Proglacial succession of biological soil crusts and vascular plants: Biotic interactions in the High Arctic

2 authors, including:

Esther Lévesque
Université du Québec à Trois-Rivières
129 PUBLICATIONS **7,514** CITATIONS

Some of the authors of this publication are also working on these related projects:

Project   Arctic Tundra Climate change Studies View project

Project   Tundra Northwest 1999 View project

Proglacial succession of biological soil crusts and vascular plants: biotic interactions in the High Arctic

Katie Breen and Esther Lévesque

Abstract: To evaluate the hypothesis that biological soil crusts facilitate the establishment and maintenance of vascular plants during succession, we studied the distribution patterns of crusts and vascular plants along a High Arctic glacier foreland and compared the success of plants growing in and out of crusted substrate. Multivariate analyses determined that distance from the glacier and crust cover were the most important variables, explaining 11% and 9% of the variance in the vegetation data, respectively. Surfaces colonized by biological soil crusts generally supported higher plant densities and showed positive associations with the most dominant, long-lived plant species such as *Saxifraga oppositifolia* L., *Salix arctica* Pall., and *Dryas integrifolia* Vahl. Crusts facilitate plant establishment and growth in early and midsuccession but may compete for available resources further along the chronosequence. This study recognizes subtle direct influences of crust on vegetation density but also draws attention to a much larger overall positive effect on community structure. Succession on this foreland proceeds via a "directional-replacement" model and supports a well-developed community of biological soil crusts and vascular plants with greater species richness, cover, and density compared with other glacier foreland vegetation communities previously investigated on Ellesmere Island, Nunavut.

Key words: Arctic, biological soil crusts, plants, succession, facilitation, glacier retreat.

Résumé : Afin d'évaluer si les croûtes biologiques facilitent la colonization et la survie des plantes vasculaires durant la succession, nous avons étudié la distribution des croûtes et des plantes vasculaires le long d'un terrain proglaciaire dans le Haut-Arctique et avons comparé le succès des plantes poussant dans et hors de la croûte. Des analyses multivariées de la végétation ont démontré que la distance du glacier et le recouvrement de la croûte étaient les variables les plus importantes, expliquant respectivement 11 % et 9 % de la variance. Les surfaces colonisées par les croûtes biologiques avaient des densités de plantes plus élevées et étaient associées positivement avec les espèces les plus dominantes et de longue vie, telles que *Saxifraga oppositifolia* L., *Salix arctica* Pall. et *Dryas integrifolia* Vahl. Nos résultats identifient des influences directes et subtiles des croûtes sur la densité de la végétation et attirent également l'attention sur un effet positif beaucoup plus grand sur la structure de la communauté. Les croûtes facilitent la colonization et la croissance des plantes au début et à la mi succession mais peuvent être en compétition pour les ressources disponibles plus loin le long du chronoséquence. La succession sur ce terrain proglaciaire suit un modèle de « remplacement-directionnel » avec des communautés bien développées de croûtes biologiques et de plantes vasculaires. De plus, ces dernières ont des valeurs de richesse spécifique, de recouvrement et de densité plus élevées comparativement à d'autres communautés de végétation proglaciaire précédemment étudiées sur l'Île d'Ellesmere, Nunavut.

Mots clés : Arctique, croûte biologique, plantes, succession, facilitation, retrait glaciaire.

Introduction

Since the end of the Little Ice Age (LIA), ca. 1850, climate warming has led to a decrease in the surface area and mass of many glaciers in the Canadian High Arctic (Dowdeswell 1995; ACIA 2005). As glaciers retreat, they expose new terrestrial environments to potential colonization by microorganisms and higher plants. As colonization proceeds, a gradient of increasing complexity is created

K. Breen[1] and E. Lévesque. Département de chimie-biologie, C.P. 500, Université du Québec à Trois-Rivières, Trois-Rivières, QC G9A 5H7, Canada; Centre d'études nordiques, Université Laval, Québec, QC G1K 7P4, Canada.

[1]Corresponding author (e-mail: kathryn.breen@uqtr.ca).

with distance from the terminus of the glacier and the resulting chronosequence is ideally suited to the study of primary colonization, succession, and changing biotic interactions such as facilitation and competition.

Given that true primary colonization of barren terrestrial environments takes place on the microbial scale, all primary succession should first be viewed as microbial in nature, a fact often overlooked in vegetation studies (Hodkinson et al. 2002). Pioneering organisms such as cyanobacteria, green algae, lichens, mosses, fungi, and heterotrophic bacteria are typically the first organisms to colonize the surface and subsurface of exposed soils (Belnap and Lange 2001). Over time, a consortium containing some or all of these microorganisms can create a firm yet flexible organic layer less than 1 cm thick on the soil surface called a biological or microbiotic soil crust (Evans and Johansen 1999; Belnap and Lange 2001). Microbiota present in biological soil crusts

can subsist in a variety of extreme habitats worldwide (Belnap and Lange 2001) including glacier ice (Skidmore et al. 2000; Mueller et al. 2001), whereas vascular plant establishment is more restricted and in the High Arctic favours microsites with higher soil temperatures, lower wind speeds, higher soil moisture content, and increased soil nitrate levels (Sohlberg and Bliss 1984).

Biological soil crusts in temperate ecosystems have positive impacts on numerous physical and ecological processes of benefit to vascular plants. Organisms present in soil crusts, such as nitrogen-fixing cyanobacteria, have been credited with increasing limiting soil nutrients as well as plant tissue concentration of several essential elements (Harper and Marble 1988; Belnap and Harper 1995; Harper and Belnap 2001). The mucilaginous properties of crusts allow them to retain moisture, reduce the harmful effects of cryoturbation (Wynn-Williams 1993; Gold and Bliss 1995), and protect the soil from erosion by wind and water (Evans and Johansen 1999; Belnap and Lange 2001). The darker and occasionally rougher surface created by soil crusts in arctic environments can lower albedo and elevate ambient soil temperatures (Gold 1998). Although recognized as important contributors to pioneer community development, there is a paucity of information regarding ecological relationships between soil crusts and vascular plants, and most published studies relate to temperate desert ecosystems. The most comprehensive study investigating the relationship between vascular plants and soil crusts in the High Arctic took place in a polar desert ecosystem on Devon Island (75°33′N, 84°40′W) (Gold and Bliss 1995; Gold 1998; Bliss and Gold 1999) where crusted surfaces were found to support higher plant diversity, biomass, seedling density, and organic matter and higher surface and soil temperatures.

With a few notable exceptions, (Tishkov 1986; Bliss and Gold 1994; Hodkinson et al. 2003; Jones and Henry 2003; Okitsu et al. 2004), successional studies on vascular plants in the High Arctic are limited, with research focusing on the succession of vascular plants along glacier forelands or exposed beach ridges. Research on plant–crust interactions has, as yet, not been considered during postglacial succession. General mechanisms of succession such as competition, facilitation, and life history traits of individual species all contribute to the pattern and rate of succession but can vary depending on environmental severity (Svoboda and Henry 1987). While abiotic factors are thought to have the most profound role in structuring extreme arctic plant communities (Billings 1987; Svoboda and Henry 1987; Matthews 1992), biotic interactions, particularly positive interactions, may play a key role in the structuring of emergent communities that subsist under environmental duress, such as those immediately following the retreat of glaciers. It is generally understood from latitudinal and alpine gradient analyses that the relative importance of positive biotic interactions will increase under increasing environmental stress (Callaway et al. 2002); however, such interactions have not been tested on a high arctic glacier foreland. Positive plant interactions, such as facilitation, allow one organism to enhance the establishment, growth, or development of a neighbouring organism by a variety of means such as changes in temperature, accumulation of nutrients, provision of shade, shelter from wind, changes in

albedo, or sequestering of propagules (Barbour et al. 1999). While facilitation is generally assumed to occur between two different vascular plants or species, we evaluate the hypothesis that facilitation can also result from biotic interactions between the consortium of organisms comprising biological soil crusts and individual plants or species, producing environmental changes that are favourable for future vascular plants along the chronosequence.

The temporal and environmental gradient created along an arctic glacier foreland presents a unique environment for investigating the relative importance of biotic interactions along a chronosequence and the potential capacity of crusts to facilitate, sustain, or interact with the ensuing colonization by higher plants. Given that high arctic plant establishment is generally favoured by microsites with higher soil temperatures, higher soil moisture content, and increased nitrogen (Sohlberg and Bliss 1984), we hypothesized that soil crusts would offer the biotic input necessary for improving conditions of growth for subsequent vascular plant species and thus increase the rate of succession following glacier retreat. The goals of this paper are (*i*) to determine whether soil crusts play a role in vascular plant community distribution patterns on a high arctic glacier foreland and, if so, (*ii*) to define the general implications of their association with plants across the successional gradient and to determine which biotic and abiotic factors are most important in explaining their distribution patterns.

Materials and methods

Site description

Field studies were undertaken during the summer of 2004 on the granite-based, north-facing foreland and adjoining older moraine of the "Teardrop Glacier" (not an official name) situated at the drainage divide of Sverdrup Pass, Ellesmere Island, Nunavut, Canada (79°10′N, 79°45′W) (Fig. 1). Sverdrup Pass is a 75 km long deglaciated valley running east–west through central Ellesmere Island and is bounded to the north and south by the Agasiz and Prince of Wales icefields and their numerous outflow glaciers.

The High Arctic is classified as an extreme environment owing to its low temperatures, short growing seasons, limited precipitation, and nutrient-poor soils (Edlund and Alt 1989) with mean July temperature of 3–5 °C and less than 150 mm of precipitation per year (Maxwell 1981). As such, the vegetation of Ellesmere Island is characterized by sparse polar desert and semidesert landscapes (Bliss and Matveyeva 1992) that support low productivity, low plant diversity, and 1%–3% plant cover, with limited areas supporting 8%–12% plant cover (Bliss and Gold 1999).

