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Plant communities of a tussock tundra landscape in the Brooks Range Foothills, Alaska

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Abstract. We present the first vegetation analysis from the Arctic Foothills of northern Alaska according to the Braun-Blanquet approach. The data are from the Innvait Creek and Toolik Lake regions. We focus on associations of dry and mesic upland surfaces and moderate snow accumulation sites; other upland plant communities, i.e. those of blockfields, non-sorted circles, and water tracks, are briefly described. Summary floristic information is presented in a synoptic table. Five associations and 15 community types are tentatively placed into seven existing syntaxonomical classes. The community descriptions are arranged according to habitat: dry exposed acidic sites, moist acidic shallow snowbeds, moist non-acidic snowbeds, moist acidic uplands, and moist non-acidic uplands. Many of the communities are Beringian vicariants of associations previously described from Greenland and the European Arctic. The described communities have a widespread distribution in northern Alaska. The relationship of the associations to complex environmental gradients are analyzed using Detrended Correspondence Analysis. Community composition is controlled primarily by mesotopographic relationships (slope position and soil moisture), microscale disturbances, and factors related to long-term landscape evolution.

Keywords: Classification; DCA; *Eriophorum vaginatum*; Gradient analysis; *Sphagnum*; Syntaxonomy; Vicariant.

Abbreviations: DCA = Detrended Correspondence Analysis; NTR = Nomenclatural type relevé.

Nomenclature: D.F. Murray, Electronic authority file, Herbarium, University of Alaska, Fairbanks, AK, USA; identifications verified by David Murray (vascular taxa) and Barbara Murray (cryptogamic taxa); voucher specimens deposited at Fairbanks.

Introduction

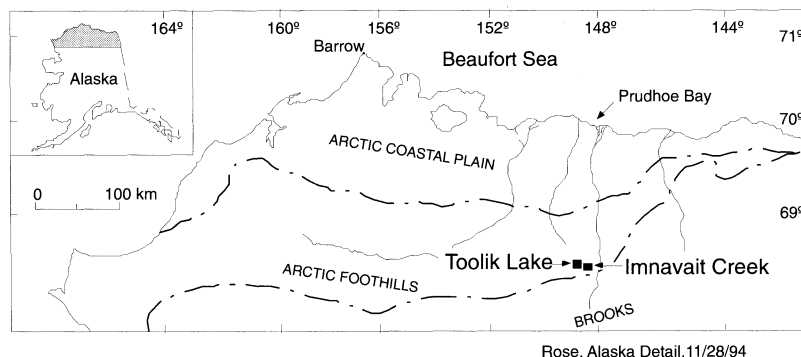
Tussock tundra dominates upland arctic landscapes in Alaska, northwestern Canada, and northeastern Russia (Bliss & Matveyeva 1992). The term 'tussock' refers

to the physiognomy of the tussock-forming sedge *Eriophorum vaginatum*. The range of *E. vaginatum* extends throughout the Arctic, except for the eastern half of North America and Greenland. Tussock tundra has been described in many areas of northern Alaska (e.g. Hanson 1951, 1953; Churchill 1955; Bliss 1956, 1962; Spetzman 1959; Douglas & Tedrow 1960; Johnson et al. 1966; Lambert 1968; D.A. Walker et al. 1982). Some of these studies have touched on the variation that occurs within tussock tundra with respect to topography, hydrology and soils, but there remains a general impression that tussock tundra is a uniform vegetation type that varies little over vast areas of the Arctic. Here we present a classification and ordination analysis of tussock tundra vegetation that accounts for some of its considerable variability, particularly along pH gradients.

The tussock tundra landscapes of the Toolik Lake and Innvait Creek region of Alaska's Brooks Range Foothills have been the focus of many ecosystem-level research programs over the past 20 years (e.g. Shaver et al. 1986, 1991; Chapin et al. 1988; Oechel 1989; Hobbie et al. in press). A multiple-scale, hierarchical geographic information system (GIS) is under development for the Innvait Creek and Toolik Lake region to support ongoing projects (D.A. Walker & M.D. Walker 1991 in press). The GIS provides a regional geobotanical framework for ecosystem models, remote-sensing studies, and other studies that extrapolate key ecosystem traits, such as soil carbon, net primary production, and trace-gas fluxes, to a broader region. The classification of the major vegetation types described here is used as a foundation for the vegetation map units in the GIS.

This is the first application of the Braun-Blanquet approach to the vegetation of the Alaskan arctic foothills. Other vegetation analyses of the North American Arctic that have used the Braun-Blanquet approach include unpublished dissertations by Lambert (1968) and Barrett (1972), and Thannheiser's (e.g. 1976, 1987 a,b) coverage of coastal and wetland vegetation of the Canadian Arctic. Cooper (1986) presented a classification of the

Fig. 1. The North Slope of Alaska, showing major physiographic provinces and locations of Toolik Lake and Imnavait Creek intensive study areas.



vegetation of the Arrigetch Creek area in the Brooks Range of Alaska, an alpine site to the south of arctic treeline. Komárková (1993, Komárková & McKendrick 1988; Komárková & Webber 1980) used the Braun-Blanquet approach to describe a wet coastal plain ecosystem at Atkasook, Alaska. Komárková's work is by far the most complete analysis of a tussock-tundra landscape, but the descriptions of the associations are not yet published. Our paper presents the first formal Braun-Blanquet descriptions from the arctic foothills. Forthcoming descriptions from Atkasook, other sites in northern Alaska, and Siberia should give a more complete picture of the regional variability of tussock tundra.

Study area

The study area encompasses two research sites, Toolik Lake and Imnavait Creek (Fig. 1). Both sites are in the Southern Arctic Foothills physiographic subprovince of the Alaskan North Slope (Wahrhaftig 1965). The region lies north of the Brooks Range, a northwestern extension of the Rocky Mountain Cordillera. It is treeless and underlain by continuous permafrost, 250–300 m thick (Osterkamp & Payne 1981). The steep mountains of the Brooks Range give way abruptly to the gently-sloping Arctic Foothills, which are characterized by broad ridges, irregular buttes, mesas, and intervening rolling tundra plains (Selkregg 1975). The terrain varies in elevation from about 180 m at the northern edge of the foothills to over 1050 m, with local relief as much as 750 m, although most hills are considerably smaller. The hills are dissected by water tracks, beaded and meandering streams, and braided rivers, the majority of which flow northward toward the Beaufort Sea (D.A. Walker et al. 1989; M.D. Walker et al. 1989; D.A. Walker & M.D. Walker in press).

The landscapes of the two sites are quite different due primarily to different glacial histories. The Imnavait Creek site (68° 37' N, 148° 18' W) is located in the headwaters of Imnavait Creek, a small beaded tributary of the Kuparuk River. The site is on Sagavanirktok

(mid-Pleistocene) glacial drift (Hamilton 1986). Hills around Imnavait Creek are mostly gently rolling, rising less than 100 m from the valley bottoms to the ridge crests, and elongated in a NNW direction. Elevation at the site varies from about 770 m to about 980 m (D.A. Walker et al. 1989).

The Toolik Lake area (68° 37' N, 149° 32' W) is a younger landscape glaciated during the late Pleistocene. It includes large areas of Itkillik I (deglaciated ca. 60 000 yr) and Itkillik II (deglaciated about 10 000 yr) glacial drifts (Hamilton 1986). The Toolik Lake landscape is dotted with small glacial lakes, kames, and moraines and is more heterogeneous than the Imnavait Creek landscape (M.D. Walker in press). Elevations range from about 670 to 850 m.

The Foothills climate has some of the warmest summer temperatures and coldest winter temperatures on the North Slope (Haugen 1982). Mean annual temperature (1985–1991) at Imnavait Creek is –7.5 °C, and total mean annual precipitation (1985–1990) is 330 mm (Hinzman et al. in press). The mean July air temperature is 10.9 °C; the mean January temperature is –21.5 °C. Ca. 33 % of the total precipitation falls as snow (10.9 cm water equivalent). Snow distribution is extremely variable due to redistribution by wind, but snow depth averages ca. 50 cm prior to melt, which occurs in early to late May. Prevailing winds, especially during winter, are primarily from the south, causing deep drifts to form on north-facing slopes. Hydrologic activity ceases in mid-September when the ground freezes. Because of its slightly higher elevation, snow remains at Imnavait Creek a few days longer than at Toolik Lake, and foggy conditions are more common, but otherwise climate differences between the sites are small (Hinzman et al. in press; Arctic LTER unpubl. data).

Methods

Field sampling

The vegetation classification is derived from 154

permanent plots, 73 at Imnavait Creek and 81 near Toolik Lake. The sampling was done during the periods of 1-10 August 1984 and 17 August - 4 September 1985 at Imnavait Creek and 1-26 August 1989 at Toolik Lake. We used the centralized replicate sampling procedure (Mueller-Dombois & Ellenberg 1974). Plot locations were subjectively chosen in areas of homogeneous vegetation that were representative of the major plant communities. Most vegetation plots were ca. 80 m², somewhat larger than the 10-50 m² recommended for heathland samples and within the 50-100 m² recommended for scrub communities (Westhoff & van der Maarel 1978). 21 plots contained mosaics of distinct homogeneous vegetation elements associated with microtopographic features such as frost scars, stone stripes and hummocks. In these cases, data from each element were kept separate, which increased the number of relevés by 11; thus in total 165 relevés were used. On the other hand, 11 samples were excluded from the classification because they represented ecotones, mixed communities, or single examples of non-extensive communities. All vascular, bryophyte, and lichen species were scored using the Braun-Blanquet cover-abundance scale (Mueller-Dombois & Ellenberg 1974). A small sample of each species was collected and returned to the laboratory for final identification.

A soil pit was dug immediately adjacent to each vegetation sample, and the soil was described and classified to the level of subgroup using U.S. Department of Agriculture standard methods (Anon. 1975). Soil samples were collected from all horizons in a subset of plots that represented the best example of each vegetation type. For the remaining plots, a single soil sample was collected from 10 cm depth (rooting zone for most tundra species). Other physical characteristics measured for each relevé were degree of slope, aspect, and rock cover. Snow depth was measured on each plot in mid-May 1994.

Percentage soil moisture was determined by drying field samples at 65 °C for 72 h and determining percentage weight loss. Organic matter was determined by the Walkley-Black procedure (Nelson & Sommers 1982). Particle size was determined by using sieves to separate the sand fraction (0.5-2 mm) and then separating silt and clay with the pipette method (Gee & Bauder 1986). Soil pH was determined with the saturated paste method (Jackson 1958) using a Chemtrix Type 400 pH meter. The terms acidic and non-acidic within this paper refer to U.S. soil taxonomy nomenclature (Anon. 1975), with acidic sites having pH < 5.0 and non-acidic sites having pH ≥ 5.0. Cations (Ca²⁺, Mg²⁺, K⁺) were extracted using the ammonium acetate method (Thomas 1982). The filtrate was analyzed using a Perkin-Elmer atomic absorption spectrophotometer model no. 2280. NO₃⁻ was

extracted with KCl (Keeney & Nelson 1982) and analyzed on a Dionex 2010i ion chromatograph (Dick & Tabatabai 1979).

Classification

Vegetation was classified using the Braun-Blanquet sorted-table method (Mueller-Dombois & Ellenberg 1974; Westhoff & van der Maarel 1978) and the specific protocol of Daniëls (1982) for distinguishing vegetation types. Community types are described as associations when we had more than 10 relevés available. All data are summarized in a synoptic table (App. 1). Individual relevé tables are presented for five formally named associations and four subassociations with the nomenclatural type relevé (NTR) indicated (Barkman et al. 1986). The faithful, differential and constant taxa comprise the set of diagnostic taxa for each community or group and forms the basis of the classification.

The synoptic table presents taxa with their constancy class in each community: r, present in < 5% of records; +, 5-10%; I, 11-20%; II, 21-40%; III, 41-60%; IV, 61-80%; V, ≥ 80%; taxa which did not reach constancy class II in at least one community, were omitted. For communities of four or fewer relevés, the actual number of occurrences is shown rather than the constancy class. Following the constancy class, the average Braun-Blanquet cover-abundance class value is shown. For the purpose of computing the average, class 'r' was converted to 0.4, and '+' to 0.7.

Ordination

Detrended Correspondence Analysis (DCA) ordination - program CANOCO, ter Braak (1987); species weighted equally, detrending by segments - was used to analyze relationships between variation in vegetation and environmental variation - five aquatic samples were not included in the ordinations because they share few or no species with the terrestrial samples, and including them gives the trivial result of separating terrestrial and aquatic sites. Following the ordination of all samples, a separate ordination was done for the dry and moist uplands (93 samples vs. 160 in the all-terrestrial sample ordination) in order to better characterize relationships within that portion of the landscape. DCA is based on a model of unimodal species response along gradients, and its performance at reconstructing gradients suffers when this assumption is not met, as well as from its rescaling algorithm, which somewhat arbitrarily repositions species along the gradient (Peet et al. 1988; van Groenewoud 1992). However, DCA, even if it does not perfectly reproduce complex gradients, produces first axes showing major directions of variation in the data

and the relationship of the classification to major environmental gradients (Peet et al. 1988; Økland 1992). Environmental variables were related to the ordination axes with biplot diagrams, which indicate the direction in the ordination diagram that has the maximum correlation with a particular environmental variable (Dargie 1984; Jongman et al. 1987).

Results: Classification

The classification resulted in five associations and 15 community types that have been provisionally placed into eight Braun-Blanquet classes (Table 1). In this section we focus on the communities of dry and mesic uplands within four classes: *Carici rupestris-Kobresietea bellardii* Ohba 74, *Cetrario-Loiseleurietea* Suzuki-Tokyo & Umezū in Suzuki-Tokyo 1964, *Oxycocco-Sphagnetum* Braun-Blanquet & Tüxen 1943 and *Scheuchzerio-Caricetum nigrae* (Nordhagen 1936) Tüxen 1937. For each type some characteristic vascular plants, mosses and lichens will be listed (indicated with v, m and l respectively). The descriptions of the vegetation types are arranged according to habitat:

- dry acidic exposed sites: *Selaginello sibiricae-Dryadetum octopetalae*, *Salici phlebophyllae-Arctietum alpinae*, *Hierochloë alpina-Betula nana* comm.;
- moist acidic shallow snowbeds: *Carici microchaetae-Cassiope tetragonae*;
- moist non-acidic shallow snowbeds: *Dryas integrifolia-Cassiope tetragona* comm.;
- moist acidic uplands: *Sphagno-Eriophoretum vaginatum*;
- moist non-acidic uplands: *Dryado integrifoliae-Caricetum bigelowii*.

Dry acidic uplands

Plant communities of dry uplands fall in two classes: *Carici rupestris-Kobresietea bellardii*, including *Dryas octopetala* dominated vegetation on exposed south facing slopes, and *Cetrario-Loiseleurietea* dry heath communities found on somewhat less exposed rocky sites.

Selaginello sibiricae-Dryadetum octopetalae **ass. nov.** (App. 1, col. 3; Table 2, NTR: TL60).

This community is dominated by the prostrate shrub *Dryas octopetala* ssp. *octopetala*, fruticose lichens, and many forbs that are locally uncommon. The association has high vascular plant and lichen diversity and relatively low moss diversity (means of 18, 22, and 5 respectively). *D. octopetala* is a faithful taxon - shared with the *Poa glauca-Arnica angustifolia* comm. (App. 1, col. 2) by virtue of its high cover and constancy; *Selaginella sibirica* has a relatively low cover but is

highly faithful to the association. Other faithful taxa are:

<i>Antennaria alpina</i> v	<i>Alectoria nigricans</i> l
<i>Melanelia septentrionalis</i> v	<i>Arctoparmelia separata</i> l
<i>Minuartia obtusiloba</i> v	<i>Coelocaulon aculeatum</i> l
<i>Oxytropis bryophila</i> v	<i>Hypogymnia subobscura</i> l
<i>Smelowskia calycina</i> v;	<i>Ochrolechia upsaliensis</i> l.

Other common taxa include:

<i>Anemone drummondii</i> v	<i>Polytrichum strictum</i> m
<i>Artemisia arctica</i> ssp. <i>arctica</i> v	<i>Rhytidium rugosum</i> m;
<i>Carex rupestris</i> v	<i>Alectoria ochroleuca</i> l
<i>Kobresia myosuroides</i> v	<i>Asahinea chrysantha</i> l
<i>Salix phlebophylla</i> v;	<i>Bryocaulon divergens</i> l
	<i>Cetraria</i> spp. l.

Typical microsites of this association include acidic, south-facing rocky hillslopes of kames, moraines, and sandstone outcrops. A somewhat depauperate version of the association occurs on rocky glacial outwash deposits. The sites are extremely windblown due to southerly wintertime katabatic winds blowing out of the Brooks Range; no snow was recorded on any of the permanent plots of this association in early May 1994, and similar snow distribution patterns have been observed in other years. The mean pH of the 11 samples in this association is 4.7 ± 0.2 . The soils thaw to depths > 100 cm by late summer. Soil organic matter content ($5.5 \pm 0.5\%$) and available $\text{NO}_3\text{-N}$ (4.5 ± 0.5 ppm) are low.

Dryas is the main vascular genus typifying dry sites throughout the Arctic, and it becomes more common at higher latitudes, where moisture is more limited (Rønning 1965; Barrett 1972; Yurtsev 1974; Aleksandrova 1980). In the Toolik Lake and Imnavait Creek region *Dryas octopetala* occurs on both acidic and non-acidic substrates and *Dryas integrifolia* occurs on non-acidic soils. In the Brooks Range, Cooper (1986) reported *D. octopetala* ssp. *alaskensis* as limited primarily to limestone areas; Elvebakk (1982) reported *D. octopetala* ssp. *octopetala* on Svalbard associated with soil pH between 5.5 and 8.0, but most abundant at pH > 7.0. In Fennoscandia, *Dryas*-dominated communities have been described from circumneutral to basic windblown sites (Nordhagen 1928; Rønning 1965). Lambert (1968), however, characterized *D. octopetala* in NW Canada as circumneutral to slightly acidic, while our data indicate that *D. octopetala* occurs primarily on acidic soils with relatively low available calcium (compared to *D. integrifolia*). Also, *D. integrifolia* is found from dry sites to moderately deep snowbeds, whereas *D. octopetala* occurs on sites with thin or no snow cover. Thus, there is apparently geographic variation in how these species respond to substrate chemistry and snow depth.

The syntaxonomic status of *Dryas*-dominated types, because of the taxonomic complexity of the genus *Dryas*, has also been in contention. Dierßen (1992) placed *Dryas octopetala* types in the *Caricion nardinae* Nordhagen 1935 and *Dryas integrifolia* types in the *Dryadion integrifoliae* (Ohba 1974) Daniëls 1982.

Table 1. Tentative class, community and association names, and habitats of the Imnavait Creek and Toolik Lake region.

Rhizocarpetea geographici	
<i>Cetraria nigricans-Rhizocarpon geographicum</i> comm.	Xeric, acidic, sandstone and conglomerate glacial erratics, and blockfields
Carici rupestris-Kobresietea bellardii	
<i>Poa glauca-Arnica angustifolia</i> comm.	Subxeric, exposed, non-acidic, animal dens, with deep rich soils
<i>Selaginello sibiricae-Dryadetum octopetalae</i>	Xeric, very exposed, acidic, rocky, south-facing slopes of kames, moraines, and sandstone outcrops
<i>Dryas integrifolia-Cassiope tetragona</i> comm.	Subxeric, well-drained, non-acidic, shallow snowbeds
Cetrario-Loiseleurietea	
<i>Carici microchaetae-Cassiope tetragona</i>	Subxeric, well drained, acidic shallow snowbeds
<i>Salici phlebophyllae-Arctoetum alpinae</i>	Subxeric, moderately exposed, acidic, rocky sites
<i>Hierochloë alpina-Betula nana</i> comm.	Subxeric, somewhat protected, acidic sites
Oxycocco-Sphagnetes	
<i>Sphagno-Eriophoretum vaginati</i>	Mesic to subhygric, acidic, uplands, moderate snow
<i>Sphagnum lenense-Salix fuscescens</i> comm.	Subhygric, acidic, hummocks, in poor fens
Scheuchzerio-Caricetea nigrae	
<i>Dryado integrifoliae-Caricetum bigelowii</i>	Mesic to subhygric, non-acidic, uplands and hummocks in fens
<i>Tomentypnum nitens-Trichophorum caespitosum</i> comm.	Subhygric, non-acidic hummocks in fens
<i>Sphagnum orientale-Eriophorum scheuchzeri</i> comm.	Hygric, acidic, poor fens
<i>Eriophorum angustifolium-Carex aquatilis</i> comm.	Hygric, non-acidic, fens
<i>Carex aquatilis-Carex chordorrhiza</i> comm.	Subhygric to hygric, non-acidic fens
<i>Hippuris vulgaris-Arctophila fulva</i> comm.	Hydric, marshes, pond margins
Potametea	
<i>Hippuris vulgaris-Sparganium hyperboreum</i> comm.	Hydric, beaded ponds, oxbow lakes
Betulo-Adenostyletea	
<i>Salix alaxensis-Salix lanata</i> comm.	Subhygric to subxeric, non-acidic, riparian margins, river bars
<i>Eriophorum angustifolium-Salix pulchra</i> comm.	Subhygric to hygric, non-acidic hillslope watertracks
Salicetea herbaceae	
<i>Salix rotundifolia</i> comm.	Mesic, non-acidic, deep snowbeds
<i>Anthelia juratzkana-Juncus biglumis</i> comm.	Subxeric, acidic, nonsorted circles.

