



Vegetation diversity and selected abiotic factors influencing the primary succession process on the foreland of Gåsbreen, Svalbard

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Abstract: The rapidly changing Arctic provides excellent opportunities for investigating primary succession on freshly deglaciated areas. Research on the Gåsbreen foreland (S Spitsbergen) traced the succession of particular groups of organisms and species, particularly lichens and bryophytes, and determined the effect of selected abiotic factors on this succession. Fieldwork in 2008, employed a continuous linear transect of phytosociological relevés (1 m²) along the foreland. Data analysis allowed to distinguish five different succession stages and three types of colonisers. Canonical correspondence analysis and a permutation test showed that distance from the front of the glacier and fine grain material in the substrate mostly influenced the distribution and abundance of vegetation, and the steepness of the moraine hills affected the colonisation process, mainly in the older part of the marginal zone.

Key words: Arctic, colonisation, glacier, lichens, bryophytes, vascular plants.

Introduction

Arctic regions offer perfect opportunities for studying primary succession processes on freshly deglaciated areas (Frenot *et al.* 1998; Jorgenson *et al.* 2015). Areas which are exposed from retreating glaciers are successively colonised by different groups of organisms such as cyanobacteria, lichens, bryophytes and vascular plants. The process of colonisation depends not only on the availability of diaspores of surrounding vegetation (Bullock *et al.* 2002; del Moral and Erin 2004; Řehouňková and Prach 2006; Jones and Del Moral 2009), but also on

a number of abiotic factors that characterise the habitat (Matthews 2008), as well as on geomorphological processes shaping the surface after the ice disappears.

On Svalbard, a progressive recession of glaciers has been observed since the end of the Little Ice Age (Błaszczuk *et al.* 2009); glaciers have been reduced both in their thickness and coverage. Measurements from north-western (*e.g.* Moreau *et al.* 2005) and southern Spitsbergen (*e.g.* Ziaja and Ostafin 2007; Ziaja *et al.* 2016a) indicate the intensification of the recession process from the 1980s onwards. Glacier volume has decreased, especially on western Svalbard (Kohler *et al.* 2007; James *et al.* 2012; Nuth *et al.* 2013).

Studies on vegetation on recently deglaciated areas on Svalbard were initiated by Kuc (1964) near the Polish Polar Station in Hornsund (southern Spitsbergen). Since the 1980s, a number of studies has been conducted on glacier forelands on the north-western coast of Spitsbergen, near Ny-Ålesund (Brossard 1985; Moreau *et al.* 2008). A significant proportion of the world's latest research related to primary succession on glacier marginal zones is based on this area and covers a variety of topics, including plant communities evolution (Hodkinson *et al.* 2003; Moreau *et al.* 2005; Moreau *et al.* 2008), pioneering species (Nakatsubo *et al.* 2010), species ecology (Nakatsubo *et al.* 2005; Uchida *et al.* 2006; Yoshitake *et al.* 2007), and the role of soil microorganisms (Bekku 2004), including mycorrhizal fungi (Fujiyoshi *et al.* 2010). Apart from the Ny-Ålesund region, research has been conducted on the western coast of Spitsbergen (Tishkov 1986), in central Spitsbergen (Ziaja and Dubiel 1996; Prach and Rachlewicz 2012), and in southern Spitsbergen (Kuc 1964; Fabiszewski 1975; Pirożnikow and Górniak 1992; Wojtuń *et al.* 2008).

The most detailed analyses on primary succession on Svalbard were associated with the successional studies of vascular plants communities (*e.g.* Pirożnikow and Górniak 1992; Nakatsubo *et al.* 2010; Prach and Rachlewicz 2012), and their interactions with mycorrhizal fungi (Těšitel *et al.* 2014; Davey *et al.* 2015). Other components of the marginal zone vegetation of the glacier (in particular bryophytes and lichens) were often overlooked or treated generally and lacked detailed species identification (*e.g.* Yoshitake *et al.* 2011). In the case of bryophytes, only Kuc (1996) included specific names of species inhabiting glacier forelands. Regarding lichens, in studies conducted near Ny-Ålesund, only large fruticose terrestrial lichenised fungi, such as *Cetrariella delisei*, were taken into account (Hodkinson *et al.* 2003; Moreau *et al.* 2005), and from the total group of bryophytes only *Sanionia uncinata* and Polytrichaceae were noted (Moreau *et al.* 2005). Only large terrestrial lichens (*Cladonia mitis*, *Cetraria* spp. and *Stereocaulon alpinum*) and bryophyte taxa, such as *Bryum* sp., *Drepanocladus* sp. and *Polytrichum* sp., were considered in their later studies (Moreau *et al.* 2009). In other Arctic regions only Jones and Henry (2003) analysed specific species of bryophytes.

