Acta Bot. Fennica 167: 3–28
Helsinki 14 September 1999
ISBN 951-9469-61-3
ISSN 0001-5369

Topographic and altitudinal patterns of heath vegetation on Vannøya and the northern Varanger Peninsula, northern Norway

Risto Virtanen, Priitta Pöyhtäri & Lauri Oksanen

Virtanen, R., Department of Biology, University of Oulu, P.O. Box 3000, FIN-90401 Oulu, Finland
Pöyhtäri, P., Kurkkionmaa, KP4, FIN-99300 Muonio, Finland
Oksanen, L., Department of Ecology and Environmental Science, Umeå University, SE-90187 Umeå, Sweden

Received 5 January 1998

Vegetation patterns of oceanic heath vegetation in northern Norway are described on the basis of systematically sampled vegetation data from two coastal mountain areas, Vannøya and northern Varanger Peninsula. The data are classified into community types by TWINSPAN clustering. On Vannøya, heaths of the *Calluna*-Bryophyta type prevail at the lowest altitudes. Woodland habitats are scattered and confined to sheltered depressions. No well developed zone with *Betula nana* heaths or scrublands is encountered. On the Varanger Penisula, neither *Calluna vulgaris* heaths nor woodland patches occur. *B. nana* has a relatively high cover in snow-protected dwarf shrub heaths. In both areas, the *Ochrolechia* type is characteristic on the wind-swept ridges of the lower and middle oroarctic zones. On sheltered slopes of Vannøya, heaths with a high cover of *Vaccinium myrtillus* have a relatively broad topographic range, whereas on the Varanger Peninsula, heaths of the *Empetrum-Dicranum*-Lichenes type dominate. In both areas, depressions are characterized by heath-like snowbed vegetation with *Salix herbacea* co-occuring with graminoids. In the middle oroarctic zone, heaths of the *Salix herbacea-Empetrum* type prevail. The highest slopes of Vannøya reach the upper oroarctic zone with patches of the *Ranunculus glacialis-Gymnomitrion* type. On Vannøya we encounter a zonation pattern where low altitude *Calluna* heaths grade into oroarctic vegetation. On the Varanger Peninsula, the climate is almost equally oceanic but the vegetation pattern approaches that typical for the oceanic sectors of the southern arctic zone.

Key words: alpine vegetation, arctic vegetation, classification, northern Fennoscandia, ordination, plant communities, vegetation zonation

CONTENTS

I. Introduction 4
II. Material and methods 4
Study areas 4
Sampling and numerical analyses 6
III. Classification and ordination 6
Betula-Myrtillus group 7
Phyllodoce-Myrtillus group 9
Calluna group 10
Arctostaphylos group 10
Juncus trifidus-Salix herbacea group 12
Juncus trifidus-Cassiope tetragona group 13
Ranunculus glacialis group 14
IV. Topographic and altitudinal patterns 15
Patterns below and at the tree-line 15
Patterns from the tree-line to the altitudinal limit of continuous vegetation 15
Patterns at high altitudes 16
V. Discussion 17
Ecological conditions of euoceanic islands 17
Zonation of euoceanic heath vegetation in northernmost Fennoscandia 18
Acknowledgements 20
References 20
Appendices 22

I. INTRODUCTION

The regional patterns in mountain birch forests of northern Fennoscandia have been extensively treated by Hämet-Ahti (1963), while treeless heaths have been dealt with by Eurola (1974), Haapasaari (1988), Engelskjøn (1994), and Oksanen and Virtanen (1995), and mires by Eurola and Vorren (1980). The studies show a change in vegetation patterns along the sharp climatic gradient from coastal areas to the interior parts of Finnmark (Hämet-Ahti 1963, Ahti *et al.* 1968, Sonesson *et al.* 1975, Dahl *et al.* 1986). These inland areas represent one of the most continental areas in northern Europe, where the amplitude of annual temperature fluctuations is high, and the precipitation is low especially during the winter months (Tuhkanen 1980, 1987, 1992, Gjaerevoll 1978). The climatic conditions on coastal islands contrast strikingly against these areas. The vegetation patterns of the coastal mountains have been less clear, because the mountains were not included in the database of Oksanen and Virtanen (1995). Consistent and systematic documentation of these vegetation complexes is also useful for a larger scale comparison along a gradient from northern Fennoscandia to the Russian Arctic (Virtanen *et al.* 1999).

The present paper has two purposes. The first is to describe topographic vegetation patterns of the oceanic parts of northernmost Fennoscandia based on systematically collected data from two sites, Vannøya, Troms, and Varanger Peninsula, Finnmark, along altitudinal gradients. Data from less oceanic areas in northern Norway and Finland have been included in the numerical analyses. Second, these patterns are then discussed in relation to arctic-oroarctic, oceanity-continentality dimensions.

II. MATERIAL AND METHODS

STUDY AREAS

We chose two localities from northern Norway lying at the outer coast of the northern Atlantic (Fig. 1). One was the Varanger Peninsula, a mountain slope at the Sandfjord about 10 km east of Berlevåg. Here mountains reach an altitude of 450 m a.s.l. The vegetation sampling was carried out on the slope with a mainly northern exposure. The other study area was in the County of Troms, the Island of Vannøya. On the southern side of the island a mountain peak called Vannkista reaches an altitude of 950 m a.s.l. The sampling was done along the southern slope which was gentle enough to provide local topographic gradients.

In both study areas, bedrock was primarily composed of siliceous material (Lindström 1987). For the sake of comparison with e.g., Haapasaari (1988), and Oksanen and Virtanen (1995) we avoided areas with calcareous bedrock and areas where indicators of calcium carbonate frequently occurred in vegetation. Consequently, the sampling was concentrated on areas that were mainly covered by oligotrophic vegetation on siliceous bedrock. A few quadrats on Vannøya had *Dryas octopetala* which is much more wide-spread on adjacent islands, e.g., Nord-Fuglöy (Engelskjøn 1970). Podzol soils prevailed up to the lower oroarctic zone. A podzol profile seemed to be weak or lacking at higher altitudes on Vannøya, and it was weakly developed on the Varanger Peninsula (Tedrow 1977).

Vannøya belongs to the Oceanic Central (OC) and Varanger Peninsula mostly to the Oceanic North eco-geo-

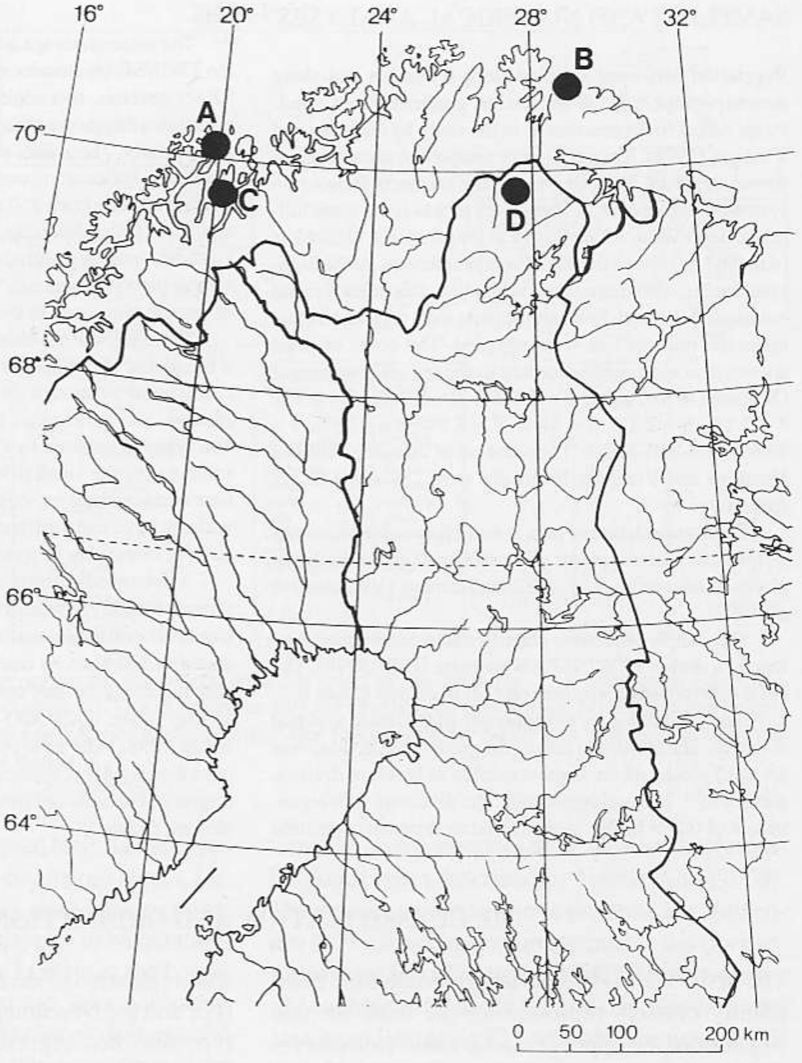

Fig. 1. Study areas in northern Fennoscandia. — A: Vannøya; — B: Varanger Peninsula; — C: Ivggegáisat (Lyngsalpene); — D: Čáhppisduottar.

graphical area (ON) delimited by Engelskjøn (1994).

The following four main climatic features have to be considered in coastal northern Norway:

1. The thermal sum (degree days, d.d.) at the sea level is much higher in the OC (mean 730 d.d.) than in ON (mean 650 d.d.). The mean temperature of the warmest month (July) are also different, being +15.0°C for OC and +12.6°C for ON (Engelskjøn 1994). The length of the growing season (days, threshold +5°C) for OC is about 140 and that for ON is 120 (Tuhkanen 1980).
2. The amplitude of annual fluctuations of temperature is slightly higher on the Varanger Peninsula than on Vannøya.
3. Winter precipitation is much lower on the Varanger Peninsula than on Vannøya.
4. The relationship between winter precipitation and thermal amplitude changes in a gradient from the west to the east. The winter precipitation markedly decreases along this gradient compared to a slower increase in thermal amplitude. This implies an increase in the arctic climate type with modest winter precipitation even in a relatively oceanic area.

For additional details *see* Tuhkanen (1980), Haapasaari (1988), and Oksanen and Virtanen (1995)

On Vannøya, grazing by sheep has a long history, presumably hundreds of years. The sheep population has been about 700 during the last few decades (A. With pers. comm. May 1995). The reindeer population decreases in summertime to about 400 individuals (A. With pers. comm. May 1995). The outer coasts of Varanger Peninsula, in Berlevåg, are only locally used for sheep husbandry (Alm *et al.* 1994), but these areas are used as summer ranges for reindeer (Oksanen *et al.* 1995).

SAMPLING AND NUMERICAL ANALYSES

Vegetation data were sampled along a transect laid along mesotopographic ridge-depression gradients from windswept ridges to depressions as in the study by Oksanen and Virtanen (1995). Transects were sampled at altitudinal intervals of 25 m. Sampling along the transects followed a systematic procedure. A rope of 15 m was fixed from hillock to depression. Along this 15 m long transect, eight plots (size 0.64 m^2) were sampled at regular intervals. At the highest altitudes, with fragmented vegetation, this method could not be used. Instead, four sample plots with vegetation closest to the transect line were sampled. The cover of plant species was estimated according to the ten scale system of Oksanen (1976), where 1 = 0.125%, 2 = 0.25%, 3 = 0.5%, 4 = 1.1%, 5 = 2.2%, 6 = 4.4%, 7 = 8.9%, 8 = 17.9%, 9 = 35.6%, and 10 = 71.2%. The numbers of sample plots from Vannøya and Varanger Peninsula were 239 and 112, respectively.

The nomenclature of taxa is according to the following references: vascular plants (Hämet-Ahti *et al.* 1998), bryophytes (Söderström *et al.* 1992) and lichens (Vitikainen *et al.* 1997).

The sample plots were classified into community clusters by a divisive TWINSPAN program (Hill 1979b). The cut levels for pseudospecies were set to default values 0, 2, 5, 10 and 20 suitable for cover classes transformed to actual %-cover. The minimum size of the group to be divided was set to 15 plots, and the highest number of levels of division was set to 7. In the classification, the divisions with eigenvalues of 0.2 or higher were treated as separate vegetation units.

The mean coverage and frequencies for each species in the TWINSPAN clusters was then computed. In the TWINSPAN analysis, two additional data sets were used to accomplish a direct comparison to the vegetational units treated in that study. These data come from Ivggegáisat (Lyngsalpene), a suboceanic mountain area in interior Troms, spanning an altitude from 250 m to 1 525 m (316 sample plots) and from Čáhppisduottar (Mt. Ailigas), northern Finnish Lapland, spanning altitudes between 350-425 m a.s.l. (32 sample plots) (Oksanen & Virtanen 1995). The total number of sample plots used in the TWINSPAN analysis was 698.

The TWINSPAN classification was used as a basis for a hierarchic classification where the higher level clusters correspond to groups of vegetation types (community groups), and the clusters below are interpreted as vegetation types as outlined by Oksanen and Virtanen (1995). In some cases, the subdivisions of the main clusters can be best characterized as variants of a community type. The variants have main differences in dominance relationships and not essentially in species composition.

A detrended correspondence analysis (DCA) was performed to analyze main vegetation gradients. To improve clarity of ordination scattergram, the size of data was reduced to 500 plots by random deletion of plots. The DCA was run using default options of the DECORANA (Hill 1979a) in the CANOCO for Windows 4.0 program (ter Braak 1998). The new program version avoids the problems discussed by Oksanen and Minchin (1997). In the scattergram of species ordination only the most important species are shown.

III. CLASSIFICATION AND ORDINATION

The first TWINSPAN division separates the community clusters representing the high altitude vegetation (the upper oroarctic zone) from the remaining sample plots (Fig. 2). The latter group contains the major categories of boreal-oroarctic heaths. This corresponds to the DCA ordination showing that the first axis of vegetational variation correlates with altitude (Fig. 3). This is then split into broad groups of chionophobous and chionophilous-snowbed types of vegetation. Accordingly, in the DCA ordination the second axis correlates with the topographic gradient from chionophilous communities in depressions to wind-exposed communities (Fig. 3). In the third level of divisions, a cluster including three community groups, the *Betula-Myrtillus* group, the *Juncus trifidus-Salix herbacea* group and the *Phyllodoce-Myrtillus* group of Oksanen and Virtanen (1995), is formed. One cluster contains entirely suboceanic vegetation of the *Betula nana*-Lichenes scrub type and the *Deschampsia flexuosa-Stereocaulon* type snowbed vegetation, and also some sample plots of the arctic *Empetrum-Vaccinium* type, *Betula nana-Cladina* type and arctic *Myrtillus*-Lichenes type (Haapasaari 1988, Oksanen & Virtanen 1995). This suboceanic vegetation of Ivggegáisat and Čáhppisduottar is not treated here in details. The chionophobous heath cluster is further dichotomized into the *Arctostaphylos* community group of Oksanen and Virtanen (1995) and vegetation characterized by *Calluna vulgaris* to be called the *Calluna* group. The community composition of the main clusters is not exclusive and the clusters contain vegetation types of other groups.