The vegetation of Sverdrup Pass has been previously described by Bergeron and Svoboda (1989) and Maycock and Fahselt (1992) and the diversity and abundance of soil algae was surveyed by Elster et al. (1999). Sverdrup Pass was classified by Bergeron and Svoboda (1989) as a polar oasis, a rare, isolated, fertile, and biologically diverse area with plant cover from near zero to 45%, which supports 75 vascular plant species. While the polar oasis distinction applies primarily to the rich wet meadows in the eastern end of the valley, most of Sverdrup Pass is represented by the more

Fig. 1. Map of Ellesmere Island (inset) and aerial photograph from 1959 of the Teardrop Glacier in Sverdrup Pass (79°10′N, 79°45′W), Ellesmere Island, Nunavut (From the National Air Photo Library 1959, © 2006. Produced under licence from her Majesty the Queen in Right of Canada, with permission of Natural Resources Canada).
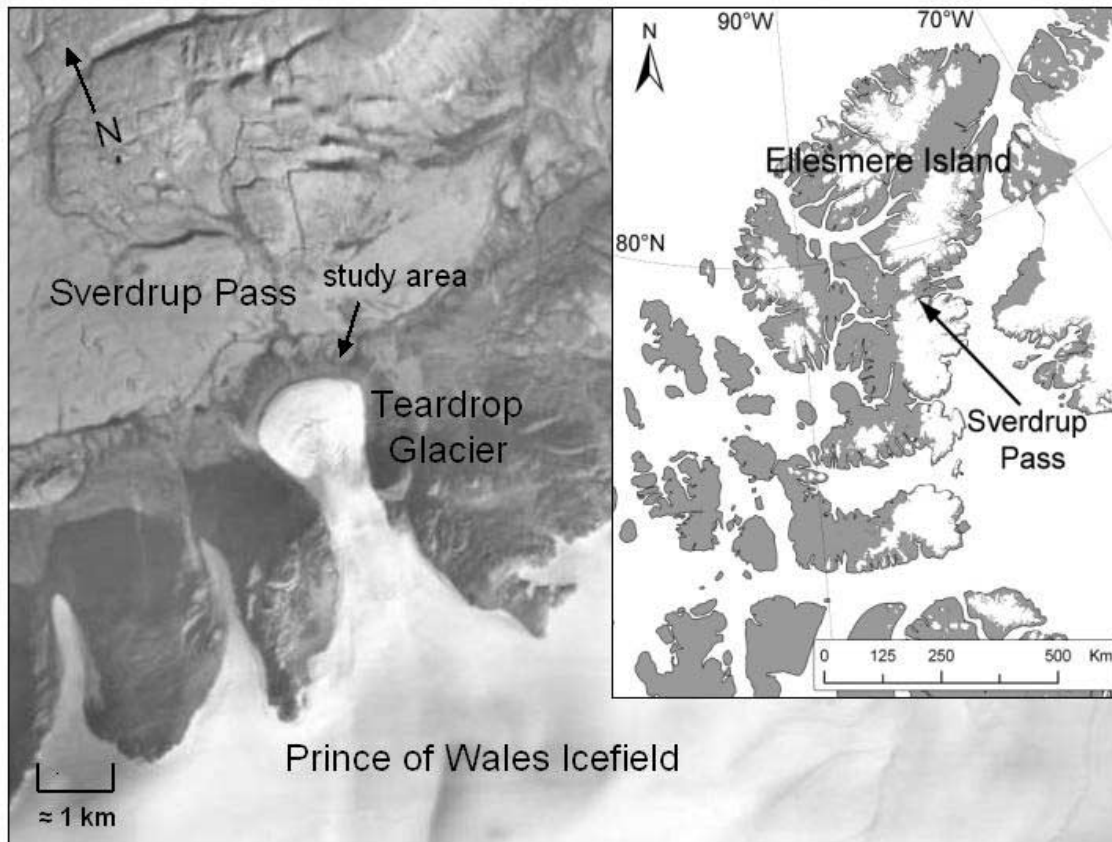
characteristic, extensive polar desert and semidesert landscapes (Lévesque 1997).

Glacier retreat in the High Arctic

The recent retreat of high arctic glaciers is attributed to the delayed response to general climatic warming since the end of the LIA (Dowdeswell 1995) and a significant increase in temperature since 1925 (Bradley 1990). A terminal moraine 190 m from the June 2004 glacier terminus marks the maximum advance of the Teardrop Glacier during the LIA. The foreland is clearly visible between the glacier and this moraine owing to the abundance of large boulders deposited during retreat and the presence of a "lichen kill zone" where the absence of macrolichens has resulted in a markedly lighter coloured terrain. The only detailed aerial photographic survey of Sverdrup Pass occurred in 1959 (Fig. 1). Comparisons between aerial photographs, in combination with in situ measurements, allowed Fahselt et al. (1988) to determine that the mean annual retreat rate of the Teardrop Glacier was 1.6 ± 0.1 SE m/year between 1959 and 1986. Measurements taken during the summer of 2004 from a preestablished stake network revealed that retreat has increased in recent years to approximately 1.88 m/year ($n = 1$) from 1987 to 1992 to 2.01 ± 0.13 SE m/year ($n = 7$) from 1992 to 2004 (Fig. 2).

Sampling design

A benchmark was established on 29 June 2004 at the glacier terminus and all distances referred to in this study are measured from this point of reference. The study area covers the entire foreland length of 190 m from the glacier to the terminal moraine and extends beyond it to 212 m to include an area on older moraines deglaciated at some point prior to the LIA. Owing to the large breadth of the glacier terminus (approximately 1.2 km across), a 200 m wide subsection of the foreland was chosen for the study area because of 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 plants and crusts along the foreland.

A north–south transect was marked out perpendicular to the glacier terminus and sites were positioned with increasing distance from the glacier. To capture changes occurring in early community development, sites were placed every 6 m along the transect for the first 60 m and every 20 m thereafter, resulting in 17 sites along the 190 m long foreland. An additional three sites were established beyond the terminal moraine (to the north), leading to a total of 20 sites. To avoid spatial periodic bias, sites were established at random distances (up to 100 m) alternating to the east or west of the north–south transect line. Sites are generally referred

Fig. 2. Teardrop Glacier foreland chronosequence, Sverdrup Pass, Ellesmere Island, Nunavut, showing the 20 vegetation sites (identified as distances from the glacier from 0 to 212 m), the six derived classification groups, and the approximate terrain ages based on measurement of glacier retreat. The terminal moraine marks the maximum extent of glacier advance during the LIA (ca. 1850).
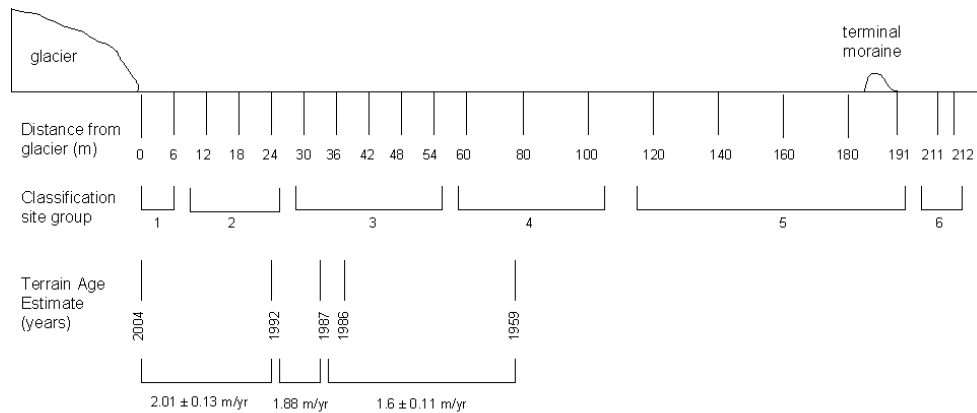
to with respect to their distance from the glacier rather than their terrain age; however, approximate ages were determined as seen in Fig. 2.

Vegetation community analysis

At each of the 20 sites, a 40 m × 5 m sampling area was established, with the longest length parallel to the glacier terminus. A general analysis of the site was obtained by randomly placing a 20 m × 5 m plot within the larger 40 m × 5 m site. A more detailed vegetation analysis of each site was undertaken using 50 cm × 50 cm quadrats randomly placed throughout the 40 m × 5 m site. Quadrat number varied among sites, since vegetation cover increased along the length of the foreland, reducing the number of quadrats required to accurately assess vegetation (Lévesque 1996). A minimum of 30 quadrats were used for each site within the first 54 m of the foreland and a minimum of 20 quadrats were used at each of the remaining sites from 60 to 212 m. Where sparse plant cover justified it, quadrats were surveyed until a minimum of 20 quadrats containing vegetation were obtained. The detailed and general analyses were compared to ensure consistency of observations. In addition to the species found in the 50 cm × 50 cm quadrats, the entire 40 m × 5 m site area was surveyed for additional species to compile a site species list. Vascular plant nomenclature generally follows Porsild and Cody (1980) except for some graminoid (Aiken et al. 2006) and *Draba* species (Mulligan 1990) and updated nomenclature is included where possible from references currently published by the Flora of North America Editorial Committee (2005).

Within both the 20 m × 5 m plots and the 50 cm × 50 cm quadrats, vascular plant cover was estimated using an abundance scale modified from Lévesque (1996), specifically designed to assess sparse vegetation at 11 levels (0%, 0%–0.5%, 0.5%–1%, 1%–2%, 2%–5%, 5%–10%, 10%–25%, 25%–50%, 50%–75%, 75%–90%, and 90%–100%). Cover estimates were made using vertical projection to ground level within each quadrat for total and individual vascular plant species as well as for biological soil crust, litter, moss, lichen, standing or moving water, feces, and paleomaterial. "Paleomaterial" refers to remnant patches of dead but preserved plant or organic soil matter released from the retreating ice margin of some high arctic glaciers owing to

the nature of cold-based glacier movement (Bergsma et al. 1984). "Moss" was determined to be moss that was growing independently of a biological soil crust, either solitary tufts or loose moss carpets. Glacial soil, pebble, rock, and small and large boulder cover were also estimated according to a modified Wentworth classification scale (Wentworth 1922; Table 1). The midpoint of each cover value range was used to determine the mean of all quadrats per site.

Density

Individual vascular plants in the 50 cm × 50 cm quadrats were identified to species level and classified as growing either in or out of biological soil crust to determine the total and individual species densities per square metre as well as species richness in each substrate. The "outside of crust" category encompassed all alternative substrates in which plants could establish, namely glacial soil, paleomaterial, moss, litter, and standing or moving water. Species were counted as either individual shoots or clumps depending on specific growth forms (Appendix A). The true or "nominal" mean density of plants was first calculated to determine the number of individuals present at each site per square metre. Three values were calculated for each of the two substrate categories (in and out of crust): (*i*) total density: the number of individual plants per square metre, (*ii*) reproductive density: the number of reproductive plants per square metre, and (*iii*) reproductive output: the number of inflorescences per square metre. These densities were calculated for individual species and total vascular plants per site. Data are mean values of all quadrats for each site.

