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Plant communities and soils in cryoturbated tundra along a bioclimate gradient in the Low Arctic, Alaska

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with 24 figures, 12 tables and 1 appendix

Abstract. Nonsorted circles and earth hummocks are important landscape components of the arctic tundra. Here we describe the vegetation on these frost-heave features at seven study sites along a N-S-transect from the Arctic Ocean to the Arctic Foothills, Alaska. We established 117 relevés in frost-heave features and surrounding tundra and classified the vegetation according to the Braun-Blanquet sorted-table method. We used Detrended Correspondence Analysis to analyze relationships between vegetation and environmental variables. We identified nine communities: *Braya purpurascens-Puccinellia angustata* community (dry nonsorted circles, subzone C); *Dryas integrifolia-Salix arctica* community (dry tundra, subzone C); Salici rotundifoliae-Caricetum aquatilis ass. nov. (moist coastal tundra, subzone C); Junco biglumis-Dryadetum integrifoliae ass. nov. (moist nonsorted circles, subzone D); Dryado integrifoliae-Caricetum bigelowii Walker et al. 1994 (moist tundra, subzone D); *Scorpidium scorpioides-Carex aquatilis* community (wet tundra, subzone D); Cladino-Vaccinietum vitis-idaeae ass. nov. (dry nonsorted circles and earth hummocks, subzone E); Sphagno-Eriophoretum vaginati Walker et al. 1994 (moist tundra, subzone E); and *Anthelia juratzkana-Juncus biglumis* community (wet nonsorted circles, subzone E).

The DCA ordination displayed the vegetation types with respect to complex environmental gradients. The first axis of the ordination corresponds to a bioclimate/pH gradient, and the second axis corresponds to a disturbance/soil moisture gradient. Frost-heave features are dominated by lichens, whereas the adjacent tundra supports more dwarf shrubs, graminoids and mosses. Frost-heave features have greater thaw depths, more bare ground, thinner organic horizons and lower soil moisture than the surrounding tundra. The morphology of frost-heave features changes along the climatic gradient, with large, barren nonsorted circles dominating the northern sites and vegetated, less active earth hummocks dotting the southern sites. Thawing of permafrost and a possible shift in plant community composition due to global warming could lead to a decline in frost-heave features and result in the loss of landscape heterogeneity.

Keywords: biocomplexity, Braun-Blanquet classification, Detrended Correspondence Analysis, earth hummocks, frost heave, nonsorted circles.

1 Introduction

The vegetation and soil patterns in many arctic tundra regions are influenced by the distribution of frost-heave features such as nonsorted circles and earth hummocks (Washburn 1980). Nonsorted circles and earth hummocks form

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in fine-grained soils with permafrost. Nonsorted circles are a form of patterned ground common in most arctic regions. They are more or less flat, bare soil patches 0.5 to 3 m across and lack a border of stones. These features are a product of differential frost heave, which occurs when ice lenses form in the soils during winter. Nonsorted circles heave more than the surrounding tundra due to deeper thaw and more ice lenses in the barren circles and also due to migration of water from the inter-circle areas (Peterson & Krantz 2003). Earth hummocks are well-vegetated, mound-shaped landforms up to 50 cm tall and 1 – 2 m in diameter. They usually have a mineral soil core and are also often caused by differential frost heave. Another prevalent process in the Arctic is contraction cracking due to desiccation and/or freezing processes (Washburn 1980). These contraction cracks form polygons, with diameter sizes ranging from centimeters to several meters. Small nonsorted contraction-crack polygons up to 40 cm in diameter form in conjunction with nonsorted circles in the High Arctic and the northern portion of our gradient.

Several aspects of frost-heave features have been studied in the past, such as geomorphology (Washburn 1956 and 1980), self-organization of patterned ground (Hallet & Prestrud 1986, Hallet 1990, Kessler et al. 2001, Kessler & Werner 2003, Peterson & Krantz 2003, Peterson et al. 2003), soil instability and cryoturbation (Sigafoos 1951, Gartner et al. 1986, Ping et al. 1998, Walker et al. 2004), and vegetation patterns (Johnson & Neiland 1983, Chernov & Matveyeva 1997, Walker et al. 2004). However, no study to date has presented a formal description and analysis of the plant communities on these unique landforms. In this study, we classify and describe the plant communities on and in between frost-heave features along a climatic gradient in the Low Arctic in Alaska. We relate soil and environmental variables to the plant communities through Detrended Correspondence Analysis and discuss the implication of these relationships with respect to a changing arctic climate.

2 Study area

2.1 Location and climate

This study was conducted along a N-S-transect from the coast of the Arctic Ocean to the Arctic Foothills along the northern segment of the Dalton Highway, Alaska, close to the Sagavanirktok River (Fig. 1). From north to south, we investigated seven study sites: Howe Island, West Dock, Deadhorse, Franklin Bluffs, Sagwon MNT (moist non-acidic tundra), Sagwon MAT (moist acidic tundra), and Happy Valley. The distance from the coast to the site farthest south (Happy Valley) is about 130 km. Howe Island, West Dock, Deadhorse and Franklin Bluffs are located in the Arctic Coastal Plain, with abundant thaw lakes dotting the landscape. The remaining sites are situated in the Arctic Foothills, where the landscape is dominated by broad sloping valleys with elevations up to 350 m. The climate of the area varies with distance from the Arctic Ocean and elevation. From north to south, temperature and precipitation increase. On the Arctic Coastal Plain,

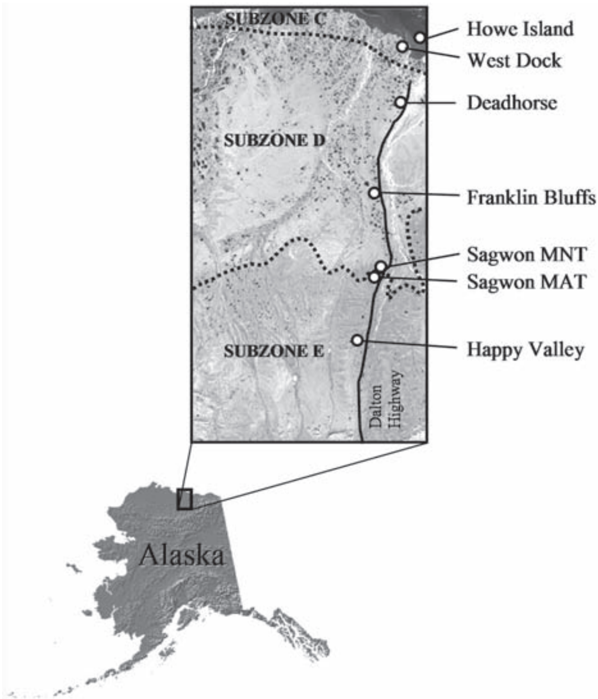

Fig. 1. Location of the three climatic subzones and the seven study sites along the northern segment of the Dalton Highway, Alaska.

the mean annual precipitation ranges from 125–140 mm and 50 % falls as snow. In the Arctic Foothills, mean annual precipitation ranges from 140–270 mm, with 40 % falling as snow (Haugen 1982).

According to the Circumpolar Arctic Vegetation Map (CAVM Team 2003) and Walker (2000), West Dock and Howe Island are part of bioclimate subzone C or the hemiprostrate dwarf-shrub subzone, with mean July temperatures from 5–7 °C. Sagwon MNT, Franklin Bluffs and Deadhorse are classified as bioclimate subzone D or the erect dwarf-shrub subzone, with mean July temperatures from 7–9 °C. Happy Valley and Sagwon MAT belong to bioclimate subzone E or the low-shrub subzone, with mean July temperatures from 9–12 °C.

2.2 Geology and soils

Howe Island, West Dock, Deadhorse and Franklin Bluffs are on the Arctic Coastal Plain, which was not glaciated during the last glaciation. It consists of alluvium and the surface is covered by predominately Holocene deposits

(Hamilton 1987). The area shows several periglacial features, such as pingos, ice-wedge polygons and nonsorted circles. Calcareous sediments are carried from limestone deposits at the headwaters of the Sagavanirktok River and redistributed as loess deposits on the coastal plain (Walker et al. 1991). Wet soils are often covered with marl due to the carbonate-rich parent material (Ping et al. 1998). The Sagwon sites are about 100 km inland on the uplands at the northern edge of the Arctic Foothills. These sites have a loess mantle over Tertiary outwash consisting of rounded gravel. Happy Valley is on a glaciated surface mapped by Hamilton (1987) as Anaktuvuk-age (early Pleistocene) till. A thin layer of loess covers the till.

All sites are located in the zone of continuous permafrost (Péwé 1975). The permafrost-affected soils, or cryosols, are in the Gelisol order of the U. S. Soil Taxonomy (Soil Survey Staff 1999), and they contain permafrost within 1 m of the soil surface (Bockheim et al. 1997). The soils show strong signs of soil mixing due to cryoturbation activity. The permafrost also acts as barrier for water percolation and leads to water-logged soils in spite of low precipitation, especially in the flat Arctic Coastal Plain. Thus, these soils commonly display gleyed features. The high soil moisture content and cold soil temperatures result in slow decomposition rates and the accumulation of thick peat horizons. Parts of the organic matter are often cryoturbated into lower parts of the active layer and can become locked up in the permafrost with changing environmental conditions (Ping et al. 1998). The chemical soil properties change along the north-south climatic gradient and with distance from the Sagavanirktok River. The northern study sites exhibit soils with high pH and free carbonates. As the Arctic Foothills rise south from the Arctic Coastal Plain, the soils become better drained, and thinner loess deposits, higher precipitation and greater leaching result in acidic soil reaction (Ping et al. 1998).

3 Methods

3.1 Field and laboratory methods

We established a total of 117 permanent plots along the bioclimate gradient, 15 at Howe Island, 5 at West Dock, 15 at Deadhorse, 37 at Franklin Bluffs, 15 at Sagwon MNT, 10 at Sagwon MAT and 20 at Happy Valley. Vegetation sampling was conducted during the summer periods of 2000 through 2003 using the centralized replicate sampling procedure (Mueller-Dombois & Ellenberg 1974). We chose the plot, or relevé, locations subjectively in areas of homogeneous vegetation that were representative of the major plant communities. The minimum sampling area was 1 m^2 per plot. We used the Braun-Blanquet cover-abundance scale to score the cover of each species (Westhoff & van der Maarel 1978). In addition, we recorded the cover of plant functional types and the average vegetation height. Nomenclature followed the PLANTS database (USDA, NRCS 2004) for vascular plants, Ignatov & Afonina (1992) for mosses, Esslinger (1997) for lichens and Konstantinova et al. (1992) for liverworts.

At each relevé, we recorded the following site information: percent bare soil, percent salt crust, cover of standing water, site moisture, glacial history, topography, site stability and elevation. We measured maximum snow depths in mid April 2002 to 2004, and maximum thaw depths in late August 2002 to 2004 using a metal probe. We correlated the vegetation information with the summer warmth index (SWI) calculated for all study sites by Walker et al. (2004). The SWI is the sum of the monthly mean air temperatures above freezing and represents an integrated value for the total amount of summer warmth available for plant growth. We examined the change in morphology of frost-heave features along the bioclimate gradient by mapping several representative nonsorted circles at selected study sites at a 1 m by 1 m scale.

At each relevé site, we measured the depth of the organic horizon and collected soil samples of the upper 10 cm of the mineral horizon, which represents the rooting zone for most tundra species. All soil samples were shipped to the University of Alaska Fairbanks Palmer Soil and Plant Analysis Laboratory for analysis. Bulk density and volumetric soil moisture were calculated by drying field samples at 105 °C for 72 hours and determining percentage weight loss. All other analyses were completed on air-dried samples. Particle size was determined using the hydrometer method, taking readings at 40 seconds and 2 hours (Gee & Bauder 1986). Soil pH values were measured using the saturated paste method with a glass electrode pH meter (Jackson 1958). Total carbon and nitrogen were determined by dry combustion using a LECO CNS 2000 analyzer at 1350 °C (Robertson et al. 1999). The availability of cations (K^+, Na^+, Ca^{2+}, Mg^{2+}) was determined with Mehlich-3 extractions (Mehlich 1984).

3.2 Classification and ordination

We classified the vegetation according to the Braun-Blanquet sorted-table method (Mueller-Dombois & Ellenberg 1974, Westhoff & van der Maarel 1978) and the protocol suggested by Dierschke (1994) for distinguishing vegetation types. The relevés were arranged in phytosociological tables to differentiate and characterize associations and community types. We placed the 117 relevés into preliminary groups based on climatic subzone, disturbance through frost action, soil pH and soil moisture content. We determined differential species and assessed the degree of fidelity of character species according to the criteria proposed by Dierschke (1994). The nomenclature of the described syntaxa is in accordance with the international code of phytosociological nomenclature (Weber et al. 2000).

Detrended Correspondence Analysis (DCA) ordinations were carried out to analyze relationships between variation in vegetation and variation in environmental variables. We used PC-ORD (4.10 for Windows) (McCune & Mefford 1999), and rare species were down-weighted and axes were rescaled based on program defaults. DCA produces first axes showing major directions of variation in the data and revealing the relationship of plant assemblages to major environmental gradients (Peet et al. 1988). To evaluate the effectiveness of the ordination, we calculated an after-the-fact coefficient to determine the variance in the main matrix explained by DCA as suggested by McCune & Mefford (1999). The ordination axes are best described as complex environmental gradients with interrelated factors (Kent & Coker 1992). Biplot diagrams were used to show the direction in the ordination diagram that has the maximum correlation with a particular environmental variable. DCA ordinations were compared with other ordination techniques available in PC-ORD (e. g. Bray-Curtis, Canonical Correspondence Analysis, Non-metric Multidimensional Scaling) using the same data set. We chose DCA as it produced results most consistent with the classification and showed strong underlying environmental gradients. An added advantage of DCA is that the output also records the length of each axis in units of the average standard deviation of species turnover (SD units), which are a measure of species turnover (beta diversity) along the axis.

3.3 Plant functional types and floristic analysis

We analyzed growth form distributions (dwarf shrubs, forbs, graminoids, mosses, lichens and liverworts) and the floristic affinities of the communities. For the latter we used a multiple-character approach modified from the criteria by Walker (1985). Each vascular species was assigned to a class according to three categories: major regional unit (coastal, arctic, arctic-alpine, arctic-boreal), northern limits of plant distributions within the four climatic zones developed by Young (1971), and geographic range (North America, North America-Asia, North America-Asia-Europe, circumpolar). Young (1971) differentiated the climatic zones based on the sum of mean monthly temperatures above 0 °C (zone 1 = 0–6 °C, zone 2 = 6–12 °C, zone 3 = 12–20 °C, zone 4 = 20–35 °C).

4 Results and discussion

4.1 Environmental and morphological characteristics

Frost-heave features differ from the surrounding tundra in several environmental characteristics. They have more bare ground than the adjacent tundra plots, and the percent of bare soil of the frost-heave features declines along the bioclimate gradient from 55 % in subzone C to 11 % in subzone E (Table 1). At all sites, nonsorted circles and earth hummocks have greater thaw depths in late summer than the surrounding tundra. The difference in thaw depths between frost-heave features and tundra in subzone C averages about 14 cm and increases toward the south to 23 cm in subzone D and 27 cm in subzone E. The thick carpets of *Sphagnum* mosses apparently insulate the stable tundra in subzone E and reduce thaw depths. The study sites are located along a strong climatic gradient, with the SWI ranging from 9.3 °C mo at Howe Island in subzone C to 30.2 °C mo at Happy Valley in subzone E (Table 2). In the northern sites, the harsh climate prevents the soil of well-vegetated sites from thawing deeply. In the southern sites, biological constraints decrease thawing processes due to insulation by

Table 1. Environmental variables and soil physical and chemical properties for the plant associations and communities of the cryoturbated tundra. Mean with standard error in parentheses.

	Braya purpurascens-Puccinellia angustata comm.	Dryas integrifolia -Salix arctica comm.	Salici rotundifoliae - Caricetum aquatilis ass.	Junco biglumis -Dryadetum integrifoliae ass.	Dryado integrifoliae - Caricetum bigelowii ass.	Scorpidium scorpioides - Carex aquatilis comm.	Cladino -Vaccinietum vitis - idaeae ass.	Sphagno-Eriophoretum vaginati ass.	Anthelia juratzkana -Juncus biglumis comm.
Thaw depth (cm)	79.4 (1.1)	65.0 (1.4)	28.0 (0.3)	88.1 (1.4)	64.9 (1.9)	70.0 (1.8)	60.3 (0.9)	33.6 (1.6)	59.8 (1.9)
Snow depth (cm)	8.1 (2.0)	13.3 (2.7)	19.2 (2.6)	27.0 (1.9)	39.8 (2.5)	58.6 (7.4)	39.7 (4.6)	60.1 (4.4)	63.2 (0.9)
O-horizon depth (cm)	0.0 (0.0)	0.4 (0.2)	26.8 (1.2)	0.2 (0.1)	15.3 (1.5)	25.4 (0.9)	6.4 (1.6)	11.9 (1.0)	0.0 (0.0)
Bare soil (%)	55.0 (11.8)	0.0 (0.3)	0.1 (0.1)	26.3 (4.8)	0.3 (0.2)	2.4 (1.1)	0.0 (0.0)	0.0 (0.0)	10.6 (4.2)
Soil moisture (vol.-%)	28.3 (2.9)	37.3 (2.6)	47.1 (0.4)	39.2 (0.9)	45.2 (2.5)	49.0 (1.9)	35.8 (1.6)	44.1 (1.3)	41.8 (3.3)
Bulk density (g/cm^3)	1.11 (0.04)	0.79 (0.03)	0.82 (0.02)	1.35 (0.04)	1.23 (0.07)	1.34 (0.04)	0.95 (0.05)	1.07 (0.04)	1.13 (0.04)
Sand content (%)	52.1 (3.3)	65.3 (2.3)	36.8 (1.6)	44.9 (2.7)	45.3 (3.3)	43.3 (2.7)	29.8 (1.4)	33.4 (1.9)	28.6 (1.9)
Silt content (%)	31.8 (2.3)	30.1 (2.6)	45.7 (2.0)	34.9 (2.6)	40.8 (3.0)	46.6 (5.8)	44.4 (1.1)	44.9 (1.1)	43.6 (1.5)
Clay content (%)	16.1 (3.9)	4.6 (0.8)	17.5 (2.2)	20.2 (0.6)	13.9 (1.2)	10.1 (3.2)	25.8 (0.8)	21.7 (1.8)	27.8 (1.8)
Soil pH	8.3 (0.1)	7.9 (0.1)	6.5 (0.1)	8.1 (0.1)	7.9 (0.1)	7.7 (0.1)	5.0 (0.1)	5.3 (0.1)	5.2 (0.1)
Total C (%)	4.77 (0.31)	6.30 (0.24)	5.34 (0.11)	5.1 (0.21)	5.78 (0.26)	5.42 (0.83)	3.73 (0.39)	3.46 (0.28)	2.68 (0.55)
Total N (%)	0.11 (0.01)	0.18 (0.03)	0.19 (0.02)	0.18 (0.01)	0.29 (0.03)	0.26 (0.05)	0.21 (0.02)	0.21 (0.02)	0.15 (0.04)
Available Ca^{2+} (me/100g)	39.8 (1.4)	48.3 (1.8)	22.0 (0.8)	67.3 (6.7)	53.2 (2.7)	40.6 (8.3)	5.4 (0.9)	9.2 (0.5)	6.0 (0.9)
Available Mg^{2+} (me/100g)	2.35 (0.12)	1.78 (0.15)	1.14 (0.08)	1.7 (0.18)	1.86 (0.21)	1.20 (0.12)	0.76 (0.10)	1.59 (0.07)	1.07 (0.11)
Available K^{+} (me/100g)	0.18 (0.01)	0.14 (0.02)	0.11 (0.01)	0.12 (0.01)	0.18 (0.02)	0.18 (0.02)	0.10 (0.01)	0.07 (0.01)	0.08 (0.01)
Available Na^{+} (me/100g)	3.18 (0.61)	0.32 (0.14)	1.42 (0.10)	0.05 (0.01)	0.06 (0.01)	0.06 (0.01)	0.02 (0.01)	0.02 (0.01)	0.02 (0.01)

Table 2. Summer warmth indices (SWI) for the study sites (after Walker et al. 2004).

Study site	Subzone	SWI (°C mo)
Howe Island	C	9.3
West Dock	C	14.0
Deadhorse	D	19.0
Franklin Bluffs	D	27.0
Sagwon MNT	D	28.2
Sagwon MAT	E	28.2
Happy Valley	E	30.2

thick vegetation mats and organic horizons. Thus, the deepest thaw depths (mean 88 cm) are found at the nonsorted circles in subzone D. Average snow depths increase along the climate gradient from north to south from 19 to 63 cm (Table 1), probably due to increased precipitation associated with higher elevation (Ping & Moore 1993). Also, stronger winds near the coast compact the snow, and much of the snow is lost due to ablation. The frost-heave features accumulate less snow than the adjacent tundra due to their raised soil surface caused by frost heave. Thinner snow cover should result in less insulated soils in the winter.

We found nonsorted circles dominating the landscape at Howe Island in subzone C (Fig. 2), periodically dotting the landscape in subzone D (Fig. 3) and being rather sporadic and inconspicuous in subzone E (Fig. 4). The

Fig. 2. Nonsorted circles dominating the landscape at Howe Island, subzone C, Alaska.

Fig. 3. Vegetated nonsorted circles at Deadhorse, subzone D, Alaska.

Fig. 4. Tussock tundra at Happy Valley, subzone E, Alaska.

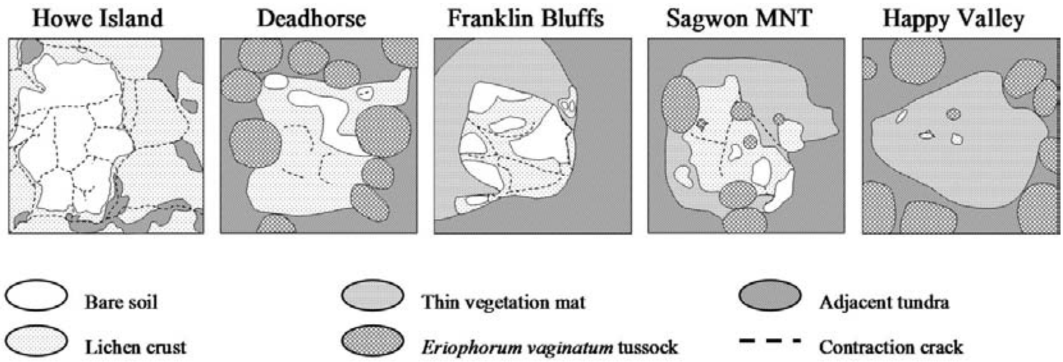

Fig. 5. Vegetation maps (1 m by 1 m) of nonsorted circles at several study sites along the bioclimate gradient from north to south.

morphological changes of nonsorted circles along the bioclimate gradient are shown in representative 1 m by 1 m maps in Fig. 5. The nonsorted circles at Howe Island at the northern end of the bioclimate gradient are large in size and exhibit high cover of bare soil. Several contraction cracks dissect the nonsorted circles and form small contraction-crack polygons. The outer parts of the nonsorted circles are covered with lichen crusts. Further south in subzone D, the nonsorted circles have less amounts of bare soil and lichen crusts, and they are encircled by a thin vegetation mat growing inward from the edges of the nonsorted circles. Fewer contraction cracks are visible. The nonsorted circles and earth hummocks at Happy Valley at the southern end of the bioclimate gradient are fully vegetated and do not show any bare soil patches.

4.2 Classification

The classification of cryoturbated tundra in the Low Arctic of Alaska resulted in five associations and four community types that have been tentatively placed into four classes (Table 3). The dry nonacidic nonsorted circles and small contraction-crack polygons of subzone C (*Braya purpurascens-Puccinellia angustata* community) could not be placed into an actually described class. The following descriptions of the vegetation types are arranged according to climatic subzones, starting with the sites farthest north. Within each subzone, the vegetation types are sorted by soil moisture. Drier sites, usually disturbed through cryoturbation activity, are mentioned first.

