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Content

| | |
|--|----|
| Ingibjörg S. Jónsdóttir | |
| Biodiversity in arctic plant communities – project introduction and summary | 3 |
| Anna Maria Fosaa, Line Nybakken and Mette Oht | |
| Vegetation and environmental relations along the western coast of Spitsbergen, Svalbard | 8 |
| Wenche Eide, Kari Klanderud and Rune Tommelstad | |
| Plant community diversity at different scales in six localities on Svalbard | 22 |
| Timo Kossonen, Lisbeth Rauff , and Åsa Lindgren | |
| Raunkiaer life forms and plant functional types on Svalbard | 40 |



Biodiversity in arctic plant communities – project introduction and summary

Ingibjörg S. Jónsdóttir

The University courses on Svalbard (UNIS), P.O. Box 156, N-9171 Longyearbyen, Norway

Introduction

Biodiversity is a widely used term in both scientific and political context. As defined by the Convention on Biological Diversity it is the variety of life on Earth and the natural patterns it forms (www.biodiv.org). In other words, it includes the variety of plants, animals and microorganisms in a very broad term and can be considered at different levels of biological organization from genes to ecosystems. In recent years, the functional role of biodiversity has received increasing attention (Chapin et al. 1998). Climate has an overriding effect on plant species diversity on a global scale and biodiversity generally decreases with increased latitude. This trend is also seen within the Arctic region both in terms of number of species and plant growth forms (Chapin and Körner 1994, Matveyeva and Chernov 2000). If quantitative aspects of diversity were considered, i.e. the dominance of species and growth forms, the large-scale decline in diversity towards the poles would become even steeper because there are relatively few species that dominate in arctic plant communities and those species tend to have a wide distribution within the Arctic or that closely related species replace each other along geographical gradients (Matveyeva and Chernov 2000). However, on smaller spatial scales, other environmental factors than climate come into play in shaping biodiversity and on such scales, biodiversity in terms of species, growth forms or reproductive strategies may not be any lower in the Arctic than elsewhere.

In July 2001 a group of students attending the graduate course AB-306 at UNIS, worked on a project focusing on four different aspects of biodiversity in the Arctic. The overall aim of the project was to assess qualitative and quantitative biodiversity patterns at two different spatial scales by considering diversity in relation to climate, bedrock type, habitat type, soil pH, active layer depth, degree of herbivory and other biological interactions. The two scales were local, i.e. along moisture gradients at each locality, and regional by comparing different localities on Svalbard. The four diversity aspects were: 1) vegetation differentiation, 2) species diversity and richness, 3) diversity of growth- and life forms and 4) diversity of reproductive strategies and detailed reports on the first three are published here. Diversity patterns on these two scales can provide valuable indication of which factors are responsible for shaping the different aspects of diversity in the Arctic.

Material and Methods

During seven days we cruised along the western coastal areas of Svalbard and the fjord systems of Spitsbergen onboard MS Stockholm and visited eight different localities, representing two bioclimatic zones (northern arctic tundra zone and middle arctic tundra zone, respectively, *sensu* Elvebakk 1997). All study sites were at south facing slopes except one, Fuglehuken at the northern tip of the island Prins Karls Forland that was facing east.

Soil moisture is one of the major factors limiting plant production in the Arctic. This factor was fixed in our study because we subjectively chose habitats according to soil moisture. At

each locality we studied two main habitat types, mesic and dry, and at two localities extremely dry habitat (semi-polar desert, more exposed than the dry habitat) was included as well. Wet habitats were excluded from the beginning for two reasons. First, they are not expected to show as large response to the large scale environmental differences among localities as the other habitat types, and secondly, wet habitats were not to be found at all localities. Extreme, late snowbeds were avoided as well since they were difficult to standardize between localities.

Two localities were only briefly visited to obtain species lists. At each of the remaining six localities we analysed the point frequency of plant species within habitat type in randomly chosen plots. For each plot the total cover of the vegetation was estimated, and the depth of the bryophyte mats (if present), the depth of the active layer. Within each habitat soil pH was measured and the grazing pressure estimated by counting droppings of different herbivores. In addition, the occurrence of other vascular species outside the plots was surveyed and subjectively quantified at each locality. At two localities, Hornsund and Blomstrandhalvøya, two study sites were included.

The students worked in four groups, each focusing on one of the aspects of diversity specified above. All groups collaborated on the data collection and then each group analysed the data for a specific aspect of diversity. Group one analysed vegetation differentiation among habitats and sites based on the point frequencies by using multivariate techniques and related it to the environmental factors (soil moisture, total vegetation cover, bryophyte depth, active layer depth, soil pH, and grazing pressure). Group two analysed species richness and species diversity in the plots combined with survey data for the vascular plant species at each locality. Group three analysed the life form spectra as defined by Raunkiear (1934) for vascular plants and then quantified both Raunkiear's life forms as well as the different growth forms (including cryptogams), or functional types. Group four analysed diversity in reproductive strategies among vascular plant species within the plots. This report is not included here. The locations we visited and further details of the methods used are given in the group reports that follow.

Result summary and Discussion

Environmental differences

The visited localities differ in a range of environmental factors. One of the criteria for the choice of the localities was that they should represent as different climates as possible within the region of west Svalbard. Unfortunately there are limited climatic records available for Svalbard so this choice had to be made intuitively. It was apparent that the localities differed both in terms of temperatures and precipitation, or rather continentality, and this was reflected in the vegetation. Due to a cold sea current from the east, rounding the south part of Spitsbergen and continuing northwards along the west coast until it meets a warmer branch of the Golf stream in level whit Isfjorden, the coldest localities of the study were in the south, i.e. Hornsund is colder than Bellsund. The warmest localities were in the inner Isfjorden, i.e. Pyramiden and Templet. Localities further north were intermediate (Prins Karl Forland and Blomstrandhalvøya). Across this temperature gradient, a continentality gradient can be assumed from the coastal sites (Prins Karl Forland, Hornsund, Bellsund) eastwards along Kungsfjorden (Blomstrandhalvøya) and into Isfjorden (Templet, Pyramiden). These climatic differences among the localities were only partly reflected in a thermophily index that one of the groups (Eide, Klanderud and Tommelstad) calculated for each locality according to Karlsen and Elvebakk (1996). This index is based on the assumption that plant species with relatively southerly distribution patterns are temperature demanding and a high representation

of such thermophilic species would thus indicate higher temperatures for that particular site than a site with low representation.