Salici phlebophyllae-Arctoetum alpinae ass. nov. (App. 1, col. 6; Table 3, cols. 14-25, NTR: TL71)

Dry shallow snow accumulation sites support stands dominated by prostrate ericaceous species and fruticose lichens. The community has relatively low vascular plant and bryophyte diversity and high lichen diversity (mean of 10, 5, and 19 respectively). The dwarf shrub *Arctous alpina* is the sole faithful taxon of this association based on its high constancy and abundance. Other common dwarf shrubs include *Salix phlebophylla*, *Vaccinium uliginosum* and *V. vitis-idaea*, any of which can be dominant. *Bistorta plumosa* and *Hierochloë alpina* are also common. Common lichens and mosses include:

<i>Bryocaulon divergens</i> m	<i>Cladina rangiferina</i> l
<i>Dicranum</i> spp. m	<i>Cladonia pyxidata</i> l
<i>Polytrichum strictum</i> m;	<i>C. macrophylla</i> l
<i>Cetraria cucullata</i> l	<i>C. uncialis</i> l
<i>C. islandica</i> l	<i>Dactylina arctica</i> l
<i>C. nivalis</i> l	<i>Sphaerophorus globosus</i> l
<i>Cladina arbuscula</i> l	<i>Thamnia</i> spp. l.

This is a common association of dry, leached, rocky sites with shallow winter snow cover, such as on moderately windblown glacial outwash deposits, kames, and moraines. Typical microsites are very shallow depressions and areas with somewhat more snow than the very

windblown *Selaginello sibiricae-Dryadetum octopetalae* (mean of 5 ± 2 cm). The soils are only somewhat more organic-rich ($9.1 \pm 2.8\%$), and the soil $\text{NO}_3\text{-N}$ values are very low, 2.2 ± 0.5 ppm. The mean soil pH of the 12 samples is 4.0 ± 0.1 .

This is apparently a Beringian association, which may represent a vicariant of *Arctostaphylo-Alectorietum octopetalae* Du Rietz 1925. We included *Salix phlebophylla* in the name as an area differential taxon for Beringia. Associations of *Arctous alpina* and *Hierochloë alpina* have been reported from other areas in Alaska (Churchill 1955), from the Foothills zone of northern Canada (Lambert 1968), and from low arctic tundra of Siberia (Aleksandrova 1980).

Hierochloë alpina-Betula nana comm. (App. 1, col. 7)

This community is dominated by dwarf and low shrubs and fruticose lichens. It is floristically poorly characterized, but *Betula nana* reaches its maximum abundance here and defines the community. *Pedicularis labradorica* is a potential diagnostic taxon, with a low presence in other local communities. Constant taxa are:

Table 2. *Selaginello sibiricae*-*Dryadetum octopetalae*. Reference no. 1 = relevé IC58A, 2 = IC54, 3 = IC53, 4 = IC52, 5 = TL60 = NTR, 6 = TL47, 7 = TL07, 8 = TL18, 9 = IC33, 10 = IC42, 11 = TL46.

Reference no.	00000000011
Number of vascular taxa	12345678901
Number of bryophyte taxa	01222221112
Number of lichen taxa	80007625381
Total number of taxa	22335856858
	11112121222
	49932835575
	2343553455
	72264206804
Faithful and differential taxa shared with the <i>Poa glauca</i>-<i>Arnica angustifolia</i> comm.:	
<i>Dryas octopetala</i> var. <i>octopetala</i>	43334333331
<i>Selaginella sibirica</i>	++11++1+r1.
<i>Minuartia obtusiloba</i>	+++++++.+
<i>Bupleurum tritridatum</i> ssp. <i>arcticum</i>	..+1++r++.
<i>Carex rupestris</i>	+...++++.1.
<i>Anemone drummondii</i>	..1.1++...
<i>Encalypta rhaetocarpa</i>	..11.++++.
<i>Poa glauca</i>	..+++.++.
<i>Arnica angustifolia</i> ssp. <i>angustifolia</i>	...1+.++.
Faithful and differential taxa of the association:	
<i>Polytrichum piliferum</i>	+++.1+1++
<i>Hypogymnia subobscura</i>	..+1++1+
<i>Antennaria alpina</i> var. <i>media</i>	..+++.++.
<i>Alectoria nigricans</i>	++...+21.
<i>Oxytropis bryophila</i>	+1++++.
<i>Ochrolechia upsaliensis</i>	1.1+1....
<i>Arctoparmelia separata</i>	++...+1.
<i>Cetraria nigricans</i>	..+++.++.
<i>Coelocaulon aculeatum</i>	..+++.++.
<i>Melanella septentrionalis</i>	..+++.++.
<i>Smelowskia calycina</i>	+++.++.
Constants:	
<i>Bryocaulon divergens</i>	211+11122+
<i>Thamnia subuliformis</i> + <i>vermicularis</i>	1121+112+1
<i>Cetraria cucullata</i>	++1+1++2
<i>Cetraria nivalis</i>	+112.111+11
<i>Asahinea chrysantha</i>	1+...+11+
<i>Alectoria ochroleuca</i>	2+...+11+
<i>Salix phlebophylla</i>	..11++12+
<i>Sphaerophorus globosus</i>	1+...+11+
<i>Cetraria islandica</i>	++...+1.
<i>Stereocaulon alpinum</i> + <i>tomentosum</i>	..111+...1.
<i>Hierochloë alpina</i>	...+...+1+
<i>Cladonia amaurocraea</i>	...+...+1+
<i>Peltigera aphthosa</i>	+1+...+1+
Other taxa:	
<i>Rhytidium rugosum</i>	...11+...1+
<i>Cladonia uncialis</i>	..+++.++.
<i>Artemisia arctica</i> ssp. <i>arctica</i>	..11+r.++.
<i>Peltigera canina</i>	..+++.++.
<i>Vaccinium vitis-idaea</i> ssp. <i>minus</i>	...+...+12
<i>Dicranum elongatum</i> + <i>groenlandicum</i>	...+...+12
<i>Polytrichum strictum</i>	...+...+11
<i>Masonhalea richardsonii</i>	...+...+11
<i>Kobresia myosuroides</i>	..111+...1.
<i>Cladonia arbuscula</i>	...+...+1+
<i>Pertusaria dactylina</i>	..+++.++.
<i>Saxifraga nivalis</i>	+1+...+1.
<i>Pedicularis capitata</i>	...+...+1.
<i>Psoroma hypnorum</i>	+...+...+1.
<i>Saxifraga bronchialis</i> ssp. <i>funstonii</i>	..+...+...+

Hierochloë alpina v
Ledum decumbens v
Aulacomnium turgidum m
Other common taxa include:
Bistorta plumosa v
Cetraria cucullata l
C. islandica l
Dicranum spadiceum m
Hylacomium splendens m
Masonhalea richardsonii m
Cladonia arbuscula l
Cladonia amaurocraea l
Sphaerophorus globosus l.

The community is found in dry, somewhat protected sites such as depressions or the lee of larger rocks on till deposits, and in the troughs of rocky high-centered polygons on glacial outwash deposits. Snow, which was on average 32 cm deep in 1994, is deeper than in the *Salici phlebophyllae*-*Arctoetum alpinae*, but somewhat shallower than in the snowbed association *Carici microchaetae*-*Cassiopeum tetragonae*. Soil pH is very

low, 3.8 ± 0.2 . Soil organic matter and available nitrate are the highest of any of the communities on dry sites, $39 \pm 14\%$ and 17 ppm respectively.

The community appears to be related to the *Empetro-Betuletum nanae* Nordhagen 1943, which is recognized by the abundance of *Betula nana*, scarcity of higher plants, the predominance of fruticose lichens, and near absence of pleurocarpous mosses. The *Hierochloë alpina*-*Betula nana* comm. is somewhat moister and has a better developed moss carpet than the *Empetro-Betuletum nanae*.

Moist acidic shallow snowbeds

Carici microchaetae-*Cassiopeum tetragonae* ass. nov. (App. 1, col. 5; Table 3, cols. 1-13, NTR: IC41).

This association is dominated by dwarf shrubs and fruticose lichens. Its relevés have a relatively high diversity - 19 vascular plants, 9 mosses and 18 lichens. *Diapensia lapponica* ssp. *obovata* and *Huperzia selago* ssp. *appressa* are faithful taxa. Constant taxa are:

Betula nana ssp. *exilis* v
Carex microchaeta v
Cassiope tetragona v
Ledum palustre ssp. *decumbens* v
Nephroma arcticum l.
Pyrola grandiflora v;
Aulacomnium turgidum m
Hylacomium splendens m;
Other common taxa include:
Salix phlebophylla v
Vaccinium uliginosum v
V. vitis-idaea v;
Peltigera aphthosa l
Thamnia spp. l.

This association occurs in moderately deep snowbeds (mean snow depth in 1994: 57 ± 13 cm) on acidic substrates. The best developed stands occur on steep north-facing, well-drained slopes, protected from winds and extreme sun with over 100 cm of snow. Poorly developed stands occur on acidic non-sorted stripes on the shoulder of some hill slopes with shallow snow drifts. Soil pH is 4.4 ± 0.2 , and the soils are organic-rich ($29.6 \pm 5\%$) mineral soils with moderate $\text{NO}_3\text{-N}$ (12 ± 7 ppm). Soil moisture is moderate and variable ($84 \pm 25\%$).

This association appears to be a western North American vicariant of the *Cassiope tetragona* (Böcher 1933) Daniëls 1982, which has an eastern North America-Greenland distribution.

Area-differential taxa for the Alaska association include:

<i>Artemisia arctica</i> ssp. <i>arctica</i> v	<i>Salix phlebophylla</i> v
<i>Bistorta plumosa</i> v	<i>S. pulchra</i> v
<i>Carex microchaeta</i> v	<i>S. reticulata</i> v
<i>Pedicularis langsдорфii</i> v	<i>S. rotundifolia</i> v
<i>Petasites frigidus</i> v	<i>Saxifraga punctata</i> v.

Moist non-acidic shallow snowbeds

Dryas integrifolia-*Cassiope tetragona* comm. (App. 1, col. 4)

This community is the non-acidic counterpart to Ass. *Carici microchaetae*-*Cassiope tetragona*. *Cassiope tetragona* is the clear dominant but *Dryas integrifolia* is also constant and abundant. Evergreen dwarf shrubs and lichens dominate the community, and there is also a well-developed moss carpet. In addition to the taxa it shares with the *Dryado integrifoliae*-*Caricetum bigelowii*, this community has the following faithful taxa:

<i>Astragalus umbellatus</i> v	<i>Radula prolifera</i> v
<i>Equisetum scirpoides</i> v	<i>Silene acaulis</i> v.
<i>Novosieversia glacialis</i> v	

The many constant taxa include:

<i>Bistorta plumosa</i> v	<i>Hypnum bambergeri</i> m
<i>Carex scirpoidea</i> v	<i>Psilidium ciliare</i> m
<i>Dryas integrifolia</i> v	<i>Rhytidium rugosum</i> m;
<i>Papaver macounii</i> v	<i>Alectoria ochroleuca</i> l
<i>Parrya nudicaulis</i> v	<i>Asahinea chrysantha</i> l
<i>Pedicularis oederi</i> v	<i>Cetraria cucullata</i> l
<i>Salix arctica</i> v	<i>C. nivalis</i> l
<i>Salix reticulata</i> v;	<i>Cladonia amaurocraea</i> l
<i>Aulacomnium turgidum</i> m	<i>C. gracilis</i> l
<i>Dicranum angustum</i> m	<i>Dactylina arctica</i> l.

The best developed stands of this community occur on steep north-facing slopes with over 100 cm of snow and non-acidic soils (pH 5.8 ± 0.1). This community also occurs on east and west-facing slopes where smaller snowdrifts form. It is normally not found on south-facing slopes due to the prevailing winds which sweep these slopes of snow. The mean measured snow depth in 1994 was 32 ± 19 cm. Soil organic matter is high ($46 \pm 9\%$) as

is calcium (41 meq/100 g). Available $\text{NO}_3\text{-N}$ is surprisingly low (8.6 ppm).

This community is a Beringian vicariant of the *Dryado-Cassiope* (Fries 1913) Hadač 1946, described from the Eurosiberian Arctic (Dierßen 1992). Similar communities have been described from the snowbeds at Prudhoe Bay (D.A. Walker 1985; D.A. Walker & Everett 1991) and pingos on the eastern Arctic Coastal Plain of Alaska (M.D. Walker 1990). Razzhivin (1994 - this issue) describes a similar provisional association from Chukotka.

Sphagno-Eriophoretum vaginati ass. nov. (App. 1, ref. 8; Table 5, NTR IC03)

This is the zonal vegetation of mesic, acidic slopes throughout the Arctic Foothills. The tussock-forming sedge *Eriophorum vaginatum* is a conspicuous dominant in most stands, although other sedges and deciduous shrubs can be dominant. There are no truly faithful taxa for the association. Nearly all the taxa are shared with other mire communities within the class. Constant taxa include:

<i>Betula nana</i> ssp. <i>exilis</i> v	<i>Sphagnum angustifolium</i> m
<i>Bistorta plumosa</i> v	<i>S. balticum</i> m
<i>Carex bigelowii</i> v	<i>S. girgensohnii</i> m
<i>Cassiope tetragona</i> v	<i>S. rubellum</i> m;
<i>Empetrum hermaphroditum</i> v	<i>Cetraria cucullata</i> l
<i>Ledum palustre</i> ssp. <i>decumbens</i> v	<i>C. islandica</i> l
<i>Pedicularis lapponica</i> v	<i>Cladonia arbuscula</i> l
<i>Petasites frigidus</i> v;	<i>C. rangiferina</i> l
<i>Anastrophyllum minutum</i> m	<i>Cladonia amaurocraea</i> l
<i>Aulacomnium turgidum</i> m	<i>C. gracilis</i> l
<i>Dicranum angustum</i> m	<i>Dactylina arctica</i> l
<i>D. groenlandicum</i> m	<i>Peltigera aphthosa</i> l.

This association covers gentle poorly drained acidic slopes in the foothills. Gravimetric soil moisture is high ($319 \pm 48\%$). The soils are relatively fine-grained compared to other vegetation types ($41 \pm 5\%$ silt, $42 \pm 5\%$ clay), probably due to their occurrence on relatively stable older slopes. The average soil pH is 4.6 ± 0.1 . Most soils have thin (15 - 25 cm) surficial organic horizons above a gleyed mineral horizon. The organic content at 10-cm depth averages $54 \pm 6\%$, and $\text{NO}_3\text{-N}$ is moderate (18 ± 3 ppm). Winter snow cover tends to be moderate (32 ± 8 cm). The combination of shallow depth of thaw (36 ± 3 cm) and high water holding capacity of the *Sphagnum* mosses tends to promote presence of numerous hygrophytic species that would normally not be present on upland surfaces. Non-sorted circles are an important component of nearly all upland surfaces. The communities found on these features (see below) form a fine scale mosaic with the *Sphagno-Eriophoretum vaginati*.

Vegetation dominated by *E. vaginatum* and *C. bigelowii* is found throughout Alaska and east to the Mackenzie River, and in Siberia from Chukotka west to

Table 3. *Carici microchaetae-Cassiopetum tetragonae* and *Salici phlebophyllae-Arctoetum alpinae*. Reference no. 1 = TL08, 2 = TL19, 3 = IC29A, 4 = IC30A, 5 = IC32A, 6 = IC44A, 7 = IC57, 8 = IC56, 9 = IC55, 10 = IC40, 11 = IC41 = NTR, 12 = TL49, 13 = TL50. Reference no. 14 = IC38, 15 = TL05, 16 = TL71 = NTR, 17 = IC09, 18 = IC28, 19 = TL63, 20 = TL65, 21 = TL69, 22 = IC39, 23 = IC43, 24 = IC60, 25 = IC51.

Reference no.	<i>Carici-Cassiopetum</i>	<i>Salici-Arctoetum</i>
Number of vascular taxa	0000000001111 11111222222	1234567890123 456789012345
Number of bryophyte taxa	111112220212 011101001111	4368741209082 511191981062
Number of lichen taxa	000001110111 000000000000	5756816317102 835564338442
Total number of taxa	2222212111120 221111112211	1003091676708 746866664054
	464445543444 433333224332	0017548285882 082431874458

Faithful and differential taxa of the *Carici microchaetae-Cassiopetum tetragonae*:

<i>Cassiope tetragona</i> ssp. <i>tetragona</i>	111122333454
<i>Hylacomium splendens</i>	.12111253.2+3
<i>Aulacomnium turgidum</i>	.12112222.111
<i>Diapensia lapponica</i> ssp. <i>obovata</i>	+++++1.++1.	..+.2..11.
<i>Ledum palustre</i> ssp. <i>decumbens</i>	1221+2112..1.	..+11.....
<i>Betula nana</i> ssp. <i>exilis</i>	11221+.1+.++.	..+1.....
<i>Racomitrium lanuginosum</i>	..+122.11.1+	...1.....
<i>Peltigera aphthosa</i>+1.....
<i>Pedicularis langsdoeffii</i>	..+1+++++.+
<i>Nephroma arcticum</i>	..+.+.+.1.
<i>Huperzia selago</i> ssp. <i>appressa</i>	..+.+.+.+.+
<i>Pyrola grandiflora</i>	..+.+.11+.+
<i>Bistorta vivipara</i>	..+.+.+.+.+
<i>Petasites frigidus</i>	..+1++.....
<i>Salix pulchra</i>	..+.1.2.....
<i>Senecio atropurpureus</i> ssp. <i>frigidus</i>+....+
<i>Chandonanthus setiformis</i>+.1.
<i>Psoroma hypnorum</i>+....+

Faithful and differential taxa of the *Salici phlebophyllae-Arctoetum alpinae*:

<i>Arctostaphylos alpina</i>	..+1.....	44432+1.122
<i>Hieracium alpina</i>	..+.+.+.1.	1+1+1+.11+
<i>Polytrichum piliferum</i>1+.	..+1+1+....
<i>Cladonia pyxidata</i>+.+1+1.
<i>Cladonia macrophylla</i>+.++....
Constants:		
<i>Vaccinium vitis-idaea</i> ssp. <i>minus</i>	++11122231+.1.	231+13333211
<i>Thamnomia subuliformis</i> + <i>vermicularis</i>	++1+++++.	+++++1+1+11+
<i>Cetraria cucullata</i>	112112111.2+.	112+12221122
<i>Cladonia gracilis</i>	++111+11121+.1.	1+1+1+1+1+1
<i>Masonhalea richardsonii</i>	..1++++111+1+	++++.1+1+1+
<i>Cetraria islandica</i>	..1+.++++11+	..11+1+1+1+
<i>Cladonia amaurocraea</i>	+++++1+1+.+	+++++1+1+
<i>Cladonia arbuscula</i>	11.2+12.222+.	++2..+212+2
<i>Dicranum elongatum</i> + <i>groenlandicum</i>	+++2221.2+1.	22+.1+21211.
<i>Cladonia rangiferina</i>	++122221121+.1.	..1..+1111+2
<i>Stereocaulon alpinum</i> + <i>tomentosum</i>	32+++..+111.1	++1..13+121
<i>Dactylina arctica</i>	++11+++1.1+	++++.+++++
<i>Bistorta plumosa</i>	+++1+11+11+	...+.1+1+
<i>Vaccinium uliginosum</i>	12111+2.1.r..	..1.1+3+33
<i>Cetraria nivalis</i>	..+11+1+1+.	21.32..+22+1
<i>Polytrichum strictum</i>	++..12..1.1+	..112+12+112
<i>Sphaerophorus globosus</i>	++++2+..+.+	21+2..+1212..
<i>Alectoria ochroleuca</i>	++1.1+....	1+11+++12..
<i>Carex microchaeta</i>	++....+11211+	..r.+++1+1.
<i>Salix phlebophylla</i>	++12221+....	..+224..12.1
<i>Cladonia uncialis</i>	+++++1.++.	++++.++++.