Three plant communities are placed in the class Carici rupestris-Kobresietea bellardii Ohba 1974. This class includes mostly meso- to xerophytic, minerotrophic dwarf shrub and grass heath communities comprised of circumpolar arctic and alpine species. The communities belong to the order Kobresio-Dryadetalia (Br.-Bl. 1948) Ohba 1974 and the North-American alliance Dryadion integrifoliae Ohba ex Daniëls 1982. The

Table 3. Class, order, alliance and association or community names and habitats of the cryoturbated tundra in the Alaskan Low Arctic.

Undescribed unit
Braya purpurascens-Puccinellia angustata comm.
Nonsorted circles and small polygons; dry nonacidic tundra; subzone C
C. Carici rupestris-Kobresietea bellardii Ohba 1974
O. Kobresio-Dryadetalia (Br.-Bl.1948) Ohba 1974
A. Dryadion integrifoliae Ohba ex Daniëls 1982
Dryas integrifolia-Salix arctica comm.
Stable, dry nonacidic tundra; subzone C
Junco biglumis-Dryadetum integrifoliae ass. nov.
Nonsorted circles; moist nonacidic tundra; subzone D
Dryado integrifoliae-Caricetum bigelowii Walker et al. 1994
Stable, moist nonacidic tundra; subzone D
C. Scheuchzerio-Caricetea nigrae (Nordh. 1936) Tx. 1937
O. Scheuchzerietalia palustris Nordh. 1936
A. Caricion lasiocarpae Vanden Berghen ap. Lebrun et al. 1949
Salici rotundifoliae-Caricetum aquatilis ass. nov.
Stable, moist nonacidic coastal tundra; subzone C
Scorpidium scorpioides-Carex aquatilis comm.
Stable, wet nonacidic tundra; subzone D
C. Loiseleurio-Vaccinietea Eggler 1952
O. Rhododendro-Vaccinietalia Br.-Bl. ap. Br.-Bl. & Jenny 1926
(A. Loiseleurio-Diapension (Br.-Bl. Et al. 1939) Daniëls 1982?)
Cladino-Vaccinietum vitis-idaeae ass. nov.
Nonsorted circles and earth hummocks; moist acidic tundra; subzone E
Sphagno-Eriophoretum vaginati Walker et al. 1994
Stable, moist acidic tundra; subzone E
C. Salicetea herbaceae Br.-Bl. 1947
O. Salicetalia herbaceae Br.-Bl. 1926
A. Saxifrago-Ranunculion nivalis Nordh. 1943 emend. Dierß. 1984
Anthelia juratzkana-Juncus biglumis comm.
Nonsorted circles; moist acidic tundra; subzone E

Dryas integrifolia-Salix arctica community belongs to the typical suballiance of the Dryadion integrifoliae. The Junco biglumis-Dryadetum integrifoliae and the Dryado integrifoliae-Caricetum bigelowii belong to the Dryadion integrifoliae suball. rhododendrenion lapponici, a new meso-hygrophytic suballiance described from Greenland by Lünterbusch & Daniëls (2004).

The moist coastal tundra of subzone C (Salici rotundifoliae-Caricetum aquatilis) and the wet nonacidic tundra of subzone D (*Scorpidium scorpioides-Carex aquatilis* community) are placed in the mire class Scheuchzerio-Caricetea nigrae (Nordh. 1936) Tx. 1937, order Scheuchzerietalia palustris Nordh. 1936, alliance Caricion lasiocarpae Vanden Berghen ap. Lebrun et al. 1949. This alliance includes wet basiphytic sedge beds on calcareous, poorly drained soils and occurs in the northern boreal zone and the Arctic.

The dry acidic nonsorted circles and earth hummocks (Cladino-Vaccinietum vitis-idaeae ass. nov.) as well as the moist acidic tundra (Sphagno-Eriophoretum vaginati Walker et al. 1994) of subzone E are placed in the class Loiseleurio-Vaccinietea Eggler 1952, order Rhododendro-Vaccinietalia Br.-Bl. ap. Br.-Bl. & Jenny 1926. This class includes dwarf shrub vegetation rich in lichens on acidic soil in alpine and arctic regions. We place the two associations provisionally within the alliance Loiseleurio-Diapension (Br.-Bl. et al. 1939) Daniëls 1982.

The small, relatively wet acidic nonsorted circles of subzone E (*Anthelia juratzkana-Juncus biglumis* community) were placed within the snow patch class Salicetea herbaceae Br.-Bl. 1947, order Salicetalia herbaceae Br.-Bl. 1926, alliance Saxifrago-Ranunculion nivalis Nordh. 1943 emend. Dierß. 1984, suballiance Luzulenion arcticae (Nordh. 1936) Gjaerevoll 1950. The class comprises alpine and arctic snow-patch communities, which often exhibit solifluction and cryoturbation features, and the alliance is tied to arctic regions with relatively wet permafrost soils. The Luzulenion arcticae includes communities with arctic species on slightly drier soils.

4.2.1 Subzone C

Braya purpurascens-Puccinellia angustata community (Fig. 6; Table 4; App. 1, ref. 1)

This community is found on the dry, nonacidic frost-heave features of subzone C, which are comprised of contraction-crack polygons and nonsorted circles. The small, nonsorted contraction-crack polygons, formed by desiccation and frost cracking, are up to 40 cm in diameter and form concentric rings around nonsorted circles measuring approximately 4 m in diameter (Fig. 7). These large frost-heave features, separated by thin strips of surrounding tundra vegetation, dominate the landscape. Cryoturbation activity is greatest at the center of the nonsorted circles, where bare mineral soil is exposed and small pebbles are heaved to the surface. The small contraction-crack polygons surrounding the nonsorted circles exhibit a thick crustose lichen cover and are more stabilized. Several small islands within and near the delta of the Sagavanirktok River exhibit these conspicuous frost-heave features. Subzone C represents only a small band along the northern coast in Alaska; thus, this community is not very common in Alaska. How-

Fig. 6. *Braya purpurascens-Puccinellia angustata* community, with the typicum variant occurring on the dry nonacidic nonsorted circles and the *Mycobilimbia lobulata* variant occurring on the small polygons surrounding the central bare area. Subzone C, Howe Island, Alaska.

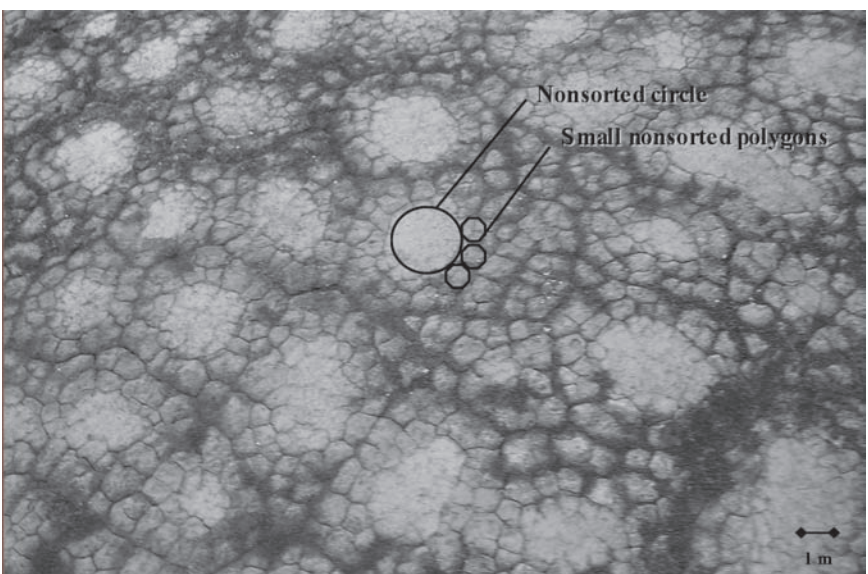

Fig. 7. Aerial view of a network of frost-heave features at Howe Island, Alaska. Note the small nonsorted polygons forming concentric rings around the nonsorted circles.

Table 4. Community table of the *Braya purpurascens-Puccinellia angustata* community.

	typicum					Mycobilimbia lobulata var.				
Relevé No.	113	114	110	24	21	25	26	115	111	23
Altitude (m.a.s.l.)	4	6	6	12	15	10	13	6	5	7
Number of vascular taxa	3	2	2	3	2	10	9	9	11	3
Number of nonvascular taxa	2	2	1	2	0	17	18	17	16	10
Total number of taxa	5	4	3	5	2	27	27	26	27	13
Ch/D: Community										
Braya glabella ssp. purpurascens	1	+	+	1	+	+	1	1	+	+
Puccinellia angustata	+	+	+	1	+	+	+	1	+	+
Polyblastia sendtneri	+	+	+	.	.	1	2	2	1	2
D: Mycobilimbia lobulata var.										
Mycobilimbia lobulata	+	+	.	.	.	3	3	3	3	4
Lecanora epibryon	.	.	.	.	.	1	1	1	2	+
Salix ovalifolia	.	.	.	.	.	1	+	+	+	+
Fulgensia bracteata	.	.	.	r	.	+	+	+	+	+
Distichium inclinatum	.	.	.	.	.	+	1	1	1	.
Chrysanthemum integrifolium	.	.	.	.	.	+	+	+	+	.
Collema sp.	.	.	.	.	.	+	+	+	+	.
Polyblastia bryophila	.	.	.	.	.	2	2	1	.	+
Hennediella heimii var. arctica	.	.	.	.	.	1	1	1	.	+
Ctenidium procerrimum	.	.	.	.	.	+	+	.	+	.
Thamnolia subuliformis	.	.	.	.	.	+	r	.	+	.
Orthothecium varia	.	.	.	.	.	+	.	+	+	.
Bryum sp.	.	.	.	.	.	.	+	+	+	.
Cerastium beeringianum	.	.	.	.	.	.	+	+	r	.
Tortula ruralis	.	.	.	r	.	.	+	+	.	+
Draba cinerea	.	.	.	.	.	r	+	.	.	.
Potentilla uniflora	.	.	.	.	.	+	.	+	.	.
Encalypta alpina	.	.	.	.	.	.	+	.	1	.
Megaspora verrucosa	.	.	.	.	.	.	+	.	+	.
Pertusaria dactylina	.	.	.	.	.	+	.	.	+	.
Cirriphyllum cirrosum	.	.	.	.	.	+	.	.	.	+
Pedicularis capitata	.	.	.	.	.	r	r	.	.	.
Cephaloziella arctica	.	.	.	.	.	+	.	+	.	.
Lophozia collaris	.	.	.	.	.	+	.	.	+	.
Artemisia campestris ssp. borealis var. borealis	.	.	.	.	.	r	.	.	r	.
Campylium stellatum	.	.	.	.	.	.	+	+	.	.
Draba sp.	.	.	.	.	.	.	.	+	+	.
Bryoerythrophyllum recurvirostre	.	.	.	.	.	.	.	+	+	.
Encalypta sp.	.	.	.	.	.	.	.	+	.	1
Others										
Androsace chamaejasme	+	.	.	.	.	r	.	.	+	.
Cochlearia groenlandica	.	.	.	+	.	+	.	+	.	.

Single occurrences: Amblystegium serpens (rel. 25: +), Rinodina roscida (25: +), Salix arctica (26: +), Aloina brevirostris (26: +), Encalypta rhaptocarpa (26: +), Arctagrostis latifolia (26: r), Ochrolechia frigida (26: r), Juncus biglumis (115: +), Didymodon rigidulus var. icmadophilus (115: +), Ditrichum flexicaule (115: +), Dryas integrifolia (111: +), Polygonum viviparum (111: +), Saxifraga oppositifolia (111: +), Didymodon sp. (111: +), Distichium capillaceum (23: +).

ever, counterparts are found in the Middle Arctic (sensu Polunin 1951) in Canada and have been described from Green Cabin on Banks Island (Walker et al. unpublished data).

We could not place this community into an existing class. The soils show a high Na^+ content due to the input of ocean spray. This agrees with Michaelson et al. (2005), who found differences in salt species and their distribution and accumulation patterns in nonsorted circles and tundra plots in the Alaskan Arctic tundra. Na^+ affected the bare microsites on coastal sites and caused smooth crusts due to soil dispersion. The vascular species of this community are all halophytic or salt tolerant, such as *Braya glabella* ssp. *purpurascens* and *Puccinellia angustata*. This suggests similarities to Type B10 Dry *Braya purpurascens-Puccinellia andersonii* forb grass barren of the coastal bluffs in the Prudhoe Bay area described by Walker (1985). The community also shows some affinities to crustose lichen-dominated plant communities at Prudhoe Bay, Types B1, B2, B3 (Walker 1985), where *Lecanora epibryon* is often dominant on mineral soils. The community shares some floristic elements with the *Puccinellia* stands of arctic coastal salt meadows described by Thannheiser (1991), although the *Braya purpurascens-Puccinellia angustata* community does not exhibit a continuous vegetation cover.

The soils are classified as Aquic Haploturbels (Michaelson et al. 2005). An organic horizon is absent, and the exposed mineral soil shows signs of desiccation cracking and/or seasonal frost cracking (Washburn 1980). The mineral soil is light brownish gray and has a sandy loam texture. Soil moisture is very low (mean 28 %, Table 1), and the soil pH is high (mean 8.3). The sparse vegetation cover acts as a poor insulator and allows for deep thaw depth (mean 79 cm). Maximum snow depth is shallow (mean 8 cm) due to the proximity to the coast.

The community is separated into two variants; the first occurs on barren nonsorted circles and the second occurs on the small contraction-crack polygons. The *Braya purpurascens-Puccinellia angustata* community typical variant is very poor in species, the only constant taxa being *Braya glabella* ssp. *purpurascens*, *Puccinellia angustata* and *Polyblastia sendtneri*. *Braya glabella* ssp. *purpurascens* and *Puccinellia angustata* are faithful. The small contraction-crack polygons feature the *Mycobilimbia lobulata* variant, which is richer in species, especially nonvascular species. A thick lichen crust consisting of *Fulgensia bracteata*, *Lecanora epibryon*, *Mycobilimbia lobulata*, *Polyblastia bryophila* and *P. sendtneri* covers the small contraction-crack polygons. The *Mycobilimbia lobulata* variant shares several taxa with the nearby *Dryas integrifolia-Salix arctica* community, including *Cerastium beeringianum*, *Chrysanthemum integrifolium* and *Salix ovalifolia*. These species are more abundant in the *Dryas integrifolia-Salix arctica* community and seem to slowly invade the edges of the contraction-crack polygons from the surrounding tundra areas.

Dryas integrifolia-Salix arctica community (Fig. 8; Table 5; App. 1, ref. 2)

This community is confined to the cracks and depressions between the large frost-heave features in subzone C. The community is not widely distributed in Alaska because subzone C covers only a narrow belt close to the Beaufort

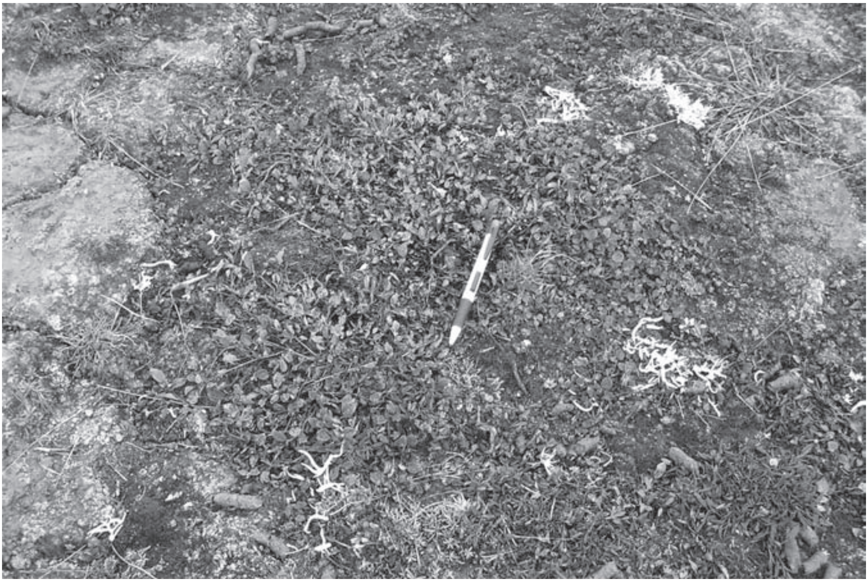

Fig. 8. *Dryas integrifolia-Salix arctica* community of the well-vegetated and stable, dry nonacidic tundra. Subzone C, Howe Island, Alaska.

Sea. We found the community on islands close to the shore of the Beaufort Sea and nearby the delta of the Sagavanirktok River. It also appears to be invading the more stabilized small contraction-crack polygons of the *Braya purpurascens-Puccinellia angustata* community. In the summer, geese nest on the islands close to the shore and have a major impact on the vegetation due to feeding on plants and excreting nitrogen-rich feces. The community is closely related to Type B2 Dry *Dryas integrifolia-Saxifraga oppositifolia-Lecanora epibryon* dwarf-shrub, crustose-lichen tundra (Walker 1985). The community is similar to the cushion plant communities described from the Canadian High Arctic polar semi-deserts by Bliss et al. (1984), which are dominated by *Dryas integrifolia*, *Salix arctica* and *Saxifraga oppositifolia* and, unlike the community described here, are poor in bryophytes.

The soils are Aquic Haploturbels and very similar to the ones associated with the *Braya purpurascens-Puccinellia angustata* community. The organic horizon is thin (0.5 cm, Table 1) and peaty. The mineral soil is grayish brown and consists of fine sandy loam. Soil moisture is low (mean 37 %) and the pH averages 7.9. Although this community is not associated with differential frost-heave features, maximum thaw depth is deep (mean 65 cm) due to the thin vegetation cover. Maximum snow depth averages 13 cm.

This community is relatively rich in vascular species. The dwarf shrubs *Dryas integrifolia*, *Salix arctica*, *S. ovalifolia* and *Saxifraga oppositifolia* and the mosses *Ctenidium procerrimum* and *Ditrichum flexicaule* dominate the

Table 5. Community table of the *Dryas integrifolia-Salix arctica* community.

Relevé No.	112	22	28	116	27
Altitude (m.a.s.l.)	6	8	13	6	17
Number of vascular taxa	16	17	16	14	17
Number of nonvascular taxa	13	8	11	17	7
Total number of taxa	29	25	27	31	24
Ch/regional D: Community					
Salix ovalifolia	2	2	2	1	3
Ctenidium procerrimum	3	3	3	1	2
Chrysanthemum integrifolium	1	1	+	1	1
Festuca baffinensis	+	+	+	1	+
Stellaria longipes	+	+	+	+	+
Cerastium beeringianum	+	+	+	+	+
Melandrium apetalum	r	+	r	+	+
Tortula ruralis	+	1	1	+	.
Draba sp.	+	+	+	.	+
Artemisia campestris ssp. borealis var. borealis	r	+	r	.	+
Didymodon asperifolius	+	+	.	+	.
Ch: Class, order and alliance					
Dryas integrifolia	4	4	3	5	4
Saxifraga oppositifolia	1	1	+	1	1
Pedicularis neoalaskanum	+	+	+	+	1
Others					
Salix arctica	2	3	2	1	2
Ditrichum flexicaule	+	2	2	+	1
Polygonum viviparum	+	+	+	+	+
Thamnolia subuliformis	+	+	+	+	+
Minuartia arctica	+	+	+	.	+
Hylocomium splendens	+	.	+	+	1
Braya glabella ssp. purpurascens	r	r	.	.	r
Distichium capillaceum	1	.	1	.	2
Androsace chamaejasme	+	.	.	1	+
Cochlearia groenlandica	.	r	r	.	+
Campylium stellatum	.	.	+	+	+
Encalypta sp.	.	.	+	+	+
Abietinella abietina	+	1	.	.	.
Tomentypnum nitens	+	.	1	.	.
Lophozia collaris	+	.	.	+	.
Rinodina roscida	+	.	.	+	.
Distichium inclinatum	.	1	.	2	.
Hypnum bambergeri	.	+	.	+	.

Single occurrences: Cephaloziella arctica (rel. 112: +), Collema sp. (112: +), Draba cinerea (22: +), Bryum pseudotriquetrum (28: +), Draba alpina (28: +), Amblystegium serpens (28: +), Aneura pinguis (28: +), Lloydia serotina (28: +), Caloplaca cerina (28: +), Carex rupestris (28: r), Didymodon rigidulus var. icmadophilus (116: +), Lecanora epibryon (116: +), Orthothecium varia (116: +).

community. Faithful taxa include *Chrysanthemum integrifolium*, *Festuca baffinensis*, *Salix ovalifolia* and *Ctenidium procerrimum*.

Salici rotundifoliae-Caricetum aquatilis Kade et al. ass. nov. (Fig. 9; Table 6, nomenclatural type relevé no. 98; App. 1, ref. 3)

The Salici rotundifoliae-Caricetum aquatilis occurs in a narrow belt of coastal circumneutral tundra in Northern Alaska. We placed this association in the class Scheuchzerio-Caricetea nigrae; however, the association is transitional to the plant communities of the Dryadion integrifoliae with regards to species composition. We found this association near West Dock at Prudhoe Bay on thin eolian silts and sands that overlie alluvial gravels of the ancient Sagavanirktok River flood plain. The coarse gravels inhibit frost heave to a large extent, and nonsorted circles were not present because of the thick gravel deposits close to the surface. The landscape is characterized by flat- and low-centered polygons with diameters of 10–15 m. Standing water can occur in spring or after heavy rain. Thick coastal fog during the summer and fall is typical.

Yurtsev (1994) placed the coastal tundra vegetation from the Cape Barrow-Prudhoe Bay area along with the eastern coast of Central Chukotka into the southern subdivision of the arctic tundra subregion and characterized the vegetation by extensive peaty wet meadows, the occasional occurrence of hypoarctic ericaceous dwarf shrub species and very low species diversity, re-

Fig. 9. Salici rotundifoliae-Caricetum aquatilis ass. nov. as part of the moist nonacidic coastal tundra. Subzone C, West Dock, Alaska.

Table 6. Community table of the Salici rotundifoliae-Caricetum aquatilis ass. nov. Nomenclatural type relevé number marked in bold.

