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Initial recruitment and establishment of vascular plants in relation to topographical variation in microsite conditions on a recently-deglaciated moraine on Ellesmere Island, high arctic Canada

Akira Mori[1†*], Takashi Osono[1], Shogo Iwasaki[2], Masaki Uchida[3,4] and Hiroshi Kanda[3,4]

[1]*Division of Environmental Science and Technology, Graduate School of Agriculture, Kyoto University, Oiwake-cho, Kitashirakawa, Sakyo-ku, Kyoto 606-8502*
[2]*Division of Geoscience, Graduate School of Environmental Earth Science, Hokkaido University, Kita-10, Nishi-5, Kita-ku, Sapporo 060-0810*
[3]*National Institute of Polar Research, Kaga 1-chome, Itabashi-ku, Tokyo 173-8515*
[4]*Department of Polar Science, School of Multidisciplinary Sciences, The Graduate University for Advanced Studies (SOKENDAI), Kaga 1-chome, Itabashi-ku, Tokyo 173-8515*
[†]*Present address: School of Resource and Environmental Management, Faculty of Applied Science, Simon Fraser University, Burnaby, British Columbia, Canada V5A 1S6*
[*]*Corresponding author. E-mail: akkym@kb3.so-net.ne.jp*

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Abstract: We investigated the effects of topographical positions (moraine ridge, upper side slope and lower side slope) within a recently-deglaciated young moraine on initial recruitment and establishment of vascular plants. Compared with the moraine ridge, the upper slope had similar/higher abundance of vascular plants in terms of percent cover, frequency occurrence, species number, and density/biomass of a dominating species, *Salix arctica*. Establishment and growth of vascular plants are generally inhibited on unstable habitats; nevertheless, on this newly-formed moraine, every attribute measured for vascular plants implied a higher probability of vascular plant recruitment on the upper slope, where substrate is less stable than on the ridge. Further, the microsite with greater vascular plant abundance, *S. arctica* density and *S. arctica* aboveground/leaf biomass accumulated more organic materials regardless of topographical positions, and such an organic accumulation was deepest on the upper slope, suggesting that relatively-successful plant establishment occurs on this site. This is further supported by the *S. arctica* population structure, which implies a relatively-constant juvenile supply on the upper slope. Along a slope, unstable gravels easily slide down hill. This topographical process may cause large rock size and high surface cover by rocks on the lower slope. On the upper slope, the percent cover by rocks had therefore become smaller, leading to high cover by fine-grained sediments, which retain moisture favorable for germination and growth of vascular plants. This would enhance the emergence of pioneer vascular plant species, probably resulting in higher vascular plant abundance, density and biomass of *S. arctica* on the upper slope. This study suggests that during primary succession following deglaciation in the high arctic the upper slope of a newly-formed glacier moraine may be an important location for the initial recruitment and establishment of pioneer vascular plant species, such as *S. arctica.*

key words: moraine ridge, moraine side slope, primary succession, *Salix arctica*, rock

Introduction

In the high arctic, well-vegetated areas, although infrequent, can be occasionally observed. Such an area is sometimes referred to as a "polar oasis" (Muc *et al.*, 1992). In such areas, vegetation succession and ecosystem development following deglaciation can be recognized in a different fashion from a harsh high arctic desert (Svoboda and Henry, 1987; Jones and Henry, 2003), which is characterized by vast expanses of barren or meagerly-vegetated terrain with no significant populations of land animals, or by icefields (Freedman *et al.*, 1992). In well-vegetated high arctic areas, the primary plant succession sometimes represents directional species addition with time (directional succession, Svoboda and Henry, 1987; Jones and Henry, 2003). However, because it is atypical (Okitsu *et al.*, 2004), this type of primary succession remains largely undocumented in the high arctic (Hodkinson *et al.*, 2003; Jones and Henry, 2003). In the high arctic, well-developed vegetation, such as a polar oasis, exists in a limited region, but provides critical habitats for biota (Bliss and Gold, 1994), strongly emphasizing importance of these areas. For further clarification of the arctic ecosystem, it is thus essential to gather more detailed information on the primary succession in the infrequent, but precious well-vegetated areas in the high arctic.