Other taxa:

<i>Asahinea chrysantha</i>	+.+.+.+.+	+++.+.++.
<i>Bryocaulon divergens</i>	+.+.+.+.+	11.22.1.12..
<i>Calamagrostis inexpectata</i>	..211+.1+.++2+.
<i>Cladonia coccifera</i>	..1+.....	+++.+.++.
<i>Cladonia pleurota</i>	..1+.....	+++.+.++.
<i>Pedicularis capitata</i>	..r+.....	+++.+.++.
<i>Anastrophyllum minutum</i>+....
<i>Dicranum acutifolium</i>21+231.+1.
<i>Pertusaria dactylina</i>+....
<i>Artemisia arctica</i> ssp. <i>arctica</i>11..	..r..1.....
<i>Empetrum hermaphroditum</i>	111.....	..+.+.++.
<i>Rhytidium rugosum</i>111.+31
<i>Cetraria kamczatica</i>+....
<i>Loiseleuria procumbens</i>	2+.....	..1.....
<i>Alectoria nigricans</i>+....	1.....
<i>Cladonia mitis</i>	..1+.....
<i>Cladonia chlorophaea</i>	..1+.....
<i>Luzula confusa</i>r+.
<i>Peltigera canina</i>+....
<i>Pertusaria panyrga</i>+....
<i>Saxifraga nelsoniana</i>+....
<i>Carex bigelowii</i>	..111.....	..r.....
<i>Cetraria andrejevii</i>+....
<i>Cetraria nigricans</i>+....
<i>Dicranum scoparium</i>+....
<i>Lophozia guttulata</i>+....

Table 3. (cont.)

Reference no.	<i>Carici-Cassiopetum</i>	<i>Salici-Arctoetum</i>
	0000000001111 11111222222	1234567890123 456789012345
<i>Pohlia nutans</i>
<i>Salix reticulata</i> ssp. <i>reticulata</i>
<i>Salix rotundifolia</i> ssp. <i>rotundifolia</i>11+.2
<i>Stellaria longipes</i>

Additional taxa with three or less occurrences: TL08: *Coleocaulon aculeatum* r, *Ochrolechia frigida* +, *Orthilia secunda* ssp. *obtusata* +, *Sphagnum rubellum* + *warnstorffii* +; TL19: *Anemone parviflora* +, *Arnica lessingii* +, *Bupleurum triradiatum* ssp. *arcticum* r, *Bryoerythrophyllum recurvirostre* +, *Carex capillaris* +, *C. scirpoidea* +, *Cladonia acuminata* +, *Dicranum undulatum* +, *Dryas integrifolia* +, *D. octopetala* var. *octopetala* +, *Equisetum scirpoides* +, *Hypogymnia physodes* +, *Nephroma expallidum* +, *Novosieversia glacialis* +, *Oxytropis arctica* r, *Pedicularis labradorica* +, *Salix glauca* +, *S. chamissonis* r, *Silene acaulis* +, *Tofieldia pusilla* +; IC29A: *Arnica lessingii* +, *Dicranum muehlenbeckii* 3, *Solorina crocea* +; IC30A: *Arnica lessingii* +, *Blepharostoma trichophyllum* ssp. *brevirete* +, *Dicranum muehlenbeckii* 1, *Peltigera scabrosa* +, *Solorina crocea* +, *Stereocaulon paschale* +; IC32A: *Arnica griseomii* ssp. *frigida* +, *Cetraria laevigata* +, *Dicranum varia* +, *Salix chamissonis* +; IC44A: *Eriophorum triste* +, *Polytrichum commune* 1, *Sphagnum lenense* +; IC57: *Andromeda polifolia* 1, *Blepharostoma trichophyllum* ssp. *brevirete* +, *Cladonia stellaris* 1, *Dactylina ramulosa* +, *Diplophyllum plicatum* +, *Luzula arctica* +, *Novosieversia glacialis* 1, *Parrya nudicaulis* s.l. +, *Poa alpigena* +, *Pogonatum urnigerum* 1, *Sanionia uncinata* +, *Sphagnum aongstroemii* +, *S. girgensohnii* 1, *S. teres* 1; IC56: *Carex misandra* +, *Dactylina ramulosa* +, *Gymnomitrium concinnatum* +, *Luzula arctica* 1, *Parrya nudicaulis* s.l. +, *Poa arctica* +, *Pogonatum urnigerum* 1, *Ptilium crista-castrensis* +, *Sanionia uncinata* +, *Sphagnum aongstroemii* +, *S. teres* +, *Tomentypnum nitens* +; IC55: *Dactylina ramulosa* +, *Dicranum muehlenbeckii* 2, *Nephroma expallidum* +, *Papaver macounii* +, *Polytrichastrum alpinum* 1, *Pogonatum urnigerum* 1, *Saxifraga bronchialis* ssp. *funstonii* +, *Sphagnum girgensohnii* 1; IC40: *Dactylina beringica* +, *Dicranum angustum* +, *Gentiana glauca* +; IC41: *Abietinella abietina* 1, *Arnica griseomii* ssp. *frigida* +, *Astragalus umbellatus* +, *Dactylina beringica* r, *Peltigera leucophlebia* r, *Poa arctica* +, *Polytrichastrum alpinum* 1, *Ptilidium ciliare* 1, *Ptilium crista-castrensis* +, *Salix chamissonis* 2, *Tomentypnum nitens* 1; TL49: *Carex scirpoidea* +, *Dicranum spadiceum* 3, *Equisetum scirpoides* +, *Minuartia arctica* r, *Novosieversia glacialis* +, *Orthilia secunda* ssp. *obtusata* +, *Pohlia cruda* +, *Saussurea angustifolia* +, *Silene acaulis* +; TL50: *Arnica angustifolia* ssp. *angustifolia* +, *Aulacomnium palustre* 2, *Boykinia richardsonii* 2, *Cardamine digitata* +, *Carex scirpoidea* +, *Dicranum angustum* 2, *D. spadiceum* 2, *Equisetum arvense* +, *Luzula arctica* +, *L. multiflora* r, *Parnassia palustris* r, *Parrya nudicaulis* s.l. +, *Plagiominium ellipticum* +, *Sanionia uncinata* 2, *Saussurea angustifolia* +, *Saxifraga nivalis* +, *Sphagnum rubellum* + *warnstorffii* 1, *Tofieldia pusilla* r, *Tomentypnum nitens* 1; IC38: *Arctoparmelia separata* +, *Polytrichum hyperboreum* 1, *Tortula ruralis* 1; TL05: *Cladonia emocyna* +, *C. pocillum* +, *Hypogymnia physodes* 1, *Melanelia septentrionalis* +, *Pedicularis lanata* r; TL71: *Ceratodon purpureus* r; IC09: *Ceratodon purpureus* +, *Eriophorum vaginatum* +, *Lecidoma demissa* +, *Tritomaria quinqueidentata* +; IC28: *Arctoparmelia separata* +, *Asahinea scholanderi* +, *Calliergon stramineum* +, *Hypogymnia subobscura* 1, *Pseudophebe pubescens* 2, *Sphaerophorus fragilis* 1; TL63: *Ochrolechia frigida* +, *Peltigera malacea* +, *Poa alpina* +; TL65: *Calamagrostis canadensis* s.l. 1, *Pedicularis labradorica* +; IC39: *Cladonia cornuta* +, *Polytrichum hyperboreum* +, *Rubus chamaemorus* +, *Tetraplodon pallidus* r; IC43: *Dactylina beringica* +, *Peltigera malacea* +, *Polytrichum hyperboreum* +; IC60: *Cetraria tilesii* +, *Cladonia alaskana* +, *Dryas octopetala* var. *octopetala* 2, *Festuca altaica* +, *Kobresia myosuroides* +, *Poa glauca* +, *P. lanata* +, *Saxifraga nivalis* r; IC51: *Dryas octopetala* var. *octopetala* +, *Peltigera malacea* 1.

the Taymyr and Yamal peninsulas (Aleksandrova 1980). However, only in unglaciated Alaska and Chukotka is this the predominant association of the uplands. Komárková & McKendrick (1988) recognized a preliminary class (not yet formally described) of upland vegetation characterized by *E. vaginatum* and *Ledum decumbens*. Lambert (1968) described a *Betulo-Eriophoretum vaginati* from the western Canadian Arctic, and although his stands were characterized by *Betula glandulosa* rather than *B. nana*, the floristic similarity between the Canadian communities and this association is high (61%).

Sphagno-Eriophoretum vaginati typicum subass. nov. (Table 4 cols. 1–26, NTR: TL54)

In the typical subassociation sedges and dwarf shrubs are dominant in the overstory and mosses in the understory. In wetter microsites, the deciduous shrubs *Salix pulchra* or *Betula nana* can be > 50 cm tall and become dominant, but sedges remain an important component of the canopy. *Eriophorum vaginatum* may be replaced by *Carex bigelowii* in some areas. In snowy

microsites, the evergreen shrub *Cassiope tetragona* is an important subdominant. *E. vaginatum* tends to be dominant on stable sites where there is no flowing water. Shrubs become more important in poorly defined ephemeral water tracks. Total species diversity of the subassociation is relatively high (mean of 41 taxa; 15 vascular plants, 14 mosses and 10 lichens). *E. vaginatum*, *Cassiope tetragona*, *Pyrola grandiflora* and *Saxifraga nelsoniana* are differential against the *betuletosum nanae*.

We recognize a *Carex bigelowii* facies of the subassociation (Table 4, cols. 21 - 26) that occurs on somewhat unstable slopes, often in conjunction with solifluction features. Here, *E. vaginatum* is absent or has a low cover in these areas.

Sphagno-Eriophoretum vaginati betuletosum nanae subass. prov. (Table 4, cols. 27 - 33, NTR: TL36)

This is a well-defined low-shrub community dominated by *Betula nana* ssp. *exilis* that is common along the margins of water tracks and on palsas and high-centered polygons in colluvial basins. There is often a deep moss mat, and summer thaw commonly does not penetrate to the mineral soil horizon. *Sphagnum teres* is a differential taxa against the subass. *typicum*. Common taxa with high cover include *Aulacomnium turgidum*, *Ledum palustre* ssp. *decumbens* and *Rubus chamaemorus* and a suite of *Sphagnum* species. Species diversity is somewhat less than in the typical subassociation with 12 vascular plants, 14 bryophytes, and 7 lichens. The subassociation contains most of the faithful and constant taxa but is missing *Eriophorum vaginatum* in most stands.

Moist non-acidic uplands

Dryado integrifoliae-Caricetum bigelowii ass. nov. (App. 1, col. 10; Table 5, cols. 1 - 14, NTR: TL43)

This is the non-acidic counterpart to the *Sphagno-Eriophoretum vaginati*, occurring on circumneutral mesic uplands and hillslopes, and limited to younger landscapes. Sedges and dwarf shrubs are dominant, and there is a well developed moss layer. Species diversity is high (26 vascular plants, 16 bryophytes, 14 lichens; total 55). The minerotrophic moss *Tomentypnum nitens* is constant and abundant. Faithful taxa are:

<i>Anemone parviflora</i> v	<i>Pyrola grandiflora</i> v
<i>Eriophorum triste</i> v	<i>Senecio resedifolius</i> v;
<i>Eutrema edwardsii</i> v	<i>Aulacomnium acuminatum</i> m
<i>Orthilia secunda</i> ssp. <i>obtusata</i> v	<i>Meesia uliginosa</i> m.

Constant taxa include:

<i>Arctous rubra</i> v	<i>Catocopium nigrum</i> m
<i>Bistorta vivipara</i> v	<i>Dicranum spadiceum</i> m
<i>Pedicularis lanata</i> v	<i>Rhytidium rugosum</i> m;
<i>Rhododendron lapponicum</i> v	<i>Cetraria islandica</i> l
<i>Salix arctica</i> v	<i>Cladonia arbuscula</i> l
<i>Vaccinium uliginosum</i> v;	<i>Cladonia amaurocraea</i> l
<i>Aulacomnium turgidum</i> m	<i>C. pyxidata</i> l.

This association occurs on mid to upper non-acidic slopes, primarily in younger landscapes. Gravimetric soil moisture is high, $381 \pm 29\%$, similar to that of the *Sphagno-Eriophoretum vaginati*. Soils are relatively coarse-grained ($57 \pm 4\%$ sand, $38 \pm 2\%$ silt, and $6 \pm 2\%$ clay). Average soil pH is 6.3 ± 0.1 , compared to only 4.6 for the *Sphagno-Eriophoretum vaginati*. Organic content of the soil is $66 \pm 5\%$, and $\text{NO}_3\text{-N}$ is low (9 ± 1 ppm). Snow depth averaged 32 ± 19 cm in 1994.

This association is placed in the *Scheuchzerio-Caricetea nigrae*, which includes the more basiphytic communities of mires and mineral-rich and moss-rich communities on poorly drained slopes. Within the class, it has affinities to the *Tofieldietalia* Preising in Oberdorfer 1949.

Dryado integrifoliae-Caricetum bigelowii caricetosum membranaceae subass. nov. (Table 5, cols. 1 - 7, NTR: TL43).

This subassociation is differentiated by *Alectoria ochroleuca*, *Anemone parviflora*, *Bryum pseudotriquetrum*, *Carex membranacea* and *Eriophorum vaginatum*. It occupies upper mesic slope positions including the dry element of non-sorted stripes.

Dryado integrifoliae-Caricetum bigelowii equisetosum arvensis subass. nov. (Table 5, cols. 8 - 14, NTR: TL45).

This subassociation is easily recognized by the abundance of *Equisetum arvense*, which gives the community a distinctive light green coloration in midsummer. It is differentiated by *Cyrtomium hymenophyllum*, *Equisetum scirpoides*, *Luzula arctica*, *Meesia uliginosa* and *Petasites frigidus*. The community is characteristically found on lower somewhat less stable slopes, often in areas of high snow cover.

Other important communities of uplands

Blockfields and glacial erratics: Cetraria nigricans-Rhizocarpon geographicum community (App. 1, col. 1).

Two relevés collected from these sites contained many epilithic cryptogams that are typical of most glacial erratics and blockfields in the region, including:

<i>Chandonanthus setiformis</i> m;	<i>Parmelia omphalodes</i> l
<i>Alectoria nigricans</i> l	<i>Porpidea flavocaerulescens</i> l
<i>Arctoparmelia centrifuga</i> l	<i>Rhizocarpon geographicum</i> l
<i>Cetraria nigricans</i> l	<i>Umbilicaria proboscidea</i> l.

The stoney glacial till and outwash deposits of the region contain many blockfields that are not covered by soil and vascular plants. Blockfields are less common on the older surfaces, but occasional glacial erratics protrude above the colluvium and peat. Most of the rocks in the region are composed of Kanayut Sandstone (Hamilton 1986).

Table 4. *Sphagno-Eriophoretum vaginati*. a. Subass. *typicum*. Reference no. 1 = relevé TL26, 2 = TL32, 3 = IC04A, 4 = **TL54** = **NTR subass.**, 5 = IC61, 6 = **IC03** = **NTR ass.**, 7 = IC50, 8 = IC62, 9 = TL25, 10 = TL73, 11 = IC07, 12 = IC17, 13 = IC24, 14 = IC01, 15 = IC08, 16 = IC13, 17 = IC67, 18 = IC35A, 19 = TL79, 20 = TL78. Reference no. 21 = IC12, 22 = **IC45** = **NTR subass.**, 23 = IC06, 24 = TL61, 25 = IC31, 26 = IC27.

b. Subass. *betuletosum nanae*. Reference no. 27 = TL75, 28 = IC48, 29 = IC05, 30 = IC10, 31 = IC46, 32 = **TL36** = **NTR subass.**, 33 = IC15. Scores of the differential species of the *Carex bigelowii* facies (cols. 21 - 26) and the subass. *betuletosum nanae* are given bold.

	<i>typicum</i>	<i>betuletosum</i>
Reference number	000000000111111111222222	2223333
Number of vascular taxa	12345678901234567890123456	7890123
Number of bryophyte taxa	11121111111111110101111111	1111111
Number of lichen taxa	33246464517225616529515547	1073002
Total number of taxa	11121111111111110100111111	0121101
	45725816313375047697665273	8325496
	11011110010011110100011111	0101000
	41251469908840873500005051	7170239
	43364443333344432321434344	2343223
	19112639728330426616175761	5468627
Faithful and differential taxa of the association:		
<i>Sphagnum rubellum</i> + <i>warnstorffii</i>	12121112211212211221221311	1+22212
<i>Rubus chamaemorus</i>	1+21+11+1222+121331.1+..	4+11242
<i>Petasites frigidus</i>	..1+.++..1..+1+.21++11.21	+111+r.
<i>Sphagnum angustifolium</i> + <i>balticum</i>	321.1.1123.11..121.+..11.	..+1.13.
<i>Tomentypnum nitens</i>	..r11r+1r.1..+..+..+..+..+	..+..+.
<i>Sphagnum girgensohnii</i>	++..+..23..+..+..33..+2+	2.11.21
<i>Pedicularis lapponica</i>	++..+..+..+..+..+..+..+..+	r++..+1
<i>Blepharostoma trichophyllum</i> ssp. <i>brevirete</i>	..+1++1.1..+..+..+..+..+.	..+..+.
<i>Pohlia nutans</i>	..+..+..+..+..+..+..+..+.	..+..+.
Differential taxa of the subass. <i>eriphoretosum vaginatum</i>:		
<i>Eriophorum vaginatum</i>	44333333332221111..21+++.	r..+..r
<i>Cassiope tetragona</i> ssp. <i>tetragona</i>	11.21+.11+++1+.1+.12r+11	..1....
<i>Pyrola grandiflora</i>	..+..+..+..+..+..+..+..+.	..+....
<i>Saxifraga nelsoniana</i>	..+..+..+..+..+..+..+..+.	..+....
Differential taxa of the subass. <i>betuletosum nanae</i>:		
<i>Sphagnum teres</i>	..1.1..2..2..2..3.2..	++32223
Constants:		
<i>Betula nana</i> ssp. <i>exilis</i>	331+11123322212221+132311.	5433443
<i>Hylacomium splendens</i>	23232222233+2+222+.223323	44323++
<i>Aulacomnium palustre</i>	..11+.11..2..122.2.121211.	312222.
<i>Vaccinium vitis-idaea</i> ssp. <i>minus</i>	23111213311111221+r121+11	+21113.
<i>Aulacomnium turgidum</i>	221122222222212221+.232222	..21222
<i>Ledum palustre</i> ssp. <i>decumbens</i>	3211111221121212+r.11121+	+111++.
<i>Cetraria cucullata</i>	++..+1+++++2+1+1+.11+++	+1++r+
<i>Polytrichum strictum</i>	++..1r12.2..2+22112+1+11	11+1112
<i>Carex bigelowii</i>	+1212221112.r222.2+.333333	+2222.r
<i>Cladina rangiferina</i>	++..+1+++++2+1.2+.1++++1	..+..+.
<i>Cetraria islandica</i>	++..+1+++++1+..+..+..+.	++..+.
<i>Cladonia amaro-cræa</i>	++..+1+++++1+.2..+1++++.	++..+.
<i>Dactylina arctica</i>	++..+1+++++1+1+1..+..+.	r++..+.
<i>Dicranum angustum</i>	1+.11111.1111+.1.1212+.1	11211.1
<i>Salix pulchra</i>	122322222+3..212.3442.1322	+12212.
<i>Bistorta plumosa</i>	11..+1+++++.11+.1+.1+.1+	++1+r.
<i>Cladonia gracilis</i>	++..+1++++.1.1+.1+.1+.1+	++r+r.
<i>Dicranum elongatum</i> + <i>groenlandicum</i>	2+.1122.221.312++..1211+.	..1.1+.
Other taxa:		
<i>Vaccinium uliginosum</i>	+111.1+.11+21+..111.1	r.1....
<i>Peltigera aphthosa</i>	+++++..+..+..+..+..+..+	++..+.
<i>Cladonia arbuscula</i>	++..+..+..+..+..+..+..+	r....+
<i>Anastrophyllum minutum</i>	+.1+1+.1+.1+.1+.1+.1+.1+	..1..+.
<i>Empetrum hermaphroditum</i>	+1+11+.1..11..r.1.2..	..+....
<i>Peltigera scabrosa</i>	..+..+..+..+..+..+..+..+	++..+.
<i>Plitidium ciliare</i>	..1+1.2..1..1.1+.1+.1+.1+	..1..+.
<i>Thamnia subuliformis</i> + <i>vermicularis</i>	++..+..+..+..+..+..+..+	++..+.
<i>Tritomaria quinqueidentata</i>	..+..+..+..+..+..+..+..+	++..+.
<i>Cladonia mitis</i>	..+..+..+..+..+..+..+..+	++..+.
<i>Pedicularis labradorica</i>	..+..+..+..+..+..+..+..+	++..+.
<i>Sanionia uncinata</i>	..1..+..+..+..+..+..+..+	..1++.
<i>Sphagnum lenense</i>	..+..+..+..+..+..+..+..+	++..+.
<i>Cetraria nivalis</i>	..+..+..+..+..+..+..+..+	++..+.
<i>Sphagnum aongstroemii</i>	..+..+..+..+..+..+..+..+	++..+.
<i>Hypnum bambergeri</i>	..+..+..+..+..+..+..+..+	++..+.
<i>Senecio atrorubescens</i> ssp. <i>frigidus</i>	..+..+..+..+..+..+..+..+	++..+.
<i>Peltigera malacea</i>	++..+..+..+..+..+..+..+	++..+.
<i>Cladonia pleurota</i>	..+..+..+..+..+..+..+..+	++..+.
<i>Dicranum acutifolium</i>	..+..+..+..+..+..+..+..+	++..+.
<i>Andromeda polifolia</i>	..+..+..+..+..+..+..+..+	++..+.
<i>Cladonia carneola</i>	..+..+..+..+..+..+..+..+	++..+.
<i>Loeskygnus badius</i>	..2+.1+.1+.1+.1+.1+.1+.1+	..1....
<i>Eriophorum angustifolium</i> ssp. <i>subarcticum</i>	..1..+..+..+..+..+..+..+	..r++.
<i>Masonhalea richardsonii</i>	++..+..+..+..+..+..+..+	++..+.
<i>Salix reticulata</i> ssp. <i>reticulata</i>	..+..+..+..+..+..+..+..+	++..+.
<i>Alectoria ochroleuca</i>	..+..+..+..+..+..+..+..+	++..+.
<i>Calliergon stramineum</i>	..+..+..+..+..+..+..+..+	++..+.
<i>Bistorta vivipara</i>	..+..+..+..+..+..+..+..+	++..+.
<i>Poa arctica</i>	..+..+..+..+..+..+..+..+	++..+.
<i>Cladonia cenotea</i>	..+..+..+..+..+..+..+..+	++..+.
<i>Arctagrostis latifolia</i> var. <i>latifolia</i>	..+..+..+..+..+..+..+..+	++..+.
<i>Barbilophozia binsteadii</i>	..+..+..+..+..+..+..+..+	++..+.
<i>Pedicularis langsdorffii</i>	..+..+..+..+..+..+..+..+	++..+.

