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Topographic, altitudinal and regional patterns in continental and suboceanic heath vegetation of northern Fennoscandia

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We sampled systematically altitudinal and topographic vegetation gradients within six northern Fennoscandian areas ranging from relatively oceanic climate in Troms to pronouncedly continental conditions in interior Finnmark and eastern Enontekiö. The sample plot material was ordinated by detrended correspondence analysis and organized into community types by means of a divisive numerical procedure (TWINSPAN). The boreal, (oro)hemiarctic and lower (oro)arctic communities thus obtained corresponded relatively well with the community types described by Hämet–Ahti (1963) and Haapasaari (1988). However, close counterparts of the Empetrum-Dicranum-Lichens type and the Myrtillus-Dicranum-Lichens type only occurred in the coastal material. Corresponding communities in inland areas were dominated by *Vaccinium vitis-idaea* and were thus regarded as a separate community type, called the arctic-hemiarctic Empetrum-Vaccinium type (aEVT). At higher altitudes, we encountered several previously undescribed community types. In continental and subcontinental areas, the topographic pattern at and somewhat above the timberline normally consists of lichen heaths, with *Betula nana* as the dominating vascular plant. Strands of aEVT sometimes occur between *Cetraria nivalis* and *Cladina* heaths. Closer to the coast, these strands become broader and form a major component of the topographic community pattern. Communities dominated by *Vaccinium myrtillus* occur only locally in edaphically warm chionophilous sites. On coastal mountains, *Empetrum hermaphroditum* is the dominating lower (oro)arctic plant. Communities rich in *V. myrtillus* occur as narrow strands between *Empetrum* heaths and grassy snow-beds. These patterns have close counterparts in low arctic areas and differ from their southern Scandinavian counterparts in the limited occurrence of communities dominated by *Phyllodoce caerulea* or *V. myrtillus* in northernmost Fennoscandia. In continental areas, boulderfields meet lower oroarctic heaths without any continuous middle oroarctic vegetation in between. Closer to the coasts, there are relatively extensive, lichen-rich middle oroarctic heaths, normally dominated by *Cassiope tetragona* and *Juncus trifidus*. Suboceanic middle oroarctic heaths are dominated by *Empetrum hermaphroditum* and *Salix herbacea*. The upper oroarctic zone is characterized by patchwise occurrence of *Luzula confusa* and *Ranunculus glacialis*. The boundaries of the hemiarctic zone have been extended to cover the major inland area of northern Fennoscandia, and the limits of the subcontinental C1 sector have been slightly revised.

Key words: altitudinal zonation, arctic ecology, continentality, geobotany, heath vegetation, horizontal zonation, northern Fennoscandia, oceanity, regional pattern, topography, tundra communities

CONTENTS

I. INTRODUCTION

The oligotrophic treeless heaths of northern Fennoscandia form a habitat complex, where many different gradients meet. The Scandinavian mountain vegetation grades into the circumpolar low arctic tundra, and there are major climatical differences between the Atlantic coast and the inland region (Regel 1950, Ahti et al. 1968, Haapasaari 1988). In addition, vegetation varies with altitude and topography. When describing the vegetational patterns of northernmost Fennoscandia, we thus need to take into account at least four independent dimensions of variation: two climatic dimensions (arctic-boreal, oceanic-continental), the altitudinal dimension (lowland-summit) and the topographic one (ridge-depression).

It would be unrealistic to pay equal attention to all dimensions in a single study. Haapasaari (1988) chose to emphasize the macroclimatic gradient and to cover northern Fennoscandia with an impressive network of sample plots. The altitudinal and latitudinal axes were also extensively covered: his sample plots ranged from the northern boreal zone to the southern arctic (lower oroarctic) zone. On balance, the material was subjectively sampled and the treatment of the topographic gradient were largely restricted to distinguishing between chionophilous and chionophobous community types.

We chose the opposite approach: consistently to sample the altitudinal and topographical gradients of six areas in northernmost Fennoscandia. With this approach, we sought to discriminate the community sequences or vegetational patterns existing along the topographic-altitudinal gradient complexes. Without data from other areas, we can, of course, engage in broader biogeographical discussions in only a limited way. Haapasaari's (1988) data sets complements ours methodologically and geographically, and we use it in concert with ours.

II. NORTHERN FENNOSCANDIA IN THE GRADIENT FROM BOREAL TO ALPINE AND ARCTIC CONDITIONS

The geography of northernmost Fennoscandia is as if designed to generate complicated and confusing climatical patterns. The warm Atlantic ocean creates a gross mismatch between vegetational zones on the eastern and western slopes of the Scandinavian mountain chain (Ahti et al. 1968). The parameters normally indicating zonal variation (mean July temperature, sum of effective temperatures; e.g. Kalela 1958, Ahti et al. 1968) do not show consistent trends with increasing latitude (Tuhkanen 1980). Consequently, along the Atlantic coast of northern Fennoscandia Ahti et al. (1968: fig. 9) drew the zonal boundaries of the middle and south boreal zones to relatively high latitudes. However, some of the interpretations of Ahti et al. (1968) are debatable and may reflect extrazonal situations, such as the warming effects of föhn (chinook) winds in the interior parts of fjords. Thus, Tuhkanen (1992), (see also Moen 1987, Haapasaari 1988: fig. 122) has somewhat revised the boundaries of the middle and south boreal zones on the Atlantic coast and assigned the coasts of northern Troms and western Finnmark in the north boreal zone. According with this are our own experiences in the Alta valley (70°N), which tends to correspond phenologically with latitudes of Kolari and Pajala (67°N). Moreover, the influence of the warm Atlantic air becomes weaker along the gradient from west to east, and in northeasternmost Norway there are coastal areas with mean July temperatures less than +10°C (Anonymous 1957). Thus, Haapasaari (1988) suggested that the northeastern coasts of Fennoscandia do not belong to the boreal zone.

Geologically, northernmost Fennoscandia consists of two different elements. The western and northern coasts belong to the Scandinavian mountain chain, characterized by overthrusting nappes (Lindström 1987). Northwards, the degree of overthrusting decreases, the topography becomes more gentle and the prevailing altitude of mountaintops decreases from about 1 500 m to 500–1 000 m (Lindström 1987). The inland area is occupied by the Fennoscandian Shield, forming a peneplane at altitudes of about 200 to 500 m a.s.l.

If Haapasaari's (1988) argument on the occurrence of at least hemiarctic conditions at sea level is accepted, then defining the limits of the Fennoscandian hemiarctic is problematic due to the geological conditions noted above. Haapasaari (1988: fig. 122) himself restricts the true hemiarctic area to the coast and regards the inland occurrence of corresponding vegetation as orohemiarctic, because the areas in question lie a few hundred metres above sea level. However, the altitudes are modest (Haapasaari 1988: fig. 9). Moreover, all biogeographic borders are influenced by altitude. Ahti et al. (1968) did not use the oro-prefix in the context of the southern extensions of the north, middle and south boreal zones in higher country, and for a good reason. If the oro-prefix were used in all situations where the slightest altitudinal component is present, problems would arise in practically all inland areas. Moreover, the practice would lead to such an excessive use of the oro-prefix that the whole concept would become largely meaningless.

For the concept to remain practical and biogeographically meaningful, we are proposing that the oro-prefix should be used only in reference to areas where the altitudinal component is strong enough to create ecological conditions essentially differing from those prevailing within the corresponding latitudinal zone.

As we are dealing with relatively modest altitudes, many attributes of high-altitude climates (e.g. intense sunshine, high winds, high amplitude of diurnal temperature variation, see Eurola 1974, Franz 1979, Ellenberg 1988) are not relevant. Nevertheless, even relatively modest altitudes force the inflowing air to rise, which can result in substantial increases in precipitation, especially during the winter when precipitation is generated by circulating air masses and shifting positions of the polar front (e.g. Schimper 1908, Flohn 1974, Browning & Hill 1981, Eurola & Kaakinen 1982, Eurola et

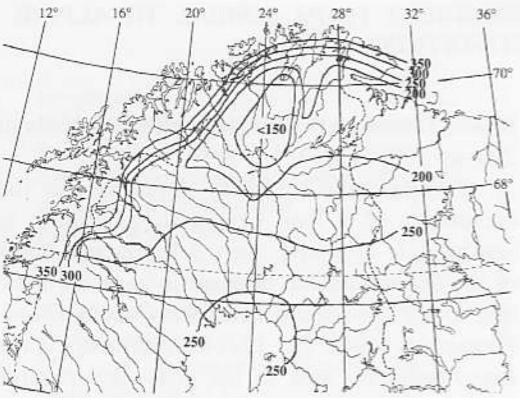


Fig. 1. Isohyets for winter (October–May) precipitation (mm) according to Norwegian, Finnish and Swedish weather station records (Anon. 1949, Wallén 1951, Helimäki 1967, Johannesen 1974).

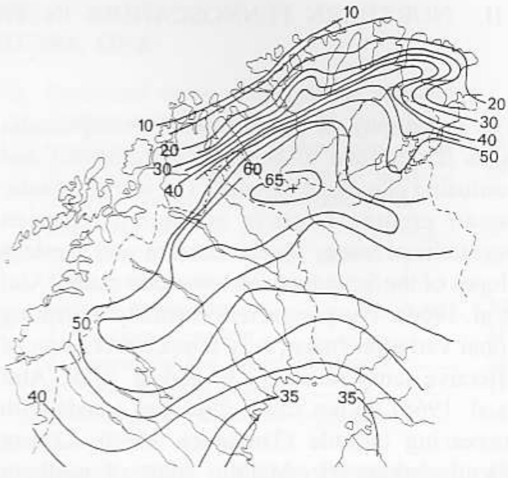


Fig. 2. Frost sums (absolute values of the sums of the negative monthly mean temperatures) in northern Fennoscandia, according to Tuhkanen (1980).

al. 1991). Conversely, winter precipitation decreases with increasing latitude because northern areas lie consistently north of the polar front. The typical arctic winter weather is clear and cold, and winter precipitation is normally less than 150 mm (Walter & Lieth 1975). Even coastal areas are characterized by thin snow cover, frigid near ground temperatures and permafrost (Schimper 1908: 698, Barry & Hare 1974, Dingman et al. 1980). In truly alpine areas, winter precipitation is much higher: 700 mm in the continental Niwot Ridge, Colorado; still higher in European Alps and in the Scandinavian mountain chain (Schröter 1908, Larcher et al. 1975, Franz 1979, Ozenda 1988, Greenland 1989), and the ground is normally frozen for only a few weeks in the autumn (Dahl 1957, Ellenberg 1988: 399).

Even relatively modest altitudes may generate profound impacts on winter precipitation and soil temperatures. This is illustrated in Finland by the distribution of areas, where frozen ground delays the onset of the growing season. In north boreal areas, the delay is longer than five days, but in the Kuusamo highlands, depicted by Ahti et al. (1968) as a southern extension of the north boreal, ground frost disappears before the onset of the growing season (Solantie 1988). Thus, there are good ecological reasons for regarding the Kuusamo area as upper oroboreal rather than truly north boreal. Similar arguments appear to apply to the treeless heaths in the northwesternmost corner of Finnish Lapland. Altitudes are modest and ecological factors, such as light, air temperatures are distinctly arctic, but soil temperatures and edaphic conditions are alpine (Eurola 1974), making the use of the oro-prefix ecologically warranted.

Isohyets for winter (October–May) precipitation according to Norwegian, Finnish and Swedish station records (Anonymous 1949, Wallén 1951, Helimäki 1967, Johannesen 1974) are presented in Fig. 1. Values below 150 mm are restricted to the interior parts of Finnmark, Norway, but only slightly higher values are typical for large parts of Finnish Lapland and for the Gárasavvon (Karesuando) area in northernmost Sweden. Conversely, winter precipitation exceeds 300 mm in most parts of the Scandinavian mountain chain, as also on the outer coast of northernmost Norway.

Winter precipitation alone is not a sufficient basis for differentiating between oroarctic and truly arctic conditions, because precipitation also varies along the continental-oceanic axis. By and large, the north Fennoscandian areas with winter precipitation below 150 mm coincide with thermally continental areas with low winter temperatures (Tuhkanen 1980, Fig. 2). Areas with somewhat higher winter precipitation need not be character-

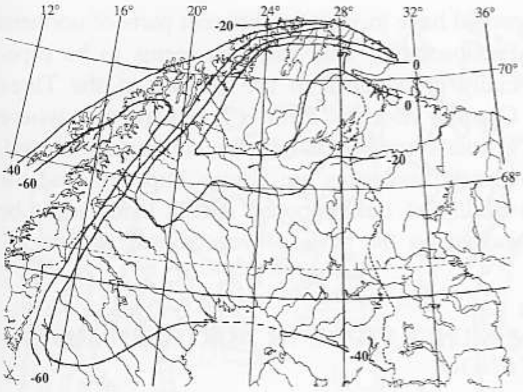


Fig. 3. The ARCT index in northern Fennoscandia.

ized by altitudinal influences, but may simply represent more oceanic sectors of the hemiarctic zone.

In order to differentiate between the impact of altitude and oceanity *per se*, we need to construct an index of arctic conditions that is not sensitive to the gradient between oceanic and continental climates. This can be done by looking at how thermal and hygric conditions covary within the low arctic zone.

The mean amplitudes of monthly temperatures and winter precipitation values for indisputably low arctic or hemiarctic climate stations are presented in Table 1. We see that the product of these two measurables hovers about the level 4 000, without showing any consistent trend between continental and oceanic areas. The only clear deviations are formed by the deepest rain shadows of East Siberia, where the product is much lower, and the Ungava Peninsula, where the arctic zone extends to exceptionally low latitudes with relatively precipitation-rich winter climate. Thus, for the purpose of distinguishing between truly arctic and oroarctic (i.e. at least slightly alpine) climatic conditions in the vicinity of the arctic timberline in western Eurasia, we propose that the following index, to be called ARCT, be used. We define the index as:

$$\mathrm{ARCT} = 40 - p_W t_a / 100,$$

where p_W is winter (October–May) precipitation and t_a is the amplitude of mean monthly temperatures.

In northernmost Fennoscandia, the area with positive ARCT values encompasses northernmost Finnish Lapland, inland areas in northernmost Norway, the shores of Várjatvuotna (Varangerfjord) and northernmost Swedish Lapland east of the thrust cliff of the Scandes (Fig. 3). The situation along the outer coasts of Norway is unclear. Slightly negative values are typical for outlying peninsulas and islands with gentle topography, whereas coastal stations in more mountainous terrain show ARCT values well below zero. The pattern in Fig. 3, where ARCT values between 0 and –20 prevail on the outermost coast, followed by a wedge of considerably larger negative ARCT values, describes an idealized coastal area with a strand of lowland between the coastal rise and the sea. The Scandinavian mountain chain and the Atlantic coast are characterized by negative ARCT values. South of Tromsö, the ARCT values of the mountains are generally below –60, i.e. at the level typical for alpine areas.

Table 1. Amplitudes of mean monthly temperatures (t_a), winter precipitation values (p_W, in mm), product $t_a p_W$ and values of the ARCT index for climatic stations in the timberline region from Kola to Labrador, computed from Walter & Lieth (1975) and Norin & Ignatenko (1975). F refers to a station within the taiga but close to the arctic timberline.

Station	t_a	p_W	$t_a p_W$	ARCT
Jan Mayen	10.5	492	5166	–12
Svjatoj Nos	18.5	189	3496	5
Sosnovez	19	212	4028	0
Morsovez	19.5	175	3412	5
Obdorsk	42	79	3318	7
Novy Port	43	68	2924	11
Ust-Jenisejsk	40.5	70	2835	9
Tolstyj Nos	46.5	91	4231	–2
Dudinka	43.5	65	2828	12
Ary-Mas	47	110	5170	–12
Hatanga (F)	46.5	131	6091	–21
Ust-Jansk	51	59	3009	10
Russkoe Uste	46.5	58	2697	13
Medvesi Mys	37.5	29	1088	29
Kresta Zaliv	27.5	105	2887	11
Saint Michael	20.5	127	2604	14
Churchill	38.5	131	5044	–10
Great Whale River	33	355	11715	–57
Fort McKenzie	37.5	276	10350	–44

The climatic parameters discussed above indicate that there is no clear answer to Eurola's (1974) question whether the conditions in the treeless highlands of northern Fennoscandia are predominantly arctic or alpine. Even if the concept alpine were used in the broadest sense, to indicate any substantial difference from truly arctic conditions (i.e. as a synonym of oroarctic), the answer would have to vary for different parts of northern Fennoscandia. This variation seems to be especially pronounced in the vicinity of the Three Country Border Point (Treriksröset), where Eurola's study was chiefly conducted. Indeed, climatic indicators are always imperfect and the validity of our proposed ARCT index must be judged on the basis of vegetational patterns.

III. LAND USE AND GEOGRAPHICAL NOMENCLATURE IN NORTHERNMOST FENNOSCANDIA

Besides being a meeting point for different climatic and geological elements, northernmost Fennoscandia is also the meeting point of West European and Arctic cultures and economies, and the open Barents Sea has protected both cultures by providing alternative resources during periods of hardship. Thus, the human population of the area is much denser than in other areas with equally cold climate (Hämet–Ahti 1963). Moreover, whenever possible both cultures have for centuries practiced two extensive forms of land use, with maximum intensity and frequently in conflict with each other: the Lappish (Sámi) reindeer husbandry and the sheep ranching of Norwegians and coastal Lapps. Thus, the lichen grounds of the area represent, at their best, an equilibrium between grazers and their critical resources. The coastal vegetation is, in turn, profoundly influenced by summer grazing sheep and reindeer. Notice, however, that reindeer is a native grazer of the area and both it and its wild counterparts seem to be chiefly limited by winter food (Kelsall 1968, Oksanen et al. 1995).

The tension between two cultures also expresses itself as an instability of the geographical nomenclature. Many localities have parallel names in Lapp and majority languages and the spelling of the Lappish names has changed with every new edition of maps. As we are dealing with the heart of Lapland, and the current trend is the restoration of the original Lappish names (Fig. 4), we regard it as fair to use Lappish names and spell them according to the rules of the Lapp languague, unless we deal with places with clearly non-Lappish population. Names in majority languages and old spellings of Lappish names are presented in parentheses, if they are better known to day. Names of weather stations are presented in the form they are written in the cited tables. As a rule, we apply the names of the "duottars" (tundras, treeless highlands), in a maximally collective sense, avoiding different names for different parts of the same duottar, if the existence of different names is due to artificial factors, such as national boundaries and differential use for reindeer grazing. The name Čáhppisduottar as used by us, includes the Veahččejávri basin and the highland west of it, normally referred to as Ánnevarri.

IV. MATERIAL AND METHODS

1. **Sampling**

Within northernmost Fennoscandia, we chose six subareas for closer vegetation studies (Fig. 5). The altitudinal ranges of the subareas are as follows: 1. Ivggegáisat (Lyngsalpene) 0–1 833 m, 2. Ráisduottar (Käsivarsi plus adjacent treeless area in Troms, Norway). 476–1 365 m, 3. Dárju (Tarju) 400–735 m, 4. Jávrisduottar (the tundra/fjeld plateau of eastern Enontekiö, and southern Finnmarksvidda) 418–588 m, 5. Čakčaduottar–Gáisat (the northern tundra/fjeld plateau of Finnmarksvidda around Lake Iešjávri) 390–1 139 m and 6. Čáhppisduottar (the eastern tundra/fjeld plateau of Utsjoki) 60–427 m.

These subareas were chosen to cover representative parts of northernmost Fennoscandia. All subareas are dominated by granitic rocks. The Fennoscandian Shield prevails in subareas 3–6, an intrusion of igneous rocks in the Scandinavian mountains in subarea 1. In subarea

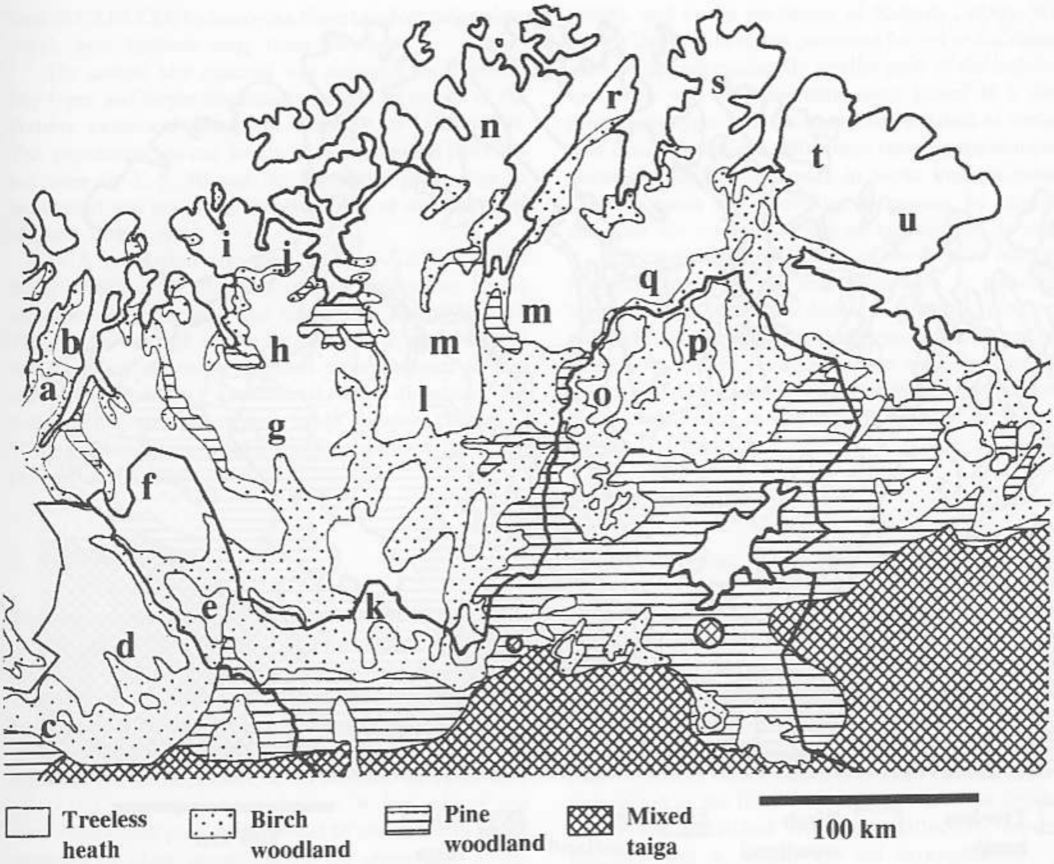


Fig. 4. Geographical outlines of the study area. The map is modified from the Atlas of Finland 1960 and 1988, applying maps of Hesselman and Lunqvist (1935), Seppälä and Rastas (1980), Dahl et al. (1986), Heikkinen and Kalliola (1988), Kullman and Engelmark (1991) and our own observations. Those treeless areas (duottar), peninsulas (njárga), highlands (Čearro) and mountains (gáisat) that are discussed in the present paper or by Oksanen et al. (1994) are indicated by lower case letters as follows: a = Ivggegáisat, b = Iddonjárga, c = Čakčačearro, d = Rostoduottar, e = Dárju, f = Ráisduottar, g = Návuonduottar, h = Silvetnjárga, i = Aksunjárga, j = Joahkkunjárga, k = Jávrisduottar, l = Čakčaduottar, m = Gáisat, n = Skuohttanjárga, o = Bajisduottar, p = Čáhppisduottar, q = Lagisduottar, r = Spiertánjarga, s = Čorgotnjárga, t = Rággonjárga, u = Várjatnjárga.

5 the Fennoscandian Shield does not reach to altitudes above 627 m, which meant that the vegetation of higher areas had to be sampled in the eocambrian Gáisa formation. However, the vegetation of the Gáisa formation does not show any indication of a nutrient-rich bedrock. Also, the uppermost parts of Ráisduottar are chiefly on the silicaceous thrust plate of fjeld schists (Uusinoka 1980). Thus, we can be fairly certain that vegetational differences between subareas reflect climatic differences. In order to avoid locally oceanic sites, our sampling did not include mountains or hills rising above the mean altitude of the summits of the subarea in question.

The sampling method was designed for studying tundra vegetation of mountainous or at least hilly areas with conspicuous small-scale topographic variation and a fair range of altitudes. Within each subarea, sampling proceeded as follows: At altitudinal intervals of 25 m a rope (15 m length) was fixed from the top of a hillock towards an adjacent depression. Eight plots of 0.8 m x 0.8 m were sampled at regular intervals along the rope. This set of sample plots is referred to as a transect. The procedure was used from the lowest altitude to the upper limit of continuous vegetation, and even higher up if possible. In the highest part of Ivggegáisat, where the vegetation fragments were too small and far apart for the rope method, plant communities were sampled upon encounter (the first 4 for each altitudinal interval of 25 metres). The cover of plants was estimated using a 10-class modification of the Scandinavian (Hult–Sernander) scale. The class centres approximately corresponded to

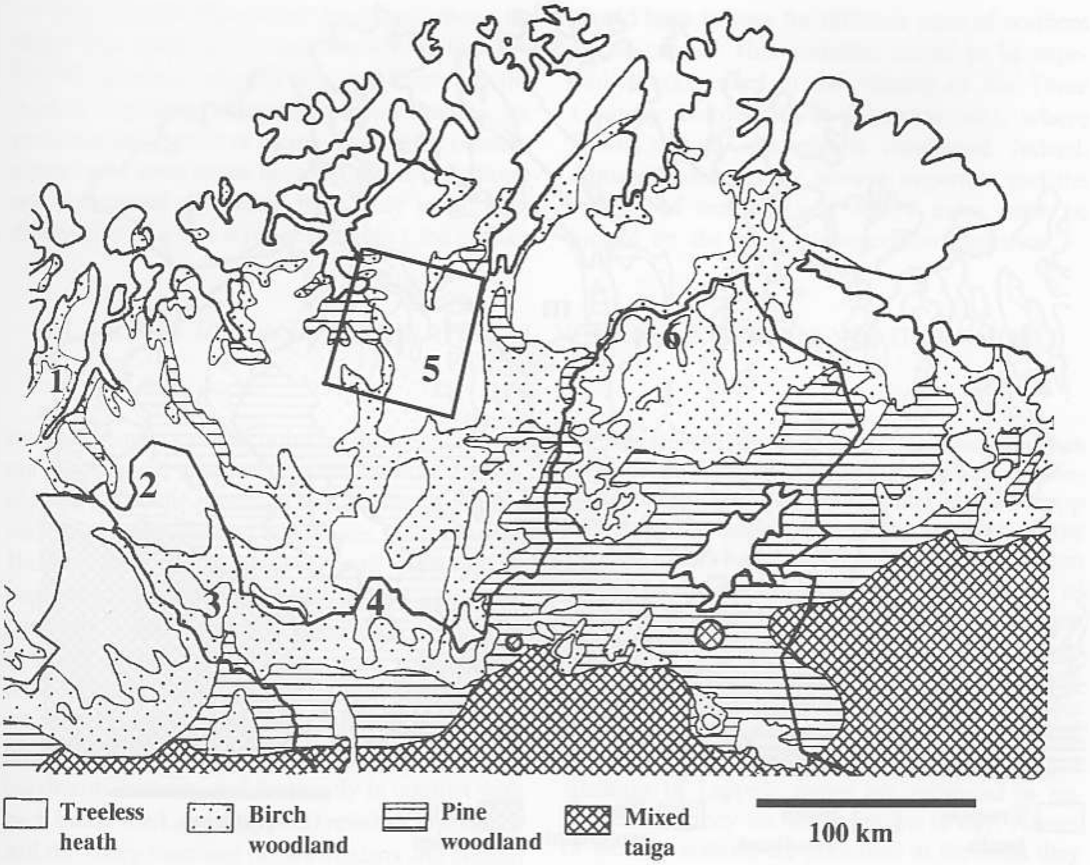


Fig. 5. Study area covering different parts of the arctic-subarctic area of northernmost Fennoscandia: 1: Ivggegáisat, 2: Ráisduottar, 3: Dárju, 4: Jávrisduottar, 5: Čakčaduottar–Gáisat and 6: Čáhppisduottar. The square is the area covered in Fig. 37.

cover percentages of 71, 35, 18, 9, 5, 2, 1, 1/2, 1/4 and 1/8 (see Oksanen 1976).

Our plots were too small to be representative of forest vegetation; forested areas were sampled chiefly to document how they grade into the treeless heaths.

Another shortcoming of the sampling method was that on Čakčaduottar and Jávrisduottar (subareas 4 and 5), where the bedrock is very gentle, glacifluvial formations with exceptionally dry and warm soils became overrepresented. In case of Čakčaduottar, we corrected this bias by including a set of 232 sample plots (size 4 m^2) systematically sampled along a reindeer fence (Oksanen 1978). The material represents winter ranges, summer ranges, intensively trampled areas along the fence and, to a limited extent, autumn ranges. The altitudinal range of this material is small (from 500 to 550 m), but the entire topographic pattern from windswept ridges to snowy depressions is represented.

2. Numerical treatment

Even without the inclusion of any published data, our material, in total 1069 sample plots, turned out to strain the space limits of standard ordination and classification programs. Thus, before the data runs, we looked for obvious discontinuities in the material, which would be used as a basis for splitting it *a priori*. The coastal Ivggegáisat (subarea 1), represented by 319 plots, was regarded as sufficiently different from the rest for this purpose. Moreover, the reindeer range study on Čakčaduottar contained 64 plots representing a peculiar local situation in the intensely trampled zone along the fence. These plots were excluded from the numerical treatment and regarded as trampled variants of the same community type to which the plots sampled in the winter range belong. This left us with 754 plots representing subareas 2–6. The number was reduced to 750 (the space limit of CANOCO) by removing those reindeer range plots which were furthest away from the fence.

The sample plot material was arranged into community types and larger community groups by means of the divisive numerical procedure TWINSPAN (Hill 1979). The pseudospecies cut levels used in the TWINSPAN run were 0, 2, 5, 10 and 20. Minimum group size to be divided was set at 11. Twelve levels of division were allowed in the run.

DCA ordination was computed by CANOCO (ter Braak 1988) using standard options detrending by 26 segments and rescaling four times with threshold 0.00. The results seemed not to be affected in any essential respect when detrending options were changed to 2nd order polynomials or an other rescaling threshold. All the numerical treatments were based on cover classes 1–10 representing a logarithmic transformation of the actual cover (see Oksanen 1976).

3. Classification

The vegetation classification basically follows the results of the TWINSPAN analysis. As a first step, TWINSPAN divisions were allowed to continue so long as groups consisted of more than 50 samples. When fewer than 50 but more than 15 samples were to be divided, the divisions with eigenvalues >0.095 were taken into account. When less than 15 samples were to be divided, an eigenvalue of >0.195 was required for division. A few solitary and very exceptional plots were pooled to clusters with larger numbers of plots, regardless of the eigenvalue of the division.

In order to put the TWINSPAN groups into a tractable classification frame, the results were processed further into a hierarchical classification scheme. At highest level are the community groups, the major TWINSPAN divisions, encompassing a roughly similar range of vegetational variation as the alliances of the Braun-Blanquet scheme. Then come the subdivisions of the community groups, the community types, which occupy an approximately equally large part of the ordination space as do the clusters that can be regarded as comparable to the site types of Hämet-Ahti (1963) and Haapasaari (1988), and to the sociations of Kalliola (1939). When the TWINSPAN division continued further to discriminate units occupying essentially smaller parts of the ordination space, the sets of these units were joined to a single community type, with the units distinguished as variants. And finally, where the differences between the units were obviously due to differences in biotic impacts (usually different kinds and intensities of grazing by reindeer), the units are referred to not as variants but as stages.

The major lines of division of the divisive numerical procedure are more or less insensitive to patterns in borderline areas with low densities of plots. Thus, if two very similar community types appeared on different sides of such lines, they were joined into a single community type. This was also done for the closely similar community types encountered in subareas 1 and 2–6.

4. Nomenclature

The nomenclature of the phanerogam species follows Hämet-Ahti et al. (1986), that of bryophytes mainly Koponen et al. (1977) and that of lichens mainly Ahti (1989) and Santesson (1984). For convenience, *Empetrum nigrum* subsp. *hermaphroditum* is hereafter called *E. hermaphroditum*, and *Luzula arcuata* subsp. *confusa* is called *L. confusa*. Some species are treated collectively: the generic taxa *Hieracium, Ochrolechia, Stereocaulon* contain several taxa. *Dicranums* may contain taxa not recognized in the field. The *Sanionia* revision (Hedenäs 1989) was published after data collection, hence *S. uncinata* and *S. nivalis* are not distinguished. The collectively treated hepatic group "*Gymnomitrion*" contains all small liverworts identifiable only with difficulty and occurring mainly at high altitudes (e.g. *Anthelia juratzkana, Gymnomitrion apiculatum, G. concinnatum, G. corallioides, Marsupella* spp., *Nardia* sp., *Pleurocladula albescens* etc.). Other crustaceous microlichens except *Ochrolechia* are named "*Lecidea*". Among *Barbilophozia* species the subgenera *Barbilophozia* and *Orthocaulis* are distinguished. Species growing on stones were excluded unless they clearly were a constituent of the terricolous vegetation. Likewise some very rare taxa were excluded from the data analysis.

V. MAIN AXES OF VEGETATION ORDINATION AND CHARACTERIZATION OF THE PLANT COMMUNITY GROUPS

The vegetation ordination of subareas 1 (Fig. 6) and 2–6 (Fig. 7) conforms to the traditional view of the two main gradients along which Fennoscandian arctic-alpine plant communities are separated from each other. The first axis reflects altitude and is presented vertically to emphasize this. The second axis represents the impact of the uneven snow cover, with com-

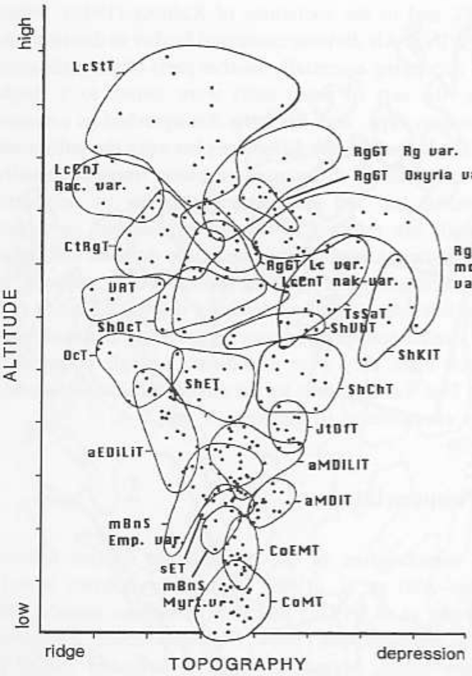


Fig. 6. The scattergram of DCA ordination of subarea 1.