Relevé No.	**98**	102	100	99	101
Altitude (m.a.s.l.)	5	5	5	5	5
Number of vascular taxa	24	16	11	8	9
Number of nonvascular taxa	44	29	23	16	16
Total number of taxa	68	45	34	24	25
Ch/regional D: Association					
Salix rotundifolia	1	+	2	3	2
Poa arctica	+	+	+	+	.
Nephroma expallidum	+	.	+	2	r
Cladonia pyxidata	.	+	+	r	r
Myurella tenerrima	+	+	+	.	.
Saxifraga cernua	+	+	.	+	.
Dicranum majus	+	+	.	+	.
Sanionia uncinata	+	+	.	+	.
Ch: Class, order and alliance					
Carex aquatilis	4	4	3	1	2
Eriophorum angustifolium ssp. triste	1	2	1	3	1
Bryum pseudotriquetrum	+	+	+	.	+
Campylium stellatum	+	+	+	.	+
Limprichtia revolvens	+	+	+	.	+
Saxifraga hirculus	+	+	.	.	+
Hierochloe pauciflora	+	.	+	+	.
Others					
Salix arctica	+	2	1	1	1
Thamnolia subuliformis	1	+	+	+	+
Cetraria islandica	+	+	+	+	+
Dactylina arctica	+	+	+	+	+
Dryas integrifolia	2	2	2	.	1
Tomentypnum nitens	2	.	1	+	+
Hylocomium splendens	+	.	+	+	+
Polygonum viviparum	+	+	+	.	.
Aulacomnium palustre	+	+	.	+	.
Distichium capillaceum	2	.	+	.	+
Salix planifolia ssp. pulchra	1	.	+	.	1
Stellaria sp.	+	.	.	+	+
Polytrichum strictum	.	.	+	+	+
Salix ovalifolia	2	+	.	.	.
Salix reticulata	1	+	.	.	.
Polytrichastrum alpinum	1	+	.	.	.
Bryoerythrophyllum recurvirostre	1	+	.	.	.
Flavocetraria cucullata	+	+	.	.	.
Cladonia pocillum	+	+	.	.	.
Pedicularis sudetica ssp. albolabiata	+	+	.	.	.
Cinclidium arcticum	+	+	.	.	.
Cladonia ecmocyna	+	+	.	.	.
Dupontia fisheri	+	+	.	.	.
Lecidea ramulosa	+	+	.	.	.
Stellaria longipes	+	+	.	.	.
Ochrolechia frigida	+	+	.	.	.
Bryum sp.	+	+	.	.	.
Distichium inclinatum	+	+	.	.	.
Orthothecium chryseum	+	+	.	.	.
Dicranum sp.	+	+	.	.	.
Oncophorus wahlenbergii	1	.	2	.	.
Hypnum bambergeri	+	.	+	.	.
Cinclidium latifolium	+	.	+	.	.
Pedicularis sp.	+	.	+	.	.
Blepharostoma trichophyllum	+	.	+	.	.
Meesia uliginosa	+	.	+	.	.
Aneura pinguis	+	.	+	.	.
Dicranum angustum	+	.	.	+	.
Peltigera aphthosa	+	.	.	.	+
Cladonia gracilis	.	+	+	.	.
Brachythecium sp.	.	+	.	+	.
Cladonia furcata	.	.	.	+	+

Single occurrences: Drepanocladus brevifolius (rel. 98: 1), Ditrichum flexicaule (98: +), Equisetum variegatum (98: +), Senecio atropurpureus (98: +), Aulacomnium turgidum (98: +), Pseudocalliergon turgescens (98: +), Carex misandra (98: +), Caloplaca tiroliensis (98: +), Equisetum scirpoides (98: +), Hypogymnia subobscura (98: +), Alectoria nigricans (98: +), Calypogeia sphagnicola (98: +), Cladonia uncialis (98: +), Salix phlebophylla (98: +), Dicranum elongatum (102: +), Melandrium apetalum (102: +), Minuartia arctica (102: +), Drepanocladus sp. (102: +), Cladonia amaurocraea (102: +), Sphaerophorus globosus (102: +); Carex bigelowii (100: 1), Dicranum spadiceum (100: +), Solorina bispora (100: +), Polytrichum sp. (100: +), Peltigera leucophlebia (99: 1), Cladonia squamosa (99: r), Aulacomnium acuminatum (101: +), Cirriphyllum cirrosum (101: +), Cochlearia groenlandica (101: r).

flecting the "youthfulness" of this type of arctic tundra. The Salici rotundifoliae-Caricetum aquatilis is equivalent to the moist to wet coastal tundra of polygon centers in the Prudhoe Bay area (Type U12 Moist *Carex aquatilis*, *Salix planifolia* ssp. *pulchra*, *Campylium stellatum* sedge, dwarf-shrub tundra) recorded by Walker (1985) and to the moist *Carex aquatilis-Oncophorus wahlenbergii* meadow in the Point Barrow area, Alaska, recorded by Webber (1978). Elias et al. (1996) described a *Dryas integrifolia-Carex aquatilis* community type on moist nonacidic coastal sites at Barter Island and a *Saxifraga cernua-Carex aquatilis* community type on more acidic flat-centered polygons, moist meadows and areas with moderate drainage from Point Barrow, Alaska. The *Saxifraga cernua-Carex aquatilis* community is most similar to that at West Dock and is dominated by *Alopecurus alpinus*, *Carex aquatilis*, *Dupontia fisheri*, *Eriophorum angustifolium*, *Petasites frigidus*, *Saxifraga cernua* and *Oncophorus wahlenbergii*.

The soils of the polygon centers are classified as Typic Historthels (Ping et al. 1998). The soils are relatively poorly drained, and standing water is sometimes present early in the summer and during rainy periods. Saturation, due to relatively high soil moisture (mean 47 %, Table 1), reduces decomposition, resulting in thick organic horizons (mean 27 cm). The mineral horizon is dark gray and gleyed. Soil texture is loam. Although part of the nonacidic tundra, the soils of this association have a relatively low pH (mean 6.5) when compared to other areas of the Prudhoe Bay region. This might be due to the coastal influence. Winds directly from the Beaufort Sea reduce the input of calcareous loess from the Sagavanirktok River delta (Walker 1985). Maximum thaw depth is shallow (mean 28 cm). The sites receive only small amounts of snow (mean 19 cm).

This sedge tundra is relatively rich in species, especially in nonvascular taxa. The association is generally dominated by *Carex aquatilis.* Other constant taxa are *Dryas integrifolia*, *Eriophorum angustifolium* ssp. *triste*, *Salix arctica*, *S. rotundifolia*, *Cetraria islandica*, *Dactylina arctica* and *Thamnolia subuliformis*. Faithful taxa include *Poa arctica*, *Salix rotundifolia*, *Cladonia pyxidata* and *Nephroma expallidum*.

4.2.2 Subzone D

Junco biglumis-Dryadetum integrifoliae Kade et al. ass. nov. (Table 7, nomenclatural type relevé no. 106; App. 1, ref. 4)

The Junco biglumis-Dryadetum integrifoliae is associated with nonsorted circles within the moist nonacidic tundra of subzone D. The association has floristic affinities to the fellfield-like *Carex rupestris-Saxifraga oppositifolia* community type of dry, exposed, east- and north-facing slopes of pingos of the Alaskan Arctic Coastal Plain (Walker et al. 1991). Walker et al. (1991) likened this group to fellfield vegetation because of its abundance of cushion and mat-forming plants and crustose lichens. Gelting (1955) described closely related *Dryas integrifolia* communities from western Greenland on basalt-rich soils, which are rich in crustose lichens such as *Lecanora epibryon*, *Ochrolechia upsaliensis* and *Pertusaria panyrga*. Chernov & Matveyeva (1997) recognized the vegetation occurring on frost scars as a separate stage in the successional formation of zonal tundra on the Taymyr Peninsula, Russia. They distinguished between several elements at this successional stage: patches of bare ground with solitary plants (which corresponds to this community type), rims with grass/dwarf-shrub/moss turf and troughs with moss turf. The process of bare-ground overgrowth is in its early stages, with an organogenic crust forming and stabilizing the ground. The thin crust is part of a micro-successional cycle, being periodically destroyed trough frost action and reestablishing itself. However, Chernov & Matveyeva (1997) viewed the vegetation growing on frost scars as part of a "spotted tundra" complex and did not describe it as a separate plant-community type.

The soil types of this association vary with site moisture conditions. Aquic Haploturbels are found on drier sites and Typic Aquiturbels on moist to wet sites (Michaelson et al. 2005). Organic horizons are very thin (0.2 cm, Table 1). The mineral soil is dark yellowish brown and has a loam texture. Soil moisture is relatively low (mean 39 %), but soils can exhibit gleyed characteristics where site moisture is locally greater. The soil pH is high (mean 8.1). The thin vegetation mat and organic horizons allow for great thaw depth (mean 88 cm). Maximum snow depth is shallow and averages 27 cm.

Taxa faithful for this association are *Carex capillaris*, *Senecio resedifolius*, *Aneura pinguis*, *Bryum wrightii*, *Cladonia pocillum* and *Solorina bispora*. Other dominant taxa are *Dryas integrifolia*, *Eriophorum angustifolium* ssp. *triste*, *Saxifraga oppositifolia*, *Ditrichum flexicaule*, *Hypnum bambergeri*, *Polyblastia sendtneri* and *Thamnolia subuliformis*.

This association has several species in common with the dry nonacidic tundra and nonsorted circles of subzone C, such as *Encalypta* sp., *Lecanora epibryon*, *Leiocolea collaris*, *Polyblastia sendtneri* and *Rinodina roscida*. It seems that the nonsorted circles in subzone D might serve as "islands" for certain species occurring in communities farther north. The disturbance through frost action creates habitat conditions similar to the physically harsh ones that are more common farther north, such as dry exposed mineral soil with greater temperature fluctuations at the surface due to the lack of insulation. Under the more favorable climatic conditions of subzone D, species occurring on these relatively rare sites would otherwise be outcompeted by species occurring in the adjacent tundra.

The association is divided into two subassociations based on cryoturbation activity and plant abundance. The Junco biglumis-Dryadetum integrifoliae typicum is found on active, barren nonsorted circles. The Junco biglumis-Dryadetum integrifoliae pedicularetosum occurs on stabilized nonsorted circles with greater plant covers.

Table 7. Community table of the *Junco biglumis-Dryadetum integrifoliae* ass. nov. Nomenclatureal type relevé numbers marked in bold.

	typicum																						pedicularetosum																			
Relevé No.	**106**	6	71	9	31	33	69	10	45	63	72	104	70	44	43	117	3	36	118	2	4	1	7	**32**	97	5	141	8	96	61	64	30	142	60	105	140	58	59	49	50	51	48
Altitude (m.a.s.l.)	20	132	280	132	123	130	275	130	20	290	280	20	280	20	20	125	128	130	125	128	128	128	133	128	128	133	128	133	128	280	280	123	127	280	20	128	281	280	20	20	20	20
Number of vascular taxa	14	19	11	16	13	14	18	22	16	13	20	16	17	10	11	14	17	13	12	14	19	14	24	28	21	26	23	22	18	25	24	21	20	24	19	19	18	19	13	16	12	10
Number of nonvascular taxa	21	23	19	25	20	15	32	18	19	27	18	16	18	24	22	18	18	18	14	12	11	17	25	23	25	25	20	23	24	28	16	17	18	24	18	18	20	12	16	19	20	17
Total number of taxa	35	42	30	41	33	29	50	40	35	40	38	32	35	34	33	32	35	31	26	26	30	31	49	51	46	51	43	45	42	53	40	38	38	48	37	37	38	31	29	35	32	27
Ch/regional D: Association																																										
Cladonia pocillum	+	+	+	+	+	+	+	+	+	+	.	.	.	+	2	+	+	+	.	.	.	.	+	1	+	+	+	+	+	+	+	+	1	+	+	+	+	1	+	+	+	.
Lecanora epibryon	+	1	+	+	+	1	1	+	+	+	+	.	.	+	.	.	+	+	.	.	.	.	1	1	+	+	+	+	+	1	+	1	2	1	+	+	+	+	+	+	+	.
Carex capillaris	+	+	1	+	+	1	+	1	.	.	+	+	+	.	.	+	1	+	+	+	+	1	+	+	+	+	+	1	+	+	.	+	+	+	.	+	+	+	.	.	.	.
Juncus biglumis	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1	+	+	+	.	.	.	.	.	.	+	.	.	.	+	.	.	.	+	+	+	.
Solorina bispora	+	+	+	+	+	.	.	.	+	+	+	+	+	+	+	+	+	+	+	+	.	.	+	r	+	+	.	+	.	.	+	r	.	.	+	.	+	+	+	+	.	.
Polyblastia sendtneri	3	2	1	2	2	2	2	2	3	2	1	3	2	.	4	1	.	3	1	2	.	1	2	1	1	1	.	+	.	.	.	+	.	.	+	.	.	.	.	1	+	.
Aneura pinguis	+	+	+	+	+	+	+	+	+	+	+	+	+	+	.	+	+	+	+	r	+	.	+	+	+	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
d: wet plots																																										
Eriophorum angustifolium ssp. subarcticum	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	1	+	+	1	+	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Juncus triglumis	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	1	+	.	+	+	1	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
D: pedicularetosum																																										
Tomentypnum nitens	.	.	+	+	.	.	+	.	+	+	+	.	.	.	+	.	+	.	.	.	+	.	1	+	1	+	2	+	1	2	1	+	2	2	1	1	+	+	.	+	+	r
Pedicularis kanei	.	.	.	r	+	r	.	+	.	.	+	.	.	.	.	.	.	.	.	.	+	.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	.	.	.
Senecio atropurpureus	.	.	+	.	.	.	.	.	+	+	.	.	.	.	+	.	+	+	.	+	.	.	+	+	+	+	+	.	+	1	+	.	+	1	1	.	1	1	+	+	+	.
Dactylina arctica	.	.	.	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	+	+	+	+	.	+	+	+	.	+	+	.	+	.	.	.	+	+	+	+
Minuartia arctica	.	+	.	.	.	.	.	+	.	.	r	.	.	.	.	.	.	.	.	.	.	.	1	1	+	1	+	+	1	.	+	1	.	.	1	+	.	.	1	+	.	.
Arctostaphylos rubra	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	+	.	.	r	.	+	+	+	+	1	r	1	+	+	.	+	+	.	+	.	.	.	.	.	.
Blepharostoma trichophyllum	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	+	+	+	+	.	.	+	+	.	.	.	.	.	.	+	+
Pedicularis capitata	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	+	+	.	+	+	+	.	.	+	+	.	+	+	.	.	.
Carex scirpoidea	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	+	+	1	+	+	+	.	+	.	.	.	.	.	+
Vulpicida tilesii	.	.	.	.	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	1	1	+	+	2	.	.	1	.	.	.	+	.	.	.	.	.	.
Papaver macounii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	+	+	.	.	+	+	.	+	.	.	.	.	.
Parrya nudicaulis	.	.	r	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	+	.	+	+	.	+	.	.	.	+	.	.	+	.	+	.	.	.	.
Cassiope tetragona	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	.	+	+	1	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Rhododendron lapponicum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	+	.	1	.	.	+	1	.	.	.	.	.	.	.	.	.	.
Pertusaria panyrga	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	2	.	2	.	1	.	.	.	+	.	.	.	+	.	.	.	.	.
Dactylina ramulosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	+	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.
Rhytidium rugosum	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	1	+	.	.	1	.	.	+	.	.	.	.	.
Lupinus arcticus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	+	.	.	+	1	.	.	.	.
Ch: Class, order and alliance																																										
Dryas integrifolia	1	1	+	1	+	+	+	1	+	+	+	1	+	+	+	+	.	1	+	1	+	+	**4**	**3**	**2**	**4**	**3**	**4**	**2**	**3**	**3**	**2**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**2**	**2**	**3**
Saxifraga oppositifolia	1	1	+	1	+	2	+	1	+	.	.	2	+	+	1	2	2	2	2	1	1	1	+	1	1	1	+	+	1	.	+	+	1	+	1	1	.	.	1	1	+	1
Hypnum bambergeri	+	+	+	+	+	.	1	+	.	+	1	.	.	+	+	+	+	.	.	+	+	+	1	1	+	+	1	1	2	.	2	1	2	1	1	1	2	.	.	+	+	+
Tofieldia pusilla	.	+	.	+	+	+	+	+	.	+	.	.	+	.	.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	.	+	+	+	.	.	.	.
Others																																										
Ditrichum flexicaule	+	+	+	+	+	+	2	+	+	+	1	1	1	+	+	+	+	+	+	+	+	.	**1**	**2**	+	+	**2**	+	**1**	**2**	**2**	+	**1**	**1**	**2**	+	**1**	**2**	**1**	**2**	+	**2**
Thamnolia subuliformis	+	+	+	+	+	+	+	+	+	+	+	+	1	+	1	+	+	r	.	r	.	+	**2**	**1**	**1**	**1**	**2**	**2**	**2**	**2**	**2**	**1**	**1**	**1**	**2**	**2**	**1**	**1**	**1**	+	+	+
Eriophorum angustifolium ssp. triste	+	+	+	+	+	+	+	+	+	+	+	1	1	+	+	.	1	+	.	+	.	+	**1**	**1**	**2**	**1**	**2**	**2**	**3**	+	+	+	**2**	**1**	**2**	**2**	+	+	**1**	**1**	**2**	**2**
Polygonum viviparum	+	+	+	+	+	+	+	+	+	.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	.	+	+	.
Distichium capillaceum	+	+	+	+	+	+	+	+	.	+	+	+	.	+	+	+	+	+	+	+	+	+	.	1	.	+	+	1	.	1	1	1	+	1	+	.	2	2	+	+	+	2
Carex membranacea	+	+	.	+	.	+	.	+	+	+	+	+	.	+	+	.	+	+	+	.	.	.	+	+	+	+	1	+	1	2	+	+	+	1	+	2	1	2	+	.	.	1
Cetraria islandica	+	+	.	+	+	.	+	.	+	+	.	.	+	+	+	.	.	+	.	.	.	.	+	+	+	.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

Cardamine hyperborea	+	.	+	.	.	.	+	r	+	+	.	+	+	+	+	.	+	.	.	+	.	.	.	+	+	+	+	+	+	+	+	.	+	+	+	+	+	+	+	+	+	.
Flavocetraria cucullata	.	+	.	+	+	+	+	.	.	+	+	.	+	.	.	+	+	r	.	.	.	.	2	+	1	1	1	2	2	1	1	+	1	2	.	1	1	+	.	.	.	.
Equisetum variegatum	+	+	.	.	.	+	+	+	+	.	+	+	.	.	+	+	.	+	+	+	+	.	+	.	+	+	+	.	.	+	.	.	+	+	+	.	.	.	.	+	+	+
Salix reticulata	+	+	.	.	.	.	.	r	+	.	.	+	.	.	.	.	r	.	.	.	r	.	+	+	.	+	.	+	+	1	.	+	.	+	+	+	2	+	.	+	+	+
Arctagrostis latifolia	+	.	.	.	.	.	.	.	+	.	+	.	+	+	+	.	.	.	.	r	.	.	.	.	+	+	+	.	+	+	.	.	+	+	+	+	+	+	+	+	+	+
Campylium stellatum	.	+	+	+	.	.	.	+	+	+	.	+	.	+	.	.	+	.	.	.	+	+	+	.	.	+	.	+	.	.	.	.	+	.	.	+	.	.	+	+	+	+
Chrysanthemum integrifolium	+	+	.	+	.	.	.	+	+	.	.	.	.	+	.	.	1	.	.	.	+	.	.	+	+	+	+	.	1	.	.	.	r	.	+	+	.	.	+	+	+	.
Bryum wrightii	+	+	+	+	+	.	.	+	1	+	+	+	.	+	.	+	.	+	+	+	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Bryum sp.	+	.	+	.	+	.	+	+	+	+	.	.	+	+	+	+	.	.	.	+	.	+	.	+	.	+	.	.	.	.	.	.	.	.	.	.	+	+	.	.	+	.
Flavocetraria nivalis	.	+	.	+	+	.	+	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	1	+	1	+	+	+	+	.	.	+	+	.	.	1	+	.	.	+	.	.
Equisetum arvense	.	1	.	+	.	.	1	.	.	+	+	.	+	.	.	.	+	.	.	+	.	+	1	.	2	.	2	.	.	1	1	.	1	1	.	.	+	+	.	.	.	.
Nostoc commune	1	.	+	.	.	.	+	.	+	+	+	.	+	+	.	+	1	1	.	.	+	+	+	+	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Eriophorum vaginatum	1	.	.	.	.	.	+	.	+	.	+	.	+	.	.	+	.	+	+	.	1	+	.	.	.	.	.	.	.	+	.	.	.	.	1	+	.	1	.	+	2	1
Salix arctica	+	.	.	.	.	.	.	.	+	.	.	+	.	+	.	.	+	.	.	.	+	+	.	.	r	+	+	+	.	.	.	1	.	+	+	.	.	.	+	+	.	+
Astragalus umbellatus	.	+	1	+	1	1	+	+	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	1	.	.	.	+	.	+	+	+	.	1	.	.	1	+	.	.	.	.
Senecio resedifolius	.	+	.	+	.	+	+	+	.	+	+	+	+	.	.	.	.	.	.	.	+	+	+	+	.	+	.	+	.	.	+	+	.	.	.	.	.	.	.	.	.	.
Encalypta sp.	1	+	.	.	+	.	+	+	.	.	+	.	+	+	+	+	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.	.	+	.	.	+	1	.	+
Distichium inclinatum	+	.	+	.	.	.	+	.	+	+	.	+	+	.	+	.	.	.	.	+	.	+	.	.	1	.	.	.	+	+	1	.	.	.	.	1	.	.	.	.	.	+
Antennaria friesiana	.	+	.	+	+	+	.	+	.	+	+	.	+	.	.	.	.	.	.	.	+	.	+	+	.	+	.	+	.	.	+	+	.	.	.	.	.	+	.	.	.	.
Orthothecium chryseum	+	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	+	+	.	.	+	.	.	+	.	+	.	+	.	.	.	.	+	.	+	.	.	.	+	+	+	+
Catoscopium nigritum	+	.	.	.	.	.	.	.	+	+	.	+	.	.	+	.	.	+	.	.	.	+	+	.	.	+	.	.	+	.	.	.	+	.	+	.	.	.	+	.	+	+
Ochrolechia frigida	+	.	.	.	+	+	+	.	1	.	.	.	.	1	1	.	1	1	.	.	.	.	+	2	.	.	.	.	.	.	.	.	.	+	.	.	+	.	+	.	.	.
Carex rupestris	.	+	.	+	+	+	.	1	.	.	.	.	.	.	+	.	.	.	.	.	.	.	+	1	+	1	+	1	.	.	.	1	+	.	.	.	.	.	.	.	.	.
Encalypta alpina	.	+	.	+	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	+	.	+	.	.	.	+	.	+	.	.	+	.	.	+	+	.	.	.	.	+	+	.
Rinodina roscida	.	+	.	.	.	+	+	.	.	.	.	.	1	.	+	+	+	.	+	.	.	.	+	.	.	+	.	.	+	.	.	+	.	.	.	.	.	.	.	.	+	.
Orthothecium strictum	.	.	.	+	+	+	+	.	.	.	+	.	+	.	.	+	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.	+	+	+	+	.	.	.	.
Minuartia rossii	.	+	.	+	.	.	.	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	+	1	+	+	.	.	.	+	.	.	1	.	.	.	.	.	.	+	.	.
Lophozia collaris	.	.	.	.	.	.	+	+	.	+	+	.	+	.	.	+	.	.	+	.	.	.	.	.	.	.	.	+	+	+	.	.	.	+	.	.	.	.	.	.	.	.
Meesia uliginosa	.	.	.	.	.	.	+	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	+	.	.	+	.	+	+	+	.	.	.	.	.
Hymenostylium recurvirostre	+	.	+	+	.	.	+	.	+	+	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Cirriphyllum cirrosum	.	.	.	.	.	.	+	.	.	.	+	.	+	.	.	.	.	.	.	.	.	+	.	.	+	.	+	.	+	+	.	.	.	+	.	.	.	.	.	.	.	.
Lloydia serotina	.	.	.	.	.	.	+	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	+	.	.	+	.	.	.	.	.
Bryum pseudotriquetrum	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	+	.	.	.
Mycobilimbia lobulata	.	+	.	.	.	+	+	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pohlia sp.	.	.	+	.	.	.	.	.	.	.	+	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Pohlia beringiensis	.	.	.	+	.	.	+	.	+	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Encalypta longicolla	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	+	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dicranum sp.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Silene acaulis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	+	1	+	.	1	.	.	.	.	.	.	.	.	.	.	.
Lophozia badensis	.	+	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cephalozia bicuspidata	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Drepanocladus sp.	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.
Hylocomium splendens	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	+	.	.	.	.	.
Saussurea angustifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	+	.	.	+	.	.	.	.	.

