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Relationships between vegetation patterns and periglacial landforms in northwestern Svalbard

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Abstract We studied the small-scale vegetation pattern in the high Arctic at Ny Ålesund to assess if the plant distribution was related to periglacial landforms. The whole area has been deglaciated for millennia but only a modest part of the area was covered by mature vegetation. The plant cover varied considerably in relation to ground patterning originated by periglacial processes, especially frost heave, frost creep, gelifluction and ice segregation, giving rise to a mosaic of microhabitats sharply differing from each other as regards physical properties and microclimate. The distributional patterns of vascular plants, lichens and bryophytes were primarily affected by complex responses to substrate texture, soil moisture content and substrate disturbance. Since global warming will probably affect both periglacial processes and plant responses to altered habitat conditions, we concluded that long-term monitoring of relationships between landforms and vegetation represents a suitable tool for assessing the impact of global change on arctic regions.

Introduction

The plant distributional pattern in arctic regions is affected by environmental factors such as air and soil

temperature, nutrient availability, soil moisture and snow depth (Wielgolaski 1997). The harsh environment, along with the short duration of the growing season, are the main causes of the low species diversity in high-arctic vegetation (Bliss and Matveyeva 1998). Substrate disturbance, due to the cryoturbation of the soil and the action of the underlying permafrost (French 1996), also represents a major environmental factor limiting plant growth in arctic regions (Jonasson and Sköld 1983). Substrate disturbance in these habitats is eventually responsible for modelling the land surface, which results in the formation of the so-called periglacial landforms (Washburn 1979; Williams and Smith 1989). Because of the complex mutual relationships among surface morphology, microclimate, substrate disturbance and plant cover, it is of great importance to understand how arctic vegetation varies in relation to periglacial landforms, and also for predicting how and to what extent the plant cover can change in response to climate warming in arctic regions.

Previous research has stressed the importance of surface micromorphology in accounting for the distributional pattern of arctic plant species (Porsild 1955; Brossard and Nimis 1984; Sohlberg and Bliss 1984; Virtanen et al. 1997). Most studies analysing relationships between vegetation and periglacial features focus on patterned ground (e.g. Raup 1971; Anderson and Bliss 1998). In particular, Jonasson (1982) demonstrated that the flora on polygon-patterned ground in northern Scandinavia differs abruptly from that on adjacent stable areas. By contrast, only occasional studies have addressed the plant cover of earth hummocks and frost boils (Britton 1957; Muc and Bliss 1977). In this paper, we aimed to assess the extent to which the small-scale plant distributional pattern in the high Arctic is affected by surface morphology. We chose a site in northwestern Svalbard for our study because, in this area, almost all typical periglacial landforms can be found within short distances of each other, with no appreciable differences in either bedrock or regional climate.

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Materials and methods

Research site

The study was carried out in Brøgger Peninsula, 78°57'N 11°34'E, close to Ny Ålesund, West Spitsbergen, Svalbard Archipelago (Fig. 1). According to climatic data from the Ny Ålesund meteorological station, the annual mean temperature in this region is -5.8°C , the mean temperature of the warmest month (July) $+5.2^{\circ}\text{C}$ and the mean annual precipitation ca. 400 mm, mainly falling as snow, which covers the ground for at least 230 days per year. The geological substrate is formed of quaternary carbonate deposits, mainly comprising marine beach deposits and weathering material or colluvium and, to a lesser extent, alluvial debris and peat. Permafrost is continuous, with a thickness of 75–450 m and an active layer 0.3–1.8 m thick (Andrè 1993).

The research site was located in the northern coastal part of Brøgger Peninsula. The site (ca. 27 km²) extends in a transect from the present coastline to the foot of the steep slope that limits the coastal deglaciated lowland from the upland glacial area (Fig. 1). Five main landscape units (Schreiber 1990; Matthews et al. 1998) were distinguished: outer raised beach, outer depression, inner raised beach, inner depression and lower slope. The whole area lies within the *Dryas octopetala* zone of the high-arctic fellfield vegetation (Brattbakk 1986). Occasionally, we observed some individuals of reindeer

in the study site but there was no apparent sign of reindeer grazing on vegetation. In areas where reindeer population density is higher, grazing by reindeer has been found to enhance grazing-tolerant species (Staa-land et al. 1993). However, the coasts of Brøgger Peninsula shelter rich colonies of barnacle goose (Tombre et al. 1998). Grazing by barnacle goose may affect to some extent all types of vegetation. However, we observed most birds commonly foraging in the lush vegetation close to the breeding cliffs, and more rarely in the sparse vegetation of fellfields.

Geomorphology

Using 1:20,000 infrared air photographs and subsequent field surveys, the periglacial landforms occurring were recorded and typified according to Tolgensbakk and Sollid (1987). Representative periglacial landforms were selected for morphometric measurements. The choice of the landforms was subjective, but the total number of the landforms selected for each periglacial feature was proportional to their frequency within the research site. Length, width, height of the centre, height of the edge and height of the border were measured, whenever appropriate, with respect to the surrounding terrain.