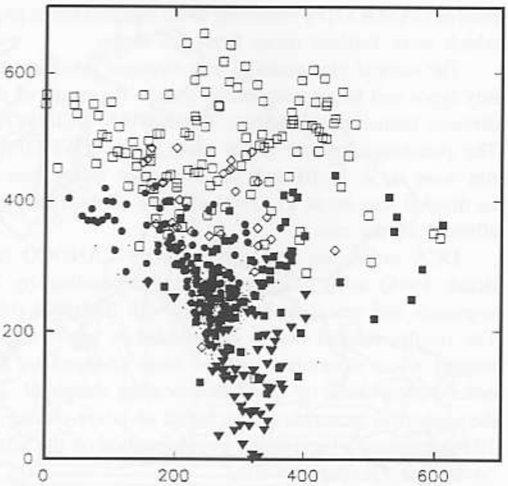


Fig. 7. The scattergram of DCA ordination of subareas 2–6. Symbols: □ high altitude vegetation, ■ Juncus trifidus-Salix herbacea group, ● Arctostaphylos group, ◊ Juncus trifidus-Cassiope tetragona group, ▲ Betula-Myrtillus group, small dots: Phyllodoce-Myrtillus group + Betula nana group.

munities on bare-blown ridges to the left and communities prevailing on snow-accumulation sites to the right.

The communities of subarea 1 separate neatly along these two axes. Conversely, in the combined material of subareas 2–6, the two first axes do not suffice to separate the community types from each other. The next two sections describe in outline the community groups, i.e. the ten main vegetation units used to organize the individual community types.

Subarea 1

In the suboceanic vegetation of subarea 1 (Ivggegáisat), the first line of the TWINSPAN division lies in a gap separating boreal and lower oroarctic communities from late snow-beds and the vegetation fragments of high altitudes (Fig. 6). Five subsequent divisions have eigenvalues of roughly 0.3, creating seven community groups altogether (Fig. 8). One of the TWINSPAN clusters is relatively inclusive, consisting of all boreal and (oro)arctic communities, which have a closed field layer: boreal vegetation, weakly chionophobous *Empetrum* heaths and communities conventionally referred to the alliance Phyllodoco-Vaccinion myrtilli (Dahl 1957, Kalliola 1939). This broad category is further divided, with an eigenvalue of only 0.195, into two subunits encompassing 1) the mesic forest floor communities and the chionophilous grass-rich oroarctic bilberry heaths (Ia) and 2) the communities dominated more pronouncedly by dwarf shrubs (Ib). These units generated by TWINSPAN do not match fully with conventional Scandinavian scheme that treats communities above and below treeline as distinct (Nordhagen 1928, 1943, Kalliola 1939, Dahl 1957). The probable reason is that the same dwarf shrubs — *Empetrum hermaphroditum* and *Vaccinium myrtillus* — prevail on both sides of the timberline, both in moderately chionophilous sites and in moderately chionophobous ones. Moreover, this division also differs from the results of the numerical analysis of the continental-subcontinental vegetation (subareas 2–6). Consequently, we have not utilized these two subunits in our

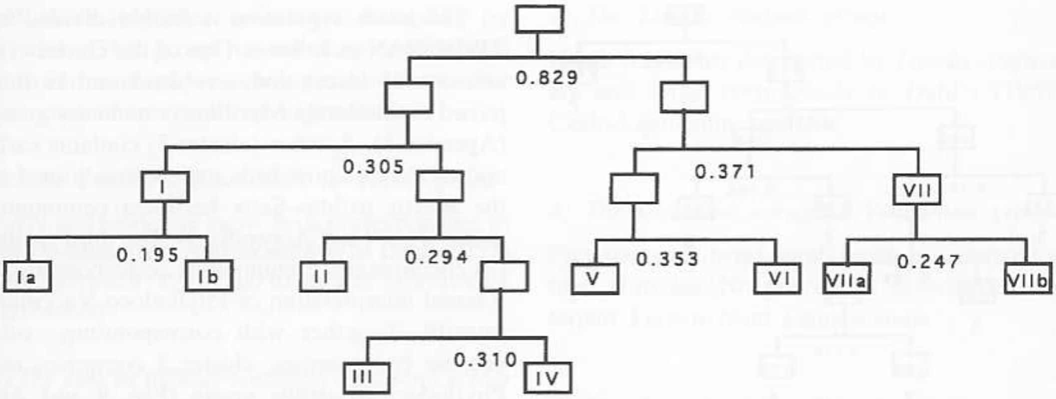


Fig. 8. Main community groups in the Ivggegáisat material after the TWINSPAN division. I = Betula-Myrtillus and Phyllodoce groups, Ia = mesic forest floors + early snow-bed vegetation, Ib = xeric forest floors and typical lower oroarctic heaths, II = Juncus trifidus-Salix herbacea group, III = Arctostaphylos group, IV = Juncus trifidus-Cassiope tetragona group, V = Salix herbacea-Kiaeria group, VI = Ranunculus glacialis group, VII = high-altitude ridge heaths; VIIa = Cassiope tetragona-Vaccinium group and VIIb = Luzula confusa group. The numbers indicate eigenvalues in TWINSPAN divisions.

classification scheme. Instead, the collective category of low altitude dwarf shrub heaths has been divided into a forested community group and a non-forested one, to be called the Betula-Myrtillus group and the Phyllodoce-Myrtillus group, respectively (Appendices 1 and 2).

The remaining three groups below the first line of the TWINSPAN division (Fig. 8) represent communities without a closed cover of erect dwarf shrubs. Thus, their shared feature is the presence of prostrate, light-loving plants. One of the groups represents vegetation of ridge heaths (roughly corresponding to Kalliola's (1939) Loiseleurieto-Arctostaphylion), and we call it the Actostaphylos community group (III, Appendix 3). Another represents moderate snow-beds (corresponding to Gjærevoll's (1956) Deschampsio-Anthoxanthion and the most early melting part of his Herbaceon), to be called the Juncus trifidus-Salix herbacea community group (II, Appendix 5). The third group encompasses middle oroarctic heaths (local counterparts of Nordhagens's (1943) Juncion trifidi Scandinavicum) referred to as the Juncus trifidus-Cassiope tetragona community group (IV, Appendix 6).

The communities above the first line of the TWINSPAN division (Fig. 8) are divided into four groups. Two groups consist of snow-beds. One of these is strongly dominated by *Salix herbacea*, sometimes with *Viola biflora* as a co-dominant, and is called the Salix herbacea-Kiaeria community group (V, Appendix 9). The other group has more varying composition of the field layer, with *Oxyria digyna*, *Ranunculus glacialis*, *Trisetum spicatum* and *Veronica alpina* as characteristic species to be called the Ranunculus glacialis community group (VI, Appendix 10). This structure does not correspond to Gjærevoll's (1956) system. The two remaining groups consist of chionophobous heaths at high altitudes. One group (VIIa) comprises communities dominated by *Luzula confusa*, and is called the Luzula confusa community group (Appendix 7), and the other (VIIb) is characterized by relatively high abundances of dwarf shrubs (mainly: *Cassiope tetragona* or *Vaccinium vitis-idaea*) and is called the Cassiope tetragona-Vaccinium community group (Appendix 8).

Subareas 2–6

The community groups of continental-subcontinental subareas 2–6 are more diffuse than those of suboceanic subarea 1 (Ivggegáisat). Only the first line of the division has an eigenvalue exceeding 0.3. In order to obtain a similar number

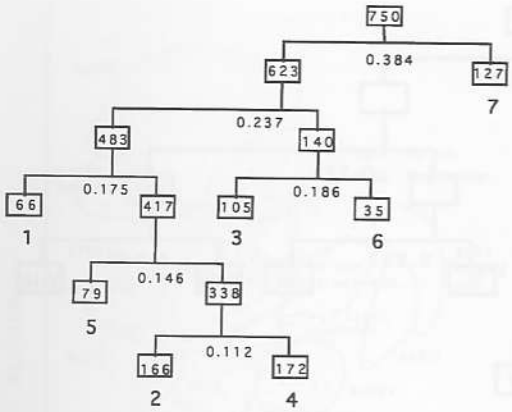


Fig. 9. The main TWINSPAN groups for subareas 2–6. 1 = Betula-Myrtillus group, 2 = Phyllodoce-Myrtillus group, 3 = Arctostaphylos group, 4 = Betula nana group, 5 = Juncus trifidus-Salix herbacea group, 6 = Juncus trifidus-Cassiope tetragona group, 7 = High-altitude vegetation.

of community groups as in the suboceanic vegetation, we must accept divisions with considerably lower eigenvalues. Nevertheless, the community group level phytosociological structure of the continental-subcontinental heath vegetation appears fairly similar to the structure of subarea 1 and to the conventional classification schemes of Scandinavian mountain vegetation.

Again, the first line of the division separates extreme snow-beds and ridge heaths at high altitudes (cluster 7) from other types of vegetation (Fig. 9). This cluster contains chiefly the Cassiope tetragona-Vaccinium, the Luzula confusa and the Ranunculus glacialis community groups (Appendices 7, 8 and 10). The late snow-beds of middle altitudes (the Salix herbacea-Kiaeria group) are not represented in the continental-subcontinental material.

The subsequent TWINSPAN divisions (Fig. 9) split the main group consisting of low and middle altitude material into smaller groups with four levels of division. The relatively well-discriminated clusters 3 and 6 represent communities resembling traditional Arctostaphy-leto-Cetrarion nivalis (our Arctostaphylos group, Appendix 3) and Juncion trifidi Scandinavicum (our Juncus trifidus-Cassiope tetragona group, Appendix 6).

The heath vegetation is further divided by TWINSPAN as follows: One of the clusters (1) consists of forest and scrubland and is thus joined to the Betula-Myrtillus community group (Apendix 1). Another (cluster 5) contains early and moderate snow-beds and is thus joined to the Juncus trifidus-Salix herbacea community group (Fig. 9 and Appendix 5). The third cluster (2) encompasses communities corresponding to a broad interpretation of Phyllodoco-Vaccinion myrtilli. Together with corresponding suboceanic communities, cluster 2 comprises our Phyllodoce-Myrtillus group (Fig. 9 and Appendix 2). The last cluster (4), which was separated from the Phyllodoce-Myrtillus group at a relatively low eigenvalue, consists of lichen heaths with *Betula nana* as the dominating vascular plant (Fig. 9 and Appendix 4). This cluster will be called the Betula nana community group.

Summary of the main community groups

1) The Betula-Myrtillus group

Forest vegetation and scrublands dominated by either *Betula pubescens* or *B. nana*.

2) The Phyllodoce-Myrtillus group

Treeless heaths, where the field layer is dominated by evergreen or semi-evergreen dwarf shrubs. The group roughly corresponds to the alliance Phyllodoce-Vaccinion myrtilli, except that it also embraces relatively chionophobous heaths with closed field layer.

3) The Arctostaphylos group

Strictly chionophobous heaths without a closed field layer thus corresponding to the most chionophobous part of the traditional alliance Loiseleurieto-Arctostaphylion.

4) The Betula nana group

Inland communities characterized by patchy occurrence of dwarf birches and by copious occurrence of fruticose lichens in areas that have not been subjected to intense trampling by reindeer. This group has no close counterparts in traditional phytosociological schemes for Fennoscandian mountain vegetation.

5) The Juncus trifidus-Salix herbacea group

Early and moderate snow-beds corresponding to the Deschampsio-Anthoxanthion of Dahl (1957) and Gjærevoll (1956) and to parts of Gjærevoll's Herbaceon.

6) The Juncus trifidus-Cassiope tetragona group

Corresponds to Juncion trifidi Scandinavicum. In the inland, the group is mainly represented by communities intermediate between typical oroarctic *Juncus trifidus* heaths and arctic *Cassiope tetragona* heaths. On Ivggegáisat, corresponding vegetation dominated by *Empetrum hermaphroditum* and *Salix herbacea*, with *Cassiope tetragona* and *J. trifidus* as subordinate components only.

7) The Luzula confusa group

Heath fragments dominated by *Luzula confusa*. By and large corresponds to Dahl's (1957) Cesio-Luzuletum confusae.

8) The Cassiope tetragona-Vaccinium group

Fragments of dwarf shrub heath encountered at high altitudes. No previously described counterpart known from Fennoscandia.

9) The Salix herbacea-Kiaeria group

Late snow-beds at middle altitudes with varying abundance of snow-bed herbs.

10) The Ranunculus glacialis group

Late and at least moderately herb-rich snow-beds at middle altitudes and snow-bed fragments encountered above the boulderfield limit.

VI. CLASSIFICATION OF VEGETATION

1. **Betula-Myrtillus community group**

Classification of the vegetation assigned to this group was conventional. By and large, differences between the eight community types created by our numerical analysis and those of Hämet–Ahti (1963) and Haapasaari (1988) were small and could be attributed to differences in the sampling procedure and to the impact of *Epirrita autumnata*. The only clear and consistent difference that we could find was the relatively sparse occurrence of *Vaccinium myrtillus* in our material. All continental community types emerging from our material are dominated by *Empetrum hermaphroditum*, usually with *Vaccinium vitis-idaea* or *V. uliginosum* as a co-dominant.

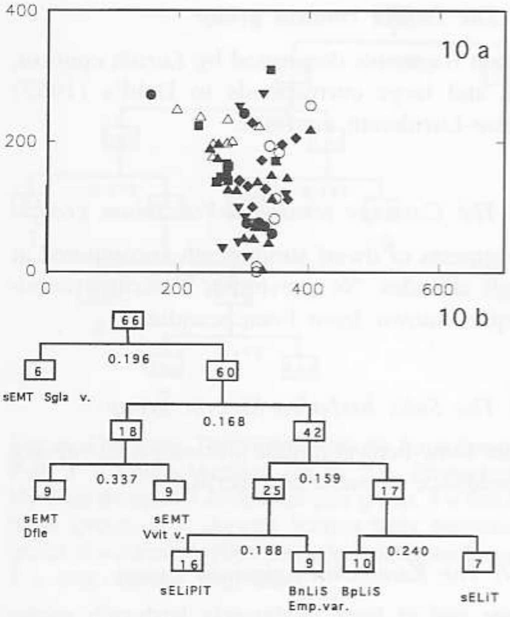
In the ordination space (Fig. 6, Fig. 10a and b), the communities tend to separate along the first axis only, although their occurrence in the field is strongly influenced by topography. However, mesic communities of depressions tend to locate at the bottom of the first axis, whereas communities of topographically elevated sites and those encountered at higher altitudes both obtain higher positions along the axis. At low altitudes, the first axis thus seems to reflect the productivity of the site, rather than altitude per se. (Appendix 1, Figs. 6, 10a and b).

1.1. *Suboceanic forest types*

The plots sampled below the timberline on Ivggegáisat were assigned to community types that can be regarded as identical with Hämet–Ahti's (1963) Cornus-Myrtillus type (CoMT), Cornus-Empetrum-Myrtillus type (CoEMT) and subalpine Empetrum type (sET).

1.2. *Subalpine Empetrum-Myrtillus type* (sEMT, Hämet-Ahti 1963)

This community type is encountered as three variants. One can be regarded as identical with



Figs. 10a–b. DCA scattergrams (10a) and TWINSPAN dendrograms (10b) for the vegetation data from subareas 2–6 witin the Betula-Myrtillus group. Letters in parentheses show the symbols of the community types in Subalpine Empetrum-Myrtillus type (sEMT): ▼ Deschampsia flexuosa variant, ■ Vaccinium vitis-idaea variant, ● Salix glauca variant; ▲ subalpine Empetrum-Lichenes-Pleurozium type (sELiPIT); ○ subalpine Empetrum-Lichenes type (sELiT); ◆ Betula pubescens-Lichenes scrub type (BpLiS); Betula nana-Lichenes scrub type (BnLiS): △ Empetrum variant.

Hämet–Ahti's Vaccinium vitis-idaea variant. The other two variants are characterized by copious abundance of *Vaccinium uliginosum* and encountered in sites with snow accumulation. The distinctive feature of the Deschampsia variant, which is mainly encountered on slopes, is constant and fairly abundant occurrence of *D. flexuosa*. The Salix glauca variant, encountered in stony depressions, is characterized by absence of *Vaccinium myrtillus* and the co-occurrence of *Salix glauca* and xerophilous lichens (*Cetraria nivalis* and *Cladina stellaris*).

Plots representing the Deschampsia variant occur in Hämet–Ahti's (1963: Appendix 6, plots 4, 23 and 37) material, but not plots representing the Salix glauca variant. The difference is probably due to sampling method (our small plots, and sampling concentrated on relatively steep slopes).

1.3. *Subalpine Empetrum-Lichenes-Pleurozium type* (sELiPlT, Hämet–Ahti 1963)

The stands representing this community type in our material are characterized by copious occurrence of *Deschampsia flexuosa*. As they mainly lie in areas where the forests have been heavily damaged by *Epirrita autumnata*, we regard this phenomenon as a transient stage only (see Lehtonen & Yli-Rekola 1979).

1.4. *Subalpine Empetrum-Lichenes type* (sELiT, Hämet–Ahti 1963)

In our material, this community type is, too, characterized by high abundance of *D. flexuosa* because of the prevalence of stands influenced by *Epirrita autumnata*.

1.5. *Betula pubescens-Lichenes scrub type* (BpLiS)

This community type is encountered right at the timberline and could be regarded as a variant of sELiT. The main difference is that scrubby mountain birches are very efficient in trapping their own detritus, and this appears to be favourable to ericaceous dwarf shrubs, *Linnaea borealis* and cup lichens. Fruticose lichens probably suffer from the litter, but this does not show up in our material because our sELiT-plots are heavily trampled by reindeer.

1.6. *Betula nana-Lichenes scrub* (BnLiS, Haapasaari 1988), *Empetrum variant*

This community type was divided into two variants, assigned to different groups. As the majority of the plots represented the typical variant, which was assigned to the Phyllodoce-

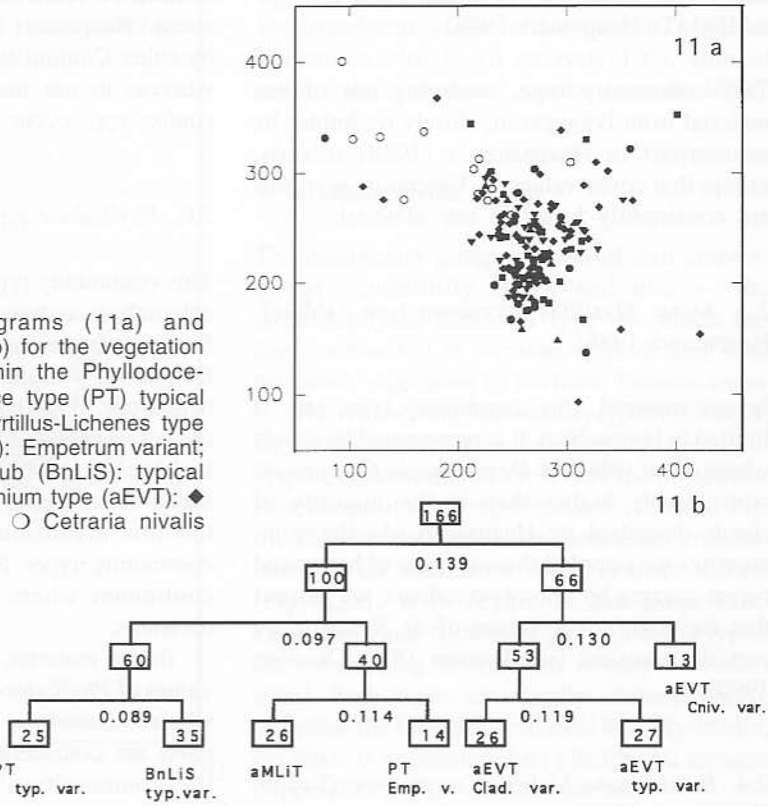


Fig. 11a–b. DCA scattergrams (11a) and TWINSPAN dendrograms (11b) for the vegetation data from subareas 2–6 within the Phyllodoce-Myrtillus group. ▲ Phyllodoce type (PT) typical variant; ■ arctic-hemiarctic Myrtillus-Lichenes type (aMLiT); ● Phyllodoce type (PT): Empetrum variant; ▼ Betula nana-Lichenes scrub (BnLiS): typical variant; arctic Empetrum-Vaccinium type (aEVT): ◆ typical and Cladina variants, ○ Cetraria nivalis variant.

Myrtillus group, this community type will be discussed in section VI.2.

2. Phyllodoce-Myrtillus group

For the most part, this group corresponds to the classical alliance Phyllodoco-Vaccinio myrtilli and is classified in accordance with conventional community type schemes. However, it also encompasses dwarf shrub heaths with low frequencies and cover values of *V. myrtillus*. One of the constituent communities — the arctic Empetrum-Vaccinium type — could not be identified with any previously described community type.

Plots assigned to this group have relatively low scores on the first DCA axis and tend to concentrate to the centre of the second one. The seven community types included overlap broadly in the ordination space defined by the two first DCA axes (Appendix 2, Figs. 6, 11a and b).

2.1. *Mossy Betula nana scrub type* (mBnS)

This community type, encountered only on Ivggegáisat, roughly corresponds to Haapasaari's (1988) Betula nana-Pleurozium-Lichenes scrub type, but is characterized by essentially lower abundances of *Pleurozium schreberi*. There are two variants: the *Empetrum* variant, characterized by relatively low cover of *B. nana*, copious abundance of *E. hermaphroditum* and a bottom layer dominated by *Dicranum fuscescens*, and the *Myrtillus* variant, with about equal cover values of *B. nana*, *E. hermaphroditum* and *V. myrtillus* and a bottom layer dominated by *Hylocomium splendens*.

2.2. *Arctic Myrtillus-Dicranum-Lichenes type* (aMDiLiT, Haapasaari 1988)

This community type, emerging out of our material from Ivggegáisat, closely resembles its counterpart in Haapasaari's (1988) records, except that cover values of *Vaccinium myrtillus* are consistently lower in our material.

2.3. *Arctic Myrtillus-Dicranum type* (aMDiT, Haapasaari 1988)

In our material, this community type, too, is limited to Ivggegáisat. It is represented by stands where cover values of *Deschampsia flexuosa* are considerably higher than in the majority of stands described by Haapasaari. As the communities we sampled showed signs of heavy and recent grazing by microtine rodents, we suspect that the high cover values of *D. flexuosa* are partially transient (see Ericson 1977, Oksanen 1990).

2.4. *Betula nana-Lichenes scrub type* (BnLiS, Haapasaari 1988)

As noted at 1.6. above, the two variants of this community type were assigned to different groups: the typical one to the present group and the Empetrum variant to the Betula-Vaccinium group. The main difference between the variants is higher abundance of ericaceous dwarf shrubs in the Empetrum variant, which was encountered chiefly on Ráisduottar (subarea 2) and can be regarded as transitional towards the mossy Betula nana scrub type. Even in the typical variant, as represented in our material, cover values of ericaceous dwarf shrubs are considerably higher than in Haapasaari's material.

2.5. *Arctic-hemiarctic Myrtillus-Lichenes type* (aMLiT, Haapasaari 1988)

This community type emerges from our material as practically identical to Haapasaari's material. The only substantial difference pertains to abundance relationships between fruticose lichens. Haapasaari described stands dominated by either *Cladina stellaris* or *Stereocaulon* spp., whereas in our material *C. mitis* and *Stereocaulon* spp. occur as co-dominants.

2.6. *Phyllodoce type* (PT, Haapasaari 1988)

This community type emerges from the numerical analysis as two variants, which do not even form a single subdivision (Fig. 11b). The Empetrum variant clustered with the arctic-hemiarctic Myrtillus-Lichenes type, whereas the typical variant was paired with the Betula nana-Lichenes scrub type. Nevertheless, the differences between the two variants are small and the low eigenvalues indicate that all three community types form a more or less diffuse continuum where random factors influence divisions.

In our material, both frequencies and cover values of *Phyllodoce caerulea* are relatively low, whereas *Empetrum hermaphroditum* and *Betula nana* are considerably more abundant than in the communities included in Haapasaari's records.

2.7. *Arctic Empetrum-Vaccinium type* (aEVT)

A large number of sample plots from continental and subcontinental areas were joined into a community type resembling the lichen-rich lingonberry (*Vaccinium vitis-idaea*) community (flechtenreiche Preisselbeer-Gesellschaft) described by Thannheiser (1975). The low, but continuous field layer and the occurrence of wind-hardy lichens creates affinities to Haapasaari's (1988) arctic Empetrum-Dicranum-Lichenes type. However, *Betula nana* and *Vaccinium vitis-idaea*, which occur sparsely on Haapasaari's plots, are co-dominants in our material. Moreover, cover values of fruticose lichens are several times higher in our plots. Two plots included in Haapasaari's arctic Empetrum-Cetraria nivalis type (Haapasaari 1988; Apendix 1, plots 5 and 32) doubtlessly represent the aEVT as defined by us.

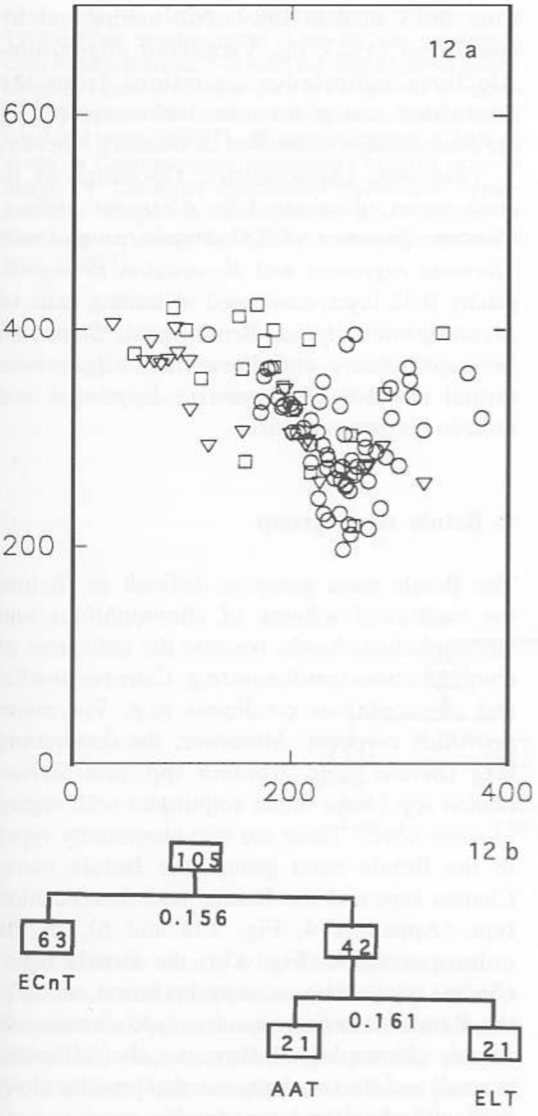


Fig. 12a–b. DCA scattergrams (12a) and TWINSPAN dendrograms (12b) for the vegetation data from subareas 2–6 within the Arctostaphylos group. Letters in parentheses show the symbols of the community types ▽ Empetrum-Cetraria nivalis type (ECnT); ☐ Empetrum-Loiseleuria type (ELT); ○ Arctostaphylos-Alectoria type (AAT).

The community type emerges as three variants (*Cladina*, typical and *Cetraria nivalis*), which range from slightly to moderately chionophobous and thus form a link between the arctic-hemiarctic Myrtillus-Lichenes type and deflation heaths.

Diagnostic features: *Cetraria nivalis* and *Sphaerophorus globosus* are present, cover of *Vaccinium vitis-idaea* exceeds 10%, sum of cover values of dwarf shrubs exceeds 50%.

3. Arctostaphylos group

The community group consists of four conventional community types and one — the Arctostaphylos-Alectoria type — which has been overlooked in previous work dealing with the heath vegetation of northern Fennoscandia.

The two oceanic community types (aEDiLiT, OcT) are well differentiated along the topographic and altitudinal axes, OcT having a more extreme position along both axes (see also Fig. 6). The distribution of the continental communities in the ordination space is more diffuse (Fig. 13a). With regard to the Empetrum-Loiseleuria and Arctostaphylos-Alectoria types, the overlapping distribution is easy to understand. Both types are equally chionophobous, but while the former is restricted to rocky terrain, the latter is encountered on glacifluvial terraces (Appendix 3, Fig. 6, 12a and b).

3.1. *Arctic Empetrum-Dicranum-Lichenes type* (aEDiLiT, Haapasaari 1988)

The distribution of this community type in our material is restricted to Ivggegáisat (subarea 1). Including strongly chionophobous heaths, as indicated by the frequent occurrence of *Loiseleuria procumbens* and wind-hardy lichens, it is somewhat more inclusive than the counterpart in Haapasaari's (1988) material.

3.2. *Ochrolechia type* (OcT, Haapasaari 1988)

Our material represents a variant in which cover values and frequencies of *Cassiope tetragona* and *Diapensia lapponica* are higher and cover values of *Loiseleuria procumbens* are lower than in Haapasaari's data. The discrepancy probably reflects altitudinal differences between the two data sets.

3.3. *Empetrum-Cetraria nivalis type* (ECnT, Haapasaari 1988)

The community type emerging from our material is practically identical with the counterparts described by Kalliola (1939; his Empetrum-Cetraria nivalis sociation) and Haapasaari (1988). However, our material includes a greater number of *Cladina*-rich plots, indicating differences in the distribution of sampling effort along the topographic gradient. TWINSPAN divided the community type into several variants or stages, but as the differences appeared small and were difficult to interpret, these are not presented separately in Appendix 3. The strongly trampled stands along the reindeer fence are presented as a separate stage, characterized by low cover values of almost all plants.

3.4. *Empetrum-Loiseleuria type* (ELT)

The community type can be regarded as identical with Kalliola's (1939) lichen-rich Diapensia-Loisleuria-Empetrum sociation. In our material, the community type is mainly represented by less extreme deflation sites, as reflected in the considerably higher cover values of lichens and lower cover values of *Diapensia lapponica* and *Loiseleuria procumbens*. Haapasaari (1988) describes corresponding sites, but does not give a name for the community type encountered there.

3.5. *Arctostaphylos-Alectoria type* (AAT)

This community type, which does not have obvious counterparts in the classification schemes of Kalliola (1939) or Haapasaari (1988), also encompasses lichen-rich vegetation of extremely chionophobous sites. It is characterized by trailing twigs of *Arctostaphylos alpina*, *Empetrum hermaphroditum* and *Vaccinium uliginosum* intermingled with *Alectoria* spp., *Bryocaulon divergens* and *Cetraria nivalis*. Counterparts of this community have been described by Neal and Kershaw (1973; their Cladina rangiferina-Alectoria ochroleuca-Vaccinium uliginosum association) from the Canadian low arctic tundra and by Nordhagen (1943; his Vaccinium uliginosum-Alectoria ochroleuca sociation) from the Sikilsdalen area in the rain shadow created by the Jotunheimen mountains of southern Norway.

Diagnostic characteristics: Discontinuous lichen cover, dominated by *Cetraria nivalis*. Constant presence of *Sphaerophorus globosus Alectoria nigricans* and *Bryocaulon divergens*, patchy field layer, composed of trailing mats of *Arctostaphylos alpina*, *Betula nana*, *Empetrum hermaphroditum* and *Vaccinium uliginosum*, virtual absence of *Diapensia lapponica* and *Loiseleuria procumbens*.

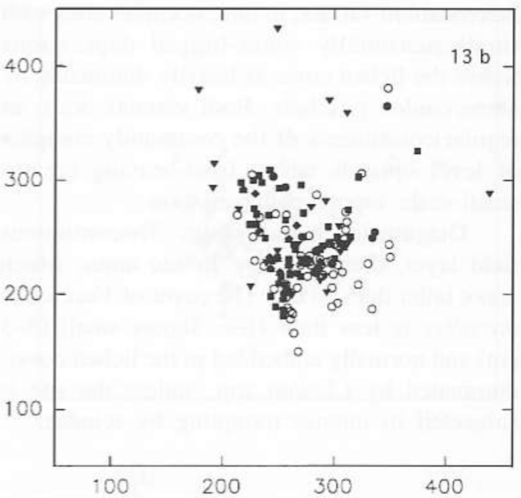
4. Betula nana group

The Betula nana group is difficult to fit into the traditional scheme of chionophilous and chionophobous heaths because the indicators of chionophobous conditions (e.g. *Cetraria nivalis*) and chionophilous conditions (e.g. *Vaccinium myrtillus*) co-occur. Moreover, the dominating taxa (*Betula nana*, *Cladina* spp. and *Stereocaulon* spp.) have broad amplitudes with regard to snow cover. There are two community types in the Betula nana group: the Betula nana-Cladina type and the Betula nana-Stereocaulon type (Appendix 4, Fig. 13a and b). In the ordination space (Fig. 13a) the Betula nana-Cladina type obtains a neutral position, whereas the Betula nana-Stereocaulon type emerges as weakly chionophilous. However, the difference is small and the two types overlap broadly along both altitudinal and topographic axes.

4.1. *Betula nana-Cladina type* (BnClT)

This community type corresponds to Kalliola's (1939) Betula nana-Empetrum-Cladina alpestris sociation and covers vast areas in the gently rolling tundra landscape of interior Finnmark. As noted by Kalliola, the dwarf birch cover is never tall enough to warrant the term 'scrubland'.

Six subtypes were distinguished within the Betula nana-Cladina type. Four of them can be interpreted as stages since the differences in



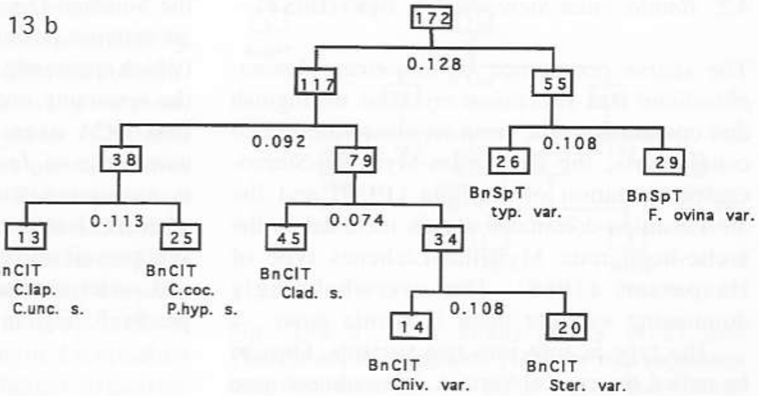


Fig. 13a–b. DCA scattergrams (13a) and TWINSPAN dendrograms (13b) for the vegetation data from subareas 2–6 witin the Betula nana group. Letters in parentheses show the symbols of the community types in the ordination figures. Betula nana-Cladina type (BnClT): ■ non-trampled (Cladina) stage, ● Calamagrostis lapponica-Cladonia uncialis stage, ▼ Cladonia coccifera-Polytrichum hyperboreum stage, ▲ Cetraria nivalis variant, ◆ Stereocaulon variant; ○ Betula nana-Stereocaulon type (BnST).

vegetation are clearly related to reindeer grazing. Two are found on opposite sides of the reindeer fence on Čakčaduottar and are thus non-trampled (*Cladina*) and trampled (graminoid) stages. Notice that plots sampled from those parts of the summer range where trampling had not been overly intensive, are grouped with the Cladina stage, apparently due to the lack of positive trampling indicators. Thus, the mean cover values of lichens reported for the Cladina stage are relatively low (compare to Oksanen 1978). A third stage is found in areas used during spring and fall migrations when trampling is less intense. The lichen carpet is low and sparse, but relatively continuous. This community we call the Calamagrostis lapponica-Cladonia uncialis stage. On the Finnish side, where continental tundra areas have long been subjected to intense summer grazing and trampling, the lichen carpet has suffered still more. The mean cover values of reindeer lichens are roughly similar to those of the Calamagrostis lapponica-Cladonia uncialis stage, but the individuals are extremely small (rarely taller than 1 cm), and cup lichens, e.g. *Cladonia coccifera*, are relatively abundant. *Festuca ovina* and especially *Polytrichum hyperboreum* abound. We call this subtype the Cladonia coccifera-Polytrichum hyperboreum stage. The summer grazed lichen heaths of Norway are probably converging towards this stage.