Over much of the Teardrop Glacier foreland, biological soil crusts are the dominant substrate. As a result, a site with a larger cover of crust would have a greater chance of supporting more individuals in the crust simply by chance, given that the crust occupies more space than any other available substrate. To compare the mean densities of species or total plants in or out of crust, densities were corrected relative to substrate availability (total density: mean number of plants per theorized 100% cover of each substrate per square metre) or converted to proportions (reproductive density: mean number of reproductive plants per total plants per square metre and reproductive output: mean number of inflorescences per

Table 1. Environmental variables and their conditional *p* values measured at 20 sites on the foreland and adjacent moraine of the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut.

Variables measured at 20 sites	Conditional *p* value
Distance from glacier (m)	**0.002**
Biological parameters	
Biological soil crust (% cover)	**0.014**
Moss (% cover)	**0.06**
Lichen (% cover)	**0.068**
Litter (% cover)	**0.042**
Feces (% cover)	0.092
Physical parameters	
Glacial soil (<0.4 cm) (% cover)	**0.066**
Paleomaterial (% cover)	**0.006**
Pebbles (0.4 – 6.4 cm) (% cover)	0.14
Rocks (6.4 –25.6 cm) (% cover)	1
Small boulders (25.6 –50 cm) (% cover)	na
Large boulders (>50 cm) (% cover)	na
Standing or moving water (% cover)	na
Volumetric water content (%)	0.098
Analyses of soil fraction <2 mm:	
Texture 5 cm deep	
Sand (%)	0.05
Silt (%)	na
Clay (%)	0.132
Chemistry 0.7 mm deep	
pH	na
C (organic) (%)	na
N (total) (%)	**0.006**
P (available) (ppm)	na
K (exchangeable) (ppm)	na
Chemistry 5 cm deep	
pH	0.1
C (organic) (%)	0.21
N (total) (%)	0.082
P (available) (ppm)	**0.052**
K (exchangeable) (ppm)	0.094

Note: An automatic forward selection in CANOCO v. 4.35 was used to select variables for further multivariate analyses. Nine variables with conditional values of $p < 0.07$ (in bold) were chosen for inclusion in the final CCA and partial CCA models. na, variables with high inflation factors or covariables.

reproductive plant per square metre). The "outside of crust" cover was determined by adding the cover values of all of the alternative substrates other than crust, listed above, in which vascular plants could establish. These corrected mean density values, referred to from now on as "relative densities," were calculated for total density, reproductive density, and reproductive output for all individual species and total vascular plants per site in and outside of crust.

Soil and substrate collections

Soil and surface substrate samples were collected at each site on 3 August 2004. Three composite samples of three randomly collected soil cores (6 cm in diameter, 5 cm deep, 1272 cm³ total sample) were randomly collected at each site. Samples of biological soil crusts were also collected randomly in each of the sites using half of an 8.8 cm diameter Petri dish as a core to extract the top 0.7 cm surface layer. Five surface cores were pooled to create one sample per site (8.8 cm in diameter, 0.7 cm deep, 213 cm³ total sample).

Soil and surface substrate samples were weighed wet to 0.01 g, frozen, and shipped south at –10 °C where they were air-dried to constant mass to determine volumetric soil moisture content. Nutrient analyses were performed on the less than 2 mm fraction of the 5 cm deep soil samples and the 0.7 cm deep substrate samples at the Forestry Soil Science Laboratory, Université Laval, Québec City, Québec, Canada. Granulometric analysis (percent sand, silt, and clay) was done by the hydrometer method (Bouyoucos 1962), pH was determined using CaCl$_2$ (McKeague 1978), organic carbon was determined using methods outlined in Yeomans and Bremner (1988), total nitrogen was extracted by the Kjeldahl method, and exchangeable potassium and available phosphorus were determined using the methods in Mehlich (1984).

Data analysis

Species–environment relationships

A two-way indicator species analysis (TWINSPAN, de-

fault settings; Hill 1979) was used for classifying the vegetation data set, which consisted of mean cover values for each of the 50 vascular plant species at each of the 20 sites. Cut levels of 0%, 0.5%, 1%, 2%, 5%, and 10% were used, since the majority of species in the analysis had relatively low mean cover values, while a few species had cover values over 5% or 10%. The minimum group size for division was set at 5.

Mean environmental and species cover data per site were used in ordination analyses using CANOCO 4.53 (Microcomputer Power, Ithaca, New York). A detrended correspondence analysis (DCA) was initially applied to the vegetation data, using default settings, to determine whether the response was unimodal or linear. Since the first two axes in the DCA had gradient lengths of 3.43 and 1.45 SD, respectively, a unimodal approach was chosen (Jongman et al. 1995). Canonical correspondence analysis (CCA) was performed to relate the environmental variables directly to the species data. Table 1 lists the variables applied to initial multivariate analyses, which included one spatial variable, the distance from the glacier (metres), and numerous environmental variables. Seven rare species, *Braya glabella* Richardson, *Braya thorild-wulffi* Ostenf., *Carex rupestris* All., *Ranunculus sulphureus* Sol., *Saxifraga hirculus* L., *Saxifraga platysepala* (Trantv.) Tolm., and *Silene acaulis* (L.) Jacq., had minimal cover and occurred either in only one sampling site or within the 40 m × 5 m site area but not within individual 50 cm × 50 cm quadrats and thus were removed from the final analysis, while additional rare species were downweighed (ter Braak and Smilauer 2004). An automatic forward selection of an initial 19 environmental variables resulted in the selection of nine explanatory variables with conditional probabilities of $p < 0.07$ (Table 1). To avoid including highly correlated variables, only variables with inflation factors less than 20 were included. The final variables were distance from the glacier (metres), mean percent cover values of crust, glacial soil, paleomaterial, lichen, moss, and litter, and the phosphorus content (parts per million) in soil cores (5 cm depth) and percent nitrogen in surface cores (0.7 cm depth).

To separate the variation in the explanatory variables, partial CCA was used for selected variables using the variable or variables of interest as predictors and all other variables as designated covariables (Borcard et al. 1992). This method allows for calculation of the proportion of variance uniquely associated with a particular variable or group of variables, in this case the environmental and spatial components as well as the individual contribution of crust cover.

Density analyses

Based on the results of the classification analysis, sites were distinguished into six distance-based groups or successional stages (Fig. 2). These classification groups served as a proxy for distance or age of terrain in all subsequent analyses. Classification groups and (or) substrate type (in or out of crust) were used as factors in one- or two-way analyses of variance (ANOVAs) on species richness as well as nominal and relative total, reproductive, and reproductive output densities for all plants to determine the importance of distance from the glacier or substrate type to each variable. ANOVAs were also used to determine whether there were

significant species-specific differences in densities in and outside of crust. These were determined for 46 out of the total 50 species that were found in the 50 cm × 50 cm quadrats (the remaining four were only found in the general 40 m × 5 m site area) using the mean densities for each classification group averaged from the original site means. If a species occurred in only one classification group, it was tested for substrate effects alone using a one-way ANOVA. Vascular plant and crust cover were tested with a one-way ANOVA to determine differences across classification groups. ANOVAs were performed using Sigma Stat 3.1 (Systat Software Inc., Point Richmond, California) followed by Tukey multiple comparison tests where appropriate to determine where significant differences occurred along the foreland. Whenever data did not meet the parametric ANOVA assumptions of normality or equal variance, they were rank transformed.
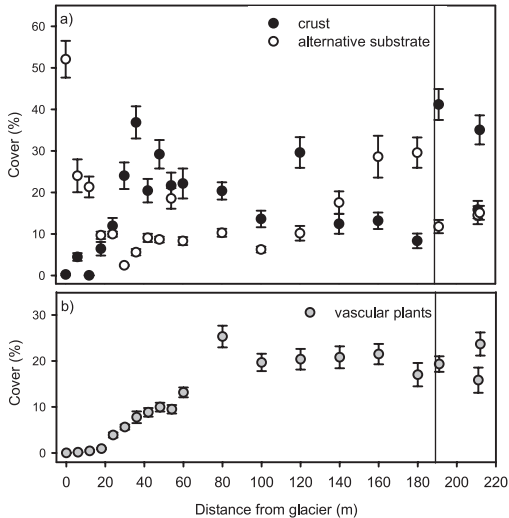
Results

General vegetation trends

A gradient of increasing complexity was observed in the vegetation along the Teardrop Glacier foreland with a general increase in vegetation cover, species richness, and density over time. Of the 75 vascular plant species identified in the polar oasis of Sverdrup Pass by Bergeron and Svoboda (1989), 50 (67%) were found on the Teardrop Glacier foreland and 51 were found across both the foreland and the old moraine. The complete list of species, representing 14 families, is found in Appendix A. Vascular plant cover, species richness, nominal and relative densities, crust cover, and all abiotic terrain features differed significantly across the classification groups ($p < 0.05$), highlighting the changes occurring across the foreland with succession and community development.

The terrain within the first 20 m of the glacier terminus, representing approximately 10 years since deglaciation, was characterized by glacial runoff, unsorted till, and intermittent patches of glacial soil and paleomaterial (Fig. 3a). Biological soil crusts were rare in this area and when found were sparse and thin, often appearing as a thin green or black layer on glacial soil or paleomaterial. As such, the dominant substrates for plant establishment within the first 20 m of the glacier terminus were glacial soil or paleomaterial. Approximately 20 m from the glacier terminus, crust cover began to increase and peaked rapidly 36 m from the glacier at 37% cover (Fig. 3a), representing the majority of substrate available for plant establishment, given that pebbles, rocks, and boulders characterized much of the foreland. Crust remained the dominant substrate across the foreland up to 140 m from the glacier, after which it declined slightly. The decline in crust cover towards the end of the foreland may have been due in part to an increase in standing water and the development of thick moss carpets, which were the dominant constituents of the "outside of crust" category in these sites. The higher crust cover observed beyond the terminal moraine was likely due to the age and undisturbed nature of the sites as well as low boulder cover, allowing for greater growth of crust.

Vascular plant colonization began within the first 6 m of the glacier terminus with the appearance, in the 200 m² surveyed, of a single individual of *Alopecurus borealis* Trin.

Fig. 3. (*a*) Soil crust and alternative substrate cover (mean ± SE) available for plant establishment at each site along the Teardrop Glacier foreland, Ellesmere Island, Nunavut. The alternative substrate or "outside of crust" category consists of all alternative substrates available for plant establishment (glacial soil, paleomatter, moss, litter, and standing water). Pebbles, rocks, and small and large boulders are excluded and complete the remaining cover types. (*b*) Vascular plant cover (mean ± SE) at each site. The vertical line indicates the terminal moraine at 190 m.