Additional taxa with three or less occurrences: Thalictrum alpinum (rel. 31: +, 5: +, 30: +), Rinodina turfacea (31: +, 61: +, 60: +), Masonhalea richardsonii (69: +, 63: +, 64: +), Carex sp. (69: +, 72: +, 70: 1), Caloplaca tiroliensis (69: +, 118: +, 61: +), Calliergon sp. (10: +, 36: +, 60: +), Peltigera sp. (10: r, 5: 1, 60: 1), Timmia austriaca (63: +, 43: +, 48: +), Rumex arcticus (63: 1, 32: +, 140: 2), Carex misandra (104: +, 117: 1, 105: +), Juncus castaneus (117: +, 3: +, 1: +), Cladonia pyxidata (96: +, 61: +, 60: 1), Cinclidium arcticum (105: +, 50: +, 51: +), Campylium polygamum (106: +, 105: +), Pedicularis langsdorfii (71: +, 32: r), Stereocaulon alpinum (9: +, 49: +), Epilobium sp. (69: +, 72: +), Ochrolechia upsaliensis (69: +, 60: +), Orthilia secunda (69: +, 60: +), Solorina saccata (69: +, 140: +), Melandrium apetalum (45: +, 50: +), Stellaria sp. (63: +, 72: r), Salix lanata ssp. richardsonii (104: r, 4: +), Pseudocalliergon turgescens (104: +, 4: +), Fissidens bryoides (70: +, 44: +), Tortula ruralis (70: +, 118: +), Tetraplodon mnioides (44: +, 43: +), Polyblastia gelatinosa (44: 1, 49: 3), Braya bartlettiana (117: 1, 118: +), Collema sp. (117: +, 118: +), Jungermannia polaris (118: +, 96: +), Tortella fragilis (1: +, 48: 1), Peltigera rufescens (7: +, 30: +), Cladonia macroceras (8: +, 96: +), Ctenidium procerrimum (96: +, 140: +), Ochrolechia inaequatula (61: +, 60: +), Peltigera didactyla (61: +, 58: +), Aulacomnium acuminatum (61: 1, 58: +), Oxytropis sp. (61: +, 59: +), Kobresia myosuroides (30: +, 142: r), Oxytropis maydelliana (60: +, 58: +), Caloplaca cerina (6: +), Cetraria aculeata (6: +), Encalypta rhaptocarpa (71: +), Lophozia sp. (71: +), Hypnum sp. (9: +), Polytrichum sp. (31: +), Didymodon rigidulus var. icmadophilus (33: +), Leptobryum pyriforme (10: +), Campylium longicuspis (10: +), Androsace chamaejasme (10: +), Braya glabella ssp. purpurascens (10: +), Polygonum bistorta var. plumosum (63: +), Didymodon sp. (63: +), Drepanocladus brevifolius (104: +), Aloina brevirostris (44: +), Bryoerythrophyllum recurvirostre (44: +), Cephaloziella arctica (117: +), Tortella tortuosa (36: +), Solorina sp. (118: +), Carex atrofusca (4: 1), Aulacomnium turgidum (1: +), Dicranum fragilifolium (1: +), Didymodon spadiceus (1: +), Myurella julacea (1: +), Vaccinium uliginosum (32: r), Hypogymnia subobscura (97: +), Cyrtomnium hymenophylloides (97: +), Ochrolechia androgyna (5: 1), Orthothecium varia (141: +), Aulacomnium palustre (141: +), Cladonia amaurocraea (8: r), Cladonia gracilis (96: +), Cladonia squamosa (61: +), Peltigera aphthosa (61: +), Pertusaria bryontha (61: +), Lagotis glauca (61: +), Bartramia ithyphylla (64: +), Alectoria nigricans (64: +), Dicranum acutifolium (60: +), Peltigera leucophlebia (60: +), Sanionia uncinata (59: 2), Stereocaulon sp. (50: +), Megaspora verrucosa (51: +).

Fig. 10. Junco biglumis-Dryadetum integrifoliae typicum subass. nov. on barren, moist nonacidic nonsorted circles. Subzone D, Franklin Bluffs, Alaska.

Junco biglumis-Dryadetum integrifoliae typicum subass. nov. (Fig. 10; Table 7, nomenclatural type relevé no. 106)

The Junco biglumis-Dryadetum integrifoliae typicum occurs on barren nonsorted circles within moist nonacidic tundra. The association colonizes nonsorted circles that show great cryoturbation activity. Up to 50 % of the soil surface is barren, and the soil commonly exhibits a "cottage cheese" structure as a result of diurnal needle-ice formation during the early summer. The association establishes itself mainly in small desiccation cracks of the nonsorted circles, where site conditions are more favorable, and expands further from there. We found this subassociation under a variety of topographic positions and soil moisture conditions. The Junco biglumis-Dryadetum integrifoliae typicum is equivalent to the Type B3 Dry *Saxifraga oppositifolia*, *Juncus biglumis* forb barrens (Walker 1985) occurring on frost scars in the Prudhoe Bay vicinity, Alaska. Walker (1985) mentions *Dryas integrifolia*, *Juncus biglumis*, *Minuartia arctica*, *Saxifraga oppositifolia*, *Bryum wrightii* and *Lecanora epibryon* as distinct taxa occurring on the dry, barren features.

The subassociation is dominated by the black crustose lichen *Polyblastia sendtneri*. At our study plots, this species is restricted to plant communities affected by soil-surface disturbance, such as the frost-heave community *Braya purpurascens-Puccinellia angustata* and the Junco biglumis-Drya-

Fig. 11. Junco biglumis-Dryadetum integrifoliae pedicularetosum subass. nov. on well-vegetated, moist nonacidic nonsorted circles. Subzone D, Franklin Bluffs, Alaska.

detum integrifoliae. In addition, *Eriophorum angustifolium* ssp. *subarcticum* and *Juncus triglumis* occur in areas with high soil moisture.

Junco biglumis-Dryadetum integrifoliae pedicularetosum subass. nov. (Fig. 11; Table 7, nomenclatural type relevé no. 32)

The Junco biglumis-Dryadetum integrifoliae pedicularetosum is associated with stabilized nonsorted circles in the moist nonacidic tundra. The nonsorted circles are well vegetated and may exhibit just a small central area of active soil churning. This subassociation represents a mid- to late-successional stage on the nonsorted circles: It invades the edges of active nonsorted circles that support the Junco biglumis-Dryadetum integrifoliae typicum in the center parts (see above), and it is dominant on less active nonsorted circles, reducing cryoturbation activity through insulation and shading. It is more or less equivalent to the Type B2 Dry *Dryas integrifolia-Saxifraga oppositifolia-Lecanora epibryon* dwarf shrub, crustose lichen tundra described from Prudhoe Bay (Walker 1985), which occurs on frost-disturbed sites. The subassociation is also very similar to the *Ochrolechia frigida-Dryas integrifolia* community type of the dry sites on Barter Island, Alaska described by Elias et al. (1996). This community type is dominated by *Dryas integrifolia* and a suite of fruticose lichens and occurs on base-rich mineral soils that are cryoturbated.

This subassociation is richer in vascular plant taxa than the Junco biglumis-Dryadetum integrifoliae typicum. Differential taxa against it include *Arctostaphylos rubra*, *Minuartia arctica*, *Pedicularis kanei*, *Senecio atropurpureus*, *Dactylina arctica* and *Tomentypnum nitens*. Most of these species are also common to the surrounding Dryado integrifoliae-Caricetum bigelowii of the moist nonacidic tundra of subzone D (see below), confirming that this subassociation represents a successional stage between the barren nonsorted circles associated with the Junco biglumis-Dryadetum integrifoliae typicum and the Dryado integrifoliae-Caricetum bigelowii of the stable tundra. This subassociation also differs morphologically from the typicum, with *Dryas integrifolia*, *Eriophorum angustifolium* ssp. *triste*, *Ditrichum flexicaule*, *Flavocetraria cucullata*, *Hypnum bambergeri* and *Thamnolia subuliformis* having distinctly greater cover abundance scores.

Dryado integrifoliae-Caricetum bigelowii Walker et al. 1994 (Fig. 12; Table 8; App. 1, ref. 5)

Walker et al. (1994) described this association as the "non-acidic counterpart to the Sphagno-Eriophoretum vaginati, occurring on circumneutral mesic uplands and hillslopes, and limited to younger landscapes". They placed the association within the mire and fen class Scheuchzerio-Caricetea nigrae, which includes basiphytic, moss-rich communities on

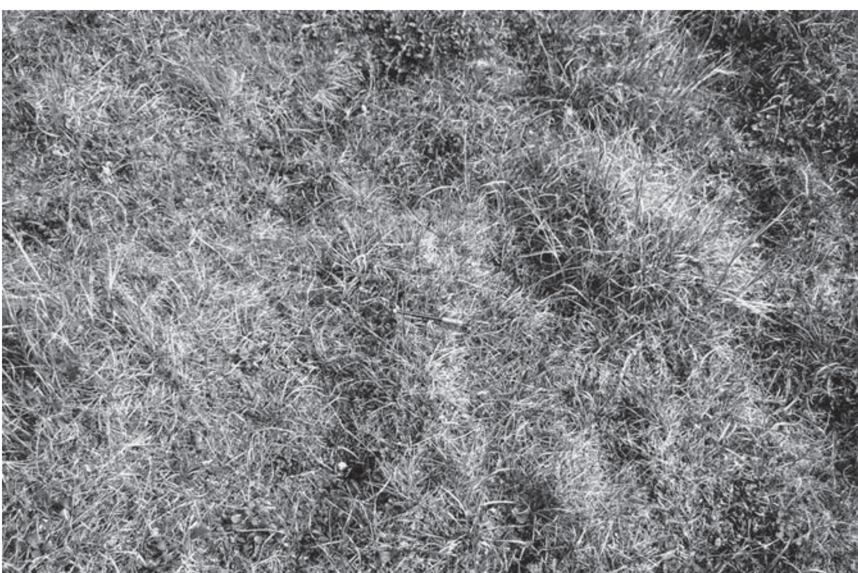

Fig. 12. Dryado integrifoliae-Caricetum bigelowii Walker et al. 1994 of the moist nonacidic tundra. Subzone D, Franklin Bluffs, Alaska.

poorly drained soils. However, we feel this association should rather be placed within the alliance Dryadion integrifoliae Ohba ex Daniëls 1982, class Carici rupestris-Kobresietea bellardii Ohba 1974, which includes dwarf shrub and grass heath communities. The Dryado integrifoliae-Caricetum bigelowii includes the Type U3 Moist *Eriophorum triste-Dryas integrifolia* sedge, dwarf-shrub tundra described from the Prudhoe Bay area by Walker (1985). They found the community type on mesic upland sites, tops of poorly developed high-centered polygons and strangs in wetter areas. They described the community type as rich in sedges (*Carex aquatilis*, *C. bigelowii*, *C. membranacea*, *Eriophorum angustifolium* ssp. *triste*) and dwarf-shrubs (*Dryas integrifolia*, *Salix arctica*, *S. reticulata*). The *Dryas integrifolia-Carex aquatilis* community type mentioned by Elias et al. (1996) is very similar in species composition and represents the most common vegetation on moist sites on Barter Island, Alaska. On the dry, exposed slopes of the Brooks Range, Alaska, the Caricetum scirpoideo-rupestris (Cooper 1986) has a similar species composition, with *Dryas octopetala* ssp. *octopetala* replacing *Dryas integrifolia*. Cooper (1986) mentions the similarity of this *Dryas*-stand type to vegetation described from Montana and eastern Canada. In addition, the *Dryas octopetala* communities described from Spitsbergen (Rønning 1965, Hartmann 1980) represent close allies. When occurring on moist to wet soils, the Dryado integrifoliae-Caricetum bigelowii is also closely allied with the *Eriophorum angustifolium-Rhododendron lapponicum* community, a fen vegetation on wet soils described from Greenland by Lünterbusch & Daniëls (2004). Another close ally is the Carici arctisibiricae-Hylocomietum alaskani described by Matveyeva (1994) from the Taimyr Peninsula in Russia, where *Dryas punctata* replaces *Dryas integrifolia*. It seems that most *Dryas*-dominated vegetation stands occur on moist to dry, circumneutral substrates under continental climatic regimes (but see Lünterbusch & Daniëls (2004) for *Dryas* communities on moist to wet soil). We found this association widely distributed on stable soils on mid slopes and hilltops in the moist nonacidic tundra of subzone D. These areas receive loess depositions from the Sagavanirktok River and favor the development of minerotrophic plant communities (Walker & Everett 1991). Nonsorted circles associated with either the Junco biglumis-Dryadetum integrifoliae or the Saxifrago oppositifoliae-Dryadetum integrifoliae represent common breaks in the association.

Similar to the Saxifrago oppositifoliae-Dryadetum integrifoliae, the soils are classified as Aquic Haploturbels on drier sites and Aquic Ochreturbels on moist sites (Michaelson et al. 2005). The organic horizons are well-developed (15 cm, Table 1) as a dark brown peaty muck. The mineral horizons often show signs of redox processes with mottled reddish dark brown and dark gray colors. Soil texture is loam, and soil moisture averages 45 %. Mean soil pH is 7.9. The soils have relatively shallow thaw depths and moderate snow depth when compared to the nonsorted circles that dot the area (means 65 cm and 40 cm, respectively).

Table 8. Community table of the Dryado integrifoliae-Caricetum bigelowii.

	Lunpinus arcticus var.					Carex scirpoidea var.										Eriophorum angustifolium ssp. subarcticum var.				
Relevé No.	29	67	55	68	65	12	34	13	11	35	46	18	19	47	20	38	41	39	40	42
Altitude (m.a.s.l.)	270	280	280	275	270	133	126	133	130	130	130	130	134	130	130	22	20	21	20	20
Number of vascular taxa	30	42	38	26	18	24	28	23	23	27	35	18	22	25	16	19	18	19	13	12
Number of nonvascular taxa	28	30	27	22	15	18	20	17	14	13	20	14	11	24	12	21	23	21	14	17
Total number of taxa	58	72	65	48	33	42	48	40	37	40	55	32	33	49	28	40	41	40	27	29
Ch/regional D: Association																				
Salix reticulata	1	2	2	2	1	1	1	+	+	+	1	+	1	2	+	2	2	1	1	2
Carex bigelowii	2	+	3	3	2	1	1	2	+	1	+	.	1	1	2	+	+	1	1	.
Arctostaphylos rubra	+	2	2	1	2	2	1	2	2	+	2	+	+	2	1	.	.	.	.	.
Papaver macounii	+	+	+	+	+	+	+	+	+	.	+	.	.	+	.	+	+	+	.	+
Saussurea angustifolia	+	+	+	+	+	1	+	+	+	1	+	+	.	.	.	.	.	.	.	.
D: Lupinus arcticus var.																				
Hylocomium splendens	3	3	4	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Aulacomnium turgidum	1	2	2	1	+	.	.	.	.	.	.	.	.	.	.	.	1	.	1	1
Rhytidium rugosum	1	+	2	1	2	+	+	+	.	1	.	.	.	.	.	.	.	.	.	.
Lupinus arcticus	+	1	1	+	+	.	1	r	.	1	.	.	.	.	.	.	.	.	.	.
Dicranum spadiceum	1	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Equisetum arvense	+	1	+	.	1	.	.	+	+	.	.	.	+	.	.	.	.	.	.	.
Saxifraga hieracifolia	+	+	r	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
Aulacomnium acuminatum	+	+	.	+	2	.	.	.	.	+	.	.	.	.	.	.	+	.	.	+
Ptilidium ciliare	+	.	1	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Masonhalea richardsonii	.	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Stellaria sp.	.	+	+	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix glauca	1	+	1	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
Cladonia pyxidata	+	+	+	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.
Tofieldia pusilla	+	+	+	.	.	.	+	.	.	.	+	.	.	+	.	.	.	.	.	.
Dicranum elongatum	+	+	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pyrola grandiflora	+	r	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Polygonum bistorta var. plumosum	+	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Silene acaulis	+	+	.	+	.	.	.	.	+	+	.	.	.	+	.	.	.	.	.	.
Saxifraga nelsoniana	r	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lagotis glauca	r	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Orthilia secunda	.	+	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Peltigera aphthosa	.	+	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Cladonia gracilis	.	+	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Stellaria longipes	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Peltigera sp.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pyrola asarifolia	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Empetrum nigrum ssp. hermaphroditum	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ledum palustre ssp. decumbens	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Peltigera leucophlebia	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Anastrophyllum minutum	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Senecio resedifolius	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
D: Carex scirpoidea var.																				
Carex scirpoidea	.	.	.	.	.	+	+	.	+	+	+	+	1	.	+	.	.	.	.	.
Cladonia pocillum	.	.	+	.	.	+	+	1	+	.	1	.	.	+	.	.	.	.	.	.
Bryum pseudotriquetrum	.	.	.	.	.	+	+	+	+	.	.	+	+	.	.	.	.	+	.	.
Kobresia myosuroides	.	.	.	.	.	1	1	.	+	1	.	.	.	.	.	.	.	.	.	.
Draba alpina	.	.	.	.	.	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.
Ctenidium molluscum	.	.	.	.	.	+	.	+	.	.	.	+	.	.	.	.	.	.	.	.
Carex rupestris	.	.	.	.	.	.	+	+	.	+	.	.	.	.	.	.	.	.	.	.

D: Eriophorum angustifolium ssp. subarcticum var.																				
Eriophorum angustifolium ssp. subarcticum	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	3	4	3	2	4
Drepanocladus brevifolius	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	2	+	2
Orthothecium chryseum	.	+	.	.	.	.	.	.	.	.	1	+	.	+	.	1	1	+	1	1
Campylium stellatum	.	+	.	.	.	+	.	.	.	.	.	.	.	.	+	+	2	+	+	2
Catoscopium nigritum	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	2	+	+	1	+
Calliergon giganteum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	+	+	+
Cinclidium arcticum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	.
Limprichtia revolvens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	.
Cirriphyllum cirrosum	.	.	.	.	.	+	.	.	.	.	+	+	.	.	.	+	+	+	.	+
Pseudocalliergon turgescens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	+	+
Pedicularis sudetica ssp. albolabiata	.	+	.	.	.	.	.	.	.	.	+	.	.	+	.	+	.	+	+	.
Drepanocladus sp.	.	+	.	.	.	.	.	.	+	.	.	+	.	.	.	.	+	+	.	+
Saxifraga oppositifolia	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	+	+	.	r
Callialaria curvicaulis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	2	.
Ch: Class, order and alliance																				
Dryas integrifolia	2	2	2	2	2	3	3	2	2	3	2	3	2	3	3	2	2	2	2	2
Hypnum bambergeri	+	.	+	2	.	2	1	2	2	1	+	.	1	+	1	+	+	.	+	+
Pedicularis capitata	+	+	+	+	+	+	+	+	+	+	+	.	+	+	+	.	.	.	.	.
Pedicularis kanei	+	+	+	.	+	.	+	+	+	+	+	+	+	+	.	+	.	.	.	.
Others																				
Tomentypnum nitens	3	3	3	2	2	3	3	3	3	2	2	3	2	3	3	2	2	2	1	3
Eriophorum angustifolium ssp. triste	+	1	2	+	+	1	+	1	1	+	2	2	1	2	2	+	+	.	+	+
Senecio atropurpureus	+	+	+	+	+	+	+	+	+	.	+	+	+	+	+	+	+	+	+	+
Polygonum viviparum	+	+	+	+	.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Thamnolia subuliformis	+	1	1	+	+	1	1	1	1	1	+	+	+	+	+	+	+	+	.	.
Carex membranacea	.	1	+	+	.	+	+	1	1	1	2	1	2	1	2	+	+	1	2	+
Ditrichum flexicaule	.	1	1	+	.	1	1	1	1	2	1	1	1	1	1	1	1	1	+	1
Flavocetraria cucullata	+	1	1	1	+	+	+	1	1	1	1	+	+	+	+	.	.	+	.	.
Cetraria islandica	+	+	+	+	+	+	+	1	+	+	+	+	+	+	+	.	.	+	.	.
Cardamine hyperborea	+	+	+	+	.	+	.	+	+	+	+	+	+	+	+	+	+	+	.	.
Salix arctica	.	.	+	.	.	1	1	1	1	2	2	1	2	2	2	2	1	2	1	1
Equisetum variegatum	.	1	.	.	.	r	+	+	+	+	+	.	+	+	+	+	+	1	+	+
Dactylina arctica	+	+	+	.	.	+	+	+	+	+	+	.	+	+	.	+	+	+	.	.
Distichium capillaceum	.	1	1	.	.	+	+	+	1	+	+	+	.	.	.	1	+	1	+	1
Cassiope tetragona	1	+	1	+	.	1	1	1	1	1	1	1	1	+	.	.	.	.	.	.
Eriophorum vaginatum	1	+	2	1	.	.	.	.	.	.	1	2	3	1	1	+	+	1	+	.
Flavocetraria nivalis	+	+	+	.	.	+	+	+	+	1	+	+	+	+	.	.	.	.	.	.
Salix lanata ssp. richardsonii	.	+	.	.	.	+	.	+	.	.	2	.	+	1	+	1	+	1	1	+
Arctagrostis latifolia	+	+	+	+	.	+	+	.	.	.	.	r	+	.	.	+	+	+	.	.
Parrya nudicaulis	+	+	+	.	.	+	+	+	+	+	+	.	+	.	.	.	.	.	.	.
Minuartia arctica	.	+	+	+	+	+	+	+	+	1	+	.	.	.	.	.	.	.	.	.
Astragalus umbellatus	.	1	+	.	+	1	1	+	1	+	.	.	.	.	.	.	.	.	.	.
Bryum sp.	.	.	.	.	.	.	.	+	.	+	+	.	+	+	.	.	.	+	.	+
Carex vaginata	.	.	.	.	.	.	.	.	.	.	+	+	+	+	+	.	.	+	r	.
Vaccinium uliginosum	.	r	+	r	.	.	+	.	.	+	+	.	.	.	.	.	.	.	.	.
Oxytropis maydelliana	.	+	+	.	+	.	+	.	.	1	r	.	.	.	.	.	.	.	.	.
Distichium inclinatum	.	+	+	.	.	.	.	.	.	.	1	.	.	1	.	+	.	.	.	.
Pedicularis langsdorfii	.	.	.	+	.	.	.	.	.	.	+	r	+	+	.	.	.	.	.	.
Solorina bispora	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	+	+	.	.	.
Orthothecium strictum	.	.	+	.	.	.	.	.	.	.	+	.	.	+	.	.	+	.	.	.
Pertusaria panyrga	+	.	r	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Cladonia amaurocraea	+	.	.	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Rumex arcticus	.	+	+	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.
Papaver sp.	.	r	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.
Carex capillaris	.	.	+	.	.	.	.	.	.	.	.	r	.	.	.	.	+	.	.	.
Carex rariflora	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	r	.	.	r
Encalypta alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	+

Additional taxa with two or less occurrences: Cetraria laevigata (rel. 29: +, 19: +), Barbilophozia barbata (29: +, 20: +), Solorina sp. (67: +, 34: +), Oxytropis sp. (67: +, 46: +), Pohlia beringiensis (67: +, 47: +), Didymodon rigidulus var. icmadophilus (67: +, 38: +), Peltigera rufescens (68: +, 12: +), Peltigera scabrosa (68: +, 13: +), Stereocaulon alpinu (34: +, 13: 1), Campylium longicuspis (34: +, 35: +), Rhododendron lapponicum (34: +, 35: +), Ctenidium procerriumum (34: +, 38: +), Chrysanthemum integrifolium (35: r, 4 r), Didymodon rigidulus (46: +, 47: +), Splachnum sp. (46: +, 47: +), Tetraplodon urceolatus (46: +, 47: +), Dicranum fragilifolium (18: +, 20: +), Scorpidium scorpioides (18: - 38: +), Tortella tortuosa (47: +, 41: +), Carex atrofusca (47: +, 39: +), C. misandra (47: +, 39: +), Meesia uliginosa (47: +, 39: +), Aulacomnium palustre (29: +), Dicranum sp. (+), Pleurozium schreberi (29: +), Tritomaria quinquedentata (29: +), Nephroma expallidum (29: r), Ochrolechia androgyna (29: r), Antennaria friesiana (67: +), Bartramia ithyphylla (67: +), Carex aquatilis (67: +), Cyrtomnium hymenophylloides (67: +), Encalypta sp. (67: +), Mycobilimbia lobulata (55: +), Vaccinium vitis-idaea (55: +), Ochrolechia frigida (55: r), O. upsaliensis (55: r), Pertusaria bryontha (55: r), Poa arctica (55: r), Rinodina turfacea (55: r), Blepharostoma trichophyllum (68: +), Cladonia coccifera (68: +), Dicranum acutifolium (68: +), Cladonia fimbriata (65: +), Peltigera malacea (65: +), Thalictrum alpinum (12: +), Abietinella abietina (34: +), Vulpicida tilesii (34: +), Lophozia sp. (13: +), Stereocaulon sp. (11: 1), Hypnum sp. (11: +), Encalypta longicolla (46: +), Caloplaca tiroliensis (47: +), Leptobryum pyriforme (47: +), Tortella fragilis (20: +), Carex rotundata (38: +), Brachythecium sp. (41: +), Carex sp. (41: +), Myurella julacea (41: +), Bryoerythrophyllum recurvirostre (39: +), Pohlia sp. (42: +).