Two of the subtypes are recognized as variants since there is no obvious association with different types of reindeer grazing. One, the Cetraria nivalis variant, is found on slightly wind-exposed sites and represents a transitional community between the Betula nana-Cladina and Empetrum-Cetraria nivalis types. The

Stereocaulon variant, in turn, occupies sites with small, seasonally water-logged depressions where the lichen cover is heavily dominated by *Stereocaulon paschale*. Both variants occur as regular constituents of the community complex of level uplands where frost-heaving creates small-scale topographic variation.

Diagnostic characteristics: Discontinuous field layer, dominated by *Betula nana*, which is not taller than 30 cm. The cover of *Vaccinium myrtillus* is less than 10%, shoots small (3–5 cm) and normally embedded in the lichen cover, dominated by *Cladina* spp., unless the site is subjected to intense trampling by reindeer.

4.2. *Betula nana-Stereocaulon type* (BnST)

The sparse occurrence of *Empetrum hermaphroditum* and *Vaccinium myrtillus* distinguish this community type from its closest described counterparts: the Empetrum-Myrtillus-Stereocaulon sociation of Kalliola (1939) and the *Stereocaulon*-dominated stands included in the arctic-hemiarctic Myrtillus-Lichenes type of Haapasaari (1988). The overwhelmingly dominating vascular plant is *Betula nana*.

The type is split into two variants. One, to be called the typical variant, is an almost pure dwarf shrub-lichen heath, whereas the other, to be called the Festuca ovina variant, is more graminoid rich and somewhat snow-bed like in its species composition. Our program pooled plots occurring on different sides of the reindeer fence, suggesting that the community is indifferent to summer grazing and relatively intense trampling. However, the most trampled sites along the reindeer fence are practically lichen-free and somewhat richer in graminoids and are thus distinguished as the graminoid stage.

Diagnostic features: the only reliable characteristic differentiating the Betula nana-Stereocaulon type from the Betula nana-Cladina type is the prevalence of *Stereocaulon* spp. Snow-bed plants (*Cassiope hypnoides*, *Diphasiastrum alpinum*, *Salix herbacea*), graminoids (especially *Deschampsia flexuosa*) and herbs (*Hieracium alpinum* and *Trientalis europaea*) are more frequent on Betula nana-Stereocaulon type.

5. **Juncus trifidus-Salix herbacea group**

Correspondence between the six types our Juncus trifidus-Salix herbacea community group, encompassing early and moderate snow-beds, and traditional categories was far from perfect. Moreover, the boundaries of the community groups generated by the numerical analysis had to be revised in order to create a consistent classification scheme for both suboceanic and continental-subcontinental snow-bed vegetation.

The two suboceanic community types (the Juncus trifidus-Deschampsia flexuosa type and the Salix herbacea-Cassiope hypnoides type) separated along the first DCA axis (Fig. 6). Among the continental-subcontinental community types, the Solidago-Deschampsia flexuosa type obtains an extreme position along the topographic axis (which apparently also reflects moisture), whereas the remaining ones overlap broadly on the two first DCA axes. This is natural, as the predominance of *Juncus trifidus* and *Cladina mitis* is associated with well-drained sandy soils, whereas *Deschampsia flexuosa* and *Stereocaulon* spp. prevail on heavy soils at the same altitudes and under similar topographic conditions (Appendix 5, Fig. 6, 14a and b).

5.1. *Juncus trifidus-Deschampsia type* (JtDfT)

This community type, based on material from Ivggegáisat (subarea 1), can be regarded as a grass heath dominated by *Deschampsia flexuosa* and *Juncus trifidus*. In the numerical treatment, it was assigned to a group that otherwise consists of dwarf shrub heaths, but it has clear counterparts in the group of snow-bed communities which emerged from corresponding treatment of continental and subcontinental vegetation (subareas 2–6). Snow-beds assigned to the Juncus trifidus-Deschampsia flexuosa type are more xerophilous than any of the snow-beds described by Gjærevoll (1956). The composition of the field layer resembles Dahl's (1957) Chiono-Juncetum trifidi, but *Vaccinium vitis-idaea* is missing and the ground layer is moss-dominated. In Nordhagen's (1928) Sylene material, one finds a mesic snow-bed with *Anthoxanthum* *odorarum*, *Deschampsia flexuosa* and moss and a more xerophilous snow-bed with *Juncus trifidus* and lichens, but not an intermediate one that would correspond to the grassy snow-beds of Ivggegáisat.

Diagnostic features: Field layer is dominated by *Deschampsia flexuosa*, *Juncus trifidus* and *Salix herbacea*. *Vaccinium myrtillus* occurs frequently, often even as a co-dominant. *Polygonum viviparum* is a constant of the field layer. Bottom layer is dominated by *Dicranum fuscescens*.

5.2. *Salix herbacea-Cassiope hypnoides type* (ShChT)

This community type, too, is characterized by frequent occurrence of erect dwarf shrubs indicating relatively long growing season. However, trailing snow-bed plants (*Cassiope hypnoides* and *Salix herbacea*) prevail. Cover values of graminoids are low. The community has some common features with Kalliola's (1939) Lycopodium alpinum-Solidago-Deschampsia flexuosa sociation (especially his plots 3 and 4), but is distinguished by lack of *Diphasiastrum alpinum* (synonym *Lycopodium alpinum*) and low cover of *Solidago virgaurea*.

Diagnostic features: *Salix herbacea* is the dominating vascular plant, *Polygonum viviparum* is constant and moderately abundant, *Cassiope hypnoides* is locally abundant, erect dwarf shrubs are present. *Juncus trifidus* is absent. The bottom layer is dominated by *Dicranum fuscescens* and species of *Barbilophozia* subgenus *Orthocaulis*.

5.3. *Deschampsia flexuosa-Stereocaulon type* (DfST)

This community type, which has no counterparts in publications known to us, is characterized by a sparse field layer with snow-bed indicators (e.g. *Cassiope hypnoides*, *Deschampsia flexuosa* and *Salix herbacea*) and a ground layer dominated by *Stereocaulon* spp. All plots assigned to this community type were sampled on Čakčaduottar. Two variants were distinguished: the typical variant with relatively high abundances of *Deschampsia flexuosa*, *Dicranum fuscescens* and *Diphasiastrum alpinum*, and the Cassiope variant where *Deschampsia flexuosa* is less abundant, but *Cassiope hypnoides* is a major constituent of the sparse vascular plant cover and the ground layer is still more heavily lichen-dominated.

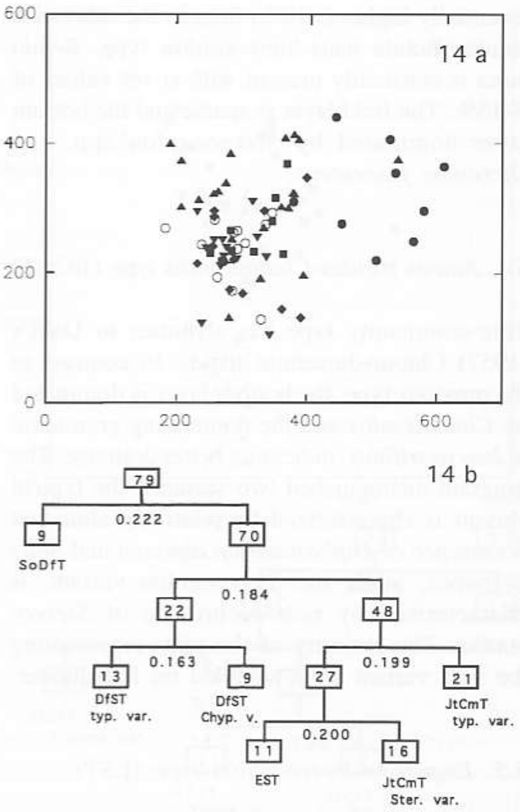


Fig. 14a–b. DCA scattergrams (14a) and TWINSPAN dendrograms (14b) for the vegetation data from subareas 2–6 within the Juncus trifidus-Salix herbacea group. Letters in parentheses show the symbols of the community types Deschampsia flexuosa-Stereocaulon type (DfST): ▼ typical variant, ■ Cassiope hypnoides variant; Juncus trifidus-Cladina mitis type (JtCmT): ▲ typical variant, ○ Stereocaulon variant, ◆ Empetrum variant; Solidago-Deschampsia type (SoDfT): ● Rubus chamaemorus variant.

Diagnostic features: Frequencies and cover values of graminoids and *Salix herbacea* are essentially higher (>10%) than in the otherwise similar Betula nana-Stereocaulon type. *Betula nana* is constantly present with cover values of 5–15%. The field layer is sparse and the bottom layer dominated by *Stereocaulon* spp. and *Dicranum fuscescens*.

5.4. *Juncus trifidus-Cladina mitis type* (JtCmT)

This community type has affinities to Dahl's (1957) Chiono-Juncetum trifidi. In contrast to the previous type, the bottom layer is dominated by *Cladina mitis* and the dominating graminoid is *Juncus trifidus*, indicating better drainage. The program distinguished two variants: the typical variant is characterized by relatively abundant occurrence of *Diphasiastrum alpinum* and *Salix herbacea*, while the Stereocaulon variant. is characterized by rich occurrence of *Stereocaulon*. The majority of the plots representing the first variant were sampled on Ráisduottar.

5.5. *Empetrum-Stereocaulon type* (EST)

According to the numerical analyses, this community type is closely associated with the *Stereocaulon* variant of the Juncus trifidus-Cladina type (see Fig. 14b). However, the field layer is heavily dominated by *Empetrum hermaphroditum*. *Vaccinium vitis-idaea* and *V. myrtillus* occur with high frequencies and locally even as co-dominants. Thus, there are affinities to Kalliola's (1939) Empetrum-Myrtillus-Stereocaulon sociation. The Empetrum-Stereocaulon type also harbours other species that are rare on snow-beds (e.g. *Linnaea borealis*, *Juniperus communis*). Except for moderate cover values of *Deschampsia flexuosa*, snow-bed plants only occur in trace amounts. The bottom layer is normally dominated by *Stereocaulon* spp. The ecology of the community type has been studied by Kyllönen (1988) and Eurola et al. (1982).

Diagnostic features: The field layer is dominated by *Empetrum hermaphroditum*. *Deschampsia flexuosa*, *Vaccinium myrtillus* and *V. vitis-idaea* are moderately abundant. The bottom layer is dominated by *Stereocaulon* spp. and *Cladina mitis*.

5.6. *Solidago-Deschampsia flexuosa type* (SoDfT)

This snow-bed type is characterized by a graminoid-rich field layer. Its closest previously described counterpart appears to be Kalliola's (1939) Lycopodium alpinum-Solidago-Deschampsia sociation. However, *Dipha–siastrum alpinum* is absent from our plots, and conversely, *Rubus chamaemorus*, which abounds in our material, is absent from Kalliola's plots. We propose that the name Solidago-Deschampsia type could be used for such moderately grass- and herb-rich early snow-beds. Kalliola's material could be referred to as the Diphasiastrum alpinum variant, and the subtype represented by our plots the Rubus chamaemorus variant.

Diagnostic features: Snow-bed graminoids (*Carex brunnescens*, *C. lachenalii* and *Deschampsia flexuosa*) are frequent and fairly abundant, broad-leaved herbs (*Rumex acetosa* and *Solidago virgaurea*, sometimes also *Rubus chamaemorus*) form a constant constituent of the community. The bottom layer is dominated by *Dicranum* and *Kiaeria* spp.

6. **Juncus trifidus-Cassiope tetragona group**

One of the community types of this group is easily identified as a northern counterpart of Juncion trifidi Scandinavicum. Also the remaining three types represent middle oroarctic heaths. They have no previously described counterparts known to us. In the numerical treatment of the suboceanic material, this community group did not emerge in a natural way; the Salix herbacea-Ochrolechia type was assigned to the Luzula confusa group.

The two suboceanic community types were differentiated along the first DCA axis (Fig. 6), while the distribution of the continental-subcontinental community types overlapped broadly along both main DCA axes (Appendix 6, Figs. 6, 15a and b).

6.1 *Juncus trifidus-Cassiope tetragona type* (JtCtT)

This community type, which we encountered only on Ráisduottar, is similar to Nordhagen's (1928) Juncus trifidus-Cetraria islandica-Cladonia sylvatica sociation, except that also *Cassiope tetragona* is moderately abundant. Three subtypes were distinguished by the numerical analysis: the Festuca ovina variant, the Trientalis variant and the Carex brunnescens variant. The first two variants are more chionophobous and have their closest previously described counterparts in Sikilsdalen, the Festuca ovina-Cetraria nivalis sociation of Nordhagen (1943), whereas the last-mentioned variant is more chionophilous and resembles the middle oroarctic heaths of Sylene. The Festuca ovina variant prevails at somewhat lower altitudes than the Trientalis variant.

Diagnostic features: The field layer is dominated by *Juncus trifidus*, alone or together with *Cassiope tetragona, Festuca ovina* and/or *Salix herbacea*. The bottom layer is dominated by *Cetraria ericetorum, C. nivalis* and/or *C. islandica*.

6.2. *Empetrum-Phyllodoce-Alectoria type* (EPAT)

This community type can be regarded as an equivalent of deflation heaths (AAT, ELT) of lower altitudes. However, middle oroarctic ridges are so stony that they accumulate some snow or they become covered by "cauliflower ice" in winter. Thus, genuine deflation surfaces do not normally develop. Instead, extreme ridge sites become dominated by *Alectoria nigricans*, somewhat less extreme ones by *Cetraria nivalis*. The dwarf shrub cover is patchy, consisting mainly of *Empetrum hermaphroditum*, *Phyllodoce caerulea* and/or *Vaccinium vitis-idaea*.

Diagnostic features: This is the only community type where *Alectoria nigricans* is actually a dominant or at least a co-dominant. Lichens are clearly dominating, with vascular plants occurring patchwise. Graminoids occur sparsely if at all. *Arctostaphylos alpina*, *Betula nana*, *Diapensia lapponica* and *Loiseleuria procumbens* are absent.

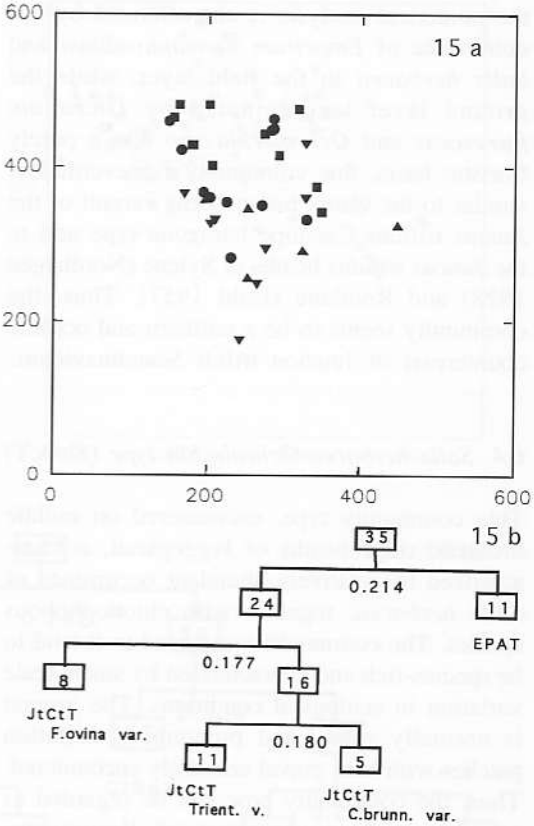


Fig. 15a–b. DCA scattergrams (15a) and TWINSPAN dendrograms for (15b) the vegetation data from subareas 2–6 within the Juncus trifidus-Cassiope tetragona group. Letters in parentheses show the symbols of the community types in the ordination figures. Juncus trifidus-Cassiope tetragona type (JtCtT): ▼ Festuca ovina variant, ▲ Carex brunnescens variant, ■ Trientalis variant; ● Empetrum-Phyllodoce-Alectoria type (EPAT).

6.3. *The Salix herbacea-Empetrum type* (ShET)

In the Ivggegáisat mountains, middle oroarctic *Juncus trifidus* grass heaths only exist if the concept is interpreted liberally. *Juncus trifidus* is present in the middle oroarctic heaths, but only with modest frequency (27%) and mean cover (1.0%). Instead, the middle oroarctic weakly chionophobous heath type identified by the numerical analysis is characterized by co-dominance of *Empetrum hermaphroditum* and *Salix herbacea* in the field layer, while the ground layer is dominated by *Dicranum fuscescens* and *Ochrolechia* spp. On a purely floristic basis, this community is nevertheless similar to the Carex brunnescens variant of the Juncus trifidus-Cassiope tetragona type and to the *Juncus trifidus* heaths of Sylene (Nordhagen 1928) and Rondane (Dahl 1957). Thus, the community seems to be a northern and oceanic counterpart of Juncion trifidi Scandinavicum.

6.4. *Salix herbacea-Ochrolechia type* (ShOcT)

This community type, encountered on middle oroarctic ridge heaths of Ivggegáisat, is characterized by relatively abundant occurrence of *Salix herbacea,* together with chionophobous species. The communities assigned to it tend to be species-rich and characterized by small-scale variation in ecological conditions. The ground is normally stony, and pronounced deflation patches with bare gravel are rarely encountered. Thus, the community type can be regarded as a suboceanic counterpart of Empetrum-Phyllodoce-Alectoria type.

Diagnostic features: This community type resembles the Ochrolechia type encountered at lower altitudes (see section 3.3.), but is distinguished from it by relatively high (>5%) cover values of *Salix herbacea*, low cover values of *Dicranum fuscescens* and *Empetrum hermaphroditum*, and absence of *Diapensia lapponica* and *Vaccinium uliginosum*. Conversely, *Cassiope hypnoides*, restricted to snow-beds at lower altitudes, is a frequent constituent, as are *Cassiope tetragona* and *Luzula confusa*.

7. **Luzula confusa group**

Vegetational patterns in the Luzula confusa group are so diffuse that the concept of community type must be used with caution. For the most part, the "communities" assigned to this group are but tiny vegetation fragments encountered on ridges and high altitude plateaux characterized by intense cryoperturbation. The distribution of the communities along the two main DCA axes is broad and diffuse (Figs. 6 and 16), indicating that they are distinguished from each other in a manner corresponding to neither altitude nor topography (Appendix 7, Figs. 6, 16a and b).

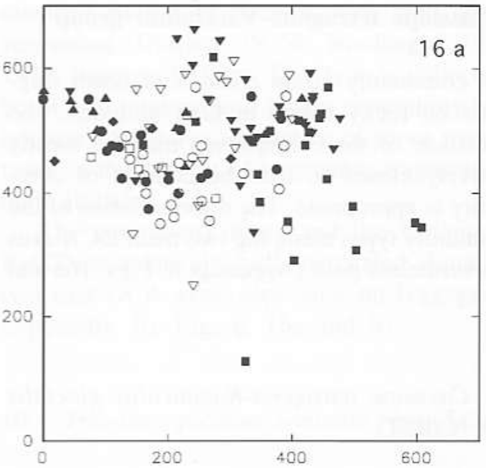
7.1. *Luzula confusa-Cetraria nivalis type* (LcCnT)

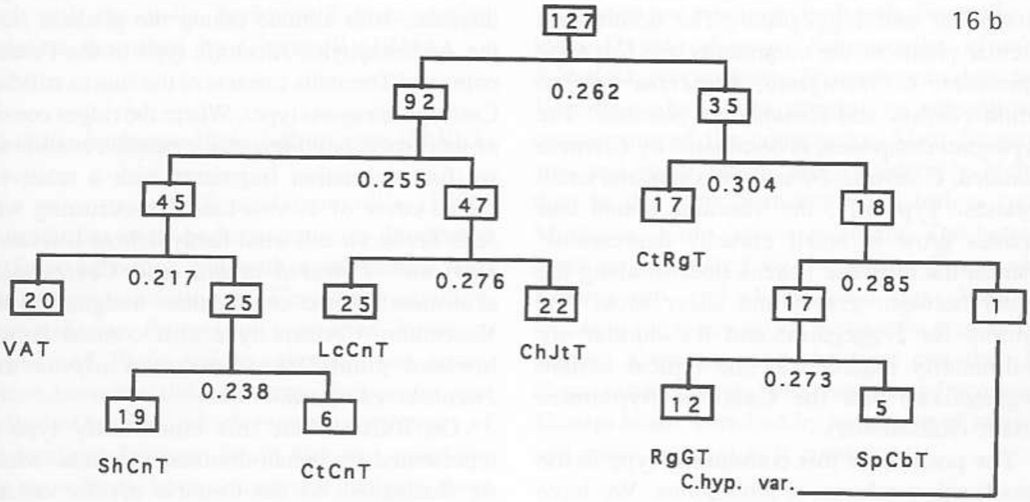
Wind-exposed sites with soil are subjected to severe cryoturbation (e.g. formation of frost-boil surfaces). The only vascular plant that appears to be adapted to cope with these conditions is *Luzula confusa*. In contact with its shoots, patches of *Cetraria nivalis* commonly occur. In the run with the Ivggegáisat material, communities of this kind formed one community type in the collective heath fragment group. The community is further subdivided into a variant with relatively abundant occurrence of *Racomitrium* spp. and a practically naked variant. (The latter is found in sites with more intense cryoperturbation). In the inland material, the computer program generated a community similar to the Racomitrium variant of the Luzula confusa-Cetraria nivalis type but with lower cover values of *Racomitrium* spp. *Cassiope hypnoides* (sparse in the suboceanic material) is a frequent and relatively abundant constituent in the inland community, which we call the Cassiope hypnoides variant of the Luzula confusa-Cetraria nivalis type.

7.2. *Cassiope hypnoides-Juncus trifidus type* (ChJtT)

The inland mountains also harbour another high-altitude heath community with copious occurrence of *Cassiope hypnoides.* In this community the cover values of *Cetraria nivalis* and *Luzula confusa* are relatively low, and *Juncus trifidus* is the characteristic graminoid. This type has affinities to the Luzuleto-Cesietum described by Dahl (1957) from Rondane, except that in Dahl's material fruticose lichens (especially *Cetraria*

Fig. 16a–b. DCA scattergrams (16a) and TWINSPAN dendrograms (16b) for the vegetation data from subareas 2–6 for high-altitude vegetation. Letters in parentheses show the symbols of the community types in the figures. ◆ Salix polaris-Carex bigelowii type (SpCbT); ▲ Ranunculus glacialis-Gymnomitrion type (RgGT): Cassiope hypnoides variant; ● Cassiope tetragona-Ranunculus glacialis type (CtRgT); ▼ Luzula confusa-Cetraria nivalis type (LcCnT): Cassiope hypnoides variant; ■ Cassiope hypnoides-Juncus tridifus type (ChJtT); ∇ Salix herbacea-Cetraria nivalis type (ShCnT); ❑ Cassiope tetragona-Cetraria nivalis type; ❍ Vaccinium-Alectoria type (VAT).





delisei) are much more abundant and *Cassiope hypnoides* is much less so.

7.3. *Luzula confusa-Saxifraga tenuis type* (LcStT)

A heterogenous community type connected to the Luzula confusa group was identified in the material from Ivggegáisat. The characteristic feature of this type is the prevalence of *Polytrichastrum sexangulare* and *Gymnomitrion* spp. in the cryptogam component. However, the two most frequent vascular plants — *Luzula confusa* and *Saxifraga nivalis* — are not snow-bed species. The outstanding feature of this community is the low cover of all plants. Many plots harbour just one shoot of *Saxifraga tenuis*, or one tuft of *Luzula confusa* shoots on what at first glance looks like bare gravel. The scanty cryptogam component normally occurs in close contact to the vascular plant. It is thus a question of a "non-community", found in the most extreme environments where interactions between plants are weak due to the combination of stressful conditions and physical disturbance (cf. Muller 1952, Savile 1960, Komárková 1993).

8. **Cassiope tetragona-Vaccinium group**

This community group consists of heath fragments on rocky ridges at high altitudes. The vegetation of these fragments may be locally relatively closed so that the concept of community is appropriate. The differentiation of the community types along the two main DCA axes is nevertheless poor (Appendix 8, Figs. 16a and b).

8.1. *Cassiope tetragona-Ranunculus glacialis type* (CtRgT)

This community type encompasses heath fragments enocountered at high altitudes on Ráisduottar and Ivggegáisat. The dominating vascular plants of the community are *Cassiope hypnoides*, *C. tetragona*, *Huperzia selago*, *Luzula confusa* and *Ranunculus glacialis*. The cryptogam component is dominated by *Cetraria islandica*, *C. nivalis*, *Ochrolechia* spp. and small hepatics. Typically, the vascular plants and hepatics grow in small gravelly depressions, whereas the fruticose lichens flourish along the border between gravel and sheer rock. The material for Ivggegáisat and Ráisduottar are preliminarily regarded as the typical variant (Ivggegáisat) and the Cassiope hypnoides variant (Ráisduottar).

The position of this community type in the classification scheme is ambiguous. We have assigned it to the Cassiope tetragona-Vaccinium group on the basis of the analysis of the suboceanic data set, but in the numerical treatment of the continental-subcontinental material, it was joined to the Ranunculus glacialis group.

8.2. *Salix herbacea-Cetraria nivalis type* (ShCnT)

This community type, which is encountered on high altitude ridges of Gáisat and Ráisduottar, embraces vegetation fragments dominated by *Cetraria nigricans*, *C. nivalis*, *Gymnomitrion* spp., *Ochrolechia* spp. and *Salix herbacea*.

8.3. *Cassiope tetragona-Cetraria nivalis type* (CtCnT)

Wind-exposed summits on Ráisduottar at altitudes between 1 000 and 1 200 m harbour vegetation fragments heavily dominated by *Cassiope tetragona*, which is entirely absent from the Salix herbacea-Cetraria nivalis type. The cover of *Cetraria nivalis* is only about 1%. The community type has thus an entirely different structural physiognomy from the Salix herbacea-Cetraria nivalis type.

8.4. *Vaccinium-Alectoria type* (VAT)

The abundance of *Vaccinium vitis-idaea* on ridges increases with altitude (along the gradient from the Arctostaphylos-Alectoria type to the Festuca ovina and Trientalis variants of the Juncus trifidus-Cassiope tetragona type). Where the ridges consist of sheer rock, providing stable edaphic conditions, we find vegetation fragments with a relatively closed cover of *V. vitis-idaea* co-occurring with *Salix herbacea* and wind-hardy lichens (*Alectoria nigricans*, *Cetraria nivalis* and *Coelocaulon aculeatum*). Some communities assigned to the Vaccinium-Alectoria type also contain typical lowland plants like *Saussurea alpina* and *Trientalis europaea*.

On Ráisduottar, this community type is represented by lichen-dominated stands, which we distinguish as the Cetraria nivalis variant. The stands sampled on Ivggegáisat, to be distinguished as the Vaccinium variant, are dominated by *V. vitis-idaea*. The Vaccinium-Alectoria type closely resembles the Empetrum-Phyllodoce-Alectoria type and could be regarded as its variant. On Ráisduottar, where the two types co-occur, the Vaccinium-Alectoria type is found on ridges with sheer rock, whereas the Empetrum-Phyllodoce-Alectoria type is encountered on ridges covered by boulders.

9. **The Salix herbacea-Kiaeria group**

The Salix herbacea-Kiaeria community group consists of late snow-bed vegetation at middle altitudes. Owing to our sampling method, such communities are poorly represented in our material. Moreover, all plots assigned to this group were on Ivggegáisat, where snow-fall is sufficient to create late snow-beds even in small-scale topographic gradients. The two community types differentiate well along the second (topographic) DCA axis (Fig. 6) and can be readily interpreted in terms of the vegetational gradients as discussed by Gjærevoll (1956) (Appendix 9, Fig. 6, 16a and b).

9.1. *Salix herbacea-Kiaeria type* (ShKiT, Gjærevoll 1956)

This community type can be regarded as identical with the Salix herbacea-Kiaeria starkei sociation described by Gjærevoll (1956).

9.2. *Salix herbacea-Viola biflora type* (ShVbT)

It is easy to infer from Gjærevoll's (1956) material that snow-bed communities dominated by *Salix herbacea*, but with a substantial herb component consisting of *Cerastium alpinum*, *Oxyria digyna*, *Polygonum viviparum*, *Veronica alpina* and *Viola biflora*, should exist somewhere between the alliances Herbaceon and Stellario-Oxyrion, which represent extremes of the gradient between heath-like and meadow-like snow-beds. In our numerical analysis, these transitory communities emerged as a distinct community type, which nevertheless should be regarded as tentative until the entire gradient between heath and meadow snow-beds has been adequately sampled.

10. **The Ranunculus glacialis group**

The group includes two previously undescribed, relatively species-rich community types — the Trisetum spicatum-Sanionia type and the Salix polaris-Carex bigelowii type — encountered at the altitudinal limit of continuous vegetation. A third member is the Ranunculus glacialis-Gymnonitrion type which is discussed in several classical studies of Scandinavian high alpine vegetation (DuRietz 1925b, Nordhagen 1928, 1943, Gjærevoll 1956). This type is collective; but it was retained as a single community type because of the limited utility of more narrow types in the context of vegetation fragments at high altitudes.

The community types and the variants of RgGT are relatively well segregated along the two first DCA axes, especially on Ivggegáisat (Appendix 10, Fig. 6, 16a and b).

10.1. *Trisetum spicatum-Sanionia type* (TsSaT)

The *Salix herbacea*-dominated snow-beds encountered at the upper limit of continuous vegetation are relatively herb-rich. Normally, at least *Oxyria digyna*, *Ranunculus nivalis*, *Sibbaldia procumbens*, *Trisetum spicatum* and *Veronica alpina* are present as subordinate constituents of the community. Their frequencies and cover values are considerably higher than in the Salix herbacea-Viola biflora type. Moreover, *Viola biflora* is absent. The bottom layer is dominated by *Dicranum fuscescens*, *Kiaeria* spp. and *Ochrolechia* spp.; *Sanionia uncinata* (or *S. nivalis*) is constantly present but seldom abundant, and the type can thus be characterized as a *Salix herbacea-Dicranum/Kiaeria* heath, enriched by indicators of moister and more nutrient-rich conditions.

10.2. *Salix polaris-Carex bigelowii type* (SpCbT)

We also encounter on Ráisduottar a relatively species-rich snow-bed community at the uppermost limit of continuous vegetation. The dominating vascular plants are *Cassiope tetragona* and *Salix polaris*, while the herbaeous component is normally represented by *Carex bigelowii*, *Festuca vivipara*, *Luzula confusa*, *Polygonum viviparum* and *Ranunculus glacialis*. The bottom layer is dominated by *Gymnomitrion* spp. Although there are obvious differences between this community type and the Trisetum spicatum-Sanionia type, they represent a basically similar phenomenon:

the occurrence of relatively species-rich vegetation at the upper limit of continuous vegetation. This 'alpine garden' phenomenon will be discussed in sections VIII and X.

10.3. *Ranunculus glacialis-Gymnomitrion type* (RgGT)

The high-altitude material of Ivggegáisat and Ráisduottar includes a community type with obvious snow-bed characteristics, with *Ranunculus glacialis* as the most conspicuous vascular plant. The bottom layer consists mainly of a thin cover of *Gymnomitrion* spp. and *Ochrolechia* spp. As defined by us, the community type encompasses Gjærevoll's (1956) Ranunculetum glacialis and also includes the naked Ranunculus glacialis association discussed by DuRietz (1925b).

This relatively collective community type is divided into five subtypes. The mossy variant is heavily cryptogam-dominated and encountered in depression sites immediately below the boulderfield limit. The mean cover of the dominating vascular plants (*Cassiope hypnoides, Luzula confusa, Ranunculus glacialis* and *Salix herbacea*) ranges only between 0.5 and 1.1%. The dominating cryptogams are *Ochrolechia* spp., *Kiaeria* spp. and *Gymnomitrion* spp. This variant corresponds to Gjærevoll's (1956) Ranunculus glacialis-Anthelia juratzkana-Gymnomitrion varians sociation.

Three more variants are encountered above the boulderfield limit on Ivggegáisat. These are placed rather far from the mossy variant by the ordination and classification procedures. However, the communities are floristically fairly similar, and there are no major differences in the composition of the field layer. The main difference lies in the entirely different abundance relationship between vascular plants and cryptogams. The fragments of Ranunculus glacialis-Gymnomitrion type encountered above the boulderfield limit are physiognomically dominated by vascular plants and at first glance seem devoid of cryptogams (see also Du Rietz 1925b), although the ground around the vascular plants normally has a thin cover of *Gymnomitrion* and *Ochrolechia* spp. The three 'naked' variants are distinguished on the basis of the vascular plant cover. One variant is dominated by Luzula confusa and thus roughly corresponds to Gjærevoll's (1956) Luzula confusa-Anthelia juratzkana-Gymnomitrion varians sociation. This variant, to be called the Luzula confusa variant of the Ranunculus glacialis-Gymnomitrion type (RgGT, Lc var), is encountered in sites subjected to intense cryoperturbation. The Oxyria variant of the Ranunculus glacialis-Gymnomitrion type (RgGT Ox var) in turn is characterized by relatively high diversity of vascular plants, the dominating species being *L. confusa*, *Oxyria digyna* and *Salix herbacea*. As such, it represents vegetation transitional between Ranunculus glacialis-Gymnomitrion type and Trisetum spicatum-Sanionia type. The Ranunculus glacialis variant (RgGT, Rg var), with *Solorina crocea* as the only relatively abundant cryptogam, corresponds to the 'naked' Ranunculus glacialis association of DuRietz (1925b).