Fig. 4. Total species richness and number of species growing in or out of crust at each site in front of the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut. The vertical line indicates the terminal moraine at 190 m.
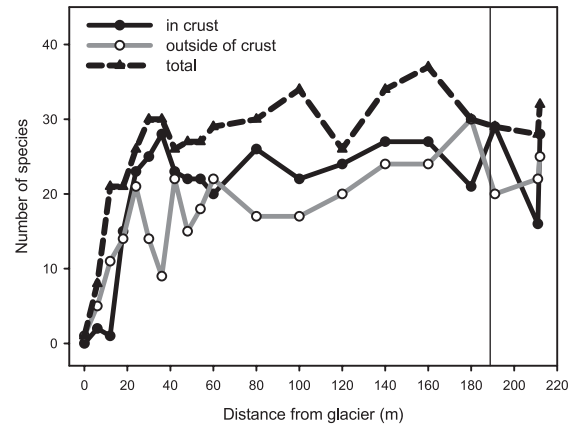

subsp. *borealis*. Although vascular plant cover was very low in the newly emerged sites and supported only scattered individual plants with 0.08% cover, it increased rapidly along the foreland before attaining a peak of 25% cover 80 m from the glacier (Fig. 3*b*). Following the peak at 80 m, vascular plant cover leveled off to roughly 20% over the rest of the foreland and sites beyond the terminal moraine. Species richness also increased rapidly along the foreland from 0 to 21 species within 18 m of the glacier (<10 years) before attaining a maximum number of species (38) 160 m from the glacier. Species richness was generally higher in crusted substrate in the majority of the 20 sites (Fig. 4); however, there was no significant difference in the total number of species or the relative species richness in and out of crust.

Certain pioneering plant species present in the early successional sites, such as *Draba oblongata* R.Br. ex DC., *Saxifraga rivularis* L., and *Puccinellia bruggemannii* T. J. Sørensen, were rarely found in later sites, as they were replaced along the chronosequence by long-lived, stress-tolerant species such as *Salix arctica* Pall., *Cassiope tetragona* (L.) D. Don subsp. *tetragona*, and *Dryas integrifolia* Vahl. Individual species presence or absence at each site highlights these successional changes (Fig. 5). Species turnover during succession is also evident among the most dominant species, those with the five highest cover and frequency values across classification groups (Table 2). The most common species, with frequency values over 70% in three or more classification groups, were *Saxifraga oppositifolia* L., *Luzula confusa* Lindberg, and *Salix arctica*.

Multivariate analyses

The divisive classification analysis (TWINSPAN) of the cover values of 50 vascular plant species at 20 sites distin-

guished eight species groups and six site groups at the third level of division. The species groupings 1–8 reveal the association of specific taxa with particular successional stages (Fig. 5). The site groupings reflect distance or terrain age, with the first division (accounting for 29% of the variance) splitting the foreland at 54 m. Subsequent divisions explained less than 20% of the variance but separated early and late successional sites into further sequential stages based on terrain age (Fig. 6).

The CCA of the same vegetation data set with nine environmental variables indicated that the community variation seen on this foreland is largely associated with the selected environmental variables in the ordination analyses. The two first axes of the CCA ordination explained 52.5% of the variation in the species cover from environmental data with a strong proportion on the first axis (38.7%). The first four axes explained 71% of the variance in species data and 86% of the variance in the species–environment data, with high species environment correlations. The variance explained by axis 1 and that explained by all canonical axes were both found to be significant ($p = 0.001$ each) (Table 3). 3). The eigenvalue of the first axis was only slightly lower compared with that in the DCA, suggesting that most of the variation was kept in the CCA analysis and that the chosen environmental variables explain most of the species variation (Jongman et al. 1995).

The CCA solution is represented in a biplot (Fig. 7) in which species are displayed according to their affinity towards each other and the environmental variables. Distance from the glacier clearly separates species along the first axis. The cover of surficial paleomaterial, found predominantly within the first 30 m of the glacier, was associated with early successional species such as *Draba oblongata*, *Draba cinerea* Adams, and *Puccinellia bruggemanni*. These species were generally found within the first 60 m of the glacier in sites with low litter and moss cover. The second axis appears to differentiate two groups of species associated with slightly different late-succession habitats. The first group of species is characterized by higher cover of crust, nitrogen content in the crust, and phosphorus in the top 5 cm of soil, which are variables that relate to soil and substrate develop-

Fig. 5. Presence of each vascular plant species across the Teardrop Glacier foreland and adjacent moraine, Sverdrup Pass, Ellesmere Island, Nunavut. Species are arranged along the *y*-axis with respect to their species classification groups (1–8). The solid vertical line marks the position of the terminal moraine at 190 m.
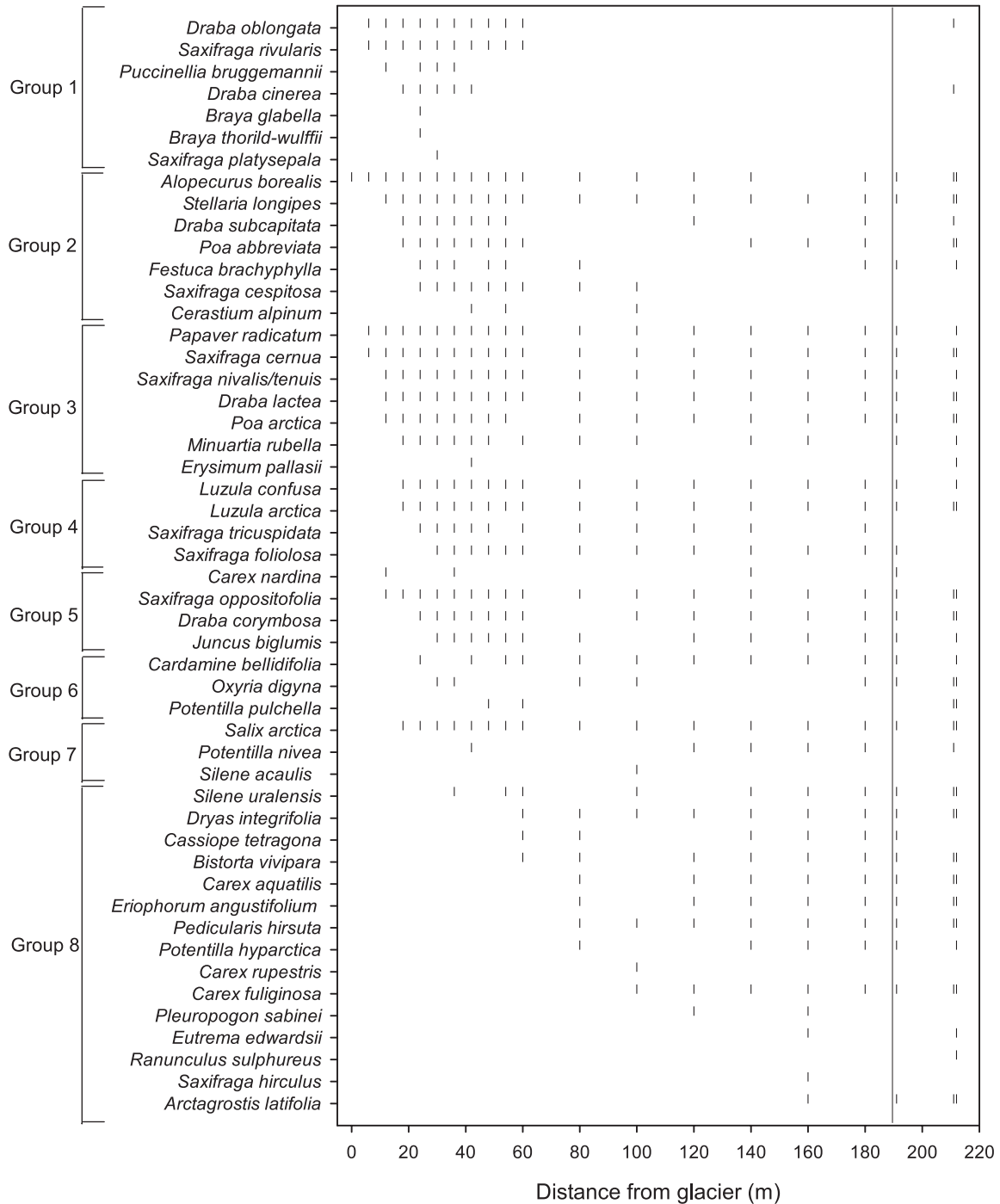
ment. This late successional group is composed of species more commonly associated with mature mesic communities and well-developed crusts such as *Cassiope tetragona* and *Dryas integrifolia* (Fig. 7). The second group of species, characterized by more substantial moss and litter cover and lower soil nutrients, are highly associated with older, moist, moss-dominated areas supporting later successional species such as *Carex aquatilis* Wahl. var. minor Boott, *Pedicularis hirsuta* L., and *Pleuropogon sabinei* R.Br. (Fig. 7). This is

consistent with observations made in some of the sites at the very end of the foreland, where moss developed to form very wet, thick carpets, unlike the mosses associated with crusts in earlier sites, suggesting that water availability can direct the development of distinct late successional plant communities.

The CCA and partial CCA attributed 82% of the variance to the selected nine variables ($p = 0.001$); the remaining 18% of the variation could not be explained by this data

Table 2. Mean cover and frequency of the five most abundant vascular plant species (highest mean cover and frequency values) in each of the six classification groups surveyed across the Teardrop Glacier foreland and adjacent moraine, Sverdrup Pass, Ellesmere Island, Nunavut.

Species	Cover (%) Classification group						Frequency (%) Classification group					
	1	2	3	4	5	6	1	2	3	4	5	6
Papaver radicatum	0.006						1.1					
Saxifraga rivularis	0.002						0.7					
Draba oblongata	0.001						0.4	23				
Saxifraga cernua	0.004	0.20					0.7	39	83			
Alopecurus borealis	0.015	0.52	0.67				2.4	21	57			
Saxifraga oppositifolia		0.32	1.4	2.5	2.1	1.7		45	78	83	75	82
Stellaria longipes		0.18	1.4	0.77					67	65		37
Luzula confusa		0.18	2.9	6.1	2.8			33	96	97	73	
Salix arctica			0.64	7.8	7.7	10.5				92	90	86
Luzula arctica				0.40						70	62	
Dryas integrifolia					1.8	0.8						
Carex aquatilis					1.4	1.5						41
Bistorta vivipara						0.8						44
Pedicularis hirsuta											55	

Note: Values are given only for the top five species in each classification group. Species may be present in other groups but do not appear in the top five.