In discussing the primary succession process, it is crucial to consider the initial recruitment process of plants (Lévesque, 2001; Cooper *et al.*, 2004). In the high arctic, it is known that the restricted availability of favorable microhabitats for recruitment and establishment of vascular plants could partially explain the low plant cover (Walker, 1995). Therefore, detecting habitats preferable for recruitment and establishment of vascular plants is of importance for further understanding of primary succession in the high arctic. For germination and subsequent establishment of vascular plants, the substrate plays an important role (Cooper *et al.*, 2004). In the retreating margin, moraines and other landforms are generally unstable (Matthews, 1992), so that in the initial process of primary succession following deglaciation, substrate instability profoundly inhibits recruitment, growth and survival of invading vascular plants (Heilbronn and Walton, 1984). Specifically, because such habitat instability is expected to have a close linkage with topography, it is significant to consider the topographical effects on initial plant recruitment in the retreating margin. The close relationship between physical environments and vegetation development has been investigated mainly on a large-scale, such as landscape level. However, this has been hardly discussed from a small-scale viewpoint, such as a variation within one recently-deglaciated moraine. Thus, the study of topographical variation of microhabitat condition along a slope of recently-deglaciated moraine and its influence on vascular plant recruitment is important for understanding the process of vegetation development in the high arctic.

In a well-vegetated area in Ellesmere Island, high arctic Canada, where the succession type is typically directional, Okitsu *et al.* (2004) have demonstrated that several vascular plant species can invade and emerge on a moraine newly-formed during the Little Ice Age, which consists of unstable fresh, sharp rocks and is sparsely covered by plants. By a field survey on different topographical positions within this young moraine, we aimed 1) to quantify topographical variation in microsite conditions and 2) to clarify its influence on initial recruitment and establishment of vascular plant species. Furthermore, we specifically focused on a pioneer vascular plant species, arctic willow (*Salix arctica*), which can occur on this youngest moraine most frequently and can continue to dominate even on the older moraines formed during the Last Ice Age on this glacier foreland (Okitsu *et al*., 2004). *Salix arctica* is a deciduous, dioecious dwarf shrub, which is one of the most common and abundant shrubs in the Canadian high arctic (Tolvanen *et al*., 2002). Among vascular plant species appeared on deglaciated moraines on this area, this species is therefore expected to have a major role in ecosystem development. Hence, by focusing on population structures of *S. arctica* within this moraine, we aimed 3) to infer the detailed initial establishment process of vascular plants. Based on the above, we provide significant information on the initial process of directional succession after glacier retreat in the marginal high arctic environment.

Materials and methods

Study site

The study site (80°52′N, 82°50′W) is located within the proglacial area in the southern front of Arklio Glacier of the Krieger Mountains, near Oobloyah Bay, Ellesmere Island, Nunavut, Canada. Although there are no available climatic data for the study site, climatic data taken by the weather station at Eureka (80°00′N, 85°56′W), 130 km south of Oobloyah Bay, shows that the study area has an extremely harsh climate (Okitsu *et al*., 2004): the monthly mean air temperature of the warmest month (July) is about 3.3°C, that of the coldest month (February) is about −38.0°C, annual mean temperature is about −19.7°C, and annual precipitation is about 64 mm. Geological features of the study site are described in King (1981) and Okitsu *et al.* (2004).

The Arklio Glacier has developed glacial moraines with different developmental periods since the Last Glacial (King, 1981). The youngest moraine was estimated as having been formed during the Little Ice Age (250 years ago; Okitsu *et al*., 2004). On the youngest moraine, although the abundance of plants was very low, several plant species could recruit and establish themselves (Okitsu *et al*., 2004). Vegetational characteristics of the deglaciated moraines in this area were described in Okitsu *et al.* (2004).

Field research

In July 2004, we established three 50 m line transects at different positions within the youngest moraine. A morphological description of the studied moraine is shown in Fig. 1. The first transect was set on the moraine ridge (Ridge site). The second was on the upper part of the moraine side slope, above the break line of the slope (Upper slope site). The third was on the lower part of the moraine side slope, below the break line of the slope (Lower slope site). Here, the investigated moraine slope was faced on the opposite side from the glacier. The mean angle of moraine ridge was 0° (min-max, 0–7°), so that the substrate at this location was relatively stable. In contrast, substrates on the side slope were unstable and susceptible to movement at any time. Especially, the mean angle of the lower slope was 37° (min-max, 30–42°) and was near the angel of repose, indicating fairly substrate instability of this location. The mean angle of the