The thickness of the active layer was measured, at 1-m intervals, along transects set up across the main axes in each of the landscape units. Measurements were made using a frost probe, according to the protocol adopted

Fig. 1 Geographic location of the research site (dotted area in the larger map)

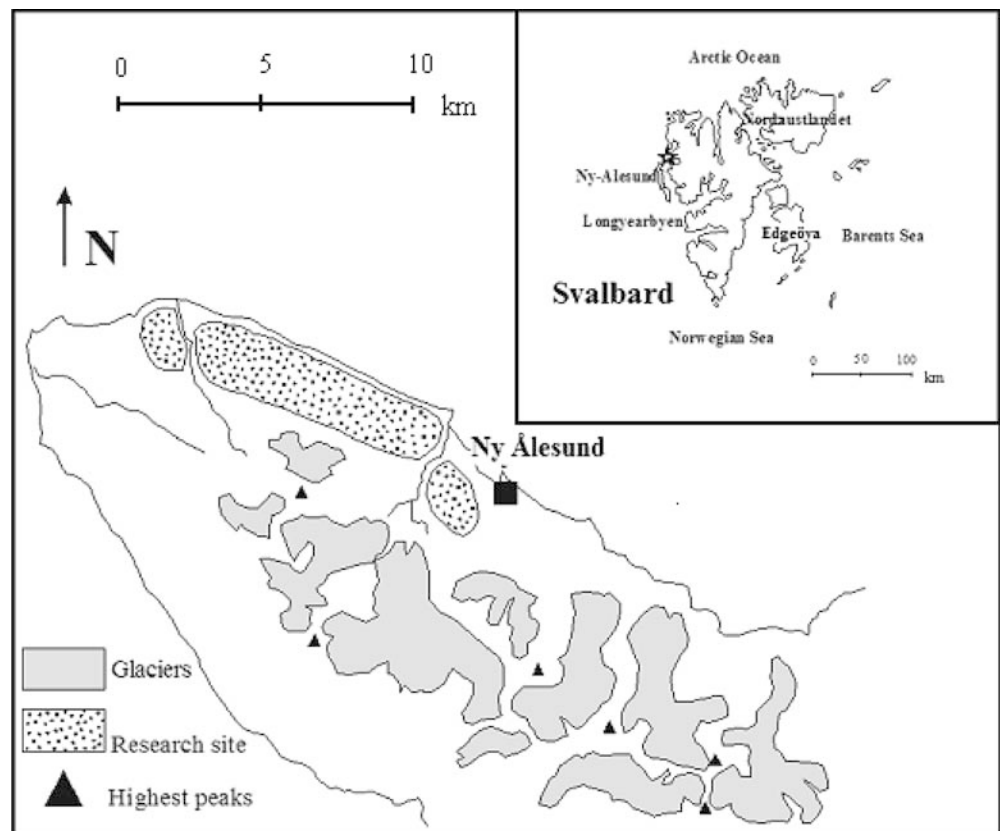


Table 1 Morphometry of the landforms. The values (as cm) are means and ranges (*ND* not determined, *HCSC* high-centred sorted circles, *LCSC* low-centred sorted circles, *SS* sorted stripes, *EH* earth hummocks, *FB* frost boils, *PHS* peat-hummock scars, *PH* peat hummocks, *GL* gelifluction lobes, *TE* terracettes)

	HCSC	LCSC	SS	EH	FB	PHS	PH	GL	TE
Length	352 (220–400)	304 (160–475)	400 (300–700)	ND	173 (85–260)	703 (101–870)	395 (340–450)	80	379 (148–610)
Width	253 (220–370)	218 (144–290)	40 (15–80)	ND	70 (63–78)	372 (170–520)	280 (200–360)	45	209 (158–260)
Edge height	10 (7–13)	12 (2.5–20)		ND	0	16 (11–21)	0		
Centre height	9 (0–11)	2 (0–4)	10 (5–14)	ND	7 (6–8)	8 (0–18)	45 (43–47)		
Scarp height								12	23 (19–27)
Active layer thickness	Centre 82 (44–125) Border 84 (48–114)	Centre 49 (27–89) Border 47 (22–89)	88 (85–93)	Centre 64 Edge 62	Centre 85 (80–91) Edge 73 (63–83)	Centre 70 (40–77) Border 54 (44–71)	Centre 30 (24–36) Border 38 (33–44)	34	96 (93–100)

by the International Active Layer Monitoring Programme (CALM; Burgess et al. 2000). In a few cases, when the frost probe could not be used owing to the presence of large boulders in the soil, the thickness of the active layer was extrapolated by means of ground temperature values measured at different depths (2, 10, 20 cm). The extrapolation was obtained by estimating the location of the 0°C isotherm based on the thermal gradient. The accuracy of the method was ± 2 cm.

A deep trench was dug into the substrate at 20 selected sites. When possible, samples of organic matter were collected for ^{14}C radiometric dating.

Vegetation survey

The vegetation was sampled in 50×50 cm plots. Two (occasionally three) plots were set up at each of the landforms selected. All of the plots were located in morphologically homogeneous microhabitats. All species occurring in the plot were recorded, including vascular plants, bryophytes and lichens, and their percentage cover estimated visually.

Microtopography and surface-soil texture were assessed visually. Species nomenclature follows Rönning (1996) for vascular plants, Elvebakk and Prestrud (1996) for lichens, and Söderström and Hedenäs (1998) for bryophytes.