Fig. 6. Classification dendrogram of vegetation produced from the cover values of 50 vascular plant species across 20 sites in front of the Teardrop Glacier at Sverdrup Pass, Ellesmere Island, Nunavut. Site numbers are distances from the glacier; the three sites beyond the terminal moraine are indicated in italics (*191, 211, 212*). Eigenvalues and indicator species are identified at each division. Species abbreviations are the first three letters of the genus and species names listed in Appendix A.
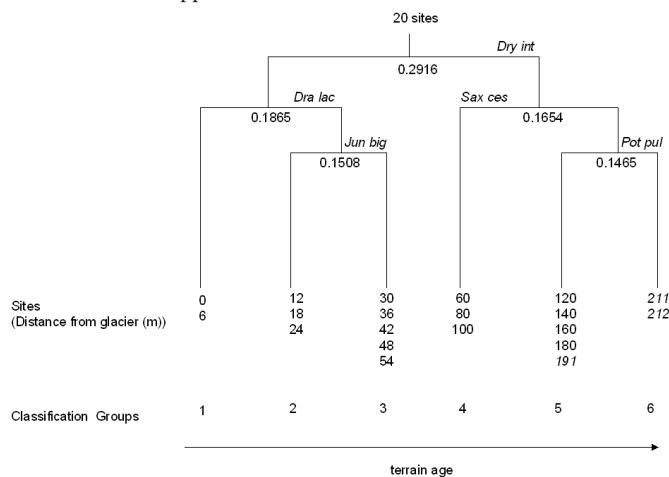
set. The nine variables were further broken down into eight environmental variables and one spatial variable as listed in Table 4. The environmental variables alone explained 52% of the variance ($p = 0.001$). After removing the effects of the environmental variables, distance from the glacier (the spatial variable) was found to explain 11% of the variance ($p = 0.002$). The proportion of variance explained by crust cover alone was 9% ($p = 0.003$) (A[1] in Table 4).

Density

The majority of vascular plant individuals were found growing in crusted rather than uncrusted substrate across the foreland as shown by the three types of nominal mean densities (total, reproductive, and reproductive ouput per square metre) per classification group (Figs. 8a–8c). Total density per site ranged from 0 to 185 plants/m^2 in crust and from 0.1 to 106 plants/m^2 outside of crust. The density of reproductive individuals in each site ranged from 0 to 60 plants/m^2 in crust and from 0 to 21 plants/m^2 outside of crust and the density of inflorescences in each site ranged from 0 to 212 inflorescenes/m^2 in crust and from 0 to 72 inflorescences/m^2 outside of crust.

Relative densities more accurately consider the cover of available substrate and all subsequent analyses and results refer to relative densities (Figs. 8d–8f). All three relative densities (total, reproductive, and reproductive output per square metre) were significantly different across the classification groups ($p = 0.001$, 0.007, and 0.006, respectively). The total relative plant density was higher in crust in all classification groups; however, the preference for crust was not statistically significant ($p = 0.059$). No significant difference was found in the relative reproductive density of plants in or out of crust or in the relative reproductive output density even though four out of the six classification groups had higher reproductive output in crust than outside of crust.

Individual species densities

Although crusted surfaces generally supported much higher nominal species densities than uncrusted surfaces, when relative densities were considered, only seven species showed significantly different densities and six of these were higher in crust than out of crust; thus, any preference for growth in crust appears to be, in part, species specific. Five species were found to have significantly higher total densities in crust than out: *Dryas integrifolia*, *Salix arctica*, *Saxifraga cespitosa* L., *Saxifraga oppositifolia*, and *Stellaria longipes* Goldie subsp. *longipes*, while *Luzula arctica* Blytt

Table 3. Summary statistics from the first four axes for indirect (DCA, vegetation data) and direct (CCA, environment and vegetation data) ordination analyses using 20 sites, mean percent cover values of 43 vascular plant species, and nine environmental variables (eight environmental and one spatial as listed in Table 1).

	DCA				CCA			
	1	2	3	4	1	2	3	4
Eigenvalue	0.391	0.099	0.045	0.012	0.376	0.134	0.106	0.070
Species–environment correlations	—	—	—	—	0.984	0.943	0.912	0.956
Cumulative % variance of species data	38.8	48.6	53.0	54.2	38.7	52.5	63.3	70.5
Cumulative % variance of species–environment	—	—	—	—	47.4	64.3	77.6	86.3
Gradient length	3.430	1.450	1.217	1.988				
Total inertia	1.009				0.972			
Sum of all eigenvalues	1.009				0.972			
Sum of all canonical eigenvalues	—				0.794			
Significance of first axis	—				0.001			
Significance of all canonical axes	—				0.001			

Note: Significance values are *p* values from Monte Carlo test with 999 permutations under reduced model.

was marginally significant (Table 5). Two species, *P. hirsuta* and *Saxifraga cespitosa* had higher reproductive densities in the crust. *D. integrifolia* had a borderline significant difference in reproductive density whereas *Saxifraga rivularis* was the only species to have a significantly higher reproductive density outside of the crust. With regard to reproductive output, *Pedicularis hirsuta* and *Saxifraga cespitosa*, had significantly higher densities in crust and *Alopecurus borealis* was marginally significant. Although only a limited number of species exhibited a significant difference in density in or out of crust, those species with higher densities in crust were among the most common and dominant species observed on the foreland (Table 2), characteristic of mature, mesic arctic environments (Bliss and Matveyeva 1992). Multiple comparison tests (Tukey) following two-way ANOVAs of species densities highlight where density was positively associated with crust along the foreland (Table 5). The results show that most species exhibiting a greater density in crust appear to show this distinction primarily in mid- or later successional sites (classification groups 3–6) where they have established populations spanning these groups.

Discussion

General vegetation trends

Previous surveys of glacier forelands on Ellesmere Island undertaken by Jones and Henry (2003) and Okitsu et al. (2004) as well as personal observations of other forelands suggest that the colonization and rate of vascular plant succession on the Teardrop Glacier foreland are exceptionally high. Despite its recent release from glaciation, the Teardrop Glacier foreland supports a vegetation cover, species richness, and density more often associated with polar oases or other richly vegetated areas in the High Arctic.

The change in vascular plant cover observed across the Teardrop Glacier is somewhat sigmoidal in form, a tendancy observed on other forelands as well, such as in the Swedish Arctic (Stork 1963), the Alps (Zollitsch 1969), and the Canadian Rockies (Sondheim and Standish 1983) as cited in Matthews (1992). The cover of vascular plants on the Teardrop foreland reached a maximum of 25% yet never exceeded 15% on the Twin Glacier foreland in the nearby polar oasis at Alexandra Fiord (78°53′N, 75°55′W) (Jones and Henry 2003). Plant cover on other marginal glacier forelands, in Oobloyah Valley, Ellesmere Island (80°50′N, 82°45′W) (Okitsu et al. 2004), the subantarctic Kerguelen Islands (49°S) (Frenot et al. 1998), and Iceland (65°N) (Arnalds et al. 1987), never exceeded 1%, 4%, and 10%, respectively. Comparative cover values of biological soil crusts along forelands are limited; however, on a glacier foreland on Svalbard (78°54′N, 12°06′E), Hodkinson et al. (2003) noted that crust became apparent 16 years after glacier retreat and reached a maximum of 35% cover within 60 years, after which time it declined as vascular species colonized the available, stabilized surface. The same study also found high vegetation cover, close to 100% after 150 years. Our results showed a more rapid rate of colonization, as crusts were visible within 4 years of retreat and attained a cover of 37% in less than 20 years yet showed a

Fig. 7. Species biplot of the first and second axes of a direct ordination analysis (CCA) of 20 sites, 50 species (triangles), and nine envir-onmental variables (arrows) sampled along the Teardrop Glacier foreland, Sverdrup Pass, Ellesmere Island, Nunavut. Environmental vari-able abbreviations: Glacial, paleo, crust, moss, lichen, and litter indicate percent cover of glacial soil, paleomaterial, crust, moss, lichen, and litter; P, available phosphorus concentration in the top 5 cm (ppm); N, total nitrogen in the top 0.7 cm (%); Dist, distance from the glacier (m). Rare species were deleted or downweighed, see text. Species abbreviations are the first 3 letters of the genus and species names listed in Appendix A.
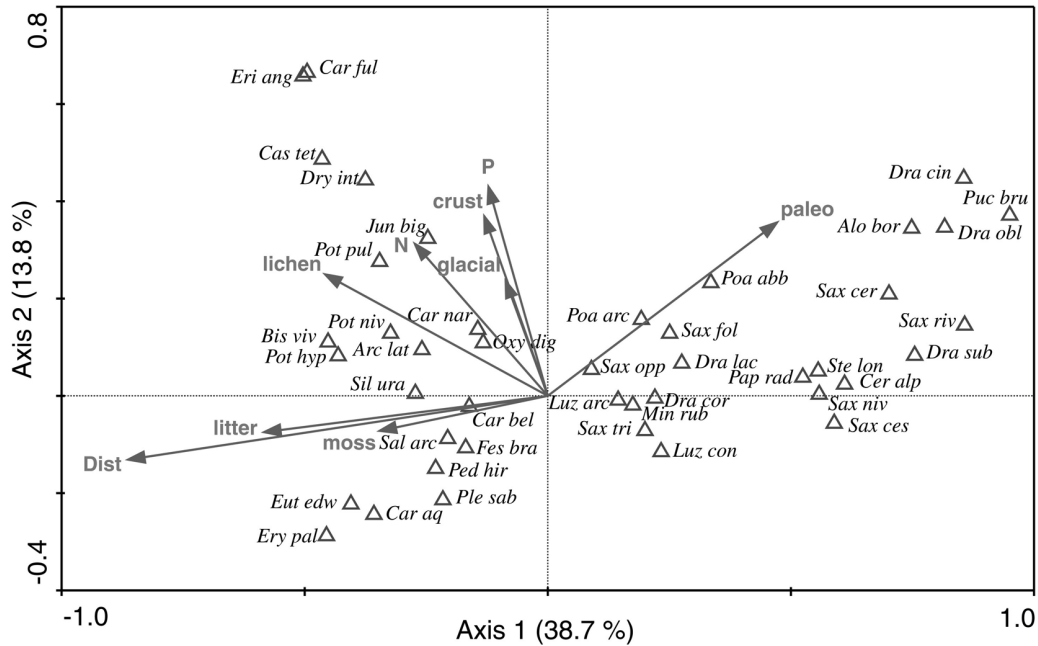

Table 4. Partial CCA variances for nine variables selected from surveys on the Teardrop Glacier foreland, Sverdrup Pass, Ellesmere Island, Nunavut.