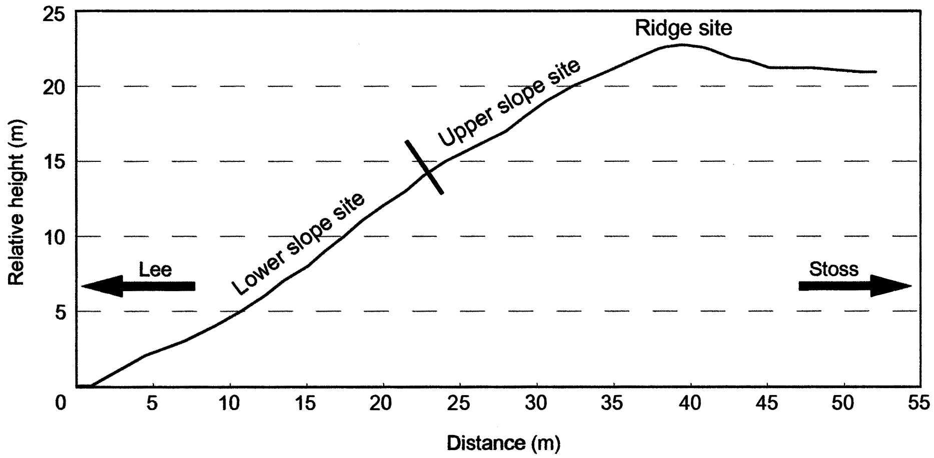

Fig. 1. A morphological description of the studied moraine. The solid line connecting the upper slope and lower slope is the break line of the moraine side slope. The ridge site was set on the ridge line, and the upper slope site and lower slope site were set horizontally along the break line.

upper slope was 30° (min-max, 24–39°); materials such as rocks at this location were also unstable and prone to falling, although materials on the upper slope seemed to be relatively stabilized compared to those on the lower slope. Therefore, the three sites could be regarded as located at different topographical positions with different substrate stabilities.

On each transect, 1×1 m quadrats were successively established at 2.5 m intervals (20 quadrats in total for each transect). Within each quadrat, we estimated microsite percent cover (%) by vascular plants, by vascular plants plus cryptogams, by rocks, and by fine-grained sediments. Rocks (≥ 2 mm) were distinguished from fine sediments (<2 mm). Here, percentage cover was assessed by eye by dividing one quadrat into one hundred 10×10 cm sections, although it is difficult to accurately distinguish vascular plants form cryptogams, and rocks from fine sediments, respectively. This was considered the most suitable recording method, since percentage cover estimations are quick, repeatable and minimally invasive (Kent and Coker, 1992).

Then within each quadrat, we recorded maximum rock size (cm), maximum accumulation depth of plant organic litter (cm), and species names of vascular plants. Within each quadrat, we measured diameter at ground level and life-stage of all *S. arctica* individuals. Aboveground and leaf biomass of *S. arctica* within each quadrat were also estimated by using a biomass-diameter relationship equation obtained from samples harvested on this moraine. The life-stages of *S. arctica* individuals were determined from their reproductive status and size. For reproductive individuals, sex was recorded. For non-reproductive ones, life-stage was determined from stem development; S-size individuals had no apparent prostrating stems, M-size individuals had prostrating stems <10 cm long, and L-size individuals had prostrating stems ≥ 10 cm long.

Statistical analyses

Differences in microsite cover (%) and attributes (maximum rock size, maximum organic accumulation depth, species abundance of vascular plants, individual density of *S. arctica*, and aboveground/leaf biomass of *S. arctica*) among site positions were evaluated using the Mann-Whitney U test. To exclude multiplicity, significance levels were adjusted according to Bonferroni's inequality. The coefficient of variation (CV; %) was also calculated for each measured parameter to quantify the magnitude of plant and microsite heterogeneity within each site (Matthews, 1992; Hirobe *et al*., 2001).

Using the 20 quadrat data within each transect, we assessed the relationships of maximum organic accumulation depth with species abundance of vascular plants, *S. arctica* density, and *S. arctica* biomass. However, there is a well-known spatial autocorrelation with reference to the plant organic accumulation (Hirobe *et al*., 2001). Thus, since the variables do not satisfy the assumption of independence, the correlation analysis cannot be performed in a typical fashion (Mitchell-Olds, 1987). Fisher's method of randomization allows a modified null hypothesis to be tested when observations are not independent (Mitchell-Olds, 1987). In this study, null distributions of the correlation coefficient (r) were generated by randomly assigning the observed attributes to the quadrats using 5000 permutations for each randomization test. The observed r-value was then compared to the null distributions to determine significance. The null hypothesis was that organic accumulation depth was independent of each plant attribute (species abundance of vascular plants, *S. arctica* density, and *S. arctica* aboveground/leaf biomass).