Another interesting difference between the localities is soil chemistry, largely affected by the extreme variation in exposed bedrocks on Svalbard, often across short distances as we observed in Hornsund. In other biomes biological activities mould the effect of bedrock to large extent. In the Arctic, however, the effect of bedrock on soil chemistry is expected to be more direct because soil processes are slow and the accumulation of organic matter is confined to the more productive mesic and wet habitats with periods of waterlogged conditions. Three of the visited sites were weakly alkaline, i.e. Templet on calcareous Permian bedrock, the sub-site at Hornsund on Middle Proterozoic marble garnet mica schist and Blomstrandhalvøya on Precambrian bedrock, with acidity ranging between pH 7 and 8. One site was close to neutral, i.e. Pyramiden on Devonian/ Carboniferous bedrock, while Bellsund, Prins Karl Forland and the second sub-site at Hornsund were weakly acidic on Carboniferous, Precambrian and Proterozoic garnet mica schist bedrocks, respectively. At all localities soil acidity tended to increase in the organic layer of the soil and as for the three alkaline sites it was generally lower in mesic habitats than in dry habitats, indicating increasing biological effects on soil chemistry. The data did not, however, allow statistical evaluation of these trends.

Grazing is a complex biological factor that can dramatically alter plant conditions set by the physical environment. We only had indirect estimates of grazing pressure at the different localities based on counting herbivore droppings per unit area. According to these estimates the highest grazing pressure by birds (geese and ptarmigan) among our study sites is in mesic habitats at the two sub-sites at Hornsund, followed by mesic habitats at Blostrandhavøya, Pyramiden and Templet, all with more than 1 dropping m^{-2} . At all other sites there were less than one bird dropping per square metre. The density of reindeer droppings was not as high. We separated between winter and summer droppings and the density of winter droppings was highest in all habitats at Templet and in mesic habitat at one sub-site at Blomstrand and in dry habitat at Bellsund (ranging between 0.16 and 0.14 m^{-2}). At all other sites the density was less than 0.1 per square metre. The density of summer droppings, however, was highest in Bellsund (dry habitat 0.64) followed by Templet (0.34 in very dry and mesic habitats). At all other localities summer dropping density was less than 0.1 per square metre. Notably, no reindeer droppings were registered at Pyramiden. We expected that these different grazing activities and grazing intensities would be reflected in the diversity patterns.

There is not a one-way interaction between the environmental factors and the vegetation. The structure of the vegetation itself affects the physical environment. Bryophytes have great insulating effect and a thick moss mat may keep the soil cool and prevent thawing at greater depth. We therefore measured the total vegetation cover, moss depth and active layer depth and treated them as environmental factors as well in the diversity analysis.

Diversity responses to the environment

Only six different plant community types were identified in the first report (Fosaa, Nybakken and Oht) and soil acidity was found to have strongest effect in differentiating these plant communities, followed by moss depth, soil moisture, active layer and grazing. Two of these communities were common to all localities while two of them were confined to cold and oceanic localities and another two were only found in some of the warmer localities. Species diversity was analysed in the second report on plot basis, rather than on community type basis (Eide, Klanderud and Tommelstad). Species diversity was generally higher in mesic habitats than in dry habitats. Interestingly difference in diversity at the regional scale was only pronounced for the more productive mesic habitats and was positively related to temperature

(indirectly estimated by calculated temperature indices). At the local scale diversity was positively related with soil pH and vegetation cover and negatively related with moss depth.

Biological spectra of vascular plant life forms based on number of plant species representing each life form has been frequently used to characterise different biomes. However, as the third report on life forms and functional types clearly demonstrates quantification of life forms is necessary to detect differences on regional and local scales (Kossonen, Rauff and Lindgren). Interesting patterns were revealed in the abundance of life forms and functional types. Three vascular plant life forms were represented in the study and on the regional scale hemicryptophytes with over-wintering buds protected in the soil surface were most abundant at colder and more oceanic localities and chamaephytes and cryptophytes with buds above and below the soil surface, respectively, were most abundant at the warmer and more continental localities in the inner fjord systems. On local scales, habitat type, i.e. soil moisture, had the strongest effect on the abundance of different categories. Hemicryptophytes were most abundant in mesic habitats while chamaephytes with over-wintering buds above the surface were equally or more abundant in dry to very dry habitats. Bryophytes were most pronounced in mesic habitats and lichens in dry habitats. Other environmental factors also affected the abundance of both life forms and functional types in various ways, but the sample size would need to be larger to fully evaluate them.

Conclusion

The diversity in terms of plant community types is low in Svalbard. Soil acidity appears to be an important factor community differentiation and biological activity is responsible for weakening the effect of difference in bedrock. Bryophytes are one component of this modifying process and thus in shaping communities and their diversity on local scale, both in terms of species, life forms and functional types. Grazing is another biological component, but a larger number of sites and a sampling design more targeted towards different grazing regimes would be needed to detect any grazing effect on biodiversity. For the relatively productive mesic habitats species diversity is primarily related to regional differences in climate.

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Vegetation and environmental relations along the western coast of Spitsbergen, Svalbard.

Anna Maria Fosaa¹, Line Nybakken² and Mette Oht³

¹Faroese Museum of Natural History, Botanical Department, Debesartrod, Fo-100 Torshavn, Faroe Islands; ²Line Nybakken, Department of Biology and Nature Conservation, Box 5014, Agricultural University of Norway, N-1432 ÅS, Norway; ³Mette Oht, Institute of Geography, University of Copenhagen, Øster Voldgade 10, 1350 Copenhagen, Denmark

Abstract. The relationship between the vegetation and different environmental parameters was investigated at six sites along the west coast of Spitsbergen and in the Inner Isfjorden area, representing a terrain with a large climatic and edaphic range. The study included 135 plots with 108 taxa. At each site the vegetation was sampled along a moisture gradient in randomly chosen plots using the objective point quadrat frequency method. Soil characteristics and moss depth were measured and the total vegetation cover and grazing pressure were estimated. The vegetation was classified into six plant communities using an agglomerative hierarchical method. The relationship between the vegetation and the environmental parameters were analysed using Canonical Correspondence Analysis (CCA). The strongest correlation with the first CCA axis was soil with pH, while vegetation cover and moss depth showed weaker correlations with that axis. Soil moisture, the active layer depth and grazing pressure were correlated with the second and third axes. This indicates that pH is the most decisive factor for plant distribution in the area studied, while grazing and moss depth might be important on a local scale.