Data treatment

Two matrices were built up, including environmental data and vegetational data, respectively, in all sampling plots. The environmental data were: landform type and microhabitat (for example: edge or centre); microtopography (raised/depressed); texture (coarse/fine); active layer thickness. The vegetational data consisted of visual estimates of percentage cover for each species using a 10%-interval scale (Heilbron and Walton 1984a, b).

The two matrices were subjected to a multivariate statistical treatment by redundancy analysis (RDA). Only the species occurring in at least 20% of the sampling plots were considered in the elaboration. A Monte Carlo permutation test was performed in order to assess

significance of differences between the patterns obtained from the ordination and random ones. All computations were performed using the CANOCO Software, version 4 (ter Braak and Šmilauer 1998).

Results

Geomorphology

Sorted circles were by far the commonest patterned-ground type. They were found on flat or very gently sloping terrain (always $< 5^\circ$). Their shape was slightly elongated along the slope or almost circular (Table 1). Two different types of sorted circles could be recognised. First, circles with a raised centre separated from the outer stone border by a low rim forming a trough (i.e. high-centred sorted circles). Second, sorted circles with a flat low centre and a raised outer stone border (i.e. low-centred sorted circles; Fig. 2). In all of the low-centred sorted circles, the base of the active layer showed a concave profile with a maximum thickness in the centre. In the high-centred sorted circles, the active layer was most often almost parallel to the ground surface. Sorted stripes (Fig. 3) were relatively rare and consisted of elongate stony stripes slightly raised above the adjacent fine-grained stripes (Table 1).



Fig. 2 Low-centred sorted circles with the stony, coarse border and the fine, depressed centre with denser plant cover



Fig. 3 Sorted stripes on the lower slope. Details of surface characteristics with alternating patterns of stony, coarse stripes and finer stripes

Among unsorted patterns, earth hummocks were confined to the inner depression, whereas frost boils (Fig. 4) were found on the outer raised beach. Both had a thicker active layer in the centre (Table 1). A peculiar type of large unsorted circle was the peat-hummock scar (see Billings and Mooney 1959), typical of depressions with peaty substrate. This type was characterised by an elliptical border of varying height, surrounding a flat or slightly domed central peaty area (Table 1). The active layer was usually thicker in the centre, as in the sorted circles. Similar to peat-hummock scars were some smaller, roughly circular, high peaty hummocks, confined to the inner depression. They were called peat hummocks, according to Billings and Mooney (1959). The inner structure of peat hummocks was similar to that described for peat mounds at Hermansenöya (Niewiarowski and Sinkiewicz 1988), where a surficial peat layer (ca. 30 cm thick) overlies a thin mineral layer and a core of probably injection ice. The active layer in the centre of peat hummocks was shallow and ran almost parallel to the surface (Table 1). Gelifluction features were frequent only on the older portion of the inner raised beach and the lower slope. Gelifluction lobes had a smaller size and a shallower active layer when compared to terracettes (Table 1).

The multivariate treatment of sampling plots and environmental data partitioned the different types of periglacial features into six main groups (Fig. 5):

- R1. Terracettes, gelifluction lobes, frost boils, earth hummocks, associated with a thick active layer (see the vector of active layer thickness in Fig. 5, insert) with two subgroups corresponding to edge (R1a) or centre (R1b) of those landforms, respectively.
- R2. Border of high-centred sorted circles and low-centred sorted circles, associated with coarse texture and raised microtopography.
- R3. Trough of high-centred sorted circles, as well as sorted stripes, located close to the origin, which indicated poor discrimination by RDA.



Fig. 4 Frost boil on the outer raised beach with the characteristic hard carapax in the centre, almost free from plant cover

- R4. Centre of high-centred sorted circles, centre of low-centred sorted circles and border of low-centred sorted circles, associated with fine texture, shallow active layer and depressed microtopography.
- R5. Peat-hummock scars, in which two subgroups could be distinguished, corresponding to border (R5a) and centre (R5b).
- R6. Peat hummocks.