Species richness is high in this association, averaging 43 species. *Arctostaphylos rubra*, *Carex bigelowii*, *Papaver macounii*, *Salix reticulata* and *Saussurea angustifolia* are faithful. The association is dominated by *Arctostaphylos rubra*, *Carex bigelowii*, *C. membranaceae*, *Dryas integrifolia*, *Eriophorum angustifolium* ssp. *triste*, *Salix arctica* and *S. reticulata*, *Ditrichum flexicaule*, *Hypnum bambergeri* and *Tomentypnum nitens*. Other constant taxa include *Cardamine hyperborea*, *Polygonum viviparum*, *Senecio atropurpureus*, *Cetraria islandica*, *Flavocetraria cucullata* and *Thamnolia subuliformis*.

The association is differentiated into three variants along the climate gradient, with mean species richness increasing from 35 to 55 species from north to south. Towards the north of subzone D at Deadhorse, the *Eriophorum angustifolium* ssp. *subarcticum* variant is found in wetter environments on level ground. Differential vascular taxa are *Eriophorum angustifolium* ssp. *subarcticum*, *Pedicularis sudetica* ssp. *albolabiata* and *Saxifraga oppositifolia*. The moss cover shows great species variety and includes numerous hygrophytic species, with *Campylium stellatum*, *Catoscopium nigritum*, *Drepanocladus brevifolius* and *Orthothecium chryseum* being differential. The *Carex scirpoidea* variant occurs in the Franklin Bluffs area on moist soils. Differential taxa include *Carex scirpoidea*, *Bryum pseudotriquetrum* and *Cladonia pocillum*. The *Lupinus arcticus* variant is found towards the warmer, southern end of subzone D on relatively well-drained slopes in the Sagwon Hills. This variant is especially rich in vascular taxa. Differential taxa include *Equisetum arvense*,

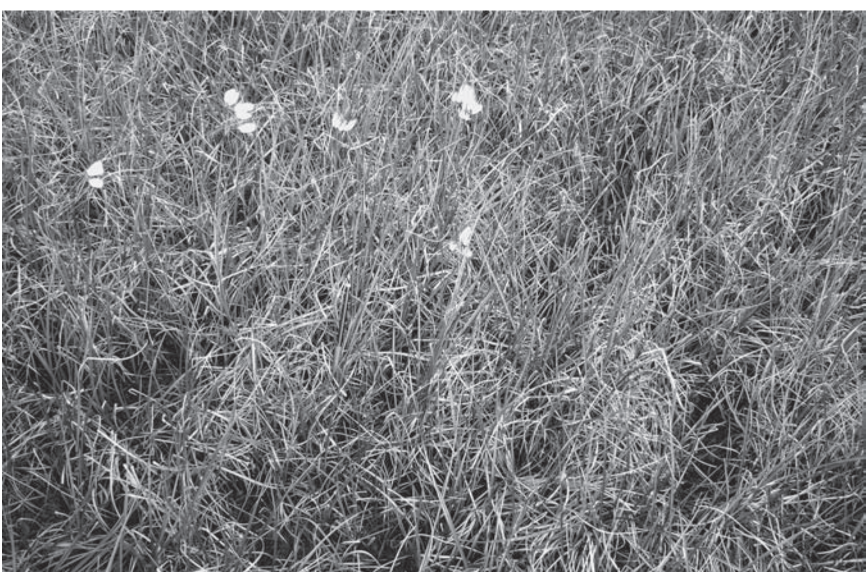

Fig. 13. *Scorpidium scorpioides*-*Carex aquatilis* community of the wet nonacidic tundra. Subzone D, Franklin Bluffs, Alaska.

Table 9. Community table of the *Scorpidium scorpioides-Carex aquatilis* community.

Relevé No.	15	14	16	17	37
Altitude (m.a.s.l.)	128	128	128	128	130
Number of vascular taxa	10	11	9	11	8
Number of nonvascular taxa	7	7	1	1	9
Total number of taxa	17	18	10	12	17
Ch/regional D: Community					
Pedicularis sudetica ssp. albolabiata	1	+	1	1	+
Carex saxatilis	+	+	+	+	.
Ch: Class, order and alliance					
Eriophorum angustifolium ssp. subarcticum	4	4	4	4	3
Scorpidium scorpioides	1	1	1	1	1
Equisetum variegatum	+	+	+	+	+
Carex aquatilis	+	+	+	.	1
Carex atrofusca	+	+	.	+	.
Campylium stellatum	+	+	.	.	+
Others					
Salix arctica	+	r	+	+	+
Eriophorum vaginatum	+	+	.	r	+
Distichium capillaceum	+	+	.	.	+
Ditrichum flexicaule	+	+	.	.	+
Catoscopium nigritum	+	+	.	.	+
Carex bigelowii	.	.	+	+	+
Limprichtia cossonii	+	+	.	.	.
Carex rariflora	+	.	.	+	.
Pedicularis parviflora	+	.	.	+	.
Salix lanata ssp. richardsonii	.	+	+	.	.

Single occurrences: Calliergon giganteum (rel. 15: +), Pseudocalliergon turgescens (14: +), Dryas integrifolia (14: r), Equisetum arvense (14: r), Equisetum scirpoides (16: +), Carex rotundata (17: +), Aneura pinguis (37: +), Bryum sp. (37: +), Carex sp. (37: +), Meesia uliginosa (37: +), Orthothecium strictum (37: +).

Lupinus arcticus, *Saxifraga hieracifolia*, *Aulacomnium turgidum*, *Dicranum spadiceum*, *Hylocomium splendens* and *Rhytidium rugosum*.

Scorpidium scorpioides-Carex aquatilis community (Fig. 13; Table 9; App. 1, ref. 6)

This wet sedge community is associated with poorly drained soils in the nonacidic tundra of subzone D. The areas usually have standing water early in the summer, and the soil surface is commonly covered with marl deposits. Almost barren nonsorted circles with thick marl deposits interrupt the otherwise closed sedge canopy. This community occurs on wetter soils than the Salici rotundifoliae-Caricetum aquatilis or the *Eriophorum angustifolium* ssp. *subarcticum* variant of the Dryado integrifoliae-Caricetum bigelowii described above. Walker & Everett (1991) described a similar wet sedge-community type from the Prudhoe Bay area (wet *Carex aquatilis-Scorpidium scorpioides* sedge tundra, Type M4 in Walker 1985), where it occurs in basins, troughs of low-centered polygons and lake margins with soil pH values above 7. They considered this community to be a transitional type between the wet and the aquatic tundra types, as it has up to 10 cm of standing water throughout the summer. This community also shows similarities to the *Eriophorum angustifolium-Carex aquatilis* community type described from hygric nonacidic fens in the Arctic Foothills of Alaska by Walker et al. (1994), and described from wet meadows and the basins of low-centered polygons with saturated soils at Point Barrow and Barter Island, Alaska, by Elias et al. (1996). The community is allied with the Paludello squarrosae-Caricetum aquatilis described from the fens and marshes of the valley bottoms of the Brooks Range, Alaska, by Cooper (1986).

The soils are Typic Historthels (Ping et al. 2004) and remain water-saturated throughout the summer. The anaerobic conditions result in thick, black, mucky organic horizons (25 cm, Table 1) due to slow decomposition rates. The upper parts of the organic horizon are often less decomposed and show recognizable plant parts in the peat. The mineral horizon is dark gray and gleyed, and soil texture is loam. Soil moisture is relatively high (mean 49 %). Soil pH averages 7.7. The soils not disturbed by cryoturbation reach a mean maximum thaw depth of 70 cm. This thaw depth is slightly greater than at the drier tundra sites of the Dryado integrifoliae-Caricetum bigelowii, probably due to the fact that wet soils conduct heat better than drier soils. The sites receive a relatively great amount of snow (mean 59 cm) due to their topographic position (depressions and toe slopes).

This community is poor in species, especially in nonvascular taxa. *Eriophorum angustifolium* ssp. *subarcticum* reaches cover values of up to 75 % and dominates the community. Faithful taxa are *P. sudetica* ssp. *albolabiata* and *Carex aquatilis*. Other constant taxa include *Equisetum variegatum*, *Salix arctica* and *Scorpidium scorpioides*.

4.2.3 Subzone E

Cladino-Vaccinietum vitis-idaeae Kade et al. ass. nov. (Fig. 14; Table 10, nomenclatural type relevé no. 91; App. 1, ref. 7)

This dwarf shrub-rich community is found on relatively dry to moist acidic nonsorted circles and earth hummocks on well-drained slopes and hilltops in subzone E. The nonsorted circles of this subzone are commonly overgrown with vegetation and exhibit only very small patches of bare soil. The earth hummocks show little cryoturbation activity as they are well insulated by the thick vegetation mat. The nonsorted circles and earth hummocks represent frequent breaks in the surrounding moist acidic tundra (Sphagno-Eriophoretum vaginati, see below). Relatively dry nonsorted circles associated with upper hill slope positions usually exhibit the Cladino-Vaccinietum vitis-idaeae; whereas wetter nonsorted circles occurring on toe slopes feature the *Anthelia juratzkana-Juncus biglumis* community (see below).

Fig. 14. Cladino-Vaccinietum vitis-idaeae ass. nov. on dry to moist nonsorted circles and earth hummocks of the acidic tundra. Subzone E, Happy Valley, Alaska.

The Cladino-Vaccinietum vitis-idaeae is similar in species composition to the Sphagno-Eriophoretum vaginati covering the surrounding moist acidic tundra. Both associations are dominated by dwarf shrubs such as *Betula nana*, *Ledum palustre* ssp. *decumbens* and *Vaccinium vitis-idaea*. However, the Cladino-Vaccinietum vitis-idaeae does not support the growth of *Sphagnum* mosses, as it is associated with the drier soils of elevated earth hummocks and higher hill-slope positions and has abundant lichen cover. The association is allied with the Salici phlebophyllae-Arctoetum alpinae Walker et al. 1994, which occurs on well drained, moderately exposed, acidic rocky sites of the Arctic Foothills. It exhibits a high diversity of fruticose lichens, such as *Cetraria cucullata*, *C. islandica*, *C. nivalis*, *Cladina arbuscula*, *C. rangiferina* and *C. uncialis*. Common dwarf shrubs include *Salix phlebophylla*, *Vaccinium uliginosum* and *V. vitis-idaea*. Cooper (1986) described two associations from the Arrigetch Creek Valley, Brooks Range, Alaska, which also show affinities to the Cladino-Vaccinietum vitis-idaeae. The Betulo glandulosae-Cladonietum stellaris Cooper 1986 occurs on relatively dry granitic glacial moraines and is dominated by *Cladonia* lichens. Here, *Betula glandulosa* replaces *Betula nana*, and both the Cladino-Vaccinietum vitis-idaeae and the Betulo glandulosae-Cladonietum stellaris have *Ledum palustre* ssp. *decumbens*, *Vaccinium vitis-idaea* and a variety of *Cladonia* species in common. The Vaccinio uliginosi-Salicetum phlebophyllae Cooper 1986 is a prostrate shrub vegetation type of windswept

Table 10. Community table of the Cladino-Vaccinietum vitis-idaeae ass. nov. Nomenclatural type relevé number marked in bold.

	Racomitrium lanuginosum var.										Carex bigelowii var.				
Relevé No.	73	78	80	90	76	92	74	**91**	88	89	93	94	95	83	82
Altitude (m.a.s.l.)	300	300	300	334	300	332	300	332	328	333	315	315	310	320	320
Number of vascular taxa	12	13	15	11	12	16	10	12	12	11	8	10	12	12	10
Number of nonvascular taxa	30	30	27	26	32	31	27	33	29	23	27	16	19	21	16
Total number of taxa	42	43	42	37	44	47	37	45	41	34	35	26	31	33	26
Ch/regional D: Association															
Anastrophyllum minutum	+	2	1	1	1	1	+	1	1	1	+	+	+	+	+
Cladina arbuscula	+	+	+	1	1	2	1	3	+	.	+	1	1	1	.
Dicranum spadiceum	+	1	2	.	1	1	1	1	+	.	+	+	.	.	.
Polytrichum hyperboreum	+	+	+	.	1	.	+	+	1	+	.	.	.	.	.
D: Racomitrium lanuginosum var.															
Racomitrium lanuginosum	3	2	2	2	3	2	3	2	2	2	.	.	2	.	.
Arctagrostis latifolia	+	2	1	1	2	2	1	+	+	+	.	.	.	.	.
Pertusaria dactylina	+	+	+	.	+	.	+	.	+	1	.	.	.	.	.
Senecio atropurpureus	1	+	+	.	+	+	+	.	.	.	.	.	.	.	+
Eriophorum vaginatum	1	+	1	1	.	.	1	.	.	.	.	1	.	.	.
Salix phlebophylla	+	1	2	.	+	.	1	.	.	.	.	.	.	.	.
Cladonia gracilis ssp. elongata	+	+	1	.	.	.	1	.	.	1	+	.	.	.	.
Rhytidium rugosum	+	1	+	.	1	.	.	.	.	.	.	.	.	.	.
Pertusaria panyrga	+	+	.	+	.	+	.	.	.	.	.	.	.	.	.
Lophozia ventricosa	+	.	.	.	+	.	+	+	.	.	.	.	.	.	.
Cladonia cenotea	.	.	+	+	+	.	.	.	.	+	.	.	.	.	.
Cladonia deformis	.	.	+	+	.	+	.	+	.	.	.	.	.	.	.
Rubus chamaemorus	.	.	.	2	.	+	.	1	.	r	.	.	.	.	.
Calamagrostis sp.	.	.	.	.	.	+	.	1	1	1	.	.	.	.	.
Cladonia pleurota	+	+	.	+	.	.	.	.	.	.	.	.	.	.	.
Nephroma expallidum	+	.	.	.	+	.	.	.	1	.	.	.	.	.	.
Cladonia gracilis	.	.	.	+	.	1	.	.	1	.	.	.	.	.	.
Barbilophozia binsteadii	.	.	.	+	.	+	.	+	.	.	.	.	.	.	.
D: Carex bigelowii var.															
Carex bigelowii	.	+	.	.	.	1	.	.	1	2	2	1	3	2	2
Cetraria islandica	.	+	.	.	+	.	+	.	.	.	+	+	+	+	.
Polytrichum strictum	.	.	.	+	.	+	.	.	.	.	+	+	.	.	+
Cladonia gracilis ssp. vulnerata	.	.	+	.	.	.	.	+	.	.	.	.	1	2	+
Andromeda polifolia	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.
Nephroma arcticum	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.
Ch: Class, order and alliance															
Vaccinium vitis-idaea	2	2	2	3	2	2	2	2	1	2	3	3	2	2	2
Dicranum elongatum	2	2	2	3	1	2	3	3	2	3	1	1	1	1	1
Ledum palustre ssp. decumbens	2	1	2	1	2	2	2	2	1	2	2	3	2	1	2
Betula nana	1	1	1	+	1	2	1	1	1	1	3	2	2	2	2
Flavocetraria cucullata	1	+	+	1	1	1	+	2	1	+	+	+	+	+	1
Empetrum nigrum ssp. hermaphroditum	1	.	1	2	+	2	.	2	1	.	2	+	2	2	2
Cladonia amaurocraea	+	+	.	+	+	+	1	+	+	+	1	.	.	.	+
Others															
Polygonum bistorta var. plumosum	1	2	2	+	1	1	1	1	+	+	1	+	2	2	1
Aulacomnium turgidum	+	1	1	1	2	1	1	1	1	+	1	+	1	1	2
Dactylina arctica	+	+	+	+	+	1	+	+	+	r	+	+	+	+	.
Cladina rangiferina	+	1	+	2	+	2	1	1	3	1	1	.	2	2	3
Hylocomium splendens	+	1	1	+	2	+	2	1	+	.	3	2	3	2	2
Cassiope tetragona	+	1	+	1	1	1	2	.	+	+	+	+	1	1	1
Petasites frigidus	.	2	1	1	2	2	.	1	+	+	.	1	1	+	1

Thamnolia subuliformis	+	+	+	+	+	+	1	+	+	+	.	.	+	.	.
Peltigera leucophlebia	+	1	1	.	+	.	.	.	1	1	1	2	+	.	1
Cladonia fimbriata	+	.	+	.	+	+	+	+	+	+	+	.	.	.	+
Dicranum acutifolium	+	1	.	+	1	.	+	.	1	+	.	.	+	+	.
Cladina stygia	.	+	+	.	.	+	.	+	.	.	2	1	1	.	+
Cladonia uncialis	1	.	.	+	.	.	.	+	1	1	.	.	+	+	.
Cladonia chlorophaea	.	.	+	.	+	+	+	+	.	.	+	+	.	.	.
Pleurozium schreberi	.	.	.	+	.	.	.	+	+	+	+	2	.	.	+
Peltigera malacea	+	+	.	.	.	+	.	+	.	.	+	.	.	.	+
Pedicularis lapponica	+	+	.	.	.	1	.	.	.	r	.	.	+	+	.
Cetraria laevigata	.	.	.	+	.	+	.	+	.	.	1	.	+	+	.
Dicranum groenlandicum	.	.	.	+	.	2	.	.	+	.	2	.	1	3	.
Ditrichum flexicaule	+	+	.	.	.	.	.	.	+	.	+	.	.	.	+
Peltigera aphthosa	.	.	.	+	.	1	1	1	.	.	.	.	.	+	.
Flavocetraria nivalis	.	.	.	.	+	.	+	.	+	.	+	.	+	.	.
Ptilidium ciliare	.	.	.	.	.	+	.	1	1	+	+	.	.	.	.
Peltigera scabrosa	.	+	.	.	.	.	.	+	.	.	.	1	.	+	.
Pedicularis labradorica	.	.	+	.	.	.	.	+	+	.	.	.	.	+	.
Pedicularis oederi	.	.	.	.	.	+	.	+	.	.	.	.	.	+	+
Cladina mitis	.	.	.	.	.	+	.	.	1	3	.	.	.	+	.
Salix planifolia ssp. pulchra	.	+	.	.	.	.	1	.	.	.	.	1	.	.	.
Lophozia jurensis	.	+	.	.	.	.	.	.	.	.	+	.	.	+	.
Vaccinium uliginosum	.	.	1	.	+	.	.	.	.	.	.	.	+	.	.
Luzula arctica	.	.	.	.	r	.	.	.	r	.	.	.	.	+	.

Additional taxa with two or less occurrences: Hypnum holmenii (rel. 73: +, 80: +), Sphaerophorus globosus (73: +, 74: +), Cladonia coccifera (78: +, 76: +), Luzula confusa (80: +, 92: +), Stellaria sp. (80: r, 92: +), Lophozia savicziae (80: +, 88: +), Dicranum angustum (80: +, 93: +), Pedicularis kanei (90: +, 91: +), Alectoria nigricans (76: +, 92: +), Lophozia excisa (76: +, 92: +), Cladonia pyxidata (76: +, 74: +), Alectoria ochroleuca (76: +, 74: r), Pohlia nutans (76: +, 83: +), Hypogymnia subobscura (74: +, 89: +), Cladonia sulphurina (91: +, 89: +), Arctostaphylos rubra (73: 2), Blepharostoma trichophyllum (73: +), Bryocaulon divergens (78: +), Pohlia sp. (78: +), Cladonia cyanipes (80: +), Ochrolechia androgyna (90: +), Aulacomnium palustre (76: +), Calypogeja muelleriana (92: +), Cladonia cornuta (92: +), Baeomyces rufus (91: +), Cladonia macroceras (91: +), Cladonia squamosa (91: +), Polytrichum sp. (91: +), Anthelia juratzkana (88: +), Lophozia sp. (88: +), Ochrolechia inaequatula (89: +), Calamagrostis canadensis (95: +), Cephalozia pleniceps (83: +), Lophozia longiflora (82: +).

ridge tops on acidic mineral soils and is dominated by *Loiseleuria procumbens*, *Salix phlebophylla*, *Vaccinium uliginosum*, *V. vitis-idaea* and several "wind lichens" such as *Cetraria kamzaticum*, *Cornicularia divergens* and *Sphaerophorus globosus*. Dierssen (1996) combined several *Racomitrium lanuginosum* heath communities described from Iceland, Greenland, Norway and Scotland into the Carici bigelowii-Racomitrietum lanuginosi (Du Rietz 1925) Dahl 1957. *Racomitrium lanuginosum* reaches its optimal vitality in this association, but in contrast to the Cladino-Vaccinietum vitis-idaeae, vascular plants play only a minor role.

The soils are classified as Ruptic-Histic Aquiturbels (Ping et al. 1998). The organic horizons range in thickness from 0 to 15 cm and consist of dark brown mucky peat. The mineral soil is yellowish brown to dark brown with clay loam texture. Soil moisture is low (mean 36 %, Table 1), and soil pH averages 5.0. Thaw depths of the nonsorted circles and hummocks average 60 cm and are shallower than the thaw depths of the more active frost-heave features in the northern subzones. Snow depth averages 40 cm.

This association is especially rich in nonvascular species; the following are faithful to this association: *Cladina arbuscula*, *Dicranum spadiceum*, *Polytrichum hyperboreum* and *Racomitrium lanuginosum*. The dominant taxa are *Betula nana*, *Cassiope tetragona*, *Empetrum nigrum* ssp. *hermaphroditum*, *Ledum palustre* ssp. *decumbens*, *Petasitis frigidus*, *Polygonum bistorta* var. *plumosum*, *Vaccinium vitis-idaea*, *Anastrophyllum minutum*, *Aulacomnium turgidum*, *Cladina rangiferina*, *Dicranum elongatum*, *Flavocetraria cucullata* and *Hylocomium splendens*. A variety of *Cladonia* and *Cladina* lichens play an important role in this association. Most species are shared with the surrounding Sphagno-Eriophoretum vaginati. However, the elevated, drier soils of the nonsorted circles and earth hummocks support a rich assortment of nonvascular species, which are differential against the Sphagno-Eriophoretum vaginati.

The association is split into two variants. The *Racomitrium lanuginosum* variant grows on flat nonsorted circles with more mineral-rich soils and moderate cryoturbation activity, and the *Carex bigelowii* variant is associated with raised, stabilized earth hummocks with more peaty soils. The *Racomitrium lanuginosum* variant is richer in nonvascular taxa and is dominated by a dense moss carpet of *Racomitrium lanuginosum*. Other differential taxa include *Arctagrostis latifolia*, *Senecio atropurpureus* and *Pertusaria dactylina*. The *Carex bigelowii* variant is differentiated by *Carex bigelowii* and *Cetraria islandica*.

Sphagno-Eriophoretum vaginati Walker et al. 1994 (Fig. 15; Table 11; App. 1, ref. 8)

Walker et al. (1994) consider the Sphagno-Eriophoretum vaginati to be the zonal vegetation of the Arctic Foothills, Alaska. It is widespread on mesic, acidic soils of the upland tundra, covering gentle, poorly drained slopes. Although occurring on uplands, this association includes some hygrophytic species due to the high water-holding capacity of the *Sphagnum* mosses. Walker et al. (1994) placed the association within the bog and wet heaths class Oxycocco-Sphagnetea Br.-Bl. & Tx. 1943 ap. Westh. et al. 1946, which comprises dwarf shrub heaths and bogs on acidic, poorly drained substrates. However, the class Oxycocco-Sphagnetea has its main distribution in nemoral and boreal areas and is only weakly developed in the Arctic. We feel the Sphagno-Eriophoretum vaginati should rather be grouped in the class Loiseleurio-Vaccinietea Eggler 1952, which includes dwarf shrub vegetation on acidic soils in alpine and arctic regions.