Introduction

The vegetation of Svalbard has been thoroughly studied compared to many other Arctic areas. Exposed ridges and sea shores are the habitats most investigated, while the open vegetation of screes, active sedimentation plains, young moraines, polar deserts and saxicolous vegetation range from almost unknown to poorly known (Elvebakk 1994). Many of the studies are local, or available only as unpublished student theses, often lacking numerical data, while many do not compare their results with other Svalbard studies.

Elvebakk (1994) made a survey of the associations and alliances from Svalbard based on all earlier published studies, where he concluded that 19 major habitat types occur. He stated that the major determinants of the spatial distribution of species and communities in the Arctic are temperature, bedrock/soil chemistry, substrate texture and topography. Partly affected by these abiotic factors are some biotic factors which may be crucial in deciding what kind of vegetation occurs in a certain place; e.g. moss depth, vegetation cover, as well as manuring and grazing by herbivores.

Vegetation studies in the Arctic seldom pay attention to the chemical preferences of plants, and several authors have concluded that this aspect is not important in relation to how plants are distributed in arctic regions (Euroala 1974; Hadac 1946). Elvebakk (1982), however, investigated fourteen different rock substrates in western Spitsbergen, and stated that there appeared to be a close correlation between different species associations and geological substrates, as well as pH values. He found a multitude of different responses among plants to the varying chemical properties of mineral substrates. His study also suggested that there

exists a change in pH preference between some species from western Spitsbergen compared with populations from regions further south, especially in Fennoscandia. When looking at vascular plants in the North American arctic tundra, Gould & Walker (1997) and Gough *et al* (2000) found that soil pH was positively correlated with species richness. Gough *et al* (2000) stated that most of the species found on acidic substrates (pH<5.5) were not confined to that soil type and also occurred on non-acidic substrates (pH>5.5).

Grazing may have a profound impact upon the composition of plant communities in the arctic in a number of ways. The most important herbivores on Svalbard are reindeer, ptarmigan and different species of geese. In a study of reindeer grazing in Adventdalen, Svalbard, Wegener & Odasz (1998) found that Svalbard reindeer do not reduce the standing crop of investigated vascular species to a constant low level, as would be expected from investigations of reindeer grazing further south. However, recent studies by van der Wal *et al.* (2001) in Ny-Ålesund, have shown that grazing by reindeer and barnacle geese do reduces moss height by means of trampling and consumption. This has a positive impact on the performance of vascular plants, as the soil temperature increased with decreasing moss layer. Lichens are also sensitive to trampling, and are among the first organisms to disappear when grazing pressure increases. Reindeer have been shown to reduce lichen cover drastically during winter grazing in the arctic (Wegener *et al.* 1992; Oullet *et al.* 1993; Manseau *et al.* 1996). In a new study van der Wal *et al.* (2001) show that the impact of Svalbard reindeer on lichens is dependent on growth form, with fruticose lichens suffering from grazing, while foliose lichens might even benefit indirectly from higher densities of reindeer or, like crustose lichens, be controlled by other factors.

In the Hudson Bay, Canada, Jano *et al.* (1998) showed that an explosion in the population of lesser snow geese led to loss of vegetation and habitat destruction. Ptarmigans are highly selective of food items of high nutritional quality, and the young chicks feed almost entirely on *Bistorta vivipara* bulbils (Unander *et al.* 1985), which can lead to decreased spread of this species.

There is a need for more comprehensive studies of Svalbard vegetation, with more than one environmental factor being taken into account. Most probably, it will appear that several factors operate simultaneously, and that some are closely associated (e.g. moisture, moss depth and vegetation cover). In this study we investigated six different localities along the western coast of Svalbard, including the inner Isfjorden area. The main aim was to look at how different abiotic (bedrock/soil pH, active layer, soil humidity) and biotic (grazing, moss depth, vegetation cover) factors correlate with the occurrence of different defined plant communities as a first step towards understanding how these factors might influence arctic vegetation. Because the vegetation in wet habitats was expected to show only small responses to climate and bedrock type, the study was limited to mesic and dry habitats.

Materials and Methods

Study sites

We investigated six different sites along the western coast of Svalbard, as shown on the map in Figure 1. At each locality, one or two mesic and dry habitats were chosen subjectively, as well as an extra dry habitat at two localities, Templet and Blomstrandhalvøya. The following is a detailed description of the localities and habitats included in the study (see also Table 1).

Site 1 – Templet, Tempelfjorden. The plant habitats range from very dry, unstable scree slopes to more stable, dry, raised beaches consisting of gravel, dry and open “fellfield” areas, a few fully vegetated mesic patches and some snowbeds. There are no true wetlands. The whole area is heavily grazed by reindeer and geese. Dominant vascular species in the dry and

extremely dry habitats are *Dryas octopetala*, *Saxifraga oppositifolia* and in the mesic: *Carex maritima*, *Poa* spp. and *Festuca rubra*.

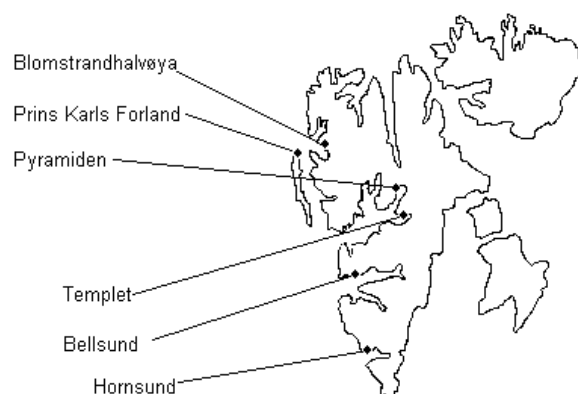


Figure 1. Map of study sites

Table 1. The location and aspect of the six localities, the numbers of mesic, dry and extra dry habitats investigated and bedrock description.

| Locality | Location | Aspect | Mesic sites | Dry sites | Extra dry sites | Bedrock |
|---------------------------------------|-------------------------------|---------|-------------|-----------|-----------------|--|
| Templet | 78°23'34.5"N, 16°48'14.8"E | 158 | 1 | 1 | 1 | Permian, calcareous, rather alkaline |
| Pyramiden, Billefjorden | 78°39'37.0"N, 16°17'51.7"E | 180 | 1 | 1 | | Devon, calcareous, some outcrops of schists |
| Fuglebergsletta Hornsund | 77°00'23N, 15°31'28E | 180 | 2 | 2 | | Middle Proterozoic marble garnet mica schist Site 2 more acidic garnet mica schist |
| Steinneset, Bellsund | 77°45'20.5"N, 14°24'38.1"E | 190 | 2 | 2 | | Carboniferous |
| Fuglehuken, Prins Karls Forland | 78°53'43.3"N, 10°28'26.8"E | 350 | 1 | 1 | | Precambrian quartzite. |
| Blomstrand, Kongsfjorden | 78°57'50.8"N, 12°02'47.7"E | 180/120 | 2 | 2 | 1 | Precambrian |

Site 2a – Adolfbukta, Billefjorden. This is a rather dry and calcareous locality where *Dryas octopetala* is the dominant species. The site was visited only briefly and not included in the final analysis.