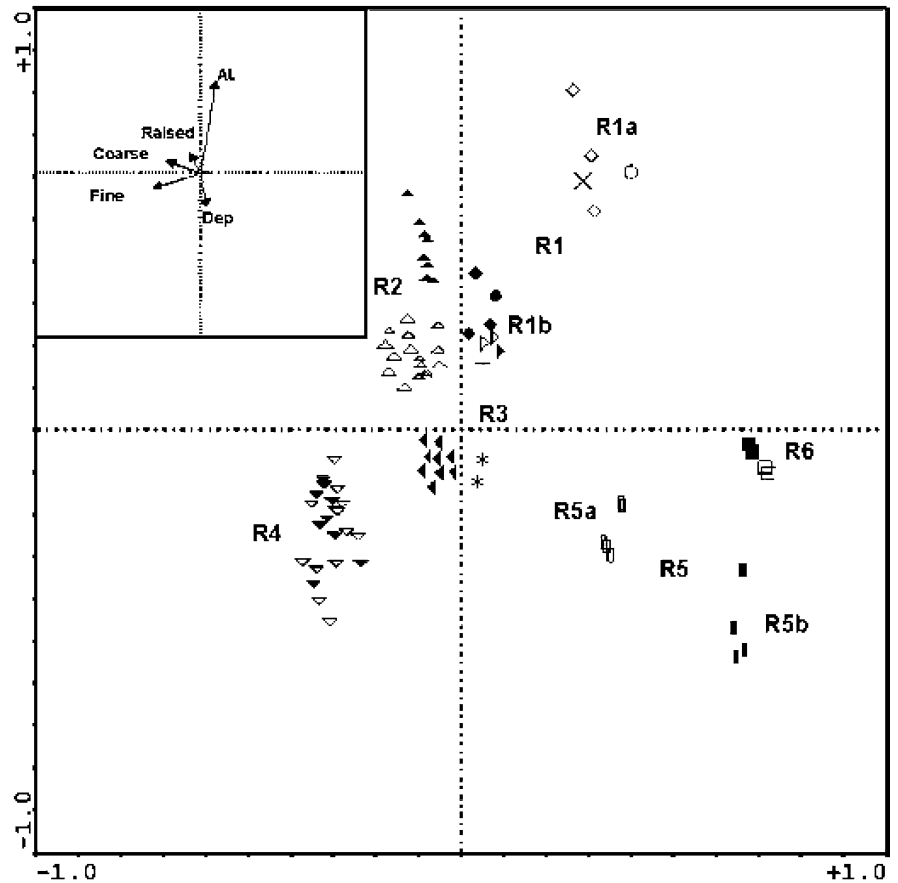
The basal 2-cm peat layer in the mire dammed by the inner raised beach had a minimum ^{14}C age of $5,180 \pm 130$ years BP (not calibrated). An organic cryoturbated layer found at a depth of ca. 30 cm under a low-centred sorted circle had a (not calibrated) ^{14}C age of 950 ± 80 years BP.

Vegetation and ecological gradients

A total of 104 species were recorded in the plots, of which 37 were vascular plants, 47 were bryophytes and 20 were lichens. In addition, two broad groups of Cyanobacteria were recognised, i.e. cyanobacterial crust and cyanobacterial jelly, the latter probably mostly formed of *Nostoc* species. The rare species, not included in the multivariate analysis (see Materials and methods), are listed in the Appendix. The species included in the multivariate analysis, along with the two Cyanobacteria groups, were clustered as follows in the RDA diagram (Fig. 6):

- S1. *Polygonum viviparum*, *Silene acaulis*, *Ditrichum flexicaule*, *Cerastium arcticum*, *Dryas octopetala*, *Oncophorus wahlenbergii*, *Minuartia rubella*, *Peltigera rufescens*.
- S2. *Ochrolechia frigida*, *Cetrariella delisei*, *Saxifraga oppositifolia*, *Lecanora epibryon*, *Bryum* sp., *Pseudocalliergon turgescens*.
- S3. Cyanobacterial crust, *Luzula confusa*, *Poa arctica*, *Blepharostoma trichophyllum*, *Mycobilimbia lobulata*,

Fig. 5 Ordination of the sampling plots on the first two RDA axes. R1–R6 plot groupings (details in the text). Symbols of landform types: ▲ HCSC border, ◄ HCSC trough, ▼ HCSC centre, △ LCSC border, ▽ LCSC centre, ★ SS, × EH edge, + EH centre, ▷ FB edge, ► FB centre, □ PHS border, ■ PHS centre, ◻ PH border, ◼ PH centre, ○ GL edge, ● GL centre, ◇ TE edge, ◆ TE centre. The weights of the environmental variables are displayed as vectors in the insert (*AL* active layer thickness, *raised* raised morphology, *dep* depressed morphology, *coarse* coarse texture, *fine* fine texture)



C. regelii, *S. cespitosa*, *Cardamine bellidifolia*, *Oxyria digyna*, *Sauteria alpina*, *Encalypta* sp., *Pohlia cruda*, *Anthelia juratzkana*.

- S4. *Dupontia pelligera*, *Scorpidium revolvens*, *Campylium stellatum*, *Orthothecium chryseon*, *Eriophorum scheuchzeri*, *Juncus biglumis*, *Tomentypnum nitens*, *Nostoc* sp., *Bryum pseudotriquetrum*, *C. nigratum*, *Calliergon giganteum*, *C. nymannii*, *Alopecurus borealis*, *S. scorpioides*, *Cladonia* sp., *Draba lactea*.
- S5. *Polytrichastrum alpinum*, *Dicranum elongatum*, *Peritularia geminipara*, *P. nutans*, *D. fuscescens*, *Equisetum arvense*, *Anastrophyllum minutum*.

By comparing the RDA ordination of species and plots in the RDA biplots (Figs. 5, 6), in relation to landform type, we found a consistent correspondence among these groupings (Fig. 7). Terracettes, gelifluction lobes, earth hummocks and frost boils (R1a, R1b) were characterised by species belonging to group S1, of which three (*Cerastium arcticum*, *Dryas octopetala* and *Peltigera rufescens*) were almost exclusive to these habitats, along with several species belonging to group S2 (Table 2). The centre of these features (subgroup R1b) was differentiated from the edge (subgroup R1a) by some species belonging to group S3, especially cyanobacterial crust (Table 2).

The plant cover on sorted circles and sorted stripes (R2–R4) was characterised by differing combinations of species belonging to groups S2 and S3. Cyanobacterial

crust, *Blepharostoma trichophyllum* and *Poa arctica* were more abundant in the trough (R3) and the centre (R4) compared to the stony border (R2) of sorted circles. Other species differentiating the centre of sorted circles with respect to the trough and the stony border were *Cerastium regelii*, *Sauteria alpina* and *Oxyria digyna*, all belonging to group S3. In addition, some moss species typical of wet soils (group S4), such as *Scorpidium revolvens*, *Campylium stellatum* and *Bryum pseudotriquetrum*, were also found in the centre but not in the drier trough and the border (Table 2).