In the main cluster of high altitude vegetation, the second division produced a dichotomy between data from Ivggegáisat and from the corresponding sample plots of Vannøya and Varanger Peninsula. Again, the vegetation types of Ivgge-

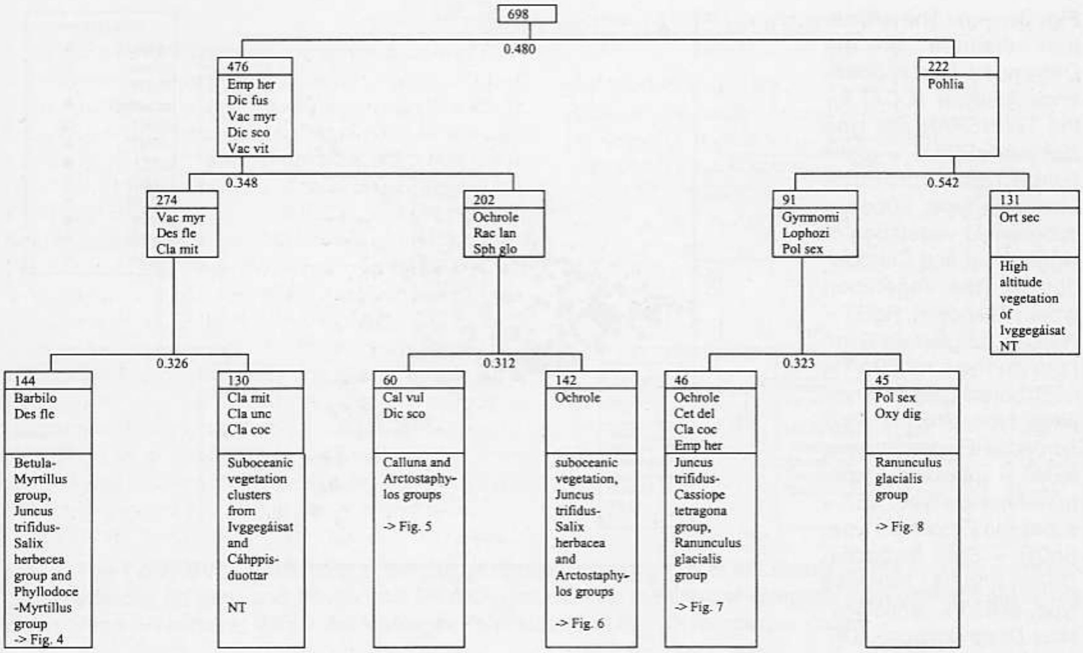

Fig. 2. The TWINSPAN dendrogram for the whole data set used in the analysis. The number of quadrats, eigenvalues and indicator species given. The divisions continue in the figures mentioned. NT = the subdivisions of material from suboceanic areas are not treated further (for the vegetation types *see* Oksanen & Virtanen 1995). *See* Fig. 3b for species codes.

gáisat are not any further treated here. These types include the *Luzula confusa-Saxifraga tenuis*, *Luzula confusa-Cetraria nivalis*, and *Cassiope tetragona-Ranunculus glacialis* types of vegetation, prevailing at altitudes above 1 050 m in the Ivggegáisat. Some plots represent the *Salix herbacea-Cassiope hypnoides*, *Salix herbacea-Kiaeria* and *Salix herbacea-Ochrolechia* type vegetation of the middle oroarctic zone (Oksanen & Virtanen 1995). This clearly indicates that also high altitude vegetation is differentiated along the axis of increasing oceanity (Fig. 3). In the third level of divisions, the snowbed communities formed a separate cluster, to be referred to as the *Ranunculus glacialis* group. In the next main division, a cluster of chionophobous vegetation characterized by *Salix herbacea* is separated. This corresponds to the *Juncus trifidus-Cassiope tetragona* group.

BETULA-MYRTILLUS GROUP

The subdivision of the cluster with vegetation of the *Betula-Myrtillus* group and snowbed vegetation (Fig. 4) incorporates three clusters that resemble forest types described by Hämet-Ahti (1963). The species composition is presented in Appendix 1. The first cluster corresponds to the *Cornus-Empetrum-Myrtillus* type (CoMT). Only two plots of Vannøya (250 m a.s.l.), and one plot from the Varanger Peninsula (25 m a.s.l.) are assigned to this cluster. This suggests that typical mesic forest types rich in *Cornus suecica* are not common in coastal mountains of northern Norway.

The other two clusters correspond to the subalpine *Empetrum-Myrtillus* type (sEMT) and the subalpine *Empetrum* type (sET) described by Hämet-Ahti (1963). These clusters only contain sample plots from Vannøya and Varanger Peninsula being thus differentiated from those encountered on Ivggegáisat. The subalpine *Empetrum-Myrtillus* type is characterized by sporadic *Betula pubescens* subsp. *czerepanovii* with *Empetrum nigrum* subsp. *hermaphroditum* and *Vaccinium myrtillus* codominant in the field layer. In the ground layer, *Pleurozium schreberi* has slightly lower cover than in the Hämet-Ahti's (1963) sample plots. *P. schre-*

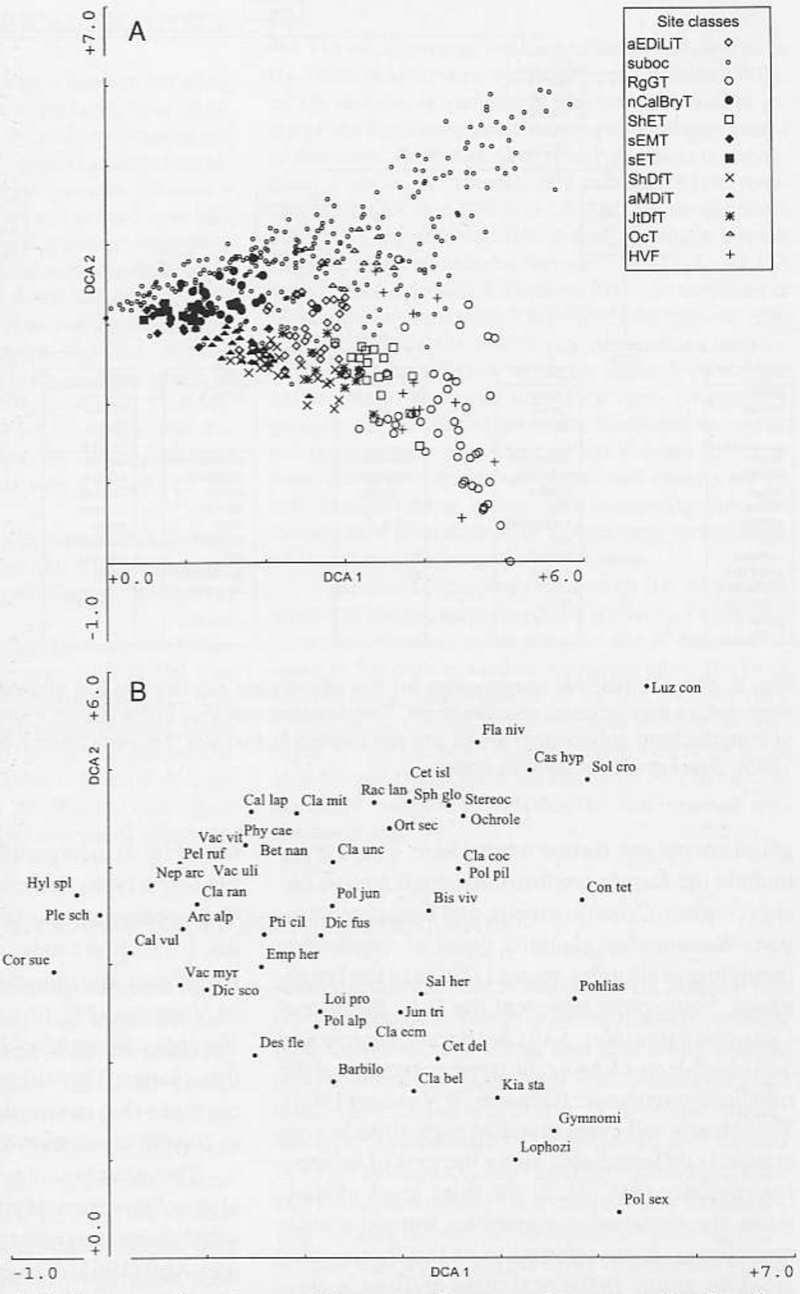

Fig. 3. — A. The ordination diagram of the Detrended Correspondence Analysis (DCA) for the TWINSPAN site type classes. aEDiLiT = arctic *Empetrum-Dicranum*-Lichenes type, suboc = suboceanic vegetation of Ivggegáisat and Čáhppisduottar (the vegetation types not shown), RgGT = *Ranunculus glacialis-Gymnomitrion* type, nCalBryT = north boreal *Calluna*-Bryophyta type, ShET = *Salix herbacea-Empetrum* type, sEMT = subalpine *Empetrum-Myrtillus* type, sET = subalpine *Empetrum* type, ShDfT = *Salix herbacea-Deschampsia flexuosa* type, aMDiT = arctic *Myrtillus-Dicranum* type, JtDfT = *Juncus trifidus-Deschampsia flexuosa* type, OcT = *Ochrolechia* type, HVF = high altitude vegetation fragments of the Varanger Peninsula. — B. The DCA ordination showing the most common species. Arc alp = *Arctostaphylos alpina*, Barbilo = *Barbilophozia* spp., Bet nan = *Betula nana*, Bis viv = *Bistorta vivipara*, Cal lap = *Calamagrostis lapponica*, Cal vul = *Calluna vulgaris*, Cas hyp = *Cassiope hypnoides*, Cet del = *Cetrariella delisei*, Cet isl = *Cetraria islandica*, Cla mit = *Cladina mitis*, Cla ran = *Cladina rangiferina*, Cla bel = *Cladonia bellidiflora*, Cla coc = *Cladonia coccifera*, Cla ecm = *Cladonia ecmocyna*, Cla unc = *Cladonia uncialis*, Con tet = *Conostomum tetragonum*, Cor sue = *Cornus suecica*, Des fle = *Deschampsia flexuosa*, Dic fus = *Dicranum fuscescens*, Dic sco = *Dicranum scoparium*, Emp her = *Empetrum nigrum* subsp. *hermaphroditum*, Fla niv = *Flavocetraria nivalis*, Gymnomi = *Gymnomitrion spp.* mainly *G. concinnatum*, Hyl spl = *Hylocomium splendens*, Jun tri = *Juncus trifidus*, Kia sta = *Kiaeria starkei*, Loi pro = *Loiseleuria procumbens*, Lophozi = *Lophozia* spp., Luz con = *Luzula arcuata* subsp. *confusa*, Nep arc = *Nephroma arcticum*, Ochrole = *Ochrolechia* spp., Ort sec = *Orthilia secunda*, Pel ruf = *Peltigera rufescens*, Phy cae = *Phyllodoce caerulea*, Ple sch = *Pleurozium schreberi*, Poa alp = *Poa alpina*, Pohlias = *Pohlia* spp., Pol alp = *Polytrichastrum alpinum*, Pol jun = *Polytrichum juniperinum*, Pol pil = *Polytrichum piliferum*, Pol sex = *Polytrichastrum sexangulare*, Pti cil = *Ptilidium ciliare*, Rac lan = *Racomitrium lanuginosum*, Sal her = *Salix herbacea*, Sol cro = *Solorina crocea*, Sph glo = *Sphaerophorus globosus*, Stereoc = *Stereocaulon* spp., Vac myr = *Vaccinium myrtillus*, Vac uli = *Vaccinium uliginosum*, Vac vit = *Vaccinium vitis-idaea*.

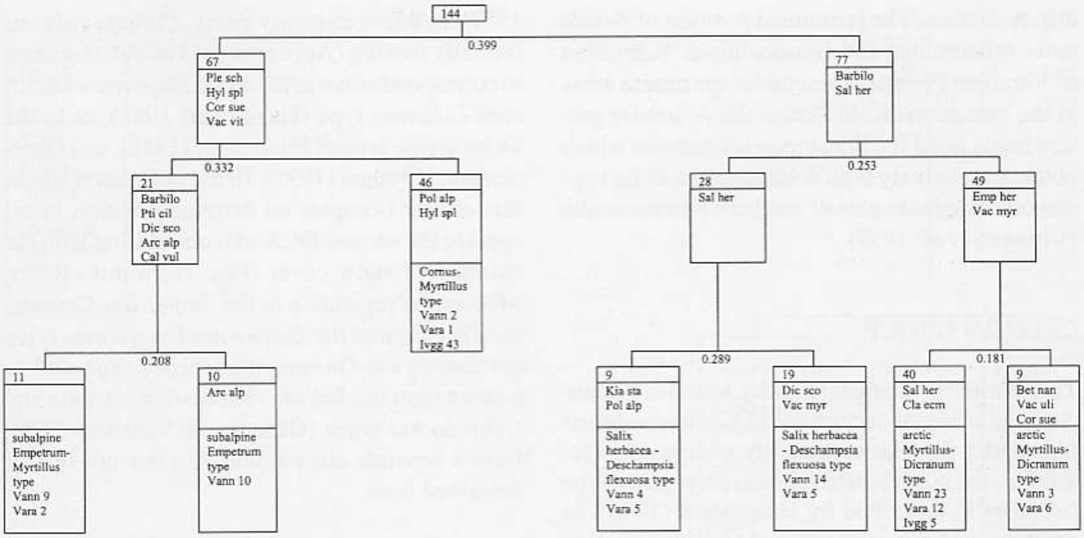

Fig. 4. The TWINSPAN subdivision of the cluster containing vegetation of the *Betula-Myrtillus*, *Juncus trifidus-Salix herbacea* (in part) and *Phyllodoce-Myrtillus* groups. The numbers of quadrats from different areas are given. Vann = Vannøya, Vara = the Varanger Peninsula. *See* Fig. 3b for species codes.

beri is a codominant with *Barbilophozia* spp., *Dicranum scoparium* and *Ptilidium ciliare*. In the sET cluster, the field layer is strongly dominated by *Empetrum nigrum* subsp. *hermaphroditum* corresponding to Hämet-Ahti's (1963) description. The only clearly distinctive feature in our material is the fairly regular occurrence of *Calluna vulgaris*. This species is much less frequent in the inner fjord areas, represented in Hämet-Ahti's (1963) or Oksanen and Virtanen's (1995) material. According to Hämet-Ahti (1963: fig. 27) the subalpine *Empetrum-Myrtillus* type is confined to inland areas of northern Finland. The sub-alpine *Vaccinium-Empetrum* heath described by Engelskjøn (1970) from Nord-Fugløy seems to represent an extreme form of this vegetation.