Variable	Variation explained	% variance explained	Significance all axes
A+ B + C + D	Total	100	
A + B + C	Environmental and spatial variables	82	0.001
A + B	Environmental variables alone	71	0.001
B + C	Spatial variable alone (distance)	30	0.001
D	Unexplained variation	18	na
A	Environment after removing effects of B	52	0.001
A[1]	Crust variable alone	9	0.003
B	Interaction between environment and spatial	19	na
C	Spatial after removing effects of B	11	0.002

Note: The eight environmental variables include the % cover of crust, glacial soil, paleomaterial, lichen, moss, and litter as well as the soil phosphorus in the top 5 cm (ppm) and nitrogen content in the top 0.7 cm (%). The spatial variable is distance from the glacier (m). The total inertia was 0.972. na, not applicable.


similar, eventual decrease in later successional sites, as vascular plant cover increased.

The high proportion of species colonization on the Tear-drop Glacier foreland (67% of the total number of species found in Sverdrup Pass) contrasts markedly with the Twin Glacier foreland, where 94 vascular species have been iden-tified in its surrounding valley (Svoboda and Freedman 1994) yet only 31 (33%) of these had colonized the foreland (Jones 1997). The rate of colonization was also higher on the Teardrop Glacier foreland, with 30 species establishing approximately 15 years after glacier retreat and a maximum of 37 species towards the end of the foreland compared with a maximum of 24 species after 20–30 years of retreat on the Twin Glacier foreland. Species richness on a compa-

rable foreland on Svalbard was also lower, increasing gradually over 100 years and stabilizing with 10–13 species. (Hodkinson et al. 2003). Species richness in Oobloyah Valley, Ellesmere Island, was extremely low, with a maximum of six species found across the LIA chronosequence (Okitsu et al. 2004). The initial peak in richness on the Teardrop

Fig. 8. Mean (± SE) (*a–c*) nominal and (*d–f*) relative total, reproductive, and reproductive output densities of vascular plants growing in and out of crust in classification groups with distance from the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut. Relative densities represent either proportions or the corrected number of individuals that would be present if substrate cover were 100% in or out of crust.
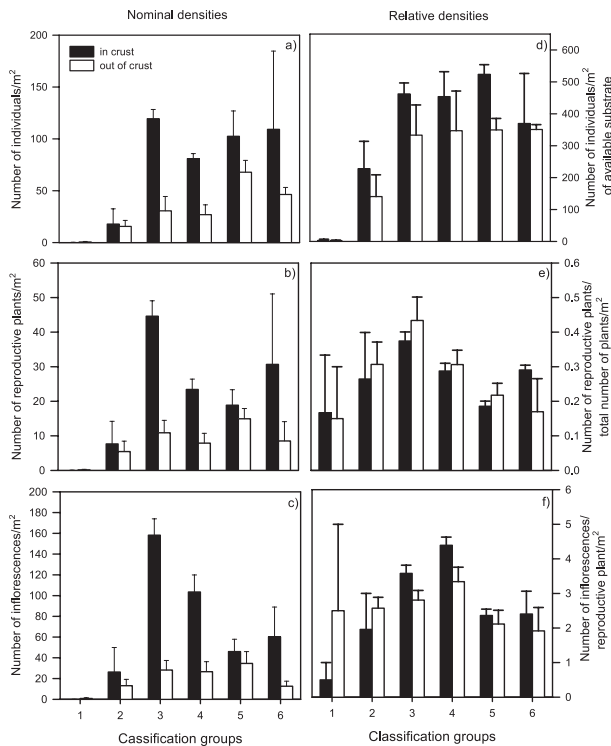
Glacier foreland between 20 and 40 m from the glacier (approximately 10–20 years following glacier retreat) appears to reflect the ability of a large number of species to colonize open spaces in the early stages of succession and also illustrates the overlap in the distribution of early and late colonizers at the same point along the chronosequence.

In addition to species colonization, the colonization of individuals, as reflected in the high nominal density values (>100 plants/m^2), highlights the successful seed dispersal and (or) clonal growth on this foreland. Comparative density values are limited; however, granitic polar desert sites in the vicinity of the Teardrop Glacier had much lower densities with averages of 28.0 ± 4.3 plants/m^2 and 3.6 ± 0.8% cover (Lévesque 1997). Although these sites were higher in elevation, they underscore the successful recruitment and establishment ability on the Teardrop foreland relative to surrounding areas. Colonization on a foreland is related to the distance from mature resident plant populations (Ryverden 1971), seed sources and a developing seed bank (Stöckling and Bäumler 1996), the presence of suitable microsites (Jumpponen et al. 1999), as well as the influence of

the glacier on microclimate (Matthews 1992). Sverdrup Pass is an extremely windy corridor and dispersal is likely achieved through aeolioan transport. Many of the early colonizing species were not found on the surrounding older moraines, suggesting some long-distance dispersal. The large boulders scattered across the foreland likely serve as traps for windblown seeds and shelter for existing plants and prevent organic matter and crusts from blowing away. Additional and perhaps significant dispersal vectors on this foreland include numerous grazing and nesting animals, including muskox, lemming, fox, and ermine as well as several bird species such as snow bunting, ptarmigan, jaeger, and gyrfalcon.

Svoboda and Henry (1987) suggested that despite successful dispersal and colonization, many plant individuals may not be able to sustain a viable population or progress beyond the initial invasion phase of succession in extreme high arctic environments such as exposed polar deserts (Lévesque 1997). However, the emergence of species at particular distances along the length of the foreland, as seen in Fig. 5, is consistent with the "directional species replacement" model of succession (Svoboda and Henry 1987), also observed on this foreland by Jones and Henry (2003), whereby species replacement occurs in seral stages with each stage distinguished by a dominant group of species. This model of succession, considered atypical in the High Arctic, is thought to occur owing to facilitation and (or) competition and is more apt to occur when environmental resistance (e.g., temperature, soil nutrients) is lower than biological driving forces (e.g., germination, establishment ability) (Svoboda and Henry 1987). The Teardrop Glacier foreland exhibits relatively low environmental resistance owing to high water availability, well-developed soil crusts, the presence of paleomaterial, and high nutrient levels (Breen 2006) as well as shelter from wind provided by the many large boulders deposited across the foreland, all of which have likely helped vegetation progress well beyond the initial invasion phase of succession.

A considerable cover of biological soil crust, as seen on this foreland, can only develop in sites exposed to adequate surface meltwater during the short growing season. Gold and Bliss (1995) suggested that the greater plant community development observed in crusted as opposed to uncrusted sites on Devon Island (75°N) was likely due to the indirect benefit of surface water facilitating the growth, maintenance, and nitrogen-fixing activities of organisms in the soil crusts. Even in barren, polar desert environments, species richness and vascular plant cover are much higher in habitats where the soil remains moist for much of the summer and supports a cover of biological soil crust (Bliss and Matveyeva 1992; Bliss et al. 1994). The Teardrop Glacier is unique compared with many glaciers in the vicinity of central Ellesmere Island in that it supports over 100 small meltwater channels evenly distributed across its terminus, averaging 30–50 cm across. Although water is available on most glacier forelands as glacial runoff, it is often discharged at such a high rate that it creates one or two large, braided streams that do not provide moisture evenly to all areas of the foreland and can hinder seed establishment and plant growth in areas of high disturbance. The unique melt patterns on the Teardrop have resulted in a glacier foreland supplied with a persistent and

Table 5. Results of two-way ANOVAs and multiple comparison tests on relative species densities in and out of crust across six classification groups on the Teardrop Glacier foreland and adjacent moraine, Sverdrup Pass, Ellesmere Island, Nunavut.

Species	Total density (no. of plants per square metre of available substrate)		Reproductive density (no. of reproductive plants per total plants per square metre)		Reproductive output density (no. of inflorescences per reproductive plant per square metre)	
	Across groups	Location and significance level	Across groups	Location and significance level	Across groups	Location and significance level
Alopecurus borealis	ns		ns		0.053	4*
Dryas integrifolia	**0.004**	5**, 6**	0.057	4*	ns	
Luzula arctica	0.055	5*	ns		ns	
Pedicularis hirsuta	ns		**0.003**	5*, 6*	**0.019**	6**
Salix arctica	**0.001**	4*, 5**, 6**	ns		ns	
Saxifraga cespitosa	**<0.001**	3***, 4***	0.029	3*, 4*	**0.018**	3**, 4*
Saxifraga oppositifolia	**<0.001**	2*, 3***, 4**, 5***, 6**	ns		ns	
Saxifraga rivularis	ns		0.027		ns	
Stellaria longipes	**0.012**	3**	ns		ns	

Note: All species were tested but only those with significantly higher density ($p \leq 0.05$, in bold) in crust rather than outside of crust across all classification groups are listed, with one exception (*Saxifraga rivularis*), which had a significantly higher reproductive density outside of crust among groups but the multiple comparison test did not detect where this difference occurred. Species with marginally significant results ($p \leq 0.06$) are also listed. Classification group numbers indicate the location (Fig. 2) of significant results of Tukey multiple comparison tests (* $p < 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$, ns = not significant). All data were rank transformed prior to analyses.

even source of water, often carrying glacial soil, paleomaterial, and nutrients that encourage colonization of soil crust microbiota (Elster et al. 1999) and subsequent vascular plants.

Plant–crust interactions

While it is widely believed that interactions between plants can change along environmental gradients (Callaway et al. 2002), our results suggest that this tenet may apply to the relationship between vascular plants and crusts along the Teardrop Glacier foreland. In very early succession, within the first few years following glacier retreat, crusts were undeveloped and plant density and cover were too low to be able to detect substrate preferences. However, a general positive association between plants and crusts seems to occur from approximately 20 to 60 m from the glacier as crust cover and vascular plant cover increase in tandem and plant species recruitment is high. Results of multiple comparison tests revealed that significant species-specific differences in densities in and out of crust became apparent approximately 30 m from the glacier or 15 years after retreat (classification groups 3–6; Table 5) and that most positive associations with crust occurred for only a handful of species. It is noteworthy that those species that exhibited significantly greater densities in crust were among those with the highest plant cover and frequency, and four of the five species, *Dryas integrifolia*, *Salix arctica*, *Saxifraga oppositifolia*, and *Stellaria longipes*, are among the most common arctic species associated with mature, mesic plant communities (Bliss and Matveyeva 1992). Of these four species, *Salix arctica*, *Saxifraga oppositifolia*, and *Stellaria longipes* first appeared approximately 20 m from the glacier (approximately 10 years after retreat) and *Dryas integrifolia* appeared after 60 m. All four species continued to be dominant members of the community along the rest of the chronosequence, highlighting a positive relationship between crusts and long-lived successional species.