Site 2b - Pyramiden, Billefjorden. The dominant vascular species at this site is *Dryas octopetala*. *Cassiope tetragona*, *Carex rupestris* and *Silene acaulis*. *Pedicularis lanata* are also rather common. The locality is heavily grazed by geese and ptarmigan, but no reindeer grazing were apparent, which was reflected in the more lush lichen vegetation than at previous sites.

Site 3 – Fuglebergsletta/Ariekammen, Hornsund. This is an extremely lush lichen heath dominated by *Cetraria delicei*, *C. nivalis*, *Cladonia arbuscula/mitis*, and moss species like *Racomitrium lanuginosum* and other *Racomitrium* spp, on the dry site. At some distance further to the west there is apparently a somewhat more acidic bedrock (garnit mica schist) with not as lush cryptogam vegetation as at the first dry sites. We also analysed both dry and mesic sites at this location. The mesic sites are moss dominated. Interestingly, no *Dryas octopetala* or *Cassiope tetragona* were found and only a few plants of *Papaver dahlianum* and *Draba* spp. *Salix reticulata* was found on the second dry site. The site is heavily grazed by geese, but not visibly influenced by reindeer. According to long-term observation by overwintering staff at the Polish research station close by reindeer came to the area only ca 10 years ago and the population is now around 150 animals.

Site 4 – Steinneset/Ingeborgfjellet/ Bellsund. The whole area is influenced by extremely heavy grazing by reindeer (> 50 animals counted) and barnacle geese. The area is very species poor, and dominated by the grasses *Poa pratensis*, *P. arctica*, *Alopecurus boreale*, *Luzula confusa* and the moss *Sanionia uncinata*. *Dryas octopetala* and *Cassiope tetragona* are totally lacking and not a single species of *Carex* was found during our fieldwork.

Site 5 – Fuglehuken, Prins Karl Forland. One dry and one mesic site close to the light house (Fuglehuken fyr), where the manuring effects from the bird cliffs are not severe, were investigated. Dominating species are *Sanionia uncinata*, *Saxifraga oppositifolia*, *S. hyperborea*, *Poa arctica*, *Festuca rubra* and the lichens *Cetraria nivalis*, *C. islandica*, *Cladonia* spp.

Site 6 – Blomstrandhalvöya, Kongsfjorden. The dominating species here, *Dryas octopetala*, *Saxifraga oppositifolia*, *Carex rupestris*, *Silene acaulis*, *Cetraria nivalis*, are the same for both the dry and mesic sites, but the vegetation cover is greater at the mesic site.

Sampling

Point frames were used to sample the frequencies of species in the different habitats and sites. The frame is 0.5m x 0.5m and consists of 25 evenly distributed points at the crossing of double layers of strings attached to the frame. Each point is without dimension, which makes it possible to hit one plant only. For each point, one hit from the field (phanerogam) layer and one from the moss/lichen (cryptogam) layer was recorded. The size of the frame should fit the vegetation type of the study. The size we sampled is as used by Kent & Coker (1992) for bryophytes and lichens, and which seemed suitable for Svalbard vegetation, with its relatively few vascular plants. Our habitats were also fairly homogeneous. Seven point frames were selected at random and sampled within each habitat (mesic/dry/extra dry), resulting in a total of 136 analysed plots across all sites and habitats.

Environmental data

For each habitat in all localities, the depth of the active soil layer, soil pH, and droppings from herbivores were quantified. Average moss depth and total vegetation cover was registered for every single point frame. The depth of the active layer was measured with a metal rod which was forced into the ground by the weight of one person, until the rod reached resistance and stopped on the permafrost table (Brown et al. submitted 2001, Molau and Mølgaard 1996). In areas where rocks are dominating (especially dry and extra dry habitats) the active layer depth

can be difficult to measure due to resistance produced by the rocks. The minimum active layer depth was then defined as the distance from the soil surface to resistance.

Soil samples were taken from the mineral layer and, where possible, from the organic layer from five frames per habitat. The pH was measured in both distilled H₂O and KCl to obtain an indication of differences in nutrient availability. An average pH was calculated for each habitat, which was used in the analysis. Droppings from herbivores were used as an estimate of the grazing pressure in the habitat. Droppings from reindeer, geese and ptarmigan were counted along a 50 x 2 m transect per habitat and calculated together as number of droppings per m². We did not differentiate between species in the analysis. The habitat classification (mesic/dry/extra dry) was used as a estimate of soil moisture in the analysis.

Average moss depth per point frame was calculated as the distance from the top of the moss layer down to the organic soil, from five diagonal points within each frame. Total vegetation cover was recorded as a subjective estimate of percentage cover inside the point frame (crustose lichens not included).

Data analysis

The frequency of each species for 135 samples and 108 taxa, was analysed in the computer programme MVSP (version 3.12c, Kovach Computing Services 1986-1999). A cluster analysis using agglomerative hierarchical technique was performed in order to classify the data. Minimum variance and squared Euclidean distance were adopted to calculate the distance between plot pairs.

The method of table sorting was performed with the method of Braun-Blanquet (1964), Mueller-Dombois & Ellenberg (1974), Westhoff & van der Maarel (1978) to identify the vegetation communities that the cluster analysis revealed. The frequency and the constancy of species hit in the point frames were used to define the communities. The constancy of species was categorised in roman numbers from I to V (see Table 2) and the relative frequency recorded as a mean percentage. The dominant species with high constancy were used to define the communities. This follows the Nordic tradition in defining plant communities (Lawesson et. Al. 2000). The result we obtained by the cluster analysis was confirmed by CA (Correspondence analysis).