PHYLLODOCE-MYRTILLUS GROUP

In the TWINSPAN analysis, a pair of clusters clearly corresponds to the traditional *Phyllodoco-Vaccinion* alliance (Nordhagen 1943), *Phyllodoco-Vaccinion myrtilli* (Dahl 1957) or the *Phyllodoce-Myrtillus* community group (Oksanen & Virtanen 1995), characteristic to sheltered slopes (Fig. 4). The closest counterparts of these clusters seem to be the arctic *Myrtillus-Dicranum*-Lichenes type and, particularly, the arctic *Myrtillus-Dicranum* type (Haapasaari 1988). An obvious difference as compared to Haapasaari's (1988) *Myrtillus-Dicranum* type, is the relatively high cover of *Empetrum nigrum* subsp. *hermaphroditum* in our material. Within this type, two regionally differentiated variants (one from Vannøya and another from Varanger Peninsula) can be recognized (Appendix 2). In the first variant with plots mainly from Vannøya, the cover value of *Empetrum* tend to be higher than that of *Vaccinium myrtillus*. In the ground layer, *Dicranum fuscescens* and *D. scoparium* are the most common species and *Cladina mitis* occurs sparsely. An additional difference compared to Haapasaari's descriptions is the relatively high abundance of *Deschampsia flexuosa* and *Barbilophozia* spp. Overall, lichens are moderately abundant, and the cluster shares features of the arctic *Myrtillus-Dicranum*-Lichenes type (Haapasaari 1988). This type grades directly into *Calluna* heaths.

In the other variant cluster with sample plots mainly from Varanger Peninsula, the cover of *Betula nana* is relatively high while *Betula pubescens* subsp. *czerepanovii* is scattered. Moreover, *Cornus suecica* and *Vaccinium uliginosum* have relatively high cover values. This cluster shows hemiarctic features and some sectorial or altitudinal differentiation. The prominent position of *Betula nana* reflects that the chionophilous vegetation of Varanger Peninsula resembles the tundra areas in the east of the Kola Peninsula. A similar pattern holds good for *Vaccinium uliginosum* which obtains a relatively high dominance in arctic vegetation complexes east of northern Fennoscandia (Virtanen *et al.* 1999).

CALLUNA GROUP

This cluster is characterized by relatively abundant and constant occurrence of *Calluna vulgaris* (Appendix 3). The community composition resembles the north boreal *Calluna*-Bryophyta type (nCalBryT) described by Haapasaari (1988). In addition to a fairly high cover of *Calluna vulgaris*, this vegetation is characterized by *Empetrum nigrum* subsp. *hermaphroditum*, which can be locally dominant. *Arctostaphylos alpina* and *Loiseleuria procumbens* occur patchily in low cover values. The ground layer is bryophyte-rich with typical species such as *Dicranum scoparium*, *Pleurozium schreberi*, *Ptilidium ciliare*, and *Racomitrium lanuginosum*. In the subdivision of TWINSPAN, this type is further split into a variant in which *C. vulgaris* and *E. nigrum* subsp. *hermaphroditum* have about equal cover and *P. schreberi* is characteristic in the ground layer. In the other variant, *E. nigrum* subsp. *hermaphroditum* is clearly dominant and *C. vulgaris* has a mean cover of less than 10%. It seems that the latter variant is confined to more exposed ridges, which is also indicated by the presence of *Sphaerophorus globosus* and *Ochrolechia frigida*, and the absence of *P. schreberi*.

This community type, almost restricted to Vannøya in our material, resembles the vegetation of the *Arctous-Calluna* association described by McVean and Ratcliffe (1962) and McVean (1964) from fairly extreme habitats of northern Scottish highlands. Hence, these heaths of northern Norway appear to represent the extreme edge of the *Calluna* heath formation typical of the oceanic north Atlantic region (Gimingham 1964).

ARCTOSTAPHYLOS GROUP

The vegetation of this group corresponds to the alliance *Arctostaphyleto-Cetrarion nivalis* (Dahl 1957). In this community group, *Calluna vulgaris* is totally lacking (Appendix 3). The clusters seem to correspond either to the arctic *Empetrum-Dicranum*-Lichenes type (Haapasaari 1988), or to the *Ochrolechia* type of Haapasaari (1988), and Oksanen and Virtanen (1995). In the ordination space, this cluster occupies an extreme position in respect to the second DCA axis correlating with the duration of snow cover (Fig. 3). In this cluster, suboceanic vegetation of the *Empetrum-Cetraria nivalis* type and the *Empetrum-Loiseleuria* type, the *Empetrum-Dicranum*-Lichenes type and to lesser extent the *Salix herbacea-Ochrolechia* and *Ochrolechia* types (Oksanen & Virtanen 1995), form a separate cluster, and they are not further described here.

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

This community type consists of four clusters (Figs. 5 and 6) that share the characteristics of the arctic *Empetrum-Dicranum*-Lichenes type (Haapasaari 1988). The dominant dwarf shrub is *Empetrum nigrum* subsp. *hermaphroditum*. In the ground layer, bryophytes and lichens occur in about equal abundances. In our clusters, typical species include *Cladina mitis*, *Dicranum fuscescens* and *Ochrolechia frigida*. In one of the subclusters assigned close to the north boreal *Calluna*-Bryophyta type by TWINSPAN (Fig. 5), there is an exceptional composition of species: *Loiseleuria procumbens* is relatively abundant (mean cover 14%), but *Empetrum* is nevertheless the dominating plant, and *Vaccinium myrtillus* occurs quite regularly while indicators of extremely sparse snow cover are missing. This community, to be called the *Loiseleuria* variant of the arctic *Empetrum-Dicranum*-Lichenes type, represents oroarctic-oceanic vegetation on upper parts of the topographic sequence. In the second cluster, the plant cover seems to be more open due to stones and and active polygons. Consequently, *Empetrum* does not reach high dominance, and open patches are occupied by *Gymnomitrion* hepatics. This variant is called the *Gymnomitrion* variant of the arctic *Empetrum-Dicranum*-Lichenes type. The third cluster is closest to the earlier characterizations of Haapasaari (1988), and Oksanen and Virtanen (1995). This cluster can thus be re-

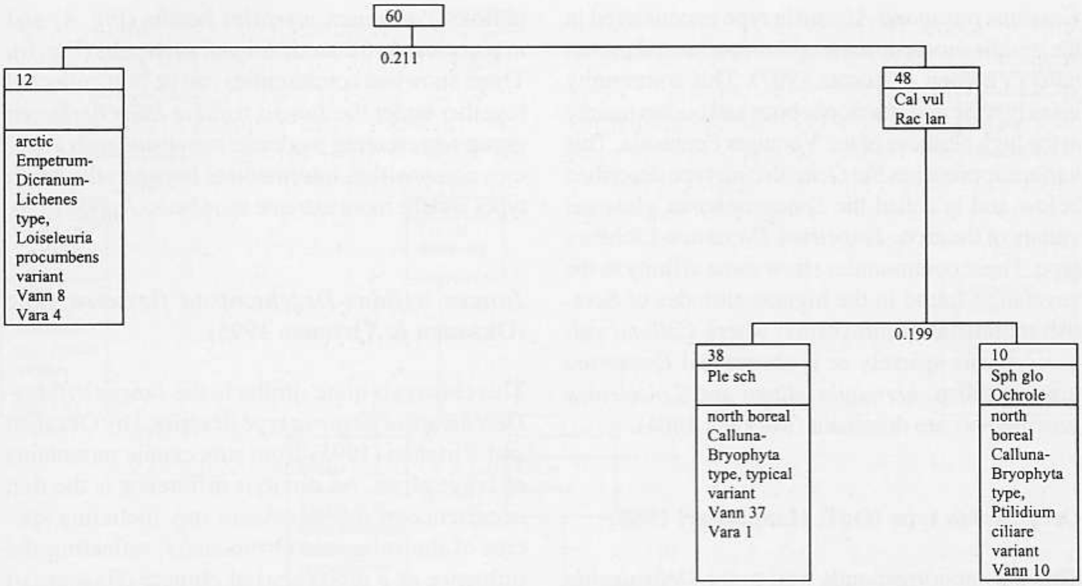

Fig. 5. The TWINSPAN subdivision of the cluster with vegetation of the *Calluna* and *Arctostaphylos* groups. *See* Fig. 3b for species codes.

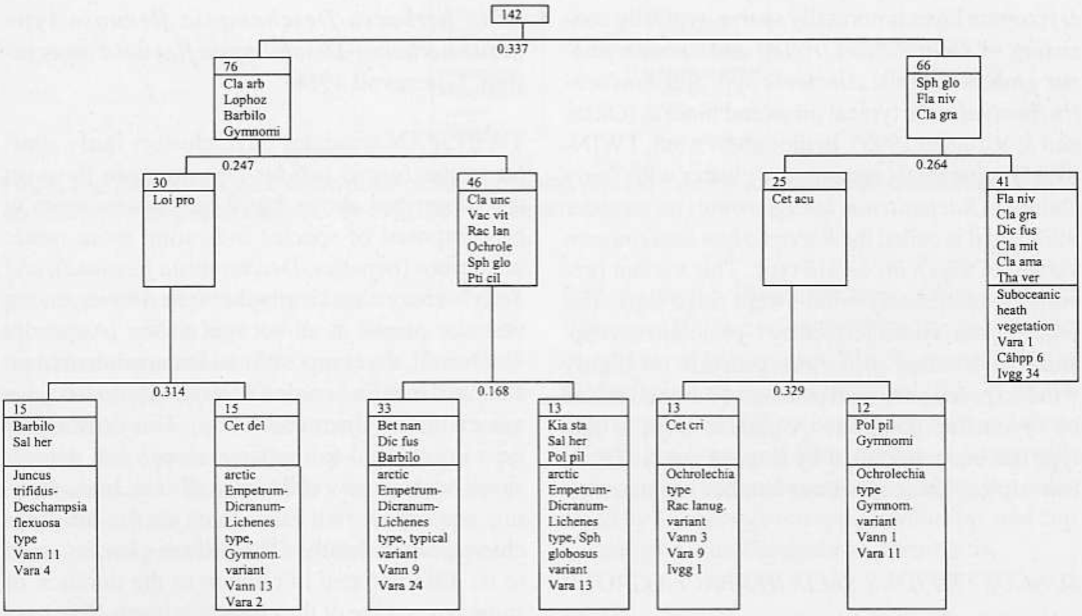

Fig. 6. The TWINSPAN subdivision of the cluster with vegetation of the *Juncus trifidus-Salix herbacea* and *Arctostaphylos* groups. Cáhpp = Čáhppisduottar; Ivgg = Ivggegáisat; Cet acu = *Cetraria aculeata*; Cet eri = *Cetraria ericetorum*; Cla ama = *Cladonia amaurocraea*; Lecidea: *Lecideaceae* sp. *See* Fig. 3b for other species codes.

garded as the typical variant of the arctic *Empetrum-Dicranum*-Lichenes type. The fourth subcluster is a fairly extreme form of the community type and has characteristics that resemble the *Empetrum-*

Cassiope tetragona-Alectoria type encountered in the middle oroarctic zone on subcontinental mountains (Virtanen & Eurola 1997). This community is fairly xeric and chionophobous and occurs mainly at the high altitudes of the Varanger Peninsula. This variant approaches the *Ochrolechia* type described below and is called the *Sphaerophorus globosus* variant of the arctic *Empetrum-Dicranum*-Lichenes type. These communities show some affinity to the vegetation found in the highest altitudes of Scottish mountains (Cairngorms) where *Calluna vulgaris* occurs sparsely or is absent and *Empetrum nigrum* subsp. *hermaphroditum* and *Loiseleuria procumbens* are dominant (McVean 1964).

Ochrolechia type (OcT, Haapasaari 1988)

This cluster corresponds well to the *Ochrolechia* type of Haapasaari (1988). The field layer is largely open with fragmented stands of *Empetrum nigrum* subsp. *hermaphroditum* and a few other dwarf shrubs creeping along the soil. Even the cryptogam layer is normally sparse, typically consisting of *Ochrolechia frigida* and *Sphaerophorus globosus*, while *Alectoria* spp. and *Flavocetraria nivalis* are typical on inland tundras (Oksanen & Virtanen 1995). In the subdivision, TWINSPAN separates a community cluster with fairly abundant *Racomitrium lanuginosum* (mean cover 9%), and it is called the *Racomitrium lanuginosum* variant of the *Ochrolechia* type. This variant prevails on moderately wind-swept ridge tops. The other cluster, characterized by *Gymnomitrion* spp. and *Polytrichum piliferum,* prevails on highly wind-exposed sites with patches of bare soil raised by cryoactive polygons. A plateau form of this type has been described by Engelskjøn (1970) as low-alpine, chionophobous heather vegetation.

JUNCUS TRIFIDUS-SALIX HERBACEA GROUP

In the material of Oksanen and Virtanen (1995), the moderate snowbeds (the alliance Herbaceon, Gjærevoll 1956) classified by TWINSPAN, coincide poorly with the traditional associations belonging to the alliance Herbaceon (Gjærevoll 1956). In the present analysis, the chionophilous vegetation is in part assigned close to the chionophilous *Vaccinium myrtillus* heaths (Fig. 4) and in part close to the arctic *Empetrum* heaths (Fig. 6). These snowbed communities can be best collected together under the *Juncus trifidus-Salix herbacea* group representing moderate snowbeds with a species composition intermediate between the heath types and the more extreme snowbeds (Appendix 4).

Juncus trifidus-Deschampsia flexuosa type (Oksanen & Virtanen 1995)

This clusters is quite similar to the *Juncus trifidus-Deschampsia flexuosa* type described by Oksanen and Virtanen (1995) from suboceanic mountains of Ivggegáisat. An obvious difference is the rich occurrence of *Barbilophozia* spp. including species of the subgenus *Orthocaulis*, reflecting the influence of a moist coastal climate (Haapasaari 1988). This heath-like snowbed type seems to be confined to the suboceanic-oceanic mountains.