In the chionophilous high altitude communities of the subcontinental Ráisduottar, *Ranunculus glacialis* occurred as a constant but subordinate constituent of vegetation fragments dominated by *Cassiope hypnoides* and *Gymnomitrion* spp. These communities are regarded as the Cassiope hypnoides variant of the Ranunculus glacialis-Gymnomitrion type (RgGT, Ch var).

VII. CONCEPTUAL ISSUES RELEVANT TO THE VEGETATION PATTERNS AND PLANT COMMUNITIES IN HEATH VEGETATION OF NORTHERN FENNOSCANDIA

1. **Objectivity of the vegetational units**

In any study of vegetational variation, it is a practical necessity to arrange the multitude of sample plots into a manageable number of community types, regardless of how continuous the vegetational gradients are in nature. The question whether or not natural discontinuities (or sections of environmental gradient with relatively rapid vegetational changes) occur, is nevertheless interesting. In a complete continuum, the cutoff points are subjective, and numerical analyses of independently sampled data sets are likely to yield different sets of community types. If on the other hand, the vegetational variation shows at least some degree of discontinuity, it is reasonable to suppose that traditional phytosociologists noticed these and defined their community types accordingly. In such a situation, numerical analyses of objectively sampled data should automatically produce community types resembling those described by traditional phytosociologists.

Except for snow-beds, where correspondence to Gjærevoll's (1956) system and to community types described by Nordhagen (1928,1943), Kalliola (1939) and Dahl (1957) is hardly better than expected by chance alone, our numerical analysis fairly faithfully recapitulated vegetation types described earlier for the same parts of the altitudinal and topographic gradients. The main exceptions were Haapasaari's (1988) altitudinal and climatic parallel types, which seem to represent subjectively chosen end points of a perfect continuum, where our material chiefly represents intermediate situations. Likewise, the higher order structure created by our analysis exhibited similarities with traditional phytosociological schemes. Thus, the correspondence between our results and previous classifications of north boreal and (oro)arctic heath types is good enough to suggest that we are not dealing with a completely amorphous continuum conforming to the ideas of the Wisconsin school (Whittaker 1956, Bray & Curtis 1957, McIntosh 1967, Austin 1985, Austin & Smith 1989).

At the same time, there were no clear-cut plant associations, either, especially not in the continental material. The lines of demarcation between different community types are so diffuse that the visual impression provided by two-dimensional ordination figures is much closer to the continuum view than to the viewpoints of plant sociologists such as Du Rietz (1921, 1922, 1924).

The existence of some objective structure in the vegetational patterns is probably due to various thresholds. Some are caused by the external environment (e.g. the boulderfield limit), while others can be regarded as due to the plants themselves. The timberline is the clearest example of thresholds of the latter type: where the birches disappear, the environmental conditions of field layer plants change radically, due to increased light intensity and wind velocity at ground level and changes in snow distribution. Other more subtle limits of the same type may occur as well (e.g. the topographic and altitudinal limits of erect dwarf shrubs), especially in oceanic heaths, where a few dwarf shrub species often monopolize the site and strongly influence the environmental conditions of other plants. Such thresholds were discussed almost 100 years ago by Cajander (1905, 1909), see also Dahl (1957) and (Shipley & Keddy 1987).

2. The concept of zonal vegetation in arctic and oroarctic areas

The conventional approach in geobotany is to distinguish a zonal community type prevailing in habitats where edaphic conditions are not extreme in any sense (Cajander 1909, 1926, Kujala 1926, Kalela 1960). The regional plant community is at least to some extent equivalent to the climatic climax of Clements (1916): a community towards which the remaining ones are converging (Cowless 1899), although so slowly that also the other community types can be regarded as practically stable.

This approach works quite well in the boreal forests of northernmost Fennoscandia (Hämet–Ahti 1963). There have also been some attempts to apply it to the arctic and oroarctic areas (Elvebakk 1985). Haapasaari (1988) chose a somewhat different approach. He described parallel community types for chionophilous and chionophobous sites without implying that one would be more regional than another. The Scandinavian classics (Nordhagen 1928, 1943, Dahl 1957) go one step further by describing sequences of varying numbers of community types from deflation heaths to snow-beds. Each altitudinal zone is characterized by some sequence of community types, while individual types may occur in more than one altitudinal zone. This approach implies that the oroarctic vegetation should be treated as a community complex in a manner analogous to the standard Nordic approach to wetland vegetation (Tuomikoski 1942, Sjörs 1948, Ruuhijärvi 1960, Eurola et al. 1984, Eurola & Holappa 1985).

The distribution of our community types along topographic and altitudinal gradients (Figs. 6 and 7) suggests that the community complex approach is the most practical one. It is usually difficult to find one or two community types covering such wide sections of topographic gradients that they could be regarded as more regional or zonal than other types. Moreover, the identification of a single zonal/regional community type is not just a practical problem. Uneven distribution of snow is an essential characteristic of all arctic and alpine areas with any degree of topographic variation, as long ago pointed out by Vestergren (1902) (see also Økland & Bendiksen 1985: 33–35). In areas where the land is level enough to make the snow cover relatively even, the lack of topographic variation itself is likely to influence edaphic conditions. It may thus be entirely misleading to identify any constituent of the topographic community sequences as the community that would prevail on perfectly level tundra.

Our observations of the vegetation in the lowland basins of Čakčaduottar, Čáhppisduottar and Jávrisduottar suggest that areas of perfectly level tundra are indeed characterized by vegetation that does not occur as a constituent of the topographic community sequences. Typically, the vegetation of such basins looks like being transitional between lichen heaths and bogs. The surface is hummocky, and bog plants (especially: *Eriophorum vaginatum*) grow in hollows. The hummocks, in turn, are dominated by *Cladina* spp. and have extremely scanty vascular plant cover, with the normally dominating species being *Vaccinium uliginosum* and *V. vitis-idaea*. The community thus shows similarities to the "tussock tundra", which is typical for those parts of arctic Russia and the North American arctic that lack small-scale topographic variation, parts such as unglaciated areas and areas subjected to recent sedimentation of fine soil particles (see Polunin 1948, Churchill 1955, Churchill & Hanson 1958, Tihomirov 1963, Raup 1965, Oberbauer & Miller 1979).

Such almost level topographic conditions represent by themselves an exceptional rather than a typical situation. Eurola (pers. comm.) has pointed out that if regional vegetations were to be defined as the community that prevails on perfectly level ground, then our concept of regional community types in the boreal zone also would have to be re-defined. For example, in the Bothnian coastlands, the regional forest type would be intermediate between forests and bogs. Thus, the vegetation complex approach to tundra vegetation is not only more practical than a search for a single regional community, but also more compatible with prevailing treatment of boreal vegetation (see also Kalela 1960).

VIII. TOPOGRAPHIC AND ALTITUDINAL PATTERNS IN OLIGOTROPHIC HEATH VEGETATION OF NORTHERN FENNOSCANDIA

The occurrence of different community types in our sample plot sequences is summarized in Fig. 18:1–6. At first glance, the main message of the material is heterogeneity. We rarely find situations where one community type prevails on chionophobous sites and another on chionophilous ones, as proposed by Haapasaari (1988). To some extent, this can be attributed to irregularities in the topography of the sampled hillocks and to differences in their steepness. There are also macrotopographical differences: some hillocks are on steep slopes, while others lie near mountain tops or on flat terraces. When these local features are eliminated, the material can be summarized in the form of a few idealized community patterns to be discussed below (Figs. 19, 25, 26 and 30).

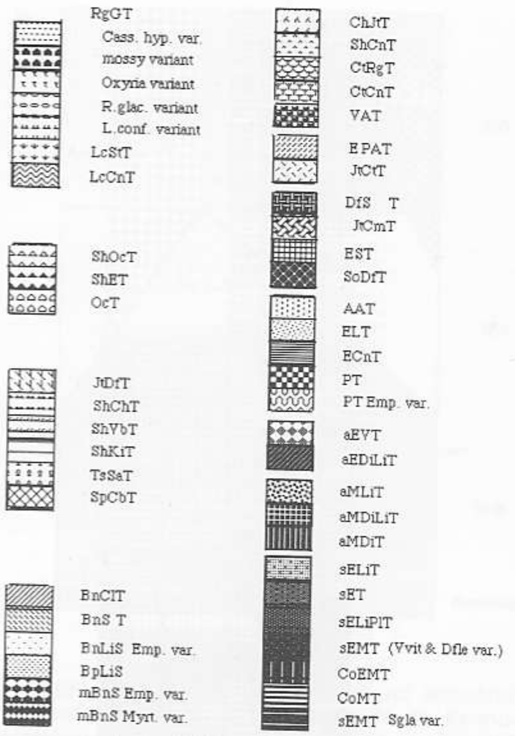


Fig. 17. Key to symbols used in the Figs. 18, 19, 25, 26 and 30. sEMT Sgla var. = subalpine Empetrum-Myrtillus type, Salix glauca variant; CoMT = Cornus-Myrtillus type; CoEMT = Cornus-Empetrum-Myrtillus type, sEMT (Vvit & Dfle var.) = subalpine Empetrum-Myrtillus type (Vaccinium vitis-idaea and Deschampsia flexuosa variants); sELiPlT = subalpine Empetrum-Lichenes-Pleurozium type sELiPlT; sET = subalpine Empetrum type; sELiT = subalpine Empetrum-Lichenes type; mBnPlT = mossy Betula nana scrub, Myrt var. = Myrtillus variant, Emp var. = Empetrum variant; BnLiS = Betula nana-Lichenes scrub; BpLiS = Betula pubescens-Lichenes scrub; BnClT = Betula nana-Cladina type; BnST = Betula nana-Stereocaulon type; aMLiT = arctic-hemiarctic Myrtillus-Lichenes type; aMDiLiT = arctic-hemiarctic Myrtillus-Dicranum-Lichenes type; aMDiT = arctic-hemiarctic Myrtillus-Dicranum type; aEDiLiT = arctic Empetrum-Dicranum-Lichenes type; aEVT = arctic Empetrum-Vaccinium type; PT = Phyllodoce type; PT Emp var. = Phyllodoce type, Empetrum variant; ECnT = Empetrum-Cetraria nivalis type; ELT = Empetrum-Loiseleuria type; AAT = Arctostaphylos-Alectoria type; DfST = Deschampsia flexuosa-Stereocaulon type; JtCmT = Juncus trifidus-Cladina mitis type; EST = Empetrum-Stereocaulon type; SoDfT = Solidago-Deschampsia flexuosa type, Rubus chamaemorus variant; JtCtT = Juncus trifidus-Cassiope tetragona type; EPAT = Empetrum-Phyllodoce-Alectoria type; VAT = Vaccinium-Alectoria type; CtCnT = Cassiope tetragona-Cetraria nivalis type; CtRgT = Cassiope tetragona-Ranunculus glacialis type; ShCnT = Salix herbacea-Cetraria nivalis type; ChJtT = Cassiope hypnoides-Juncus tridifus type; SpCbT = Salix polaris-Carex bigelowii type; TsSaT = Trisetum spicatum-Sanionia type; ShKiT = Salix herbacea-Kiaeria type; ShVbT = Salix herbacea-Viola biflora type; ShChT = Salix herbacea-Cassiope hypnoides type; JtDfT = Juncus trifidus-Deschampsia flexuosa type; OcT = Ochrolechia type; ShET = Salix herbacea-Empetrum type; ShOcT = Salix herbacea-Ochrolechia type; LcCnT = Luzula confusa-Cetraria nivalis type; LcStT = Luzula confusa-Saxifraga tenuis type; RgGT = Ranunculus glacialis-Gymnomitrion type (Cassiope hypnoides, mossy, Oxyria, Ranunculus glacialis and Luzula confusa variants).

1. **Continental pattern**

Genuine boreal birch forests are rare in the Čakčaduottar and Jávrisduottar area. Even the valley between the two tundras is largely occupied by a mosaic of stunted woodlands and dwarf birch scrublands (Haapasaari 1988). However, Hämet–Ahti's (1963) material from adjacent boreal valleys suggests that the subalpine Empetrum-Lichenes type is the overwhelmingly dominating forest type both on glacial till soils and on glacifluvial formations. Birch forests of the subalpine Empetrum-Lichenes type also prevail on the level forelands of Dárju (Fig. 18:3).

At an altitude of about 300 m a.s.l. the continuous birch forests give way to complexes of woodland and scrubland. At first this is expressed by the appearence of patches of the Betula nana-Lichenes scrub type in depressions and along bog margins. At the same altitudes, birch forests on wind-exposed hilltops get shrubby and acquire some characteristics of the Empetrum-Loiseleuria type.

With increasing altitude, the topographic range of birch woodlands decreases. At altitudes of 400–460 m, birch woodlands become restricted to south-facing slopes and to moist and nutrient-rich sites. Ridges are occupied by seemingly lower (oro)arctic chionophobous

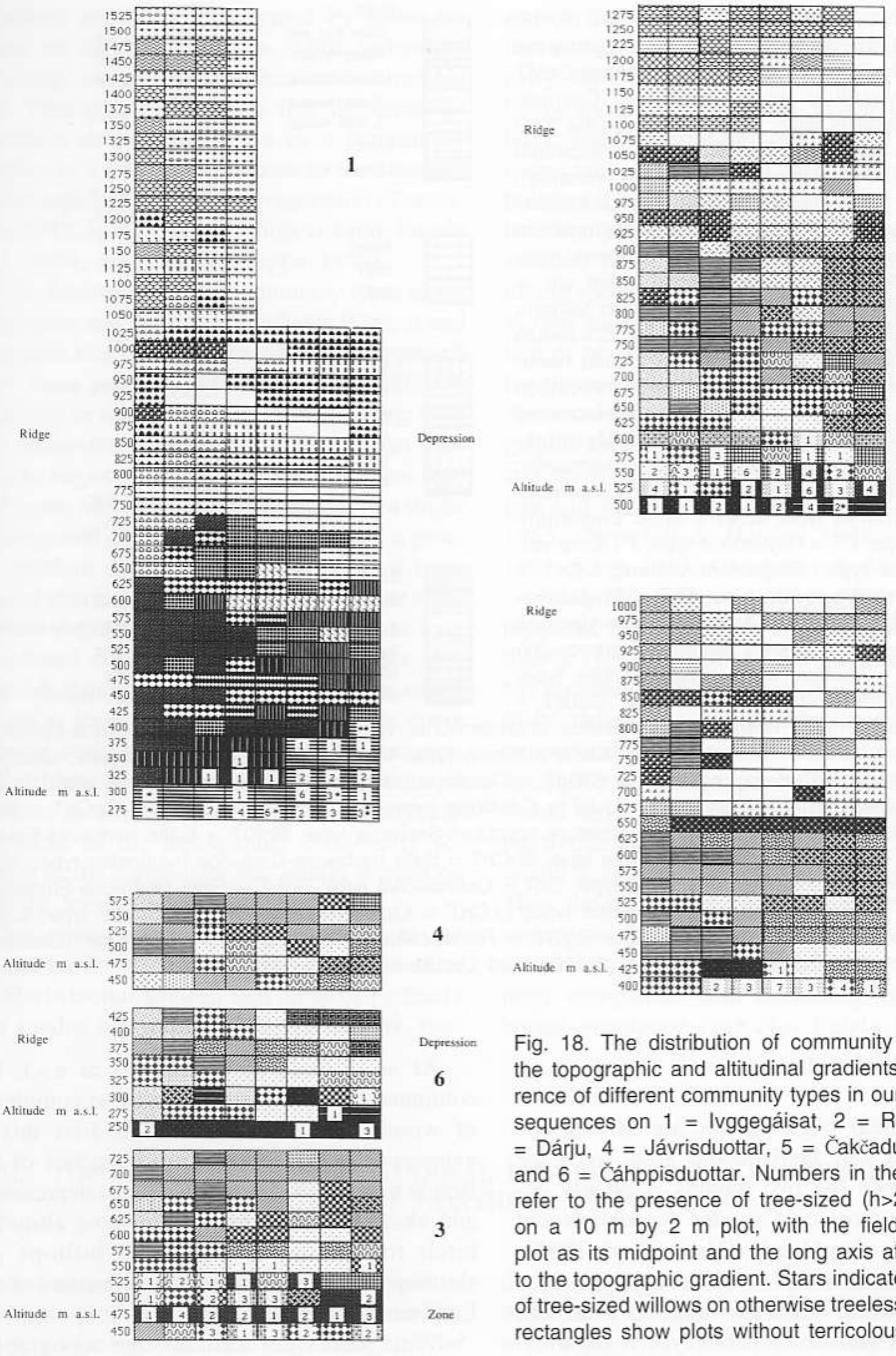


Fig. 18. The distribution of community types along the topographic and altitudinal gradients. The occurrence of different community types in our sample plot sequences on 1 = Ivggegáisat, 2 = Ráisduottar, 3 = Dárju, 4 = Jávrisduottar, 5 = Čakčaduottar–Gáisat and 6 = Čáhppisduottar. Numbers in the illustrations refer to the presence of tree-sized (h>2 m) birches on a 10 m by 2 m plot, with the field layer study plot as its midpoint and the long axis at slight angle to the topographic gradient. Stars indicate the number of tree-sized willows on otherwise treeless plots. Blank rectangles show plots without terricolous vegetation.

heaths. Patches of mountain birch scrubland (the Betula pubescens-Lichenes scrub type) occur on slopes, while depressions are occupied by dwarf birch scrublands (the Betula nana-Lichenes scrub type) (see fig. 3 in Oksanen et al. 1995). In areas that are summer-grazed by reindeer, Betula pubescens-Lichenes scrublands have been largely eliminated (Oksanen et al. 1995).

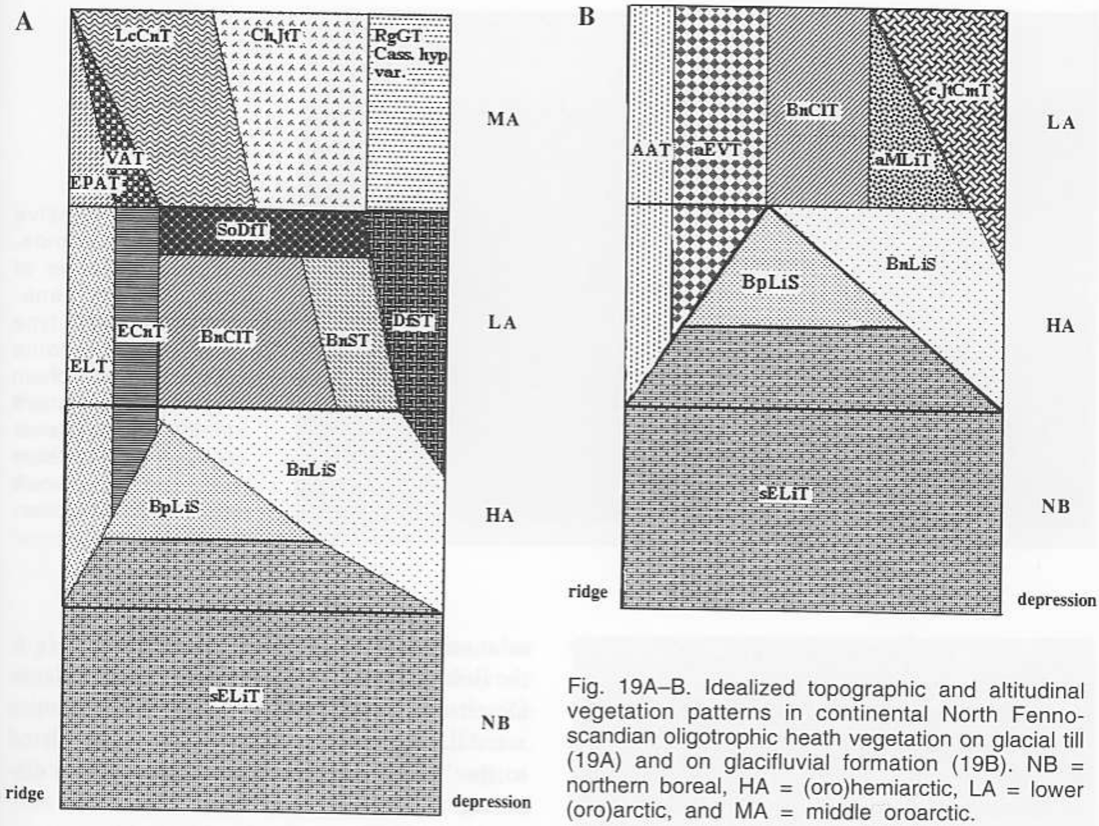


Fig. 19A–B. Idealized topographic and altitudinal vegetation patterns in continental North Fennoscandian oligotrophic heath vegetation on glacial till (19A) and on glacifluvial formation (19B). NB = northern boreal, HA = (oro)hemiarctic, LA = lower (oro)arctic, and MA = middle oroarctic.

There, the uppermost indicators of hemiarctic conditions are scattered mountain birches (see fig. 7 in Oksanen et al. 1995) and *Betula nana* scrublands.

At altitudes where the woodlands become discontinuous, edaphic conditions begin to have an impact on the topographic community pattern. On glacifluvial formations, extreme ridge sites are occupied by deflation heaths of the Arctostaphylos-Alectoria type (Fig. 19B), whereas on rocky ridges the Empetrum-Loiseleuria type prevails (Fig. 19A) On till-covered hills the Empetrum-Cetraria nivalis type occupies somewhat less extreme ridge sites. On glaciofluvial formations the Empetrum-Cetraria nivalis type is at least partially replaced by the arctic-hemiarctic Empetrum-Vaccinium type. These chionophobous heath types occur both in the (oro)hemiarctic zone, where they grade into *Betula nana* or *B. pubescens* scrublands, and in the lower oroarctic zone, where they grade into the Betula nana-Cladina type (Figs. 20 and 21). On glaciofluvial formations the Betula nana-Cladina type is frequently replaced by the arctic-hemiarctic Myrtillus-Lichenes type. Lower slopes of hills covered by glacial till are normally occupied by the Betula nana-Stereocaulon type, which grades into snow-beds of Deschampsia flexuosa-Stereocaulon type. Well-drained snow-bed sites are occupied by the Juncus trifidus-Cladina mitis type (Fig. 22).

The inland tundras are characterized by gentle topography. Thus, heaths of the Betula nana-Cladina type and the Betula nana-Stereocaulon type are the overwhelmingly dominating community types throughout the tundra landscape (Table 2, Figs. 20 and 23, see also Heikkinen & Kalliola 1988). Deflation heaths of the Empetrum-Loiseleuria type are only common in the vicinity of major valleys, where slopes are steeper and ridges sharper than on the plateaux. The occurrence of the Arctostaphylos-Alectoria type is virtually restricted to flat-topped glaciofluvial formations, where fairly extensive stands are encountered.

Fig. 20. Extensive transitional stands, showing features of both Betula nana-Lichenes scrub type and the Cladonia coccifera-Polytrichum hyperboreum variant of the Betula nana-Cladina type at 520 m a.s.l. on the Finnish side of Jávrisduottar.

Snow-beds are only a minor constituent of the landscape.

Within the Fennoscandian Shield, even the highest part of the inland tundras remain within the lower oroarctic zone. At the northern edge of Čakčaduottar, lichen-dominated continental heaths come in contact with the Gáisa formation, with summits rising to altitudes of about 1 000–1 150 m. Here, lichen heaths are abruptly replaced by boulderfields at an altitude of about 600 m (Fig. 24). The lowermost part of the boulderfield zone is characterized by patches of relatively grass- and herb-rich vegetation (e.g. the Rubus chamaemorus variant of the Solidago-Deschampsia flexuosa type). These communities are still, clearly, lower oroarctic. They are related to the "alpine garden" phenomenon to be discussed in section X.

Table 2. Areas occupied by each main community group as percentage of total area sampled in line transects of 30 km.

Community group	(Oro-) hemiarctic	Lower oroarctic
Arctostaphylos group	20	14
Betula nana group	42	43
Phyllodoce-Myrtillus group	7.6	4.9
Juncus trifidus-Salix herbacea group	< 0.1	8.6
dry meadows	2.6	2.0
moist meadows and willow thickets	1.1	0.1
bogs	26	27

Above 650 m, the boulderfields are extremely barren, except for saxicolous lichens and tiny patches of the Luzula confusa-Cetraria nivalis type. Fragments assigned to the Cassiope hypnoides-Juncus trifidus and Salix herbacea-*Cetraria nivalis* types are encountered in sites where the vegetation fragments are larger. Only two of the plots sampled in the boulderfield zone were assigned to snow-bed communities, probably on the basis of the cryptogam vegetation there. The characteristic vascular plants of middle oroarctic snow-beds (e.g. *Cardamine bellidifolia*, *Oxyria digyna* and *Ranunculus glacialis*) are extremely rare and were not found on any plot sampled by us.

Up to 925 m, patches of lichen-rich dwarf shrub heath (the Vaccinium-Alectoria type and Empetrum-Phyllodoce-Alectoria type) are encountered on rocky ridges. These communities are also found on more oceanic mountains, where they belong to the middle oroarctic community complex (see below). Thus, boulderfields below the 900 m contour can be

Fig. 21. Heath of the Betula nana-Cladina type with patches of the Betula nana-Stereocaulon type in depressions, Čearro plateau.

regarded as middle oroarctic. The absence of these indicator communities from the plots we sampled at 950, 975 and 1 000 m may be due to the marked convexity of the terrain. Hence, the occurrence of truly upper oroarctic vegetation within the Gáisa formation must be regarded as uncertain.

2. **Pattern on low inland mountains**

The vegetation on the slopes of Dárju between 500 and 650 m, does not conform to the pattern described above, suggesting that vegetation patterns on the low inland mountains are inherently different from those encountered on inland plateaux. Although the inland mountains were poorly represented in our material, Kalliola (1939) and Haapasaari (1988) covered them extensively, and the vegetational patterns of Pallas-Ounastunturi area have been documented by Eeronheimo et al. 1992 (in figs. 15–17). Idealized vegetation patterns derived from these sources and from Dárju are summarized in Fig. 25.

The uppermost forests of mountain slopes tend to be more mesic than the forests encountered in the valleys of interior Finnmark. In the orohemiarctic and lower oroarctic zones of mountains, moderately chionophobous sites are occupied by the Empetrum variant of the Phyllodoce type or by the arctic-hemiarctic Empetrum-Vaccinium type. Moderately

Fig. 22. The Juncus trifidus-Cladina mitis type on a well-drained slope.

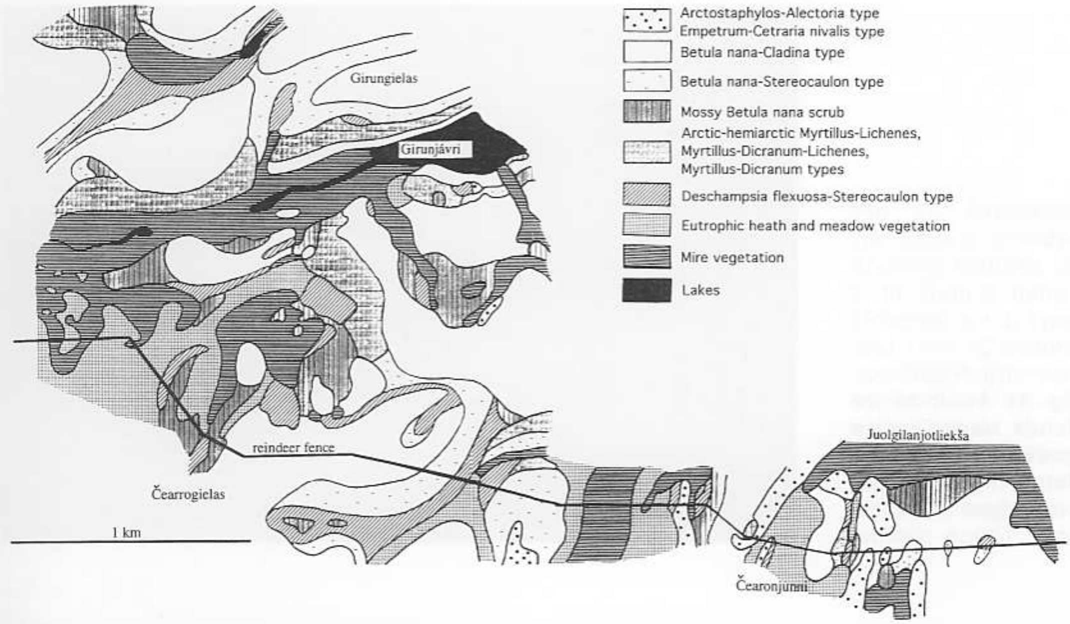


Fig. 23. Vegetation map for the northern part of the Cearro highlands on Čakčaduottar.

Fig. 24. Borderline terrain between the lower oroarctic habitat complex and the boulderfield zone on Gáisat at 550 m a.s.l.

chionophilous sites harbour the typical variant of the Phyllodoce type or the arctic Myrtillus-Lichenes type, which grade into snow-beds of Juncus trifidus-Cladina mitis type. On hills with gentle topography and at lower altitudes, this community type is replaced by the Empetrum-Stereocaulon type or the Empetrum variant of Phyllodoce type, which can thus occur both on ridges and in depressions. *Phyllodoce* heaths seem to occur in more convex and wind-exposed terrain, whereas the arctic Myrtillus-Lichenes type and the arctic-hemiarctic Empetrum-Vaccinium type are most frequently encountered on steeper slopes. On mountains with relatively gentle topography, the two variants of the Phyllodoce type thus frequently cover the entire range of topographic conditions within the lower oroarctic zone.

The existence of truly middle oroarctic conditions on the isolated mountains of our study area is doubtful, although both Kalliola (1939) and Haapasaari (1988) regard the highest parts of Pallastunturi (summit altitude 807 m) as middle oroarctic. However, the relatively isolated Roahppi mountain (summit altitude 944 m) northwest of Dárju can be regarded as middle oroarctic above the 850 m countour. The middle

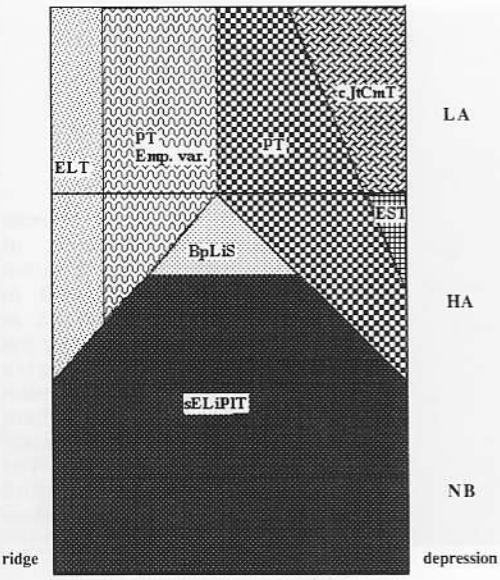


Fig. 25. Idealized topographic and altitudinal vegetation pattern on low inland mountains. Codes: see Fig. 17.

oroarctic vegetation complex seems to be dominated by ridge heaths of Empetrum-Phyllodoce-Alectoria type and snow-beds of Juncus trifidus-Cladina mitis type (Piirainen & Piirainen 1991). Similar topographic patterns have been documented by Eeronheimo et al. (in prep.) around the summit of Pallastunturi.

3. **Subcontinental pattern**

The vegetational patterns on the eastern slopes of Ráisduottar (Fig. 26) begin rather similarly to the patterns on isolated inland mountains. In the neighbourhoods of the Scandinavian mountain chain, lichen-dominated mountain birch forests are replaced by somewhat less xeric forest types, mainly by the subalpine Empetrum-Myrtillus type (Hämet–Ahti 1963). Slightly above the 500 m contour, forests become discontinuous. Deflation heaths of Empetrum-Loiseleuria type appear on extreme ridges, with heaths of arctic-hemiarctic Empetrum-Vaccinium type on slightly less exposed sites. Depressions are occupied by the Empetrum variant of Phyllodoce type or by the Empetrum-Stereocaulon type. The uppermost birch woodlands represent the subalpine Empetrum-Lichens type, which suggests that the prevalence of subalpine Empetrum-Myrtillus type in the lowermost sample plot transects may be a local phenomenon, caused by the lack of obstacles between the Galpajávri (Kilpisjärvi) basin and passes extending into the oceanic areas to the west and north of Galpajávri (see Hämet–Ahti 1963: 100–102).

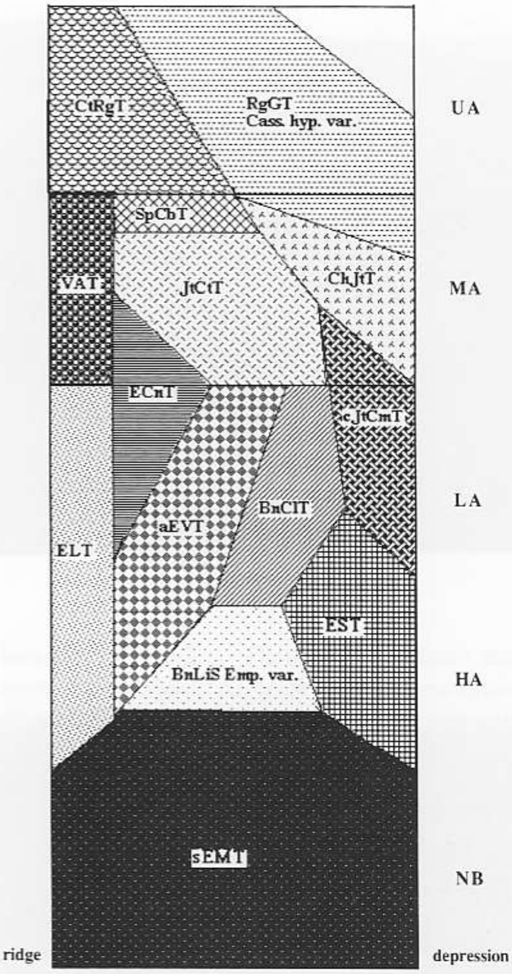


Fig. 26. Idealized topographic and altitudinal pattern in subcontinental oligotrophic heath vegetation in northern Fennoscandia. The pattern is based on the material from Ráisduottar. Blank shows permanent snow-fields.

In the lower (oro)arctic zone, however, the subcontinental pattern diverges from the pattern

Fig. 27. Lower oroarctic habitat complex at Suolojávri, Finnish Ráisduottar, 700 m a.s.l. The hillock is mainly occupied by the arctic-hemiarctic Empetrum-Vaccinium type. On the slope there is a zone of the Betula nana-Cladina type. The depression harbours the Empetrum stereocaulon type.