Additional taxa with three or less occurrences:

TL26: *Dicranum spadicum* 2; *Nephroma arcticum* +; *Peltigera canina* +; *Stereocaulon alpinum* + *tomentosum* +; **TL32:** *Chandonanthus setiformis* +; *Dicranum scoparium* +; *Rhytidium rugosum* r; *Stereocaulon alpinum* + *tomentosum* +; **IC04A:** *Meslia uliginosa* +; *Sarmenthyphnum sarmentosum* 1; **TL54:** *Arctous rubra* +; *Cladonia chlorophaea* +; *Dicranum spadicum* +; *D. scoparium* +; *Dryas integrifolia* r; *Equisetum arvense* +; *Eriophorum triste* +; *Limprichtia revolvens* +; *Meslia triquetra* +; *M. uliginosa* +; *Nephroma arcticum* r; *Ochrolechia upsaliensis* +; *Orthilia secunda* ssp. *obtusata* +; *Orthothecium chryseum* +; *Paludella squarrosa* r; *Pedicularis capitata* r; *Peltigera polydactyla* +; *Plagiomnium medium* +; *Rhytidium rugosum* +; *Sphagnum contortum* 1; *Stellaria longipes* +; **IC61:** *Valeriana capitata* +; **IC03:** *Arctous alpina* 1; *Limprichtia revolvens* +; *Peltigera polydactyla* +; *Pleurozium schreberi* +; *Rhizomnium andrewsianum* +; **IC50:** *Alectoria nigricans* +; *Cladonia deformis* +; *C. uncialis* +; **IC62:** *Cetraria fastigiata* +; *Cladonia uncialis* +; *Limprichtia revolvens* +; *Meslia uliginosa* +; *Saxifraga cernua* +; **TL25:** *Pedicularis oederi* r; *Peltigera canina* +; *Sphagnum fimbriatum* 1; **TL73:** *Cladonia pyxidata* +; *C. subfurcata* +; *Dicranum spadicum* 1; *Peltigera canina* +; *Sphagnum fimbriatum* 2; **IC45:** *Peltigera horizontalis* +; **IC06:** *Bryocaulon divergens* r; *Cetraria kamezatica* +; *Cladonia fimbriata* +; *C. uncialis* +; *Pertusaria dactylina* +; **TL81:** *Arctous rubra* r; *Cladonia pyxidata* r; *Eriophorum triste* +; **IC31:** *Cetraria inermis* +; *Cirriophyllum cirrosum* +; *Cladonia coccifera* +; *Dactylina ramulosa* +; *Pertusaria dactylina* +; **IC27:** *Anemone parviflora* +; *Arnica grisei* ssp. *frigida* +; *Dactylina ramulosa* +; *Dicranum muehlenbeckii* 2; *Pedicularis albolabata* +; *P. capitata* +; **IC48:** *Cladonia macrophylla* +; *C. subfurcata* +; *Lophozia guttulata* +; *Sarmenthyphnum sarmentosum* 1; **IC05:** *Arctous alpina* r; *Campylium stellatum* +; *Pedicularis albolabata* r; *Sarmenthyphnum sarmentosum* +; *Scapania paludicola* 1; *Sphagnum imbricatum* 3; **IC07:** *Campylium stellatum* +; *Luzula wahlenbergii* r; *Politrachastrum alpinum* 1; *Scapania paludicola* +; *Sphagnum capillifolium* 1; **IC01:** *Cladonia sulphurina* +; *Rhizomnium andrewsianum* +; *Polytrichum commune* 2; **IC24:** *Alectoria nigricans* r; *Carex rariflora* r; *C. rotundata* r; *Cladonia chlorophaea* +; *C. deformis* +; *Dactylina ramulosa* r; *Mylia anomala* +; *Politrachastrum alpinum* +; *Salix fuscescens* +; **IC08:** *Bryocaulon divergens* +; *Lobaria linita* r; *Racomitrium lanuginosum* +; *Salix phlebophylla* 1; *Sphaerophorus globosus* r; **IC13:** *Cetraria fastigiata* +; *Melanella septentrionalis* +; *Polytrichum commune* +; *Scapania paludicola* +; *Tuckermannopsis sepicola* +; **IC67:** *Alectoria nigricans* +; *Cladonia ecmocyna* +; **IC10:** *Cladonia fimbriata* +; *Festuca altaica* 1; *Melanella septentrionalis* +; *Polemonium acutiflorum* +; *Politrachastrum alpinum* +; *Sphaerophorus globosus* +; *Tuckermannopsis pinastri* +; **TL36:** *Luzula wahlenbergii* +; **IC15:** *Carex aquatilis* s.l. 1; *C. rotundata* +; *Cladonia chlorophaea* +; *Eriophorum scheuchzeri* var. *scheuchzeri* +; *Salix fuscescens* 1; *Sphagnum compactum* +; *S. magellanicum* 2; *Tuckermannopsis sepicola* +; **IC35A:** *Paludella squarrosa* +; **TL79:** *Pedicularis oederi* r; *Polytrichum commune* +; **TL78:** *Anemone parviflora* +; *A. richardsonii* +; *Sphagnum squarrosum* 3; *Warnstorffia exannulata* +.

Rhizocarpon geographicum-dominated lichen-covered rock is common throughout the foothills and Brooks Range (Lambert 1968; Pegau 1968; Anderson 1974; Webber et al. 1979; Cooper 1986; M.D. Walker 1990). In Europe and Japan alpine silicate-rock lichen vegetation with *R. geographicum* belongs to the *Rhizocarpetea geographici* (Wirth 1972; Roux 1978; Ellenberg 1988). Daniëls (1975) placed the rock lichen communities of SE Greenland into the *Rhizocarpetea geographici*, and our stands also appear to fit there.

Animal dens: Poa glauca-*Arnica angustifolia* community (App. 1, col. 2)

This community type occurs primarily around the dens of the arctic ground squirrel. The most important physical characteristics of these sites are their coarse soils (58% sand), a pH of 5.4 ± 1.0 and relatively high amounts of soil nutrients (11.6 meq/100 g Ca, 41.8 ppm P). Most of these sites are on ridge tops or other high points in the landscape; none of the plots had any snow cover when it was measured in May 1994.

The community is rich in vascular plants (22 spp., particularly grasses and forbs), and relatively poor in bryophytes (five spp.) and lichens (four spp.). *Potentilla hookeriana* and *Bryum argenteum* are faithful to this community alone, which shares many faithful taxa with the *Selaginello sibiricae*-*Dryadetum octopetalae*:

<i>Anemone drummondii</i> v	<i>Kobresia myosuroides</i> v
<i>Arnica angustifolia</i> v	<i>Minuartia obtusiloba</i> v
<i>Artemisia arctica</i> v	<i>Poa glauca</i> v
<i>Bupleurum triradiatum</i> v	<i>Saxifraga nivalis</i> v
<i>Carex obtusata</i> v	<i>S. tricuspidata</i> v
<i>C. rupestris</i> v	<i>Salix phlebophylla</i> v;
<i>Dryas octopetala</i> v	<i>Encalypta rhaptocarpa</i> m

Forb-rich vegetation in the Arctic is confined to local situations, often on fairly steep, south-facing slopes (Yurtsev 1974; D.A. Walker 1985; Zanolka 1989; M.D. Walker 1990; M.D. Walker et al. 1991). Typical habitats include stream banks and pingos, and burrowing and denning animals are often associated with these same sites, which may have soil temperatures elevated as much as 15 °C above those found on level surfaces (M.D. Walker et al. 1991). These stands have been classified physiognomically as meadow or steppe. Because of their limited extent and local nature, there is minimal information available on this type of vegetation, but a common feature is the presence of locally uncommon forbs, often to the north of their main distributional limit. For this reason associations are probably highly localized; many more data will be necessary before the status of higher units will be clear.

Non-sorted circles: Anthelia juratzkana-*Juncus biglumis* community (App. 1, col. 20)

Juncus biglumis, *Luzula arctica* and *Anthelia juratz-*

kana are faithful. In addition, there are seven constant taxa. Total species diversity is low, ranging from as few as three to as many as 22 species in our samples. *Racomitrium lanuginosum* occasionally forms mats on what were apparently once barren frost scars, which may represent a successional sequence that occurs when the frost action is moderated for some reason.

Non-sorted circles (also called frost scars or frost boils) are small areas, about 0.5 to 1.5 m in diameter, of highly disturbed mineral soil created by cryoturbation processes (Washburn 1956). They are common features of most hillslopes and are particularly common on ridge crests and shoulders, wherever there is mineral material near the soil surface (Everett 1980; D.A. Walker et al. 1989). The amount of vegetation covering the disturbed patches varies considerably depending on the cryoturbation activity of the site. Non-sorted circles can cover more than 50 % of the soil surface in favorable sites, and are thought to occupy as much as 15 - 30 % of most foothill interfluvial areas. In some areas they are masked by the surrounding tussocks. The two most distinguishing physical characteristics of these sites are their extremely low organic matter and their high degree of cryoturbation. The average soil organic matter of stands within this association is only 5 %, compared to 54 % for the *Sphagno-Eriophoretum vaginati*, which makes up the matrix surrounding the non-sorted circles.

Other authors (e.g. Matveyeva 1994 - this issue) have included frost scars as part of a complex community, but functionally and floristically they are quite distinct from tussock tundra. There is considerable floristic differentiation of non-sorted circles occurring on acidic vs. non-acidic substrates. For example, the circles at Prudhoe Bay, Alaska (pH = 7.4) are characterized by a suite of basiphilous species including *Bryum wrightii*, *Chrysanthemum integrifolia*, *Minuartia rubella*, *M. arctica* and *Saxifraga oppositifolia* (D.A. Walker 1985). The non-sorted circle habitat is a unique arctic disturbance regime.

Water tracks: Eriophorum angustifolium-*Salix pulchra* community (App. 1, col. 18).

Hillslope water tracks are shallow channels that conduct meltwater during the thaw season and runoff after rain events. On the older surfaces they often form networks of parallel drainages that are spaced tens of meters apart and give many hills a ribbed appearance (D.A. Walker et al. 1982). They have been called 'horse-tail drainages' because of their unique appearance from the air (Cantlon 1961). The best developed water tracks carry water throughout the summer. Many of these have medium high (50 - 100 cm) *Salix pulchra* with an *Eriophorum angustifolium* understory.

Species diversity is low (average of 16 spp. per relevé

Table 5. *Dryado integrifoliae-Caricetum bigelowii*, a. subass. *caricetosum membranaceae*. Reference no. 1 = relevé TL22, 2 = TL23, 3 = TL77, 4 = TL39, 5 = TL42, 6 = TL43 = NTR (ass. and subass.), 7 = TL56; b. subass. *equisetosum arvensis*. 8 = TL53, 9 = TL45 = NTR (subass.), 10 = TL52, 11 = TL24, 12 = TL10, 13 = TL21, 14 = TL41.

	<i>caricetosum</i>	<i>equisetosum</i>
Reference number	0000000	0011111
Number of vascular taxa	1234567	8901234
Number of bryophyte taxa	2222221	2232222
Number of lichen taxa	9322789	6965391
Total number of taxa	2111111	1111111
	2842468	5634865
	1111111	1111101
	1142658	5726184
	6554555	5665555
	2206795	6215230

Faithful and differential taxa of the association:

<i>Carex bigelowii</i>	2332232	3233233
<i>Thamnochloa subuliformis</i> + <i>vermicularis</i>	+++++1+	+r+1.+
<i>Pedicularis capitata</i>	++++++.	+++++++
<i>Equisetum arvense</i>	++++.1.	+322232
<i>Peltigera aphthosa</i>	++++.	+++++++
<i>Eriophorum triste</i>	11..112	+1+1..1
<i>Cassiope tetragona</i> ssp. <i>tetragona</i>	111..+	1++12+
<i>Masonhalea richardsonii</i>	..++.	++E+++
<i>Pyrola grandiflora</i>	++.	+++++
<i>Polytrichum strictum</i>	..++.	+++++++
<i>Bistorta plumosa</i>r+	+++++++
<i>Eriophorum vaginatum</i>	2r+13r.	++++.
<i>Dicranum elongatum</i> + <i>groenlandicum</i>	11+11.1	++++.1
<i>Stereocaulon alpinum</i> + <i>tomentosum</i>	..++.	r++.
<i>Saundersia angustifolia</i>	++++.	++1..
<i>Tritomaria quinqueidentata</i>	++++.	++.
<i>Senecio atropurpureus</i> ssp. <i>frigidus</i>	++.	++.
<i>Eutrema edwardsii</i>	++++.	++.
<i>Vaccinium vitis-idaea</i> ssp. <i>minus</i>	r++.	r++.
<i>Papaver macounii</i>	..++.	++.
<i>Hypnum bambergeri</i>	++.	++.
<i>Saxifraga hirculus</i>	++.	++.
<i>Dicranum angustum</i>	+1+.	++.
<i>Arctagrostis latifolia</i> var. <i>latifolia</i>	++.	++.
<i>Anastrophyllum minutum</i>	++.	++.

Differential taxa of the subass. *caricetosum membranaceae*:

<i>Carex membranacea</i>	++11+12
<i>Limprichtia revolvens</i>	++.	..1.
<i>Alectoria ochroleuca</i>	++.	..r
<i>Anemone parviflora</i>	++++.	++.
<i>Bryum pseudotriquetrum</i>	++++.	++.

Differential taxa of the subass. *equisetosum arvensis*:

<i>Meesia uliginosa</i>	++.	++.
<i>Equisetum scirpoides</i>	++.	++.
<i>Petasites frigidus</i>	++.	..1+.
<i>Luzula arctica</i>	++.	++.
<i>Cyrtomium hymenophyllum</i>	++.	++.

Constants:

<i>Tomentypnum nitens</i>	3334432	2313233
<i>Hylocomium splendens</i>	22322+2	4242432
<i>Dryas integrifolia</i>	3333331	2313232
<i>Cladina rangiferina</i>	+++++1	++r+++
<i>Cetraria cucullata</i>	+1+++2	++r+1++
<i>Salix reticulata</i> ssp. <i>reticulata</i>	2..13321	1331122
<i>Aulacomnium turgidum</i>	11111+1	2..++1++
<i>Bistorta vivipara</i>	++++++.	++r++
<i>Vaccinium uliginosum</i>	+++++.2	+1r++r.
<i>Ptilidium ciliare</i>	111.1+1	..1+11+1
<i>Cetraria islandica</i>	+++++1	++r+++
<i>Cladina arbuscula</i>	++++.1	++.
<i>Dactylina arctica</i>	++.	++r++.
<i>Rhytidium rugosum</i>	+++++	r1..+1
<i>Pedicularis lanata</i>	++.	++.
<i>Ditrichum flexicaule</i>	1+..+1.	..1+..+
<i>Pedicularis oederi</i>	++.	++r++.
<i>Dicranum spadicum</i>	++.	+1+2..
<i>Rhododendron lapponicum</i>	++.	+1+1
<i>Salix arctica</i>	..111+	+1+..+1
<i>Campylopus stellatum</i>	++.	++.
<i>Arctous rubra</i>	+++++1.	++.
<i>Cladonia pyxidata</i>	++++++.	++.
<i>Cladonia gracilis</i>	++++.	++r++.
<i>Cladonia amaurocraea</i>	++++.	++.
<i>Catoscopium nigrum</i>	++.	..+1.

Other taxa:

<i>Andromeda polifolia</i>	++.	++.
<i>Tofieldia pusilla</i>	++.	++.
<i>Asahinea chrysantha</i>	++.	++.
<i>Aulacomnium acuminatum</i>	++.	..1+..
<i>Cetraria nivalis</i>	++.	++.
<i>Sphagnum rubellum</i> + <i>warnstorffii</i>	++.	++r++.
<i>Barbilophozia barbata</i>	++.	++.
<i>Betula nana</i> ssp. <i>exilis</i>	++.	++r++.
<i>Aulacomnium palustre</i>	++.	..11....

Table 5. (cont.)

Reference number	0000000	0011111
	1234567	8901234
<i>Lagotis glauca</i>	..++.	..++.
<i>Ledum palustre</i> ssp. <i>decumbens</i>	r++.	++.
<i>Stellaria longipes</i>	++.	++r++.
<i>Distichium capillaceum</i>	..++.	..2..+1
<i>Orthilia secunda</i> ssp. <i>obtusata</i>	++.	++.
<i>Pertusaria dactylina</i>	++.	++.
<i>Pedicularis langsdorffii</i>	++.	++.
<i>Rubus chamaemorus</i>	r++.	++r++.
<i>Senecio resedifolius</i>	++.	++r++.
<i>Thalictrum alpinum</i>	++.	++.