Since spore-bearing organisms, bryophytes and lichens, are the main tundra components (Pointing *et al.* 2015) it is important to supplement the information on their occurrence in these areas. There is still a need for a comprehensive research

of the primary succession process that takes into account these organisms as well as vascular plants. The main objectives of the current study were to (1) trace the succession of particular groups of organisms and species, and their possible replacements, with a special focus on lichens and bryophytes, (2) identify the main successional stages on the studied glacier foreland, (3) identify 'early' and 'late' colonisers, and (4) determine those abiotic factors affecting the succession.

Material and methods

Study area. — Gåsbreen glacier is located in the north-western part of Sørkapp Land, on the southern shore of Hornsund (south Spitsbergen) (Fig. 1). It is a medium-sized valley glacier, *c.* 7.3 km in length and 14.3 km² in area, with a volume of 1.6 km³ in the 1990s (Hagen *et al.* 1993). Since the end of the 19th century, Gåsbreen has been systematically studied, the oldest information about its extent derived from a map made in 1899 by De Geer (1923, after: Ziaja and Ostafin 2007). The glacier was mapped in 1938, 1983–1984 and 1990 (Ziaja and Ostafin 2007), and data for the recent years has been obtained from images provided by the Terra ASTER satellite (NASA).

According to the Circumpolar Arctic Vegetation Map (Walker *et al.* 2005), Gåsbreen is located in bioclimatic subzone B. The vegetation in this subzone is dominated by lichens and mosses (30–60%). The vegetation is 5–10 cm in height and covers 20–80% of the surface area. The vegetation map created by Elvebakk (2005) presents three major vegetation units which can be identified in the north-western Sørkapp Land: (1) mesic, circumneutral tundra with *Luzula nivalis*; (2) mesic, acidic tundra characterized by *Luzula confusa*, and (3) *Deschampsia alpina* mires. Ziaja *et al.* (2016b) mention several different plant communities that occur in the north-western Sørkapp Land, including the *Racomitrium lanuginosum* community, the *Flavocetraria nivalis*-*Cladonia rangiferina* community, the *Gymnomitrium coralloides* community, the *Cetrariella delisei* community, and the *Bistorta vivipara* community.

Fieldwork and data analyses. — Fieldwork was carried out in the summer of 2008. A continuous linear transect consisting of phytosociological relevés was designated from the glacier front to the oldest part of the Gåsbreen marginal zone (Fig. 1); it was located in such a way as to cross the longest possible part of the marginal zone. Phytosociological relevés were made using a 1 × 1 m frame, divided into 100 squares, each of 10 × 10 cm. One square corresponded to 1% cover of taxon. In certain relevé the percentage cover of each species was determined from 1% to 100% scale. For each relevés, the total percentage cover of vascular plants, mosses and lichens was determined, as well as the exposure and steepness of the substrate of relevé.