Fig. 28. Middle oroarctic heaths of the Juncus trifidus-Cassiope tetragona type at Guonjarvárri, Finnish Ráisduottar, 900 m a.s.l.

of isolated inland mountains. *Phyllodoce* heaths, which are rather poorly represented even at lower altitudes, disappear, and the Empetrum-Stereocaulon type becomes restricted to weakly concave sites. The Empetrum-Cetraria nivalis type emerges as a regular constituent of topographic sequences occurring between the Empetrum-Loiseleuria type and the arctic-hemiarctic Empetrum-Vaccinium type. Sites with better snow cover are occupied by the Betula nana-Cladina type, which normally grades into snow-beds of the Juncus trifidus-Cladina mitis type along gradients of increasing snow depth (Fig. 27). The lower oroarctic pattern is thus rather similar to its counterpart on continental plateaux. Communities with high cover values of *Phyllodoce caerulea* or *Vaccinium myrtillus* do not form regular constituents of topographic sequences, whereas fruticose lichens and *Betula nana* abound from

Fig. 29. Upper oroarctic *Cassiope tetragona-Ranunculus* glacialis heath of Ráisduottar, Ritničohkka.

ridges to depressions. The main difference as compared with the continental tundras is that the arctic-hemiarctic Empetrum-Vaccinium type is regularly a major constituent of the community sequence.

At an altitude of 850 m, the arctic-hemiarctic Empetrum-Vaccinium and Betula nana-Cladina types both become replaced by the Juncus trifidus-Cassiope tetragona type (Fig. 28). In our opinion, this transition can be interpreted as the limit between lower and middle oroarctic zones. The 850 m contour also roughly corresponds to the altitudinal limit of *Vaccinium myrtillus* (Kyllönen 1988). On extreme ridges, the Empetrum-Loiseleuria type gives way to the two middle oroarctic deflation heath types, which we have already encountered on Gáisat. The Vaccinium-Alectoria type is the common one, while the Empetrum-Phyllodoce-Alectoria type is encountered in terrain covered by boulders. However, the Empetrum-Cetraria nivalis type remains a regular constituent of community sequences, as does the chiefly lower oroarctic Juncus trifidus-Cladina mitis type.

Sampling at altitudes above 1 000 m was performed rather close to summits (up to 1075 m on Guonjarvárri, at 1 100–1 150 m on Gahpperusvárri, at 1 175–1 275 m on Ritničohkka), which makes it difficult to distinguish between the impacts of altitude and micro- and macrotopography. At least two communities seem to be typical for middle oroarctic summits and do not belong to the small-scale topographic sequences of mountain slopes: the Salix herbacea-Cetraria nivalis type and the Cassiope tetragona-Cetraria nivalis type. Heaths of the Cassiope hypnoides-Juncus trifidus type, in turn, seem to form a regular constituent of community sequences, replacing snow-beds of Juncus trifidus-Cladina mitis type at higher altitudes.

At an altitude of about 1 150–1 200 m, middle oroarctic grass-dwarf shrub heaths give way to boulderfields. The transition is accompanied by the emergence of the Salix polaris-Carex bigelowii type in the upper part of the topographic gradient. Within the boulderfield zone, the vegetation consists of small fragments, occupying sites affected by solifluction or embedded in a matrix of stones and gravel. The prevalent community type of high-altitude inland mountains, the Luzula confusa-Cetraria nivalis type, is relatively uncommon in our material from Ráisduottar. The most common community types encountered are the Ranunculus glacialis-Gymnomitrion type, occurring in sheltered depresssions, and heath fragments of the Cassiope tetragona-Ranunculus glacialis type, encountered on more chionophobous sites (Fig. 29).

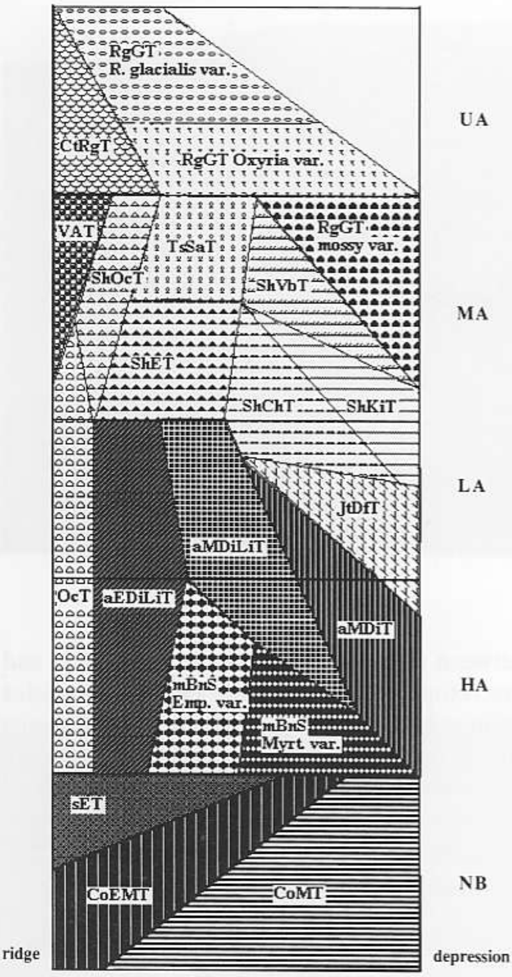


Fig. 30. Idealized topographic and altitudinal pattern in suboceanic oligotrophic heath vegetation in northern Fennoscandia. The pattern is based on the material from Ivggegáisat.

This vegetational pattern is similar to the upper oroarctic pattern encountered on Ivggegáisat (see below), and the co-occurrence of extremely chionophilous and extremely chionophobous elements in a single community is in itself an upper oroarctic feature. Thus, we propose that the highest summits of Ráisduottar are truly upper oroarctic. There are some reasonable counter-arguments. *Cassiope tetragona* is a chiefly middle (oro)arctic species (Nordhagen 1955), and also *Luzula confusa* heaths are sometimes regarded as middle oroarctic (Federley & Vuokko 1980). However, by these criteria, the middle oroarctic zone of Ivggegáisat would become untenably wide, encompassing altitudes from 800 m to at least 1 530 m (see below).

The contrast between continental and subcontinental patterns in northernmost Fennoscandia has parallels with Dahl's (1957) records from eastern and western slopes of Rondane. The lower oroarctic zone is characterized by similar lichen-dominated communities on both slopes, but middle oroarctic grass heaths are only encountered on the more oceanic west slopes. On east slopes, seemingly upper oroarctic boulderfields meet directly lower oroarctic lichen-dwarf shrub heaths. The main difference between the patterns of inland northern Fennoscandia and Rondane is the copious occurrence of two arctic dwarf shrubs, *Betula nana* and *Cassiope tetragona*, and the much sparser occurrence of *Juncus trifidus* and *Vaccinium myrtillus* in northern Fennoscandia. The lower (oro)arctic lichen heaths are thus more similar to their arctic counterparts (Larsen 1965, Larsen & Kershaw 1975) than to the lichen heaths of mountains in southern Norway. The middle oroarctic heaths of Ráisduottar, in turn, are intermediate between southern Scandinavian *Juncus trifidus* heaths (Nordhagen 1928, 1943, Dahl 1957) and middle arctic *Cassiope tetragona* heaths (Böcher 1963, Bliss 1977, Cooper 1986).

4. **Suboceanic pattern on Ivggegáisat**

The lowermost slopes of Ivggegáisat are covered by woodlands of Cornus-Myrtillus type (Hämet-Ahti 1963), although the tree cover on hillocks and ridges is scanty and patches of the Cornus-Empetrum-Myrtillus type regularly occur on crests (Fig. 30, Oksanen et al. 1995: fig. 6). Above the 300 m contour, the treeless patches of hilltops quickly become larger and are occupied by heaths of the subalpine Empetrum type. Sparsely wooded heaths of Cornus-Empetrum-Myrtillus type prevail on slopes, and stands of the Cornus-Myrtillus type have receded to depressions. This seemingly orohemiarctic complex is replaced

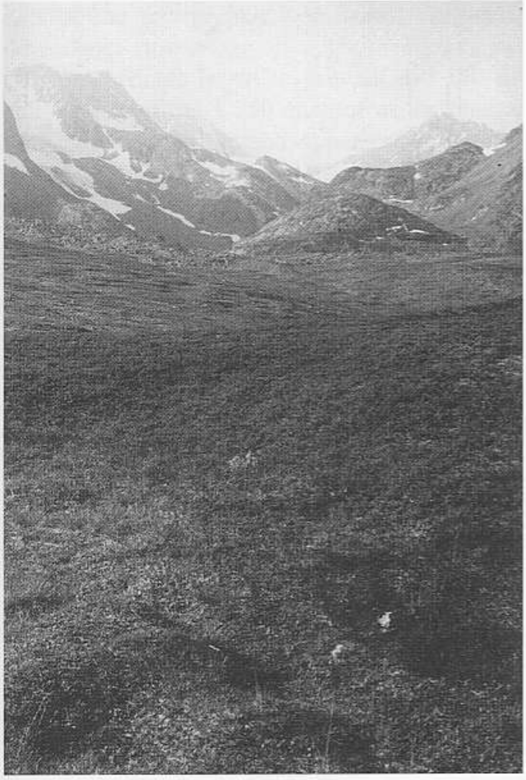


Fig. 31. Lower oroarctic community complex on Jorbbavárri, Ivggegáisat 550 m a.s.l. The hillock is mainly occupied by the Empetrum-Dicranum-Lichenes type, which grades into a grassy stage of the Myrtillus-Dicranum type in the depression.

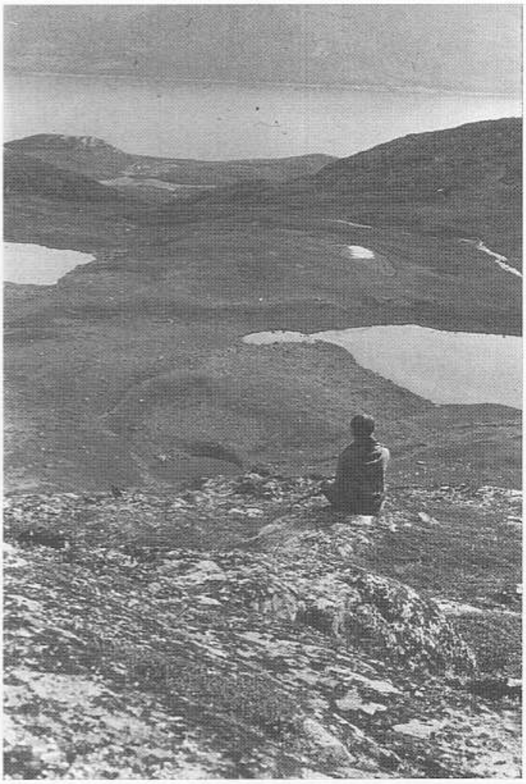


Fig. 32. Middle oroarctic landscape on Jorbbavárri, Ivggegáisat 800–900 m a.s.l. Hillocks are occupied by mixed *Empetrum hermaphroditum* and *Salix herbacea* heaths.

by treeless heaths at an altitude of 400 m. However, in sites inaccesible to sheep, individual trees occur up to 540 m (Oksanen et al. 1995). We thus regard the complexes of woodlands and heaths between 300 m and 400 m as at least mainly north boreal (or upper oroboreal) and suggest that sheep grazing accounts for the lack of continuous tree cover (Haapasaari 1988, Oksanen et al. 1995).

According to this interpretation, the treeless heaths between the altitudes of 400 m and 550 m are orohemiarctic. Nevertheless, the topographic sequence only harbours one community type with affinities to Haapasaari's (1988) hemiarctic heath types: the mossy *Betula nana* scrub. Depressions are occupied by the arctic Myrtillus-Dicranum-Lichenes and Myrtillus-Dicranum types, and ridges are characterized by rather extensive stands of the arctic Empetrum-Dicranum-Lichenes type (Fig. 31). Due to macrotopographic conditions, our material from these altitudes does not include extreme ridge sites, but stands representing our Diapensia-Ochrolechia type have been described by Haapasaari (1988) from the same area at altitudes corresponding to our orohemiarctic zone. We thus tentatively include this community type in the orohemiarctic community sequence.

The main diagnostic feature of truly lower oroarctic conditions, as we interpret them, is that the arctic Empetrum-Dicranum and Myrtillus-Dicranum-Lichenes types normally meet without any *Betula nana* scrubland in between. Another characteristic lower oroarctic feature is the occurrence of snow-beds as regular constituents of the topographic community sequence. At relatively low altitudes, they are mainly represented by the Juncus trifidus-Deschampsia flexuosa type. With increasing altitude, the most

Fig. 33. Luzula confusa dominated patch of the Salix herbacea-Ochrolechia type on a middle oroarctic ridge on Jorbbavárri, Ivggegáisat 950 m a.s.l.

Fig. 34. A fragment of the Ranunculus glacialis-Gymnomitrion type in the upper oroarctic zone, Jorbbavárri, Ivggegáisat, 1 100 m a.s.l.

extreme depressions become occupied by late snow-beds of the Salix herbacea-Kiaeria type. At altitudes between 600 and 700 m, the abundance of graminoids in early and moderate snow-beds sharply declines. In our material, this is reflected as the replacement of the Juncus trifidus-Deschampsia flexuosa type by the Salix herbacea-Cassiope hypnoides type.

Above 700 m, neither *Empetrum hermaphroditum* nor *Vaccinium myrtillus* manage to grow as closed stands. Thus, *Salix herbacea* can spread from snow-beds to crests of ridges, becoming a co-dominant in almost all constituents of the topographic community sequence (Fig. 32). Between 700 arctic and 750 m, stands intermediate between the Myrtillus-Dicranum-Lichenes type and the Salix herbacea-Cassiope hypnoides type are common. Above the 750 m contour *Vaccinium myrtillus* is only occasionally encountered. This we regard as the line of demarcation between the lower and middle oroarctic zones.

Immediately above the 750 m contour, the arctic Empetrum-Dicranum-Lichenes and Myrtillus-Dicranum-Lichenes types are replaced by the Salix herbacea-Empetrum type, but other constituents of the community sequence are familiar from the lower oroarctic zone. At somewhat higher altitudes, the Ochrolechia type of the ridges grades into the Salix herbacea-Ochrolechia type (Fig. 33). The Vaccinium-Alectoria type is patchily encountered on rocky ridges. Heaths of the *S*alix herbacea-Empetrum type are replaced by the "alpine gardens" of the Trisetum-Sanionia type, and snow-beds of Salix herbaea-Kiaeria type give way to the Salix herbacea-Viola biflora type. The mossy variant of the Ranunculus glacialis-Gymnomition type appears in extreme depressions, and with increasing altitude it occupies a successively larger part of the topographic community sequence (Fig. 34).

Boulderfields begin to prevail at 1 150 m, and we regard the 1 150 contour as the natural limit between middle and upper oroarctic vegetation. The upper oroarctic vegetation pattern is similar to the one described from Ráisduottar. Patches of the Cassiope tetragona-Ranunculus glacialis type are encountered on rocky ridges, while fragments of the Luzula confusa-Cetraria nivalis type occur on ridge sites subjected to intense cryoperturbation. More shelterd sites harbour patches of the Ranunculus glacialis-Gymnomitrion type, the Oxyria variant prevailing in lower parts of the boulderfield zone and the Ranunculus glacialis variant at higher altitudes. The Luzula confusa variant is conditioned by intense cryoperturbation and the Luzula confusa-Saxifraga tenuis type occurs on extensive high altitude plateaux. We have therefore excluded these two community types from the scheme of idealized altitudinal and topographic vegetation patterns of Ivggegáisat (Fig. 30).

IX. GEOBOTANICAL INTERPRETATION OF VEGETATIONAL PATTERNS IN NORTHERN FENNOSCANDIA

1. **Arctic and alpine features in heath vegetation of northern Fennoscandia**

The climatic indicators discussed in section 2 suggest that conditions within the Scandinavian mountain chain up to the Three Country Border Point (Treriksröset) differ from those of the circumpolar tundra. Winter precipitation is greater than in arctic areas with equally oceanic climate and this is reflected as relatively warm soil conditions and absence of any indicators of permafrost (Eurola 1974). East of the mountain chain, however, winter precipitation is as low as in corresponding arctic areas. Palsa bogs prevail on both sides of the timberline, indicating the presence of at least discontinuous permafrost (Fries 1913, Ruuhijärvi 1960, Thannheiser 1975, Gjærevoll 1978, Vorren 1979, Eurola & Vorren 1980, own observations).

Patterns of heath vegetation correlate well with the climatic indicators discussed above. The two characteristic dwarf shrubs of Scandinavian oroarctic heaths, *Phyllodoce caerulea* and *Vaccinium myrtillus* (see Nordhagen 1928, 1943, Dahl 1957), which have limited occurrence in the circumpolar low arctic zone (Hultén 1958, 1968, Hultén & Fries 1986), abound on the small isolated mountains of Finnish Lapland (Kalliola 1939, Haapasaari 1988). Moreover, *V. myrtillus* is among the predominating components of mountain heaths in southern and central Troms (Haapasaari 1988, our data). Conversely, in the inland plateaux and on the eastern slopes of the mountains north of Duordnosjávri (Torneträsk), the field layer of lower oroarctic heaths is normally dominated by *Betula nana*, which is much less abundant on the mountains of southern Scandinavia (Nordhagen 1928, 1943, Dahl 1957) and in continental Europe is restricted to wetlands (Hegi 1957, Ellenberg 1988). Corresponding *Betula nana* heaths form a dominating component of the vegetation of the circumpolar hemiarctic zone and of southern arctic areas resembling northern Fennoscandia in topography and glacial history (e.g. Canada, Greenland; see, Böcher 1933, 1954, 1963, Larsen 1965).

The circumpolar affinities are not restricted to heath vegetation. Also the hemiarctic meadow vegetation of the inland plateaux mainly consists of relatively dry communities with clear circumpolar affinities (Jonasson 1982, Oksanen 1995a). Communities assigned to the primarily lower oroarctic (low alpine) alliance Lactucion alpinae occur along permanent creeks, as pointed out by Eurola (1974). However, these communities are invariably willow thickets with tall herbs only as a subordinate constituent of the vegetation (Kalliola 1939, Gjærevoll 1978 Jonasson 1983). Identical communities are encountered in corresponding sites within the circumpolar hemiarctic and southern arctic zones (Larsen 1965, Aleksandrova 1970).

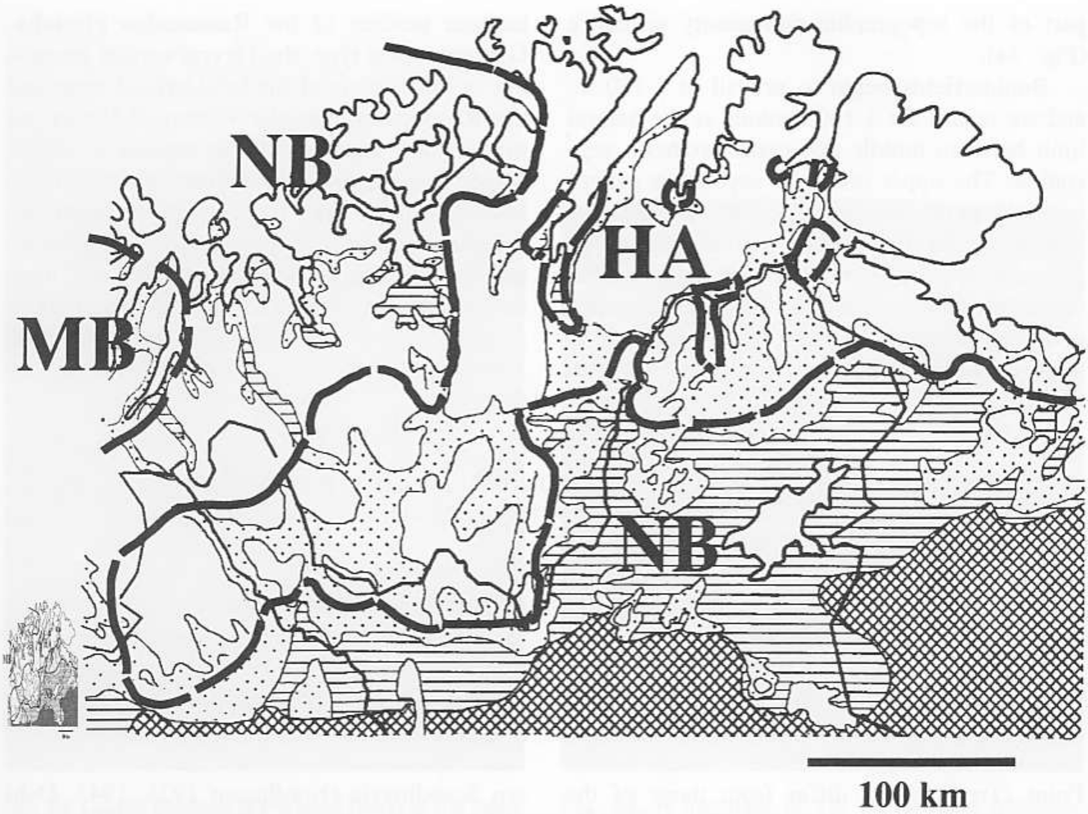


Fig. 35. Revised zonal divisions of northernmost Fennoscandia on the basis of Ahti et al. (1968), Jonasson (1981), Dahl et al. (1986), Seppälä and Rastas (1980), Haapasaari (1988), Heikkinen and Kalliola (1988), Piirainen and Piirainen (1991) and our data. HA = hemiarctic zone, NB = northern boreal zone, MB = middle boreal zone.

Genuine tall herb meadows are only common on mountains south of Duordnosjávri (Anonymous 1975–1983).

In coastal areas east of North Cape, treeless heaths are normally dominated by *Empetrum hermaphroditum*, whereas communities dominated by *V. myrtillus* are restricted to sites with concave topography (Haapasaari 1988). This pattern is basically similar that encountered in the hemiarctic and southern arctic areas of coastal Greenland (Böcher 1933, 1958, 1963).

Both climatic and vegetational indicators thus suggest that peninsulas east of North Cape, the adjacent inland tundra plateaux and the eastern slopes of Scandes north of Duordnosjávri (Torneträsk) are parts of the circumpolar arctic-hemiarctic zone (Fig. 35). Notice, however that north boreal conditions occur locally in major valleys (Fig. 35).

According to Haapasaari (1988: fig. 122), the northeastern coasts of Norway are at least partially low arctic. The chief argument for this view is that low arctic heath types cover extensive areas on Várjatnjárga (Varangerhalvöya) and Čorgotnjárga (Nordkinnhalvöya), especially in terrain with convex topography (Haapasaari 1988: 163–164). However, the supposedly low arctic heath types are common in the hemiarctic (and orohemiarctic) zone, especially in convex terrain, which is unfavourable for the development of *Betula nana* scrublands (see our discussion on vegetational patterns of Ivggegáisat). Moreover, Haapasaari's hemiarctic Empetrum-Pleurozium type is reported to be a "frequent and dominant" heath community along the northeastern coasts of Norway (Haapasaari 1988: fig. 85 and 114), which also harbour birch scrublands and tall willow thickets in the mouths of all rivers and substantial creeks (Ahti et al. 1968, Hämet–Ahti 1963, Oksanen et al. 1995: fig. 4). It thus seems safe to attribute the existence of coastal areas with seemingly southern arctic vegetation to local topographic conditions.

With regard to the southern arctic/lower oroarctic zone in northernmost Fennoscandia, the use of the oro-prefix can be justified by the lack of a physical connection to the southern arctic at sea level. Moreover, the lower oroarctic areas appear normally to be sufficiently elevated to have milder thermal conditions and/or thicker snow-cover than the surrounding hemiarctic landscape. Almost all palsa bogs that we encountered in interior Finnmark lie at altitudes where mountain birches still occur in topographically and edaphically favourable sites, i.e. within the hemiarctic zone. Moreover, oroarctic *Myrtillus-Lichenes* heaths were well-represented in our lower oroarctic transect material from Čakčaduottar. However, the existence of oroarctic features in the vegetation appears to depend on altitudinal differences rather than on altitude *per se*: oroarctic *Phyllodoce* and *Myrtillus-Lichenes* heaths are encountered on slopes, whereas basins at the same altitudes are occupied by arctic *Betula nana-Cladina* heaths.

The vegetation of middle oroarctic elevations is normally clearly different from its latitudinal counterparts. However, the middle oroarctic vegetation in northernmost Fennoscandia is not identical with its South Scandinavian counterpart either. The dwarf willow, *Salix herbacea,* heaths of Ivggegáisat are quite unlike the middle oroarctic *Juncus trifidus* heaths of southern Scandinavia and at least physiognomically resemble the middle arctic *Salix arctica* heaths (Porsild 1951, Elvebakk 1985). On the subcontinental eastern slopes of Ráisduottar, middle oroarctic sites are normally occupied by a mixture of the arctic dwarf shrub *Cassiope tetragona* and the oroarctic graminoid *Juncus trifidus*.

Similarities between northern and southern Fennoscandia are at their greatest at the highest elevations. The Luzula confusa-Ranunculus glacialis communities of northernmost Fennoscandia have practically identical counterparts in southern Norway (Nordhagen 1928, 1943, Gjærevoll 1956, Dahl 1957) and only weakly resemble typical polar deserts of the high arctic (Bliss et al. 1984, Aleksandrova 1988). However, the uppermost vegetation fragments of Fennoscandian mountains are also unlike their counterparts on the mountains of middle latitudes. To illustrate this, we sampled 40 plots the boulderfields of the Grossglockner, Austrian Alps group, and 40 plots in the polar desert landscape of Louisfjellet and Breineset, Adventdalen area,

Table 3. Frequencies and mean cover values in high alpine vegetation fragments in the Grossglockner group sampled by the same methods as applied in the high-altitude Ivggegáisat plots. n = 20 in both groups.

	Alt. <2900 m		Alt. >2900 m	
	Freq.	cover	Freq.	cover
Aster alpinus	5	0.01	–	–
Androsace helvetica	5	0.01	–	–
Artemisia genipi	10	0.22	–	–
Arabis pumila	5	0.01	–	–
Cardamine resedifolia	40	0.05	–	–
Carex sp.	5	+	–	–
Cerastium alpinum	10	0.04	5	0.01
Cerastium latifolium	–	–	15	0.26
Draba aizoides	5	0.01	5	0.01
Linaria alpina	35	0.25	5	0.03
Poa alpina	25	0.12	–	–
Saxifraga exigata	10	0.12	5	0.02
Saxifraga oppositifolia	25	0.94	55	9.28
Saxifraga rudolphiana	35	1.91	20	5.41
Saxifraga microphylla	15	0.02	–	–
Silene acaulis	20	5.52	–	–
Sagina saginoides	5	+	–	–
Saxifraga bryoides	–	–	35	1.96
Saxifraga moschata	–	–	5	0.11
Vascular plants		9.23		17.08
Andreaea sp.	–	–	40	3.67
Kiaeria sp.	5	0.01	20	0.47
Lecidea sp.	–	–	35	0.94
Ochrolechia sp.	–	–	15	0.30
Stereocaulon sp.	–	–	5	0.06
Polytrichastrum sexangulare	–	–	10	0.12
Cladonia verticillata	–	–	25	1.20
Cryptogamic plants		0.01		6.76

Table 4. Frequencies and mean cover values in high oroarctic-polar-desert vegetation fragments in inner Spitsbergen sampled by the same methods as used in the high altitude Ivggegáisat plots.

	Alt. 375–425 m		Alt. 450–600 m	
	Freq.	cover	Freq.	cover
Alopecurus alpinus	20	0.35	–	–
Cardamine bellidifolia	5	0.05	25	0.25
Cerastium arcticum	45	0.45	25	0.3
Draba adamsii	10	0.10	15	0.15
Draba fladnizensis	5	0.05	–	–
Draba sp.	30	0.30	35	0.4
Dryas octopetala	10	0.25	–	–
Koenigia islandica	5	0.05	–	–
Luzula arctica	15	0.55	20	0.4
Luzula arcuata	45	0.9	–	–
Minuartia rubella	5	0.05	20	0.2
Oxyria digyna	5	0.05	15	0.15
Papaver dahlianum	80	0.8	55	1.1
Pedicularis hirsuta	5	0.05	–	–
Poa arctica	85	1.15	35	0.55
Polygonum viviparum	10	0.15	–	–
Potentilla hyparctica	40	0.65	–	–
Ranunculus sulphureus	20	0.2	–	–
Sagina nivalis	10	0.1	–	–
Salix polaris	65	3.25	10	0.2
Saxifraga cernua	50	0.55	15	0.15
Saxifraga cespitosa	60	0.65	40	0.5
Saxifraga flagellaris	15	0.15	–	–
Saxifraga nivalis	10	0.1	10	0.15
Saxifraga oppositifolia	55	1.25	35	0.7
Stellaria crassipes	20	0.2	30	0.45
Deschampsia alpina	–	–	10	0.1
Draba alpina	–	–	5	0.05
Luzula confusa	–	–	45	1.35
Phippsia algida	–	–	10	0.1
Poa alpigena	–	–	5	0.05
Saxifraga hyperborea	–	–	30	0.35
Vascular plants		12.4		7.45
Hylocomium splendens	40	1.2	–	–
Hypnum revolutum	80	2.3	15	0.25
Racomitrium canescens	85	1.85	25	0.5
Sanionia spp.	75	2.05	25	0.45
Tortula ruralis	65	1.0	10	0.1
Psoroma hypnorum	75	1.0	–	–
Stereocaulon spp.	90	1.4	20	0.25
Pogonatum sp.	–	–	40	1.0
Anthelia juratzkana	5	0.15	30	1.2
Scapania tundrae	–	–	15	1.15
Ochrolechia spp.	50	0.9	35	1.55
Cryptogamic plants		11.85		6.45
Cover of other cryptogams		17.3		9.55
Cryptogams total		29.15		16.00

Spitsbergen, using the same method as on the boulderfields of northernost Fennoscandia. On the basis of altitude we divided the material between extreme and moderately extreme sites. In the Glossglockner material, extreme sites lie at altitudes of 2 900–3 200 m, and less extreme sites between 2 600 and 2 900 m. In Svalbard, the altitudes of extreme sites are 450–600 m and those of less extreme sites 375–425 m. The data from Grossglockner are presented in Table 3, the data from Svalbard in Table 4.

In the Grossglockner material the overwhelmingly dominating component of the high alpine vegetation consists of cushion plants (Saxi*fraga oppositifolia*, *S. rudolphiana* and *Silene acaulis*). Note that alpine populations of *S. oppositifolia* have a much more compact growth form than the Scandinavian populations (see also Hauri & Schröter 1914, Vierhapper 1927, Krivonogova 1965). With increasing altitude, the vegetation fragments become less frequent in the largely sterile boulderfield landscape, but the sizes of individual cushions increase (Reisigl & Pitschmann 1958). The role of terricolous cryptogams is negligible, though greatest at the highest altitudes, where the relatively large cushions trap soil and thus create a habitat for cryptogams.

In the polar desert of Svalbard, the uppermost vegetation fragments can be characterized as scattered sets of herbs (e.g. *Papaver dahlianum* and *Saxifraga hyperborea*) and graminoids growing among stones and gravel (see also Bliss & Svoboda 1984, Bliss et al. 1984, Aleksandrova 1988). The cover of terricolous cryptogams tends to be higher than the cover of vascular plants, although vascular plants dominate physiognomically, and probably also in terms of biomass. In terms of the distribution of different morphological categories, the upper oroarctic of the whole of Fennoscandia is thus more similar to the vegetation of polar deserts than to the vegetation of truly high alpine habitats, which is heavily dominated by cushion plants.

2. Sectorial division in northern Fennoscandia

Today, we have two different treatments of sector groups in northernmost Fennoscandia.

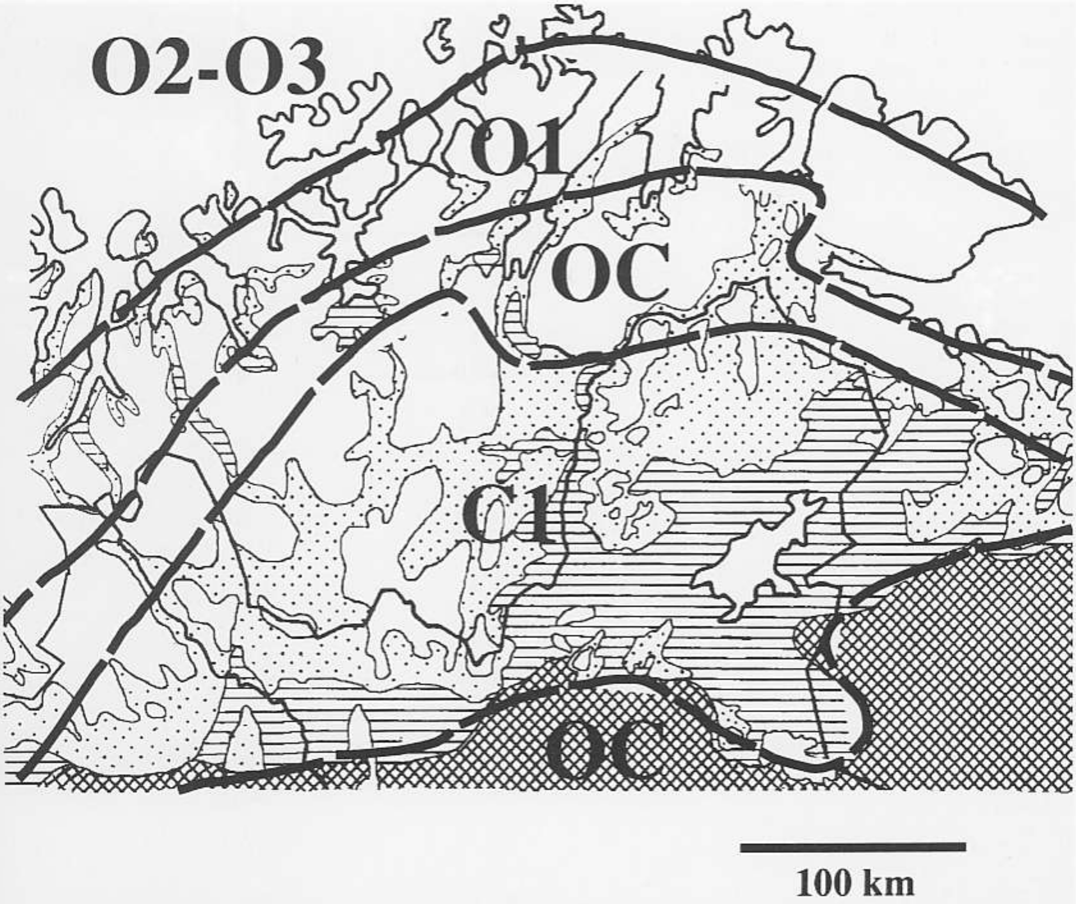


Fig. 36. Revised sectoral divisions in northernmost Fennoscandia on the basis of Ahti et al. (1968), Jonasson (1981), Haapasaari (1988), Heikkinen and Kalliola (1988), Piirainen and Piirainen (1991) and our data. O2-O3 = oceanic, O1 = suboceanic, OC = subcontinental and C1 = continental sectors (sector groups).