Table 2. Constancy of species hit in point frames

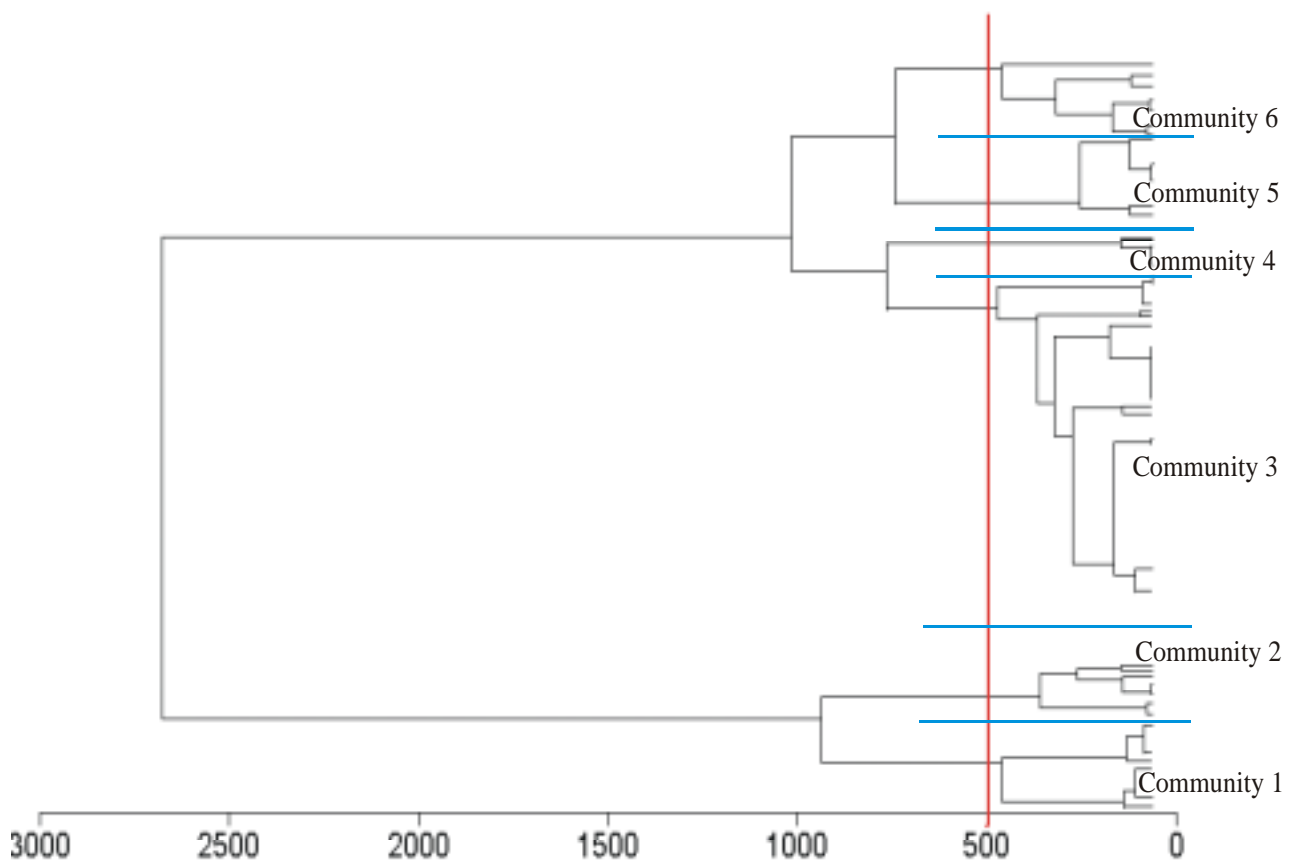
| <i>Constancy code</i> | <i>Constancy in %</i> |
|-----------------------|-----------------------|
| I | 1-5 |
| II | 6-25 |
| III | 26-50 |
| IV | 51-75 |
| V | 76-100 |

In order to find the relationship between environmental factors and plant communities, a direct gradient analysis was performed in terms of a CCA (Canonical Correspondence Analysis).

Results

Classification and ordination

We choose to divide the cluster diagram into six plant communities (Figure 2). The Correspondence Analysis (CA) revealed the same groupings as in the agglomerative dendrogram (Fig. 3a). A summary of the CA results is shown in Table 3. The eigenvalues are



relatively high, with a strong Axis 1.

Figure 2. Dendrogram with communities 1-6

Table 3. Summary of the results from the CA (Correspondence Analysis). Eigenvalues and % of variance explained.

| | Axis 1 | Axis 2 | Axis 3 | Axis 4 |
|-----------------|--------|--------|--------|--------|
| Eigenvalues | 0.694 | 0.631 | 0.575 | 0.569 |
| Percentage | 4.708 | 4.279 | 3.899 | 3.858 |
| Cum. Percentage | 4.708 | 8.987 | 12.885 | 16.743 |