Salix herbacea-Deschampsia flexuosa type (*Salix herbacea-Deschampsia flexuosa* association, Gjærevoll 1956)

TWINSPAN separates three clusters fairly similar to the *Juncus trifidus-Deschampsia flexuosa* type described above, but these clusters seem to be composed of species indicating more mesic conditions (hepatics, *Deschampsia flexuosa*), and *Salix herbacea* has clearly the highest cover among vascular plants, in all but one cluster (Appendix 4). Overall, the compositional features seem to resemble the *Salix herbacea-Deschampsia flexuosa* association of Gjærevoll (1956). This community type is confined to sheltered slopes and depressions, where snow remains well into June, melting a week or two later than on the adjacent chionophilous heaths. These three clusters seem to be differentiated in relation to the duration of snow cover. One of the clusters is heath-like, having a relatively high cover of *Empetrum nigrum* subsp. *hermaphroditum*, thus to be called as the *Empetrum* variant of the type. The second cluster has a relatively high cover of *Dicranum* spp. and characteristic of chionophilous heaths, and is thus described as the *Dicranum* variant of the type. The third cluster is much like genuine snowbeds with

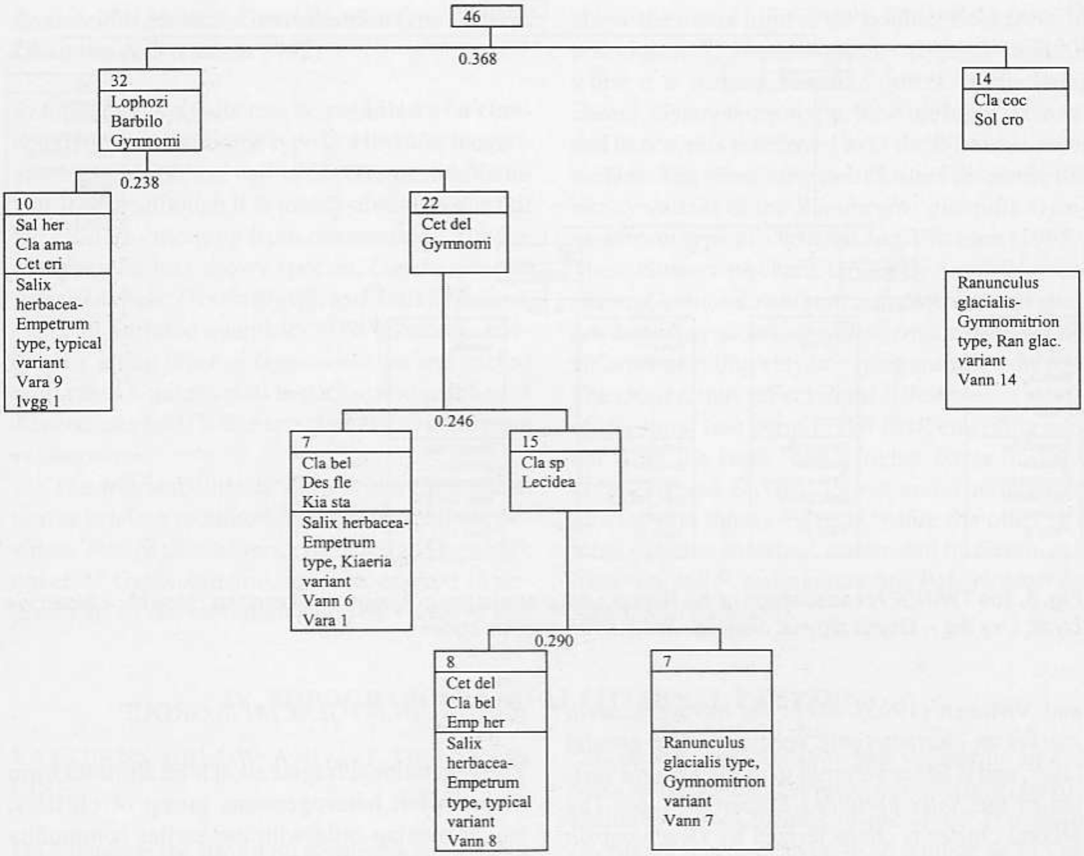

Fig. 7. The TWINSPAN subdivision of the cluster containing vegetation of the *Juncus trifidus-Cassiope tetragona* and *Ranunculus glacialis* groups. *See* Fig. 3b for species codes.

only sporadic occurrences of evergreen dwarf shrubs and with a high cover of *Kiaeria starkei*, typical of the relatively late snowbeds. This variant is thus called as the *Kiaeria* variant of the *Salix herbacea-Deschampsia flexuosa* type. It resembles the *Salix herbacea-Cassiope hypnoides* type of Oksanen and Virtanen (1995), but the high cover of *Deschampsia flexuosa* in the former type is a distinguishing feature between these two types.

JUNCUS TRIFIDUS-CASSIOPE TETRAGONA GROUP

This community group represents at least weakly snow-protected vegetation of the middle oroarctic zone and our present material from coastal mountains forms clusters which closely resemble the *Salix herbacea-Empetrum* type of Oksanen and Virtanen (1995) encountered on the suboceanic mountains of Ivggegáisat. This type vegetation is further split into three subclusters (Fig. 7) with a fragmented field layer. *Empetrum nigrum* subsp. *hermaphroditum* and *Salix herbacea* occur with approximately equal cover, and open patches colonized by *Gymnomitrion* spp., *Pohlia* spp. and cup lichens of genus *Cladonia* (Appendix 5).

***Salix herbacea-Empetrum* type (ShET, Oksanen & Virtanen 1995)**

In the three clusters representing this community type, *Empetrum nigrum* subsp. *hermaphroditum* and *Salix herbacea* are codominant. One of the clusters is similar to that described by Oksanen

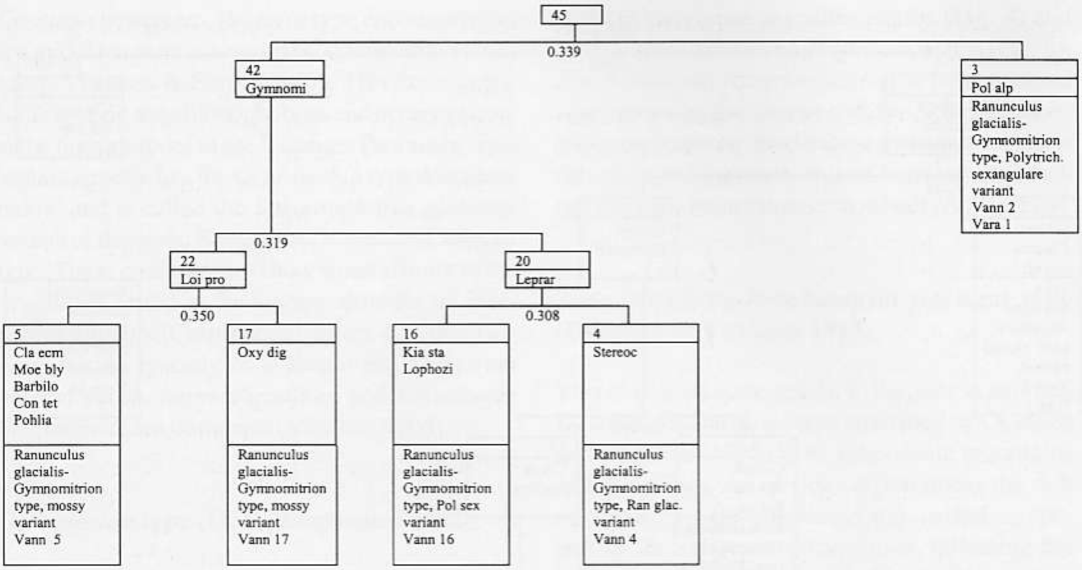

Fig. 8. The TWINSPAN subdivision of the *Ranunculus glacialis* group. Leprar = *Lepraria* sp.; Moe bly = *Moerckia blyttii*; Oxy dig = *Oxyria digyna*; *See* Fig. 3b for other species codes.

and Virtanen (1995), exept for having *Kiaeria starkei* as characteristic species in the ground layer, and is hence referred to as the *Kiaeria* variant of the *Salix herbacea-Empetrum* type. The second cluster is characterized by *Deschampsia flexuosa* and even *Vaccinium myrtillus* occurs only fragmentarily. This community type occurs adjacent to moderate snowbeds in areas transitional between the lower and middle oroarctic zones. The third cluster consists of somewhat chionophobous vegetation of the middle oroarctic zone and closely related to the *Ocholechia* type (*see* above). The indicators of wind-swept heaths are meager or absent and are replaced by species extending their range into higher altitudes (e.g., *Cetrariella delisei*), where both chionophobous and chionophilous species occur in the community. A factor contributing to this is the cryoperturbation which breaks up *Empetrum* clones and forms open space for colonizing small hepatics, such as *Gymnomitrion concinnatum*, *Marsupella condensata* and *Pohlia* spp. We name this cluster the *Gymnomitrion* variant of the *Salix herbacea-Empetrum* type. This type corresponds to the middle-alpine, chionophobous heaths of Engelskjøn (1970).

RANUNCULUS GLACIALIS GROUP

The vegetational fragments at high altitudes form a somewhat heterogeneous group of clusters, which overlap little with the earlier community types of Oksanen and Virtanen (1995). They concluded that a collective community concept is sensible when dealing with the small fragments of vegetation encountered in upper oroarctic boulderfields, because conditions varied locally even within these patches and because the vascular plant component of these communities was probably profoundly influenced by founder effects. This vegetation was collectively assigned to the *Ranunculus glacialis-Gymnomitrion* type (RgGT) consisting of several variants. The present material also includes clusters that are relatively similar to this type vegetation. Nevertheless, even in light of the DCA ordination (Fig. 3) the emerging clusters in our material seem to have a composition that is not equal with the variant types recognized by Oksanen and Virtanen (1995). We found it useful to combine some of the subclusters generated by TWINSPAN (Figs. 2, 7 and 8), and finally could recognize four variants within the type (Appendix 6).

Ranunculus glacialis-Gymnomitrion type (RgGT, Oksanen & Virtanen 1995)

Ranunculus glacialis can be regarded as a characteristic species for the type in a broader biogeographic scale (Gjærevoll 1956, Oksanen & Virtanen 1995), although it is totally absent in most of the clusters emerging from our material. The accompanying less showy species, *Luzula arcuata* subsp. *confusa*, *Oxyria digyna* and *Salix herbacea*, occur in variable quantities. The ground is covered by a thin layer of *Gymnomitrion* spp. mixed with other similar small hepatics, and patches of *Kiaeria starkei*, *Pohlia* spp. and *Polytrichastrum sexangulare*.

The four subclusters show some differentiation in relation to altitudinal and topographic position. Two of the clusters, characterized by a high cover of *Gymnomitrion*, are encountered in depressions of the mountain slope of Vannøya just above the lower limit of the boulder field zone. In one cluster *R. glacialis* occurs (typical variant), while it is lacking from the others. In the latter cluster, *Gymnomitrion* spp. have the highest cover, and hence, this is referred to as the *Gymnomitrion* variant. The remaining two clusters resemble the mossy variant of the *Ranunculus glacialis-Gymnomitrion* type of Oksanen and Virtanen (1995). These clusters are characterized by *Anthelia juratzkana*, *Gymnomitrion concinnatum*, *Kiaeria starkei*, *Lophozia sudetica* and *Polytrichastrum sexangulare*, indicating very late lying snow conditions. The clusters may reflect slight differences in length of the snow free period. The first, emerging earlier from the snow, has a higher cover of *Salix herbacea* and *Oxyria digyna* and a number of mosses (the mossy variant), while the other is a more extreme snowbed, dominated by *Gymnomitrion* spp. and *P. sexangulare* (the *Polytrichastrum sexangulare* variant).

IV. TOPOGRAPHIC AND ALTITUDINAL PATTERNS

PATTERNS BELOW AND AT THE TREE-LINE

On Vannøya, the sites with mountain birch forest are scattered, and reach an altitude of only 100 m. In some places, even the lowest altitudes are characterized by the treeless heaths of the north boreal *Calluna*-Bryophyta type, which forms the prevalent vegetation up to the altitude of 200 m (Fig. 9). In depressions of the lower slopes of Vannøya, the subalpine *Empetrum* type prevails together with the subalpine *Empetrum-Myrtillus* type. On the Varanger Peninsula, forested habitats are completely lacking, but some stands of the lower slopes represent boreal heath types.

PATTERNS FROM THE TREE-LINE TO THE ALTITUDINAL LIMIT OF CONTINUOUS VEGETATION

On Vannøya, with increasing altitude, the *Calluna*-Bryophyta type grades into the arctic *Empetrum-Dicranum*-Lichenes type and to the *Ochrolechia* type (Fig. 9). Above an altitude of 200 m, depressions harbour snowbed vegetation of the *Salix herbacea-Deschampsia flexuosa* type, and on sheltered slopes, heaths of the arctic *Myrtillus-Dicranum* type prevail up to an altitude of 475 m. No communities dominated by *Betula nana* occur. The *Empetrum-Dicranum*-Lichenes type extends up to an altitude of 500 m. The uppermost fragments of *Myrtillus* heaths reach the same altitude.

On the Varanger Peninsula, ridges from the lowest altitudes upwards are characterized by wind-swept heaths of the *Ochrolechia* type, while sheltered slopes are covered by the arctic *Empetrum-Dicranum*-Lichenes type (Fig. 9). The arctic *Myrtillus-Dicranum* type occurs regularly in snow protected slopes. The upper limit of this type in our material lies at ca. 250–275 m a.s.l. The vegetation pattern differs from that of inland areas of northern Fennoscandia. For instance, *Phyllodoce caerulea* is considerably less frequent and less abundant in the oceanic sectors of northern Fennoscandia than on the isolated subcontinental mountains (Kalliola 1939, Haapasaari 1988, Oksanen & Virtanen 1995).