Additional taxa with three or less occurrences: TL22: *Blepharostoma trichophyllum* ssp. *brevirete* +, *Cardamine digitata* +, *Cinclidium arcticum* +, *C. stygium* +, *Empetrum hermaphroditum* r, *Mesoptychia sahlbergii* +, *Orthothecium chryseum* +, *Peltigera malacea* +, *Salix glauca* r, *S. phlebophylla* r, *Saxifraga hieracifolia* +, *Scapania simmonsii* +, *Sphagnum aongstroemii* r, *Timmia norvegica* +; TL23: *Carex podocarpa* r, *C. scirpoides* r, *Cinclidium arcticum* +, *Lophozia rupeana* +, *Ochrolechia frigida* +, *Philonotis fontana* var. *pumila* +, *Scapania simmonsii* +; TL77: *Carex aquatilis* s.l. r, *Peltigera canina* +, *P. malacea* +, *P. polydactyla* +, *Racomitrium lanuginosum* +, *Salix lanata* ssp. *richardsonii* 2; TL39: *Cladonia coccifera* +, *C. uncialis* +, *Equisetum variegatum* +, *Poa arctica* +; TL42: *Carex aquatilis* s.l. r, *Cinclidium latifolium* +, *C. subrotundum* +, *Cladonia pleurota* +, *C. subfurcata* +, *Empetrum hermaphroditum* r, *Pedicularis labradorica* +, *Peltigera polydactyla* +, *Potentilla biflora* r; TL43: *Carex capillaris* +, *C. rariflora* r, *Minuartia arctica* r, *Oncophorus wahlenbergii* +, *Pannaria pezizoides* +, *Potentilla biflora* r, *Racomitrium lanuginosum* +, *Sphaerophorus globosus* r, *Tofieldia coccinea* +, *Tortella tortuosa* +; TL56: *Carex capillaris* +, *Fissidens osmundioides* +, *Lecanora epibryon* r, *Loeskyum badius* +, *Orthothecium chryseum* +, *Racomitrium lanuginosum* 2, *Scapania simmonsii* +, *Tofieldia coccinea* +; TL53: *Barbilophozia binsteadii* +, *Cladonia uncialis* r, *Lyellia aspera* +, *Paludella squarrosa* r, *Peltigera canina* +, *Salix chamissonis* +, *Salix glauca* +, *S. planifolia* ssp. *pulchra* 1, *Sphagnum girgensohnii* +, *S. lenense* +, *S. warnstorffii* +; TL45: *Cetraria laevigata* +, *Cladonia macrophylla* +, *Draba alpina* +, *Festuca altaica* 1, *Gentiana prostrata* +, *Hypnum cupressiforme* +, *Juncus biglumis* r, *Montia bostockii* +, *Nephroma expallidum* r, *Novostevia glacialis* +, *Oncophorus wahlenbergii* 3, *Peltigera didactyla* r, *Potentilla biflora* +; TL52: *Anemone richardsonii* 1, *Arnica lessingii* +, *Boykinia richardsonii* +, *Carex scirpoides* +, *Dodecatheon frigidum* +, *Gentiana prostrata* r, *Lyellia aspera* +, *Parnassia kotzebuei* +, *Parrya nudicaulis* s.l. +, *Pohlia cruda* +, *Rhizomnium andrewsianum* +, *Salix rotundifolia* ssp. *rotundifolia* 3, *Sanionia uncinata* +, *Saxifraga nelsoniana* +; TL24: *Cardamine bellidifolia* +, *Carex vaginata* r, *Cladonia coccifera* +, *C. pleurota* +, *Montia bostockii* +, *Ochrolechia upsaliensis* +, *Peltigera canina* +, *Pyrola asarifolia* +; TL10: *Anemone richardsonii* r, *Arctous alpina* +, *Blepharostoma trichophyllum* ssp. *brevirete* +, *Brachythecium turgidum* +, *Calliergon megalophyllum* +, *Dicranum acutifolium* +, *Equisetum variegatum* +, *Loeskyum badius* +, *Sanionia uncinata* +; TL21: *Arnica angustifolia* ssp. *angustifolia* +, *Blepharostoma trichophyllum* ssp. *brevirete* +, *Boykinia richardsonii* +, *Cardamine digitata* +, *Fissidens osmundioides* +, *Loeskyum badius* +, *Pedicularis sudetica* ssp. *interior* +, *Rhizomnium andrewsianum* +, *Salix pulchra* +, *Sphagnum teres* +; TL41: *Carex atrofusca* +, *C. scirpoides* +, *Cladonia coccifera* +, *Lecanora epibryon* +, *Oncophorus wahlenbergii* +, *Sphaerophorus globosus* +, *Tofieldia coccinea* +.

compared with 41 in the streamside riparian areas), and the stands are floristically distinct from the mesic tussock tundra that surrounds them. Faithful taxa are *Calliergon stramineum*, *Eriophorum angustifolium* ssp. *subarcticum* and *Salix pulchra*; differential taxa against other riparian types are *Rubus chamaemorus*, *Sphagnum girgensohnii* and *S. warnstorffii*. These sites are relatively rich in forbs and include many typical riparian species such as *Anemone richardsonii*, *Paludella squarrosa*, *Polemonium acutiflorum* and *Valeriana capitata*. The community is tentatively placed in the *Betulo-Adenostyletea* Braun-Blanquet 1948, including nutrient-rich subalpine and subarctic shrub communities associated with flowing water, but it may also belong to the *Scheuchzerio-Caricetea nigrae*.

Water tracks are an important component of the suite of upland vegetation communities, often dominating lower portions of slopes, especially where there is deep winter snow cover. Many carry only intermittent water flow, and the vegetation associated with the water tracks varies according to the volume of water that the track normally carries. Channels of the better developed water tracks have a distinctive *Eriophorum angustifolium*-*Salix pulchra* willow community. Poorly defined tracks that carry only small amounts of water have

shrub facies of the *Sphagno-Eriophoretum vaginati* subass. *typicum* (see above). The margins of the well-developed water tracks with distinctive channels often have well-developed shrub communities assigned to the *Sphagno-Eriophoretum vaginati betuletosum nanae*.

Well-developed water tracks are less common on the rocky till surfaces at Toolik Lake, and more distinctive riparian communities form along creek margins - *Salix alaxensis*-*S. pulchra* community type, App. 1, col. 17. The riparian communities of our study represent only a small part of the total riparian diversity. The streamside communities of the foothills region are extremely diverse, including everything from the vegetation of small water tracks to the extensive floodplains of major rivers, including both the Kuparuk and Sagavanirktok within the area studied.

Results: Ordination

DCA ordination of all relevés captured two important environmental gradients (Fig. 2a). Axis 1 corresponds to a complex mesotopographic gradient (*sensu* Billings 1973) with communities of dry exposed sites (A, B, C, F) on the right side of the diagram, snowbeds (D, E, Q), moist slopes (H, J) in the central-right portion, and bogs and fens on the left (K, L, M, N). The starburst of arrows within the ordination space (biplot diagram) displays the principal direction of variation and strength of correlation for major environmental variables. Environmental factors related to drier conditions (rock cover, sand, slope) increase toward the right, and factors related to wetter conditions increase toward the left (soil moisture, soil organic matter). The trend of higher nutrients (Ca, Mg, K, and NO_3) toward the left portion of the diagram is controlled by the minerotrophic water track and riparian communities on the left side (P and O in Fig. 2a) and the leached, nutrient-poor acidic dry communities on the right side (C, E, and F in Fig. 2a). The vertical axis corresponds to a complex landscape age gradient with pH increasing and soil clay content decreasing.

The effect of snow was not captured in the ordination diagrams, probably because it is neither correlated with, nor orthogonal to, the overriding moisture and pH gradients. The snowbed types are in the intermediate portion of the moisture gradient; however, the acidic and non-acidic snowbed types separate out along the pH gradient, and snow has a relatively high correlation with axis 4 of the ordination (Table 6). When only the dry upland plots are ordinated (not shown), snow has the strongest correlation with axis 1.

Although each of the community types occupies a relatively narrow range within the ordination space (Fig.

2a), there is considerable expected overlap because of intersecting Gaussian species distributions along environmental gradients. When the communities are grouped into the six terrestrial syntaxonomic classes, there is even greater overlap of the syntaxonomic units, but again, the general patterns reflect the influence of the mesotopographic gradient (Fig. 2b). The dry class *Carici-Kobresietea bellardii* is on the right side of the diagram; the wet class *Scheuchzerio-Caricetea nigrae* is on the left side, and classes with communities of intermediate moisture status are in the middle.

The ellipses enclosing the classes *Scheuchzerio-Caricetea nigrae* and *Betulo-Adenostyletea* are very large and the overlap between these ellipses and that of the *Oxycocco-Sphagnetes* is a consequence of the broad range of environmental conditions and species composition within these classes. The *Anthelia juratzkana-Juncus biglumis* community of non-sorted circles falls almost completely within the *Cetrario-Loiseleurietea* in the ordination diagram, suggesting that it has strong floristic compositional ties to that class.

The species ordination (Fig. 2c) shows the central distribution points for species along the same gradients. Species found in dry sites (e.g. *Dryas octopetala*, *Carex rupestris*) appear on the right side of the diagram and wet species are on the left (e.g. *Carex aquatilis*, *C. chondorrhiza*). Species found on young and highly disturbed sites (e.g. *Salix alaxensis*, *Poa glauca*) occur toward the top of the diagram, and species found in acidic stable sites (e.g. *Sphagnum lenense*, *Eriophorum scheuchzeri*) occur toward the bottom. Species typical of mesic and snowbed sites (e.g. *Tomentypnum nitens*, *Cassiope tetragona*) are in the middle of the diagram.

Ordination of the dry and moist uplands (without the mires, riparian communities, non-sorted circles, block-fields, and deep snowbeds) reveals a similar set of gradients (Fig. 3, Table 6). Axis 1 has dry, exposed sites to the right and sites with higher soil moisture to the left. Axis 2 is related to landscape age and substrate pH, with higher pH and nutrient conditions in the upper part of the diagram and increasing clay in the lower part. The lower-level syntaxa (associations and community types) are relatively well separated in the diagram. However, the *Carici microchaetae-Cassiope tetragonae* has considerable overlap with several vegetation types, probably due to its central location with respect to several environmental gradients (pH, soil moisture, snow).

Discussion

Relevance to other ecological research

The major landscape-level environmental variables controlling vegetation patterns within the Toolik Lake and Imnavait Creek region are a combination of conditions related to hillslope topography and landscape age. The topographic control of soil, vegetation, and geochemical properties has been illustrated in numerous studies of the Arctic (e.g. Cantlon 1961; de Molenaar 1987; Shaver et al. 1991; D.A. Walker et al. 1989; D.A. Walker & Everett 1991); however, the influence of geologic-scale terrain evolution on arctic vegetation patterns has only recently been recognized. Locally in the Arctic Foothills, Hamilton (1986) described the effects of different Pleistocene glaciations on landscape morphology. Jorgenson (1984) and D.A. Walker et al. (1989, in press) linked Hamilton's glacial units to a hypothesis of vegetation evolution, whereby peat formation (paludification) and ice aggradation on older surfaces leads to restricted drainage, a general acidification of the soils, and the introduction of *Sphagnum* mosses to wet hillslopes. The advent of the mosses changes the soil chemistry, hydrology and soil thermal properties, resulting in peat formation, acidic mires in colluvial basins, extensive water track development, and tussock tundra on gentle hill slopes. Differences in degree of paludification are the main factors controlling the distribution of acidic tussock tundra, *Sphagno-Eriophoretum vaginatum*, and its non-acidic counterpart *Dryado integrifoliae-Caricetum bigelowii*. The association *Dryado integrifoliae-Caricetum bigelowii* is also found in association with a variety of other natural disturbances including loess deposition, solifluction, cryoturbation, and alluvial processes (e.g. D.A. Walker & Everett 1991).

Well-developed tussock tundra appears to form only under conditions of long-term site stability. The two associations *Sphagno-Eriophoretum vaginatum* and *Dryado integrifoliae-Caricetum bigelowii* are important throughout the uplands of the foothills, and are also apparently abundant in similar topographic positions in far eastern Siberia (Razzhivin 1994 - this issue). The *Sphagno-Eriophoretum vaginatum* includes a variety of dominance types, including both sedge mires and shrublands, corresponding to local variation in moisture, exposure and nutrients. The physiognomic variation within the association is very important from an ecosystem-function perspective. For example, the relative cover and size of deciduous shrubs can strongly affect microclimate, net primary productivity (NPP), and animal habitat characteristics. Physiognomic differences of plant communities are not necessarily reflected

Fig. 2. DCA ordination of all terrestrial samples. **a.** Samples-environment biplot, with samples coded by association or community type. **b.** Samples grouped according to tentative syntaxonomic class. **c.** Position of major characteristic taxa for the classes, associations, and community types. Arrows along each DCA axis indicate direction of principal environmental gradients. Letters represent associations and communities:

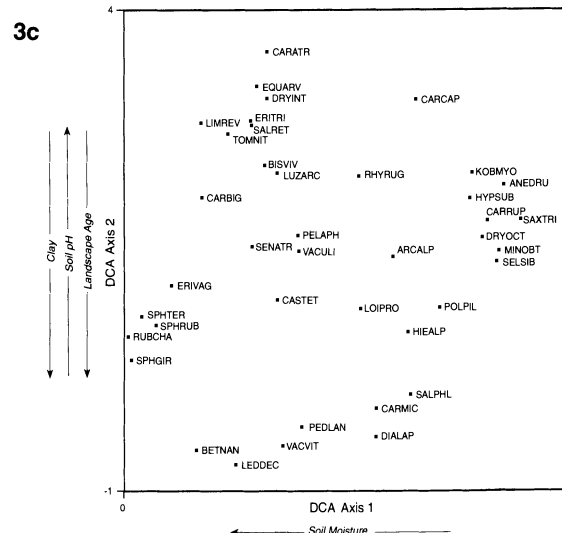
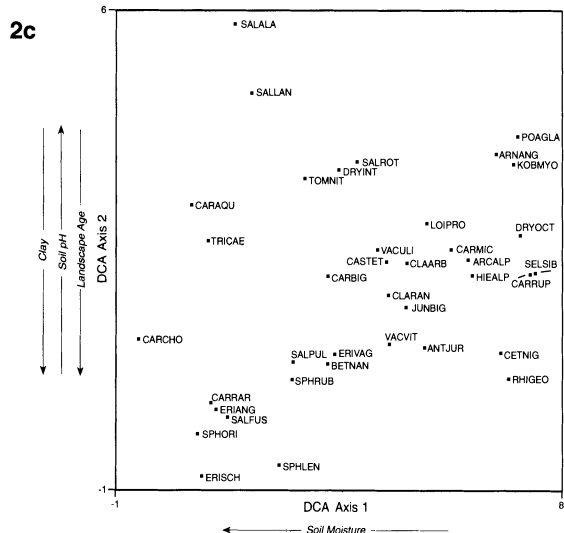
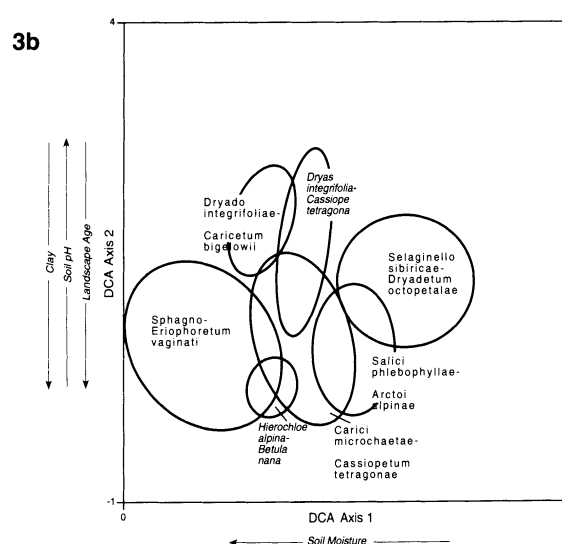
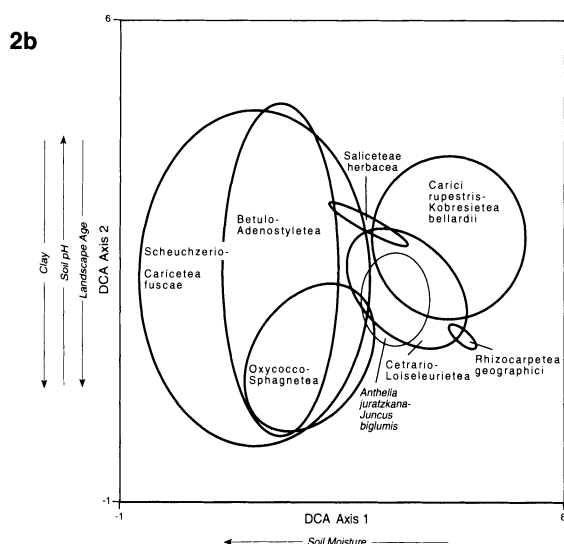
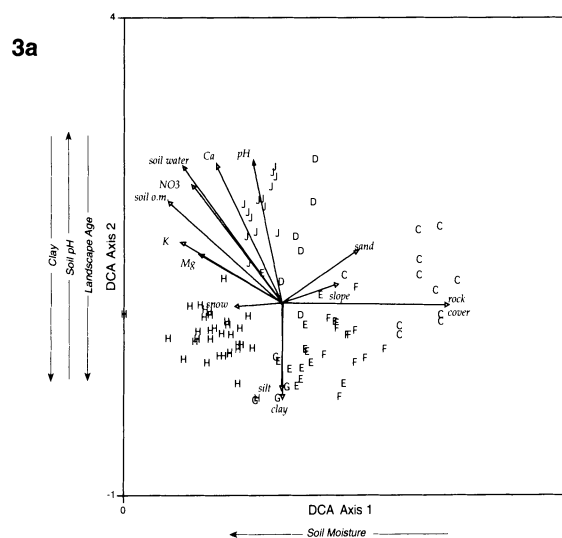
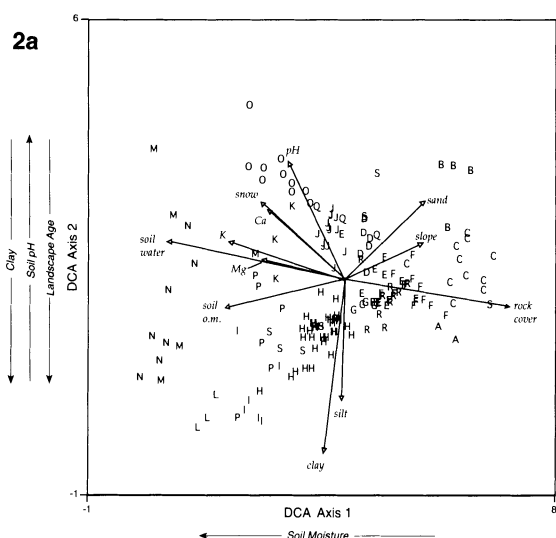
A, *Cetraria nigricans-Rhizocarpon geographicum* comm.; B, *Poa glauca-Arnica angustifolia* comm.; C, *Selaginella sibiricae-Dryadetum octopetalae*; D, *Dryas integrifolia-Cassiope tetragona* comm.; E, *Carici microchaetae-Cassiope tetragona*; F, *Salici phlebophyllae-Arctietum alpinae*; G, *Hierochloë alpina-Betula nana* comm.; H, *Sphagno-Eriophoretum vaginatum*; I, *Sphagnum lenense-Salix fuscescens* comm.; J, *Dryado integrifoliae-Caricetum bigelowii*; K, *Tomentypnum nitens-Trichophorum caespitosum* comm.; L, *Sphagnum orientale-Eriophorum scheuchzeri* comm.; M, *Eriophorum angustifolium-Carex aquatilis* comm.; N, *Carex aquatilis-Carex chordorrhiza* comm.; O, *Salix alaxensis-Salix lanata* comm.; P, *Eriophorum angustifolium-Salix pulchra* comm.; Q, *Salix rotundifolia* comm.; R, *Anthelia juratzkana-Juncus biglumis* comm.; S, not classified.

Species codes are:

ANTJUR *Anthelia juratzkana*, ARCALP *Arctous alpina*, ARNANG *Arnica angustifolia*, BETNAN *Betula nana*, CARAQU *Carex aquatilis*, CARBIG *Carex bigelowii*, CARCHO *Carex chordorrhiza*, CARMIC *Carex microchaeta*, CARRAR *Carex rariflora*, CARRUP *Carex rupestris*, CASTET *Cassiope tetragona*, CETNIG *Cetraria nigricans*, CLAARB *Cladina arbuscula*, CLARAN *Cladina rangiferina*, DRYINT *Dryas integrifolia*, DRYOCT *Dryas octopetala*, ERIANG *Eriophorum angustifolium*, ERISCH *Eriophorum scheuchzeri*, ERIVAG *Eriophorum vaginatum*, HIEALP *Hierochloë alpina*, JUNBIG *Juncus biglumis*, KOBMYO *Kobresia myosuroides*, LOIPRO *Loiseleuria procumbens*, POAGLA *Poa glauca*, RHIGEO *Rhizocarpon geographicum*, SALALA *Salix alaxensis*, SALFUS *Salix fuscescens*, SALLAN *Salix lanata*, SALPUL *Salix pulchra*, SALROT *Salix rotundifolia*, SELSIB *Selaginella sibirica*, SPHLEN *Sphagnum lenense*, SPHORI *Sphagnum orientale*, SPHRUB *Sphagnum rubellum*, TOMNIT *Tomentypnum nitens*, TRICAE *Trichophorum caespitosum*, VACULI *Vaccinium uliginosum*, VACVIT *Vaccinium vitis-idaea*.