The Sphagno-Eriophoretum vaginati is common in upland regions of northwestern Canada and northeastern Russia (Bliss & Matveyeva 1992, Chernov & Matveyeva 1997). It is the predominant association on the uplands in unglaciated tundra areas of Beringia with ice-rich permafrost. The association is dominant on the mesic slopes and hilltops of the acidic tundra in subzone E, commonly interspersed with large, often inactive nonsorted circles and earth hummocks (Cladino-Vaccinietum vitis-idaeae). Not so common and restricted to slightly wetter areas are small and barren active

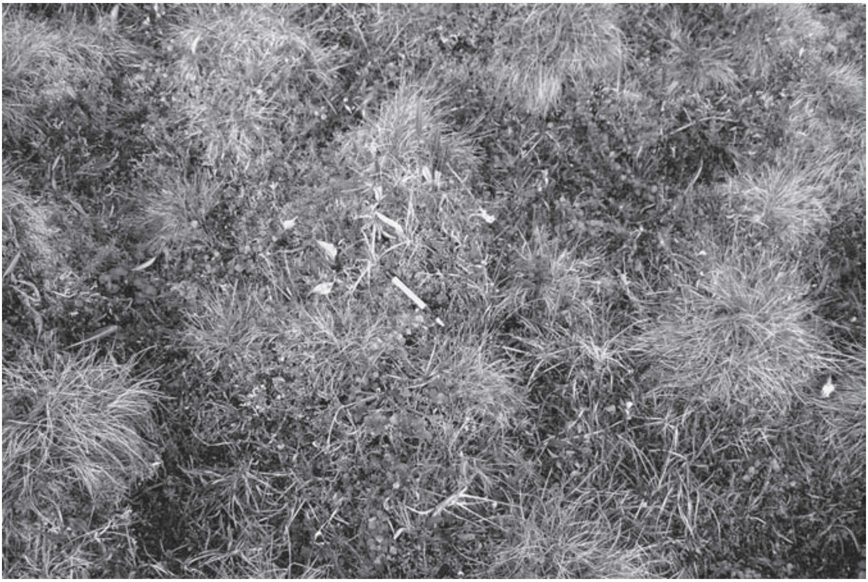

Fig. 15. Sphagno-Eriophoretum vaginati Walker et al. 1994 of the moist acidic tundra. Subzone E, Sagwon MAT, Alaska.

nonsorted circles (*Anthelia juratzkana-Juncus biglumis* community, see below).

The soils are classified as Histic Aquiturbels (Ping et al. 1998). Organic horizons are about 12 cm thick (Table 1) and consist of dark brown mucky peat. They overlay dark gray, gleyed mineral horizons with loam texture. In places with better drainage, mineral soils lack gleyed features and are dark yellowish brown. Soil moisture averages 44 % and soil pH is low (mean 5.3). The soils are insulated by a deep *Sphagnum* moss cover and exhibit shallow thaw depths (mean 34 cm). Maximum snow depth averages 60 cm.

The association is rich in nonvascular taxa (mean 28 taxa) but relatively poor in vascular taxa, especially in comparison to the Dryado integrifoliae-Caricetum bigelowii (means 14 and 24 vascular species, respectively). Faithful taxa are *Pedicularis lapponica*, *Salix planifolia* ssp. *pulchra*, *Sphagnum angustifolium*, *S. girgensohnii* and *S. warnstorfii*. The abundant tussock-forming sedge *Eriophorum vaginatum* gives this vegetation type its characteristic look. Together with *Eriophorum vaginatum*, the dwarf shrubs *Betula nana*, *Cassiope tetragona*, *Empetrum nigrum*, *Ledum palustre* ssp. *decumbens*, *Salix planifolia* ssp. *pulchra* and *Vaccinium vitis-idaea* are dominant in the overstory. Thick moss mats of *Aulacomnium turgidum*, *Hylocomium splendens* and a variety of *Dicranum* and *Sphagnum* species are found in the small depressions next to the tussocks. This association shares many species with the Cladino-Vaccinietum vitis-idaeae, with *Eriophorum vagina-*

Table 11. Community table of the Sphagno-Eriophoretum vaginati.

Relevé No.	86	77	75	84	87	81	85	62	79	66
Altitude (m.a.s.l.)	320	300	300	315	315	300	320	300	290	315
Number of vascular taxa	16	13	13	14	12	15	16	16	11	12
Number of nonvascular taxa	23	28	33	23	21	42	26	32	30	20
Total number of taxa	39	41	46	37	33	57	42	48	41	32
Ch/regional D: Association										
Eriophorum vaginatum	3	3	3	3	3	3	3	3	3	3
Sphagnum warnstorfii	2	1	+	2	2	1	2	2	2	2
Salix planifolia ssp. pulchra	1	1	2	2	2	2	1	2	2	1
Sphagnum girgensohnii	+	1	2	1	1	1	1	2	.	.
Pedicularis lapponica	+	+	+	+	+	.	+	.	+	.
Sphagnum angustifolium	2	+	+	2	1	.	1	.	.	2
Saxifraga nelsoniana	+	+	+	.	.	+	.	+	+	.
Ch: Class, order and alliance										
Betula nana	3	2	2	3	3	2	3	2	2	2
Ledum palustre ssp. decumbens	2	2	1	2	2	2	2	2	1	1
Vaccinium vitis-idaea	1	2	1	2	2	2	2	2	1	2
Flavocetraria cucullata	+	+	+	+	+	1	+	1	+	.
Dicranum elongatum	+	+	+	+	+	2	.	.	2	+
Empetrum nigrum ssp. hermaphroditum	2	.	+	2	1	+	2	+	.	1
Cladonia amaurocraea	.	+	.	+	+	+	.	+	+	+
Others										
Hylocomium splendens	2	3	2	2	2	1	3	2	2	1
Cassiope tetragona	1	2	2	1	1	2	1	1	2	1
Aulacomnium turgidum	2	1	1	2	1	1	2	1	2	+
Polygonum bistorta var. plumosum	2	2	1	1	1	1	+	1	+	+
Dactylina arctica	+	+	+	+	+	+	+	1	+	+
Petasites frigidus	+	+	+	+	+	.	1	+	+	+
Senecio atropurpureus	+	+	+	+	.	+	+	+	+	.
Cladina stygia	1	+	+	.	+	+	+	.	+	+
Anastrophyllum minutum	+	+	1	.	.	2	+	+	2	+
Tomentypnum nitens	+	.	r	+	+	+	+	.	+	+
Ptilidium ciliare	+	.	+	1	1	.	+	.	+	+
Cladina rangiferina	1	.	.	+	+	1	+	+	+	.
Peltigera leucophlebia	1	+	+	+	+	1	.	.	.	.
Cladina arbuscula	+	+	+	.	+	+	.	+	.	.
Polytrichum sp.	+	+	+	.	.	+	+	.	+	.
Peltigera scabrosa	+	+	+	.	.	.	+	+	.	+
Pleurozium schreberi	+	.	+	1	1	.	.	.	+	+
Carex bigelowii	1	.	.	1	1	.	1	+	.	+
Blepharostoma trichophyllum	.	1	1	.	.	+	.	+	1	+
Cetraria islandica	+	+	.	+	.	+	.	.	+	.
Thamnolia subuliformis	.	+	+	.	.	+	.	+	+	.
Dicranum acutifolium	.	2	.	+	.	1	+	.	1	.
Dicranum angustum	.	.	2	+	.	+	.	.	+	+
Cetraria laevigata	.	.	.	+	+	r	+	.	.	+
Dicranum groenlandicum	1	.	.	1	1	.	1	.	.	.
Vaccinium uliginosum	1	.	.	1	.	.	.	+	.	+
Nephroma arcticum	+	.	.	.	.	+	+	+	.	.
Barbilophozia binsteadii	.	+	+	.	.	+	.	.	+	.
Arctagrostis latifolia	.	+	+	.	.	+	.	+	.	.
Peltigera malacea	.	+	.	.	+	.	+	+	.	.

Hypnum holmenii	.	.	+	.	.	+	+	.	+	.
Pedicularis labradorica	+	.	.	.	+	.	+	.	.	.
Ditrichum flexicaule	+	.	.	.	.	+	.	.	+	.
Nephroma expallidum	.	+	+	.	.	.	+	.	.	.
Tritomaria quinquedentata	.	+	+	.	.	.	.	.	.	+
Pedicularis oederi	.	+	.	r	.	.	r	.	.	.
Aulacomnium palustre	.	+	.	.	.	+	.	1	.	.
Sphagnum balticum	.	+	.	.	.	.	+	+	.	.
Lophozia ventricosa	.	.	+	.	.	.	.	.	+	+
Cladonia gracilis ssp. vulnerata	.	.	.	+	+	+	.	.	.	.
Cladonia cyanipes	.	.	.	.	.	+	+	.	+	.
Cladonia fimbriata	.	.	.	.	.	+	+	+	.	.
Cladonia deformis	.	.	.	.	.	+	.	+	.	+
Peltigera aphthosa	.	.	.	.	.	.	1	1	+	.
Cephalozia pleniceps	.	+	+	.	.	.	.	.	.	.
Calypogeia sphagnicola	.	+	.	.	.	+	.	.	.	.
Dicranum spadiceum	.	.	+	.	.	+	.	.	.	.
Barbilophozia kunzeana	.	.	+	.	.	.	.	.	+	.
Calypogeia muelleriana	.	.	+	.	.	.	.	.	+	.
Dicranum sp.	.	.	.	+	.	.	.	2	.	.
Salix phlebophylla	.	.	.	.	.	+	.	+	.	.
Flavocetraria nivalis	.	.	.	.	.	+	.	+	.	.
Sphaerophorus globosus	.	.	.	.	.	+	.	+	.	.

Single occurrences: Andromeda polifolia (rel. 86: r), Cephalozia bicuspidata (75: +), Peltigera sp. (75: +), Rhytidium rugosum (84: +), Polytrichum strictum (87: +), Calamagrostis sp. (81: +), Saussurea angustifolia (81: +), Cladonia cenotea (81: +), C. pocillum (81: +), C. uncialis (81: +), Drepanocladus sp. (81: +), Lophozia savicziae (81: +), Pertusaria dactylina (81: +), Rinodina turfacea (81: +), Luzula arctica (81: r), Calamagrostis canadensis (85: +), Stellaria sp. (85: r), Salix arctica (62: +), Alectoria nigricans (62: +), A. ochroleuca (62: +), Bryocaulon divergens (62: +), Cetraria aculeata (62: +), Cladonia coccifera (62: +), C. cornuta (62: +), C. gracilis (62: +), Dactylina ramulosa (62: +), Polytrichastrum alpinum (62: +), Lophozia longiflora (79: +), Pertusaria panyrga (79: +), Pedicularis capitata (66: +), Aneura pinguis (66: +).

tum, *Salix planifolia* ssp. *pulchra* and the *Sphagnum* mosses being differential against it.

Anthelia juratzkana-Juncus biglumis community (Fig. 16; Table 12; App. 1, ref. 9)

Walker et al. (1994) described this unit occurring on nonsorted circles as a distinct community within the tussock tundra of the Alaskan North Slope. We found this community associated with small, active, barren nonsorted circles of the moist acidic tundra in subzone E. These nonsorted circles represent a rather inconspicuous component of the surrounding Sphagno-Eriophoretum vaginati. These small features, measuring only up to 40 cm in diameter, are restricted to the wetter inter-tussock sites and are common on toe slopes of hills at Happy Valley. They are usually placed 15 m or more apart and can be difficult to spot as they are sometimes hidden under *Eriophorum vaginatum* tussocks and dwarf-shrub branches.

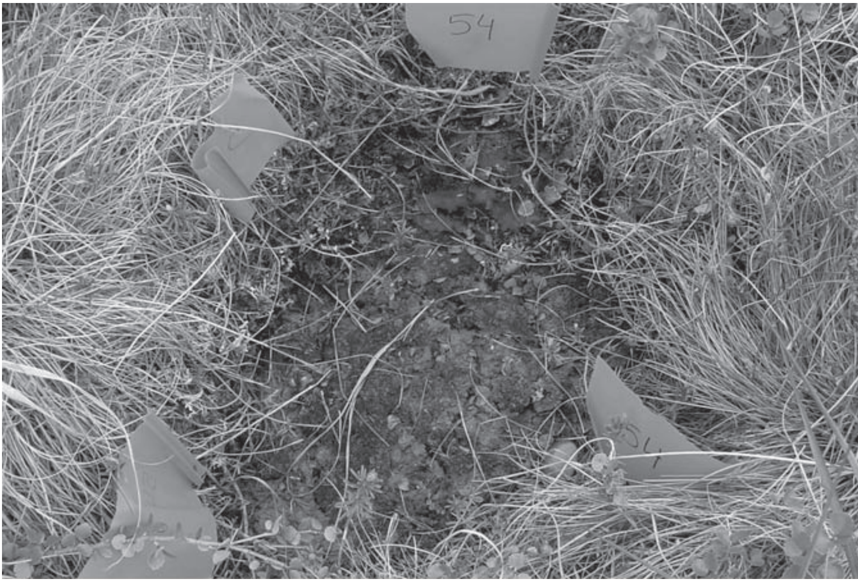

Fig. 16. *Anthelia juratzkana-Juncus biglumis* community on relatively wet acidic frost boils. Subzone E, Happy Valley, Alaska.

The soils are classified as Typic Aquiturbels (Ping et al. 2004). Organic horizons are absent, and the mineral soil surface is either bare or covered by a thin layer composed of cryptogamic liverworts, mosses and lichens that readily peels off the mineral soil. The mineral soils have very dark gray, gleyed horizons and a clay loam texture. Soil moisture content averages 42 % (Table 1) and soil pH averages 5.2. The lack of a thick insulative vegetation mat or organic horizon results in deep thaw (mean 60 cm). The low position along the hill slope is responsible for snow accumulation, and maximum snow depth is rather deep, averaging 63 cm.

The community is dominated by nonvascular species. The nonvascular species composition of this community is similar to several moss synusia of snow patch communities compiled by Dierssen (1996). The leafy liverwort *Anthelia juratzkana* forms an almost continuous carpet on most of the nonsorted circles. Faithful taxa are *Cephalozia bicuspidata*, *Dicranella subulata* and *Jungermannia confertissima*. *Juncus biglumis* and *Luzula arctica* are also restricted to these barren areas. In addition, there are several constant taxa that are invading from the surrounding Sphagno-Eriophoretum vaginati: *Betula nana*, *Eriophorum vaginatum*, *Ledum palustre* ssp. *decumbens*, *Vaccinium vitis-idaea* and *Hylocomium splendens*. This community shares a few species with the associations occurring on nonacidic nonsorted circles, such as *Juncus biglumis*, *Dactylina ramulosa* and *Pohlia* sp.

Table 12. Community table of the *Anthelia juratzkana-Juncus biglumis* community.

Relevé No.	57	54	53	52	56
Altitude (m.a.s.l.)	305	310	305	305	305
Number of vascular taxa	9	6	8	11	7
Number of nonvascular taxa	19	16	24	16	7
Total number of taxa	28	22	32	27	14
Ch/regional D: Community					
Dicranella subulata	1	1	2	+	+
Jungermannia sp.	+	+	2	.	+
Jungermannia confertissima	+	+	+	.	.
Cephalozia bicuspidata	+	+	+	.	.
Juncus biglumis	+	+	.	1	.
Ch: Class, order and alliance					
Anthelia juratzkana	2	2	+	4	3
Luzula arctica	+	.	2	2	.
Others					
Vaccinium vitis-idaea	2	+	1	1	+
Hylocomium splendens	1	1	2	+	+
Eriophorum vaginatum	1	+	+	1	1
Ledum palustre ssp. decumbens	1	r	+	1	+
Betula nana	+	r	+	r	+
Cetraria islandica	1	+	+	r	.
Cassiope tetragona	1	.	1	+	+
Dactylina arctica	+	+	+	.	.
Cladina rangiferina	2	+	.	r	.
Cladonia fimbriata	+	+	.	.	+
Cladonia amaurocraea	+	.	+	+	.
Aulacomnium turgidum	+	.	r	r	.
Empetrum nigrum	+	.	+	.	1
Flavocetraria cucullata	.	+	2	+	.
Vaccinium uliginosum	.	.	+	r	+
Lophozia sudetica var. sudetica	+	+	.	.	.
Lophozia ventricosa	+	+	.	.	.
Anastrophyllum minutum	+	.	+	.	.
Salix planifolia ssp. pulchra	r	.	.	r	.
Cladonia gracilis	.	+	+	.	.
Pohlia cruda	.	+	+	.	.
Peltigera leucophlebia	.	2	.	.	1
Cladonia chlorophaea	.	.	1	+	.
Cladina mitis	.	.	r	+	.
Lophozia sp.	.	.	+	.	+

Single occurrences: Cladonia uncialis (53: +), Dicranum spadiceum (53: +), Peltigera rufescens (53: +), Pohlia sp. (53: +), Polytrichum hyperboreum (53: +), Ptilidium ciliare (53: +), Pertusaria panyrga (57: 2), Didymodon spadiceus (57: 1), Baeomyces rufus (57: +), Lophozia excisa (57: +), Dactylina ramulosa (52: 2), Cladonia occifera (52: 1), Bryum sp. (52: +), Cladina stygia (52: +), Ditrichum flexicaule (52: +), Peltigera sp. (52: +), Polygonum bistorta var. plumosum (52: +), Pedicularis lapponica (52: r), Arctagrostis latifolia (54: +).

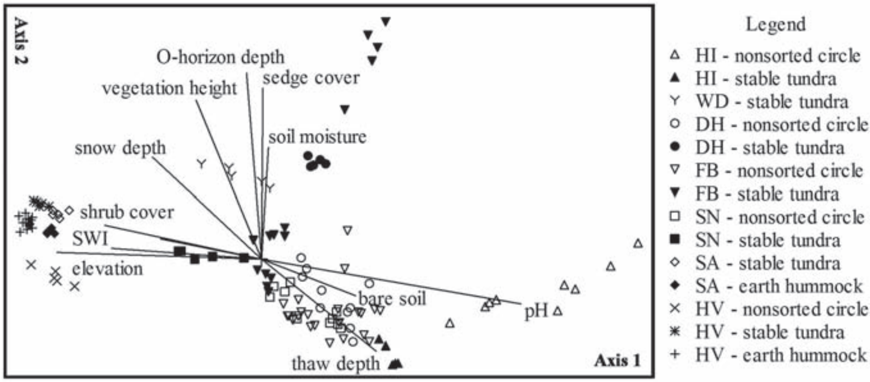

Fig. 17. DCA ordination of all relevés. The biplot diagram displays variables correlated with the plot distributions and indicates the direction and strength of correlation of variables with $R^2 > 0.35$. The sample plots are coded according to the location of the study sites: HI – Howe Island, WD – West Dock, DH – Deadhorse, FB – Franklin Bluffs, SN – Sagwon MNT, SA – Sagwon MAT, HV – Happy Valley.

4.3 Ordination

The DCA ordination diagram shows the relationship between plant communities and environmental variables (Fig. 17). The ordination axes show the major directions of variation in the data; the first axis explains 53 % and the second axis explains 11 % of the variation. The arrows within the biplot diagram display the principal direction of variation and strength of correlation for major environmental variables. Only environmental variables with $R^2 > 0.35$ are shown.

Axis 1 of the DCA ordination is interpreted as a more or less complex bioclimate/pH gradient, which corresponds to the south-to-north negative trend in temperature and positive trend in soil pH. Soil pH, thaw depth and the amount of bare ground increase along axis 1, and air temperature as measured by the SWI, elevation, snow depth and cover of erect dwarf shrubs decrease along axis 1. Thaw depth increases along axis 1 along with decreasing vegetation cover, which allows the soil to warm up more in the summer. Snow depth increases towards the south with increasing elevation. Communities of subzone E occupy the left end of the gradient and communities of subzone C the right end. The coastal tundra plots at West Dock are an exception.

Axis 2 is interpreted as a complex environmental gradient associated with disturbance through cryoturbation. Low soil moisture and vegetation height, shallow depth of snow and the organic horizon are characteristic of frost-heave features and decrease along axis 2, whereas thaw depth increases along this axis. In general, tundra plots are grouped towards the upper part of the ordination space, and frost-heave features occupy the lower part. The dry tundra plots at Howe Island represent an exception.

The results obtained by the classification are reflected in the ordination analysis (Fig. 18). The Cladino-Vaccinietum vitis-idaeae, the Sphagno-Eriophoretum vaginati and the *Anthelia juratzkana-Juncus biglumis* community are clustered in the left portion of the ordination space, which is correlated with low soil pH, warm air temperatures and high shrub cover. The plant communities of the Dryadion integrifoliae (*Dryas integrifolia-Salix arctica* community, Junco biglumis-Dryadetum integrifoliae and Dryado integrifoliae-Caricetum bigelowii) occupy the center of the ordination diagram. They are arranged along a soil moisture and disturbance gradient, with soil moisture increasing and cryogenic activity decreasing from the *Dryas integrifolia-Salix arctica* community toward the Dryado integrifoliae-Caricetum bigelowii. The plant communities of the Scheuchzerio-Caricetea nigrae (Salici rotundifoliae-Caricetum aquatilis and *Scorpidium scorpioides-Carex aquatilis* community) are located in the upper part of the ordination space, corresponding to high soil moisture conditions, thick organic horizons and shallow thaw depth. The *Braya purpurascens-Puccinellia angustata* community occupies the lower right corner of the diagram, which corresponds to low soil moisture conditions, cool air temperature and great thaw depth.

The DCA axes are scaled in units of the average standard deviation of species turnover (SD, Fig. 18). Along a gradient, a complete turnover in species composition of plots occurs in about 4 SD (Hill & Gauch 1980).

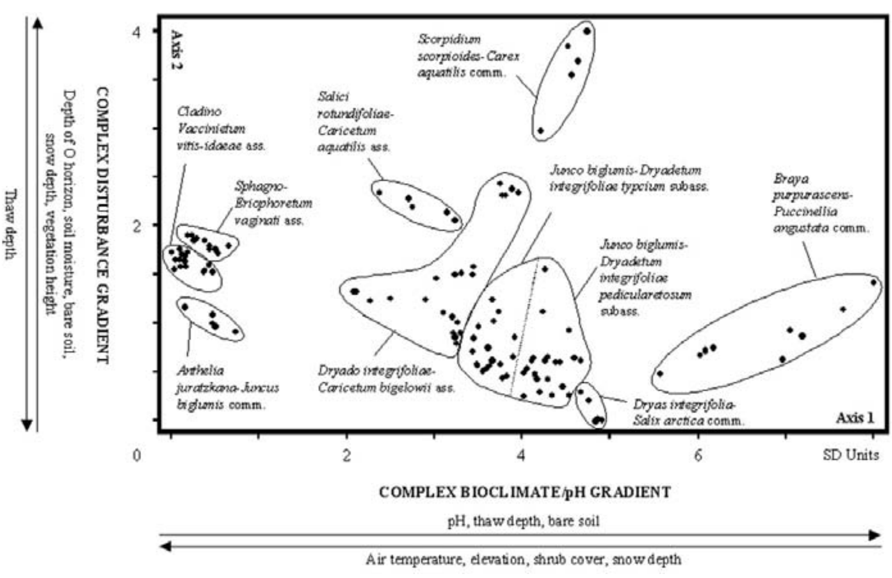

Fig. 18. DCA ordination of all relevés. The sample plots are grouped according to association or community. Arrows along each DCA axis indicate the direction of the principal environmental gradients. Axes are labeled in SD units (see text for interpretation).

Along the complex bioclimate/pH gradient, an almost entire species turnover occurs from the acidic plant communities to the communities of the Dryadion integrifoliae, and another full turnover in species composition occurs between the Dryadion integrifoliae and the *Braya purpurascens-Puccinellia angustata* community. Along the complex disturbance gradient, an almost complete species turnover occurs between the *Scorpidium scorpioides-Carex aquatilis* community and most of the remaining communities.