On the Varanger Peninsula, *Betula nana* obtains higher cover values in both arctic *Empetrum*-

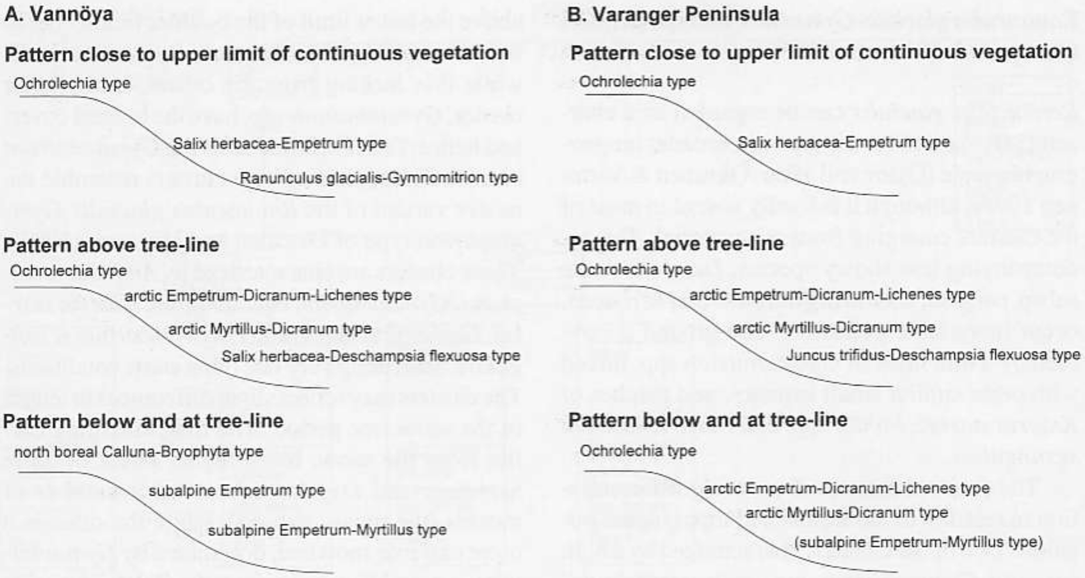

Fig. 9. The community complexes along the ridge-depression topographic sequences. — A: Vannøya; — B: The Varanger Peninsula.

Dicranum-Lichenes type and arctic *Myrtillus-Dicranum* type (about 10%) than in the corresponding communities on Vannøya (Appendices 2 and 3). This suggests that the vegetation character on the Varanger Peninsula resembles that of subcontinental areas in interior Finnmark (Oksanen & Virtanen 1995), subcontinental-suboceanic mountains (Jonasson 1981, Haapasaari 1988, Oksanen & Virtanen 1995), or hemiarctic tundras east of the Kola Peninsula (Virtanen *et al.* 1999). On Vannøya, *Vaccinium myrtillus* heaths are much more characteristic in the lower oroarctic vegetation, while on the Varanger Peninsula, *Empetrum* heaths dominate.

At altitudes of 500 m, the vegetation of Vannøya changes fairly abruptly due to the change in macrotopography. The mountain slope is strongly concave, with jagged peaks rising from the "shoulders" with relatively gentle topography. At this transition boulders start to dominate while the characteristic vegetation types include the *Ochrolechia* type on the ridges, the *Salix herbacea-Empetrum* type in more sheltered slopes, and the *Ranunculus glacialis-Gymnomitrion* type in depressions (Fig. 9). This pattern corresponds to the middle oroarctic vegetation compelexes encountered on the suboceanic Ivggegáisat mountains (Oksanen & Virtanen 1995). On the Varanger Peninsula, macrotopography becomes flat or convex at altitudes of about 300 m. Above this limit topographic variation becomes very modest and places of substantial snow accumulation do not occur. The vegetation of somewhat sheltered slopes represents the *Salix herbacea-Empetrum* type which is the characteristic element of the middle oroarctic zone.

PATTERNS AT HIGH ALTITUDES

On Vannøya at altitudes above 750 m, the vegetation pattern is similar to the one encountered on the suboceanic Ivggegáisat above the altitude of 1 100 m, with various variants of the *Ranunculus glacialis-Gymnomitrion* type (Oksanen & Virtanen 1995). The details differ, however. *R. glacialis* is less abundant on Vannøya. The *Polytrichastrum sexangulare* variant of the *Ranunculus glacialis-Gymnomitrion* type, dominating at altitudes between 750 and 900 m is without a close counterpart in the material from Ivggegáisat, but approaches the *Anthelia juratzkana-Polytrichastrum sexangulare* type described from subcontinental Finnish mountains (Virtanen & Eurola 1997) or the bryophyte-rich high-altitude communities described by Engelskjøn (1994) or from Jan Mayen (Virtanen *et al.* 1997). Fragments of *Luzula confusa* heath, which abound on the upper oroarctic ridges of Ivggegáisat, are not encountered on Vannøya at all. Even another heath fragment type typical for suboceanic mountains, the *Cassiope tetragona-Ranunculus glacialis* type (Oksanen & Virtanen 1995), is lacking. These vegetational differences are reflected in the DCA ordination showing a clear segregation in the high altitude vegetation (Fig. 3).

V. DISCUSSION

ECOLOGICAL CONDITIONS OF EUOCEANIC ISLANDS

The lowland vegetation of outer coasts in northern Norway is shaped in part by the cool coastal climate type, in part by restricted tree growth, and in part part by human activity. It is likely that formerly forested areas to some extent have become replaced by treeless heaths during this process. Hence, the *Calluna* heaths at low altitudes must be regarded as secondary vegetation created by sheep and reindeer plus logging for fuel (Hämet-Ahti 1963, Haapasaari 1988, Oksanen *et al.* 1995), as is the entire Atlantic *Calluna* formation (Gimingham 1964, McVean 1964, Gwynne *et al.* 1974). Widespread occurrences of *Calluna* heaths extend to the central oceanic area (OC, Engelskjøn 1994) of northern Troms (Skogen 1974), which is also the northern limit of the common occurrence of some temperate Atlantic mosses, such as *Rhytidiadelphus loreus*. In this area *Calluna* heaths merge into the arctic-oroarctic tundra heaths (Tuhkanen 1987).

A striking difference between suboceanic and euoceanic heath communities is the overwhelming predominance of evergreen plants, mainly ericaceous dwarf shrubs, on euoceanic heaths. This was unexpected because deciduous dwarf shrubs and herbs increase with increasingly oceanic climate along the gradient from continental to suboceanic areas (Oksanen and Virtanen 1995, *see* also Hämet-Ahti 1963). Moreover, vegetation of the subalpine *Empetrum-Myrtillus* type typical to subcontinental mountains re-emerged on the euoceanic outer coasts. A likely underlying reason is a difference in the duration of the snowy season. The suboceanic parts of northernmost Fennoscandia are characterized by copious snow cover. As summer conditions are moist, deciduous dwarf shrubs and herbs (e.g., *Cornus suecica*) with good capacity to transpire water, are favoured. On the outer coasts, however, the vegetation indicates "Scottish" winter conditions, with only periodic snow cover, which gives possibilities for photosynthesis in late winter, especially on the Atlantic coast where the thermal climate is mild. The prevalance of *Calluna vulgaris* is probably associated with these climatic conditions (Barkman 1990).

Even the co-occurrence of the chionophilous bilberry which is sensitive to freeze-drying (Sjörs 1989) and chionophobous evergreen dwarf shrubs (e.g., *Loiseleuria procumbens*) is probably a consequence of mild winters, weak freezing of the soil and cool springs. Under such conditions, bilberry twigs survive on sites with thin snow cover, because they are unlikely to be exposed to the combination of desiccating sunshine and frozen ground. On the other hand, evergreen cushion-forming plants can be competitive even outside the most extreme ridge sites, because of their capability of trapping warm air is especially advantageous in cool, windy habitats (Gauslaa 1984).

In the lower oroarctic zone, the clearest difference between suboceanic and euoceanic vegetation patterns is the high abundance of graminoids (especially *Deschampsia flexuosa*) in euoceanic snowbeds. This feature is probably a straightforward consequence of moisture conditions. Moderate snowbeds irrigated by temporary creeks tend to be graminoid-dominated even in inland areas (Gjærevoll 1956).

At higher altitudes, bryophytes (e.g., *Gymnomitrion* spp. and *Polytrichastrum sexangulare*) are common in euoceanic vegetation. The uppermost vegetation fragments of suboceanic mountains are typically patches of high alpine herbs or wood rushes, and scanty lichens (e.g. *Solorina crocea*) and mosses on bare ground (Du Rietz 1925, Engelskjøn 1994, Oksanen & Virtanen 1995). On Vannøya, however, mosses are the dominating component of these fragments, whereas *Ranunculus* *glacialis* is relatively uncommon. Mosses are probably favoured by the cool and moist summers and by the mild, snowy winters, when cold erosion is not likely to be intense (Nordhagen 1928, Engelskjøn 1986). High alpine herbs, which reproduce mainly or exclusively sexually (Oksanen & Virtanen 1997) are, in turn, likely to have problems coping with the moss cover (Söyrinki 1938).

On the northern coast of the Varanger Peninsula, facing the Barents Sea, deciduous dwarf shrubs (e.g. *Betula nana*) are relatively abundant, and among evergreens, the primarily arctic *Empetrum nigrum* subsp. *hermaphroditum* is the overwhelmingly dominating species. Moreover, the topographic amplitude of *Vaccinium myrtillus* heaths is relatively narrow and ridges are occupied by *Ochrolechia* heaths, just as in suboceanic areas, whereas *Calluna* heaths are virtually absent. It might be argued that the north-facing coasts of the Barents Sea are not as oceanic as the west-facing Atlantic coasts. However, the vegetation patterns described from the outer coasts of western Greenland (Böcher 1954, 1963, Elvebakk 1985) are quite similar to those encountered on the northern shores of the Varanger Peninsula. We thus propose that the main reason for the vegetational differences between Vannøya and the Varanger Peninsula is a shift from oroarctic to arctic conditions, where even oceanic areas have relatively cold winters and considerably less winter precipitation than what is typical for correspondingly oceanic mountains, rising from the boreal zone. Hence, freeze-drying is a problem even in oceanic sectors of the arctic zone, favouring deciduous plants and desiccation-tolerant evergreens.

ZONATION OF EUOCEANIC HEATH VEGETATION IN NORTHERNMOST FENNOSCANDIA

On Vannøya, areas below the altitude of 250 m harbour plant communities with clearly boreal or even temperate affinities. In spite of the scanty occurrence and partial absence of mountain birches, these areas are thus to be regarded as boreal or (oro)hemiarctic (Fig. 10). However, it is difficult to decide whether the lowermost parts of this *Calluna* zone are truly boreal. Data from adjacent suboceanic and continental areas (Oksanen & Virtanen 1995) suggest that the hemiarctic zone is normally a mosaic of boreal and (oro)arctic community types, with few distinctive vegetation types of its own. The outer coasts of Troms were assigned to the hemiarctic zone by Dahl *et al.* (1986) and to the boreal zone by Haapasaari (1988). However, the vertical width of the (oro)hemiarctic was normally about 150 m (Oksanen & Virtanen 1995). If this criterion is applicable to the outer coasts, then the areas below 100 m belong to the boreal zone, and cultural factors (logging, sheep grazing) account for their hemiarctic physiognomy. Engelskjøn (1970) does not discuss the delimitation of boreal and hemiarctic zones, but according to him, the vertical range of the collective subalpine zone on adjacent Nord-Fuglöy Island extend to an altitude of 250 m.

In the Sandfjord area on the northern coast of the Varanger Peninsula, communities with boreal affinities were encountered in the lowermost transect only. At the same altitudes, the gravel bars in a creek mouth support willow stands up to 3 m tall (pers. obs.). Hence, at least a narrow hemiarctic zone seems to be present on the northern shores of the Varanger Peninsula. The seemingly southern arctic landscapes of adjacent peninsulas probably owe their arctic physiognomy to the lack of sheltered sites, not to their zonal position, contrary to the arguments of Haapasaari (1988).

If the upper limit of the lower oroarctic zone is defined by the disappearance of bilberry heaths, it lies at 500 m on Vannøya and at 275 m on Varanger Peninsula. In both areas, the vertical width of the lower oroarctic zone would thus be 250 m, which is a typical figure throughout the Scandinavian mountain chain (Kalliola 1939, Nordhagen 1943, Dahl 1957, Holten 1983, Oksanen & Virtanen 1995). We suspect, however, that we have for methodological reasons underestimated the positions of both limits on the northern coast of the Varanger Peninsula. In this area, almost all slopes have a northern exposition and are thus microclimatically unfavourable. The proper place for the upper limit of the hemiarctic zone lies at the altitude (or latitude), where boreal communities disappear even from sites with maximally favourable microclimate. On the few south-facing slopes found in the area, we have observed shrubby vegetation rich in *Cornus suecica* and *Gymnocarpium dryopteris* up to an altitude of

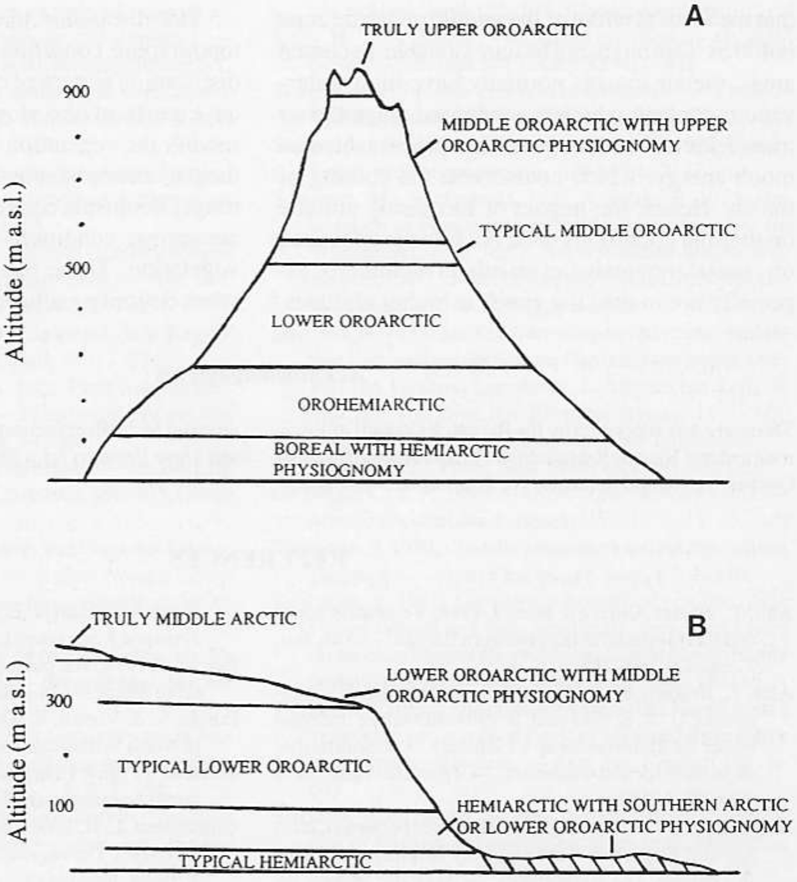

Fig. 10. The altitudinal zonation of euoceanic heath vegetation in northernmost Fennoscandia. — A: Vannøya; — B: the Varanger Peninsula. Hatched area denotes outer coasts with exposed capes and headlands.