The higher nutrient requirements of later successional species, such as *Bistorta vivipara* (L.) Gray, *Cassiope tetragona* and *Dryas integrifolia*, may have delayed their entry but may also have been facilitated in part by their associations with mycorrhizal or free-living bacteria (Hodkinson et al. 2003). These trends concur with the multivariate analyses, which revealed that terrain age followed by crust cover were the best explanatory variables of community composition. Terrain age and substrate composition have also been shown to play a vital role in vascular plant relationships in temperate deserts where they also promote primarily species-specific responses to crust presence (Evans and Johansen 1999).

The facilitation of plants by crusts in early succession is likely promoted by high moisture and nutrient levels in crusted soils (Breen 2006) leading to increased growth of existing plant structures and (or) the production of new individuals (increased cover and (or) density). The reproductive and reproductive output densities do not show significant substrate preferences but nonetheless show an increase in reproduction in midsuccession. The predominance of crust as a ground cover at this point along the foreland likely creates favourable conditions in both crusted and adjacent uncrusted substrate. The increase in the relative number of inflorescen-

ces on plants growing in crust in site groups 3 and 4 also suggests that crusts provide conditions that encourage reproductive resource allocation, essential for increasing cover and density across the foreland. If colonization were exclusively age dependent, the number of individuals per square metre would continue to increase across the foreland. However, the total density and cover of plants begin to stabilize following their respective peaks, approximately 40 and 80 m from the glacier. The high number of individuals appears to ensure the sustained cover but growth limitations appear to exist beyond 80 m from the glacier.

Crusts improve conditions for growth in early and midsuccession and continue to be important constituents of late-succession communities; however, the increase and subsequent stabilization of vascular plant cover coincide with a decrease in crust cover, as was also noted on Svalbard by Hodkinson et al. (2003). Although rare, competition has been observed in the High Arctic primarily in biotically rich environments, such as wet meadows, or polar oases where vegetation cover can reach 100% in mature communities (Svoboda and Freedman 1994). Given the high density and plant cover observed on this foreland, competition between plants and between plants and crust is possible and may occur in late succession owing to plants outcompeting crusts for limiting resources, including nutrients, ground cover, and (or) light. For example, the increasing horizontal growth of maturing plants such as *Salix arctica* may compete by physically smothering crusted surfaces. Evans and Lange (2001) suggested that crusts develop best where harsh environments limit the growth of higher plants. Our results show that plants that can colonize rapidly can take advantage of the superior properties of developing crusts such as increased nitrogen and water retention (Breen 2006), those that survive will be sustained by these properties but will eventually experience a slower growth rate, and those that colonize later may be outcompeted by existing vegetation. This is of particular interest for those dominant shrub species that do not recruit easily in other parts of the valley (Lévesque and Svoboda 1995). Crust may therefore play a crucial role facilitating the establishment of structuring species such as *Salix arctica*.

Despite the potential for competition in late succession, as vascular plant cover exceeded that of crusts, the majority of plants were still found to be growing within crusted rather than uncrusted terrain, suggesting that crusts continue to provide a superior substrate for growth despite their eventual decline in cover. The particular significance of crusts to plants is difficult to identify in later succession given that even plants growing "out of crust" are still likely benefiting from the ubiquitous presence of surrounding crusts, since even the noncrusted areas on this foreland supported higher densities than adjacent polar deserts (Lévesque 2001). The trends noted in this study show that crusts can modify vascular plant community structure; however, further research is needed to explore the physiological, biochemical, and (or) ecological relationships between crusts and vascular plants to determine precise mechanisms of facilitation and (or) competition. Field experiments undertaken to test the hypothesis that crusts provide a superior substrate for germination and seedling survival yielded inconclusive results;

however, the results of preliminary laboratory experiments, using crusts collected across the foreland, suggest that germination success and leaf growth are greater in plants grown on crusted soils (Breen 2006).

As the Arctic continues to respond to global climate change (ACIA 2005), increased melting of glaciers will have consequences for existing and future proglacial community development, which will be highly dependent on precipitation regimes and the melt pattern of individual glaciers and ice sheets. As can be seen from the atypical Teardrop Glacier foreland, melt patterns that promote a steady supply of water to new terrain can nurture the colonization of biological soil crusts, which may have subsequent impacts on plant cover, richness, density, biomass accumulation and, carbon budgets and as such can promote a "greening of the North". The study of interactions that influence the overall rate and direction of succession will add to our knowledge of the revegetation potential of marginal habitats and disturbed areas across the High Arctic.

Acknowledgements

References

ACIA. 2005. Impacts of a warming Arctic. Arctic climate impact assessment scientific report 1042. Cambridge University Press, New York.

Aiken, S.G., Dallwitz, M.J., Consaul, L.L., McJannet, C.L., Gillespie, L.J., Boles, R.L., Argus, G.W., Gillett, J.M., Scott, P.J., Elven, R., LeBlanc, M.C., Brysting, A.K., and Solstad, H. 2006. Flora of the Canadian Arctic Archipelago: descriptions, illustrations, identification, and information retrieval [online]. Available from http://www.mun.ca/biology/delta/arcticf/ [accessed January 2006].

Arnalds, O., Aradottir, A.L., and Thorsteinsson, I. 1987. The nature and restoration of denuded areas in Iceland. Arct. Alp. Res. **19**: 518–525.

Barbour, M.G., Burk, J.H., Pitts, W.D., Gilliam, F.S., and Schwartz, M.W. 1999. Terrestrial plant ecology. Benjamin/Cummings, Menlo Park, Calif.

Belnap, J., and Harper, K.T. 1995. The influence of cryptobiotic soil crusts on elemental content of tissue of two desert seed plants. Arid Soil Res. Rehabil. **9**: 107–115.

Belnap, J., and Lange, O.L. (*Editors*). 2001. Biological soil crusts: structure, function and management. Springer, Berlin.

Bergeron, J.F., and Svoboda, J. 1989. Plant communities of Sverdrup Pass, Ellesmere Island, N.W.T. Musk-Ox, **37**: 76–85.

Bergsma, B., Svoboda, J., and Freedman, B. 1984. Entombed plant communities released by a retreating glacier at central Ellesmere Island, Canada. Arctic, **37**: 49–52.

Billings, W.D. 1987. Constraints to plant growth, reproduction and establishment in arctic environments. Arct. Alp. Res. **19**: 357–365.

Bliss, L.C., and Gold, W.G. 1994. The patterning of plant communities and edaphic factors along a high arctic coastline: implications for succession. Can. J. Bot. **72**: 1095–1107.

Bliss, L.C., and Gold, W.G. 1999. Vascular plant reproduction, establishment, and growth and the effects of cryptogamic crusts within a polar desert ecosystem, Devon Island, N.W.T., Canada. Can. J. Bot. **77**: 623–636. doi:10.1139/cjb-77-5-623.

Bliss, L.C., and Matveyeva, N.V. 1992. Circumpolar arctic vegetation. *In* Arctic ecosystems in a changing climate: an ecophysiological perspective. *Edited by* F.S. Chapin, R.L. Jefferies, G.R. Reynolds, G.R. Shaver, and J. Svoboda. Academic Press, New York. pp. 59–89.

Bliss, L.C., Henry, G.H.R., Svoboda, J., and Bliss, D.I. 1994. Patterns of plant distribution within two polar desert landscapes. Arct. Alp. Res. **26**: 46–55.

Borcard, D., Legendre, P., and Drapeau, P. 1992. Partialling out the spatial component of ecological variation. Ecology, **73**: 1045–1055. doi:10.2307/1940179.

Bouyoucos, G.V. 1962. Hydrometer method improved for making particle size analysis of soils. Agron. J. **54**: 464–465.

Bradley, R.S. 1990. Holocene paleoclimatology of the Queen Elizabeth Islands, Canadian High Arctic. . Quat. Sci. Rev. **9**: 365–384.

Breen, K. 2006. Le rôle des croûtes biologiques dans la succession des plantes vasculaires sur un terrain proglaciaire dans le Haut-Arctique canadien. Mémoire de maîtrise, Département de chimie-biologie, Université du Québec à Trois-Rivières, Trois-Rivières, Qué.

Callaway, R.M., Brooker, R.W., Choler, P., Zaal, K., Lortie, C.J., Michalet, R., Paolini, L., Pugnaire, F.I., Newingham, B., Aschehoug, E.T., Armas, C., Kikodze, D., and Cook, B.J. 2002. Positive interactions among alpine plants increase with stress. Nature, **417**: 844–848. doi:10.1038/nature00812. PMID:12075350.

Dowdeswell, J.A. 1995. Glaciers in the High Arctic and recent environmental change. A: Philos. Trans. R. Soc. Lond., **352**: 321–334.

Edlund, S.A., and Alt, B.T. 1989. Regional congruence of vegetation and summer climate patterns in the Queen Elizabeth Islands, Northwest Territories, Canada. Arctic, **42**: 3–23.

Elster, J., Lukesova, A., Svoboda, J., Kopecky, J., and Kanda, H. 1999. Diversity and abundance of soil algae in the polar desert, Sverdrup Pass, central Ellesmere Island. Polar Rec. **35**: 231–254.

Evans, R.D., and Johansen, J.R. 1999. Microbiotic crusts and ecosystem processes. Crit. Rev. Plant Sci. **18**: 183–225.

Evans, R.D., and Lange, O.L. 2001. Biological soil crusts and ecosystem nitrogen and carbon dynamics. *In* Biological soil crusts: structure, function and management. *Edited by* J. Belnap and O.L. Lange. Springer, Berlin. pp. 263–279.

Fahselt, D., Maycock, P.F., and Svoboda, J. 1988. Initial establishment of saxicolous lichens following recent glacial recession in Sverdrup Pass, Ellesmere Island, Canada. Lichenologist, **20**: 253–268.

Flora of North America Editorial Committee. 2005. Flora of North America [online]. Available from http://hua.huh.harvard.edu/FNA/ [accessed January 2006].

Frenot, Y., Gloaguen, J.C., Cannavacciuolo, M., and Bellido, A. 1998. Primary succession on glacier forelands in the subantarctic Kerguelen Islands. J. Veg. Sci. **9**: 75–84. doi:10.2307/3237225.

Gold, W.G. 1998. The influence of cryptogamic crusts on the thermal environment and temperature relations of plants in a high

arctic polar desert, Devon Island, N.W.T., Canada. Arct. Alp. Res. **30**: 108–120.

Gold, W., and Bliss, L. 1995. Water limitations and plant community development in a polar desert. Ecology, **76**: 1558–1568. doi:10.2307/1938157.

Harper, K.T., and Belnap, J. 2001. The influence of biological soil crusts on mineral uptake by associated vascular plants. J. Arid Environ. **47**: 347–357. doi:10.1006/jare.2000.0713.