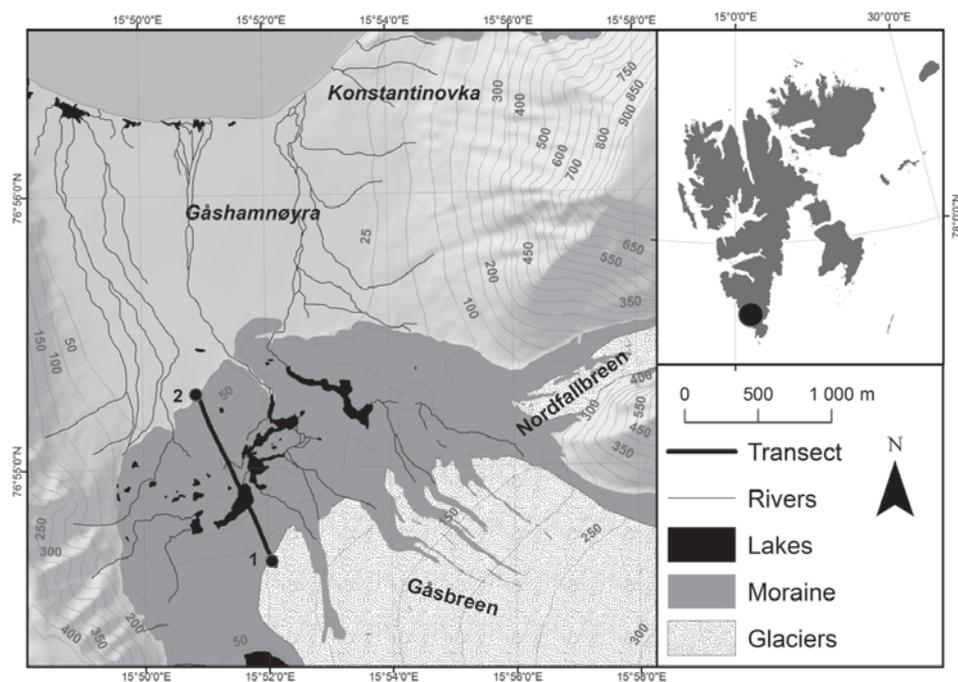


Fig. 1. Location of the study area and linear transect on the Gåsreen marginal zone (extent of glacier from 2001–2010): 1 – first relevé; 2 – last relevé (© Norwegian Polar Institute 2014: <http://geodata.npolar.no/>).

Based on collected data, list of recorded species of vascular plants, bryophytes and lichens was prepared (Table 1). To determine the dominant species in term of abundance (Table 1) and to distinguish the primary succession stages (Fig. 2), the cover percentages for each species were calculated on the Braun-Blanquet scale. The succession stages were distinguished based on the changes in species composition such as the appearance and disappearance of species, changes in percentage cover of both, certain species abundance and general coverage of vegetation group (Braun-Blanquet 1964). Additionally, the succession stages were graphically interpreted taking into account the geomorphological features of moraine along the transect (Fig. 2). To create a sequential graph of changes in the total percentage cover of vascular plants, bryophytes and lichens along the transect the percentage values were used. In these graphs, also the first records of species were marked (Fig. 2).

Canonical correspondence analysis (CCA) and Monte Carlo permutation tests were used to determine the main factors affecting primary succession. In case of vegetation, the percentage cover was taken to perform statistical analyses. The terrain relief along the transect varied according to substrate age; in the area exposed from the ice since 1936, most of the surface was flat, with only small

hills (< 3 m). Higher moraines occurred at approximately 950 m of transect. The older part, exposed from the ice before 1936, was much hillier, with higher (> 30 m) and steeper hills. To determine the age of the individual parts of the marginal zone, the map created by Ziája *et al.* (2016a) containing data on changes of the glacier since 1983, and maps showing the extent of the glacier in 1899 (De Geer 1923, after: Ziája and Ostafin 2007), 1936 (C13 Sørkapp 1947), and 1983 (C13 Sørkapp 1986) were used. Due to above-mentioned differences in landform features in the younger and the older part of the transect, additional CCA analysis was performed separately for each part. For the statistical analyses the following factors were chosen: *distance* – distance from the front of the glacier in

Table 1

The list of species recorded on the Gåsbreen foreland which characterise the distinguished succession stages. Also, the maximum abundance of each species is given. ‘Stage of succession’ corresponds to Fig. 2. Symbols used: P = vascular plants, B = bryophytes, and L = lichens. The cover percentages for each species were calculated on the Braun-Blanquet scale according to: r – 1%, + – 2%, 1 – 3–4%, 2 – 5–25%.

Stage of succession	Species		Maximum coverage
1	<i>Carex lachenalii</i> Schkuhr.	P	+
	<i>Cochlearia groenlandica</i> L.	P	+
	<i>Sagina nivalis</i> (Lindbl.) Fr.	P	+
	<i>Poa alpina</i> var. <i>vivipara</i> L.	P	+
	<i>Cerastium regelli</i> Ostenf.	P	1
	<i>Saxifraga cernua</i> L.	P	1
	<i>Saxifraga cespitosa</i> L.	P	1
	<i>Saxifraga oppositifolia</i> L.	P	2
	<i>Bryum pseudotriquetrum</i> (Hedw.) P. Gaertn.	B	+
	<i>Brachythecium turgidum</i> (Hartm.) Kindb.	B	+
	<i>Cerastium arcticum</i> Lange	P	2
2	<i>Draba oxycarpa</i> Sommerf.	P	2
	<i>Draba alpina</i> L.	P	2
	<i>Salix polaris</i> Wahlenb.	P	+
3	<i>Polyblastia cupularis</i> A. Massal.	L	+
	<i>Protoblastenia rupestris</i> (Scop.) J. Steiner	L	r
	<i>Puccinellia vahliana</i> (Liebm.) Scribn. <i>et</i> Merr.	P	1
	<i>Micranthes nivalis</i> L.	P	r
	<i>Hypnum bambergeri</i> Schimp.	B	+
	<i>Silene acaulis</i> (L.) Jacq.	P	+