100 m, which is probably an appropriate altitudinal limit of the hemiarctic zone in this area. The disappearance of bilberry heaths at an altitude of 300 m is, in turn, probably influenced by the convex macrotopography of the plain which starts at this altitude. The proper limit between the lower and the middle oroarctic zones should be determined by looking at the vegetation patterns on the few protruding hilltops with concave slopes. We consider that the limit lies at least at an altitude of 350 m (Fig. 10).

Even the upper limit of bilberry heaths in our material from Vannøya may provide a biased estimate of the transition between lower and middle oroarctic zones, because even strongly concave macrotopography may be unfavourable, as such areas accumulate copious amounts of snow during the winter. On adjacent Nord-Fugløy Island, bilberry heaths extend to an altitude of 600 (or even 650) m on the southern side of the island (Engelskjøn 1970), which suggests that there is either considerable variation between near-by islands or the real transition occurs at the altitude of about 600 m. Moreover, it is possible that Engelskjøn (1970) refers to the uppermost heath fragments with some bilberry twigs, which our method would probably treat as snowbeds or as *Salix herbacea-Empetrum* heaths. Due to the uncertainties of the situation, we preliminarily accept the 500 m limit (Fig. 10).

On Vannøya, the continuous middle oroarctic vegetation was only found within an altitudinal interval of 50 m. From 550 m upwards, there was just steep, rocky slopes without continuous vegetation. On the other hand, the mossy variant of the *Ranunculus glacialis* type, which in many ways resembles middle oroarctic heaths and snow-beds, occurred up to an altitude of 900 m. The proper border between middle and upper oroarctic zones might thus be as high as 900 m, which would imply that the vertical width of the middle oroarctic zone is 400 m. This might not be unreasonable. In coastal areas, the air masses normally have high water-vapour content, which is condensed when the air mass rises and cools down. This process releases much energy, which counteracts the cooling of the air. Hence, the impact of increasing altitude on thermal conditions need not be as pronounced on coastal mountains as on inland mountains, especially not in the "fog zone" at higher altitudes.

The discussion above indicates that macrotopographic conditions may strongly affect the distribution pattern of community types. The concave parts of the slopes on Vannøya strongly modify the vegetation complex and contribute to the prevalence of snowbed vegetation. On the Varanger Peninsula convex upper slopes tend to create reverse conditions favouring chionophobous vegetation. These factors have to be considered when delimiting altitudinal zones (Fig. 10).

Acknowledgements

The study was supported by the Research Council of Environment and Natural Resources of Finland and the Swedish Council for Natural Sciences. We thank an anonymous referee and M. Walker for useful comments on the manuscript, and Dave Henman for a linguistic check.

REFERENCES

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968: Vegetation zones and their sections in northwestern Europe. — *Ann. Bot. Fennici* 5: 169–211.

Alm, T., Bråthen, K. A., Karlsen, S. R., Nordtug, B., Sommersel, G.-A. & Øiesvold, S. 1994: Botaniske undersøkelser av kulturlandskap i Finnmark. 3. Lokalitetsbeskrivelser for Øst-Finnmark. — *Tromura Naturvitenskap* 77: 1–258.

Barkman, J. J. 1990: Ecological differences between *Calluna*- and *Empetrum*-dominated dry heath communities in Drenthe, The Netherlands. — *Acta Bot. Neerl.* 39: 75–92.

Böcher, T. W. 1954: Oceanic and continental vegetation complexes in southwest Greenland. — *Meddel. Grønland* 148: 1–336.

Böcher, T. W. 1963: Phytogeography of Middle West Greenland. — *Meddel. Grønland* 148(3): 1–289.

Dahl, E. 1957: Rondane. Mountain vegetation in South Norway and its relation to the environment. — *Skrifter Norske Videnskaps-Akad. Oslo, I. Matem.-Naturvidensk. kl.* 1956(3): 1–374.

Dahl, E., Elven, R., Moen, A. & Skogen, A. 1986: Vegetasjonsregionkart over Norge 1:1 500 000. — *Nasjonalatlas for Norge, Statens Kartverk.*

Du Rietz, G. E. 1925: Die regionale Gliederung der skandinavischen Vegetation. — *Svenska Växtsoc. Sällsk. Handl.* 8: 1–60.

Elvebakk, A. 1985: Higher phytosociological syntaxa on Svalbard and their use in subdivision of the Arctic. — *Nordic J. Bot.* 5: 273–284.

Engelskjøn, T. 1970: Flora of Nord-Fuglöy, Troms. — *Astarte* 3: 63–82.

Engelskjøn, T. 1986: Zonality of climate and plant distributions in some Arctic and Antarctic regions. — *Norsk Polarinst. Rapportserie* 30: 1–49.

Engelskjøn, T. 1994: High- and mid-alpine vegetation in North Scandinavia. Ecology and thermal relations. — *Tromura Naturvitenskap* 74: 1–65.

Eurola, S. 1974: The plant ecology of Northern Kiölen, arctic or alpine? — *Aquilo, Ser. Bot.* 13: 10–22.

Eurola, S. & Vorren, K.-D. 1980: Mire zones and sections in North Fennoscandia. — *Aquilo, Ser. Bot.* 17: 39–56.

Gauslaa, Y. 1984: Heat resistance and energy budget in different Scandinavian plants. — *Holarctic Ecol.* 7: 1–18.

Gimingham, C. H. 1964: Dwarf shrub heaths. — In: Burnett, J. H. (ed.), *The vegetation of Scotland*: 232–279. Oliver & Boyd, Edinburgh.

Gjærevoll, O. 1956: The plant communities of the Scandinavian alpine snow-beds. — *Kongel. Norske Videnskabers Selsk. Skrifter* 1956(1): 1–405.

Gjærevoll, O. (ed.) 1978: Finnmarksvidda, natur – kultur. — *Norges offentlige utredninger* 1978(18 A): 1–332. Universitetsforlaget, Oslo.

Gwynne, D., Milner, C. & Hornung, M. 1974: The vegetation and soils of Hirta. — In: Jewell, P. A., Milner, C., Boyd, M. J. (eds), *Island survivors: the ecology of the soay sheep of St Kilda*: 37–87. Athlone Press, London.

Haapasaari, M. 1988: The oligotrophic heath vegetation of northern Fennoscandia and its zonation. — *Acta Bot. Fennica* 135: 1–219.

Hämet-Ahti, L. 1963: Zonation of the mountain birch forests in northernmost Fennoscandia. — *Ann. Bot. Soc. Zool. Bot. Fennicae Vanamo* 34(4): 1–127.

Hämet-Ahti, L., Suominen, J., Ulvinen, T. & Uotila, P. (eds.) 1998: *Retkeilykasvio*, ed. 4. Finnish Museum of Natural History, Botanical Museum. Helsinki. 656 pp.

Hill, M O. 1979a: *DECORANA — A FORTRAN program for detrended correspondence analysis and reciprocal averaging.* — Ecology and systematics, Cornell University, Ithaca, NY. (reissued by Microcomputerpower, Ithaca).

Hill, M. O. 1979b: *TWINSPAN — A FORTRAN program for* *analyzing multivariate data in an ordered two-way table by classification of individuals and attributes.* — Ecology and systematics, Cornell University, Ithaca, NY.

Holten, J. I. 1983: Kriterier for avgrensning av vegetasjonssoner i Norge. — *Kungl. N. Vidensk. Sellsk. Museet Rapport Serie* 7: 76–94.

Jonasson, S. 1981: Plant communities and species distribution of low alpine *Betula nana* heaths in northernmost Sweden. — *Vegetatio* 44: 51–64.

Kalliola, R. 1939: Pflanzensoziologische Untersuchungen in der alpinen Stufe Finnisch-Lapplands. — *Ann. Bot. Soc. Zool. Bot. Fennicae Vanamo* 13(2):1–321.

Lindström, M. 1987: Northernmost Scandinavia in the geological perspective. — *Ecol. Bull.* 38: 17–37.

McVean, D. N. & Ratcliffe, D. A. 1962: Plant communities of the Scottish Highlands. — *Monographs of the Nature Conservancy* 1. London. 445 pp.

McVean, D. N. 1964: Dwarf shrub heaths. — In: Burnett, J. H. (ed.), *The vegetation of Scotland*: 481–495. Oliver & Boyd, Edinburgh.

Nordhagen, R. 1928: Die Vegetation und Flora des Sylenegebietes. I. Die Vegetation. — *Skrifter Norske Videnskaps-Akad. Oslo, I. Matem.-Naturvidenskapelig kl.* 1927(1): 1-612.

Nordhagen, R. 1943: Sikilsdalen og Norges fjellbeiter. En plantesosiologisk monografi. — *Bergens Mus. Skrifter* 22: 1–607.

Oksanen, J. & Minchin, P. R. 1997: Instability of ordination results under changes in input data order: explanations and remedies. — *J. Veg. Sci.* 8: 447–454.

Oksanen, L. 1976: On the use of the Scandinavian type class system in coverage estimation. — *Ann. Bot. Fennici* 13: 149–153.

Oksanen, L., Moen, J. & Helle, T. 1995: Timberline patterns in northernmost Fennoscandia: the relative importance of climate and grazing. — *Acta Bot. Fennica* 153: 93–105.

Oksanen, L. & Virtanen, R. 1995: Topographic, altitudinal and regional patterns in continental and suboceanic heath vegetation of northern Fennoscandia. — *Acta Bot. Fennica* 153: 1–80.

Oksanen, L. & Virtanen, R. 1997: Adaptation to disturbance as a part of the strategy of arctic and alpine plants. — In: Crawford, R. M. M. (ed.), *Disturbance and recovery in Arctic lands*: 91–113. Kluwer, Dordrecht.

Sjörs, H. 1989: Blåbär, Vaccinium myrtillus — ett växtporträtt. — *Svensk Bot.Tidskr.* 83: 411–428.

Skogen, A. 1974: Den vest-norske lyngheien — et kulturlandskap i endring. — *Forskningsnytt* 19: 4–6.

Söderström, L., Hedenäs, L. & Hallingbäck, T. 1992: Checklista över Sveriges mossor. — *Myrinia* 2: 13–56.

Sonesson, M., Wielgolaski, F. E. & Kallio, P. 1975: Description of Fennoscandian tundra ecosystems. — In: Wielgolaski, F. E. (ed.), *Fennoscandian tundra ecosystems*, Part 1: 3–28. Ecological Studies. Analysis and Synthesis, Vol. 16. Springer. Berlin.

Söyrinki, N. 1938: Studien über die generative und vegetative Vermehrung der Samenpflanzen in der alpinen Vegetation Petsamo-Lapplands. I. Allgemeine Teil. — *Ann. Bot. Soc. Zool. Bot. Fennicae Vanamo* 11: 1–323.

Tedrow, J. C. F. 1977: *Soils of the polar landscapes.* — Rutgers Univ. Press, New Brunswick, NJ. 638 pp.

ter Braak, C. J. F. 1998: *CANOCO for Windows 4.0.* — Microcomputerpower, Ithaca, NY.

Tuhkanen, S. 1980: Climatic parameters and indices in plant geography. — *Acta Phytogeogr. Suec.* 67: 1–110.

Tuhkanen, S. 1987: The phytogeographical position if the Faeroe Islands and their ecoclimatic correspondences on the other continents: problems associated with highly oceanic regions. — *Ann. Bot. Fennici* 24: 111–135.

Tuhkanen, S. 1992: The climate of Tierra del Fuego from a vegetation geographical point of view and its ecocline counterparts elsewhere. — *Acta Bot. Fennica* 145: 1–64.

Virtanen, R. & Eurola, S. 1997: Middle oroarctic vegetation of Finland and middle-northern arctic vegetation on Svalbard. — *Acta Phytogeogr. Suec.* 82: 1–60.

Virtanen, R., Lundberg, P. A., Moen, J. & Oksanen, L. 1997: Topographic and altitudinal patterns in plant communities on European arctic islands. — *Polar Biol.* 17: 95–113.

Virtanen, R., Oksanen, L. & Razzhivin, V. Yu. 1999: Topographic and regional patterns of tundra heath vegetation from northern Fennoscandia to the Taimyr Peninsula. — *Acta Bot. Fennica* 167: 29–83.

Vitikainen, O., Ahti, T., Kuusinen, M., Lommi, S. & Ulvinen, T. 1997: Checklist of lichens and allied fungi of Finland. — *Norrlinia* 6: 1–123.