Fig. 3. DCA ordination of dry and moist upland samples. **a.** Samples-environment biplot, with samples coded by association or comm. type as in Fig. 2. **b.** Samples grouped according to association or comm. **c.** Position of major characteristic taxa for the associations and community types. Arrows and association abbreviations as in Fig. 2. Species codes are:

ANEDRU *Anemone drummondii*, ARCALP *Arctous alpina*, BETNAN *Betula nana*, BISVIV *Bistorta vivipara*, CARATR *Carex atrofusca*, CARBIG *Carex bigelowii*, CARCAP *Carex capillaris*, CARRUP *Carex rupestris*, CASTET *Cassiope tetragona*, DIALAP *Diapensia lapponica*, DRYINT *Dryas integrifolia*, DRYOCT *Dryas octopetala*, EQUARVE *Equisetum arvense*, ERITRI *Eriophorum triste*, ERIVAG *Eriophorum vaginatum*, HIEALP *Hierochloë alpina*, HYP SUB *Hypogymnia subobscura*, KOBMYO *Kobresia myosuroides*, LEDDEC *Ledum palustre* ssp. *decumbens*, LIMREV *Limprichtia revolvens*, LOIPRO *Loiseleuria procumbens*, LUZARC *Luzula arctica*, MINOBT *Minuartia obtusiloba*, PEDLAN *Pedicularis lanata*, PELAPH *Peltigera aphthosa*, POLPIL *Polytrichum piliferum*, RHYRUG *Rhytidium rugosum*, RUBCHA *Rubus chamaemorus*, SALPHL *Salix phlebophylla*, SALRET *Salix reticulata*, SAXTRI *Saxifraga tricuspidata*, SELSIB *Selaginella sibirica*, SENATR *Senecio atropurpureus*, SPHGIR *Sphagnum girgensohnii*, SPHRUB *Sphagnum rubellum*, SPHTER *Sphagnum teres*, TOMNIT *Tomentypnum nitens*, VACULI *Vaccinium uliginosum*, VACVIT *Vaccinium vitis-idaea*.



in a purely floristic classification, especially in low-arctic tundra ecosystems, because of the rather constant composition of the dominance types and the variable height of the dominant species. Vegetation mapping units that are useful for a wide variety of arctic ecological studies can be based on the Braun-Blanquet associations but require finer differentiation corresponding to dominant species and growth forms.

Recently, landscape age at Toolik Lake has been linked to remotely-sensed patterns of vegetation biomass. Older landscapes have higher mean normalized difference vegetation index (NDVI) and greater amounts of standing biomass (D.A. Walker et al. in press). The NDVI is a greenness index derived from the red and infrared bands of multispectral data (e.g. Paruelo et al. 1993). The higher NDVI values for the older landscapes are due in part to relative proportions of dry, moist and wet vegetation types on different aged surfaces; generally drier vegetation types dominate the younger surfaces. Of greater regional significance is the difference in biomass and NDVI of vegetation growing on moist upland surfaces. The biomass of the *Sphagno-Eriophoretum vaginatum* tussock tundra is ca. 25 % greater than its non-acidic counterpart, the *Dryado integrifoliae-Caricetum bigelowii* (512 g/m² vs. 403 g/m²; D.A. Walker et al. in press). Other studies have derived regional maps of leaf-area index and biomass based on this knowledge (Shippert et al. in press), and these data will be used in regional models of fluxes of trace gases, water, and energy from tundra surfaces (Weller et al. in press). Until recently, the *Dryado integrifoliae-Caricetum bigelowii* was not recognized as distinct from acidic tussock tundra by arctic ecologists. However, many of its functional properties are quite different from tussock tundra, and consideration of its areal extent could influence estimates of important ecosystem variables such as NPP, soil carbon, leaf area index, and evapotranspiration.

The *Dryado integrifoliae-Caricetum bigelowii* and related associations, e.g. *Dryas integrifolia-Cassiope tetragona*, are also important with respect to regional biodiversity. These associations have the highest species diversity of any of the communities sampled in this study. Several of the species have local, Beringian, or western North American distributions, e.g. *Claytonia bostockii*, *Lagotis glauca*, *Novosieversia glacialis*, *Parrya nudicaulis* ssp. *septentrionalis*, *Potentilla biflora* and *Saussurea angustifolia*. Additionally, the effects of landscape age upon total regional plant and animal diversity and abundance have not been studied in any detail. The Toolik Lake region offers a pristine environment with a young heterogeneous landscape the biodiversity of which contrast with that of old stable landscapes.

Table 6. Correlation coefficients of environmental variables with species axes derived by DCA ordination. Variables are sorted by their degree of correlation with the first axis. The five highest absolute values for each axis are in bold type, and variables that fall into that category for either of the first two axes are also shown in bold type.

All terrestrial samples (160):	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	.634	.474	.326	.274
Gradient length	6.81	4.74	4.21	4.55
All terrestrial samples (160):	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	.634	.474	.326	.274
Gradient length	6.81	4.74	4.21	4.55
Overall correlation	.726	.594	.519	.548
Soil water	-.514	.020	.158	.310
Rock cover	.475	.001	-.358	-.230
Soil organic matter	-.358	-.093	.251	.300
K	-.334	.041	.176	.144
Sand	.250	.190	-.143	.082
Mg	-.239	.012	.195	-.004
Slope angle	.238	.101	-.046	-.282
Snow depth	-.233	.130	-.158	-.128
Ca	-.214	.118	.131	.151
NO ₃	-.173	.082	.189	.293
Soil pH	-.147	.223	-.033	.136
Clay	-.092	-.358	.079	-.154
Silt	-.029	-.246	.016	-.183
Dry and moist uplands (93):				
Eigenvalue	.561	.294	.185	.146
Gradient length	5.28	2.53	2.53	2.43
Overall correlation	.783	.668	.558	.535
Rock cover	.650	.030	-.210	-.052
Soil organic matter	-.437	.253	-.009	-.141
K	-.392	.145	.173	.194
Soil water	-.378	.353	-.010	-.281
NO ₃ -.342	.302	.090	-.008	
Mg	-.322	.115	-.122	-.110
Sand	.301	.161	-.192	.096
Ca	-.246	.364	-.261	-.110
Slope angle	.218	.065	-.217	.073
Snow depth	-.189	-.022	-.140	.240
Soil pH	-.102	.381	-.249	-.052
Silt	-.012	-.236	-.166	.146
Clay	-.007	-.261	-.109	-.091

Toward a Braun-Blanquet circumpolar vegetation classification

A circumpolar vegetation classification would be highly desirable to extend the results of these and other studies to the entire arctic region. We tentatively assigned the associations and community types to seven existing Braun-Blanquet classes. However, the formal assignment of Alaskan and Siberian vegetation to circumpolar syntaxonomic units will require reassessment of existing high level units that emphasizes circumpolar taxa in their definition. 35 - 80 % of any Arctic flora are species with acircumpolar distribution (Yurtsev 1994 - this issue). Many cryptogamic taxa also

have circumpolar distributions, giving vegetation communities of similar habitats strong floristic similarities throughout.

Much of the Arctic phytosociological work has focused on the Scandinavian mountains and Greenland (e.g. de Molenaar 1974, 1976; Daniëls 1975, 1982, 1994 - this issue; Thannheiser 1987a, b; Dierßen 1992). Units that were described as sociations may be redefined as associations under conditions summarized by Moravec (1993). The floristic ties between these regions and Beringia are strong enough that it should be possible to apply the European units, or revisions of them, to Alaska.

Plant taxa with more restricted distributions can be used to define local associations or differentiate vicarious representatives of broader associations. Several of our associations appear to be vicariants of previously described associations from Scandinavia and Greenland, and we differentiated our associations on the basis of common Beringian taxa. Alaska is one of the floristically richest areas in the Arctic due to the presence of an unglaciated land bridge that existed between Alaska and Siberia during Pleistocene glacial maxima (Hopkins 1982). This ice-free area, known as Greater Beringia, was the only extensively unglaciated region of the Arctic during the Pleistocene, and today it supports an extensive endemic flora (Hultén 1968; Yurtsev 1994 - this issue). Some authors have been inclined to define an entirely new set of syntaxonomic units for Beringia (e.g. Cooper 1986, Komárková & McKendrick 1988). To do this, however, denies the strong floristic similarities of communities in similar habitats in geographically disjunct regions of the Arctic.

It may be better to define relatively broad circumpolar alliances with associations based on regional vicariant taxa, recognizing that some associations will not have a set of vicariants forming a circumpolar group. For example, the *Sphagno-Eriophoretum vaginati* is primarily a Beringian association without a good corresponding vicariant association in Europe. Although *Eriophorum vaginatum* has a circumpolar distribution, it does not dominate extensive landscapes outside of Beringia (Aleksandrova 1980). Other arctic tundra landscapes with similar topography support very different vegetation. For example, on the Taymyr Peninsula in north central Siberia, an association of *Carex bigelowii* and *Dryas octopetala*, the *Carici arctisibiricae-Hylocomietum alaskani* (Matveyeva 1994 - this issue) predominates on mesic uplands that are otherwise similar to the tussock-tundra landscapes of northern Alaska. This association has strong relationships to the *Dryado integrifoliae-Caricetum bigelowii* described in our study. It may be that these other regions are simply not old enough to develop the soil conditions necessary for extensive stands of tussock tundra.

The applications mentioned above require a vegetation classification based on accurate floristic information and which can be applied to broad regions of the arctic. Of the many vegetation classification systems that have been used in northern Alaska, only the Braun-Blanquet approach has the potential for creating a framework based on the strong similarities of vegetation occurring in similar habitats throughout the circumpolar region yet also recognizing important floristic variation within these units.

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References (* = in Russian; ** = with English summary)

- Anon. 1975. *Soil taxonomy, a basic system of soil classification for making and interpreting soil surveys*. Soil Conservation Service, U.S. Department of Agriculture Handbook No. 436. Washington, DC.
- Aleksandrova, V.D. 1980. *The Arctic and Antarctic: Their division into geobotanical areas*. Cambridge University Press, New York, NY.
- Anderson, J.H. 1974. *Plants, soils, phytocenology and primary production of the Eagle Summit Tundra Biome Site*. U.S. Tundra Biome data report 74-42. Fairbanks, AK.
- Barkman, J.J., Moravec, J. & Rauschert, S. 1986. Code of phytosociological nomenclature. *Vegetatio* 67: 145-158.
- Barrett, P.E. 1972. *Phytogeocoenoses of a coastal lowland ecosystem, Devon Island, N.W.T.* Ph.D. Thesis, University of British Columbia, Vancouver.
- Billings, W.D. 1973. Arctic and alpine vegetations: similarities, differences, and susceptibility to disturbances. *BioScience* 23: 697-704.
- Bliss, L.C. 1956. A comparison of plant development in microenvironments of arctic and alpine tundras. *Ecol. Monogr.* 26: 303-337.
- Bliss, L.C. 1962. Adaptations of arctic and alpine plants. *Biol. Rev.* 43: 481-529.
- Bliss, L.C. & Matveyeva, N.V. 1992. Circumpolar arctic vegetation. In: Chapin, F.S., Jefferies, R.L., Reynolds, J.F., Shaver, G.R., Svoboda, J. & Chu, E.W. (eds.) *Arctic ecosystems in a changing climate: an ecophysiological*

- perspective, pp. 59-89. Academic Press, San Diego, CA.
- Böcher, T.W. 1933. Studies on the vegetation of the east coast of Greenland. *Medd. Grönl.* 104(4): 1-56.
- Braun-Blanquet, J. 1948-1950. Übersicht der Pflanzengesellschaften Rätens. I-VI. *Vegetatio* 1: 29-41, 1: 129-146, 1: 285-316; 2: 20-37, 2: 213-237, 2: 341-360.
- Braun-Blanquet, J. & Tüxen, R. 1943. *Übersicht der höheren Vegetationseinheiten Mitteleuropas*. S.I.G.M.A. Comm. 84, Montpellier.
- Cantlon, J.E. 1961. *Plant cover in relation to macro-, meso- and microrelief*. Report Grants #ONR-208 and 216, Office of Naval Research, Washington, DC.
- Chapin, F. S., III, Fetcher, N., Kielland, K., Everett, K. R. & Linkins, A. E. 1988. Productivity and nutrient cycling of Alaskan tundra: enhancement by flowing soil water. *Ecology* 69: 693-702.
- Churchill, E.D. 1955. Phytosociological and environmental characteristics of some plant communities in the Umiat region of Alaska. *Ecology* 36: 606-627.
- Cooper, D.J. 1986. Arctic-alpine tundra vegetation of the Arrigetch Creek Valley, Brooks Range, Alaska. *Phytocoenologia* 14: 467-555.
- Daniëls, F.J.A. 1975. Vegetation of the Angmagssalik District, Southeast Greenland. III. Epilithic macrolichen communities. *Medd. Grönl.* 198(3): 1-32.
- Daniëls, F.J.A. 1982. Vegetation of the Angmagssalik District, Southeast Greenland, IV. Shrub, dwarf shrub and terricolous lichens. *Medd. Grönl. Biosci.* 10: 1-78.
- Daniëls, F.J.A. 1994. Vegetation classification in Greenland. *J. Veg. Sci.* 5: 781-790.
- Dargie, T.C.D. 1984. On the integrated interpretation of indirect site ordinations: a case study using semi-arid vegetation in south-eastern Spain. *Vegetatio* 30: 15-32.
- de Molenaar, J.G. 1974. Vegetation of the Angmagssalik District, Southeast Greenland I. Littoral vegetation. *Medd. Grönl.* 198(1): 1-98.
- de Molenaar, J.G. 1976. Vegetation of the Angmagssalik District, Southeast Greenland II. Herb and snow-bed vegetation. *Medd. Grönl.* 198(2): 1-265.
- de Molenaar, J.G. 1987. An ecohydrological approach to floral and vegetational patterns in Arctic landscape ecology. *Arct. Alp. Res.* 19: 414-424.
- Dick, W.A. & Tabatabai, M.A. 1979. Ion chromatographic determination of sulfate and nitrate in soils. *Soil Sci. Am. J.* 43: 899-904.
- Dierßen, K. 1992. Zur Synsystematik nordeuropäischer Vegetationstypen. 1. Alpine Vegetation und floristisch verwandte Vegetationseinheiten tieferer Lagen sowie der Arktis. *Ber. R.-Tüxen-Ges.* 4: 191-226.
- Douglas, L.A. & Tedrow, J.C.F. 1960. Tundra soils of arctic Alaska. In: *Proceedings of the 7th International Congress of Soil Scientists*, pp. 291-304. Int. Congress of Soil Scientists, 4. Madison, WI.
- DuRietz, G.E. 1925. Zur Kenntnis der flechtenreiche Zwergstrauchheiden im kontinentalen Südnorwegen. *Sven. Växtsociol. Sällsk. Handl.* 4: 1-80.
- Ellenberg, H. 1988. *Vegetation ecology of central Europe*. 4th ed., transl. by G.K. Strutt. Cambridge University Press, New York, NY.
- Elvebakk, A. 1982. Geological preferences among Svalbard plants. *Inter-Nord* 16: 11-31.
- Everett, K.R. 1980. Landforms. In: Walker, D.A., Everett, K.R., Webber, P.J. & Brown, J. (eds.) *Geobotanical atlas of the Prudhoe Bay region, Alaska*, pp. 14-19. CRREL Report #80-14. U.S. Army Cold Regions Research and Engineering Laboratory, Hanover, NH.
- Fries, T.C.E. 1913. *Botanische Untersuchungen im nördlichsten Schweden*. Doctoral Thesis, Uppsala University.
- Gee, G.W. & Bauder, J.W. 1986. Particle size analysis. In: Klute, A. (ed.) *Methods of soil analysis, Part 1: Physical and mineralogical methods*, pp. 383-411. Agronomy Society of America and Soil Science Society of America, Madison, WI.
- Hadač, E. 1946. The plant-communities of Sassen Quarter, Vestspitsbergen. *Stud. Bot. Českoslov.* 7: 127-164.
- Hamilton, T.D. 1986. Late Cenozoic glaciation of the Central Brooks Range. In: Hamilton, T.D., Reed, K.M. & Thorson, R.M. (eds.) *Glaciation in Alaska: the geologic record*, pp. 9-49. Alaska Geological Society, Fairbanks, AK.
- Hanson, H.C. 1951. Characteristics of some grassland, marsh, and other plant communities in western Alaska. *Ecol. Monogr.* 21: 317-378.
- Hanson, H.C. 1953. Vegetation types in northwestern Alaska and comparisons with communities in other arctic regions. *Ecology* 34: 111-148.
- Haugen, R. K. 1982. *Climate of remote areas in north-central Alaska, 1975-1979 summary*. CRREL Report #82-35, U.S. Army Cold Regions Research and Engineering Laboratory, Hanover, NH.
- Hinzman, L.D., Kane, D.L., Benson, C.S. & Everett, K.R. In press. Thermal and hydrologic processes in the Imnavait Creek watershed. In: Reynolds, J.F. & Tenhunen, J.D. (eds.) *Landscape function: Implications for ecosystem disturbance, a case study in arctic tundra*. Springer-Verlag, Berlin.
- Hobbie, J.E., Deegan, L.A., Peterson, B.J., Rastetter, E.B., Shaver, G.R., Kling, G.W., O'Brien, W.J., Chapin, F.S., Miller, M.C., Kipphut, G.W., Bowden, W.B., Hershey, A.E. & McDonald, M.E. In press. Long-term measurements at the arctic LTER site. In: Steele, J. (ed.) *Ecological time series*. Chapman and Hall, New York, NY.
- Hopkins, D. 1982. Aspects of the paleogeography of Beringia during the late Pleistocene. In: Hopkins, D.M., Matthews, J.V., Jr., Schweger, C.E., & Young, S.B. (eds.) *Palaeoecology of Beringia*, pp. 3-28. Academic Press, New York, NY.
- Hultén, E. 1968. *Flora of Alaska and neighboring territories: A manual of the vascular plants*. Stanford University Press, Stanford, CA.
- Jackson, M.L. 1958. *Soil chemical analysis*. Prentice-Hall, Inc., Englewood Cliffs, NJ.
- Johnson, A.W., Viereck, L.A., Johnson, R.E. & Melchior, H. 1966. Vegetation and flora. In: Wilimovsky, N.J. & Wolfe, J.N. (eds.) *Environment of the Cape Thompson Region, Alaska*, pp. 277-354. Publication PNE-481, U.S. Atomic Energy Commission, Oak Ridge, TN.
- Jongman, R.H.G., ter Braak, C.J.F. & van Tongeren, O.F.R. 1987. *Data analysis in community and landscape ecology*. Pudoc, Wageningen.
- Jorgenson, T. 1984. The response of vegetation to landscape