Results

Microsite conditions

Microsite conditions at each site are shown in Table 1. The percent cover by rocks significantly increased in the order of lower slope site, ridge site and upper slope site. The coefficient of variation (CV) of rock cover was highest at the lower slope site compared to the other two sites. Also, the percent cover by fine-grained sediment significantly increased at the upper slope site, ridge site and lower slope site, while the CV value of fine sediment cover decreased in the same order. Maximum rock size was significantly different between the site positions, smallest at the upper slope site and largest at the lower slope site. The CV value of rock size was highest at the upper slope site. Maximum organic accumulation depth was greatest at the upper slope site and smallest at the lower slope site. Notably, the CV of organic accumulation showed quite high values ranging from the smallest value of 121% at the upper slope site to the highest value of 229% at the lower slope site.

Community attributes

Community attributes at each site are shown in Table 2. Although significant differences were not detected for percent cover by vascular plants, there was a slight tendency for vascular plant cover to increase in the order of upper slope site, ridge site, and lower slope site. The CV of vascular plant cover showed quite high values ranging from the smallest value of 205% at the upper slope site to the highest value of 447% at

Table 1. Envoronmental properties within 1×1 m quadrats at each site. Differences were tested with the Mann-Whitney test. To exclude multiplicity, significant levels were adjusted. The same letter indicates no significant difference at $P<0.05$. CV indicates the coefficient of variation (%).

Property	Position		
	Ridge site	Upper slope site	Lower slope site
Cover by rocks (%)			
Mean	82.5[a]	56.5[b]	92.0[c]
CV	12	37	125
Cover by fine-grained sediments (%)			
Mean	15.8[a]	42.5[b]	7.5[c]
CV	69	50	151
Maximum rock size (cm)			
Mean	36.3[a]	26.1[b]	48.7[c]
CV	41	78	47
Maximum organic accumulation (cm)			
Mean	0.3[a]	0.9[a]	0.1[b]
CV	131	121	229

Table 2. Community attributes within 1×1 m quadrats at each site. Differences were tested with the Mann-Whitney test. To exclude multiplicity, significant levels were adjusted. The same letter indicates no significant difference at $P<0.05$. CV indicates the coefficient of variation (%).

Property	Position		
	Ridge site	Upper slope site	Lower slope site
Cover by vascular plants (%)			
Mean	0.8[a]	1.0[a]	0.3[a]
CV	244	205	447
Cover by vascular plants and cryptogams (%)			
Mean	1.8[a]	1.0[a]	0.5[a]
CV	168	205	308
Species abundance of vascular plants (species/m^2)			
Mean	0.6[a]	1.0[a]	0.0
CV	113	86	—
Individual density of *Salix arctica* (no./m^2)			
Mean	0.2[a]	0.9[a]	0.0
CV	205	194	—
Aboveground biomass of *Salix arctica* (g/m^2)			
Mean	0.5[a]	3.9[a]	0.0
CV	321	203	—
Leaf biomass of *Salix arctica* (g/m^2)			
Mean	0.1[a]	0.6[a]	0.0
CV	263	196	—

the lower slope site. The percent cover and CV of vascular plants plus cryptogams were also smallest and greatest at the lower slope site, respectively. For species abundance of vascular plants, *S. arctica* density, and aboveground and leaf biomass of *S. arctica*, differences were tested between the ridge site and the upper slope site, because there are no vascular plants at the lower slope site; although statistical differences were not detected for these variables, they tended to be greater at the upper slope site than at the ridge site, and the CV values for plant abundance were greater at the ridge site than the at upper slope site.