Ahti et al. (1968) define sectors and sector groups primarily on the basis of forest vegetation, whereas Haapasaari's (1988) point of departure is the vegetation of treeless heaths. Although the two treatments conform in many ways, the continental (C1) sectors are almost non-overlapping. The continental sector of Ahti et al. (1968) encompasses the Anarjávri (Inarinjärvi) basin and the highlands south of it and stretches towards the southwest to the area around of Gällivare without including substantial pieces of Norwegian territory. Haapasaari's C1 sector, in turn, starts at the northern border of this area and is at its widest in the interior parts of northern Norway.

We regard it as most natural to define sector groups primarily with reference to the zone that prevails in the area as a whole. Exceptionally elevated habitats tend to receive more precipitation (e.g. Flohn 1974, Barry 1987, Barry & Chorley 1992). But exceptionally low-lying areas, too, are likely to be subjected to unusual climatic conditions. Although precipitation in itself normally decreases with decreasing altitude, forested valleys may act as snow traps and slopes may receive moisture from subsurface runoff. Thus, depending on the relative strengths of these two factors, valleys may be either moister or drier than the surrounding uplands.

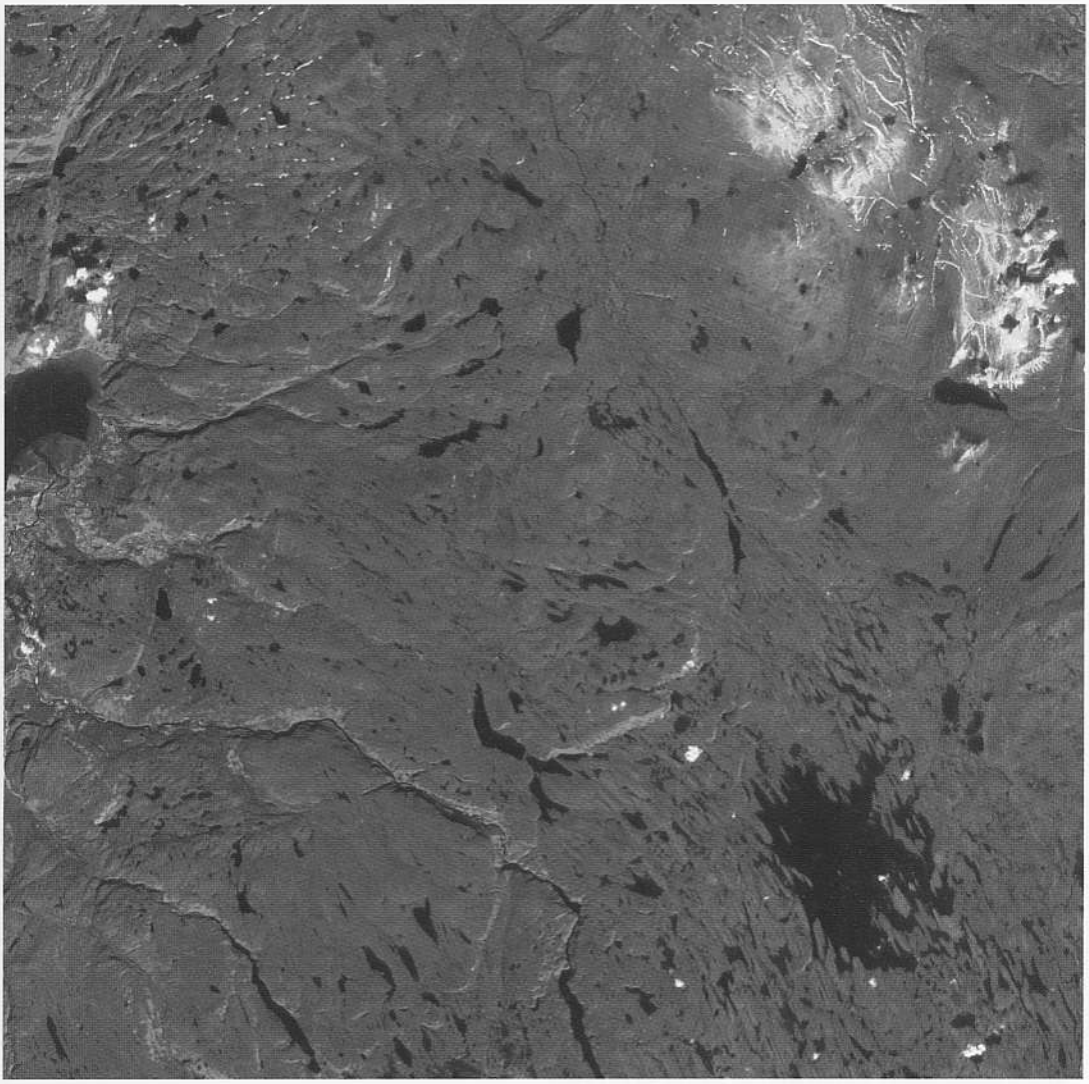


Fig. 37. SPOT satellite photograph of Iešjávri basin shows that the highlands northeast of it and the western slopes of the Gáisa formation belong to the C1 sector. The light greyish color reflects abundant lichen grounds. Reddish colour is reflected chiefly by eutrophic vegetation. The area covered in the vegetation map (Fig. 23) is delimited in the right margin of the figure.

If sector groups are delimited on the basis of the prevailing vegetation zone — forest vegetation in the boreal region and hemiarctic vegetation in the predominantly hemiarctic region — the C1 sector will include both the area proposed by Ahti et al. (1968) and the area proposed by Haapasaari (1988). Within Finnish Lapland, Haapasaari's boundaries are supported by the recent vegetation maps and the vegetational data (Heikkinen & Kalliola 1988, Eeronheimo et al. 1992, Piirainen & Piirainen 1991, present data.) The exact borders in the northwest need slight revision: our data suggest that the Iešjávri basin, the highlands northeast of it, and the western slopes of the Gáisa formation belong to the C1 sector (Fig. 36). Satellite photographs (Fig. 37) further strengthen this impression.

X. ECOLOGICAL CONDITIONS SUSTAINING THE VEGETATIONAL PATTERNS

The main function of descriptions of vegetational patterns is to provide a point of departure for ecological studies. Speculations based on observed patterns are always on uncertain ground, and need to be checked experimentally (Tilman 1988, Keddy 1989). So far, this has rarely been done in northern Fennoscandia. It is nevertheless useful to review proposed ecological explanations and present own interpretations for the vegetational patterns, as a means of stimulating experimental ecological studies.

Summer temperatures and snow

Summer temperatures and snow depth are traditionally regarded as the main factors responsible for the existence of altitudinal and topographic variation in Fennoscandian arctic and oroarctic vegetation. These factors have been extensively discussed in many studies (Gjærevoll 1956, Dahl 1957, Eurola et al. 1986) and textbooks (Økland & Bendiksen 1985).

Nutrients

Nutrients are in short supply in the majority of arctic habitats (Chapin & Shaver 1985, Berendse & Jonasson 1992) and the dramatic impact of nutrient-rich bedrock on Scandinavian oroarctic vegetation has long been noticed (see Nordhagen 1928). Although our material is restricted to areas with nutrient-poor bedrock, indicators of nutrient-rich conditions are encountered in the boulderfield zone and immediately below it. Cryoperturbation appears to create relatively nutrient-rich conditions at high altitudes (Jonasson & Sköld 1983, Jonasson 1986). In the boulderfield zone, nutrients released by cryoperturbation probably percolate into the boulderfield and run downwards over the surface of intact bedrock. At the lower limit of the boulderfield zone, this deep subsurface runoff comes up to the surface and the nutrients carried along become available for plants. We regard this as the main reason for the species-rich "alpine gardens" (the Trisetum spicatum-Sanionia type on Ivggegáisat, the Salix polaris-Carex bigelowii type on Ráisduottar and the Solidago-Deschampsia type on Gáisat) occurring immediately below the boulderfield zone.

Physical disturbance

Physical disturbance is often intense in the upper oroarctic zone, where it probably influences the occurrence and composition of the vegetation fragments (Muller 1952, Benninghoff 1952, Sigafoos 1952, Raup 1969, Bliss & Wein 1972). Jon Moen (pers. comm.) experimentally sowed gravelly patches in the boulderfield zone of Vuorasnjarháldi (Alta, Norway, alt. 850 m) with a roadside grass seed mixture and observed that the productivity was as high as or higher than the productivity of moderate oligotrophic snowbeds at an altitude of 620 m. This suggests that the virtual lack of vegetation in this area was primarily due to intense physical disturbance. Moreover, the dominating vascular plant of continental boulderfields — *Luzula confusa* — is clearly disturbance adapted and allocates heavily to generative reproduction (Addison & Bliss 1984, Oksanen & Ranta 1992).

Physical disturbance appears to be quite important even at lower altitudes (e.g. Fox 1981). Dahl (1957) pointed out that, in spite of their trailing growth habit, many arctic-alpine plants have a strong taproot and few or no adventitious roots. Thus, they can only reproduce generatively (Söyrinki 1939). This growth form may be essential for coping with the soil movements typical of arctic-alpine habitats (Raup 1969, Jonasson 1986, Jonasson & Callaghan 1992). Dahl (1957) has proposed that this is the main reason why *Phyllodoce caerulea,* which has only weak adventitious roots, replaces *Vaccinium myrtillus* on slopes with unstable soils. The same explanation might also apply to the relationship between *P. caerulea* and *V. vitis-idaea*. Both species are relatively mesomorphic evergreen dwarf shrubs and could thus be expected to claim similar sites. According to our data, *V. vitis-idaea* flourishes on rocky ridges and sandy heathlands, where soils are relatively stable, while *P. caerulea* appears more abundantly on stony ridges and slopes.

Soil temperatures

Soil temperatures appear to be the main proximate factor responsible for the varying degrees of arctic and alpine (oroarctic) features in Fennoscandian (oro)arctic vegetation (see Eurola 1974). In typical oroarctic areas, thick snow cover prevents the freezing of the soil (Dahl 1957), whereas typical arctic areas are characterized by permafrost and low soil temperatures even in the active layer. High soil temperatures increase the rate of nutrient mineralization, which is likely to favour herbaceous plants over dwarf shrubs. Cool but unfrozen soils, in turn, are likely to favour evergreen dwarf shrubs over deciduous ones, because the non-frozen soil allows evergreens to start photosynthesizing in spring as soon as the snow cover is thin enough that light can penetrate to canopy level. If, however, the ground remains frozen after the snowmelt, evergreen and semi-evergreen trees and dwarf shrubs like *Vaccinium myrtillus* (Karlsson 1985), may be heavily damaged (Kullman 1989). We regard this as at least a contributing factor for the existence of oroarctic *Phyllodoce* and *Myrtillus* heaths in sites that are dominated by lichens and *Betula nana* in more arctic climatic conditions and by graminoids in corresponding truly alpine habitats at middle latitudes. Note that the distribution of *Phyllodoce*-dominated lower oroarctic heaths correlates well with the distribution of spruce-dominated timberline forests (Widstrand 1965, Haapasaari 1988), suggesting that unfrozen soil favours evergreen plants in both the tree layer and the field layer (see Oksanen 1995b).

The traditional explanation for the absence of *Vaccinium myrtillus* from chionophobous sites is its inability to tolerate low temperatures (Nordhagen 1928, Dahl 1957). Results obtained by Eurola et al. (1980), and by Havas (1965, 1971) for Central Finland support this view, although the relative importance of cold per se and freeze-drying in late winter (Tranquillini 1957, Havas 1971) is in need of further study. The cold-sensitivity of *V. myrtillus* is also of relevance to the issue of arctic and alpine features in heath vegetation of northern Fennoscandia. In the Arctic, mean temperatures at the ground are just as frigid as mean air temperatures; the snow cover only protects against thermal extremes (Dingman et al. 1980). Thus, the Arctic is off limits for cold-sensitive plants. By and large this also applies to oceanic sectors of the Arctic zone, for even there winter precipitation is low by alpine standards, and the cold-hardy *Empetrum hermaphroditum* is the overwhelmingly dominating dwarf shrub (Böcher 1954, 1963). It is for this reason that we emphasize the abundance relationship between *E. hermaphroditum* and *V. myrtillus* when discussing the occurrence of arctic coastal vegetation in northernmost Fennoscandia.

Freezing of vegetation

Freezing of vegetation in solid ice is a major problem for reindeer husbandry in northernmost Fennoscandia, especially when cold autumns are followed by mild winters, as in the winter 1992/1993. Meltwaters may then percolate through the snow and freeze upon reaching the frozen soil (Per–Mikael Utsi, pers. comm.). Hayfields in northernmost Norway also frequently suffer from 'burning' of the ground due to the formation of ice lenses (own observations). The fatefulness for natural oroarctic vegetation of freezing in solid ice is discussed by Dahl (1957), who backed his interpretation with observations concerning the impact of road construction on drainage conditions. According to Dahl, *Stereocaulon* spp. tolerate freezing in solid ice, whereas *Cladina* spp. and *Vaccinium myrtillus* do not.

Freezing in solid ice appears to be the main factor responsible for the existence of extensive

Fig. 38. Accumulated early winter snow covers a patch of Betula nana-Stereocaulon type, while *Betula nana-Cladina* heaths are still snow-free.

Stereocaulon heaths in northern Fennoscandia. As stated above, these heaths normally occur on the slopes of flat-topped hills, and according to our observations, these sites obtain a relatively thick snow cover during the first blizzards (Fig. 38). Late autumn thaws, which subsequently melt the snow from upland sites, often leave slopes covered with an icy crust. The copious occurrence of Stereocaulon heaths in northern Fennoscandia is thus probably not due to reindeer grazing, as proposed by Du Rietz (1925a) but rather due to the arctic climate, creating a situation where meltwaters tend to freeze upon reaching the frozen ground.

Grazing by sheep

Grazing by sheep is more or less restricted to the Atlantic coast, where the animals can be kept out-of-doors throughout the year and where the need for supplementary winter food is relatively small (Haapasaari 1988). Besides depressing the timberline of Ivggegáisat by at least 200 m (Oksanen et al. 1995), sheep grazing may contribute to the high abundances of the relatively unpalatable *Empetrum hermaphroditum* on treeless boreal and orohemiarctic heaths. In the forest zone, the abundances of graminoids (especially: *Deschampsia cespitosa* and *D. flexuosa*) are conspicuously high in the vicinity of settlements, where sheep grazing is most intense.

Grazing by reindeer

Grazing by reindeer is doubtless crucially important for inland tundra vegetation. In areas where wild reindeer were reduced to low levels already in ancient times and where reindeer husbandry has not developed, *Cladina stellaris* builds thick carpets, largely excluding other lichens and causing major problems for vascular plants (Du Rietz 1925a, Söyrinki 1939, Nordhagen 1943, Brown & Mikola 1974). Persistent heavy grazing and trampling decimates the *Cladina* carpet. The ability of *Stereocaulon* spp. to invade such sites seems to be overrated (L. Kärelampi pers. comm., Oksanen 1978, present data). Instead of creating secondary *Sterero-caulon* heaths, intense grazing and trampling seem to encourage an expansion of *Polytrichum hyperboreum* and *P. piliferum* (inedible for reindeer). Thus *Cladina* heaths subjected to persistent, intense summer grazing appear to converge towards the *Polytrichum hyperboreum* stage. Even prudently used winter ranges are characterized by much lower lichen biomass and much higher species diversity than the *Cladina stellaris* dominated heaths of ungrazed areas (Oksanen 1978, Helle & Aspi 1983, Du Rietz 1925a, Dahl 1957).

Summer grazing by reindeer also is likely to be a major factor influencing the composition of snow-bed vegetation. During warm summer days, reindeer typically rest on snowfields and prefer to graze the emerging shoots along their edges (Skjenneberg & Slagsvold 1968, own observations). On our snow-bed plots sampled slightly below the boulderfield limit on Ivggegáisat, practically all herbaceous plants with erect, robust shoots (e.g. *Luzula confusa*, *Oxyria digyna* and *Ranunculus glacialis*) had been heavily grazed by reindeer. When sampling the vegetation fragments in the boulderfield zone, we systematically recorded evidence for grazing on our plots, assigning all species on plots to one of the following categories: (1) intact (no evidence for vertebrate grazing), (2) nibbled (at least one inflorescence severed, no substantial amounts of foliage removed) and (3) grazed (large amounts of foliage lost). Nibbling is probably the work of rock ptarmigans (*Lagopus mutus*), which were observed to consume inflorescences of *R. glacialis.* Grazing, on the other hand, is probably mainly due to reindeer, although some grazed graminoids grew in places that were only accessible to microtine rodents.

The results (Table 5) reflect the combined impact of grazer preference and accessibility and must therefore not be over-interpreted. Nevertheless, they show that there is substantial grazing even in the boulderfield zone, especially on ridges where the *Luzula confusa* heaths are found. Moreover, reindeer appears to prefer herbaceous plants with robust, erect shoots. The altitudinal distribution of grazing appears to be uneven: all grazed stands of *Ranunculus glacialis* and the majority of grazed *Luzula confusa* stands lie in the lower part of the boulderfield zone.

Table 5. Grazing observations (%) for the most common constituents of upper oroarctic plant communities on Ivggegáisat.

Species	n	grazed	nibbled	intact
Ranunculus glacialis	23	13	30	57
Luzula confusa	44	48	7	45
Salix herbacea	19	0	0	100
Cardamine bellidifolia	19	0	0	100
Cassiope hypnoides	21	0	0	100
Cassiope tetragona	10	0	0	100
Saxifraga nivalis	12	0	0	100

The observations summarized above suggest that grazing by reindeer may be a major cause of the relative rarity of *Luzula confusa* and *Ranunculus glacialis* in the middle oroarctic zone. Moreover, as Du Rietz (1925b) long ago noticed, *Salix herbacea* is abundant in the lower parts of the boulderfield zone, whereas higher up *R. glacialis* monopolizes corresponding sites. This, too, may reflect the grazing by reindeer in the lower parts of the boulderfield zone.

While the impact of reindeer grazing on robust, erect herbs and erect woody plants is clearly negative (Höglund & Eriksson 1973), prostrate plants and small herbs are likely to gain from the elimination of superior competitors and from the mechanical disturbance of the moss carpet. Normally disturbance promotes species diversity (Harper 1969, Grime 1973, 1977, Fox 1985), and reindeer may thus contribute to the species-richness of the 'alpine gardens' at the boulderfield limit.

The profound impact of reindeer on lichen heath and snow-bed vegetation is not a consequence of extremely high numbers (Skjenneberg & Slagsvold 1968, Kurkela 1978). In the subareas included in our study, summer densities of reindeer range from 2–5 to 10 animals per km^2 (Oksanen et al. 1995: fig. 1). Average year-around densities are still lower. Rather than being a consequence of high grazer densities, the current strong influence of reindeer on the heath and snow-bed vegetation of northern Fennoscandia appears to be a consequence of the low productivity of these habitats, creating a situation where moderate grazer density suffices to generate intense grazing pressure. This implies that the current impact of reindeer may not be essentially stronger than would be associated with wild reindeer at their natural equilibrium density (Kelsall 1968, Oksanen 1988).

Microtine rodents

In arctic and subarctic habitats, microtine rodents are at least as important consumers as the ungulates (Wielgolaski 1975, Bliss 1977, Batzli et al. 1980). The impact of microtine rodents is at its highest on chionophilous sites, which are periodically eaten bare by lemmings (*Lemmus lemmus*) (Kalela 1961, 1971, Kalela & Koponen 1971, Oksanen & Oksanen 1981). Nordhagen (1928) early pointed out that this must have a major impact on nutrient cycling. The periodic removal of mosses is also likely to have direct impacts on snow-bed vegetation. In the absence of lemmings, moss biomass of snow-bed sites increases continuously (Kyllönen & Laine 1980, Oksanen 1983, Moen et al. 1993), and such a development could lead to the establishment of moss banks, from which vascular plants would be virtually eliminated. An example is provided by the lemming-free arctic islands, Jan Mayen and Bear Island (Virtanen et al., in prep., see also Söyrinki 1938). Lemmings do not eat dwarf shrubs, but they remove whatever is preventing their access to mosses, and often sever dwarf shrubs in great quantities (pers. comm. by H. Henttonen, own observations). Thus, in spite of their short-term negative impact on graminoids (Moen et al. 1993), lemmings may favour graminoids over dwarf shrubs of oroarctic heaths, as illustrated by our plots representing the arctic Myrtillus-Dicranum type.

Grey-sided voles (*Clethrionomys rufocanus*) are the dominating microtine species of northern Fennoscandia (Lahti et al. 1976, Oksanen & Oksanen 1981, 1992, Andersson & Jonasson 1986). They use dwarf shrubs as winter food (Kalela 1957, Emanuelsson 1984, Oksanen et al. 1987). On islands, where predation pressure is low, they can inflict up to 100% shoot mortality on all woody plants (Oksanen et al. 1987, H. Henttonen, pers. comm., P. Lundberg, in prep.). Grey-sided voles periodically reduce the dwarf shrub cover (Oksanen et al. 1981, 1987, Oksanen 1988) and influence interspecific interactions between dwarf shrubs (Callaghan & Emanuelsson 1985).

In areas with more oceanic or oroarctic conditions, field voles (*Microtus agrestis*) and root voles (*Microtus oeconomus*) may be abundant in the lower oroarctic zone, especially during microtine peaks with low lemming numbers (Henttonen et al. 1977). We are unaware of detailed studies on their impact on north boreal and oroarctic vegetation.

Invertebrate herbivores

Two invertebrate herbivores are important for the timberline by periodically defoliating and sometimes even killing large numbers of mountain birch: these are *Operopthera brumata* in coastal areas and *Epirrita autumnata* in the inland (Tenow 1972, Kallio & Lehtonen 1973). After outbreaks, birch are able to recover by means of basal sprouts, but the sprouts are then vulnerable to vertebrate grazing. Thus, in combination with grazing by reindeer, hares and microtine rodents, defoliation by folivorous insects may transform forest areas to tundra (Seppälä & Rastas 1980, Lehtonen 1981). Outbreaks of these species do not occur in the continental-hemiarctic areas, where low winter temperatures result in heavy egg mortality (Tenow & Nilsson 1990).

The differences in grazing can only explain broad patterns in the abundance relationships between erect and prostrate plants (see Oksanen & Ranta 1992). And in our own opinion even these patterns are ultimately ascribable to the physical environment (high grazing pressure being a consequence of the low primary productivity see Fretwell 1977 and Oksanen et al. 1981). Low grazing pressure is again encountered in the boulderfield zone, where grazers cannot survive (Fretwell 1977 and Oksanen et al. 1981, Oksanen 1988, 1990, Oksanen & Oksanen 1989).

As for typical (oro)arctic heaths and snow-beds, we propose that natural grazing pressure is uniformly high and has always been so. Consequently, differences in (oro)arctic heath and snow-bed vegetation cannot normally be attributed to grazing alone, but must be due to differences in the physical environment or to the interaction between the physical environment and grazing.

Interaction between grazing and nutrient availability

The most obvious interaction is between grazing and nutrient availability. Under nutrient-rich conditions, grazing favours graminoids and other rapidly growing plants, whereas the combination of intense grazing and low nutrient availability favours dwarf shrubs with high concentrations of carbon-based defensive chemicals (Bryant et al. 1983, Oksanen 1990; Herms & Mattson 1992). This trade-off seems to explain many local and large-scale patterns in arctic and oroarctic vegetation. On oceanic and northern Ivggegáisat (see above) and on coastal Greenland (Böcher 1933, 1954, 1963), where soils are cold and thus nutrient-poor, there are no altitudinal or latitudinal grass heath zones. On mountains of middle latitudes, grass heaths are the main constituent of the alpine zone, whereas dwarf shrub heaths are restricted to the vicintity of the timberline (Braun–Blanquet 1948–50, Ellenberg 1988, Ozenda 1988). In southern and continental parts of the temperate zone, the dwarf shrub zone disappears and even subalpine communities are dominated by herbaceous plants (Hämet–Ahti 1978b). In areas with nutrient-rich rocks, however, low alpine grass heaths occur even in Fennoscandia (Nordhagen 1928). Patches of grass heath can also be found in generally oligotrophic areas in locally nutrient-rich conditions, e.g. around arctic fox dens and reindeer carcases, and can be experimentally created by fertilizing (Bliss 1971, Heil & Diemont 1983, Chapin & Shaver 1985, Jonasson 1992, D. Grellman, in prep.). The broad geographical patterns evident in the vertical extent of the oroarctic grass heath zone thus seem to reflect differences in soil fertility, probably ultimately due to differences in soil temperatures which influence the rate of nutrient mineralization.

Together with our considerations on the direct impacts of soil temperatures, the above argument implies that high abundance of evergreen ericaceous shrubs is basically a boreal-oroarctic phenomenon (cf. Rundel 1991). In truly arctic areas, the frozen soil reduces the advantages of the evergreenness in vascular plants, which leads to the prevalence of cryptogams and deciduous dwarf shrubs, except in oceanic areas with mild winters (e.g. the coastal *Empetrum* heaths of Greenland; Böcher 1933, 1954, 1963) and in sites that remain unfrozen for edaphic reasons (e.g. the *Cassiope tetragona* heaths on ridges covered by coarse gravel, see Muc & Bliss 1977). In truly alpine conditions at middle latitudes, in turn, the generally more nutrient-rich conditions favour graminoids and other herbaceous plants over dwarf shrubs. This is reflected in the distribution pattern of *Phyllodoce caerulea* and *P. aleutica* (Hultén 1958, 1968), where the centre of gravity lies on boreal mountains and where the broadest latitudinal range is observed in oceanic areas, where also the combination of edaphic conditions postulated to be favourable for evergreen ericoids (cool but not frozen soils) occurs over a wide range of latitudes and altitudes.

Interactions between plants

Direct and indirect interactions between plants are the proximate factors shaping plant communities. The scene is set by the physical environment, and by variations in the intensity of herbivory, but the name of the game is struggle for existence. In environments that are both extremely stressful and physically disturbed, plants may occasionally happen to help each other, as proposed by Grime (1977, 1979), Callaghan & Emanuelsson (1985) and Callaghan (1987). The occurrence of terricolous cryptogams around the shoots of *Luzula confusa* on high alpine ridges may qualify as an example of this phenomenon, although it is unclear whether the impact of cryptogams on *Luzula confusa* is positive or negative.

However, the Grime´s statement (1977, 1979) that the importance of competition decreases along gradients of intensifying stress is logically problematic. In any undisturbed habitat, plant biomass will build up until the available space is fully occupied. Stress will influence the amount of space available for plants, and the rate at which it becomes occupied after disturbance. Moreover, stress will have an impact on the optimal tactics of resource competition (Tilman 1988). However, we cannot see how stress alone would change the nature of plant-plant interactions. We thus expect that struggle for existence between plants is just as intense in a physically stable *Ranunculus glacialis* snow-bed as in a mesic boreal forest. Moen's (1993) experiment on the establishment of *Oxyria digyna* seedlings within *Ranunculus glacialis* snow-beds supports this view.

Intense herbivory, which probably prevails between the timberline and the boulderfield limit (Oksanen 1988, 1990), reduces the importance of classical resource competition and replaces it to some extent by apparent competition (consumer-mediated indirect negative interactions, Holt 1977). On strongly grazed sites, the success of plants depends on their ability to sustain grazing better than their neighbours (i.e. have higher ratio of growth rate to loss rate). Thus, one category of negative plant-plant interactions is at least partially replaced by another, but the intensity of the struggle for existence between plants is by no means reduced.

There is nothing new in our emphasis on the importance of negative plant-plant interactions in shaping plant communities. After having reviewed the impacts of various physical and biotic factors Cajander (1905) almost 100 years ago pointed out that the composition of vegetation cannot be understood without due consideration of one more factor: the struggle for existence between plants, which ultimately creates regular communities out of the sets of species capable of coping with the environment.

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APPENDICES

Appendix 1. Mean percentage cover of plants in community types of the Betula–Myrtillus group. The frequencies of taxa in each community type are indicated as follows: bold, frequency >66.7%; underline, frequency 33.3–66.7%; normal text, frequency <33.3%. CoMT = Cornus–Myrtillus type, CoEMT = Cornus–Empetrum–Myrtillus type, sET = subalpine Empetrum type, sEMT = subalpine Empetrum–Myrtillus type, Dfle var. = Deschampsia flexuosa variant, Vvit var. = Vaccinium vitis–idaea variant, Sgla var. = Salix glauca variant, sELiPIT = subalpine Empetrum–Lichenes–Pleurozium type, sELiT = subalpine Empetrum–Lichenes type, BpLiS = Betula pubescens–Lichenes scrub. m refers to the number of plots assigned to the community type.

	CoMT	**CoEMT**	**sET**	**sEMT**			**sELiPIT**	**sELiT**	**BpLiS**
				Dfle var.	Vvit var.	Sgla var.			
Anthoxanthum odoratum alpinum	0.1	–	–	–	–	–	–	5.2	–
Betula nana	1.8	0.7	0.3	–	0.1	0.7	2.3	–	0.6
Betula pubescens czerepanovii	0.4	0.1	0.1	–	0.3	**18.1**	0.1	–	**10.0**
Calamagrostis lapponica	–	–	–	–	1.0	+	–	–	–
Carex bigelowii	–	–	–	–	–	0.1	–	–	–
Carex lachenalii	–	–	–	–	–	+	–	–	–
Cornus suecica	**36.1**	**27.2**	**7.0**	0.1	0.1	–	–	–	–
Deschampsia flexuosa	**7.2**	**0.8**	0.3	**3.9**	–	+	**14.7**	16.6	11.4
Diphasiastrum alpinum	–	–	–	–	–	–	+	–	+
Diphasiastrum complanatum	–	–	–	–	–	–	+	2.7	–
Empetrum nigrum hermaphroditum	**6.9**	**29.1**	**44.2**	**36.0**	**34.0**	**36.2**	**23.0**	11.0	**30.7**
Empetrum nigrum nigrum	–	–	–	–	–	–	–	+	–
Equisetum pratense	0.3	–	–	–	–	–	–	–	–
Festuca ovina	0.1	0.1	0.1	–	+	–	2.4	0.1	+
Gymnocarpium dryopteris	**1.7**	0.1	–	–	–	–	–	–	–
Hieracium sp.	0.1	–	–	–	–	–	–	–	–
Huperzia selago	–	–	0.1	–	–	–	–	–	–
Juncus trifidus	0.1	–	0.5	–	–	–	–	–	–
Juniperus communis	0.4	0.1	–	2.9	2.0	–	8.4	0.4	–
Ledum palustre	–	–	–	6.0	4.6	–	–	–	–
Linnaea borealis	0.1	–	–	0.2	0.1	0.2	0.1	–	4.5
Lycopodium annotinum	0.3	0.7	0.7	–	–	–	0.5	0.4	0.5
Melampyrum sylvaticum	0.1	–	–	–	–	–	–	–	–
Pedicularis lapponica	0.3	0.1	–	±	–	–	+	–	–
Phyllodoce caerulea	4.4	2.8	0.8	–	–	–	2.6	–	0.1
Polygonum viviparum	–	0.1	–	–	–	–	–	–	–
Rubus chamaemorus	–	0.1	0.1	–	–	–	–	–	–
Salix borealis	0.1	0.2	–	–	–	–	–	–	–
Salix caprea	0.1	0.1	–	–	–	–	–	–	–
Salix glauca	–	0.1	–	–	–	6.7	–	–	–
Salix herbacea	0.1	0.1	–	–	–	–	–	–	–
Salix phylicifolia	0.8	–	–	–	–	–	–	–	–
Solidago virgaurea	0.3	–	–	–	–	–	**1.8**	0.1	–
Trientalis europaea	0.1	0.1	–	0.1	–	–	–	–	–
Vaccinium myrtillus	**25.2**	**22.4**	**13.7**	11.1	8.9	–	**9.1**	0.1	8.3
Vaccinium uliginosum	5.3	0.3	1.2	**24.6**	0.3	**21.0**	–	–	–
Vaccinium vitis-idaea	**8.2**	7.6	6.2	**15.7**	**18.7**	**6.5**	**24.2**	**7.6**	**19.1**
Dicranum bergeri	–	–	–	0.6	+	–	–	–	–
Dicranum fuscescens	–	–	15.5	–	**0.3**	3.8	**12.9**	2.2	**10.9**
Dicranum scoparium	1.7	**10.5**	**11.5**	+	–	–	0.1	–	1.2
Hylocomium splendens	**37.9**	**42.0**	**20.0**	+	+	–	1.1	–	–

Appendix 1. Continued

	CoMT	CoEMT	sET	sEMT			sELiPIT	sELiT	BpLiS
				Dfle var.	Vvit var.	Sgla var.			
Pleurozium schreberi	**21.1**	**21.1**	**17.4**	**29.1**	**14.8**	18.0	**23.9**	**5.3**	7.7
Pohlia nutans	–	–	0.1	+	0.1	+	+	0.2	+
Polytrichastrum alpinum	**1.1**	**0.3**	1.1	0.1	–	+	**17.4**	–	0.4
Polytrichum juniperinum	0.1	0.1	**0.7**	–	+	–	2.3	**8.7**	**1.7**
Polytrichum piliferum	–	–	–	+	–	–	–	+	–
Rhodobryum roseum	0.1	–	–	–	–	–	–	–	–
Barbilophozia spp.	–	–	–	**0.7**	0.1	±	7.9	0.9	**0.9**
Lophozia spp.	–	–	–	–	0.1	–	+	–	–
Orthocaulis spp.	3.8	**4.5**	**0.6**	–	–	–	0.3	–	–
Ptilidium ciliare	–	0.7	1.1	0.1	**0.8**	–	+	5.3	**0.5**
Cetraria cucullata	–	–	–	–	+	–	–	–	–
Cetraria ericetorum	–	–	–	–	–	–	–	+	–
Cetraria islandica	–	–	0.1	+	–	–	0.1	–	+
Cetraria nivalis	–	–	–	+	0.1	–	–	–	0.1
Cetraria delisei	–	–	–	–	–	6.0	–	–	–
Cladina mitis	0.1	0.4	1.1	**1.4**	**4.9**	**0.1**	**15.6**	**7.2**	**5.4**
Cladina rangiferina	–	0.2	0.8	**4.2**	**8.5**	6.5	**9.2**	**0.6**	**8.5**
Cladina stellaris	–	–	–	+	–	12.0	0.1	+	+
Cladonia amaurocraea	0.1	0.1	0.4	–	**0.1**	–	–	–	0.1
Cladonia bellidiflora	–	–	0.2	–	+	–	0.1	+	0.1
Cladonia carneola	–	–	–	–	+	–	+	+	–
Cladonia chlorophaea	–	–	0.1	–	+	–	+	0.1	0.1
Cladonia coccifera	–	0.1	**0.2**	+	0.1	–	0.1	0.1	0.1
Cladonia crispata	–	–	0.2	–	–	0.1	0.1	**0.1**	+
Cladonia deformis	–	0.1	0.1	–	–	–	+	–	–
Cladonia ecmocyna	0.1	0.1	0.1	**0.2**	0.2	0.1	**0.4**	**0.1**	0.1
Cladonia gracilis dilatata	–	–	–	–	+	–	–	–	–
Cladonia gracilis elongata	–	0.1	**0.4**	+	**0.1**	–	0.1	**0.1**	0.1
Cladonia macrophylla	–	0.1	**0.1**	–	–	–	+	+	+
Cladonia pyxidata	–	–	0.1	–	–	–	–	–	+
Cladonia sulphurina	–	–	–	–	±	–	±	+	+
Cladonia uncialis	0.1	0.1	**0.3**	0.3	0.1	–	±	0.8	0.4
Ichmadophila ericetorum	–	–	–	–	–	–	+	–	+
Lecidea spp.	–	–	–	–	0.1	–	0.7	–	0.5
Nephroma arcticum	**5.5**	**13.4**	**8.0**	4.0	+	–	+	–	–
Ochrolechia spp.	–	–	–	–	0.1	–	–	–	–
Peltigera rufescens	0.1	**3.0**	1.5	–	+	–	–	–	–
Stereocaulon spp.	–	–	–	+	0.3	+	2.6	**10.4**	7.2
n	26	14	8	9	9	6	16	7	10