- evolution on glacial till near Toolik Lake, Alaska. In: Inventorying forest and other vegetation of the high latitude and high altitude regions, In: *Proceedings of an International Symposium, Society of American Foresters Regional Technical Conference, 23-26 July 1984*, pp. 134-141. Fairbanks, AK.
- Keeney, D.R. & Nelson, D. W. 1982. Nitrogen-inorganic forms. In: Page, A.L., Miller R.H. & Kenney, D.R. (eds.) *Methods of soil analysis, Part II: Chemical and microbiological properties*, pp. 643-698. Soil Science Society of America, Madison, WI.
- Komárková, V. 1993. Vegetation type hierarchies and landform disturbance in arctic Alaska and alpine Colorado with emphasis on snowpatches. *Vegetatio* 106: 155-181.
- Komárková, V. & McKendrick, J.D. 1988. Patterns in vascular plant growth forms in arctic communities and environment at Atkasook, Alaska. In: Werger, M.J.A., van der Aart, P.J.M., During, H.J. & Verhoeven, J.T.A. (eds.) *Plant form and vegetation structure*, pp. 45-70. SPB Academic Publishing, The Hague.
- Komárková, V. & Webber, P.J. 1980. Two low arctic vegetation maps near Atkasook, Alaska. *Arct. Alp. Res.* 12: 447-472.
- Lambert, J.D.H. 1968. *The ecology and successional trends in the Low Arctic subalpine zone of the Richardson and British Mountains of the Canadian western arctic*. Ph.D. Thesis, University of British Columbia, Vancouver.
- Matveyeva, N.V. Floristic classification and ecology of tundra vegetation of the Taymyr Peninsula, northern Siberia. *J. Veg. Sci.* 5: 813-828.
- Moravec, J. 1993. Syntaxonomic and nomenclatural treatment of Scandinavian-type associations and socations. *J. Veg. Sci.* 4: 833-838.
- Mueller-Dombois, D. & Ellenberg, H. 1974. *Aims and methods of vegetation ecology*. John Wiley and Sons, New York, NY.
- Nelson, D.W. & Sommers, L.E. 1982. Total carbon, organic carbon and organic matter. In: Page, A.L., Miller, R.H. & Keeney, D.R. (eds.) *Methods of soil analysis, Part 2. Chemical and microbiological properties*, pp. 539-580. American Society of Agronomy and Soil Science Society of America, Madison, WI.
- Nordhagen, R. 1928. Die Flora und Vegetation des Sylenegebietes. *Nor. Vidensk. Akad. Skr. Oslo* 1:1-612.
- Nordhagen, R. 1935. Om *Arenaria norvegica* Wb. og dens betydning for utforskningen av Scandinavias eldste floraelement. *Berg. Mus. Årbok Naturvidensk. R.* 1935,1: 1-183.
- Nordhagen, R. 1936. Versuch einer neuen Einteilung der subalpinen-alpinen Vegetation Norwegens. *Berg. Mus. Årb. Naturvid. R.* 1936,7: 1-88.
- Nordhagen, R. 1943. Sikilsdalen og Norges fjellbeiter. En Plantensosiologisk monografi. *Berg. Mus. Skr.* 22: 1-607.
- Oberdorfer, E. 1949. *Pflanzensoziologische Exkursionsflora für Südwestdeutschland und die angrenzenden Gebiete*. Ulmer, Stuttgart.
- Oechel, W.C. 1989. Nutrient and water flux in a small arctic watershed: an overview. *Holarct. Ecol.* 12: 229-237.
- Ohba, T. 1974. Vergleichende Studien über die alpine Vegetation Japans. I. *Carici rupestris-Kobresietea bellardii*. *Phytocoenologia* 1: 339-401.
- Økland, R.H. 1992. Studies in SE Fennoscandian mires: relevance to ecological theory. *J. Veg. Sci.* 3: 279-284.
- Osterkamp, T.E., & Payne, M.W. 1981. Estimates of permafrost thickness from well bogs in northern Alaska. *Cold Reg. Sci. Tech.* 5: 13-27.
- Paruelo, J.M., Aguiar, M.R., Golluscio, R.A., León, R.J.C. & Pujol, G. 1993. Environmental controls of NDVI dynamics in Patagonia based on NOAA-AVHRR satellite data. *J. Veg. Sci.* 4: 425-428.
- Peet, R.K., Knox, R.G., Case, J.S. & Allen, R.B. 1988. Putting things in order. The advantages of detrended correspondence analysis. *Am. Nat.* 129: 434-448.
- Pegau, R.E. 1968. Growth rates of important reindeer forage lichens on the Seward Peninsula, Alaska. *Arctic* 21: 255-259.
- Razzhivin, V.Yu. 1994. Snowbed vegetation of far northeastern Asia. *J. Veg. Sci.* 5: 829-842.
- Rønning, O.I. 1965. Studies in Dryadion of Svalbard. *Skr. Nor. Polarinst.* 134: 1-52.
- Roux, C. 1978. Complément à l'étude écologique et phytosociologique des peuplements lichéniques saxicoles-calciocoles du SE de la France. *Bull. Mus. Hist. Nat. Mars.* 38: 65-186.
- Selkregg, L.L. 1975 *Alaska regional profiles: arctic region*. University of Alaska, Fairbanks, AK.
- Shaver, G.R., Chapin, F.S., III & Gartner, B.L. 1986. Factors limiting seasonal growth and peak biomass accumulation in *Eriophorum vaginatum* in Alaskan tussock tundra. *J. Ecol.* 74: 257-278.
- Shaver, G., Nadelhoffer, K.J. & Giblin, A.E. 1991. Biogeochemical diversity and element transport in a heterogeneous landscape, the North Slope of Alaska. *Ecol. Stud. Anal. Synth.* 82: 105-125.
- Shippert, M.M., Walker, D.A., Auerbach, N.A. & Lewis, B.E. In press. Biomass and leaf area index maps derived from SPOT images for the Toolik Lake and Imnavait Creek area, Alaska. *Polar Rec.*
- Spetzman, L.A. 1959. *Vegetation of the arctic slope of Alaska*. United States Geological Survey Professional Paper 302-B. U.S. Government Printing Office, Washington, DC.
- Suzuki Tokyo 1964. *Übersicht auf die alpinen und subalpinen Pflanzengesellschaften im inneren Kurobegebiet*. Synth. Sci. Res. Org., Toyama University, Toyama.
- ter Braak, C.J.F. 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. *Vegetatio* 69: 69-78.
- Thannheiser, D. 1976. Ufer- und Sumpfvegetation auf dem westlichen kanadischen Arktis-Archipel und Spitzbergen. *Polarforschung* 46: 71-82.
- Thannheiser, D. 1987a. Die Vegetationszonen in der westlichen kanadischen Arktis. *Hamburg. Geogr. Stud.* 43: 159-177.
- Thannheiser, D. 1987b. Vergleichende ökologische Studien an der Küsten-vegetation am Nordatlantik. *Berlin. Geogr. Stud.* 25: 285-299.
- Thomas, G.W. 1982. Exchangeable cations. In: Page, A.L., Miller, R.H. & Keeney, D.R. (eds.) *Methods of soil analysis, Part 2. Chemical and microbiological properties*, pp. 159-166. Agronomy Ser.No. 9. American Society of Agronomy and Soil Science Society of America, Madison, WI.

- Tüxen, R. 1937. Die Pflanzengesellschaften Nordwestdeutschlands. *Mitt. Flor.-soziol. Arbeitsgem.* 3: 1-170.
- van Groenewoud, H. 1992. The robustness of Correspondence, Detrended Correspondence, and TWINSpan Analysis. *J. Veg. Sci.* 3: 239-246.
- Wahrhaftig, C. 1965. *Physiographic divisions of Alaska*. U.S. Geological Survey Professional Paper 482. U.S. Government Printing Office, Washington, DC.
- Walker, D.A. 1985. *Vegetation and environmental gradients of the Prudhoe Bay region, Alaska*. CRREL Report 85-14, U.S. Army Cold Regions Research and Engineering Laboratory, Hanover, NH.
- Walker, D.A. & Everett, K.R. 1991. Loess ecosystems of northern Alaska: regional gradient and toposequence at Prudhoe Bay. *Ecol. Monogr.* 61: 437-464.
- Walker, D.A. & Walker, M.D. 1991. History and pattern of disturbance in Alaskan arctic terrestrial ecosystems: a hierarchical approach to analysing landscape change. *J. Appl. Ecol.* 28: 244-276.
- Walker, D.A. & Walker, M.D. In press. Terrain and vegetation of the Imnavait Creek Research Site. In: Reynolds, J. F. & Tenhunen, J. D. (eds.) *Landscape function: Implications for ecosystem disturbance, a case study in arctic tundra*. Springer-Verlag, Berlin.
- Walker, D.A., Auerbach, N.A., & Shippert, M.M. In press. NDVI, biomass, and landscape evolution of glaciated terrain in northern Alaska. *Polar Rec.*
- Walker, D.A., Binnian, E., Evans, B.M., Lederer, N.D., Nordstrand, E. & Webber, P.J. 1989. Terrain, vegetation and landscape evolution of the R4D research site, Brooks Range Foothills, Alaska. *Holarct. Ecol.* 12: 238-261.
- Walker, D.A., Everett, K.R., Acevedo, W., Gaydos, L., Brown, J. & Webber, P.J. 1982. *Landsat-assisted environmental mapping in the Arctic National Wildlife Refuge, Alaska*. CRREL Report #82-27, U.S. Army Cold Regions Research and Engineering Laboratory, Hanover, NH.
- Walker, M.D. 1990. Vegetation and Floristics of Pingos, Central Arctic Coastal Plain, Alaska. *Diss. Bot.* 149.
- Walker, M.D. In press. Patterns and causes of arctic plant community diversity. In: Chapin, F.S. Körner, C.H. (eds.) *Arctic and alpine biodiversity: patterns, causes, and ecosystem consequences*. Springer-Verlag, Berlin.
- Walker, M.D., Walker, D.A. & Everett, K.R. 1989. *Wetland soils and vegetation, Arctic Foothills, Alaska*. Report 89 (7), U.S. Fish and Wildlife Service, Department of the Interior, Washington, DC.
- Walker, M.D., Walker, D.A., Everett, K.R. & Short, S.K. 1991. Arctic steppe on south-facing slopes of pingos, central Arctic Coastal Plain, Alaska. *Arct. Alp. Res.* 23: 170-188.
- Washburn, 1956. Classification of patterned ground and review of suggested origins. *Geol. Soc. Am. Bull.* 67: 823-866.
- Webber, P.J., Komárková, V., Walker, D.A. & Werbe, N. 1979. *Geobotanical studies along a latitudinal gradient between the Yukon River and Prudhoe Bay, Alaska*. CRREL Internal Report 585, U.S. Army Cold Regions Research and Engineering Laboratory, Hanover, NH.
- Weller, G., Chapin, F.S., Everett, K.R., Hobbie, J.E., Kane, D., Oechel, W.C., Ping, C.L., Reeburgh, W.S., Walker, D. & Walsh, J. In press. The arctic flux study: a regional view of trace gas release. *Glob. Ecol. Biogeogr. Lett.*
- Westhoff, V. & van der Maarel, E. 1978. The Braun-Blanquet approach. In: Whittaker, R.H. (ed.) *Classification of plant communities*, pp. 287-399. Junk, Den Haag.
- Wirth, V. 1972. Die Silikatflechten-Gemeinschaften im oberalpinen Zentraleuropa. *Diss. Bot.* 17.
- Yurtsev, B.A. 1974**. The steppe associations of the Chukotka tundra and the Pleistocene 'tundra steppe.' *Bot. Zh. (Leningr.)* 59: 484-501.
- Yurtsev, B.A. 1994. Floristic division of the Arctic. *J. Veg. Sci.* 5: 765-776.
- Zanokha, L.L. 1989*. *Grasslands of the tundra zone (with Taymyr as an example)*. Thesis, Komarov Botanical Institute, Leningrad.

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App. 1. Synoptic table of all vegetation communities. Species with constancy < 1 are omitted. Bold boxes indicate faithful and differential taxa for classes and associations. Other boxes show taxa preferential to multiple groups.

Class Rhizocarpetea geographici. Reference no. 1: *Cetraria nigricans*-*Rhizocarpon geographicum* comm.

Class Carici rupestris-Kobresietea bellardii. 2: *Poa glauca*-*Arnica angustifolia* comm., 3: *Selaginella sibirica*-*Dryadetum octopetalae*; 4: *Dryas integrifolia*-*Cassiope tetragona* comm.

Class Cetrario-Loiseleurietea. 5. *Carici microchaetae*-*Cassiope tetragona*; 6. *Salici phlebophyllae*-*Arctostaphylos alpina*; 7. *Hierochloë alpina*-*Betula nana* comm.

Class Oxycocco-Sphagnetes. 8. *Sphagno-Eriophoretum vaginatum*; 9. *Sphagnum lenense*-*Salix fuscescens* comm.

Class Scheuchzerio-Caricetea nigrae. 10. *Dryas integrifolia*-*Caricetum bigelowii*; 11. *Tomentypnum nitens*-*Trichophorum caespitosum* comm.; 12. *Sphagnum orientale*-*Eriophorum scheuchzeri* comm.; 13. *Eriophorum angustifolium*-*Carex aquatilis* comm.; 14. *Carex aquatilis*-*Carex chordorrhiza* comm.; 15. *Hippuris vulgaris*-*Arctophila fulva* comm.

Class Potametea. 16. *Hippuris vulgaris*-*Sparganium hyperboreum* comm.

Class Betulo-Adenostyletea. 17. *Salix alaxensis*-*Salix lanata* comm.; 18. *Eriophorum angustifolium*-*Salix pulchra* comm.

Class Salicetea herbaceae. 19. *Salix rotundifolia* comm.

- 20. *Anthelia juratzkana*-*Juncus biglumis* comm.

Reference no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Number of relevés	2	4	11	6	13	12	4	33	6	14	3	3	5	7	2	3	10	6	3	7
<i>Cetraria cucullata</i>	1/+	3/+	V/+	V/1	V/1	V/2	4/+	V/+	III/+	V/+	3/+	I/+	.	.	III/+
<i>C. islandica</i>	2/+	1/+	V/+	V/+	V/+	V/+	4/+	IV/+	I/+	V/+	2/+	I/+	.	1/+	III/+
<i>Polytrichum strictum</i>	1/+	2/+	III/+	V/1	III/1	V/1	4/1	V/1	I/2	III/+	1/r	1/+	II/+	II/+	1/+	III/+
<i>Cladonia pyxidata</i>	1/+	3/+	II/+	II/+	I/+	III/+	1/+	+/+	.	IV/+	3/+	.	.	I/+	III/+	.
<i>Cetraria nivalis</i>	2/+	1/r	V/1	V/1	IV/2	IV/2	2/+	II/+	.	III/+	1/1	I/+	.	.	.
<i>Cladonia amaurocraea</i>	2/+	.	IV/+	V/+	V/+	V/+	4/+	IV/+	.	IV/+	2/+	III/+
<i>Cladonia arbuscula</i>	2/1	.	II/+	V/1	IV/1	V/1	4/2	III/+	.	V/+	2/r	I/+	.	.	III/+
<i>C. rangiferina</i>	2/1	.	II/+	V/1	V/2	IV/1	4/1	IV/+	I/+	V/+	1/+	I/+	.	.	III/+
<i>Thamnolia subuliformis+vermicularis</i>	2/+	.	V/1	V/+	V/+	V/+	2/+	II/+	I/+	V/+	1/r	I/+	.	.	V/+
<i>Dactylina arctica</i>	1/+	.	II/+	V/+	V/+	IV/+	4/+	IV/+	I/+	IV/+	2/+	I/+	.	1/r	III/+
<i>Cladonia gracilis</i>	2/1	.	I/+	IV/+	V/1	V/+	2/+	IV/+	.	IV/+	1/+	1/+	II/+
<i>Racomitrium lanuginosum</i>	2/1	.	II/+	IV/1	IV/1	I/+	1/r	r/+	.	II/1	1/+	1/+	I/1
<i>Cladonia uncialis</i>	2/+	.	III/+	II/+	IV/+	III/+	2/+	+/+	.	I/+	1/+	1/+	.
<i>Bryocaulon divergens</i>	2/2	.	V/1	II/+	II/+	III/1	1/+	+/+	.	.	1/+
<i>Rhizocarpon geographicum</i>	2/2
<i>Cetraria nigricans</i>	2/2	.	III/+	.	+/+	II/+
<i>Chandonanthus setiformis</i>	2/2	.	.	I/+	II/+	+/+	.	r/+	1/+	.
<i>Arctoparmelia centrifuga</i>	2/2
<i>Umbilicaria proboscidea</i>	2/1	+/+
<i>Porpidea flavocaerulescens</i>	2/1
<i>Parmelia omphalodes</i>	2/+
<i>Alectoria nigricans</i>	2/+	.	III/+	I/+	II/+	I/+	.	+/+
<i>Salix reticulata</i> ssp. <i>reticulata</i>	.	1/+	.	V/1	II/+	.	.	I/+	.	V/2	3/+	III/2	II/+	1/1	.
<i>Bistorta vivipara</i>	.	1/+	+/+	IV/+	II/+	.	.	I/+	I/+	V/+	3/+	II/+	I/r	.	.	.	III/+	II/+	2/+	II/+
<i>Rhytidium rugosum</i>	.	4/1	III/+	V/1	II/+	II/2	2/+	+/+	.	IV/+	2/+	I/+	.	.	.
<i>Empetrum hermaphroditum</i>	.	.	+/1	I/+	II/1	II/+	1/+	III/+	.	I/r	1/r	III/1
<i>Asahinea chrysantha</i>	.	.	V/+	V/+	III/+	III/+	2/+	.	.	III/+	3/+	I/+
<i>Ledum palustre</i> ssp. <i>decumbens</i>	.	1/+	.	II/+	IV/1	III/+	4/2	V/1	.	II/+	I/+	.	.	I/1
<i>Cassiope tetragona</i> ssp. <i>tetragona</i>	.	.	+/+	V/2	V/2	II/+	1/1	IV/1	I/r	IV/1	I/r	.	1/+	IV/+
<i>Alectoria ochroleuca</i>	2/1	1/+	V/+	IV/+	IV/+	V/1	1/+	I/+	.	II/+
<i>Pedicularis capitata</i>	.	4/+	II/+	IV/+	IV/+	II/+	.	+/+	.	V/+	II/+	.	2/+	.
<i>Cladonia pleurota</i>	1/+	.	.	.	II/+	III/+	2/+	I/+	.	I/+	I/+	.	.	.
<i>Peltigera canina</i>	.	3/+	III/+	II/+	II/+	+/	1/+	+/+	.	II/+	1/+	I/r
<i>Salix phlebophylla</i>	.	1/+	V/+	I/+	IV/1	IV/2	1/r	r/1	.	+/+	I/+
<i>Hierochloë alpina</i>	2/+	1/+	IV/+	II/+	II/+	V/+	4/+	1/+	.
<i>Carex microchaeta</i>	.	.	II/+	III/+	IV/1	IV/+	2/+	2/+	.
<i>Artemisia arctica</i> ssp. <i>arctica</i>	1/+	1/+	III/+	.	II/+	III/+	I/r	.	.	.	III/+	.	2/+	.
<i>Dryas octopetala</i> var. <i>octopetala</i>	.	4/+	V/3	I/+	+/+	I/1
<i>Kobresia myosuroides</i>	.	3/+	II/+	II/+	.	+/+
<i>Saxifraga reflexa</i>	.	2/+	I/+	I/+
<i>Lecanora epibryon</i>	.	1/+	II/+	I/+	I/+
<i>Minuartia arctica</i>	.	1/+	I/+	II/+	+/+	+/
<i>Stellaria longipes</i>	.	4/+	+/+	III/+	I/+	I/+	.	r/+	.	II/+	.	.	I/+	.	.	.	II/+	I/+	2/+	.
<i>Anemone drummondii</i>	.	4/+	III/+
<i>Poa glauca</i>	.	3/2	III/+	.	+/+
<i>Bupleurum triradiatum</i> ssp. <i>arcticum</i>	.	2/+	IV/+	.	+/+
<i>Minuartia obtusiloba</i>	.	1/+	V/+
<i>Selaginella sibirica</i>	.	1/+	V/+
<i>Saxifraga tricuspidata</i>	.	3/1	II/+
<i>Carex rupestris</i>	.	1/+	III/+
<i>Encalypta rhaptocarpa</i>	.	1/+	III/+
<i>Saxifraga nivalis</i>	.	1/+	II/+	.	+/+	+/+	I/r	.	1/+	.
<i>S. bronchialis</i> ssp. <i>funstonii</i>	.	1/+	II/+	.	+/+	1/+	.
<i>Potentilla nivea</i>	.	2/+	I/+
<i>Trisetum spicatum</i>	.	2/+	+/+
<i>Thalictrum alpinum</i>	.	1/+	+/+	II/+	I/+	.	.	.

App. 1. (Cont.)