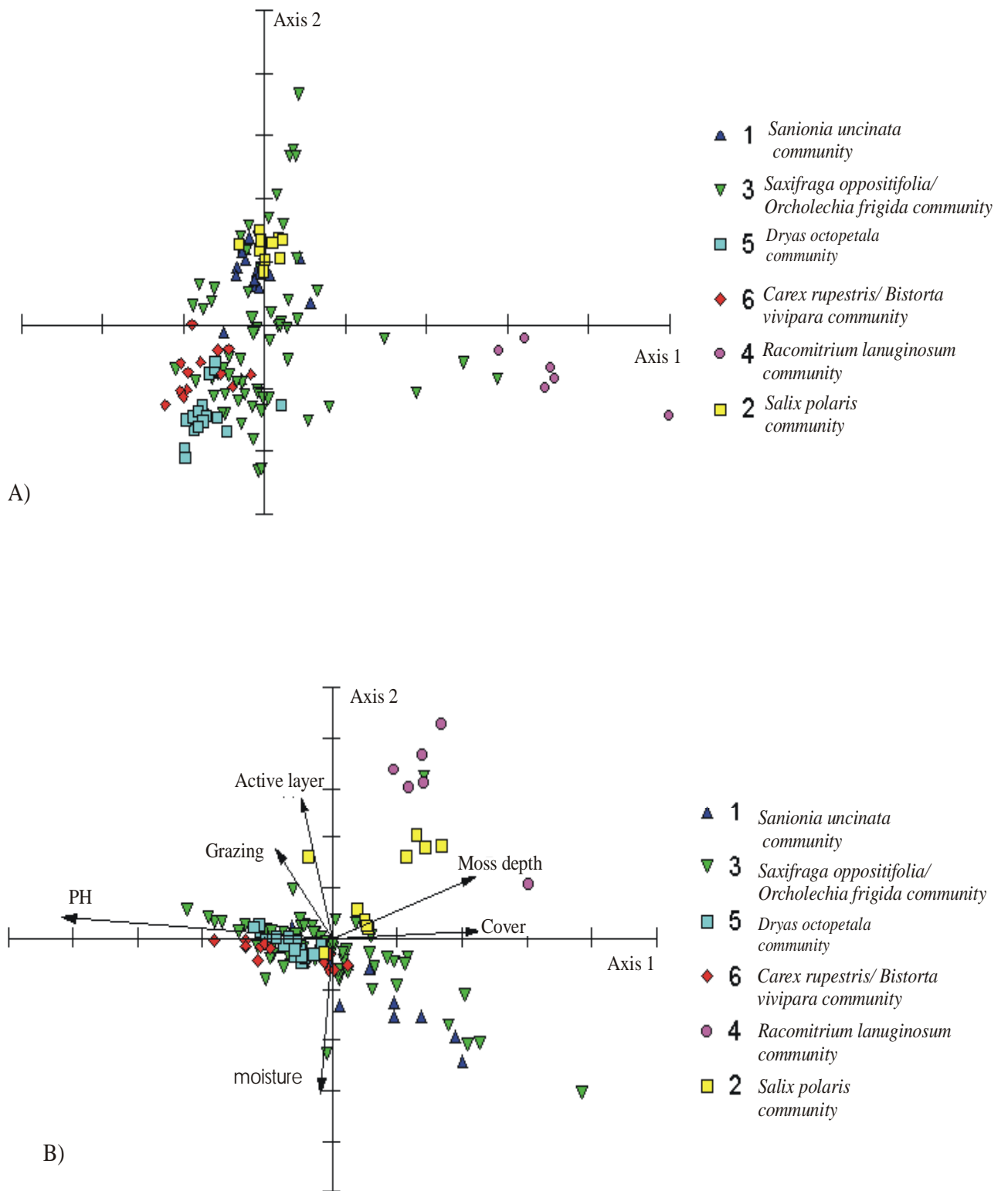


Figure 3. A) CA of plant communities. B) CCA of six communities and six environmental variables

The results from the CCA analysis showed that, the environmental parameters, such as vegetation cover and moss depth, are positively correlated with the first ordination axis while pH is negatively correlated to the first axis (Fig. 3B, Table 4 and 5). Active layer and grazing are positively correlated with the second axis, and moisture is negatively correlated with the second axis (Table 5).

Axis 1 explains 25% of the species variance with a species-environment correlation of 0.75. Axis 2 explains 23% of the species variance with a species-environment correlation of 0.72. Axis 3 explains 19 % of the species variance with a species-environment correlation of 0.70.

Community 1, 2 and 4 are correlated with cover and moss depth. Community 3 shows a large spread in relation to pH and moisture, and also to some degree in cover. Communities 5 and 6 are correlated with pH (Fig. 3B).

Table 4. Summary of the results from the CCA (Canonical Correspondence Analysis). Eigenvalues, % of variance explained and species environmental correlation.

| | Axis 1 | Axis 2 | Axis 3 | Axis 4 |
|-------------------------|--------|--------|--------|--------|
| Eigenvalues | 0.308 | 0.276 | 0.177 | 0.126 |
| Percentage | 2.086 | 1.868 | 1,197 | 0.853 |
| Cum. Percentage | 2.086 | 3.954 | 5.151 | 6.005 |
| Cum.Constr.Percentage | 29.058 | 55.081 | 71.753 | 83.637 |
| Spec.-env. Correlations | 0.782 | 0.746 | 0.686 | 0.623 |

Table 5. Intraset correlations between environmental variables and constrained site scores

| | Envi. Axis 1 | Envi. Axis 2 | Envi. Axis 3 | Envi. Axis 4 |
|--------------|--------------|--------------|--------------|--------------|
| Cover | 0.450 | 0.031 | 0.364 | 0.017 |
| Moss depth | 0.436 | 0.243 | -0.096 | 0.186 |
| Moisture | -0.036 | -0.604 | 0.511 | 0.272 |
| Active layer | -0.093 | 0.553 | 0.756 | -0.288 |
| Grazing | -0.172 | 0.350 | 0.543 | 0.525 |
| pH | -0.822 | 0.081 | -0.371 | -0.297 |

Plant communities

1. *Sanionia uncinata* community. The character species for this community is *Sanionia uncinata* (V/44). *Salix polaris* also has a relatively high constancy in the community (IV/13). The community is found in all sites, except Pyramiden, and on moist habitats, except for one plot from a dry site. The vegetation cover is high (86% on average). The total number of species in the cluster is 43, the number of species in the plots ranges from a minimum of five to a maximum of nine, and soil acidity varied between pH 6.91 (max) and 6.12 (min).

2. *Salix polaris* community. The character species for this community is *Salix polaris* (V/27). Other species of high constancy in the community are *Sanionia uncinata* (V/13), *Cetrariella delisei* (V/4), and *Aulacomium palustre* (IV/13). The community has a high vegetation cover (84 % on average), and the total number of species in the cluster is 18. The community is found in mesic habitats in Hornsund. The number of species in the plots ranges from a minimum of four to a maximum of nine, and soil acidity varied between pH 7.21 (max) and 6.39(min).

3. *Saxifraga oppositifolia*- *Ochrolechia frigida* community. The character species of this community are *Saxifraga oppositifolia* (IV/7) and *Ochrolechia frigida* (III/12). Most of the species in the community have both low frequency and low constancy. The community is also characterised by a relatively low vegetation cover (41 % on average). The total number of species is high (84) for the whole cluster, and the community includes more than 50 % of all plots in the study. The community is represented at all sites, mostly in dry and extra dry habitats, but ten plots are in mesic habitats. The number of species in the plots ranges from a minimum of one to a maximum of eleven. Soil acidity varied between pH 8.11 (max) and 6.03(min).

4. *Racomitrium lanuginosum* community. The character species for this community is *Racomitrium lanuginosum* (V/32). Another species of high frequency is *Cladonia uncialis* (V/7). The community is small, with only 6 plots and 22 species. The vegetation cover is 57 % on average. The community was found in dry habitats in Hornsund and in one plot in Bellsund. The number of species in the plots ranges from a minimum of seven to a maximum of eight and soil acidity was at pH 6.56.

5. *Dryas octopetala* community. The character species for the community is *Dryas octopetala* (V/44). Other species of high constancy in the community are *Carex rupestris* (IV/12) and *Saxifraga oppositifolia* (IV/6). The number of plots in the community is 18 and the number of species is 22. This community is found on both moist and dry habitats on the localities of Pyramiden and Blomstrandhalvøya. The number of species in the plots ranges from a minimum of two to a maximum of nine and soil acidity varied between pH 8.02 (max) and 6.76 (min).