Appendix 2. Mean percentage cover of plants in community types of the Phyllodoce-Myrtillus group. The frequencies of taxa in each community type are indicated as follows: bold, frequency >66.7%; underline, frequency 33.3–66.7%; normal text, frequency <33.3%. mBnS = mossy Betula nana scrub, Myrt. var. = Myrtillus variant, Emp. var. = Empetrum variant, aMDiT = arctic–hemiarctic Myrtillus–Dicranum type, aMDiLiT = arctic–hemiarctic Myrtillus–Dicranum–Lichenes type, BnLiS = Betula nana–Lichenes scrub, typ. var. = typical variant, Emp. var. = Empetrum variant, aMLiT = arctic–hemiarctic Myrtillus–Lichenes type, PT = Phyllodoce type, typ. var = typical variant, Emp. var. = Empetrum variant, aEVT = arctic–hemiarctic Empetrum–Vaccinium type, Emp. var. = Empetrum variant, Clad. var. = Cladina variant, typ. var. = typical variant, Cniv var. = Cetraria nivalis variant.

	mBnS		aMDiT	aMDiLiT	BnLiS		aMLiT	PT		aEVT		
	Myrt. var.	Emp. var.			typ. var.	Emp. var.		typ. var.	Emp. var.	Clad var.	typ. var.	Cniv var.
Alchemilla sp.	–	–	0.3	–	–	–	–	–	–	–	–	–
Antennaria dioica	–	–	–	–	–	–	–	–	–	+	–	–
Arctostaphylos alpina	–	1.5	–	1.8	–	–	–	–	1.4	–	2.7	12.5
Betula nana	**22.1**	7.7	3.2	6.0	**27.1**	**16.6**	**17.2**	**14.0**	**13.4**	**20.1**	**17.2**	12.5
Betula pubescens czerepanovii	–	–	–	–	–	2.0	–	+	1.6	1.6	0.7	–
Calamagrostis lapponica	0.7	2.5	–	0.9	1.1	–	0.2	5.1	+	3.2	3.2	0.5
Carex bigelowii	–	0.1	–	0.1	1.5	4.6	0.9	**3.2**	0.1	+	+	0.2
Carex brunnescens	–	–	–	–	–	–	+	+	–	–	–	–
Carex vaginata	–	–	–	–	–	+	–	–	–	–	–	–
Cassiope hypnoides	–	–	–	0.1	–	–	–	–	–	–	–	–
Cassiope tetragona	–	–	–	–	–	–	–	–	–	0.2	–	–
Cornus suecica	–	2.7	–	–	–	–	–	–	+	–	–	–
Deschampsia flexuosa	**0.8**	0.3	**11.9**	2.6	3.6	1.2	3.4	**0.4**	**7.4**	0.2	0.2	+
Diapensia lapponica	–	–	–	–	–	–	–	–	+	–	–	+
Diphasiastrum alpinum	–	0.1	0.1	0.1	+	–	1.7	0.1	0.2	–	0.1	–
Diphasiastrum complanatum	–	–	–	–	–	–	–	–	–	–	1.5	–
Empetrum nigrum hermaphroditum	**26.5**	**39.2**	**19.9**	**16.9**	**21.3**	**28.0**	**17.4**	**16.1**	**24.5**	**16.1**	**24.9**	**19.8**
Festuca ovina	–	0.4	–	–	+	+	–	0.1	+	1.4	0.2	+
Hieracium Alpina coll.	–	–	0.1	0.1	+	–	–	–	–	–	–	0.2
Huperzia selago	–	0.1	–	–	–	–	+	–	–	–	–	+
Juncus trifidus	–	0.1	0.1	0.3	0.1	–	1.7	+	0.2	0.1	0.3	+
Juniperus communis	–	–	–	–	–	+	–	–	3.8	–	0.7	–
Ledum palustre	–	–	–	–	0.1	–	–	–	–	–	–	–
Linnaea borealis	–	–	–	–	–	0.1	–	–	0.2	–	+	–
Loiseleuria procumbens	–	0.4	–	–	0.5	–	0.2	–	–	–	1.4	1.4
Lycopodium annotinum	–	–	0.1	0.1	–	–	–	+	+	–	1.3	–
Pedicularis lapponica	–	0.1	0.1	0.1	+	+	–	–	0.1	–	+	–
Phyllodoce caerulea	–	0.5	0.1	0.5	7.0	5.2	7.3	15.6	7.4	1.4	2.2	1.4
Polygonum viviparum	–	0.1	–	–	–	–	–	–	–	–	–	–
Rubus chamaemorus	–	0.1	–	–	0.1	–	–	–	–	–	–	–
Salix glauca	–	–	–	–	+	0.1	–	–	+	–	–	–
Salix herbacea	–	1.1	2.1	8.1	0.2	–	+	–	1.5	–	–	–
Silene acaulis	–	0.3	–	–	–	–	–	–	–	–	–	–
Solidago virgaurea	–	0.1	0.1	0.1	0.1	0.1	–	0.1	0.1	+	+	–
Trientalis europaea	–	–	–	–	–	+	–	–	+	+	0.1	–
Vaccinium myrtillus	**19.2**	12.6	**37.3**	**13.4**	17.5	**14.1**	**20.8**	6.7	3.7	9.1	6.3	0.5
Vaccinium uliginosum	0.4	2.8	0.3	1.9	2.7	2.6	+	0.4	1.9	0.3	2.0	6.0
Vaccinium vitis-idaea	**11.4**	5.6	0.1	**3.2**	**9.6**	**9.9**	**10.4**	**6.7**	**5.6**	**13.8**	**17.2**	**24.4**
Aulacomnium turgidum	–	0.1	–	–	–	–	–	–	–	–	–	–
Dicranum bergeri	–	–	–	–	–	–	–	–	+	+	–	–
Dicranum fuscescens	3.7	**30.1**	**6.2**	**40.2**	**23.1**	**6.6**	**21.9**	**31.2**	**16.7**	**13.4**	**7.7**	**10.0**
Dicranum scoparium	**9.6**	2.8	**3.0**	1.6	+	0.2	–	+	–	+	+	+
Hylocomium splendens	**38.4**	8.1	1.3	7.7	–	–	–	–	–	–	–	–
Kiaeria starkei	–	–	–	–	–	–	0.7	–	–	–	–	–

Appendix 2. Continued

	mBnS		aMDiT	aMDiLiT	BnLiS		aMLiT	PT		aEVT		
	Myrt. var.	Emp. var.			typ. var.	Emp. var.		typ. var.	Emp. var.	Clad var.	typ. var.	Cniv var.
Pleurozium schreberi	**5.0**	**8.4**	**4.9**	7.2	1.1	**4.1**	–	+	–	+	0.2	–
Pohlia nutans	–	–	0.1	0.1	–	–	+	0.1	–	+	0.1	0.1
Polytrichastrum alpinum	**0.3**	0.3	**0.7**	1.0	1.9	0.7	2.1	8.3	7.0	0.1	–	+
Polytrichum hyperboreum	–	–	–	0.5	0.1	–	0.2	+	1.4	2.4	3.1	0.8
Polytrichum juniperinum	0.1	0.1	0.1	2.1	0.1	0.1	2.9	3.9	0.4	2.2	1.7	+
Polytrichum piliferum	–	–	–	–	+	+	+	0.3	+	+	0.7	+
Racomitrium lanuginosum	–	–	–	0.2	–	–	–	–	–	–	–	–
Sanionia uncinata	–	–	–	0.1	–	–	–	–	–	–	–	–
Anastrophyllum minutum	–	–	0.1	0.1	–	–	–	–	–	–	–	–
Barbilophozia spp.	–	–	–	–	1.1	**5.9**	+	+	3.3	0.2	1.5	+
Orthocaulis spp.	**2.5**	6.8	**24.6**	**2.5**	1.4	2.3	2.3	1.1	–	0.9	–	–
Ptilidium ciliare	**1.7**	8.2	0.1	–	+	–	–	+	0.1	5.0	0.4	1.6
Tetralophozia setiformis	–	–	–	0.1	1.0	–	–	+	–	+	0.1	+
Alectoria nigricans	–	–	–	–	–	–	–	–	–	+	+	+
Alectoria ochroleuca	–	–	–	–	–	–	–	0.2	–	+	–	+
Bryocaulon divergens	–	–	–	–	–	–	+	–	–	–	–	+
Cetraria cucullata	0.1	0.1	–	0.1	–	–	+	–	+	±	+	3.1
Cetraria ericetorum	–	–	–	0.1	0.1	±	0.5	3.0	0.4	0.5	+	0.3
Cetraria islandica	**0.2**	0.1	–	**0.2**	0.4	0.2	2.5	**3.0**	0.4	0.2	+	–
Cetraria nivalis	–	0.1	–	–	+	–	0.8	+	+	**2.8**	+	**15.8**
Cladina arbuscula	–	–	–	–	+	–	–	–	–	–	+	–
Cladina mitis	**2.5**	**3.0**	**0.6**	**3.8**	**23.6**	**15.3**	**21.5**	**23.4**	**17.2**	**22.7**	**16.0**	**15.2**
Cladina rangiferina	**0.5**	**0.5**	0.1	**0.8**	**8.1**	**13.8**	**4.0**	0.4	**4.1**	**8.1**	**3.2**	0.3
Cladina stellaris	–	–	–	–	**17.7**	4.1	**12.8**	**11.8**	**4.9**	**8.3**	+	0.2
Cladonia amaurocraea	0.1	–	0.1	0.1	+	+	+	–	+	2.9	0.1	0.4
Cladonia bellidiflora	**0.1**	0.1	0.1	**0.1**	0.1	+	**0.3**	**0.5**	0.1	0.1	+	+
Cladonia carneola	–	–	–	–	–	–	+	+	+	–	–	–
Cladonia chlorophaea	0.1	–	–	0.1	+	+	**0.1**	0.1	0.1	0.1	**0.1**	+
Cladonia coccifera	0.1	0.1	0.1	0.6	1.1	+	**2.0**	**9.4**	0.1	**0.3**	0.1	+
Cladonia crispata	0.1	0.1	0.1	**0.4**	**0.1**	0.1	0.2	**0.5**	**0.4**	**0.3**	0.1	+
Cladonia deformis	–	0.1	–	0.1	+	+	+	–	+	–	+	+
Cladonia delessertii	–	0.1	0.1	0.1	–	–	+	–	–	–	–	–
Cladonia ecmocyna	0.1	0.1	**0.3**	**0.2**	0.2	0.2	+	+	0.1	0.1	**0.2**	+
Cladonia furcata	–	–	–	–	–	–	+	–	–	–	–	–
Cladonia gracilis elongata	**0.1**	**0.2**	–	**0.3**	**0.6**	0.2	**2.0**	**0.4**	**0.2**	**5.4**	**0.3**	**0.2**
Cladonia gracilis dilatata	–	–	–	0.1	+	–	+	+	+	+	–	–
Cladonia macrophylla	–	–	–	–	0.1	+	+	0.1	+	+	+	+
Cladonia sulphurina	–	–	–	–	0.1	+	0.2	**1.0**	+	0.1	0.2	+
Cladonia uncialis	0.1	**0.9**	0.1	**0.7**	**5.4**	0.6	**8.8**	**0.7**	**4.6**	**6.1**	**3.2**	2.9
Coriscium viride	–	–	–	–	+	–	–	–	–	+	–	–
Ichmadophila ericetorum	–	–	–	0.1	+	–	+	+	–	–	+	–
Lecidea spp.	–	–	–	–	1.1	±	6.8	5.4	1.5	0.1	3.5	–
Nephroma arcticum	**33.9**	**17.2**	2.4	**33.9**	–	4.1	+	+	–	0.1	+	–
Ochrolechia spp.	–	1.4	–	0.4	–	–	**6.1**	+	+	0.3	0.2	4.8
Peltigera rufescens	0.1	1.8	0.1	**1.0**	–	–	–	–	–	–	–	–
Peltigera scabrosa	–	0.1	–	–	0.1	+	0.2	+	–	–	–	–
Psoroma hypnorum	–	0.1	–	0.1	–	–	–	–	–	–	+	–
Sphaerophorus fragilis	–	–	–	–	–	–	–	–	–	+	–	–
Sphaerophorus globosus	–	0.1	–	–	–	–	–	–	–	0.1	+	0.5
Stereocaulon spp.	–	0.1	–	0.7	**24.1**	**12.6**	12.6	**26.6**	**25.9**	**18.4**	**20.2**	12.8
Thamnolia vermicularis	–	0.1	–	0.1	–	–	–	–	–	–	–	–
n	7	18	14	20	35	9	26	25	14	26	27	13

Appendix 3 Mean %-cover of plants in community types of the Arctostaphylos group. The frequencies of taxa in each community type are indicated as follows: bold, frequency >66.7%; underline, frequency 33.3–66.7%; normal text, frequency <33.3%. aEDiLiT = arctic–hemiarctic Empetrum–Dicranum–Lichenes type, OcT = Ochrolechia type, ECnT = Empetrum–Cetraria nivalis type, ELT = Empetrum–Loiseleuria type, AAT = Arctostaphylos–Alectoria type.

	aEDiLiT	OcT	ECnT		ELT	AAT	
				trampled stage			trampled stage
Arctostaphylos alpina	1.5	–	+	–	5.0	10.0	1.7
Betula nana	**10.6**	**0.5**	**18.1**	**8.1**	6.0	**6.8**	**7.2**
Calamagrostis lapponica	0.9	0.6	0.6	+	0.1	–	–
Carex bigelowii	–	–	0.3	0.1	1.9	+	+
Carex brunnescens	–	–	–	–	1.7	–	–
Carex vaginata	–	–	0.1	–	+	–	–
Cassiope tetragona	–	0.6	0.1	–	–	–	–
Deschampsia flexuosa	0.1	–	–	–	0.9	–	–
Diapensia lapponica	0.9	1.5	–	–	+	–	–
Empetrum nigrum hermaph.	**28.1**	**11.3**	**15.5**	**6.2**	**18.5**	**25.9**	**10.7**
Festuca ovina	–	0.1	0.3	–	0.3	–	–
Hieracium Alpina coll.	–	–	+	–	–	–	–
Hierochloë alpina	–	–	+	–	0.1	–	–
Huperzia selago	–	–	–	–	+	–	–
Juncus trifidus	0.5	–	0.2	+	+	+	+
Linnaea borealis	–	–	0.1	–	–	–	–
Loiseleuria procumbens	0.9	0.1	0.2	–	2.8	0.1	–
Luzula arcuata confusa	–	0.1	+	–	0.1	+	–
Luzula spicata	0.1	–	–	–	–	–	–
Lycopodium annotinum	–	–	+	–	–	–	–
Pedicularis lapponica	–	–	+	–	–	–	–
Phyllodoce caerulea	–	–	4.7	1.0	–	0.1	–
Polygonum viviparum	0.1	0.1	–	–	–	–	–
Rubus chamaemorus	0.1	–	–	–	–	–	–
Salix glauca	–	–	–	–	+	–	–
Salix herbacea	0.7	**2.4**	0.1	–	0.2	+	–
Trientalis europaea	–	–	+	–	–	–	–
Vaccinium myrtillus	–	–	2.6	1.0	2.6	–	–
Vaccinium uliginosum	**3.8**	**2.3**	0.8	–	2.5	**4.5**	1.8
Vaccinium vitis-idaea	**6.3**	**4.2**	**8.1**	**0.6**	**4.0**	**4.6**	**1.6**
Aulacomnium turgidum	0.4	0.4	–	–	–	–	–
Dicranum fuscescens	**18.5**	16.4	**10.3**	**5.5**	0.9	3.5	**0.3**
Dicranum majus	0.1	–	–	–	–	–	–
Dicranum scoparium	1.0	0.1	–	–	–	–	–
Hylocomium splendens	7.1	0.1	–	–	–	–	–
Pleurozium schreberi	5.8	1.8	–	–	–	–	–
Pohlia nutans	–	–	+	–	0.1	–	–
Polytrichastrum alpinum	–	0.1	+	0.2	–	–	–
Polytrichum hyperboreum	2.4	0.3	3.3	**0.6**	4.8	**0.8**	–
Polytrichum juniperinum	0.5	2.2	0.2	0.2	+	1.7	–
Polytrichum piliferum	0.1	0.1	0.1	–	2.0	0.5	+
Racomitrium lanuginosum	0.1	**2.6**	+	–	+	+	–
Anastrophyllum minutum	0.1	–	+	–	0.1	+	–
Lophozia spp.	–	–	+	–	–	+	–
Ptilidium ciliare	9.0	1.8	+	–	–	1.9	–
Tetralophozia setiformis	0.8	**1.1**	0.5	–	–	–	–

Appendix 3. Continued

	aEDiLiT	OcT	ECnT		ELT	AAT	
				trampled stage			trampled stage
Alectoria nigricans	0.1	**0.4**	**1.1**	±	**5.3**	**0.4**	+
Alectoria ochroleuca	–	0.1	0.2	–	**5.7**	0.1	+
Bryocaulon divergens	1.0	0.1	+	–	**7.7**	**0.1**	–
Cetraria cucullata	0.1	0.1	**0.3**	+	**2.8**	**0.2**	+
Cetraria delisei	–	–	+	+	–	–	–
Cetraria ericetorum	0.1	0.1	**2.5**	**0.1**	3.2	**0.3**	+
Cetraria islandica	0.1	–	0.1	+	+	–	–
Cetraria nigricans	–	–	+	–	+	–	–
Cetraria nivalis	0.1	1.1	**23.9**	**0.7**	**12.8**	**11.6**	**0.5**
Cladina arbuscula	–	–	–	–	–	+	–
Cladina mitis	**1.3**	1.1	**14.1**	**0.1**	**3.2**	**2.2**	**0.1**
Cladina rangiferina	0.1	0.1	**1.3**	–	+	0.1	±
Cladina stellaris	–	–	0.2	+	+	+	+
Cladonia amaurocraea	**0.1**	0.2	**0.3**	+	±	±	–
Cladonia bellidiflora	0.1	0.1	0.1	+	+	0.1	–
Cladonia chlorophaea	–	–	0.1	–	0.1	+	–
Cladonia coccifera	0.2	**0.2**	**0.2**	+	0.1	0.1	+
Cladonia crispata	0.1	0.1	0.2	–	+	+	–
Cladonia deformis	0.1	–	+	–	–	–	–
Cladonia delessertii	–	–	+	–	–	–	–
Cladonia ecmocyna	0.1	–	–	–	–	+	–
Cladonia furcata	–	–	+	–	–	–	–
Cladonia gracilis elongata	0.1	**0.1**	**0.9**	+	+	0.1	+
Cladonia macrophylla	0.1	–	±	–	+	+	+
Cladonia pyxidata	0.1	–	–	–	+	–	–
Cladonia sulphurina	–	–	+	–	–	+	–
Cladonia uncialis	**0.6**	**0.5**	**0.6**	±	0.3	**0.1**	+
Cladonia verticillata	–	–	+	–	0.2	–	–
Coelocaulon aculeatum	0.1	0.1	–	–	–	+	–
Coriscium viride	–	–	+	–	+	+	±
Lecidea spp.	–	–	**7.4**	**1.7**	**16.8**	**6.5**	+
Nephroma arcticum	1.5	–	+	0.1	–	+	–
Ochrolechia spp.	**14.6**	**22.6**	**8.2**	0.1	**4.6**	1.8	+
Peltigera rufescens	0.4	0.1	–	–	–	–	–
Peltigera scabrosa	–	–	+	–	–	–	–
Psoroma hypnorum	0.1	–	+	–	–	–	–
Solorina crocea	0.4	0.1	–	–	+	–	–
Sphaerophorus fragilis	–	–	–	–	–	+	–
Sphaerophorus globosus	**3.9**	**8.5**	**2.2**	0.1	**10.4**	**0.3**	**0.2**
Stereocaulon spp.	0.2	0.1	4.3	0.1	0.3	1.5	+
Thamnolia vermicularis	**0.2**	**0.1**	+	–	+	+	–
n	21	10	63	12	21	21	8

Appendix 4. Mean percentage-cover of plants in community types of the Betula nana group. The frequencies of taxa in each community type are indicated as follows: bold, frequency >66.7%; underline, frequency 33.3-66.7%; normal text, frequency <33.3%. BnClT = Betula nana-Cladina type, ClapCunc s = Calamagrostis lapponica-Cladonia uncialis stage, CcocPhyp s = Cladonia coccifera-Polytrichum hyperboreum stage, Cla s = Cladina stage, Cniv var = Cetraria nivalis variant, Ster var = Stereocaulon variant. BnST = Betula nana-Stereocaulon type, typ var = typical variant, gram s = graminoid stage, Fovi var = Festuca ovina variant.

	BnClT						**BnST**		
	Clap Cunc s	Ccoc Phyp s	gram s	Cla s	Cniv var	Ster var	typ var	gram s	Fovi var
Betula nana	**17.4**	**13.7**	**7.5**	**24.3**	**27.0**	**21.6**	**26.1**	**17.5**	**25.0**
Calamagrostis lapponica	3.5	+	0.5	0.4	+	0.5	1.5	–	1.3
Carex bigelowii	**6.6**	4.6	**3.7**	**0.4**	**3.8**	**4.6**	**1.5**	**5.8**	**4.4**
Carex brunnescens	+	0.2	0.3	+	+	–	+	0.4	0.1
Carex lachenalii	–	–	–	–	–	–	–	–	–
Carex vaginata	+	+	0.2	–	0.4	–	0.1	**0.7**	+
Cassiope hypnoides	–	–	–	–	–	–	+	–	–
Cassiope tetragona	–	0.2	–	–	–	–	–	–	–
Deschampsia flexuosa	–	1.8	0.1	+	+	1.8	0.1	0.5	0.7
Diphasiastrum alpinum	–	+	–	+	–	+	+	–	+
Empetrum nigrum hermaph.	0.4	2.4	0.1	8.9	2.9	**15.5**	5.0	0.4	3.3
Festuca ovina	0.3	**2.1**	**3.1**	+	0.1	1.0	**0.6**	**3.3**	**4.8**
Hieracium Alpina coll.	+	–	–	+	–	–	+	0.1	+
Huperzia selago	–	–	–	+	–	–	–	–	–
Juncus trifidus	0.1	0.6	+	0.1	–	+	0.2	0.1	0.2
Juniperus communis	–	0.1	–	–	–	–	–	–	–
Luzula arcuata confusa	+	–	–	–	–	–	–	–	–
Luzula spicata	+	–	+	–	–	–	–	+	0.1
Nardus stricta	–	–	–	–	–	–	–	0.2	–
Pedicularis lapponica	+	–	–	–	–	–	–	–	+
Phyllodoce caerulea	3.0	3.8	+	2.0	2.7	2.3	0.8	–	0.5
Polygonum viviparum	–	–	–	–	–	–	–	+	–
Rubus chamaemorus	+	–	–	–	+	–	–	–	–
Salix glauca	–	1.5	–	–	–	+	0.8	–	–
Salix herbacea	**1.5**	+	+	+	0.1	+	0.1	0.4	0.2
Solidago virgaurea	–	+	0.1	–	–	+	+	+	–
Trientalis europaea	+	–	0.2	–	0.3	–	0.1	**0.6**	0.1
Vaccinium myrtillus	0.7	5.2	–	3.1	0.8	3.8	0.8	0.5	5.3
Vaccinium uliginosum	–	0.2	+	–	+	–	–	–	–
Vaccinium vitis-idaea	**3.3**	**4.7**	**0.5**	**8.1**	**3.8**	**5.8**	**0.8**	**0.2**	**0.9**
Conostomum tetragonum	–	–	–	–	–	–	–	–	+
Dicranum fuscescens	**28.6**	**16.9**	**8.1**	**17.7**	**19.6**	**24.2**	**36.2**	**27.1**	**47.8**
Dicranum scoparium	–	–	–	–	–	+	–	+	–
Hylocomium splendens	–	–	–	–	–	–	–	–	0.2
Pleurozium schreberi	–	–	–	–	–	0.9	–	–	–
Pohlia nutans	–	+	–	+	–	+	+	–	–
Polytrichastrum alpinum	0.1	1.	+	0.5	0.4	0.1	**1.1**	**1.8**	**4.5**
Polytrichum hyperboreum	**6.5**	**18.5**	**0.5**	**8.3**	**8.1**	3.8	3.4	3.1	1.3
Polytrichum juniperinum	+	+	+	1.5	+	0.1	1.6	**1.1**	**5.3**
Polytrichum piliferum	+	1.5	–	+	–	+	–	–	–
Anastrophyllum minutum	+	+	–	–	–	–	–	–	+
Orthocaulis spp.	+	1.6	–	+	–	+	–	–	0.1
Ptilidium ciliare	+	0.4	–	0.1	–	0.1	–	–	–

Appendix 4. Continued

	BnClT						BnST		
	Clap Cunc s	Ccoc Phyp s	gram s	Cla s	Cniv var	Ster var	typ var	gram s	Fovi var
Alectoria nigricans	+	+	+	0.1	**0.1**	0.1	+	–	–
Alectoria ochroleuca	–	+	–	0.1	–	–	–	–	–
Cetraria cucullata	–	0.2	–	0.1	0.1	0.1	+	–	+
Cetraria delisei	+	0.1	–	+	–	–	–	–	+
Cetraria ericetorum	**0.9**	4.1	–	**3.7**	**0.1**	0.2	+	–	+
Cetraria islandica	**4.0**	2.5	+	0.4	**1.1**	**2.0**	**0.7**	**0.2**	**2.6**
Cetraria nivalis	**1.1**	**6.7**	**+**	**7.3**	**12.3**	**2.9**	**1.1**	+	0.1
Cladina mitis	**17.1**	**23.2**	+	**27.8**	**12.6**	**15.1**	**4.8**	+	**8.3**
Cladina rangiferina	**0.2**	**3.3**	+	**8.5**	**2.3**	**2.5**	**0.6**	+	**3.0**
Cladina stellaris	**1.8**	**13.8**	+	**18.0**	**5.9**	**7.9**	**6.3**	+	**2.6**
Cladonia amaurocraea	+	+	–	+	0.1	+	+	–	–
Cladonia bellidiflora	**0.3**	**0.3**	–	0.1	0.1	+	0.1	+	0.1
Cladonia chlorophaea	0.1	0.1	–	+	0.1	0.1	+	–	+
Cladonia coccifera	**1.3**	**6.4**	–	**0.6**	0.1	**0.1**	**0.1**	+	0.1
Cladonia crispata	**0.4**	0.3	–	**0.1**	0.1	0.1	+	–	+
Cladonia deformis	–	–	+	–	–	+	–	–	–
Cladonia ecmocyna	+	+	–	+	–	+	–	–	+
Cladonia gracilis dilatata	–	+	–	–	–	–	–	–	–
Cladonia gracilis elongata	**0.3**	**0.7**	+	**3.0**	**0.5**	**0.4**	**0.1**	+	**0.9**
Cladonia macrophylla	0.1	0.1	–	+	+	+	+	+	+
Cladonia pyxidata	–	+	–	–	–	–	–	–	–
Cladonia sulphurina	0.1	0.1	–	0.2	+	+	+	–	+
Cladonia uncialis	**8.8**	**2.5**	+	**0.4**	**0.2**	**0.5**	**0.2**	**0.1**	**1.3**
Cladonia verticillata	–	+	–	–	–	–	–	–	–
Coelocaulon divergens	–	–	–	+	–	–	–	–	–
Coriscium viride	–	–	–	+	–	–	–	–	+
Ichmadophila ericetorum	–	0.1	–	+	+	–	–	–	–
Lecidea spp.	**8.2**	10.0	–	0.2	0.2	+	+	+	–
Nephroma arcticum	+	–	+	0.3	0.3	0.1	**0.9**	**0.3**	**6.3**
Ochrolechia spp.	**8.5**	**9.8**	–	2.7	**0.1**	0.1	+	+	0.3
Peltigera scabrosa	+	–	–	0.1	+	0.2	+	–	0.4
Solorina crocea	–	–	–	–	–	–	–	–	+
Sphaerophorus globosus	–	–	+	+	0.1	–	+	–	–
Stereocaulon spp.	13.9	**16.7**	+	**8.6**	**6.2**	**20.4**	**15.4**	**1.3**	**4.0**
Thamnolia vermicularis	–	–	–	–	–	+	–	–	–
n	13	25	16	45	14	20	26	12	29

Appendix 5. Mean percentage–cover of plants in community types of the Juncus trifidus–Salix herbacea group. The frequencies of taxa in each community type are indicated as follows: bold, frequency >66.7%; underline, frequency 33.3–66.7%; normal text, frequency <33.3%. JtDfT = Juncus trifidus–Deschampsia flexuosa type, ShChT = Salix herbacea–Cassiope hypnoides type, DfST = Deschampsia flexuosa–Stereocaulon type, typ var. = typical variant, Chyp var. = Cassiope hypnoides variant, JtCmT = Juncus trifidus–Cladina mitis type, typ. var. = typical variant, Ster. var. = Stereocaulon variant, EST = Empetrum–Stereocaulon type, SoDfT = Solidago–Deschampsia flexuosa type.