Frequency occurrence (%) of vascular plants at each line transect is shown in Table 3. A total of six vascular plant species were recorded in this study. On the ridge site, four vascular plant species were observed, and 50% of the quadrats had no vascular plant species. On the upper slope site, five vascular plant species were observed, and 30% of the quadrats had no vascular plant species. Especially, the frequency occurrence of each vascular plant species tended to be higher at the upper slope site, compared to the ridge site. On the lower slope site, there were no vascular plants. For the lower slope site, the foliage part of one vascular plant individual growing on the location adjacent to the edge of a studied quadrat on this site covered the surface of this quadrat. So, in spite of the absence of vascular plants within 20 studied quadrats on this site (Table 3), the percent surface cover by vascular plants on this site

Table 3. Frequency occurrence (%) of vascular plants at each site.

Vascular plant species	Position		
	Ridge site	Upper slope site	Lower slope site
Epilobium latifolium	30	30	0
Salix arctica	20	40	0
Stellaria monantha	5	10	0
Dryas integrifolia	5	0	0
Papaver radicatum	0	10	0
Oxyria digyna	0	10	0
All species	50	70	0

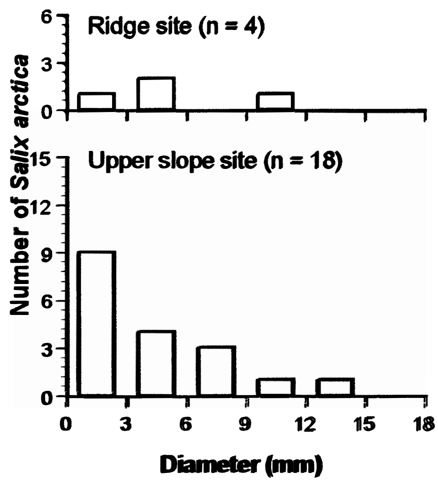

Fig. 2. Frequency size (diameter at ground level) distribution of *Salix arctica* on the ridge and upper slope sites. At the lower slope site, there was no *Salix arctica* individual.

accounted for 0.3% (Table 2).

Population structures of *Salix arctica*

Figure 2 shows the diameter frequency distribution of *S. arctica* at the ridge site and the upper slope site. On the upper slope site, *S. arctica* showed an inverse J-shaped size distribution. The life-stage distributions of *S. arctica* showed that two sites had female individuals of *S. arctica*; especially on the upper slope site, S-sized individuals showed the highest proportion within the population (Table 4).

Correlations between plant and microsite attributes

On both the ridge site and the upper slope site, maximum organic accumulation depth was significantly positively correlated with species abundance of vascular plants, *S. arctica* density, and aboveground and leaf biomass of *S. arctica* (Table 5).

Table 4. Proportion (%) of *Salix arctica* individuals within each site.

Life stage	Position		
	Ridge site ($n=4$)	Upper slope site ($n=18$)	Lower slope site ($n=0$)
Non-reproductive individuals			
S-size	0.0	38.9	—
M-size	25.0	16.7	—
L-size	25.0	16.7	—
Reproductive individuals			
Male	0.0	0.0	—
Female	50.0	27.8	—

Table 5. Correlation coefficient (r) of maximum organic accumulation depth with species abundance of vascular plants, density of *Salix arctica*, and aboveground biomass of *Salix arctica* within each 1×1 m quadrat. Significance levels were based on the 5000 randomization test. Significant levels: **$P<0.01$, *$P<0.05$.

Quadrat properties	Position	
	Ridge site	Upper slope site
Species abundance of vascular plants (species/m^2)	0.649**	0.572**
Individual density of *Salix arctica* (no./m^2)	0.587**	0.558**
Aboveground biomass of *Salix arctica* (g/m^2)	0.599**	0.511*
Leaf biomass of *Salix arctica* (g/m^2)	0.644**	0.551*

Discussion

In deglaciated terrains, plant recruitment is a key event that regulates primary plant succession (Jumpponen *et al*., 1999; Lévesque, 2001). Initial plant recruitment and establishment on recently-deglaciated terrains is profoundly determined by physical environmental conditions of microsites (Jumpponen *et al*., 1999). Here, to assess the initial recruitment and establishment of vascular plants in the retreating margin, this study specifically focused on differences in the relationship of plant occurrence to microsite conditions among spatial positions within a recently-deglaciated moraine.