6. *Carex rupestris*-*Bistorta vivipara* community. The character species for the community are *Carex rupestris* (V/12) and *Bistorta vivipara* (V/7). Other species of high frequency in the community are *Sanionia uncinata* (IV/11), *Tomentypnum nitens* (IV/13), *Saxifraga oppositifolia* (V/8), *Dryas octopetala* (IV/5), *Silene acaulis* (IV/6), and *Cassiope tetragonia* (IV/13). The vegetation cover is high (81 % on average) and the total number of species for the cluster is 37. The community is found in mesic habitats, on the sites of Templet, Pyramiden and Blomstrandhavøya. The number of species in the plots ranges from a minimum of seven to a maximum of thirteen and soil acidity varied between pH 7.13 (max) and 6.73 (min).

For a complete list of species with frequency and constancy represented in each community see Table 6.

Table 6. Synoptic table of the six plant communities. Roman numbers record constancy of species in samples, arabic numbers are mean percentage relative frequencies of a species in a community and '+' indicates frequency less than 1%

| Community | 1 | 2 | 3 | 4 | 5 | 6 |
|-------------------------------|--------|-------|--------|-------|-------|-------|
| Number of relevés (plots) | 17 | 10 | 71 | 6 | 18 | 13 |
| % vegetation cover | 86 | 84 | 41 | 57 | 58 | 81 |
| Number of species | 43 | 19 | 84 | 22 | 21 | 37 |
| Ave moss depth (cm) | 2.1 | 3.5 | 4.4 | 5.7 | 1.8 | 1.4 |
| Active layer(cm) | 32 | 51 | 26 | 23 | 31 | 50 |
| <u>Character species</u> | | | | | | |
| Sanionia uncinata | V/44 | V/13 | III/5 | | III/6 | IV/11 |
| Salix polaris | IV/13 | V/27 | III/12 | | II/3 | III/3 |
| Saxifraga oppositifolia | II/2 | II/1 | IV/7 | | IV/6 | V/8 |
| Ochrolechia frigida | II/+ | III/1 | III/12 | III/4 | II/1 | III/4 |
| Racomitrium lanuginosum | I/+ | V/32 | | | | |
| Dryas octopetala | II/3 | | II/3 | | V/44 | IV/5 |
| Carex rupestris | II/+ | | II/1 | | IV/12 | V/12 |
| Tomentypnum nitens | III/5 | | II/1 | | | IV/13 |
| Frequent phanerogams | | | | | | |
| Silene acaulis | II/+ | | I/+ | | III/3 | IV/6 |
| Bistorta vivipara | II/+ | | II/3 | | III/3 | V/7 |
| Cassiope tetragona | | | | | IV/9 | |
| <u>Frequent cryptogams</u> | | | | | | |
| Cetrariella delisei | III/3 | V/4 | III/9 | III/3 | II/1 | II/1 |
| Cetraria islandica | II/1 | II/+ | II/3 | III/7 | II/2 | II/2 |
| Polytrichastrum alpinum | III/3 | II/+ | II/4 | III/5 | | II/+ |
| Cetraria nivalis | II/+ | II/+ | II/1 | | II/+ | II/+ |
| Ditrichum flexicaule | II/1 | | II/2 | III/8 | III/7 | IV/7 |
| Campyllum stellatum | III/11 | II/2 | II/+ | | II/+ | |
| Aulacomnium palustre | II/2 | IV/13 | I/+ | II/3 | | |
| Ptilidium ciliare | II/1 | IV/12 | | II/5 | | |
| <u>Other phanerogams</u> | | | | | | |
| Luzula arcuata ssp confusa | III/3 | | II/3 | III/3 | | II/+ |
| Carex misandra | II/+ | | | | III/2 | II/+ |
| Luzula arctica | | | I/+ | II/+ | | II/+ |
| Oxyria digyna | II/+ | II/+ | | | | |
| Cochlearia groenlandica | III/3 | | II/2 | | | |
| Poa arctica | II/+ | | I/+ | | | |
| Saxifraga cespitosa | II/+ | | I/+ | | | |
| Cerastium arcticum | II/+ | | I/+ | | | |
| Saxifraga hyperborea | III/1 | | I/+ | | | |
| Equisetum variegatum | | II/+ | | II/+ | | |
| Festuca rubra ssp arctica | | II/+ | | | II/+ | |
| Equisetum arvense ssp boreale | I/+ | | | II/+ | | |
| Festuca baffinensis | | | | II/+ | II/+ | |
| Draba daurica | II/+ | | | | | |
| Equisetum scirpoides | II/+ | | | | | |
| Phippsia algida | II/+ | | | | | |
| Alopecurus borealis | II/+ | | | | | |
| Draba corymbosa | | I/+ | | | | |
| Saxifraga hirculus | | I/+ | | | | |
| Stellaria longipes | | | I/+ | | | |
| Carex maritima | | II/+ | | | | |
| Carex nardina | | | II/+ | | | |
| Cerastium alpinum | | I/+ | | | | |
| Pedicularis hirsuta | | | | | II/+ | |
| Poa species | | | | | | II/+ |
| Gastrolychnis uranlensis | | | | | | II/+ |
| <u>Other cryptogams</u> | | | | | | |
| Cetraria ericetorum | II/+ | II/+ | I/+ | II/1 | II/4 | |
| Aulacomnium turgidum | II/+ | III/6 | I/+ | | II/+ | II/+ |
| Cladonia species | II/+ | | II/+ | II/1 | | II/+ |
| Cladonia uncialis | II/+ | | I/+ | V/7 | | + |
| Sphaerophorus fragilis | | III/3 | II/+ | III/3 | | + |
| Barbilophozia species | II/+ | II/+ | I/+ | | | |
| Table 6, continued | | | | | | |
| Cladonia arbuscula | II/+ | | I/3 | II/3 | | |
| Stereocaulon species | | II/2 | | II/3 | II/+ | |