Reference no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	18	17	19	20
<i>Arnica angustifolia</i> ssp. <i>angustifolia</i>		4/+	II/+	.	+/+	+/+
<i>Abietinella abietina</i>		3/2	.	I/+	+/+
<i>Calamagrostis purpurascens</i>		3/2	+/+
<i>Potentilla hookeriana</i>		3/+
<i>Bryum argenteum</i>		3/+
<i>Carex obtusata</i>		3/+	I/+	I/+
<i>Ceratodon purpureus</i>		2/+	.	I/+	.	I/+
<i>Poa alpina</i>		2/+	.	I/+	.	+/+
<i>Pohlia cruda</i>		2/+	.	.	+/+	+/+	I/+	.	I/+	I/+
<i>Vaccinium vitis-idaea</i> ssp. <i>minus</i>		1/+	III/1	II/+	V/1	V/2	4/3	V/1	III/+	III/+	I/+	.	IV/+	IV/+
<i>V. uliginosum</i>			II/1	V/2	IV/1	V/1	2/1	III/+	III/+	V/+	1/r	III/2	.	.	.
<i>Masonhalea richardsonii</i>			III/r	V/+	V/+	V/+	4/2	II/+	.	IV/+	2/+	.
<i>Dicranum elongatum</i> + <i>groenlandicum</i>			III/1	II/1	IV/1	V/1	2/3	IV/1	.	III/+	I/+	.	.	.
<i>Stereocaulon alpinum</i> + <i>tomentosum</i>			IV/+	V/+	V/1	IV/1	3/+	+/+	.	III/+	I/+	.	3/+	I/+
<i>Sphaerophorus globosus</i>	2/+	.	V/+	IV/+	IV/+	IV/1	.	+/+	.	I/+
<i>Pertusaria dactylina</i>			II/+	III/1	II/+	III/+	.	+/+	.	II/+	I/r
<i>Cladonia coccifera</i>	1/+		II/+	I/+	III/+	III/+	.	r/+	.	II/+
<i>Ochrolechia frigida</i>	1/+		II/+	I/+	+/+	+/+	.	.	.	+/+
<i>Loiseleuria procumbens</i>			II/+	.	II/1	II/+	I/r	.	.	I/+
<i>Psoroma hypnorum</i>	1/+		II/+	.	II/+	+/+	1/+	.
<i>Bryoerythrophyllum recurvirostre</i>			+/+	.	+/+
<i>Polytrichum hyperboreum</i>			II/+	.	.	II/+
<i>Cetraria andrejevii</i>			+/+	.	II/+	+/+
<i>Pertusaria panyrga</i>			+/+	.	I/+	II/+	.	.	.	II/+
<i>Hypogymnia subobscura</i>			V/+	I/+	.	+/+
<i>Polytrichum piliferum</i>			V/+	.	II/+	IV/+	1/+	.
<i>Arctoparmelia separata</i>	1/+		III/+	.	I/+
<i>Antennaria alpina</i>			IV/+
<i>Ochrolechia upsaliensis</i>			III/+	r/+	.	+/+	I/+	.	.	.
<i>Coelocaulon aculeatum</i>			III/+	.	+/r
<i>Oxytropis bryophila</i>			III/+
<i>Melanelia septentrionalis</i>			II/+	.	.	+/+	.	+/+
<i>Douglasia ochotensis</i>			II/+
<i>Smelowskia calycina</i>			II/+
<i>Androsace chamaejasme</i> ssp. <i>lehmanniana</i>			II/+
<i>Hylacomium splendens</i>			IV/2	V/2	.	3/2	V/2	I/+	V/2	3/+	I/r	IV/1	IV/1	2/2	III/+
<i>Aulacomnium turgidum</i>			V/+	V/2	.	4/2	V/2	V/2	V/1	3/1	1/+	.	I/+	.	.	.	I/+	I/+	.	II/+
<i>Peltigera aphthosa</i>			IV/+	V/+	IV/+	1/+	III/+	.	V/+	I/+	I/+	2/+	II/+
<i>Carex bigelowii</i>			IV/1	II/1	+/r	1/1	V/2	I/+	V/3	.	.	.	II/+	.	.	.	I/+	II/+	2/+	.
<i>Dicranum spadicum</i>			I/+	I/2	.	4/1	+/+	+/+	IV/+	1/+	I/+	.	.	.
<i>Pedicularis labradorica</i>			I/+	+/+	+/+	3/+	II/+	.	+/+
<i>Dicranum scoparium</i>			I/1	II/+	.	2/3	+/+
<i>Peltigera malacea</i>			I/+	.	II/+	2/+	I/+	.	I/+	I/+	I/r	1/+	II/+
<i>Cladina mitis</i>			I/+	I/+	II/+	2/+	II/+	I/+	.	1/+
<i>Cetraria kamczatica</i>			I/+	II/+	.	1/+	r/+	1/+	.
<i>Cladonia ecmocyna</i>			.	.	+/+	2/+	r/+	1/+	.
<i>Dactylina ramulosa</i>	1/+		II/+	II/+	.	+/+
<i>Tomentypnum nitens</i>			V/1	II/+	.	.	III/+	.	V/3	3/3	.	I/1	III/+	.	.	.	V/1	V/+	1/2	.
<i>Psilidium ciliare</i>			V/1	+/+	.	1/+	III/+	I/+	V/+	1/1
<i>Dryas integrifolia</i>		+/+	V/2	+/+	.	.	r/r	.	V/2	2/2	.	.	I/r	.	.	.	I/+	.	1/+	.
<i>Tofieldia pusilla</i>			IV/+	II/+	III/+	3/+	II/+	.	1/+	.
<i>Ditrichum flexicaule</i>			III/+	IV/+	3/+	.	.	I/+	.	.	.	II/+	.	.	.
<i>Rhododendron lapponicum</i>			III/+	IV/+	2/+	I/+	.	.	.
<i>Salix arctica</i>			III/+	IV/+	2/+	.	.	I/r
<i>Pedicularis oederi</i>			IV/+	.	.	+/r	.	.	IV/+	1/r
<i>Carex scirpoidea</i>			V/+	.	II/+	.	.	.	II/+	1/+	I/+	.	.	.
<i>Pedicularis lanata</i>			II/+	II/+	.	+/r	.	.	IV/+	1/r	1/+	.
<i>Equisetum variegatum</i>			II/+	I/+	2/+	I/+	.	.	.
<i>Bryum pseudotriquetrum</i>			I/+	II/+	2/+	.	II/+	I/+	.	.	.	IV/+	I/1	1/+	.
<i>Fissidens osmundioides</i>			I/+	I/+	2/+	.	.	I/+	.	.	.	I/+	.	.	.
<i>Distichium capillaceum</i>			I/1	II/1	1/2	II/+	.	.	.
<i>Barbilophozia barbata</i>		+/+	I/+	II/+	1/+	I/+	.	.	.
<i>Equisetum arvense</i>		+/+	IV/1	.	.	.	r/+	.	V/2	.	.	I/r	IV/1	I/1	2/+	.
<i>Saussurea angustifolia</i>		+/+	V/+	.	I/+	.	.	.	III/+
<i>Papaver macounii</i>			III/+	+/+	III/+	I/+	.	1/+	.
<i>Hypnum bambergeri</i>			III/+	+/+	.	.	II/+	.	III/+
<i>Parrya nudicaulis</i> s.l.			III/+	.	II/+	.	.	.	+/+	1/+	.
<i>Saxifraga hirculus</i>			I/r	III/+	I/+	.	1/+	.
<i>Potentilla biflora</i>			II/+	II/+
<i>Carex vaginata</i>			II/+	+/r	I/+	.	.	.
<i>Lagotis glauca</i>			I/+	II/+	I/+	.	.	.
<i>Scapania simmonsii</i>			I/+	II/+
<i>Tofieldia coccinea</i>			+/+	I/+	II/+
<i>Bistorta plumosa</i>	2/+	I/+	V/2	V/+	III/+	3/+	IV/+	III/+	III/+	.	.	I/r	III/+	II/+	1/+	.
<i>Dicranum angustum</i>			V/2	I/1	.	2/1	V/1	IV/+	III/+	II/+	I/+	.	.
<i>Novosieversia glacialis</i>			+/r	V/+	II/+	.	.	.	+/+
<i>Equisetum scirpoides</i>			IV/+	I/+	II/+	III/+	.	.	.
<i>Astragalus umbellatus</i>			III/1
<i>Silene acaulis</i>			III/+	I/+	1/+	.
<i>Radula prolifera</i>			III/+	+/+	+/+
<i>Cetraria tilesii</i>			+/+	II/+
<i>Oxytropis maydelliana</i>			I/+	II/+
<i>Trichostomum arcticum</i>			II/+	I/+

App. 1. (Cont.)

Reference no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	18	17	19	20
<i>Diapensia lapponica</i> ssp. <i>obovata</i>	.	.	+1	I/+	V/+	II/1	1/+	.
<i>Pedicularis langsdorffii</i>	.	.	+1	I/+	IV/+	I/+	.	I/+	I/+	II/+	I/+	.	1/+	.
<i>Nephroma arcticum</i>	.	.	I/+	I/+	IV/+	.	1/+	+1
<i>Dicranum acutifolium</i>	2/+	.	+1	III/+	II/2	II/+	2/+	I/1	.	+1	1/+	I/+	.	.	.
<i>Calamagrostis inexpectata</i>	.	.	+1	I/+	III/1	II/1	1/+	I/+
<i>Huperzia selago</i> ssp. <i>appressa</i>	.	.	I/+	I/+	III/+	.	.	.	II/+	.	1/+	1/+	.
<i>Dicranum muehlenbeckii</i>	.	.	+1	I/+	II/2	.	.	r/2
<i>Pogonatum urnigerum</i>	.	.	+1	.	II/1	1/+	I/+
<i>Arctous alpina</i>	.	2/+	I/1	I/1	I/+	V/2	.	+1	.	+1
<i>Cladonia macrophylla</i>	.	.	+1	.	+1	III/+	.	r/+	.	+1	I/+	.	.	.
<i>Betula nana</i> ssp. <i>exilis</i>	.	.	.	III/+	IV/1	II/+	4/4	V/2	V/1	II/+	1/r	1/+	II/+	IV/1	.	I/+
<i>Carex rariflora</i>	r/r	V/1	+1	2/1	3/2	I/+	III/+
<i>Salix fuscescens</i>	.	.	.	I/+	.	.	.	+1	V/2	.	3/+	3/+	I/1	III/+
<i>Sphagnum rubellum</i> + <i>warnstorffii</i>	I/+	.	.	V/2	V/2	III/+	1/1	2/+	I/1	.	.	.	III/+	V/1	1/+	.
<i>Eriophorum scheuchzeri</i> var. <i>scheuchzeri</i>	r/+	IV/2	.	1/+	3/1	II/+	I/+
<i>Carex rotundata</i>	+1	IV/1	.	1/1	3/1	I/2	V/2
<i>Andromeda polifolia</i>	+1	.	.	II/+	IV/+	III/+	3/+	3/+	.	II/r	.	.	II/+	.	.	.
<i>Pedicularis albobaiata</i>	.	.	.	I/+	.	.	.	+1	III/+	.	2/+	3/+	III/+	IV/+	.	.	I/+	.	.	.
<i>Tritomaria quinqueidentata</i>	.	.	+1	I/+	.	+1	.	II/+	IV/+	III/+	1/+	I/+	I/+	I/+	.	.
<i>Limprichtia revolvens</i>	+1	II/+	3/+	1/+	I/3	III/+	.	.	.	II/+	.	.	.
<i>Sphagnum angustifolium</i> + <i>balticum</i>	IV/1	IV/1	.	.	2/3	II/1	.	.
<i>S. fimbriatum</i>	+1	IV/+	.	.	1/+	I/1	I/1	.	.
<i>Scapania paludicola</i>	+1	II/+	.	.	2/+	II/+	.	.
<i>Peltigera scabrosa</i>	+1	.	1/+	III/+
<i>Cladonia carneola</i>	II/+
<i>Rubus chamaemorus</i>	V/2	IV/+	II/+	I/+	V/+	.	I/+
<i>Eriophorum vaginatum</i>	+1	.	IV/2	.	III/1	III/+
<i>Petasites frigidus</i>	.	.	.	II/+	II/+	.	.	IV/+	.	II/+	.	.	I/+	.	.	.	III/+	V/1	2/+	I/+
<i>Sphagnum teres</i>	I/+	.	.	III/2	I/1	+1	II/+	.	.
<i>S. girgensohnii</i>	.	.	.	I/+	I/1	.	.	III/1	.	I/+	1/1	III/1	.	.
<i>Blepharostoma trichophyllum</i> ssp. <i>brevirete</i>	I/+	.	.	III/+	II/+	II/+	.	1/+	I/+	I/+	.	.
<i>Sphagnum lenense</i>	+1	.	.	II/1	V/2	+1
<i>Pedicularis lapponica</i>	III/+	V/2
<i>Sphagnum aongstroemii</i>	I/+	.	.	II/+	IV/+	+1
<i>Pohlia nutans</i>	.	.	+1	.	+1	II/+	.	II/+	III/+	II/+	.	.
<i>Sphagnum compactum</i>	r/+	II/+
<i>Campylopus stellatus</i>	+1	.	IV/+	2/1	.	II/1	III/+	.	.	III/+	I/2	1/+	.
<i>Arctous rubra</i>	+1	.	IV/+	2/+	II/+	.	.	.
<i>Aulacomnium acuminatum</i>	III/+	1/+	I/+	.	.	.
<i>Catocopium nigrum</i>	III/+	1/+	.	.	I/r	.	.	I/+	.	.	.
<i>Meesia uliginosa</i>	+1	.	II/+	1/+
<i>Eriophorum triste</i>	.	.	.	II/+	+1	.	.	+1	.	IV/1	1/+	I/+
<i>Senecio atropurpureus</i> ssp. <i>frigidus</i>	.	1/+	+1	.	II/+	.	.	II/+	.	III/+	1/+	.
<i>Pyrola grandiflora</i>	.	.	.	I/+	III/+	.	.	II/+	.	IV/+	I/+	.	1/+	.
<i>Eutrema edwardsii</i>	III/+
<i>Senecio resedifolius</i>	II/+
<i>Orthilia secunda</i> ssp. <i>obtusata</i>	.	.	.	I/+	I/+	.	.	r/+	.	II/+	1/+	.
<i>Anemone parviflora</i>	+1	.	.	+1	.	II/+	.	.	.	I/+	.	.	II/+	.	1/+	.
<i>Trichophorum caespitosum</i>	3/2	.	.	III/+
<i>Carex atrofusca</i>	+1	3/+	.	.	III/+
<i>C. capillaris</i>	.	.	II/+	II/+	+1	I/+	3/+	.	.	II/+	.	.	I/+	.	.	.
<i>Kobresia simpliciuscula</i>	3/+	.	.	.	I/+
<i>Oncophorus wahlenbergii</i>	.	.	.	I/+	II/2	3/+	.	.	I/+
<i>Salix chamissonis</i>	.	.	.	I/+	II/1	.	.	I/2	+1	2/+	.	.	I/3	.	.	.	III/1	I/1	1/+	.
<i>Sphagnum orientale</i>	II/+	.	.	.	3/3
<i>S. imbricatum</i>	III/2	.	.	.	3/1
<i>Carex aquatilis</i> s.l.	r/1	II/2	I/r	2/2	.	V/3	V/1	.	.	II/2	I/2	.	.
<i>Saxifraga cernua</i>	r/+	III/+	.	.	.	I/+	I/+	.	.
<i>Cardamine pratensis</i>	II/+	I/r	.	.
<i>Saxifraga foliolosa</i>	I/+	.	.	II/+
<i>Caltha palustris</i> ssp. <i>arctica</i>	II/+	.	1/+
<i>Chrysosplenium tetrandrum</i>
<i>Carex chordorrhiza</i>	1/+
<i>Juncus triglumis</i>	V/2	IV/+
<i>Hippuris vulgaris</i>	2/1	2/+
<i>Arctophila fulva</i>	I/+	.	2/3
<i>Scorpidium scorpioides</i>	I/1	V/1
<i>Ranunculus pallasii</i>	I/r	.	2/+
<i>Sparganium hyperboreum</i>	3/3
<i>Sphagnum lindbergii</i>	2/2
<i>S. squarrosum</i>	r/3	I/+	.	2/+	.	.	I/3	.	.
<i>Polemonium acutiflorum</i>	r/+	V/+	V/+	3/+	.
<i>Sanionia uncinata</i>	.	.	.	II/+	I/1	.	.	II/2	I/+	I/+	.	.	I/3	.	.	.	V/1	IV/2	3/2	.
<i>Aulacomnium palustre</i>	.	.	.	I/+	+1	.	1/1	IV/2	I/2	II/2	.	.	I/2	.	.	.	IV/2	V/1	1/2	.
<i>Arctagrostis latifolia</i> var. <i>latifolia</i>	.	.	.	I/+	.	.	.	I/+	.	III/+	III/+	III/+	3/+	.
<i>Valeriana capitata</i>	r/+	I/+	.	.	.	II/+	.	.	.	IV/+	III/+	.	.
<i>Paludella squarrosa</i>	+1	.	+1	.	.	I/1	.	1/+	.	II/+	III/+	.	.

App. 1. (Cont.)

Reference no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	18	17	19	20
<i>Dodecatheon frigidum</i>	+/+	V/1	.	1/+	.
<i>Anemone richardsonii</i>	.	.	.	I/+	+1	.	.	r/+	.	I/+	V/+	I/+	1/1	.
<i>Carex membranacea</i>	.	.	.	I/r	III/1	1/1	.	.	I/+	.	.	IV/1	.	.	.
<i>Aconitum delphinifolium</i> ssp. <i>paradoxum</i>	.	3/+	+r	IV/+	.	.	.
<i>Climacium dendroides</i>	.	.	.	I/+	IV/+	.	1/+	.
<i>Pentaphylloides floribunda</i>	IV/+	.	.	.
<i>Salix lanata</i> ssp. <i>richardsonii</i>	+2	1/+	III/3	.	.	.
<i>Calamagrostis canadensis</i> s.l.	+1	2/+	III/2	.	.	.
<i>Carex podocarpa</i>	+r	III/1	.	1/+	.
<i>Festuca altaica</i>	.	.	+/+	.	.	+/+	1/+	r/1	.	+1	III/+	.	.	.
<i>Hypnum lindbergii</i>	III/+	.	.	.
<i>Senecio lugens</i>	III/+	.	.	.
<i>Wilhelmsia physodes</i>	II/+	.	.	.	III/+	.	.	.
<i>Plagiomnium ellipticum</i>	.	1/+	III/+	.	.	.
<i>Rubus arcticus</i> ssp. <i>acaulis</i>	II/1	.	.	.
<i>Philonotis fontana</i> var. <i>pumila</i>	+/+	II/+	.	.	.
<i>Hypnum pratense</i>	I/+	.	.	.	II/+	.	.	.
<i>Parnassia palustris</i>	+/+	I/r	.	.	II/+	.	.	.
<i>Pedicularis sudetica</i> ssp. <i>interior</i>	+/r	+/+	.	.	.	I/+	.	.	II/+	.	.	.
<i>Epilobium latifolium</i>	II/+	.	.	.
<i>Solidago multiradiata</i> var. <i>multiradiata</i>	II/+	.	.	.
<i>Eriophorum angustifolium</i> ssp. <i>subarcticum</i>	II/+	II/+	.	2/+	2/+	V/2	IV/1	.	.	I/+	V/3	.	.
<i>Salix pulchra</i>	II/1	.	1/+	V/2	II/1	I/+	.	.	I/1	.	.	.	II/2	V/3	1/+	.
<i>Calliergon stramineum</i>	.	1/+	I/+	II/+	I/1	III/1	.	.
<i>Pohlia andrewsii</i>	II/+	.	.	.
<i>Salix rotundifolia</i> ssp. <i>rotundifolia</i>	II/1	+/3	I/1	.	3/4	.
<i>Saxifraga nelsoniana</i>	.	.	+r	III/+	II/+	+r	.	II/+	.	+/+	.	.	I/+	.	.	.	II/+	IV/+	3/+	.
<i>Politrachastrum alpinum</i>	1/+	1/+	.	.	I/1	.	.	+/+	II/2	.	.	.	I/1	2/1	.
<i>Anastrophyllum minutum</i>	.	.	I/+	I/+	III/+	II/+	1/+	III/+	II/+	III/+	I/+	.	2/+	.
<i>Aconitum delphinifolium</i> ssp. <i>delphinifolium</i>	I/+	I/+	.	2/+	.
<i>Arnica lessingii</i>	.	1/+	I/+	.	II/+	.	.	.	+/+	+/+	I/+	.	2/+	.
<i>Cladonia chlorophaea</i>	.	.	+/+	.	II/+	I/+	.	+/+	2/+	.
<i>Poa paucispicula</i>	2/+	.
<i>P. arctica</i>	.	1/1	I/+	I/+	I/+	+/+	.	I/+	I/r	+/+	.	.	I/+	.	.	.	II/+	II/+	2/+	.
<i>Juncus biglumis</i>	.	.	.	II/+	+/r	V/1
<i>Anthelia juratzkana</i>	V/2
<i>Luzula arctica</i>	.	.	.	IV/+	II/+	II/+	1/+	V/+
<i>Loeskypnum badius</i>	II/+	.	II/+	.	1/+
<i>Polytrichum commune</i>	+1	.	.	+1	II/2	I/+	I/1	.	1/+
<i>Cyrtomium hymenophyllum</i>	II/+	II/+	.	1/+	.
<i>Aneura pinguis</i>	.	.	.	I/+	1/+	II/+
<i>Comarum palustre</i>	II/+	.	.	1/+