Harper, K.T., and Marble, J.R. 1988. A role for nonvascular plants in management of arid and semiarid rangelands. *In* Vegetation science: applications for rangeland analysis and management. *Edited by* P.T. Tueller. Kluwer Academic Publishers, Dordrecht, Netherlands. pp. 135–169.

Hill, M.O. 1979. TWINSPAN: a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University, Ithaca, N.Y.

Hodkinson, I.D., Webb, N.R., and Coulson, S.J. 2002. Primary community assembly on land-the missing stages: why are heterotrophic organisms always there first? J. Ecol. **90**: 569–577. doi:10.1046/j.1365-2745.2002.00696.x.

Hodkinson, I.D., Coulson, S.J., and Webb, N.R. 2003. Community assembly along proglacial chronosequences in the High Arctic: vegetation and soil development in north-west Svalbard. J. Ecol. **91**: 651–663. doi:10.1046/j.1365-2745.2003.00786.x.

Jones, G.A. 1997. Primary plant succession on the Twin Glacier Foreland, Alexandra Fjord, Ellesmere Island, Canadian High Arctic. M.Sc. thesis, Geography Department, University of British Columbia, Vancouver, B.C.

Jones, G.A., and Henry, G.H.R. 2003. Primary plant succession on recently deglaciated terrain in the Canadian High Arctic. J. Biogeogr. **30**: 277–296. doi:10.1046/j.1365-2699.2003.00818.x.

Jongman, R.H.G., ter Braak, C.T.F., and Van Tongeren, O.F.R. 1995. Data analysis in community and landscape ecology. Cambridge University Press, Cambridge, UK.

Jumpponen, A., Väre, H., Mattson, K.G., Ohtonen, R., and Trappe, J.M. 1999. Characterization of 'safe sites' for pioneers in primary succession on recently deglaciated terrain. J. Ecol. **87**: 98–105. doi:10.1046/j.1365-2745.1999.00328.x.

Lévesque, E. 1996. Minimum area and cover-abundance scales as applied to polar desert vegetation. Arct. Alp. Res. **28**: 156–162.

Lévesque, E. 1997. Plant distribution and colonization in extreme polar deserts, Ellesmere Island, Canada. Ph.D. thesis, Botany Department, University of Toronto, Toronto, Ont.

Lévesque, E. 2001. Small scale plant distribution within a polar desert plateau, central Ellesmere Island, Canada. Ecoscience, **8**: 350–358.

Lévesque, E., and Svoboda, J. 1995. Germinable seed bank from polar desert stands, Central Ellesmere Island, Canada. *In* Proceedings of the International Conference on Global Change and Arctic Terrestrial Ecosystems, 21–26 August 1993, Oppdal, Norway. *Edited by* T.V. Callaghan, U. Molau, M.J. Tyson, J.I. Holten, W.C. Oechel, T. Gilmanov, B. Maxwell, and B. Sveinobojorrnossen. Ecosystems Research Report 10, European Commission, Brussels. pp. 97–107.

Matthews, J.A. 1992. The ecology of recently-deglaciated terrain: a geoecological approach to glacier forelands and primary succession. Cambridge University Press, Cambridge, UK.

Maxwell, J.B. 1981. Climatic regions of the Canadian Arctic Islands. Arctic, **34**: 225–240.

Maycock, P.F., and Fahselt, D. 1992. Vegetation of stressed calcareous screes and slopes in Sverdrup Pass, Ellesmere Island, Canada. Can. J. Bot. **70**: 2359–2377.

McKeague, J.A. 1978. Manual on soil sampling and methods of analysis. 2nd ed. Canadian Society of Soil Science, Ottawa, Ont.

Mehlich, A. 1984. Mehlich 3 soil test extractant: a modification of Mehlich 2 extractant. Commun. Soil Sci. Plant Anal. **18**: 1003–1015.

Mueller, D.R., Vincent, W.F., Pollard, W.H., and Fritsen, C.H. 2001. Glacial cryoconite ecosystems: a bipolar comparison of algal communities and habitats. Nova Hedwigia Beih. **123**: 173–197.

Mulligan, G.A. 1990. Key to the Brassicaceae (Cruciferae) of Canada and Alaska. No. 38. Eastern Cereal and Oilseed Research Center, Agriculture and Agri-Food Canada, Central Experimental Farm, Ottawa, Ont.

Okitsu, S., Sawaguchi, S., Hasegawa, H., and Kanda, H. 2004. Vegetation development on the glacier moraines in Oobloyah Valley, Ellesmere Island, high arctic Canada. Polar Biosci. **17**: 83–94.

Porsild, A.E., and Cody, W.J. 1980. Vascular plants of continental Northwest Territories, Canada. National Museum of Natural Sciences, Ottawa, Ont.

Ryverden, L. 1971. Studies in seed dispersal: trapping of diaspores in the alpine zone at Finse, Norway. Norw. J. Bot. **18**: 215–226.

Skidmore, M.L., Foght, J.M., and Sharp, M.J. 2000. Microbial life beneath a high arctic glacier. Appl. Environ. Microbiol. **66**: 3214–3220. doi:10.1128/AEM.66.8.3214-3220.2000. PMID:10919772.

Sohlberg, E., and Bliss, L.C. 1984. Microscale patterns of vascular plant distribution in two high arctic communities. Can. J. Bot. **62**: 2033–2042.

Sondheim, M.W., and Standish, J.T. 1983. Numerical analysis of a chronosequence, including assessment of variability. Can. J. Soil Sci. **63**: 501–517.

Stöckling, J., and Bäumler, E. 1996. Seed rain, seedling establishment and clonal growth strategies on a glacier foreland. J. Veg. Sci. **7**: 45–56.

Stork, A. 1963. Plant immigration in front of retreating glaciers, with examples from the Kebnekajse area, northern Sweden. Geogr. Ann. **45**: 1–22.

Svoboda, J., and Freedman, B. 1994. Ecology of a polar oasis, Alexandra Fjord, Ellesmere Island, Canada. Captus University Publications, Toronto, Ont.

Svoboda, J., and Henry, G.H.R. 1987. Succession in marginal arctic environments. Arct. Alp. Res. **19**: 373–384.

ter Braak, C.T.F., and Smilauer, P. 2004. CANOCO for Windows. Biometrics-Plant Research International, Wageningen, Netherlands.

Tishkov, A.A. 1986. Primary succession in arctic tundra on the west coast of Spitsbergen (Svalbard). Polar Geogr. Geol. **10**: 148–156.

Wentworth, C.K. 1922. A scale of grade and class terms for clastic sediments. J. Geol. **30**: 377–392.

Wynn-Williams, D.D. 1993. Microbial processes and initial stabilization of fellfield soil. *In* Primary succession on land. *Edited by* J. Miles and D.W.H. Walton. Blackwell Scientific Publications, Oxford, UK. pp. 17–32.

Yeomans, J.C., and Bremner, J.M. 1988. A rapid and precise method for routine determination of organic carbon in soil. Commun. Soil Sci. Plant Anal. **19**: 1467–1476.

Zollitsch, B. 1969. Die Vegetationsentwicklung im Pasterzenvorfeld. Wissenschaftliche Alpenvereinsheft (München), **21**: 267–290.

Appendix A

Appendix appears on the following page.

Table A1. List of vascular plant species and growth form used in density analyses (i, individual; c, clump) on the foreland and adjacent moraine of the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut.

Family and species	Growth form
Brassicaceae	
Braya glabella Richardson	i
Braya thorild-wulffii Ostenf.	i
Cardamine bellidifolia L.	i
Draba cinerea Adams	i
Draba corymbosa R.Br. ex DC.	i
Draba oblongata R.Br. ex DC.	i
Draba subcapitata Simmons	i
Draba lactea auct. non Adams	i
Erysimum pallasii (Pursh) Fernald	i
Eutrema edwardsii R.Br.	i
Caryophyllaceae	
Cerastium alpinum L. subsp. *lanatum* (Lam.) Aschers. & Graebn.	c
Minuartia rubella (Wahlenb.) Hiern	c
Silene acaulis (L.) Jacq.*	—
Silene uralensis (Rupr.) Bocquet subsp. *uralensis*	i
Stellaria longipes Goldie subsp. *longipes*	c
Cyperaceae	
Carex aquatilis Wahl. var. minor Boott	i
Carex fuliginosa Schkuhr.	c
Carex nardina Fries s.lat.	i
Carex rupestris All.*	—
Eriophorum angustifolium subsp. *triste* (T. Fries) Hultén	i
Ericaceae	
Cassiope tetragona (L.) D. Don subsp. *tetragona*	c
Juncaceae	
Juncus biglumis L.	i
Luzula arctica Blytt in M.N. Blytt & A.G. Blytt	c
Luzula confusa Lindberg	c
Onagraceae	
Chamerion latifolium (L.) Holub[†]	—
Papaveraceae	
Papaver radicatum Rottb. s.lat.	c
Poaceae	
Alopecurus borealis Trin. subsp. *borealis*	i
Arctagrostis latifolia (R.Br.) Griseb. subsp. *latifolia*	i
Festuca brachyphylla J.A. Schultes ex J.A. Schultes & J.H. Schultes	c
Pleuropogon sabinei R.Br.	i
Poa abbreviata R.Br.	c
Poa arctica R.Br. s.lat.	c
Puccinellia bruggemannii T.J. Sørensen	i
Polygonaceae	
Bistorta vivipara (L.) Gray	i
Oxyria digyna (L.) Hill	c
Ranunculaceae	
Ranunculus sulphureus Sol.	i
Rosaceae	
Dryas integrifolia Vahl	c
Potentilla hyparctica Malte	c
Potentilla nivea L.	c
Potentilla pulchella R.Br.	c
Salicaceae	
Salix arctica Pall.	c
Saxifragaceae	
Saxifraga cespitosa L.	c

Table A1 (*concluded*).

Family and species	Growth form
Saxifraga cernua L.	c
Saxifraga foliolosa R.Br.	c
Saxifraga hirculus L.*	—
Saxifraga nivalis/tenuis	c
Saxifraga oppositifolia L.	c
Saxifraga platysepala (Trantv.)Tolm.*	—
Saxifraga rivularis L.	c
Saxifraga tricuspidata Rothb.	c
Scrophulariaceae	
Pedicularis hirsuta L.	i
Total = 51 species	

*Species not found in the 50 cm × 50 cm quadrats but found within the 40 m × 5 m site.

[†]Additional species seen on the foreland but not encountered in either the 40 m × 5 m site or the 50 cm × 50 cm quadrats.