Table 1

Stage of succession	Species		Maximum coverage
4	<i>Distichum inclinatum</i> (Hedw.) Bruch <i>et</i> Schimp.	B	+
	<i>Pohlia cruda</i> (Hedw.) Lindb.	B	r
	<i>Andreaea blyttii</i> Schimp.	B	l
	<i>Polyblastia hyperborea</i> Th. Fr.	L	+
	<i>Thelidium papulare</i> (Fr.) Arnold	L	r
	<i>Verrucaria obsoleta</i> Lyngé	L	r
	<i>Carbonea vorticosa</i> (Flörke) Hertel	L	r
	<i>Polyblastia theleodes</i> (Sommerf.) Th. Fr.	L	+
	<i>Aspicilia disperspens</i> (Zahlbr.) Räsänen	L	+
	<i>Aspicilia aquatica</i> Körb.	L	r
	<i>Physcia caesia</i> (Hoffm.) Hampe <i>ex</i> Fűrnr.	L	+
	<i>Eiglera flavida</i> (Hepp) Hafellner	L	+
	<i>Lecidea plana</i> (J. Lahm) Nyl.	L	r
	<i>Xanthoria elegans</i> (Link) Th. Fr.	L	+
	<i>Rhizocarpon geminatum</i> Körb.	L	r
	<i>Verrucaria acrotella</i> Ach.	L	r
	<i>Protothelenella sphinctrinoides</i> (Nyl.) H. Mayrhofer <i>et</i> Poelt	L	+
<i>Stereocaulon depressum</i> (Frey) I.M. Lamb	L	+	

meter values; *fine grain* – percentage of particles < 2 cm diam. in soil; *exposure* – exposure of moraine hills determined using magnetic compass and divided into four categories: S: 135°–225°, N: 315°–45°, E: 45°–135°, W: 226°–314°); *steepness* – steepness of moraine hills determined with inclinometer; *age category* – two categories of absolute age of the substrate: the younger exposed from the ice between 1936 and 1983 (25–72 years) and the older revealed prior to 1936 (> 72 years). The youngest part of transect (< 25 years) was not taken into analyses, because of complete lack of vegetation. Data were normalised using log₁₀ transformation provided by CANOCO v. 4.5 (Ter Braak and Šmilauer 2002). Analyses were carried out using STATISTICA v. 9.0 (<http://www.statsoft.com>) and CANOCO v. 4.5. Taxonomical nomenclature followed Rønning (1996), Index Fungorum (<http://www.mycobank.org/>), Frisvoll and Elvebakk (1996), Hill *et al.* (2006) and Ochyra *et al.* (2008).