Peat-hummock scars (R5) were characterised by a high frequency of species belonging to group S4 (Table 2), all typical of waterlogged mineral soils and fens. The border of peat-hummock scars (R5a) was differentiated by the rather frequent occurrence of species indicating somewhat drier soil conditions, especially *Cetrariella delisei*, *Ochrolechia frigida*, and *Distichium capillaceum*, which were not found in the moister central part (R5b) of this feature. Peat hummocks (R6) were characterised by species belonging to group S5, especially *Pohlia nutans*, *Dicranum fuscescens* and *Polytrichastrum alpinum* (Table 2).

All other species had a centroid located close to the origin, indicating poor discriminating power, and were thus not indicated in the biplot diagram for clarity of presentation.

Fig. 6 Ordination of species (abbreviations as in Table 2) on the first two RDA axes. *S1–S5* species groupings (details in the text)

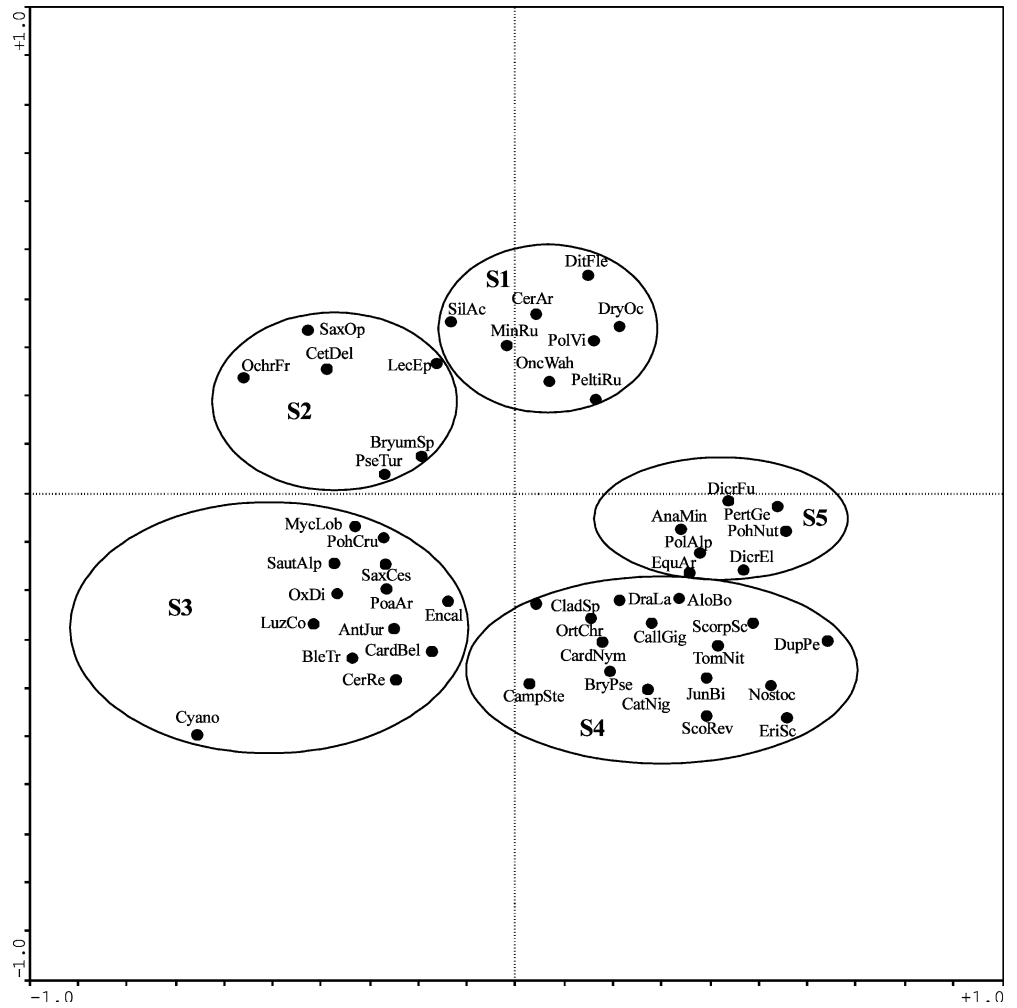


Fig. 7 Joint ordination of species groupings (*S1–S5*), plot groupings (*R1–R6*) and landform types (abbreviations as in Table 1) along environmental gradients. The height of the *light-grey bars* indicates frost-heave intensity