Appendix 1. Mean percentage cover of clusters of the *Betula-Myrtillus* group. The frequencies are indicated as follows: bold = *f* > 66.7%; underlined = 33.3% < *f* < 66.7%; normal text = *f* < 33.3%. sEMT = subalpine *Empetrum-Myrtillus* type, sET = subalpine *Empetrum* type, CoMT = *Cornus-Myrtillus* type.

	sEMT	sET	CoMT
Alchemilla spp.	–	–	0.1
Andromeda polifolia	0.8	0.3	–
Anthoxanthum odoratum subsp. *alpinum*	–	–	2.2
Arctostaphylos alpina	+	**6.9**	–
Betula nana	–	–	4.6
Betula pubescens subsp. *czerepanovii*	2.8	1.3	0.2
Bistorta vivipara	–	–	+
Calamagrostis lapponica	–	–	0.4
Calluna vulgaris	4.7	21.7	–
Carex lachenalii	–	–	0.2
Cornus suecica	**3.5**	**1.2**	**28.9**
Deschampsia flexuosa	**2.1**	0.2	**5.3**
Empetrum nigrum subsp. *hermaphroditum*	**36.4**	**60.5**	**13.3**
Equisetum arvense	–	–	+
Equisetum pratense	–	–	0.1
Equisetum sylvaticum	–	–	+
Festuca ovina	–	–	+
Gymnocarpium dryopteris	–	–	1.0
Hierochloë alpina	–	–	+
Juncus trifidus	–	–	+
Juniperus communis	6.5	–	0.3
Linnaea borealis	–	–	+
Loiseleuria procumbens	0.4	1.9	–
Luzula pilosa	–	–	+
Luzula spicata	+	–	–
Lycopodium annotinum	–	–	0.4
Melampyrum pratense	+	–	–
Melampyrum sylvaticum	0.2	–	+
Nardus stricta	2.2	–	–
Orthilia secunda	–	–	4.1
Pedicularis lapponica	–	–	0.2
Phyllodoce caerulea	+	–	+
Rhodiola rosea	–	–	+
Rubus chamaemorus	–	–	+
Salix arbuscula	–	–	0.1
Salix glauca	–	–	+
Salix hastata	–	–	+
Salix herbacea	–	–	0.8
Salix myrtillus	–	–	0.1
Salix phylicifolia	–	–	0.4
Solidago virgaurea	–	–	0.2
Phegopteris connectilis	–	–	0.1
Trientalis europaea	–	–	0.1
Vaccinium myrtillus	**10.9**	**5.0**	**23.4**

	sEMT	sET	CoMT
Vaccinium uliginosum	**2.4**	+	3.3
Vaccinium vitis–idaea	**2.2**	**5.1**	6.2
Anthelia juratzkana	–	–	0.1
Barbilophozia spp.	**5.0**	0.2	**0.9**
Calypogeia sp.	–	+	–
Lophozia spp.	+	+	–
Ptilidium ciliare	**4.5**	1.8	0.1
Scapania sp.	–	–	0.1
Aulacomnium turgidum	–	–	+
Dicranum fuscescens	1.5	**2.3**	1.0
Dicranum majus	–	+	–
Dicranum scoparium	**11.2**	**9.8**	3.3
Hylocomium splendens	1.2	6.0	**34.1**
Kiaeria starkei	–	–	1.5
Plagiothecium sp.	+	–	–
Plagiothecium undulatum	–	+	–
Pleurozium schreberi	8.5	**8.5**	**18.6**
Pohlia nutans	–	–	0.1
Polytrichastrum alpinum	–	–	0.8
Polytrichastrum sexangulare	–	–	+
Polytrichum juniperinum	–	–	+
Racomitrium lanuginosum	–	0.4	–
Rhytidiadelphus loreus	2.4	–	–
Cetraria islandica subsp. *crispiformis*	–	–	+
Cetraria islandica	–	–	+
Cetrariella delisei	–	–	+
Cladina mitis	1.3	0.3	0.1
Cladina rangiferina	0.3	**1.3**	+
Cladonia amaurocraea	–	–	+
Cladonia bellidiflora	+	–	+
Cladonia chlorophaea	+	0.1	–
Cladonia coccifera	+	+	+
Cladonia crispata	–	–	+
Cladonia deformis	–	–	+
Cladonia ecmocyna	+	+	+
Cladonia spp.	+	–	–
Cladonia subfurcata	–	–	+
Cladonia uncialis	–	+	+
Flavocetraria cucullata	–	–	+
Nephroma arcticum	–	1.0	6.6
Ochrolechia spp.	–	–	+
Peltigera aphthosa	–	–	+
Peltigera rufescens	–	–	0.9
Peltigera scabrosa	–	–	+
Stereocaulon spp.	–	–	+

Appendix 2. Mean percentage cover of clusters of the Phyllodoce-Myrtillus group. The frequencies are indicated as follows: bold = $f > 66.7\%$; underlined = $33.3\% < f < 66.7\%$; normal text = $f < 33.3\%$. aMDiT = arctic *Myrtillus-Dicranum* type, with two (regional) variant clusters.

	aMDiT var. 1	aMDiT var. 2
Arctostaphylos alpina	+	–
Betula nana	0.5	**9.9**
Betula pubescens subsp. *czerepanovii*	–	3.9
Bistorta vivipara	+	+
Calluna vulgaris	0.5	–
Carex bigelowii	–	+
Carex lachenalii	–	+
Cornus suecica	1.3	**7.0**
Deschampsia flexuosa	**9.0**	**8.4**
Empetrum nigrum subsp. *hermaphroditum*	**36.8**	**35.6**
Hieracium sp.	+	+
Huperzia selago	0.1	–
Juncus trifidus	0.1	–
Loiseleuria procumbens	0.8	1.3
Nardus stricta	0.2	2.0
Orthilia secunda	3.7	–
Phyllodoce caerulea	0.5	–
Pyrola minor	+	–
Rubus chamaemorus	–	0.3
Salix herbacea	**5.5**	0.2
Solidago virgaurea	+	0.1
Trientalis europaea	–	0.5
Vaccinium myrtillus	**22.0**	**33.6**
Vaccinium uliginosum	0.6	**10.1**
Vaccinium vitis-idaea	0.4	0.6
Barbilophozia spp.	**17.7**	**23.1**
Diplophyllum taxifolium	+	–
Gymnomitrion spp.	0.1	–
Lophozia spp.	0.1	+
Ptilidium ciliare	0.6	0.1
Dicranum fuscescens	**29.1**	**22.5**
Dicranum scoparium	**16.2**	**22.1**
Hylocomium splendens	+	–
Kiaeria starkei	2.0	2.0
Plagiothecium sp.	+	+
Pleurozium schreberi	0.4	0.6
Pohlia nutans	–	+
Pohlia sp.	+	–
Polytrichastrum alpinum	0.2	–
Polytrichum commune	–	1.0
Polytrichum hyperboreum	+	–
Polytrichum juniperinum	+	–
Polytrichum piliferum	+	–
Racomitrium lanuginosum	+	–
Racomitrium microcarpon	+	–
Rhytidiadelphus loreus	0.2	–
Cetraria aculeata	+	–
Cetraria islandica subsp. *crispiformis*	0.3	–
Cetraria islandica subsp. *islandica*	0.5	4.0
Cetraria ericetorum	+	–
Cetrariella delisei	+	+
Cladina mitis	**4.9**	**2.2**
Cladina rangiferina	1.4	0.1
Cladonia amaurocraea	0.1	0.1
Cladonia bellidiflora	2.4	0.1
Cladonia chlorophaea	0.1	+
Cladonia coccifera	+	0.1
Cladonia deformis	+	–
Cladonia ecmocyna	0.3	+
Cladonia fimbriata	0.1	–
Cladonia gracilis	0.1	–
Cladonia macrophylla	0.3	–
Cladonia pleurota	+	–
Cladonia spp.	+	0.1
Cladonia subfurcata	+	–
Cladonia uncialis	0.1	–
Nephroma arcticum	0.4	–
Ochrolechia spp.	0.9	–
Peltigera rufescens	+	–
Stereocaulon sp.	+	–
Thamnolia vermicularis	+	–

Appendix 3. Mean percentage cover of clusters of the *Calluna* and *Arctostaphylos* groups. The frequencies are indicated as follows: bold = *f* > 66.7%; underlined = 33.3% < *f* < 66.7%; normal text = *f* < 33.3%. nCalBryT = north boreal *Calluna*-Bryophyta type, typ.var. = typical variant, Pcil var. = *Ptilidium ciliare* variant, aEDiLiT = arctic *Empetrum-Dicranum*-Lichenes type, Lpro var. = *Loiseleuria* variant, Gym var. = *Gymnomitrion* variant, type var. = typical variant, OcT = *Ochrolechia* type, Sglo var. = *Sphaerophorus globosus* variant, Rlan var. = *Racomitrium lanunginosum* variant, Gym var. = *Gymnomitrion* variant.

	nCalBryT		aEDiLiT				OcT	
	typ. var.	Pcil var.	Lpro var.	Gym var.	typ. var.	Sglo var.	Rlan var.	Gym var.
Andromeda polifolia	0.1	–	–	–	–	–	–	–
Antennaria dioica	+	+	–	–	–	–	0.2	–
Arctostaphylos alpina	4.8	2.4	0.8	0.3	0.6	–	0.7	0.1
Betula nana	0.2	+	5.2	–	7.1	–	1.6	0.6
Betula pubescens subsp. *czerepanovii*	–	–	2.9	–	–	–	–	–
Bistorta vivipara	–	–	–	–	–	+	–	–
Calluna vulgaris	**19.9**	**8.2**	–	–	–	–	–	–
Cardamine bellidifolia	–	–	–	–	–	–	+	–
Carex bigelowii	+	–	+	–	–	–	–	–
Carex rupestris	–	–	–	–	–	–	–	+
Cornus suecica	0.1	+	–	–	–	–	–	–
Deschampsia flexuosa	0.3	–	5.6	0.6	0.4	–	–	–
Diapensia lapponica	+	–	–	0.2	0.1	–	0.2	1.5
Dryas octopetala	+	–	–	–	–	–	+	0.1
Empetrum hermaphroditum	**33.0**	**22.9**	**37.8**	**20.8**	**36.9**	**20.9**	10.3	**4.5**
Festuca ovina	–	0.1	+	–	0.3	–	0.2	+
Huperzia selago	+	–	–	–	+	0.3	+	–
Juncus trifidus	0.2	0.3	+	2.2	0.7	2.2	0.7	**1.7**
Loiseleuria procumbens	3.5	2.4	**14.1**	**8.0**	**1.9**	**0.7**	0.7	**0.9**
Luzula arcuata subsp. *confusa*	–	–	–	–	+	0.1	0.2	–
Nardus stricta	0.2	–	–	–	–	–	–	–
Pedicularis lapponica	+	–	–	–	–	–	–	–
Pinguicula vulgaris	–	+	–	–	–	–	+	+
Poa alpina	–	–	–	–	–	–	+	–
Pyrola minor	–	–	–	–	11.1	–	–	–
Ranunculus glacialis	–	–	–	–	–	–	+	–
Rubus chamaemorus	–	–	+	–	–	–	–	–
Salix herbacea	–	+	1.6	0.3	0.2	**1.2**	0.9	**0.1**
Silene acaulis	–	+	–	–	–	0.2	–	–
Solidago virgaurea	–	–	0.1	–	+	–	+	–
Thalictrum alpinum	+	–	–	–	–	–	–	–
Tofieldia pusilla	–	+	–	–	–	–	–	–
Vaccinium myrtillus	0.3	–	6.2	+	0.5	1.0	+	–
Vaccinium uliginosum	2.6	0.8	1.9	0.3	+	0.3	1.9	1.7
Vaccinium vitis–idaea	0.4	–	1.3	–	0.8	**0.5**	1.1	0.3
Anthelia juratzkana	–	–	–	0.6	–	0.1	–	–
Barbilophozia spp.	0.4	0.2	**9.4**	0.2	**1.7**	0.2	+	–
Diplophyllum taxifolium	+	–	–	–	+	0.1	–	–
Gymnomitrion spp.	–	0.2	+	**9.6**	1.2	**2.2**	0.3	**4.6**
Lophozia spp.	+	–	0.4	1.2	0.4	**0.3**	0.5	–
Ptilidium ciliare	**11.6**	**17.2**	**13.9**	4.6	–	1.6	0.4	–
Tetralophozia setiformis	–	–	–	–	+	+	0.3	–
Conostomum tetragonum	–	–	–	+	+	–	–	–
Dicranum drummondii	–	–	+	–	–	–	–	–
Dicranum elongatum	–	–	0.1	–	–	–	–	–
Dicranum fuscescens	2.9	0.3	**16.7**	**4.5**	**10.1**	0.7	2.2	+
Dicranum majus	0.9	–	–	–	–	–	–	–
Dicranum scoparium	**6.2**	**4.5**	**11.7**	–	2.4	2.7	1.1	–
Dicranum sp.	–	–	–	–	–	–	0.2	–

Continued

Appendix 3. Continued.

	nCalBryT		aEDiLiT				OcT	
	typ. var.	Pcil var.	Lpro var.	Gym var.	typ. var.	Sglo var.	Rlan var.	Gym var.
Grimmia sp.	–	+	–	–	–	–	–	–
Heterocladium dimorphum	+	–	–	–	–	–	–	–
Hylocomium splendens	0.9	–	–	–	–	–	0.3	–
Kiaeria starkei	–	–	12.2	5.6	3.4	**7.5**	0.3	+
Oligotrichum hercynicum	–	–	–	+	+	–	–	–
Plagiothecium sp.	+	–	–	–	+	–	–	+
Pleurozium schreberi	**8.2**	–	0.4	–	–	–	+	–
Pohlia spp.	+	**0.1**	+	0.1	0.1	+	+	+
Polytrichastrum alpinum	+	0.1	0.1	+	–	+	–	–
Polytrichastrum sexangulare	–	+	–	+	+	–	–	–
Polytrichum hyperboreum	–	+	0.1	+	+	+	0.7	+
Polytrichum juniperinum	+	–	–	+	–	–	–	+
Polytrichum piliferum	+	–	–	0.4	0.2	1.9	–	**0.3**
Pterigynandrum filiforme	0.2	0.1	–	–	–	–	–	–
Racomitrium canescens	–	–	–	0.1	–	–	–	–
Racomitrium lanuginosum	**9.8**	12.6	0.4	1.2	2.2	**3.3**	**9.1**	0.6
Racomitrium microcarpon	–	–	–	–	–	0.1	–	–
Sanionia uncinata	+	+	–	–	–	–	–	–
Tetraplodon mnioides	–	+	–	–	–	–	–	–
Tortella tortuosa	+	+	–	–	–	–	–	–
Alectoria nigricans	–	–	–	–	–	+	0.1	0.2
Bryocaulon divergens	+	+	–	–	–	–	+	+
Cetraria aculeata	+	+	–	–	0.2	0.2	0.1	0.3
Cetraria ericetorum	+	+	–	0.3	0.2	1.2	2.8	0.1
Cetraria hepatizon	–	+	–	–	–	–	–	–
Cetraria islandica subsp. *crispiformis*	+	0.1	+	–	1.2	1.3	**1.7**	+
Cetraria islandica	+	–	–	–	0.1	–	–	–
Cetrariella delisei	–	+	0.1	**3.7**	0.7	+	+	0.4
Cladina mitis	**1.5**	**0.5**	**10.3**	**4.9**	**4.1**	**3.3**	0.1	+
Cladina rangiferina	1.4	0.1	0.6	–	0.1	–	–	–
Cladina stellaris	–	–	–	–	–	0.2	–	–
Cladonia amaurocraea	–	–	+	–	0.4	0.3	–	–
Cladonia bellidiflora	+	+	0.2	0.7	0.9	0.2	0.1	+
Cladonia chlorophaea	+	–	–	–	–	–	–	–
Cladonia coccifera	0.1	0.5	0.1	0.9	0.2	0.4	0.7	0.1
Cladonia ecmocyna	+	–	0.1	0.1	0.1	–	–	–
Cladonia gracilis	+	–	+	–	–	–	0.1	–
Cladonia macrophylla	+	+	0.7	**3.6**	+	0.5	0.6	–
Cladonia pyxidata	–	+	–	–	–	–	–	–
Cladonia spp.	+	+	0.2	0.1	+	–	+	+
Cladonia subfurcata	0.1	0.2	0.3	0.4	0.7	–	+	0.1
Cladonia uncialis	0.2	0.1	0.5	+	**0.4**	**0.4**	0.1	+
Flavocetraria nivalis	+	+	–	–	+	–	–	–
Lecidea spp.	0.1	–	–	1.2	0.1	+	–	+
Nephroma arcticum	0.1	+	–	–	0.7	0.2	–	–
Ochrolechia spp.	0.2	**2.7**	0.4	**6.8**	**17.1**	**17.6**	**15.4**	**27.8**
Parmelia omphalodes	–	–	–	–	–	1.0	+	–
Peltigera rufescens	–	+	–	–	–	–	–	–
Pertusaria dactylina	–	–	–	–	–	+	–	–
Pseudephebe minuscula	–	–	+	–	–	–	+	0.1
Psedephebe pubescens	–	–	–	–	+	+	0.4	0.4
Psoroma hypnorum	0.1	–	+	+	–	2.8	–	–
Solorina crocea	–	–	–	–	+	–	–	–
Sphaerophorus globosus	+	**0.9**	–	–	1.0	**2.1**	**6.1**	**8.2**
Stereocaulon spp.	0.1	+	+	+	0.4	+	–	0.1
Thamnolia vermicularis	–	–	–	–	–	+	+	–

Appendix 4. Mean percentage cover of clusters of the *Juncus trifidus-Salix herbacea* group. The frequencies are indicated as follows: bold = $f > 66.7\%$; underlined = $33.3\% < f < 66.7\%$; normal text = $f < 33.3\ \%$. ShDfT = *Salix herbacea-Deschampsia flexuosa* type, Kiaeria var. = *Kiaeria* variant, Dicr var. = *Dicranum* variant, Eher var. = *Empetrum hermaphroditum* variant, JtDfT = *Juncus trifidus-Deschampsia flexuosa* type.