	JtDfT	ShChT	DfST		JtCmT		EST	SoDfT
			typ. var.	Chyp var.	typ. var.	Ster. var.		
Agrostis mertensii	–	–	–	–	–	–	–	0.7
Antennaria dioica	–	0.1	–	–	–	+	–	–
Anthoxanthum odor.alpinum	1.7	0.2	0.1	+	–	–	–	–
Betula nana	0.1	–	**13.7**	**5.8**	0.6	6.8	1.7	–
Betula pubescens czerepanovii	–	–	–	–	–	+	+	–
Calamagrostis lapponica	0.1	0.2	–	–	+	–	0.1	–
Carex bigelowii	0.1	1.0	**6.1**	**9.5**	0.1	4.8	0.5	–
Carex brunnescens	–	–	0.2	0.7	0.1	+	–	5.7
Carex lachenalii	–	0.1	0.4	0.1	–	–	–	**4.8**
Carex vaginata	–	–	0.2	–	–	–	–	–
Cassiope hypnoides	0.1	7.4	+	**5.1**	+	–	–	–
Cassiope tetragona	–	–	–	–	1.8	–	–	–
Cerastium alpinum	–	0.1	–	–	–	–	–	–
Cerastium cerastoides	–	–	–	–	–	–	–	0.1
Cornus suecica	–	–	2.8	–	–	–	–	–
Deschampsia flexuosa	**5.2**	0.8	**13.4**	**4.7**	4.5	1.0	**8.0**	12.3
Diapensia lapponica	0.1	–	–	–	–	–	–	–
Diphasiastrum alpinum	0.3	–	**5.7**	0.7	6.1	**5.1**	0.1	–
Empetrum nigrum hermaphroditum	5.1	0.6	**11.1**	**5.2**	4.5	**10.8**	**34.8**	0.6
Festuca ovina	–	0.2	3.0	**0.9**	0.3	0.4	0.1	–
Festuca vivipara	–	0.1	–	–	–	–	–	–
Gnaphalium supinum	**0.2**	0.6	+	+	+	–	–	+
Hieracium Alpina coll.	0.1	**0.2**	0.1	0.9	0.1	0.1	+	+
Huperzia selago	–	0.1	+	+	+	–	–	+
Juncus trifidus	**6.9**	–	0.1	**0.7**	**15.4**	12.8	–	–
Juniperus communis	–	–	–	–	2.0	0.2	5.0	–
Linnaea borealis	–	–	–	–	–	–	3.8	–
Loiseleuria procumbens	0.1	0.1	0.4	0.1	+	+	–	–
Luzula arcuata confusa	–	0.1	–	–	+	–	–	–
Luzula parviflora	–	–	–	–	–	–	–	0.1
Luzula spicata	0.1	0.1	+	0.1	+	+	–	0.4
Minuartia biflora	–	0.1	–	–	–	–	–	+
Nardus stricta	–	–	+	0.9	–	–	–	–
Pedicularis lapponica	0.1	–	–	+	–	+	–	–
Phyllodoce caerulea	0.1	0.8	0.6	**5.0**	4.7	3.7	2.5	–
Poa alpina	–	0.1	–	–	–	–	–	–
Polygonum viviparum	**0.8**	**4.3**	–	0.4	+	–	–	–
Pyrola minor	–	–	+	–	–	–	–	–
Rubus chamaemorus	–	–	–	–	–	+	–	8.5
Rumex acetosa lapponica	–	–	–	–	–	–	–	**2.2**
Salix glauca	–	–	+	–	–	0.1	–	–
Salix herbacea	**17.9**	**23.6**	**11.2**	**13.8**	5.1	0.2	0.5	–
Saxifraga cernua	–	0.1	–	–	–	–	–	–
Sibbaldia procumbens	0.1	0.2	+	0.1	0.3	–	–	4.3
Silene acaulis	–	1.5	–	–	–	–	–	–
Solidago virgaurea	0.1	0.5	0.1	0.8	0.1	0.3	0.6	0.5
Taraxacum croceum	–	0.1	–	–	–	–	–	+
Trientalis europaea	–	–	–	–	–	+	–	–
Trisetum spicatum	–	0.1	–	–	–	–	–	+
Vaccinium myrtillus	8.3	4.4	**10.8**	4.1	6.1	9.5	10.1	0.1
Vaccinium uliginosum	–	–	–	–	+	2.3	–	–
Vaccinium vitis-idaea	0.1	0.1	**0.3**	**0.4**	**3.2**	**2.2**	**10.8**	–
Vahlodea atropurpurea	–	0.1	–	–	–	–	–	–
Veronica alpina	0.1	0.1	–	–	–	–	–	0.1
Viola biflora	–	2.0	–	–	–	–	–	–

Appendix 5. Continued

	JtDfT	**ShChT**	**DfST**		**JtCmT**		**EST**	**SoDfT**
			typ. var.	Chyp var.	typ. var.	Ster. var.		
Andreaea spp.	–	–	–	–	–	–	–	+
Conostomum tetragonum	–	0.1	0.1	0.6	–	–	–	–
Dicranum fuscescens	**24.5**	**12.1**	**33.0**	**16.9**	**10.8**	**24.8**	**4.1**	**5.8**
Dicranum majus	–	0.1	–	–	–	–	–	–
Dicranum scoparium	2.5	1.3	+	**7.8**	–	–	–	4.0
Hylocomium splendens	0.1	0.5	–	–	–	–	–	–
Kiaeria starkei	1.3	0.3	+	8.2	0.5	–	–	+
Pleurozium schreberi	0.1	0.1	–	–	–	+	–	–
Pohlia nutans	0.1	0.1	+	–	0.1	–	0.3	–
Polytrichastrum alpinum	0.1	**0.5**	**4.3**	**2.0**	1.7	5.8	2.1	+
Polytrichum hyperboreum	–	0.5	+	0.7	0.4	+	–	–
Polytrichum juniperinum	**3.5**	1.3	0.4	**6.2**	+	2.4	**3.8**	**1.0**
Polytrichum piliferum	–	0.1	+	0.1	**1.0**	+	0.5	0.1
Racomitrium lanuginosum	–	–	–	–	+	–	–	–
Anastrophyllum minutum	0.2	0.1	–	–	3.6	0.3	–	+
Barbilophozia spp.	–	–	–	–	–	+	3.3	0.2
Gymnomitrion spp.	–	–	–	–	–	–	–	0.1
Lophozia spp.	–	–	–	–	–	–	–	**11.2**
Orthocaulis+Anthelia spp.	3.2	**13.4**	0.1	–	+	0.5	–	0.2
Ptilidium ciliare	–	0.3	–	–	–	+	–	–
Tetralophozia setiformis	–	–	–	0.1	–	–	3.3	–
Alectoria nigricans	–	–	–	–	+	–	–	–
Alectoria ochroleuca	–	–	–	–	+	+	–	–
Cetraria delisei	–	–	0.1	**0.8**	1.1	–	–	+
Cetraria ericetorum	–	0.1	–	–	6.8	**0.9**	1.7	–
Cetraria islandica	0.1	0.1	**2.8**	**6.7**	**6.4**	**5.1**	0.1	**1.2**
Cetraria nivalis	–	0.1	–	–	+	–	–	–
Cladina mitis	0.7	**3.3**	**3.0**	**5.3**	**18.1**	**21.6**	**7.1**	**0.7**
Cladina rangiferina	0.1	0.2	0.4	–	0.1	1.4	+	+
Cladina stellaris	–	–	+	–	0.1	2.8	+	+
Cladonia amaurocraea	–	–	–	–	+	–	+	–
Cladonia bellidiflora	**0.2**	0.1	**0.1**	**0.1**	0.5	**0.8**	**0.1**	**0.7**
Cladonia chlorophaea	0.1	0.1	+	0.1	0.1	+	+	0.1
Cladonia coccifera	**0.1**	**0.2**	**0.8**	**0.7**	**6.0**	**5.9**	**3.4**	**1.1**
Cladonia crispata	0.1	0.1	–	+	0.2	**0.2**	**0.3**	–
Cladonia deformis	–	–	–	–	–	–	–	0.4
Cladonia delessertii	0.1	0.1	–	–	0.4	–	+	–
Cladonia ecmocyna	0.1	0.1	–	–	+	+	0.2	0.2
Cladonia furcata	–	–	–	–	–	+	–	–
Cladonia gracilis elongata	0.4	0.1	**0.1**	**0.8**	0.5	**0.9**	**0.1**	**0.8**
Cladonia macrophylla	–	0.1	+	–	0.1	0.1	–	+
Cladonia pyxidata	–	0.1	–	–	–	–	–	–
Cladonia sulphurina	–	–	+	+	0.1	2.3	+	–
Cladonia uncialis	0.2	**0.5**	**0.5**	**5.1**	**2.9**	**8.7**	**4.0**	**4.7**
Cladonia verticillata	–	–	–	–	+	–	–	–
Ichmadophila ericetorum	–	–	+	–	–	–	0.1	–
Lecidea spp.	–	–	+	1.1	**9.9**	**6.5**	1.7	2.1
Nephroma arcticum	3.1	1.3	**4.0**	0.2	+	1.1	–	4.0
Ochrolechia spp.	0.6	**4.2**	**3.4**	**1.6**	**8.4**	1.1	–	**2.9**
Peltigera canina	–	–	–	–	–	–	–	+
Peltigera leucophlebia	–	0.1	–	–	–	–	–	+
Peltigera rufescens	**0.4**	0.1	–	–	–	–	–	+
Peltigera scabrosa	–	–	+	–	–	+	–	–
Psoroma hypnorum	–	0.1	–	–	–	–	–	+
Solorina crocea	–	–	–	–	+	–	–	–
Sphaerophorus fragilis	–	–	–	+	–	–	–	–
Stereocaulon spp.	0.2	0.5	**20.8**	**30.1**	6.3	**28.2**	**11.0**	+
Thamnolia vermicularis	–	–	–	–	+	–	–	–
n	7	19	13	9	21	16	11	9

Appendix 6. Mean percentage–cover of plants in community types of the Juncus trifidus–Cassiope tetragona group. The frequencies of taxa in each community type are indicated as follows: bold, frequency >66.7%; underline, frequency 33.3–66.7%; normal text, frequency <33.3%. JtCtT = Juncus trifidus–Cassiope tetragona type, Fovi var. = Festuca ovina variant, Trient var. = Trientalis variant, Cbru var. = Carex brunnescens variant, EPAT = Empetrum–Phyllodoce–Alectoria type, ShET = Salix herbacea–Empetrum type, ShOcT = Salix herbacea–Ochrolechia type.

	JtCtT			EPAT	ShET	ShOcT
	Fovi var.	Trient var.	Cbru var.			
Antennaria alpina	–	–	–	–	0.1	0.1
Betula nana	**16.1**	–	–	–	–	–
Calamagrostis lapponica	–	–	–	–	0.6	0.1
Cardamine bellidifolia	–	–	–	–	–	0.1
Carex bigelowii	–	–	0.2	–	–	–
Carex brunnescens	–	–	7.2	–	–	–
Cassiope hypnoides	+	0.3	–	–	0.4	1.1
Cassiope tetragona	4.6	9.8	10.9	3.5	0.6	1.1
Empetrum nigrum hermaph.	0.1	–	–	8.5	7.0	1.8
Erigeron uniflorus	–	–	–	–	–	0.1
Festuca ovina	10.0	0.5	0.2	–	0.1	0.1
Gnaphalium supinum	+	–	–	–	–	0.1
Hieracium alpinum	–	–	–	–	0.7	–
Huperzia selago	–	–	–	–	0.1	0.1
Juncus trifidus	**14.0**	**17.0**	**11.0**	0.1	1.0	0.1
Luzula arcuata confusa	+	3.3	0.1	0.1	–	**1.3**
Luzula spicata	–	–	–	–	0.1	0.1
Phyllodoce caerulea	–	+	3.8	8.5	0.3	0.1
Ranunculus nivalis	–	–	–	–	–	0.1
Salix herbacea	+	8.7	**15.2**	+	**11.9**	**8.8**
Solidago virgaurea	–	+	–	–	–	–
Trientalis europaea	+	3.8	+	+	–	–
Trisetum spicatum	–	–	–	–	0.1	0.1
Vaccinium myrtillus	–	–	3.6	–	–	–
Vaccinium uliginosum	–	–	–	–	1.5	–
Vaccinium vitis-idaea	**9.3**	**5.0**	**2.3**	**5.9**	1.7	0.2
Veronica alpina	–	–	–	–	–	0.1
Conostomum tetragonum	–	–	–	–	0.1	0.1
Dicranum fuscescens	+	–	**2.3**	2.6	**19.3**	**4.1**
Gymnomitrion spp.	–	–	–	0.2	–	–
Kiaeria starkei	–	–	–	+	–	0.5
Pleurozium schreberi	–	–	–	–	0.7	–
Pohlia nutans	+	–	–	–	–	0.4
Polytrichastrum alpinum	–	–	–	–	0.1	0.1
Polytrichum hyperboreum	5.8	**4.1**	1.1	3.4	1.6	3.2
Polytrichum juniperinum	–	0.5	–	+	1.7	–
Polytrichum piliferum	**12.0**	**4.1**	**0.4**	0.1	0.9	1.7
Racomitrium lanuginosum	–	–	–	–	0.1	0.4
Sanionia uncinata	–	–	–	–	0.4	–
Lophozia spp.	–	–	–	+	–	–
Orthocaulis spp.	–	–	0.1	+	**3.2**	**0.9**
Ptilidium ciliare	–	–	–	–	5.9	0.3
Tetralophozia setiformis	+	–	0.1	1.0	2.2	1.0
Alectoria nigricans	5.5	**8.5**	0.1	**16.8**	–	–
Alectoria ochroleuca	+	–	–	+	0.1	–

Appendix 6. Continued

	JtCtT			EPAT	ShET	ShOcT
	Fovi var.	Trient var.	Cbru var.			
Bryoocaulon divergens	**3.0**	**5.6**	+	0.1	0.1	0.1
Cetraria cucullata	**5.3**	**0.4**	+	+	–	–
Cetraria delisei	–	+	0.2	–	0.1	0.1
Cetraria ericetorum	**18.6**	**11.7**	**7.5**	**2.8**	0.1	**0.4**
Cetraria islandica	+	**16.9**	**15.5**	0.1	0.1	–
Cetraria nigricans	+	–	0.1	**1.4**	–	–
Cetraria nivalis	**16.4**	**20.6**	**1.2**	**25.0**	0.7	**0.6**
Cladina mitis	**9.5**	**10.4**	**5.5**	**1.1**	**2.5**	0.1
Cladina rangiferina	+	±	0.1	3.3	0.1	–
Cladina stellaris	–	–	–	+	–	–
Cladonia amaurocraea	+	+	0.1	**0.4**	0.1	0.1
Cladonia bellidiflora	+	0.1	**0.6**	0.1	0.2	0.1
Cladonia chlorophaea	+	+	0.1	+	0.1	–
Cladonia coccifera	0.1	**0.7**	0.6	**0.3**	**0.4**	**1.4**
Cladonia crispata	0.1	+	0.7	0.1	–	–
Cladonia deformis	–	–	–	–	0.1	–
Cladonia delessertii	+	0.1	1.0	–	0.1	0.1
Cladonia ecmocyna	+	–	–	–	–	0.1
Cladonia furcata/subfurcata	–	–	–	+	0.1	–
Cladonia gracilis elongata	0.2	**0.2**	0.3	**3.5**	**0.3**	**0.2**
Cladonia macrophylla	+	0.1	**0.1**	0.1	0.1	–
Cladonia sulphurina	–	+	+	+	–	–
Cladonia uncialis	0.4	–	1.2	+	**0.5**	0.1
Cladonia verticillata	0.1	**0.2**	0.1	0.1	–	–
Coelocaulon aculeatum	+	0.7	+	+	–	0.4
Lecidea spp.	**19.1**	**7.6**	**8.1**	6.7	–	–
Ochrolechia spp.	**3.1**	**18.5**	**22.2**	**10.6**	**15.3**	**28.3**
Peltigera rufescens	–	–	–	–	0.1	0.1
Pseudephebe pubescens	–	–	–	+	–	–
Solorina crocea	+	+	–	+	0.1	0.2
Sphaerophorus fragilis	–	–	–	+	–	–
Sphaerophorus globosus	+	0.1	–	7.1	0.7	0.5
Stereocaulon spp.	0.8	–	–	–	0.2	0.6
Thamnolia vermicularis	0.1	0.1	+	–	0.1	0.1
n	8	11	5	11	12	8

Appendix 7. Mean percentage–cover of plants in community types of the Luzula confusa group. The frequencies of taxa in each community type are indicated as follows: bold, frequency >66.7%; underline, frequency 33.3–66.7%; normal text, frequency <33.3%. LcCnT = Luzula confusa–Cetraria nivalis type, Chyp var. = Cassiope hypnoides variant, ChJtT = Cassiope hypnoides–Juncus trifidus type, LcStT = Luzula confusa–Saxifraga tenuis type.

	LcCnT			**ChJtT**	**LcStT**
	Rac var.	naked var.	Chyp var.		
Cardamine bellidifolia	0.1	0.1	+	+	0.1
Carex bigelowii	–	–	0.7	1.6	–
Carex brunnescens	–	–	–	0.3	–
Carex lachenalii	–	0.1	+	–	–
Cassiope hypnoides	0.1	**0.1**	6.1	6.4	0.5
Cassiope tetragona	0.1	0.1	–	0.1	–
Deschampsia flexuosa	–	–	–	0.8	–
Empetrum hermaphroditum	–	0.1	–	–	–
Huperzia selago	–	0.1	–	+	–
Juncus trifidus	0.3	–	–	3.3	–
Luzula arcuata confusa	**2.9**	2.2	**7.5**	**2.7**	1.7
Minuartia biflora	–	–	+	–	–
Oxyria digyna	–	–	–	–	0.1
Phyllodoce caerulea	–	0.1	0.4	+	0.1
Poa alpina	–	–	–	–	0.1
Ranunculus glacialis	0.4	0.2	–	–	0.2
Salix herbacea	0.1	**0.8**	–	+	0.4
Saxifraga aizoides	–	–	–	–	0.1
Saxifraga rivularis	–	0.1	–	–	–
Saxifraga tenuis	–	0.1	–	–	0.1
Silene acaulis	–	0.1	–	+	–
Trientalis europaea	–	–	–	1.9	–
Vaccinium vitis-idaea	–	–	0.1	+	–
Conostomum tetragonum	0.1	0.1	–	+	–
Kiaeria starkei	–	0.1	0.2	–	–
Oligotrichum hercynicum	–	–	+	–	–
Pogonatum spp.	–	–	+	–	–
Pohlia spp.	0.1	0.1	–	–	0.3
Polytrichastrum alpinum	–	–	–	–	–
Polytrichastrum sexangulare	**0.7**	**0.3**	+	–	**1.6**
Polytrichum hyperboreum	–	0.8	0.9	2.2	–
Polytrichum piliferum	0.1	1.6	0.4	0.1	–
Racomitrium l anuginosum	1.0	–	–	–	0.8
Racomitrium microcarpon	–	–	0.2	0.8	–
Sanionia spp.	–	0.1	–	–	–
Anastrophyllum minutum	–	–	–	+	+
Gymnomitrion spp.	0.7	+	**18.0**	2.0	2.1
Orthocaulis spp.	–	0.3	–	+	0.3
Lophozia spp.	–	–	–	+	–
Alectoria nigricans	0.3	0.1	**0.1**	+	–
Alectoria ochroleuca	0.6	0.1	+	–	0.1
Bryocaulon divergens	0.1	–	+	+	–
Cetraria delisei	–	–	+	0.1	–
Cetraria ericetorum	0.1	0.1	+	+	–
Cetraria islandica	–	0.1	0.1	**3.8**	–

Appendix 7. Continued

	LcCnT			ChJtT	LcStT
	Rac var.	naked var.	Chyp var.		
Cetraria nigricans	–	–	0.2	+	–
Cetraria nivalis	1.9	0.1	**8.1**	0.1	–
Cladina mitis	–	–	+	–	–
Cladonia amaurocraea	–	–	+	–	–
Cladonia bellidiflora	–	–	+	1.7	0.1
Cladonia chlorophaea	–	–	+	+	–
Cladonia coccifera	–	–	**0.1**	**0.2**	–
Cladonia crispata	0.1	–	–	–	0.1
Cladonia delessertii	–	–	–	+	–
Cladonia gracilis elongata	–	–	0.1	0.4	–
Cladonia macrophylla	–	0.1	+	+	–
Cladonia subfurcata	–	–	0.1	+	–
Cladonia sulphurina	–	–	+	+	–
Cladonia verticillata	–	**0.1**	+	–	–
Coelocaulon aculeatum	–	–	+	+	–
Lecidea spp.	–	–	3.4	0.8	–
Ochrolechia spp.	0.9	**6.3**	**10.4**	**8.4**	0.1
Solorina crocea	0.1	0.6	0.2	–	0.1
Sphaerophorus fragilis	0.3	–	+	–	–
Sphaerophorus globosus	–	–	1.7	–	–
Stereocaulon spp.	–	0.1	+	±	0.1
Umbilicaria spp.	–	–	+	–	–
n	4	4	25	22	19

Appendix 8. Mean percentage–cover of plants in community types of the Cassiope tetragona–Vaccinium group. The frequencies of taxa in each community type are indicated as follows: bold, frequency >66.7%; underline, frequency 33.3–66.7%; normal text, frequency <33.3%. CtRgT = Cassiope tetragona–Ranunculus glacialis type, Cbig var. = Carex bigelowii variant, Chyp var. = Cassiope hypnoides variant, ShCnT = Salix herbacea–Cetraria nivalis type, CtCnT = Cassiope tetragona–Cetraria nivalis type, VAT = Vaccinium–Alectoria type, Vvit var. = Vaccinium vitis–idaea variant, Cniv var. = Cetraria nivalis variant.

	CtRgT		**ShCnT**	**CtCnT**	**VAT**	
	hyp var.	typical var.			Vvit var.	Cniv var.
Antennaria alpina	–	0.1	–	–	–	–
Betula nana	–	–	–	–	–	+
Cardamine bellidifolia	**0.2**	0.1	+	–	–	+
Carex bigelowii	0.1	–	+	0.1	–	–
Carex lachenalii	–	0.1	0.1	–	–	–
Cassiope hypnoides	**7.0**	0.8	0.1	–	–	+
Cassiope tetragona	0.1	0.9	0.1	**13.2**	–	–
Cerastium alpinum	–	–	–	–	0.1	–
Empetrum nigrum hermaph.	–	–	0.1	–	–	7.3
Festuca ovina	–	–	–	–	–	0.1
Festuca vivipara	+	–	–	–	–	–
Huperzia selago	–	+	+	+	0.1	0.9
Juncus biglumis	+	–	–	–	–	–
Juncus trifidus	–	2.5	–	–	–	–
Luzula arcuata confusa	**1.3**	**0.5**	**2.5**	**1.1**	0.1	1.1
Oxyria digyna	+	–	–	–	–	–
Phyllodoce caerulea	–	–	–	–	–	2.0
Ranunculus glacialis	**0.5**	1.7	+	–	–	–
Salix glauca	–	–	–	–	–	+
Salix herbacea	0.6	0.2	2.3	–	1.9	3.7
Salix polaris	0.1	–	0.3	–	–	–
Saussurea alpina	–	–	–	–	2.2	–
Saxifraga oppositifolia	–	–	–	–	0.1	–
Silene acaulis	–	–	–	–	–	0.1
Trisetum spicatum	–	–	–	–	0.1	–
Vaccinium uliginosum	–	–	–	–	–	+
Vaccinium vitis-idaea	–	–	2.0	–	**14.7**	**5.6**
Veronica alpina	–	0.1	–	–	–	–
Andreaea spp.	+	–	+	–	–	+
Arctoa fulvella	+	–	–	–	–	–
Conostomum tetragonum	0.1	0.3	–	–	–	–
Dicranum fuscescens	–	–	+	–	**0.1**	+
Dicranum scoparium	–	–	–	0.2	–	–
Kiaeria starkei	+	0.2	+	–	0.6	–
Oligotrichum hercynicum	**0.2**	–	+	0.4	–	+
Pogonatum spp.	+	–	–	–	–	–
Pohlia spp.	–	–	–	–	0.1	–
Polytrichastrum sexangulare	**1.1**	0.2	+	–	0.1	+
Polytrichum hyperboreum	+	0.6	0.4	0.2	0.1	0.4
Polytrichum piliferum	–	–	0.2	0.3	0.2	0.6
Racomitrium lanuginosum	0.3	0.6	0.1	0.8	**0.1**	–
Racomitrium microcarpon	0.1	–	0.2	–	–	+
Sanionia spp.	–	0.1	–	–	–	–
Anastrophyllum minutum	–	+	–	–	–	–
Gymnomitrion spp.	**24.9**	**1.5**	**9.8**	**18.8**	–	4.6
Lophozia spp.	–	–	–	–	–	+

Appendix 8. Continued

	CtRgT		ShCnT	CtCnT	VAT	
	hyp var.	typical var.			Vvit var.	Cniv var.
Orthocaulis spp.	–	0.1	–	–	0.5	+
Ptilidium ciliare	–	–	–	–	–	+
Tetralophozia setiformis	–	–	0.1	+	–	+
Alectoria nigricans	+	0.1	**0.6**	**0.3**	**1.1**	**5.3**
Alectoria ochroleuca	–	0.2	0.1	0.2	0.3	0.3
Bryocaulon divergens	–	0.2	0.3	0.1	0.1	**0.8**
Cetraria cucullata	+	–	+	**0.6**	**0.1**	2.1
Cetraria delisei	0.2	0.6	+	–	–	0.1
Cetraria ericetorum	**0.1**	1.1	+	–	**0.1**	**2.8**
Cetraria islandica	+	1.4	+	**0.6**	0.1	1.2
Cetraria nigricans	+	0.1	**2.2**	0.8	–	4.2
Cetraria nivalis	**0.1**	1.9	**3.4**	**1.0**	**4.0**	**15.5**
Cladina mitis	0.1	0.1	+	+	–	0.1
Cladina rangiferina	–	0.1	–	0.1	–	+
Cladonia amaurocraea	–	–	+	+	0.1	–
Cladonia bellidiflora	–	0.1	+	+	–	+
Cladonia chlorophaea	–	0.1	–	–	–	+
Cladonia coccifera	0.1	0.1	**0.1**	0.1	**0.1**	**0.1**
Cladonia deformis	–	–	–	–	–	+
Cladonia crispata	–	–	+	–	–	+
Cladonia delessertii	–	–	–	+	–	+
Cladonia ecmocyna	–	0.1	–	–	–	–
Cladonia gracilis dilatata	–	–	–	–	–	+
Cladonia gracilis elongata	**0.1**	0.1	0.1	0.1	**0.1**	0.1
Cladonia macrophylla	–	0.1	0.1	–	+	–
Cladonia subfurcata	+	–	+	0.1	–	+
Cladonia uncialis	+	–	–	–	+	+
Cladonia verticillata	–	–	–	0.1	–	0.1
Coelocaulon aculeatum	–	–	0.1	0.2	0.2	0.2
Lecidea spp.	–	–	0.2	+	–	7.5
Ochrolechia spp.	**0.4**	**2.5**	**6.0**	9.5	**15.0**	**11.4**
Pseudephebe pubescens	–	–	0.2	0.3	–	+
Solorina crocea	0.1	0.3	0.1	**0.3**	+	+
Sphaerophorus fragilis	–	–	0.2	+	0.1	+
Sphaerophorus globosus	–	0.1	**0.7**	**0.2**	**2.0**	0.5
Stereocaulon spp.	**0.2**	0.2	+	–	–	+
Thamnolia vermicularis	–	0.1	+	+	0.1	0.1
Umbilicaria spp.	–	–	+	–	–	+
n	13	10	19	6	4	20

Appendix 9. Mean percentage-cover of plants in community types of the Salix herbacea-Kiaeria group. The frequencies of taxa in each community type are indicated as follows: bold, frequency >66.7%; italics, frequency 33.3–66.7%; normal text, frequency <33.3%. ShKiT = Salix herbacea-Kiaeria type, ShVbT = Salix herbacea-Viola biflora type.

	ShKiT	ShVbT
Antennaria alpina	–	**0.4**
Anthoxanthum odoratum	1.3	–
Calamagrostis lapponica	–	*0.1*
Carex bigelowii	–	0.1
Carex lachenalii	0.1	0.1
Cassiope hypnoides	0.3	*0.8*
Cerastium alpinum	–	*0.3*
Festuca ovina	0.1	**0.8**
Gnaphalium supinum	**2.2**	–
Hieracium alpinum	0.1	0.1
Huperzia selago	–	*0.1*
Luzula arcuata confusa	–	0.1
Luzula spicata	–	*0.1*
Minuartia biflora	–	*0.1*
Oxyria digyna	0.3	0.2
Phyllodoce caerulea	0.1	–
Poa alpina	0.7	*0.2*
Polygonum viviparum	**2.1**	**0.7**
Rumex actosa	0.2	–
Salix herbacea	**39.2**	**26.5**
Saxifraga cernua	0.1	–
Sibbaldia procumbens	*0.1*	*0.8*
Silene acaulis	0.1	–
Solidago virgaurea	0.3	–
Taraxacum croceum	0.1	–
Trisetum spicatum	0.1	*0.1*
Vaccinium vitis-idaea	–	*0.9*
Vahlodea atropurpurea	**0.2**	
Veronica alpina	**0.2**	*0.2*
Viola biflora	*1.0*	**3.8**
Conostomum tetragonum	0.6	0.1
Dicranum fuscescens	0.6	**8.3**
Dicranum scoparium	–	0.1
Kiaeria starkei	**20.2**	*1.6*
Pohlia nutans	–	*0.1*
Polytrichastrum alpinum	–	*0.3*
Polytrichum hyperboreum	–	0.1
Polytrichum juniperinum	3.0	0.1
Polytrichum piliferum	–	**0.4**
Sanionia uncinata	0.2	–
Gymnomitrion spp.	2.5	0.5
Orthocaulis sp.	**14.7**	**6.2**
Tetralophozia setiformis	–	0.2
Cetraria ericetorum	–	*0.1*
Cetraria islandica	0.1	**0.1**
Cladina mitis	**0.1**	**0.4**
Cladina rangiferina	–	0.1
Cladonia amaurocraea	–	*0.1*
Cladonia bellidiflora	–	0.1
Cladonia coccifera	–	**1.0**
Cladonia crispata	–	0.1
Cladonia deformis	–	0.1
Cladonia ecmocyna	*0.1*	–
Cladonia gracilis elongata	–	**0.1**
Cladonia uncialis	0.1	**1.8**
Nephroma arcticum	–	0.1
Ochrolechia spp.	0.1	**15.5**
Peltigera apthosa	–	0.1
Peltigera rufescens	–	0.1
Peltigera scabrosa	–	0.1
Psoroma hypnorum	–	*0.1*
Solorina crocea	0.3	**0.2**
Stereocaulon sp.	**0.1**	**2.6**
n	7	5

Appendix 10. Mean percentage–cover of plants in community types of the Ranunculus glacialis group. The frequencies of taxa in each community type are indicated as follows: bold, frequency >66.7%; underline, frequency 33.3–66.7%; normal text, frequency <33.3%. TsSaT = Trisetum spicatum–Sanionia type, SpCbT = Salix polaris–Carex bigelowii type, RgGT = Ranunculus glacialis–Gymnomitrion type, moss–v = mossy variant, Ox–v = Oxyria variant, Rg–v = Ranunculus glacialis variant, Lc–v = Luzula confusa variant, Ch–v = Cassiope hypnoides variant.

	TsSaT	**SpCbT**	**RgGT**				
			moss-v	Ox-v	Rg-v	Lc-v	Ch–v
Antennaria alpina	0.1	±	0.1	–	–	0.1	–
Cardamine bellidifolia	0.1	0.1	0.1	–	0.1	0.1	**0.2**
Carex bigelowii	–	1.1	–	0.4	–	–	0.1
Carex lachenalii	1.2	–	0.1	–	0.1	–	0.1
Cassiope hypnoides	1.5	**1.4**	1.1	0.9	0.1	1.4	**7.0**
Cassiope tetragona	–	**3.8**	0.1	–	–	0.1	0.1
Cerastium alpinum	0.1	–	0.1	–	–	0.1	–
Cerastium cerastoides	0.1	–	0.1	–	–	–	–
Deschampsia flexuosa	0.1	–	–	–	–	–	–
Erigeron uniflorus	0.1	–	–	–	–	–	–
Festuca ovina	0.1	–	–	–	0.1	–	–
Festuca vivipara	0.1	**0.8**	0.1	–	–	0.4	+
Gnaphalium supinum	**0.2**	–	0.1	–	–	–	–
Huperzia selago	0.1	+	–	–	–	–	–
Juncus biglumis	–	0.1	–	–	–	–	+
Loiseleuria procumbens	0.1	–	–	–	–	–	–
Luzula arcuata confusa	0.1	**0.5**	0.7	**1.0**	1.9	**2.3**	**1.3**
Luzula spicata	0.1	–	–	–	–	0.1	–
Minuartia biflora	0.1	–	0.1	–	–	–	–
Oxyria digyna	0.9	+	0.1	0.8	–	–	0.1
Pedicularis lapponica	–	+	–	–	–	–	–
Phyllodoce caerulea	0.1	–	–	0.1	0.1	0.2	–
Poa alpina	0.3	–	0.4	–	–	0.1	–
Polygonum viviparum	0.2	**0.3**	0.1	–	–	0.1	–
Ranunculus glacialis	–	0.1	0.5	0.4	**1.3**	0.8	**0.5**
Ranunculus nivalis	0.6	–	0.1	–	–	–	–
Ranunculus pygmaeus	–	–	0.1	–	–	–	–
Salix herbacea	**15.1**	–	1.0	**2.1**	–	1.9	0.6
Salix polaris	–	**3.1**	–	–	–	–	0.1
Saxifraga cernua	–	–	0.1	–	0.1	–	–
Saxifraga cespitosa	–	–	–	–	0.2	–	–
Saxifraga foliolosa	–	±	–	–	–	–	–
Saxifraga oppositifolia	–	–	0.1	–	–	0.4	–
Saxifraga rivularis	–	–	0.1	–	–	–	–
Saxifraga tenuis	0.1	–	0.1	–	0.1	–	–
Sibbaldia procumbens	0.5	–	–	–	–	–	–
Silene acaulis	0.1	+	–	–	–	0.4	–
Trisetum spicatum	**1.0**	–	0.2	0.1	0.2	0.1	–
Vaccinium vitis-idaea	–	–	–	–	–	0.1	–
Vahlodea atropurpurea	–	–	0.1	–	–	–	–
Veronica alpina	**0.2**	–	0.1	0.1	–	–	–
Viola biflora	–	–	0.1	–	–	–	–
Andreaea spp.	–	0.2	–	–	–	–	0.1
Arctoa fulvella	–	0.2	–	–	–	–	0.1
Conostomum tetragonum	**1.6**	–	**2.9**	**1.8**	0.3	0.1	0.1
Dicranum fuscescens	1.7	–	–	–	–	0.1	–

Appendix 10. Continued

	TsSaT	**SpCbT**	**RgGT**				
			moss-v	Ox-v	Rg-v	Lc-v	Ch–v
Dicranum scoparium	0.6	0.5	–	–	–	–	–
Hylocomium splendens	0.3	+	–	–	0.1	–	–
Kiaeria starkei	**5.4**	0.2	**6.1**	0.1	-	0.1	0.1
Oligotrochum hercynicum	–	**0.4**	–	–	–	–	**0.2**
Pogonatum sp.	–	–	–	–	–	–	0.1
Pohlia spp.	0.5	–	**3.9**	**0.3**	**0.5**	0.2	**0.2**
Polytrichastrum sexangulare	0.1	0.2	0.1	**5.9**	0.3	0.5	**1.2**
Polytrichum hyperboreum	–	0.1	–	–	–	0.1	0.1
Polytrichum juniperinum	–	–	0.1	–	–	–	–
Polytrichum piliferum	0.1	–	0.1	–	–	**0.1**	–
Racomitrium lanuginosum	–	**1.4**	–	–	–	–	0.3
Racomitrium microcarpon	–	–	–	–	–	–	0.1
Sanionia uncinata	3.3	+	0.1	–	0.1	0.4	–
Anastrophyllum minutum	0.1	–	–	0.1	0.1	–	–
Gymnomitrion sp.	–	**13.5**	–	–	–	–	**24.9**
Hepaticae spp.	–	–	–	–	0.6	1.8	–
Orthocaulis sp.	**6.9**	–	**6.8**	1.0	**0.2**	**0.1**	–
Tetralophozia setiformis	–	–	–	–	–	0.1	–
Alectoria nigricans	–	–	–	–	–	0.1	0.1
Bryocaulon divergens	–	–	0.1	–	–	0.1	–
Cetraria cucullata	–	–	–	–	–	–	0.1
Cetraria delisei	0.1	**0.2**	0.1	–	0.1	0.1	0.2
Cetraria ericetorum	–	0.1	0.1	–	–	**0.1**	**0.1**
Cetraria islandica	**0.4**	–	0.1	–	0.1	0.3	+
Cetraria nigricans	–	–	–	–	–	–	0.1
Cetraria nivalis	0.1	0.5	0.1	–	–	0.1	**0.1**
Cladina mitis	0.1	**0.2**	0.1	–	–	0.1	0.1
Cladina rangiferina	0.1	+	–	–	–	–	0.1
Cladonia amaurocraea	–	+	–	–	–	0.1	–
Cladonia bellidiflora	0.1	–	0.1	–	–	0.1	0.1
Cladonia cervicornis vertic.	–	–	–	–	–	0.1	0.1
Cladonia chlorophaea	–	–	0.1	–	–	–	–
Cladonia coccifera	**0.3**	**0.1**	**0.6**	0.1	0.1	1.1	0.1
Cladonia crispata	0.1	–	0.1	–	–	0.1	–
Cladonia ecmocyna	**0.2**	0.1	0.1	–	–	0.1	–
Cladonia gracilis	0.1	–	**0.1**	0.2	–	0.1	–
Cladonia gracilis elongata	0.6	**0.1**	0.1	–	0.1	0.2	**0.1**
Cladonia macrophylla	–	–	0.1	0.1	–	0.1	–
Cladonia subfurcata	–	+	–	–	–	–	0.1
Cladonia uncialis	0.1	0.1	–	–	–	0.1	–
Coelocaulon aculeatum	–	–	–	–	–	–	–
Ochrolechia spp.	**13.5**	**1.0**	**8.6**	**10.7**	**1.3**	**7.5**	**0.4**
Peltigera rufescens	0.1	–	–	–	0.1	–	–
Peltigera scabrosa	0.5	–	–	–	–	–	–
Psoroma hypnorum	–	–	0.1	–	–	–	–
Solorina crocea	0.3	0.1	0.8	0.1	2.2	**1.7**	0.1
Sphaerophorus globosus	0.1	+	–	–	–	0.1	–
Stereocaulon sp.	1.0	0.1	**1.2**	0.1	0.2	0.7	**0.2**
Thamnolia vermicularis	0.1	0.1	–	–	0.1	0.1	–
n	15	5	26	6	10	10	13