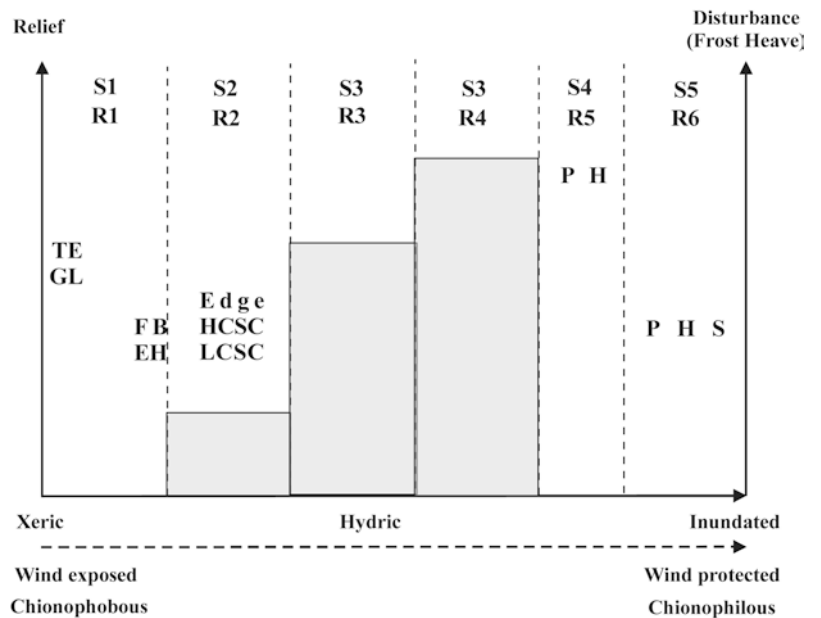


Table 2 Percentage frequencies of the species within the plot groupings. *In parentheses* are the abbreviations used for the species displayed in Fig. 6

Species groupings	Plot groupings							
	R1a	R1b	R2	R3	R4	R5a	R5b	R6
Group S1								
<i>Polygonum viviparum</i> (PolVi)	80	88	15	40	33	67	50	25
<i>Silene acaulis</i> (SilAc)	60	33	11	30	18	–	–	–
<i>Ditrichum flexicaule</i> (DitFle)	80	33	18	10	3	–	–	–
<i>Cerastium arcticum</i> (CerAr)	40	44	4	10	7	–	–	–
<i>Dryas octopetala</i> (DryOc)	60	33	–	–	–	–	–	–
<i>Oncophorus wahlenbergii</i> (OncWah)	20	11	15	–	–	17	–	–
<i>Minuartia rubella</i> (MinRu)	20	22	11	–	–	–	–	–
<i>Peltigera rufescens</i> (PeltiRu)	20	22	–	–	–	–	–	–
Group S2								
<i>Ochrolechia frigida</i> (OchrFr)	80	89	89	80	96	83	17	–
<i>Cetrariella delisei</i> (CetDel)	80	67	85	70	67	50	–	–
<i>Saxifraga oppositifolia</i> (SaxOp)	80	89	59	80	85	–	–	–
<i>Lecanora epibryon</i> (LecEp)	40	44	18	40	15	–	–	–
<i>Bryum</i> sp. (BryumSp)	20	–	11	30	22	–	–	–
<i>Pseudo-calliergon turgescens</i> (PseTur)	–	–	22	–	26	–	–	–
Group S3								
Cyanobacterial crust (Cyano)	–	89	59	80	100	67	33	–
<i>Luzula confusa</i> (LuzCo)	20	11	26	30	74	50	–	–
<i>Poa arctica</i> (PoaAr)	–	44	11	60	41	17	17	–
<i>Blepharostoma trichophyllum</i> (BleTr)	–	11	11	60	55	–	17	–
<i>Mycobilimbia lobulata</i> (MycLob)	–	11	22	30	30	17	17	–
<i>Cerastium regelii</i> (CerRe)	–	–	4	10	48	17	17	25
<i>Saxifraga cespitosa</i> (SaxCes)	–	11	26	–	55	17	–	–
<i>Cardamine bellidifolia</i> (CardBel)	–	11	15	30	18	–	17	–
<i>Oxyria digyna</i> (OxDi)	–	–	7	10	30	–	–	–
<i>Sauteria alpina</i> (SautAlp)	–	–	4	10	26	–	–	–
<i>Encalypta</i> sp. (Encal)	–	22	–	–	15	–	–	–
<i>Pohlia cruda</i> (PohCru)	–	–	4	10	15	–	–	–
<i>Anthelia juratzkana</i> (AntJur)	–	–	–	10	15	–	–	–
Group S4								
<i>Dupontia pelligera</i> (DupPe)	–	–	–	–	–	67	67	75
<i>Scorpidium revolvens</i> (ScoRev)	–	11	–	20	15	17	83	–
<i>Campyllum stellatum</i> (CampSte)	–	–	11	20	22	33	50	–
<i>Orthothecium chryseon</i> (OrtChr)	20	22	–	10	18	33	33	–
<i>Eriophorum scheuchzeri</i> (EriSc)	–	–	–	–	–	33	83	–
<i>Juncus biglumis</i> (JunBi)	–	11	–	10	4	–	83	–
<i>Tomentypnum nitens</i> (TomNit)	–	–	–	–	–	50	50	–
<i>Nostoc</i> (Nostoc)	–	–	–	–	–	–	100	–
<i>Bryum pseudotriquetrum</i> (BryPs)	–	–	4	–	11	50	33	–
<i>Catocopium nigrum</i> (CatNig)	–	–	–	10	4	–	67	–
<i>Calliergon giganteum</i> (CallGig)	–	–	–	–	4	50	17	–
<i>Cardamine nymannii</i> (CardNym)	–	–	–	10	4	33	17	–
<i>Alopecurus borealis</i> (AloBo)	–	–	–	–	–	33	17	–
<i>Scorpidium scorpioides</i> (ScorpSc)	–	–	–	–	–	17	33	–
<i>Cladonia</i> sp. (CladSp)	–	–	–	–	7	33	–	–
<i>Draba lactea</i> (DraLa)	–	–	–	–	–	33	–	–
Group S5								
<i>Polytrichastrum alpinum</i> (PolAlp)	20	11	–	10	11	33	–	75
<i>Dicranum elongatum</i> (DicrEl)	–	–	–	–	–	17	–	100
<i>Pertusaria geminipara</i> (PertGe)	–	–	–	10	–	–	–	100
<i>Pohlia nutans</i> (PohNut)	–	–	–	–	–	17	17	75
<i>Dicranum fuscescens</i> (DicrFu)	–	–	–	–	–	–	–	75
<i>Equisetum arvense</i> (EquAr)	–	–	–	–	–	33	–	25
<i>Anastrophyllum minutum</i> (AnaMin)	–	–	–	–	–	–	–	50
Other species								
<i>D. corymbosa</i>	20	11	7	10	22	17	17	–
<i>S. cernua</i>	–	11	30	20	41	33	–	25
<i>S. hieracifolia</i>	–	–	7	–	7	17	–	–
<i>S. nivalis</i>	–	–	4	–	11	17	–	–
<i>Salix polaris</i>	80	78	30	90	37	100	67	–
<i>Cyrtomnium</i> sp.	–	11	4	–	37	17	–	–
<i>D. capillaceum</i>	20	33	15	20	30	50	–	–
<i>D. inclinatum</i>	–	–	4	10	4	17	–	–
<i>Sanionia uncinata</i>	20	44	52	70	70	83	–	–