4.4 Plant functional types and floristic analysis

The analyses of plant functional types and floristic affinities show pronounced differences between frost-heave communities and adjacent tundra plots as well as changes along the bioclimate gradient. Total species richness peaks in plant communities in subzone D and is lower in subzone C and E (Fig. 19) possibly because subzone D is warmer than subzone C and has more mineral-rich soils than subzone E. The floristic richness is greatest in the Junco biglumis-Dryadetum integrifoliae with 164 species. The Dryado integrifoliae-Caricetum bigelowii has also a great floristic richness with 155 species, which is consistent with the exceptionally high diversity noted by Matveyeva (1994) in the corresponding Carici arctisibiricae-Hylocomietum alaskani of the Taymir Peninsula, Russia. The wet sedge *Scorpidium scorpioides-Carex aquatilis* community has the poorest floristic diversity with 26 species. Species numbers in all communities are driven by nonvascular species, which usually make up more than 60 % of the total species. When comparing frost-heave communities to the surrounding tundra counterparts, frost-heave features usually have relatively greater lichen and liverwort diversity. In contrast, stable tundra communities show greater diversity in forbs and mosses. The species richness of liverworts increases along the bioclimate gradient from north to south, whereas the species richness of forbs, graminoids and mosses peaks in subzone D.

Total plant cover is usually greater in tundra plots than in frost-heave communities (Fig. 19). In general, the tundra communities have greater dwarf shrub, graminoid and moss cover, while frost-heave communities support a greater lichen and liverwort cover. The cover of graminoids plays an important role especially in the wet Salici rotundifoliae-Caricetum aquatilis (67 %) and *Scorpidium scorpioides-Carex aquatilis* community (73 %). The cover of forbs is low in all community types (0–6 %), but is highest in the *Dryas integrifolia-Salix arctica* community. Along the bioclimate gradient, total plant cover of frost-heave features increases from north to south from 49 to 140 %, and total plant cover of the surrounding tundra remains relatively constant (79–131 %). The cover of lichens decreases along the bioclimate gradient, whereas the importance of mosses and liverworts increases from north to south.

Frost-heave features and adjacent tundra communities also show pronounced differences when considering the cover and growth form of li-

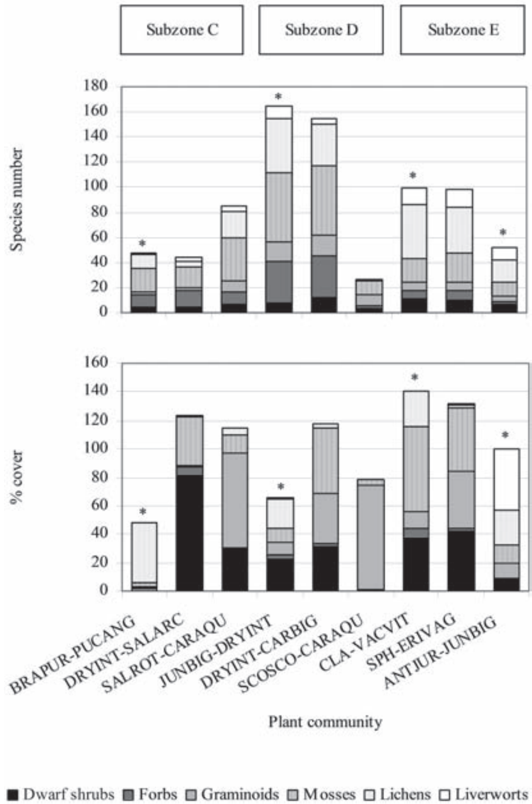

Fig. 19. Analysis of the species richness and plant functional types of the cryoturbated tundra communities. Plant functional types are shown as species numbers and percent cover values. Key to plant communities: BRAPUR-PUCANG = *Braya purpurascens-Puccinellia angustata* comm., DRYINT-SALARC = *Dryas integrifolia-Salix arctica* comm., SALROT-CARAQU = Salici rotundifoliae-Caricetum aquatilis, JUNBIG-DRYINT = Junco biglumis-Dryadetum integrifoliae, DRYINT-CARBIG = Dryado integrifoliae-Caricetum bigelowii, SCOSCO-CARAQU = *Scorpidium scorpioides-Carex aquatilis* comm., CLA-VACVIT = Cladino-Vaccinietum vitis-idaeae, SPH-ERIVAG = Sphagno-Eriophoretum vaginati, ANTJUR-JUNBIG = *Anthelia juratzkana-Juncus biglumis* comm. Plant communities associated with cryoturbation activity are marked with *.

chens (Fig. 20). Nonsorted circles exhibit lichen cover values ranging from 21 to 43 %, whereas the surrounding tundra plots reach a maximum of only 5 %. Nonsorted circles support all three growth forms of lichens, with crustose lichens reaching their maximum cover in the northern sites and fruticose lichen covers increasing towards the south. Foliose lichens are rare on northern nonsorted circles and are only a minor component in the south. In contrast, stable tundra communities do not support the growth

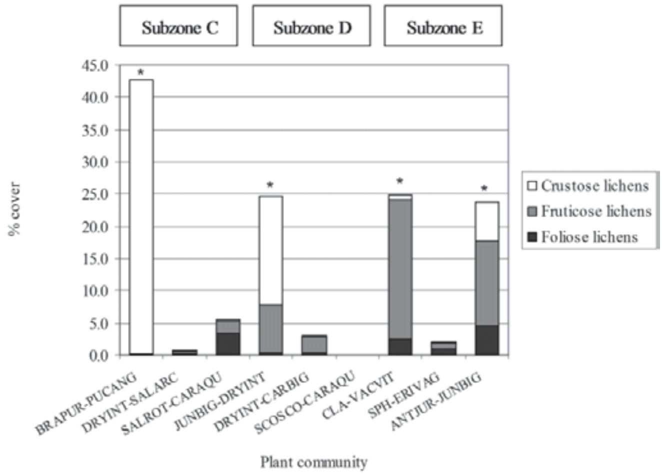

Fig. 20. Analysis of lichen cover of the cryoturbated tundra communities based on their growth form. See Fig. 19 for key to plant communities.

of crustose lichens but have small amounts of both fruticose and foliose lichens.

An analysis of the floristic affinities of the vascular plants within each plant community is presented in Fig. 21. The analysis considers the flora in three ways modified from the criteria by Walker (1985): major regional units, northern limits of species distribution and geographic range. When comparing plant communities of nonsorted circles and adjacent tundra areas within a subzone, differences are slight. All communities are dominated by arctic-alpine species, which proportion ranges from 39–70 %. In general, nonsorted circles seem to support a slightly larger proportion of species with distribution limits farther in the north. Nonsorted circles in subzones C and D support also relatively more North American species, whereas the surrounding tundra communities show a greater proportion of circumpolar species.

Along the bioclimate gradient, the proportion of coastal and arctic-alpine species decreases towards the south from 18 to 0 % and from 70 to 39 %, respectively, whereas the importance of arctic-boreal species increases from 0 to 31 % (Fig. 21). The plant communities at the northern end of the bioclimate gradient have a great proportion of species with northern distribution limits in Zone 1 or 2 (up to 36 % and 48 %, respectively), whereas more than half of the species in southern communities have their distribution limits in Zone 3. However, species with rather warm distribution limits in Zone 4 do not occur in the southern plant communities in subzone E. Most Zone 4 species are *Carex* species limited to the moist nonacidic graminoid tundra in subzone D in this study. All communities are dominated by species with circumpolar ranges, with the importance of circumpolar species increasing towards the south. In contrast, species with their geo-

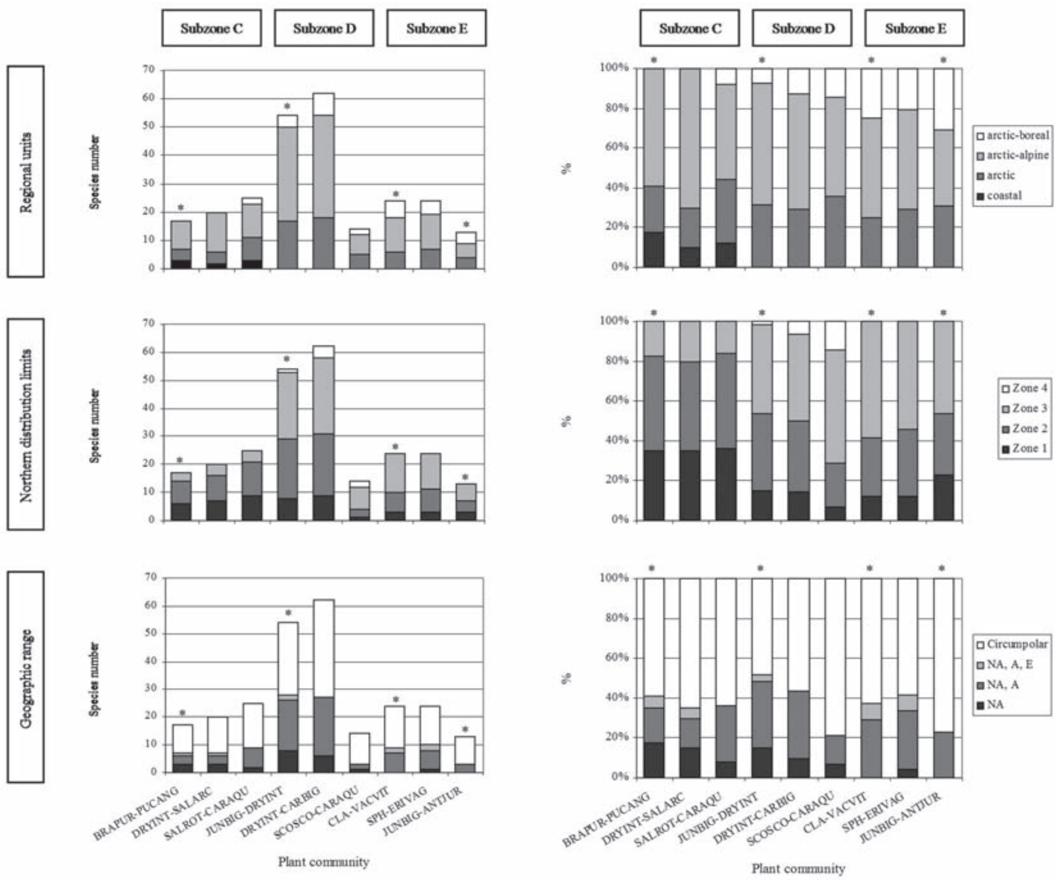

Fig. 21. Floristic analysis for vascular species of the cryoturbated tundra communities. The major regional units, northern distribution limits and geographic ranges are shown as total species numbers and percent values. See Fig. 19 for key to plant communities. Key to geographic range units: NA = North America, A = Asia, E = Europe.

graphic range limited to Northern America occur mostly in the northern sites.

4.5 Soil properties

Physical soil properties vary among the different plant communities. Frost-heave communities have greater amounts of bare soil and very thin organic horizons, resulting in lower moisture values of the mineral soil due to evaporation when compared to adjacent tundra communities (Fig. 22). The amount of bare ground decreases along the climate gradient from north to south. The depth of the organic horizons and soil moisture are greatest in

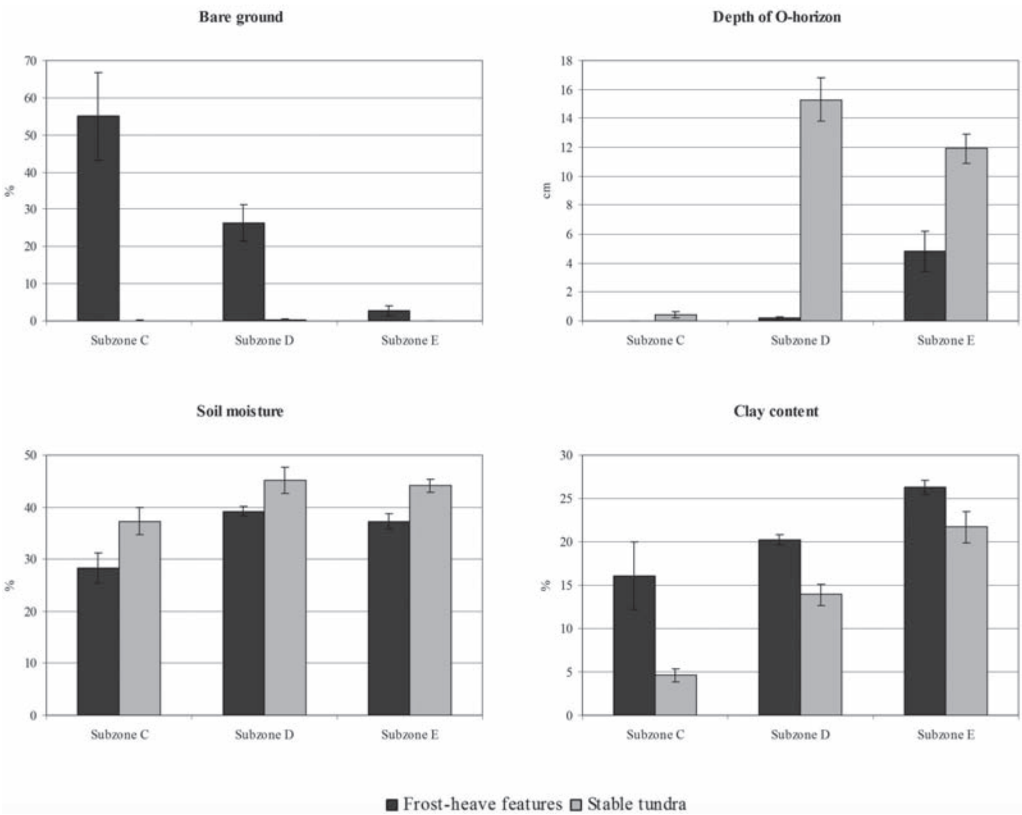

Fig. 22. Soil physical properties of frost-heave features and adjacent stable tundra sites for the different climatic subzones. Means and standard errors for the cover of bare ground, depth of the organic horizon, volumetric soil moisture and clay content are shown.

the stable tundra in subzone D and lowest for the bare nonsorted circles in subzone C. Bulk density of the mineral soil is generally slightly greater for the frost-heave communities than the surrounding tundra, which might be explained by the different soil textures. When comparing frost-heave features and adjacent tundra within a subzone, the frost-heave features have greater clay contents and less coarse-textured materials (Fig. 22), indicating that sorting caused by frost heave is moving coarser materials to the edges of the frost-heave features. Soil texture also varies along the climate gradient, with clay content increasing from north to south. This is caused by the older, more weathered glacial surfaces at the southern end of the gradient when compared to the relatively young alluvial and eolian parent materials on the coastal plain.

The chemical characteristics of the mineral soils associated with the different plant communities depend strongly on soil reaction. Soil pH averages 8.1 in the nonacidic nonsorted circles and 7.7 in the nonacidic stable tundra and drops to 5.2 in the acidic tundra (Fig. 23). Frost-heave features have often slightly higher pH values than the adjacent tundra, which can be explained by the lack of thick organic horizons and thus less input of leached organic acids. Total C is greater in the nonacidic tundra than in acidic tundra communities (Fig. 23). Inorganic C in the form of carbonates, e.g. $CaCO_3$, is most likely responsible for the greater total C values at

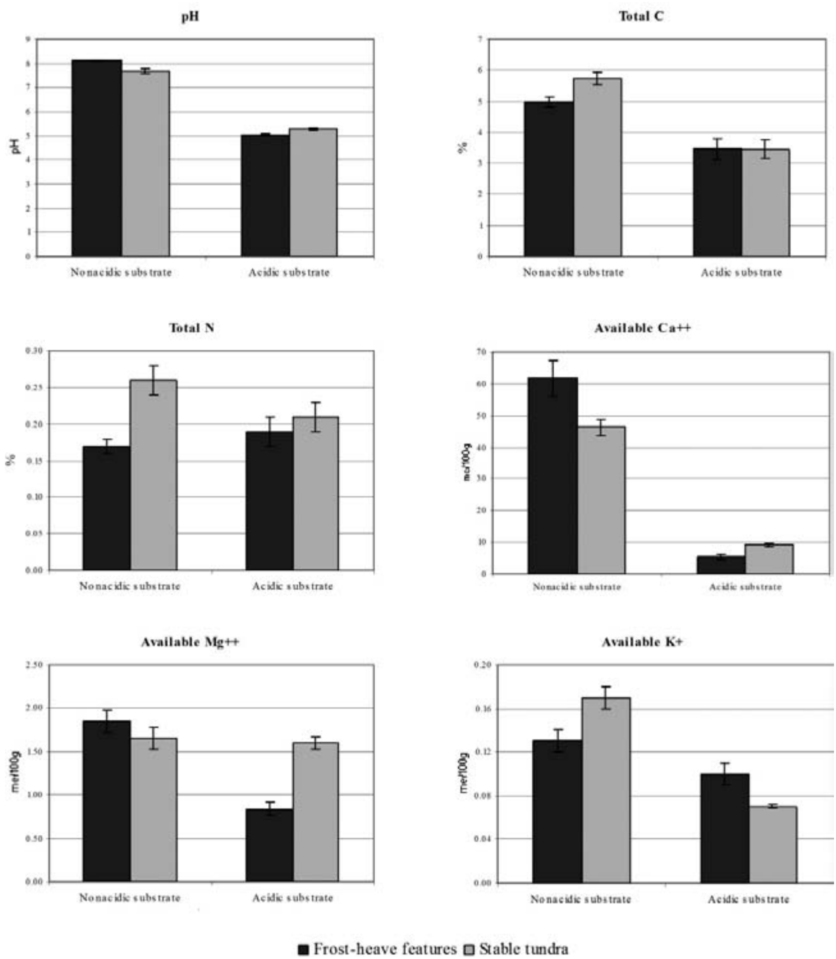

Fig. 23. Soil chemical properties of frost-heave features and stable tundra sites on nonacidic and acidic substrates. Means and standard errors for pH, total C, total N, available Ca^{2+}, available Mg^{2+} and available K^+ are shown.

nonacidic sites (Ping, pers. comm.), which is supported by the high Ca^{2+} contents at these sites. The calcium-rich carbonates are blown into the sites from the Sagavanirktok River in the form of loess. Total C is slightly lower in the nonacidic frost-heave features (5.0 %) than in the surrounding tundra (5.8 %). Total N shows a similar pattern, with 0.17 % and 0.19 % in nonacidic and acidic frost-heave features, respectively, and 0.26 % and 0.21 % in the adjacent tundra sites (Fig. 23). These results can be explained by less plant biomass in the frost-heave communities and therefore less decomposable material in the soils.

Loess input and pH levels also affect the availability of soil nutrients. The nonacidic nonsorted circles and stable tundra sites have relatively high contents of available Ca^{2+} (means 62 and 46 me/100g, respectively), Mg^{2+} (means 1.85 and 1.65 me/100g) and K^{+} (means 0.13 and 0.17 me/100g, Fig. 23). In contrast, the acidic frost-heave features and stable tundra are low in available Ca^{2+} (means 6 and 9 me/100g, respectively), Mg^{2+} (means 0.84 and 1.59 me/100g) and K^{+} (means 0.10 and 0.07 me/100g). Available Na^{+} in the mineral soil decreases along the climate gradient from 2.23 me/100g in the north to 0.01 me/100g in the south (Fig. 24). The decrease in Na^{+} is correlated with increasing distance from the ocean and thus decreased salt inputs from the ocean spray. The nonsorted circles and small contraction-crack polygons in subzone C have especially high Na^{+} values. Proximity to the ocean and high evaporation from these barren features result in high salt concentrations in the surface horizon when compared to surrounding tundra areas. High Ca^{2+} concentrations were measured for soils of the Junco biglumis-Dryadetum integrifoliae, where thick $CaCO_3$ deposits cover the soil surface as marl.

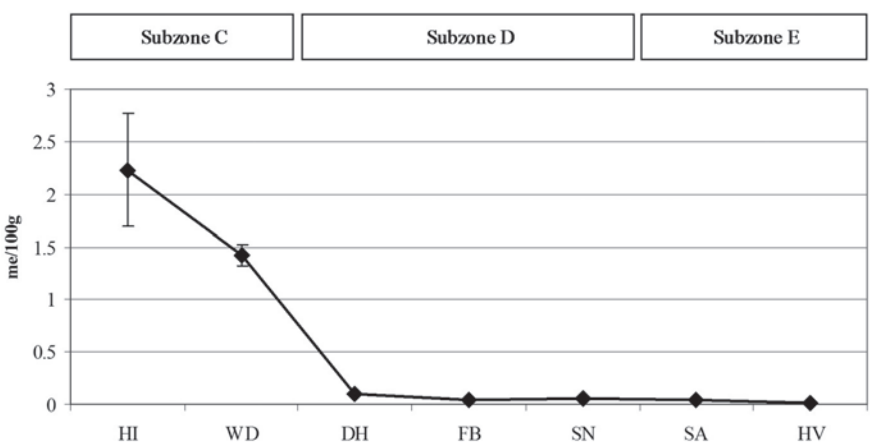

Fig. 24. Available Na^{+} of the mineral soils of the cryoturbated tundra. Means and standard errors are shown for each study site, which are listed from north to south. See Fig. 17 for key to the study sites.

4.6 Linkages between climate, frost heave and vegetation

The morphology of frost-heave features is strongly controlled by climate (Chernov & Matveyeva 1997, Walker et al. 2004). We found that at the northern sites in subzone C, the physical constraints of the harsh environment result in low plant cover and thin organic horizons on both frost-heave features and surrounding tundra. Further south in subzone D, physical processes dominate on frost-heave features and result in sparse vegetation. In contrast, biological processes dominate in the surrounding tundra due to the moderate climate, allowing for denser vegetation and thicker organic layers. Under the warmer climate of the southern-most sites in subzone E, biological processes dominate the landscape morphology and result in poorly developed frost-heave features. Both frost-heave features and the surrounding tundra are completely covered with vegetation and have thick organic horizons.

Climate change in arctic ecosystems is expected to have major effects on vegetation patterns, recession of permafrost and nutrient cycling (Chapin et al. 2004, Hinzman et al. 2005). An alteration of temperature and moisture regimes caused by global climate change will likely result in shifts of vegetation zones and species composition (Chapin et al. 1995). Cryogenic features are most strongly expressed in subzone C and become more vegetated towards the south. They should be highly susceptible to environmental change (Walker et al. 2004). A potential decline in cryoturbation activity due to increased biomass and permafrost degradation due to thawing (Chapin et al. 2004) could lead to local disappearance of frost-heave features in the arctic tundra and a decrease in landscape heterogeneity and biodiversity.

5 Conclusion

We found that well developed frost-heave features display tight linkages among soil, vegetation and cryoturbation activity. Frost-heave features show strong soil-surface disturbance due to needle-ice formation and frost cracking, having a negative impact on plant roots and resulting in little vegetation cover and shallow organic horizons. In turn, the sparse plant canopy provides only minimal insulation at the soil surface, which results in great thaw depths in late summer, reinforcing frost-heave activity.

We identified and described nine plant associations and communities in the cryoturbated arctic tundra: *Braya purpurascens-Puccinellia angustata* community (dry nonsorted circles, subzone C); *Dryas integrifolia-Salix arctica* community (dry tundra, subzone C); Salici rotundifoliae-Caricetum aquatilis ass. nov. (moist coastal tundra, subzone C); Junco biglumis-Dryadetum integrifoliae ass. nov. (moist nonsorted circles, subzone D); Dryado integrifoliae-Caricetum bigelowii Walker et al. 1994 (moist tundra, subzone D); *Scorpidium scorpioides-Carex aquatilis* community (wet tundra, subzone D); Cladino-Vaccinietum vitis-idaeae ass. nov. (dry nonsorted circles and earth hummocks, subzone E);

Sphagno-Eriophoretum vaginati Walker et al. 1994 (moist tundra, subzone E); and *Anthelia juratzkana-Juncus biglumis* community (wet nonsorted circles, subzone E).