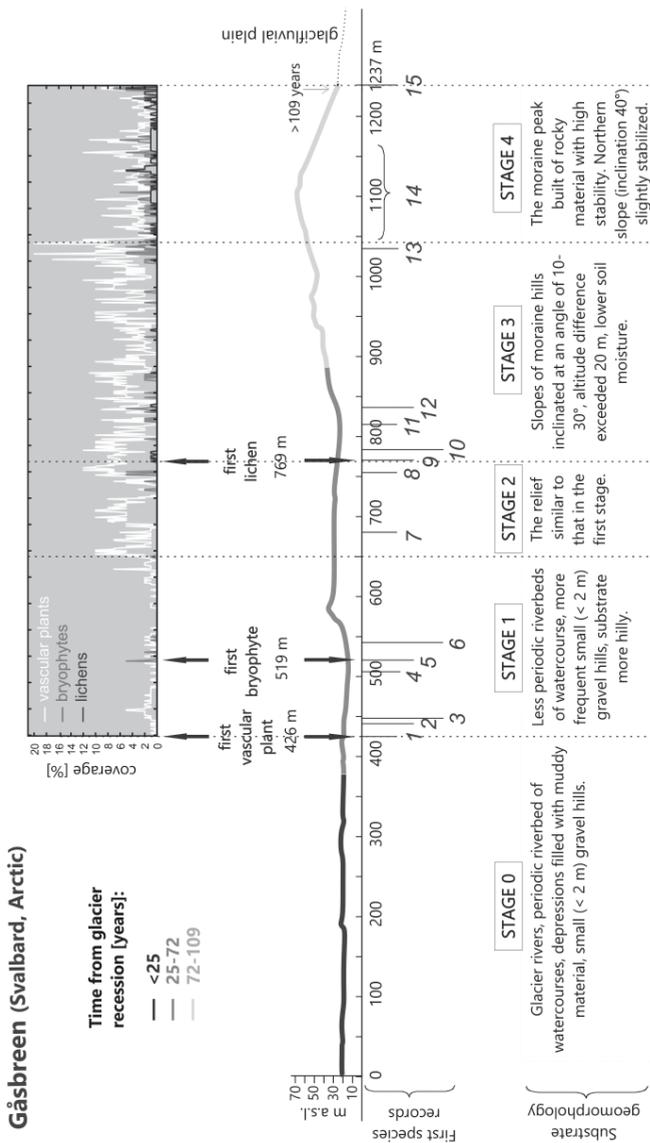


Fig. 2. Stages of succession on the Gåsbeen foreland (the first records of species and altitude graph were taken from Olech *et al.* 2011 and modified). The geomorphological characteristic of the substrate as well as the species recorded in each stage are presented. The arrows mark the first records of vascular plants, bryophytes and lichens. The numbers 1–15 refer to first records of taxa: 1 – *Carex lachenalii*, *Cochlearia groenlandica*; 2 – *Sagina nivalis*, *Poa alpina* var. *vivipara*; 3 – *Cerastium regelli*, *Saxifraga cernua*, *Saxifraga oppositifolia*; 4 – *Saxifraga oppositifolia*; 5 – *Bryum pseudotriquetrum*, *Brachythecium turgidum*; 6 – *Cerastium arcticum*; 7 – *Draba oxycarpa*, *Draba alpina*; 8 – *Salix polaris*; 9 – *Polyblastia cupularis*, *Protoblastenia rupestris*; 10 – *Puccinellia vahliana*; 11 – *Micranthes nivalis*; 12 – *Hypnum bambergeri*; 13 – *Silene acaulis*; 14 – *Distichum inclinatum*, *Pohlia cruda*, *Andreaea blyttii*, *Polyblastia hyperborea*, *Thelidium papulare*, *Verrucaria obsoleta*, *Carbonea vorticosa*, *Polyblastia theleodes*, *Aspicilia dissepens*, *Aspicilia aquatica*, *Physcia caesia*, *Eiglera flavida*, *Lecidea plana*, *Xanthoria elegans*, *Rhizocarpon geminatum*, *Verrucaria acrotella*; 15 – *Protothelenella sphinctrinoides*, *Stereocaulon depressum*.

Results

Within the Gåsbreen marginal zone, 15 species of vascular plants, 6 species of bryophytes and 17 species of lichens were recorded (Table 1). Vascular plants appeared first on the transect and were the predominant group of organisms (present in 48.1% of relevés), and also reached the highest (up to 20%) cover; the first recorded species were *Carex lachenalii* and *Cochlearia groenlandica*. In terms of frequency, the dominant species were *Saxifraga oppositifolia* (32.7% of relevés), *Cerastium arcticum* (12.9% of relevés), *Saxifraga cespitosa* (12.7% of relevés) and *Sagina nivalis* (10.8% of relevés). All these taxa covered up to 10%.

The second most frequent group were lichens, present in 10.3% of the relevés. The first observed species were *Polyblastia cupularis* and *Protoblastenia rupestris*. The least numerous group were bryophytes (6.95% of relevés), the first recorded being *Bryum pseudotriquetrum* and *Brachythecium turgidum*. The percentage cover of both bryophytes and lichens did not exceed 5%. Five succession stages and three types of colonisers were distinguished on the glacier marginal zone (Fig. 2; Table 2).

Distance from the front of the glacier proved to be the main factor influencing the distribution and frequency of particular species along the whole transect ($F = 46.11$; $p < 0.05$) (Fig. 3a). The fine-grained substrate also had a strong influence on the distribution and frequency of species ($F = 20.56$; $p < 0.05$) (Fig. 3a). Permutation test results showed that age category, exposure, and steepness were statistically insignificant when analysing the whole transect. When dividing the transect into two parts, in the younger part (Fig. 2; Fig. 3b), only the distance from the glacier front was statistically significant ($F = 15.92$; $p < 0.05$); in the older part (Fig. 3c), all factors except the exposure were statistically significant: distance from the glacier front ($F = 39.33$; $p < 0.05$), fine-grained material ($F = 5.49$; $p < 0.05$), and steepness ($F = 5.36$; $p < 0.05$).

Discussion

Primary succession is an extremely complex process which depends on numerous biotic and abiotic factors. While analysing the succession on the Gåsbreen foreland it can be concluded that the last observed stage of succession is not the final one. Only in the oldest part of the marginal zone lichens from the genus *Stereocaulon*, which are considered as an indicator of nearly mature plant communities, occurred (Moreau *et al.* 2009). The relevés located in the oldest part of the foreland were still different in terms of species composition and coverage in comparison to the surrounding tundra. The plant communities around the examined glacier foreland are primarily characterised by a higher degree of vegetation cover and a higher proportion of bryophytes and lichens (Ziaja *et al.* 2016b).

Table 2

Type of colonisers distinguished along the transect on the Gåsbreen foreland.