Table 2 (Contd.)

Species groupings	Plot groupings							
	R1a	R1b	R2	R3	R4	R5a	R5b	R6
<i>Encalypta alpina</i>	–	11	11	10	7	17	–	–
<i>Cladonia pocillum</i>	–	22	–	–	7	17	–	–
<i>P. oculata</i>	–	–	4	20	4	–	–	–
<i>Solorina bispora</i>	–	11	4	–	4	–	–	–

Discussion

The northern coast of Brøgger Peninsula was deglaciated ca. 11–13,000 years ago. Since then, sea level has changed several times as an effect of glacio-isostatic rebound, with a major marine transgression in mid-Holocene (Forman et al. 1987). Our radiocarbon dating of the basal peat in the mire dammed by the highest raised beach confirms that the whole area above this level has been free from ice, and not submerged by the sea, for at least 5,000 years. Soil development and plant colonisation on deglaciated ground in high-arctic regions proceed at considerably slower rates compared to climatically more favourable regions (Forbes 1996). However, a recent study in an arctic area close to Brøgger Peninsula has shown that ca. 100 years were required for plants to cover almost totally the ground on stable areas (Hodkinson et al. 2003). Since only a very limited portion of our research site showed a 100% plant cover, this means that substrate instability or some other limiting factor must have hindered the establishment of mature vegetation on most of the area. The only radiocarbon dating available for cryoturbated organic material underneath sorted circles suggested that substrate disturbance giving rise to patterned ground has been active for several centuries.

Substrate disturbance in periglacial regions is determined by four main processes: frost heave, frost creep, gelifluction and ice segregation. These are responsible for the microhabitat differentiation within and among landform types. Gelifluction lobes and terracettes are mostly developed on moderately sloping terrain. This accounts for the coarser substrate texture and the thicker active layer, both of which enhance water drainage (Fig. 7). As a consequence, the plant cover in these habitats consisted of xerophytic vascular (*Dryas octopetala*, *Minuartia rubella*, *Silene acaulis* and *Cerastium arcticum*), lichen (*Peltigera rufescens*) and bryophyte (*Ditrichum flexicaule*) species. On gelifluction landforms, substrate disturbance is brought about by en masse sliding along the top of the permafrost table, related to two-sided freezing (Mackay 1981) or plug-flow (Washburn 1997). Those processes do not affect the integrity of the upper soil layer, as demonstrated by the abundance of species typical of mature vegetation, such as *Dryas octopetala* and *Silene acaulis*, in these habitats (Table 2). In particular, *Dryas octopetala* is a mat-forming dwarf shrub typical of exposed ridges

with a modest snow cover. Individual clones of *Dryas* can live >100 years, usually spreading by vegetative lateral growth on relatively stable ground (McGraw 1985).

By contrast, frost heave exerts disturbance on flat ground where sorted circles are by far the commonest feature. This accounts for the presence of stress-tolerant species that do not occur, or are very rare, on gelifluction landforms: *Oxyria digyna*, *Saxifraga cespitosa*, *Cardamine bellidifolia* and *Cerastium regelii* (Edlund and Alt 1989). Strong substrate disturbance by frost heave results in sharp habitat differentiation within sorted circles. Indeed, microtopography and substrate texture differed greatly between centre, trough and stony borders of sorted circles, with further differences between high-centred and low-centred stone circles. Frost-heave measurements have shown that surface heave is >80 mm per year in the centre against ca. 20 mm per year in the stony border and 60 mm in the trough (Hallet 1998). As a consequence, all of the stress-tolerant species cited above were much more abundant in the centre compared to the border and the trough (Table 2). *Oxyria digyna* has also been found to indicate intense substrate movement in a periglacial area in the Italian Alps (Cannone and Gerdol 2003).