The most important environmental factors resulting in the characteristic species composition of the community types described above are disturbance through cryoturbation, climate, soil pH and soil moisture. The DCA ordination displayed the vegetation types with respect to complex environmental gradients. The first axis of the DCA ordination corresponds to a complex bioclimate/pH gradient, where the percentage of bare soil and pH increase, while air temperature, elevation and shrub cover decrease. The second axis corresponds to a complex disturbance/soil moisture gradient.

Frost-heave features support a greater lichen and liverwort cover, whereas the adjacent tundra areas have a greater cover of dwarf shrubs, graminoids and mosses. The cover of lichens decreases along the bioclimate gradient, whereas the importance of mosses and liverworts increases from north to south. All communities are dominated by arctic-alpine species and taxa with circumpolar geographic ranges.

Frost-heave features have greater amounts of bare ground, thinner organic horizons and lower soil moisture when compared to the surrounding tundra. Soils in the nonacidic tundra are richer in plant-available nutrients than acidic soils, with coastal sites showing high Na^+ concentrations and having smooth soil surfaces due to soil dispersing. Ca^{2+} accumulates in nonsorted circles further inland and results in "cottage cheese" crusts due to aggregation and needle-ice formation.

In correspondence with other studies (Chernov & Matveyeva 1997, Walker et al. 2004), we found that the morphology of frost-heave features changes along the climatic gradient. Large, almost barren nonsorted circles with a high degree of contraction cracking dominate the landscape in the dry nonacidic tundra in subzone C. In subzone D, nonsorted circles show more vegetation cover and are smaller in diameter. Farther south, the less active nonsorted circles and earth hummocks have thick vegetation mats and resemble the adjacent tundra areas in species composition. Active nonsorted circles are small and sparsely distributed in subzone E.

Thawing of permafrost and a possible shift in plant community composition and vegetation zones might lead to a decline in frost-heave features. The potential loss of frost-heave features and the associated plant communities would especially impact areas with great floristic differences between frost-heave features and adjacent tundra and result in the loss of landscape heterogeneity.

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Appendix

Synoptic table of all vegetation communities. Species occurring in only one community type with constancy < II are omitted. Key to reference numbers: 1 *Braya purpurascens-Puccinellia angustata* comm., 2 *Dryas integrifolia-Salix arctica* comm., 3 Salici rotundifoliae-Caricetum aquatilis, 4 Junco biglumis-Dryadetum integrifoliae, 5 Dryado integrifoliae-Caricetum bigelowii, 6 *Scorpidium scorpioides-Carex aquatilis* com., 7 Cladino-vaccinietum vitis-idaeae, 8 Sphagno-Eriophoretum vaginati, 9 *Anthelia juratzkana-Juncus biglumis* comm.

Reference No.	1	2	3	4	5	6	7	8	9
Number of relevés	10	5	5	42	20	5	15	10	5
D Braya purpurascens-Puccinellia angustata comm.									
Braya glabella ssp. purpurascens	V^{1}	III	.	r^{+}	.	.	.	.	.
Fulgensia bracteata	V^{+}	.	.	.	.	.	.	.	.
Puccinellia angustata	V^{+}	.	.	.	.	.	.	.	.
Mycobilimbia lobulata	IV^{3}	.	.	I^{+}	r^{+}	.	.	.	.
Polyblastia bryophila	IV^{2}	.	.	.	.	.	.	.	.
Hennediella heimii var. arctica	IV^{1}	.	.	.	.	.	.	.	.
Potentilla uniflora	II^{+}	.	.	.	.	.	.	.	.
D Dryas integrifolia-Salix arctica comm.									
Salix ovalifolia	III^{+}	V^{2}	II^{2}	.	.	.	.	.	.
Ctenidium procerrimum	II^{+}	V^{2}	.	r^{+}	+$^{+}$	.	.	.	.
Chrysanthemum integrifolium	II^{+}	V^{1}	.	III^{+}	+	.	.	.	.
Festuca baffinensis	.	V^{+}	.	.	.	.	.	.	.
Cerastium beeringianum	II^{+}	V^{+}	.	.	.	.	.	.	.
Melandrium apetalum	.	V^{+}	I^{+}	r^{+}	.	.	.	.	.
Stellaria longipes	.	V^{+}	II^{+}	.	+$^{+}$	.	.	.	.
Tortula ruralis	II^{+}	IV^{1}	.	r^{+}	.	.	.	.	.
Artemisia campestris ssp. borealis var. borealis	I	IV^{+}	.	.	.	.	.	.	.
Didymodon asperifolius	.	III^{+}	.	.	.	.	.	.	.
Abietinella abietina	.	II^{1}	.	.	r^{+}	.	.	.	.
D Salici rotundifoliae-Caricetum aquatilis									
Salix rotundifolia	.	.	V^{2}	.	.	.	.	.	.
Nephroma expallidum	.	.	IV^{2}	.	r	.	I^{+}	II^{+}	.
Cladonia pyxidata	.	.	IV^{+}	+$^{+}$	II^{+}	.	I^{+}	.	.
Poa arctica	.	.	IV^{+}	.	r^{+}	.	.	.	.
Saxifraga cernua	.	.	III^{+}	.	.	.	.	.	.
Dicranum majus	.	.	III^{+}	.	.	.	.	.	.
Myurella tenerrima	.	.	III^{+}	.	.	.	.	.	.
Sanionia uncinata	.	.	III^{+}	r^{2}	.	.	.	.	.
Polytrichastrum alpinum	.	.	II^{1}	.	.	.	.	+$^{+}$	.
Cladonia ecmocyna	.	.	II^{+}	.	.	.	.	.	.
Cladonia furcata	.	.	II^{+}	.	.	.	.	.	.
Lecidea ramulosa	.	.	II^{+}	.	.	.	.	.	.
D Junco biglumis-Dryadetum integrifoliae									
Cladonia pocillum	.	.	II^{+}	V^{+}	II^{+}	.	.	+$^{+}$	.
Carex capillaris	.	.	.	IV^{+}	I^{+}	.	.	.	.
Aneura pinguis	.	I^{+}	II^{+}	IV^{+}	.	I^{+}	.	+$^{+}$	.
Solorina bispora	.	.	I^{+}	IV^{+}	I^{+}	.	.	.	.
Senecio resedifolius	.	.	.	III^{+}	+$^{+}$	.	.	.	.
Bryum wrightii	.	.	.	III^{+}	.	.	.	.	.
Vulpicida tilesii	.	.	.	II^{1}	r^{+}	.	.	.	.
Antennaria friesiana	.	.	.	II^{+}	r^{+}	.	.	.	.
Juncus triglumis	.	.	.	II^{+}	.	.	.	.	.
Minuartia rossii	.	.	.	II^{+}	.	.	.	.	.
Hymenostylium recurvirostre	.	.	.	II^{+}	.	.	.	.	.
Nostoc commune	.	.	.	II^{+}	.	.	.	.	.
D Dryado integrifoliae-Caricetum bigelowii									
Carex bigelowii	.	.	I^{1}	.	V^{2}	III^{+}	III^{2}	III^{1}	.
Salix reticulata	.	.	II^{1}	III^{1}	V^{2}	.	.	.	.
Arctostaphylos rubra	.	.	.	II^{+}	IV^{2}	.	+^{2}	.	.
Papaver macounii	.	.	.	I^{+}	IV^{+}	.	.	.	.
Saussurea angustifolia	.	.	.	+$^{+}$	III^{+}	.	.	+$^{+}$	.

Carex vaginata	.	.	.	.	II^{+}	.	.	.	.
Oxytropis maydelliana	.	.	.	r^{+}	II^{+}	.	.	.	.
Pedicularis langsdorfii	.	.	.	r^{+}	II^{+}	.	.	.	.
Saxifraga hieracifolia	.	.	.	.	II^{+}	.	.	.	.
D Scorpidium scorpioides-Carex aquatilis comm.									
Pedicularis sudetica ssp. albolabiata	.	.	II^{+}	.	II^{+}	V^{1}	.	.	.
Carex saxatilis	.	.	.	.	.	IV^{+}	.	.	.
Pedicularis parviflora	.	.	.	.	.	II^{+}	.	.	.
Limprichtia cossonii	.	.	.	.	.	II^{+}	.	.	.
D Cladino-Vaccinietum vitis-idaeae									
Cladina arbuscula	.	.	.	.	.	.	V^{2}	III^{+}	.
Racomitrium lanuginosum	.	.	.	.	.	.	IV^{2}	.	.
Dicranum spadiceum	.	.	I^{+}	.	II^{+}	.	IV^{1}	I^{+}	I^{+}
Cladonia uncialis	.	.	I^{+}	.	.	.	III^{1}	+$^{+}$	I^{+}
Pertusaria dactylina	I^{+}	.	.	.	.	.	III^{+}	+$^{+}$	.
Polytrichum hyperboreum	.	.	.	.	.	.	III^{+}	.	I^{+}
Rubus chamaemorus	.	.	.	.	.	.	II^{2}	.	.
Cladonia gracilis ssp. elongata	.	.	.	.	.	.	II^{1}	.	.
Cladonia cenotea	.	.	.	.	.	.	II^{+}	+$^{+}$	.
Lophozia ventricosa	.	.	.	.	.	.	II^{+}	.	.
D Sphagno-Eriophoretum vaginati									
Salix planifolia ssp. pulchra	.	.	III^{1}	.	.	.	I^{1}	V^{2}	II
Sphagnum warnstorfii	.	.	.	.	.	.	.	V^{2}	.
Sphagnum angustifolium	.	.	.	.	.	.	.	IV^{2}	.
Sphagnum girgensohnii	.	.	.	.	.	.	.	IV^{2}	.
Pedicularis lapponica	.	.	.	.	.	.	II^{+}	IV^{+}	I
Saxifraga nelsoniana	.	.	.	.	I^{+}	.	.	III^{+}	.
Cladonia cyanipes	.	.	.	.	.	.	+$^{+}$	II^{+}	.
Sphagnum balticum	.	.	.	.	.	.	.	II^{+}	.
Tritomaria quinquedentata	.	.	.	.	r^{+}	.	.	II^{+}	.
D Anthelia juratzkana-Juncus biglumis comm.									
Anthelia juratzkana	.	.	.	.	.	.	+$^{+}$	.	V^{1}
Dicranella subulata	.	.	.	.	.	.	.	.	V^{1}
Luzula arctica	.	.	.	.	.	.	I^{+}	+	III^{2}
Cephalozia bicuspidata	.	.	.	+$^{+}$	.	.	.	+$^{+}$	III^{+}
Jungermania confertissima	.	.	.	.	.	.	.	.	III^{+}
Lophozia sudetica var. sudetica	.	.	.	.	.	.	.	.	II^{+}
Pohlia cruda	.	.	.	.	.	.	.	.	II^{+}
Didymodon spadiceus	.	.	.	r^{+}	.	.	.	.	I^{1}
D Carici rupestris-Kobresietea bellardii: Dryadion integrifoliae									
Dryas integrifolia	+$^{+}$	V^{4}	IV^{2}	V^{2}	V^{2}	I	.	.	.
Hypnum bambergeri	.	II^{+}	II^{+}	IV^{1}	IV^{1}	.	.	.	.
Minuartia arctica	.	IV^{+}	I^{+}	II^{1}	III^{+}	.	.	.	.
Saxifraga oppositifolia	+$^{+}$	V^{1}	.	V^{1}	II^{+}	.	.	.	.
Pedicularis capitata	I	V^{+}	.	II^{+}	IV^{+}	.	.	+$^{+}$	.
Carex rupestris	.	I	.	II^{+}	I^{+}	.	.	.	.
Lloydia serotina	.	I^{+}	.	I^{+}	.	.	.	.	.
Pedicularis kanei	.	.	.	III^{+}	IV^{+}	.	I^{+}	.	.
Tofieldia pusilla	.	.	.	IV^{+}	II^{+}	.	.	.	.
Carex scirpoidea	.	.	.	II^{+}	II^{+}	.	.	.	.
Silene acaulis	.	.	.	I^{1}	II^{+}	.	.	.	.
Rhododendron lapponicum	.	.	.	I^{1}	+$^{+}$	.	.	.	.
Kobresia myosuroides	.	.	.	r^{+}	I^{1}	.	.	.	.
D Scheuchzerio-Caricetea nigrae									
Carex aquatilis	.	.	V^{3}	.	r^{+}	IV^{+}	.	.	.
Campylium stellatum	I^{+}	III^{+}	IV^{+}	III^{+}	II^{1}	III^{+}	.	.	.
Equisetum variegatum	.	.	I^{+}	III^{+}	IV^{+}	V^{+}	.	.	.

Eriophorum angustifolium ssp. triste	.	.	V^{2}	V^{1}	V^{3}	.	.	.	.
Bryum pseudotriquetrum	.	I^{+}	IV^{+}	I^{+}	II^{+}	.	.	.	.
Limprichtia revolvens	.	.	IV^{+}	.	I^{+}	.	.	.	.
Hierochloe pauciflora	.	.	III^{+}	.	.	.	.	.	.
Saxifraga hirculus	.	.	III^{+}	.	.	.	.	.	.
Oncophorus wahlenbergii	.	.	II^{2}	.	.	.	.	.	.
Cinclidium arcticum	.	.	II^{+}	$+^{+}$	I^{+}	.	.	.	.
Cinclidium latifolium	.	.	II^{+}	.	.	.	.	.	.
Dupontia fisheri	.	.	II^{+}	.	.	.	.	.	.
Eriophorum angustifolium ssp. subarcticum	.	.	.	I^{1}	II^{3}	V^{4}	.	.	.
Scorpidium scorpioides	.	.	.	.	$+^{+}$	V^{1}	.	.	.
Carex atrofusca	.	.	.	r^{1}	$+^{+}$	III^{+}	.	.	.
Carex rariflora	.	.	.	.	.	II^{+}	.	.	.
D Loiseleurio-Vaccinietea									
Betula nana	.	.	.	.	.	.	V^{2}	V^{2}	V^{+}
Ledum palustre ssp. decumbens	.	.	.	.	.	.	V^{2}	V^{2}	V^{1}
Vaccinium vitis-idaea	.	.	.	.	r^{+}	.	V^{2}	V^{2}	V^{1}
Flavocetraria cucullata	.	.	II^{+}	IV^{1}	IV^{1}	.	V^{1}	V^{+}	III^{2}
Dicranum elongatum	.	.	I^{+}	.	I^{2}	.	V^{2}	IV^{1}	.
Empetrum nigrum ssp. hermaphroditum	.	.	.	.	+	.	IV^{2}	IV^{2}	III^{+}
Cladonia amaurocraea	.	.	I^{+}	r	I^{+}	.	IV^{+}	IV^{+}	III^{+}
D Non-sorted circles									
Lecanora epibryon	III^{1}	I^{+}	.	IV^{1}	.	.	.	.	.
Polyblastia sendtneri	IV^{2}	.	.	IV^{2}	.	.	.	.	.
Juncus biglumis	$+^{+}$	.	.	IV^{+}	.	.	.	.	III^{+}
D Subzone C and non-sorted circles in subzone D									
Androsace chamaejasme	II^{+}	III^{+}	.	r^{+}	.	.	.	.	.
Lophozia collaris	I^{+}	II^{+}	.	II^{+}	.	.	.	.	.
Rinodina roscida	$+^{+}$	II^{+}	.	II^{+}	.	.	.	.	.
Orthothecium varia	II^{+}	I^{+}	.	r^{+}	.	.	.	.	.
D Nonacidic tundra									
Distichium capillaceum	$+^{+}$	III^{2}	III^{2}	V^{1}	IV^{1}	III^{+}	.	.	.
Salix arctica	$+^{+}$	V^{2}	V^{1}	III^{+}	IV^{2}	V^{+}	.	$+^{+}$	.
Polygonum viviparum	$+^{+}$	V^{+}	III^{+}	V^{+}	V^{+}	.	.	.	.
Distichium inclinatum	II^{1}	II^{2}	II^{+}	II^{+}	II^{1}	.	.	.	.
Didymodon rigidulus var. icmadophilus	$+^{+}$	I^{+}	.	r^{+}	$+^{+}$	.	.	.	.
Cirriphyllum cirrosum	I^{+}	.	I^{+}	II^{+}	II^{+}	.	.	.	.
Ochrolechia frigida	+	.	II^{+}	II^{1}	r	.	.	.	.
Bryoerythrophyllum recurvirostre	I^{+}	.	II^{1}	r^{+}	r^{+}	.	.	.	.
Cochlearia officinalis	II^{+}	III^{+}	I	.	.	.	.	.	.
Encalypta alpina	I^{1}	.	.	II^{+}	I^{+}	.	.	.	.
Meesia uliginosa	.	.	II^{+}	II^{+}	$+^{+}$	I^{+}	.	.	.
Pseudocalliergon turgescens	.	.	I^{+}	r^{+}	I^{+}	I^{+}	.	.	.
Orthothecium chryseum	.	.	II^{+}	II^{+}	III^{1}	.	.	.	.
Drepanocladus brevifolius	.	.	I^{1}	r^{+}	II^{2}	.	.	.	.
Aulacomnium acuminatum	.	.	I^{+}	r^{1}	II^{1}	.	.	.	.
Carex misandra	.	.	I^{+}	$+^{+}$	$+^{+}$	.	.	.	.
Caloplaca tiroliensis	.	.	I^{+}	$+^{+}$	r^{+}	.	.	.	.
Catoscopium nigritum	.	.	.	II^{+}	II^{1}	III^{+}	.	.	.
Equisetum arvense	.	.	.	III^{1}	II^{+}	I	.	.	.
Salix lanata ssp. richardsonii	.	.	.	r^{+}	III^{2}	II^{+}	.	.	.
Orthothecium strictum	.	.	.	II^{+}	I^{+}	I^{+}	.	.	.
Carex membranacea	.	.	.	IV^{1}	V^{1}	.	.	.	.
Cardamine hyperborea	.	.	.	IV^{+}	IV^{+}	.	.	.	.
Astragalus umbellatus	.	.	.	III^{+}	II^{1}	.	.	.	.
Parrya nudicaulis	.	.	.	II^{+}	III^{+}	.	.	.	.
Lupinus arcticus	.	.	.	I^{1}	II^{1}	.	.	.	.

D Moist tundra									
Cetraria islandica	.	.	V^{+}	IV^{+}	IV^{+}	.	III^{+}	III^{+}	IV^{+}
Dactylina arctica	.	.	V^{+}	II^{+}	IV^{+}	.	V^{+}	V^{+}	III^{+}
Peltigera leucophlebia	.	.	I^{1}	r^{+}	$+^{+}$	.	IV^{1}	III^{+}	II^{2}
Cladonia gracilis	.	.	II^{+}	r^{+}	I^{+}	.	I^{1}	$+^{+}$	II^{+}
Blepharostoma trichophyllum	.	.	II^{+}	II^{+}	r^{+}	.	$+^{+}$	III^{1}	.
Senecio atropurpureus	.	.	I^{+}	III^{+}	V^{+}	.	III^{+}	IV^{+}	.
Peltigera aphthosa	.	.	II^{+}	r^{+}	I^{+}	.	II^{1}	II^{1}	.
Aulacomnium palustre	.	.	III^{+}	r^{+}	r^{+}	.	$+^{+}$	II^{+}	.
Cassiope tetragona	.	.	.	I^{+}	IV^{1}	.	V^{1}	V^{2}	IV^{1}
Vaccinium uliginosum	.	.	.	r	II^{+}	.	I^{+}	II^{1}	III^{+}
Pertusaria panyrga	.	.	.	I^{2}	I^{+}	.	II^{+}	$+^{+}$	I^{2}
Alectoria nigricans	.	.	I^{+}	r^{+}	.	.	I^{+}	$+^{+}$	.
Flavocetraria nivalis	.	.	.	III^{+}	III^{+}	.	II^{+}	I^{+}	.
Rhytidium rugosum	.	.	.	I^{+}	III^{1}	.	II^{1}	$+^{+}$	.
Hypogymnia subobscura	.	.	I^{+}	r^{+}	.	.	I^{+}	.	.
Cladonia squamosa	.	.	I	r^{+}	.	.	$+^{+}$	.	.
Polytrichum strictum	.	.	III^{+}	.	.	.	II^{+}	$+^{+}$	.
Dicranum angustum	.	.	II^{+}	.	.	.	I^{+}	III^{1}	.
Sphaerophorus globosus	.	.	I^{+}	.	.	.	I^{+}	I^{+}	.
D Acidic tundra									
Aulacomnium turgidum	.	.	I^{+}	r^{+}	II^{2}	.	V^{1}	V^{2}	III^{+}
Cladina rangiferina	.	.	.	.	.	.	V^{2}	IV^{+}	III^{2}
Polygonum bistorta var. plumosum	.	.	.	r^{+}	I^{+}	.	V^{2}	V^{1}	I^{+}
Anastrophyllum minutum	.	.	.	.	$+^{+}$	.	IV^{1}	IV^{1}	II^{+}
Cladina stygia	.	.	.	.	.	.	III^{1}	IV^{+}	I^{+}
Cladonia fimbriata	.	.	.	.	r^{+}	.	III^{+}	II^{+}	III^{+}
Ptilidium ciliare	.	.	.	.	I^{1}	.	II^{1}	IV^{+}	I^{+}
Cladonia coccifera	.	.	.	.	r^{+}	.	I^{+}	$+^{+}$	I^{1}
Petasites frigidus	.	.	.	.	.	.	IV^{2}	V^{+}	.
Dicranum acutifolium	.	.	.	r^{+}	r^{+}	.	III^{+}	III^{1}	.
Pleurozium schreberi	.	.	.	.	r^{+}	.	III^{1}	III^{+}	.
Cetraria laevigata	.	.	.	.	$+^{+}$	.	II^{+}	III^{+}	.
Peltigera scabrosa	.	.	.	.	$+^{+}$	.	II^{+}	III^{+}	.
Dicranum groenlandicum	.	.	.	.	.	.	II^{2}	II^{1}	.
Cladonia gracilis ssp. vulnerata	.	.	.	.	.	.	II^{1}	II^{+}	.
Cladonia deformis	.	.	.	.	.	.	II^{+}	II^{+}	.
Pedicularis labradorica	.	.	.	.	.	.	II^{+}	II^{+}	.
Pedicularis oederi	.	.	.	.	.	.	II^{+}	II^{+}	.
Peltigera malacea	.	.	.	.	r^{+}	.	II^{+}	II^{+}	.
Salix phlebophylla	.	.	I^{+}	.	.	.	II^{1}	I^{+}	.
Barbilophozia binsteadii	.	.	.	.	.	.	I^{+}	II^{+}	.
Hypnum holmenii	.	.	.	.	.	.	I^{+}	II^{+}	.
Nephroma arcticum	.	.	.	.	.	.	I^{+}	II^{+}	.
Cladonia chlorophaea	.	.	.	.	.	.	III^{+}	.	II^{1}
Cladina mitis	.	.	.	.	.	.	II^{2}	.	II^{+}
Lophozia excisa	.	.	.	.	.	.	I^{+}	.	I^{+}
Lophozia ventricosa	.	.	.	.	.	.	.	II^{+}	II^{+}
Other taxa									
Ditrichum flexicaule	$+^{+}$	V^{2}	I^{+}	V^{1}	V^{1}	III^{+}	II^{+}	II^{+}	I^{+}
Thamnolia subuliformis	II^{+}	V^{+}	V^{+}	V^{1}	V^{1}	.	IV^{+}	III^{+}	.
Hylocomium splendens	.	IV^{+}	IV^{+}	$+^{+}$	II^{3}	.	V^{2}	V^{2}	V^{1}
Arctagrostis latifolia	+	.	.	III^{+}	III^{+}	.	IV^{2}	II^{+}	I^{+}
Eriophorum vaginatum	.	.	.	III^{1}	IV^{2}	IV^{+}	II^{1}	V^{3}	V^{1}
Tomentypnum nitens	.	II^{1}	IV^{1}	IV^{1}	V^{3}	.	.	IV^{+}	.