	Type of coloniser	Species
1. early colonisers – species appeared first on the exposed substrate in the first stage of primary succession (Fig. 2)	1.a. vascular plants appearing in the first succession stage and disappearing in the later stages	<i>Carex lachenalii</i> , <i>Cochlearia groenlandica</i>
	1.b. vascular plants appearing in the first stage of succession, which, although not disappeared in subsequent stages, reached the maximum occurrence early on the transect	<i>Saxifraga cespitosa</i> , <i>Saxifraga cernua</i> , <i>Sagina nivalis</i> , <i>Poa alpina</i> var. <i>vivipara</i> , <i>Cerastium regelli</i>
	1.c. bryophytes appearing in the first succession stage and decreasing their number in the later stages	<i>Bryum pseudotriquetrum</i> , <i>Brachythecium turgidum</i>
	1.d. species present in the most of the transect, appeared in the first stage of succession, but reached the maximum occurrence in the final stage of succession	<i>Saxifraga oppositifolia</i> , <i>Cerastium arcticum</i>
2. ‘intermediate’ group – plants that appeared for the first time in the second stage of primary succession (Fig. 2)		<i>Draba</i> sp., <i>Salix polaris</i>
3. late colonisers – species which appeared for the first time at a considerable distance from the beginning of the transect in the third or fourth stage of succession (Fig. 2)		<i>Puccinellia vahliana</i> , <i>Micranthes nivalis</i> , <i>Silene acaulis</i> , all lichens

In the 20th century, the theory of a linear character of primary succession begun to be questioned (Pickett and White 1985; Walker and Del Moral 2003). The results of our studies confirmed this viewpoint (3a–c). The distance from the front of the glacier (which is indirectly considered as the substrate age), was the main factor influencing the distribution and abundance of vegetation, and the fine-grained material and slope steepness was also important. The occurrence of vascular plants and terrestrial lichens was associated with a more stable and fine-grained substrates with slight inclines. The stability of the substrate increases with its age. In contrast, poorer vegetation, mainly composed of bryophytes and algae, occur in wet and unstable places, periodically eroded due to activity of glacial rivers (Węgrzyn and Wietrzyk 2015). Water from the glacial rivers that flow out mainly in the younger part of the Gåsbreen marginal zone affects the succession process, regularly destroying the first colonisers. Moraine erosion caused by glacial rivers activity has already been analysed in the context of primary succession (Moreau *et al.* 2008). Within strongly eroded regions, younger succession stages are observed in contrast to the same aged