Seemingly paradoxical was our finding that species indicating longer snow cover and moister soil (such as *Anthelia juratzkana*, *Pohlia cruda* and *Luzula confusa*; see Table 2 and Fig. 7) were more frequent in the centre than in the depressed trough of high-centred stone circles. A possible reason is that the cyanobacterial crust covering most of the area in the circle centre reduces the albedo (Gold 1998), thus increasing surface temperature and spring thaw. The concave profile of the permafrost table determines subsurface water flow towards the central part of the stone circles where water availability thus increases. A further effect of the cyanobacterial crust consists of nitrogen fixation, which can improve the nutrient status in the upper soil horizon (Dickson 2000).

Ice segregation constitutes the main process inducing heave in peat hummocks. Peat-hummock scars represent relict landforms (Table 3). The uplift of the peat hummock progressively modifies the relief, in turn affecting microhabitat (Seppälä 1990). Therefore, soil moisture rather than substrate disturbance per se is the main factor affecting floristic composition on this landform type.

The plant cover on peat-hummock scars closely resembles that of arctic fens. Svalbard fens are mostly

Table 3 Synthesis of the periglacial processes acting in the different landform types

Landform type	Processes			
	Frost heave	Frost creep	Gelifluction	Ice segregation
Patterned ground	<i>Sorted polygons</i> High-centred sorted circles (HCSC) Low-centred sorted circles (LCSC) Sorted stripes (SS) <i>Unsorted polygons</i> Frost boils (FB)			Frost boils (FB)
Slope features	Earth hummocks (EH) Gelifluction lobes (GL)	Gelifluction lobes (GL)	Gelifluction Lobes (GL)	
Permafrost features	Terracettes (TE) Peat hummocks (PH) Peat-hummock scars (PHS)	Terracettes (TE)	Terracettes (TE)	Peat hummocks (PH) Peat-hummock scars (PHS)

characterised by *Dupontia pelligera* and *Eriophorum scheuchzeri* (Elvebakk 1994), both occurring with high frequency and cover in the centre of peat-hummock scars (Table 2). The ground is covered by brown mosses typical of alkaline and subneutral fens, such as *Scorpidium revolvens*, *Calliergon giganteum*, *Campylium stellatum* and *S. scorpioides*, along with a cyanobacterial jelly indicating almost permanently waterlogged soil. In contrast, the substrate in the border of peat-hummock scars is somewhat drier due to the slightly raised micromorphology (Table 1) and the coarser substrate texture.

Peat hummocks are palsa-like features (Salvigsen 1977), raised above the surrounding terrain due to the presence of a thick ice core. Contrary to peat-hummock scars, the surface peat layer on peat hummocks is only occasionally, if ever, waterlogged, which results in drier well-oxygenated conditions. This promotes the establishment of moss species intolerant of soil anoxia, especially *Dicranum elongatum*, *D. fuscescens* and *Polytrichum alpinum*, whose undecomposed tissues create an acidic peat layer. *Anastrophyllum minutum*, a small liverwort, usually has a patchy distribution indicating some degree of surface erosion (Philippi 1973).

Conclusion

Small-scale patterned ground in Svalbard plays a major role in determining plant distributional patterns. Periglacial processes affect vegetation, either through a direct effect on substrate stability, or through an indirect effect on microhabitat conditions. Therefore, periglacial landforms and vegetation are both components of a complex system. The balance between substrate disturbance and microhabitat conditions probably represents the mechanism regulating the dynamical equilibrium between the two components of the system. Since environmental changes associated with global warming are likely to affect not only the type and the magnitude of periglacial processes but also the plant responses to altered habitat conditions, long-term monitoring of the relationships between periglacial landforms and vegeta-

tion represents a suitable tool for assessing the impact of global change on arctic regions.

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Appendix

List of the rare species, not included in the RDA elaboration

Vascular plants *Carex misandra*, *C. rupestris*, *Cassiope tetragona*, *D. arctica*, *D. subcapitata*, *E. scirpoides*, *Pedicularis dasyantha*, *P. irsuta*, *P. alpina vivipara*, *Ranunculus spetsbergensis*, *R. sulphureus*, *S. aizoides*, *S. uralensis*, *Stellaria crassipes*.

Bryophytes *Platydictya jungermannioides*, *Aneura pinguis*, *Aplodon wormskioldii*, *Ceratodon purpureus*, *D. groenlandicum*, *Hylocomium splendens*, *Meesia triquetra*, *M. uliginosa*, *Mnium thomsonii*, *Myurella julacea*, *O. strictum*, *Paludella squarrosa*, *Polytrichum* sp., *Pseudo-calliergon trifarium*, *Ptilidium ciliare*, *Scapania gymnostomophila*, *Tetraplodon* sp., *Tortella fragilis*, *Tritomaria scitula*.

Lichens *Biatora subduplex*, *Caloplaca jungermanniae*, *C. coccifera*, *Dacampia hookeri*, *Flavocetraria nivalis*, *Fulgensia bracteata*, *L. hageni*, *Leciophysma finmarkicum*, *P. lepidophora*, *Phaeorrhiza nimbosa*.

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