	ShDfT			JtDfT
	Kiaeria var.	Dicr var.	Eher var.	
Agrostis mertensii	–	–	–	0.3
Anthoxanthum odoratum subsp. *alpinum*	0.5	**1.0**	2.0	–
Bistorta vivipara	0.8	–	–	0.4
Carex bigelowii	–	1.3	–	1.2
Carex brunnescens	0.2	+	–	–
Carex lachenalii	1.2	0.3	2.0	0.6
Carex rupestris	–	–	–	0.6
Carex sp.	0.2	–	–	–
Carex vaginata	2.0	–	2.7	–
Cassiope hypnoides	–	–	–	0.3
Cornus suecica	–	0.3	+	–
Deschampsia flexuosa	**23.7**	**17.8**	**20.9**	6.7
Empetrum nigrum subsp. *hermaphroditum*	1.0	3.9	**16.1**	–
Equisetum arvense	–	–	–	+
Festuca ovina	–	–	–	0.1
Gnaphalium supinum	0.2	0.2	–	0.3
Hieracium sp.	+	–	0.1	+
Hierochloë alpina	–	–	+	–
Huperzia selago	+	0.1	0.3	0.1
Juncus trifidus	0.2	–	0.3	2.1
Loiseleuria procumbens	+	0.3	0.1	1.5
Nardus stricta	–	1.5	1.8	–
Phyllodoce caerulea	–	–	1.8	4.7
Rubus chamaemorus	–	–	0.4	0.3
Rumex acetosa	0.3	0.1	–	–
Salix herbacea	**36.6**	**42.5**	**19.6**	**17.7**
Saussurea alpina	–	–	+	–
Sibbaldia procumbens	–	–	–	0.3
Solidago virgaurea	–	1.8	0.2	0.1
Trientalis europaea	0.5	–	–	–
Trisetum spicatum	–	–	0.7	–
Vaccinium myrtillus	0.5	12.3	**19.3**	4.2
Vaccinium uliginosum	–	–	1.8	1.2
Vaccinium vitis–idaea	+	–	–	–
Veronica alpina	–	–	–	+
Viola canina	–	–	0.1	–
Viola sp.	+	–	–	–
Anthelia juratzkana	–	–	–	0.1
Barbilophozia spp.	37.6	**45.5**	**46.8**	**18.1**
Gymnomitrion spp.	0.2	–	–	1.2
Lophozia spp.	0.2	1.1	–	**6.1**
Moerckia blyttii	+	+	–	–
Ptilidium ciliare	0.2	–	–	0.8
Conostomum tetragonum	0.1	–	–	0.2
Dicranum fuscescens	5.0	10.0	**19.7**	**29.1**
Dicranum scoparium	4.4	**23.8**	**24.1**	0.3
Dicranoweisia crispula	–	+	–	+
Kiaeria starkei	**29.2**	–	–	15.7
Plagiothechium sp.	–	–	–	+
Pleurozium schreberi	–	–	+	–
Pohlia spp.	0.3	+	–	0.5
Polytrichastrum alpinum	**1.9**	0.1	–	1.2
Polytrichastrum sexangulare	0.5	0.1	–	1.9
Polytrichum commune	–	2.0	–	–
Polytrichum hyperboreum	–	+	0.3	0.3
Polytrichum juniperinum	–	0.1	0.7	0.1
Polytrichum piliferum	1.0	–	–	0.6
Racomitrium microcarpon	–	–	+	+
Rhytidiadelphus loreus	0.5	0.1	0.9	+
Sanionia uncinata	–	–	1.8	–
Cetraria ericetorum	–	–	–	+
Cetraria islandica subsp. *crispiformis*	–	+	–	+
Cetraria islandica	–	0.3	–	–
Cetrariella delisei	–	–	–	0.1
Cladina mitis	+	+	0.9	**2.8**
Cladonia bellidiflora	0.2	0.4	+	**2.2**
Cladonia chlorophaea	–	0.5	–	–
Cladonia coccifera	–	–	+	0.4
Cladonia ecmocyna	0.8	0.3	0.1	1.0
Cladonia macrophylla	+	+	0.2	0.8
Cladonia pleurota	–	–	+	–
Cladonia spp.	0.2	+	0.1	+
Cladonia subfurcata	–	–	–	0.2
Cladonia uncialis	–	–	+	0.1
Lepraria sp.	+	–	–	–
Nephroma arcticum	–	0.2	–	–
Ochrolechia spp.	–	–	–	0.2
Stereocaulon sp.	–	–	–	+

Appendix 5. Mean percentage cover of clusters of the *Juncus trifidus-Cassiope tetragona* group. The frequencies are indicated as follows: bold = *f* > 66.7%; underlined = 33.3% < *f* < 66.7%; normal text = *f* < 33.3%. ShET = *Salix herbacea* type, Kiaeria var. = *Kiaeria* variant, Gymn var. = *Gymnomitrion* variant, typ. var. = typical variant.

	ShET		
	Kiaeria var.	Gymn var.	typ. var.
Bistorta vivipara	0.9	+	–
Cardamine bellidifolia	+	–	–
Carex bigelowii	–	+	–
Carex brunnescens	–	–	+
Carex lachenalii	0.3	–	–
Cassiope hypnoides	–	–	–
Deschampsia flexuosa	0.1	**3.9**	+
Empetrum nigrum subsp. *hermaphroditum*	6.2	10.1	**17.1**
Gnaphalium supinum	0.2	0.8	1
Huperzia selago	+	+	–
Juncus trifidus	2.4	1.3	2.1
Loiseleuria procumbens	–	–	2.9
Luzula arcuata subsp. *confusa*	0.1	–	–
Luzula spicata	0.5	1.9	0.3
Oxyria digyna	+	–	–
Rhodiola rosea	–	1.3	–
Rubus chamaemorus	+	–	–
Rumex acetosa	+	–	–
Salix herbacea	**6.1**	5.6	3.4
Sibbaldia procumbens	–	0.3	–
Solidago virgaurea	–	–	+
Vaccinium myrtillus	0.4	5.1	–
Anthelia juratzkana	0.1	0.6	0.2
Barbilophozia spp.	2.0	0.6	–
Diplophyllum taxifolium	0.2	–	–
Gymnomitrion spp.	1.6	**10.9**	**7.1**
Lophozia spp.	**1.1**	**10.9**	**2.8**
Ptilidium ciliare	–	0.6	1.7
Conostomum tetragonum	–	0.3	0.2
Dicranum fuscescens	1.8	–	–
Kiaeria starkei	26.7	**10.5**	1.7
Oligotrichum hercynicum	–	0.3	0.1
Pohlia spp.	**0.2**	**2.7**	**0.1**
Polytrichastrum alpinum	0.3	–	–
Polytrichastrum sexangulare	–	+	–
Polytrichum hyperboreum	0.2	–	+
Polytrichum piliferum	0.1	3.8	0.2
Racomitrium microcarpon	+	+	0.3
Cetraria ericetorum	1.2	–	–
Cetraria islandica	–	–	+
Cetraria sp.	–	–	+
Cetrariella delisei	0.2	**0.7**	**4.3**
Cladina mitis	0.6	2.0	0.1
Cladina rangiferina	–	0.1	+
Cladonia amaurocraea	0.9	+	–
Cladonia bellidiflora	1.1	**4.4**	2.8
Cladonia coccifera	1.1	0.3	0.6
Cladonia gracilis	–	–	1.1
Cladonia macrophylla	0.1	0.6	0.3
Cladonia spp.	+	–	0.4
Cladonia subfurcata	0.2	0.3	0.6
Cladonia uncialis	+	0.3	–
Lecidea spp.	1.1	0.3	**1.7**
Lepraria sp.	0.2	+	–
Ochrolechia spp.	**6.7**	2.7	**15.7**
Pertusaria dactylina	0.1	–	–
Solorina crocea	+	–	–
Stereocaulon sp.	–	+	–
Thamnolia vermicularis	+	–	–

Appendix 6. Mean percentage cover of clusters of the *Ranunculus glacialis* group. The frequencies are indicated as follows: bold = *f* > 66.7%; underlined = 33.3% < *f* < 66.7%; normal text = *f* < 33.3%. RgGT = *Ranunculus glacialis-Gymnomitrion* type, mossy variant, Psex var. = *Polytrichastrum sexangulare* variant, Gymn var. = *Gymnomitrion* variant, Rgla var. = *Ranunculus glacialis* variant.

	RgGT			
	mossy var.	Psex var.	Gymn var.	Rgla var.
Agrostis mertensii	–	0.2	–	–
Antennaria alpina	–	0.4	–	–
Bistorta vivipara	–	0.1	–	–
Cardamine bellidifolia	–	–	0.1	+
Carex bigelowii	–	1.5	–	–
Carex brunnescens	0.4	–	0.3	–
Carex lachenalii	+	+	0.5	0.6
Carex sp.	+	–	–	–
Cassiope hypnoides	–	–	0.6	+
Deschampsia flexuosa	0.1	+	–	0.6
Empetrum nigrum subsp. *hermaphroditum*	–	–	1.9	–
Gnaphalium supinum	0.2	0.4	–	+
Juncus trifidus	0.3	–	3.8	–
Loiseleuria procumbens	–	–	–	+
Luzula arcuata subsp. *confusa*	–	–	–	1.5
Oxyria digyna	2.7	–	–	–
Ranunculus glacialis	–	–	–	0.5
Rhodiola rosea	–	+	–	–
Salix herbacea	**11.3**	**0.2**	**1.3**	–
Sibbaldia procumbens	1.6	0.1	–	–
Trisetum spicatum	0.4	–	–	0.7
Vaccinium myrtillus	–	+	–	–
Veronica alpina	0.1	–	–	–
Viola spp.	–	+	–	–
Anthelia juratzkana	5.5	1.3	–	–
Barbilophozia spp.	5.1	+	–	0.8
Diplophyllum taxifolium	+	–	–	–
Gymnomitrion spp.	**3.4**	**6.9**	**11.4**	**17.2**
Moerckia blyttii	0.2	–	–	–
Lophozia spp.	**8.7**	5.3	**2.8**	0.5
Andreaea rupestris	–	–	–	+
Bartramia ithyphylla	0.2	–	–	–
Bryum sp.	–	–	–	+
Conostomum tetragonum	0.1	+	0.6	+
Dicranella sp.	–	–	–	+
Dicranoweisia crispula	0.1	0.4	–	–
Dicranum elongatum	–	–	–	+
Dicranum fuscescens	4.9	–	–	+
Dicranum scoparium	–	0.4	–	+
Dicranum spp.	–	0.2	–	0.1
Ditrichum sp.	–	+	–	+
Kiaeria starkei	**8.8**	4.3	**3.1**	0.2
Oligotrichum hercynicum	–	0.2	–	0.2
Pohlia spp.	0.7	**0.4**	**0.8**	**0.3**
Polytrichastrum alpinum	0.4	1.0	–	–
Polytrichastrum sexangulare	4.4	**7.7**	0.7	1.1
Polytrichum hyperboreum	–	–	–	0.1
Polytrichum piliferum	–	–	0.1	–
Racomitrium fasciculare	0.1	–	–	–
Racomitrium ellipticum	–	+	–	–
Racomitrium lanuginosum	–	–	–	+
Racomitrium microcarpon	3.4	0.2	0.2	+
Sanionia uncinata	0.2	–	–	–
Schistidium spp.	0.1	–	–	+
Cetraria islandica subsp. *crispiformis*	0.4	–	–	0.4
Cetrariella delisei	–	–	2.6	0.1
Cladina mitis	+	–	–	–
Cladonia bellidiflora	0.9	1.2	–	+
Cladonia coccifera	0.1	–	0.3	**0.7**
Cladonia ecmocyna	0.9	–	–	–
Cladonia gracilis	0.2	–	–	0.3
Cladonia macrophylla	–	–	0.6	–
Cladonia spp.	+	0.1	2.6	–
Cladonia subfurcata	–	–	0.9	–
Flavocetraria nivalis	–	–	–	0.2
Lecidea spp.	0.1	0.1	**1.8**	0.1
Lepraria sp.	0.1	1.4	–	–
Ochrolechia spp.	–	0.1	0.2	**2.3**
Solorina crocea	–	0.6	–	0.5
Sphaerophorus globosus	–	–	–	1.6
Stereocaulon spp.	–	0.1	–	0.1
Thamnolia vermicularis	–	–	–	+