The slope of recently-formed moraines with negligible vegetation is unstable, and is therefore susceptible to mass movement, such as rockfall and debris flow (Matthews, 1992). So, among the site locations within this investigated moraine, the ridge site seems to be a relatively stabilized location. However, compared with the ridge, the upper slope site had similar/higher abundance of vascular plants in terms of plant cover, species number, density/biomass of indicator species *S. arctica* (Table 2), and frequency occurrence of each vascular plant species (Table 3). Establishment and growth of plants are generally inhibited on unstable habitats (Heilbronn and Walton, 1984); nevertheless, on this recently-deglaciated moraine, every attribute measured for vascular plants suggested a higher probability of vascular plant emergence on the upper part of the side slope, expected to be less stable than the ridge top.

High recruitment of vascular plants onto the upper slope can also be inferred by relationships between plant and microsite attribues; microsites with greater species abundance of vascular plants, higher *S. arctica* density and greater *S. arctica* above-ground/leaf biomasses, accumulated more organic materials regardless of the site position (Table 5). The spatial distribution of primary production directly affects the spatial distribution of organic matter through litter input (Hirobe *et al*., 2001). The results of CVs (Tables 1 and 2) indicate that organic accumulation depth and plant abundance were highly spatially heterogeneous on each site within the moraine; nevertheless, these two were closely correlated (Table 5). Accumulation depth of organic matter may therefore imply duration after plant establishment. Accordingly, the deepest organic accumulation on the upper slope (Table 1) suggests that gradual but relatively-successful plant establishment occurs on this site.

Moreover, it is interesting to focus on population structures of *S. arctica* at each investigated position. The upper slope site had *S. arctica* individuals belonging to all life-stages from non-reproductive smaller individuals to reproductive ones except for males (Table 4), although the dry conditions of this moraine might lead to the sex ratio of reproductive individuals being biased to females (Pielou, 1994). Specifically, it is worth noting that only on the upper slope did *S. arctica* juveniles seem to be relatively constantly provided to the site, as indicated by the inverse J-shaped size distribution (Fig. 2) suggesting a stable population structure (Mori and Takeda, 2004). These structural characteristics of this species on the upper slope seem to account for the important role of this position within the new moraine for population establishment of *S. arcitica* as a dominating pioneer vascular plant species. This may further suggest an importance of this position for initial appearance of the more general vascular plant community, although information about populations of other co-occurring vascular plant species was unfortunately lacking in this study.

These facts must be related to microhabitat properties of the upper slope, which profoundly affect the recruitment, establishment and growth of appearing vascular plants. Initially steep slope angles are lowered down by a variety of many processes including slope wash, creep, gelifluction, slumping and sediment flow (Matthews, 1992). Especially, among these slope processes, it appears that unstable materials on the upper slope can easily fall down to the lower slope, resulting in decrease in slope angle to below the angle of repose (Fig. 1). The results that maximum rock size and percent cover by rocks were significantly largest on the lower slope site (Table 1) may derive from such a topographical process. On the upper slope site, rock cover had therefore become smaller, leading to high surface cover by fine-grained sediments (Table 1). Remaining substrates on the upper slope, such as boulders, which are expected to be relatively stable compared to those that have fallen, might play a role in retaining fine-grained sediments. Fine-grained sediments retain moisture favorable for germination and growth of vascular plants (Mizuno, 1998). This would enhance the emergence of pioneer vascular plants, probably resulting in higher tendency in vascular plant abundance, *S. arctica* density and *S. arctica* biomass on the upper slope of this recently-deglaciated moraine.

It is notable that, although the results of this study demonstrate the subtle effects of moraine topography on recruitment and establishment of vascular plants, mainly on *S. arctica*, this effect may be due to the conditions of the microsite itself, resulting from topographical processes, rather than the topography itself. Jumpponen *et al.* (1999) similarly emphasized the importance of physical conditions of a microsite for plant occurrence on a deglaciated foreland. Because several other agents affecting plant recruitment, such as microtopography, particular substrate quality, seed source, and dispersability of each speices (Harper, 1977; Chapin *et al*., 1994; Lévesque, 2001; Cooper *et al*., 2004; Mori *et al*., 2004), are not documented in this study, further study is needed to clarify the recruitment process of vascular plants into vacant space in the retreating margin. Furthermore, moraine morphology largely differs depending on several conditions, such as the glacier itself and periglacial processes, probably leading to different plant invasion patterns. However, during primary plant succession following deglaciation, it is worth noting that, within a newly-formed steep glacier moraine as in this study, the upper part of the side slope may be an important location for the initial recruitment and establishment of pioneer vascular plants in a well-vegetated area in the high arctic.

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