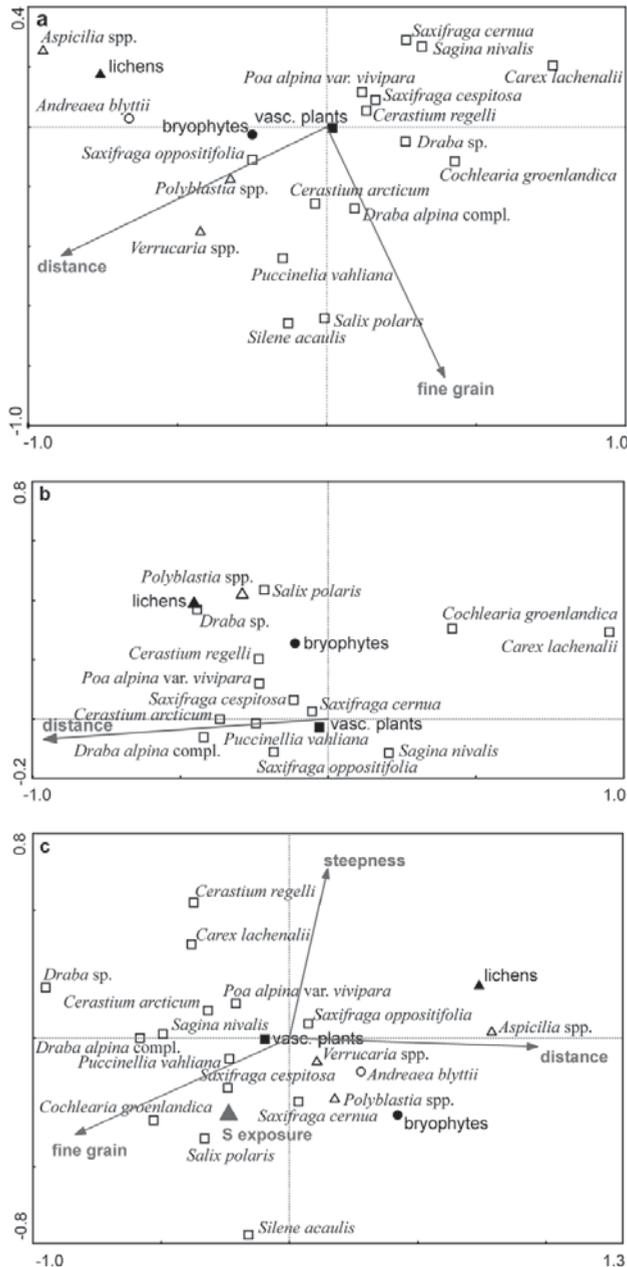


Fig. 3a–c. Ordinations of species and vegetation groups along the first and second canonical correspondence analysis (CCA) axes: a – whole transect; b – younger part of transect (25–72 years); c – older part of transect (> 72 years). Symbols used: squares = vascular plants, circles = bryophytes, triangles = lichens. Environmental variables were pre-selected using the Monte Carlo permutation test: *distance* – distance from the front of glacier; *fine grain* – percentage of particles < 2 cm diam. in soil; *S exposure* – southern exposure of moraine hills, and *steepness* – steepness of moraine hills.

but unflooded parts of the moraine (Moreau *et al.* 2008). Wojtuń *et al.* (2008) also observed the relationship between the substrate type and the occurrence of particular groups of plants, while Kuc (1996) emphasised the preference of lichens for stable substrates. Furthermore, Cannone *et al.* (2004) claimed that substrate stability arising from periglacial processes, especially frost creep (downslope soil movement caused by frost heaving and thawing), frost heave (upward soil movement caused by its swelling during freezing condition), gelifluction (flowing down-slope of material over a permafrost layer) and ice segregation (development of discrete ice structures in minerals or soil in periglacial conditions), are important factors. These processes are responsible for the development of microhabitats that are inhabited by different groups of organisms (Cannone *et al.* 2004).

Plant life forms and their mode of spreading also influence the colonisation potential of individual species (Cooper *et al.* 2004). Vascular plants recorded on the Gåsbreen foreland were mostly solitary growing species, forming rosettes or small tussocks, except mat-forming *Saxifraga oppositifolia* and *Salix polaris*. Individually growing and young individuals were most likely to be found in early succession stages (Table 1).

The majority of the plant species reproduces mainly sexually, producing large amounts of seeds with high germination capacity (Cooper *et al.* 2004; Alsos *et al.* 2013). Despite the fact that the germination level in the field is usually much lower than under experimental conditions (Müller *et al.* 2011; Alsos *et al.* 2013) seed production seems to play an important role in the succession process. Three main ways of pollination occur among the studied species: by insects (*Saxifraga* spp., *Draba* spp.), by wind (*Carex lachenalii*, *Puccinellia vahliana* and *Salix polaris*) and self-pollination (*Cochlearia groenlandica*, *Sagina nivalis*, *Micranthes nivalis*, also partially *Saxifraga cespitosa*). Seeds of some species (e.g. *Carex lachenalii*, *Cochlearia groenlandica*) are effectively dispersed by traveling downstream with water. This means that glacier rivers and meltdown streams are important paths of plant dispersal. Wind also plays an essential role in seed dispersal (e.g. *Salix polaris*). Seeds of several species (e.g. *Draba* spp.) have special adaptations to being dispersed by animals, mainly birds feeding on them (<http://svalbardflora.no/> and references therein). However, due to the lack of large bird colonies or feeding grounds in the vicinity of the studied moraine, this factor seems to be of a small importance.

Seed bank in the soil of glacier forelands is much smaller than in the mature tundra communities of Svalbard, however, an effective colonisation of glacier marginal zones by seedlings germinating from the seed bank is probable (Cooper *et al.* 2004). *Micranthes nivalis* seems to have an especially strong capacity of germinating from the seed bank (Cooper *et al.* 2004). A so-called cascade effect, as observed on glacier forelands in the central Alps (Erschbamer *et al.* 2008), is also possible when germination takes place faster in places already overgrown

by vegetation in contrast to areas lacking plant cover. Further research is needed to gain deeper insight into this subject.

The dominant species on the entire length of the Gåsbreen transect, *Saxifraga oppositifolia* and *Cerastium arcticum*, can effectively reproduce vegetatively, by fragmentation of mats and producing runners, respectively. For *Saxifraga oppositifolia*, vegetative reproduction seems to be much more effective than producing seeds which germinate only in about 2% under natural outdoor conditions on a moraine (Müller *et al.* 2011; Alsos *et al.* 2013). The group of species reproducing mostly vegetatively includes also *Cerastium regelli* and *Saxifraga cernua*. Pseudoviviparous reproduction also facilitates succession as exemplified by *Poa alpina* var. *vivipara* which is present along the entire transect on Gåsbreen, confirming its effective adaptation to polar climatic conditions. The significant participation of species spreading vegetatively was also observed in the Alps (Stöcklin and Bäumler 1996).

The order of entry of particular groups of organisms (Fig. 2) and composition of early and late coloniser groups (Table 2) on the Gåsbreen foreland are similar to other glacier moraines of Spitsbergen. Vascular plants and bryophytes appear first, while lichens enter later, when the substrate is more stable (Moreau *et al.* 2005, 2008). Similarly, differentiation of succession stages (Fig. 2) is an effect not only of the substrate age but also of its morphology and microhabitat conditions (Cannone *et al.* 2004; Moreau *et al.* 2005, 2009). *Saxifraga oppositifolia* is the dominant species in deglaciated areas, both in the north (Hodkinson *et al.* 2003; Moreau *et al.* 2005) and in the south of Spitsbergen (Pirożnikow and Górniak 1992; Wojtuń *et al.* 2008). *Cerastium arcticum*, *Cochlearia groenlandica*, *Sagina nivalis* and *Saxifraga cespitosa* occur in the younger part (*c.* 30 years old) of the Midtre Lovénbreen marginal zone (Moreau *et al.* 2008), and also in the younger fragment of the Werenskiöldbreen marginal zone (Wojtuń *et al.* 2008). Although *Salix polaris* and *Silene acaulis* are already present in the youngest part of moraines, they reach a high frequency only at the *c.* 100 years old fragment of the Midtre Lovénbreen (Moreau *et al.* 2008). *Puccinellia vahliana* appears as a late coloniser on the Werenskiöldbreen foreland (Wojtuń *et al.* 2008). Just as in Gåsbreen, terrestrial lichens appear on the Midtre Lovénbreen moraine only in the oldest parts of the moraine hills (Moreau *et al.* 2009). Species of *Stereocaulon* are among the first terrestrial lichens colonising the Gåsbreen, Midtre Lovénbreen (Moreau *et al.* 2009) and Werenskiöldbreen (Wojtuń *et al.* 2008) forelands. Thalli of these species (except those with a *Chlorophyta* photobiont) also contain cyanobacterial symbionts with an ability to bind atmospheric nitrogen, on the one hand influencing the colonisation potential of these lichens (Sancho *et al.* 2011), and on the other probably playing an important role in soil-forming processes.

Some aspects of succession are different on the Gåsbreen foreland than on moraines of other Svalbard glaciers. *Cerastium regelii* and *Sagina nivalis*, which are present from the beginning of the succession process on the Gåsbreen

moraine, are included by Wojtuń *et al.* (2008) in the late coloniser group on the Werenskiöldbreen foreland, and Moreau *et al.* (2008) observed the withdrawal of *Saxifraga cespitosa* from the oldest parts of the Midtre Lovénbreen marginal zone, which is not recorded on Gåsbreen. These differences may be caused by different habitat conditions, including the stability of the moraines or water availability. The species composition of the first coloniser group of the Gåsbreen moraine and the five glacier moraines of Petuniabukta is similar, but in the Petuniabukta area there is no species exchange but only the arrival of additional species (Prach and Rachlewicz 2012). A different sequence of colonisation in this region can be due to the influence of the microclimate; Petuniabukta being located in the warmest and driest part of Spitsbergen.

The succession rate and the time of the first plant appearance vary for the glacier forelands in different regions of Spitsbergen. On the Midtre Lovénbreen foreland (Hodkinson *et al.* 2003) and glaciers around Petuniabukta (Prach and Rachlewicz 2012), the first plants appear much earlier (two years after deglaciation) than on the Gåsbreen marginal zone. The most probable factors determining this difference are the less stable substrate and harsher climate of the Gåsbreen foreland. The substrate stability in combination with higher participation of fine grain material on the Midtre Lovénbreen moraine may also explain the occurrence of areas with almost complete vegetation cover, as well as the presence of species whose coverage exceeds 10%, such as *Salix polaris*, *Racomitrium lanuginosum*, *Cladonia* spp. and *Cetraria* spp.

The primary succession research in Gåsbreen provides important additional data on the dynamics of vegetation development on glacier forelands in southern Spitsbergen. Except for the research on Werenskiöldbreen, primary succession has only been studied in central and northern Spitsbergen. The current results provide an opportunity to compare data with past and future research in terms of the observed rapid climate change.

Currently, Arctic warming is contributing to glacier recession, but it does not always influence directly the improvement of thermal conditions of plant growth on glacier forelands (Wojtuń *et al.* 2008). However, if the scenarios predicting the acceleration of the climate change in the coming years become a reality, the dynamics of succession processes taking place on the glacier moraines, such as their speed, intensity and type of interaction between species, will continue to increase. This opens up new research possibilities, including long-term monitoring programmes.

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