| | | | | | |
|-----------------------------|-------|------|-------|------|------|
| Bryum species | II/+ | | II/+ | | II/+ |
| Ochrolechia species | II/1 | II/3 | II/4 | | |
| Cladonia gracilis | II/1 | | I/+ | | |
| Dicranum species | II/2 | | II/+ | | |
| Cetraria species | | | I/+ | II/1 | |
| Ephebe species | | I/+ | II/+ | | |
| Sphaerophorus globosus | | II/1 | III/2 | | |
| Physconia muscigena | | II/+ | | II/+ | |
| Scorpidium cossoni | | II/+ | | II/1 | |
| Tortella species | | I/+ | | II/2 | |
| Distichium inclinatum | | II/2 | | | II/+ |
| Gymnostomum species | | I/+ | | | + |
| Oncophorus wahlenbergii | | II/+ | | | II/+ |
| Pohlia species | | | II/+ | | II/+ |
| Scoliosporum species | | | | | |
| Timmia austriaca | | I/+ | | II/+ | |
| Tortula ruralis | | | I/+ | | II/+ |
| Pleurozium schreberi | II/+ | | | | |
| Stereocaulon alpinum | II/+ | | | | |
| Peltigera canina | II/+ | | | | |
| Lopadium species | II/+ | | | | |
| Cetrariella speciesl | III/3 | | | | |
| Cinclidium stygium | II/1 | | | | |
| Dicranum scoparium | II/+ | | | | |
| Meesia uliginosa | | I/+ | | | |
| Thamnotia vermicularis | | I/+ | | | |
| Physconia species | | I/+ | | | |
| Andreaea species | | I/+ | | | |
| Aneura pinguis | | | I/+ | | |
| Polytrichum hyperboreum | I/+ | | | | |
| Racomitrium microcarpon | I/+ | | | | |
| Rinodina species | | I/+ | | | |
| Sanionia species | | | I/+ | | |
| Schistidium apocarpum | I/+ | | | | |
| Sphaerophorus species | I/+ | | | | |
| Hylocomium species | | I/+ | | | |
| Hylocomium splendens | | | I/+ | | |
| Lecidea species | | I/+ | | | |
| Orthothecium chryseon | | I/+ | | | |
| Parmelia species | | II/+ | | | |
| Encalypta alpina | | I/+ | | | |
| Encalypta rhaptocarpa | | I/+ | | | |
| Distichium capillaceum | | I/+ | | | |
| Collema ceraniscum | | II/+ | | | |
| Cladonia pocillum | | I/+ | | | |
| Cladium species | | I/+ | | | |
| Catoscopium nigratum | | I/+ | | | |
| Barbula species | | I/+ | | | |
| Brodoa oroarctica | | I/+ | | | |
| Bryum argenteum | | I/+ | | | |
| Cladonia crispata | | | | II/6 | |
| Cladonia macrophylla | | | II/1 | | |
| Blepharostoma species | | | | | II/+ |
| Ditrichum species | | | | | II/+ |
| Cyrtomnium hymenophylloides | | | | | II/+ |

Discussion and conclusions

It is generally accepted that climate determines the large-scale distribution of vegetation, while edaphic, topographic, grazing and human factors operate on a more local scale (Woodward 1987). In our study the vegetation at all sites was sampled along a moisture gradient, while the sites differed in climate, grazing intensity and bedrock.

Defining plant communities is not easy, since a gradual transition from one community to another makes it difficult to determine borders. Normally, very common species, or species that do not have any special preferences, are not considered as character species for a community. In the Arctic, however, plant communities do not seem to be as well differentiated as in most other biomes. There may be several reasons for this, as for example low competition intensity, which does not act as a restriction for species occurrence. Because of this, we found it necessary to define species such as *Saxifraga oppositifolia*, *Sanionia*

uncinata and *Salix polaris* as character species, even though they are common in several plant communities.

Of the six communities defined in this study, communities 1 (*Sanionia uncinata* community), 2 (*Salix polaris* community) and 6 (*Carex rupestris*- *Bistorta vivipara* community) were found only in mesic habitats. Elvebakk (1994) defined a community rich in *Dryas octopetala*, *Tomentypnum nitens* and *Carex misandra* on mesic plains/slopes on calcareous substrates in the warmer areas of Svalbard. This community is similar to our community 6 (*Carex rupestris*- *Bistorta vivipara* community), which has a frequent representation of *Dryas octopetala* and *Tomentypnum nitens*, but differs in that *Carex misandra* is missing in our community. Elvebakk also mentioned that *Cassiope tetragona* is lacking in this community since it avoids pure limestone. In our community *Cassiope tetragona* is frequent, which is explained by the fact that the localities where we found it had both calcareous and schist bedrocks.

At most sites, grazing (quantified by droppings) appeared to be more pronounced than expected. The communities 3 (*Saxifraga oppositifolia* community), 5 (*Dryas octopetala* community) and 6 (*Carex rupestris*-*Bistorta vivipara*) were influenced by grazing, as shown by the CCA analysis. These plant communities were found at Pyramiden, Blomstrandhalvøya and Templet, which also were among the areas on Svalbard with the most favourable climate. The site at Bellsund, which had the highest density of droppings, consisted mostly of plots belonging to community 3. In Hornsund the vegetation was little influenced by grazing, as a thick lichen and moss layer covered the ground. Here the Svalbard reindeer were low in number ten years ago, but since then the population has increased enormously. Researchers staying at the Polish station nearby have also noted a change of the vegetation; one example being *Saxifraga oppositifolia*, which has increased its flowering in recent years. (pers. comm. Polish research station). Prins Karls Forland was expected to be an area without reindeer, but several animals were in fact observed during our stay on the island.

The differences in bedrock are expected to be best reflected in the vegetation in areas where soil forming processes are slow, such as in the Arctic. In this study pH is closely correlated to bedrock, and varies from pH 6 to 8. Elvebakk (1982) studied the geological preferences among Svalbard plants. He grouped eighty species into eight classes connected to particular pH preferences. *Saxifraga oppositifolia*, *Dryas octopetala*, *Carex rupestris* and *Bistorta vivipara* are all mentioned as circumneutral species, with preference for weakly basic soils. In our study, these species are recognised as character species for communities 3, 5 and 6 respectively, and the communities show weak correlation with pH, according to Figure 3b and therefore support the classification system of Elvebakk (1982).

The biplot of the CCA splits Community 6 into two parts. This seems to be due to lack of *Tomentypnum nitens*, which according to Elvebakk (1982), is a calcareous species, but was absent in four of our quadrats. The part of the community where *T. nitens* is represented seems to be better correlated with pH than the rest of the community. All the sites visited during our study were more or less alkaline, except for Hornsund. The highest soil pH values were found in Pyramiden, where the *Dryas octopetala* community dominated the vegetation. Elvebakk (1982) characterised *Salix polaris* as indifferent to pH, while the CCA in this study shows a negative correlation with pH for the *Salix polaris* community. The plots from this community are all located in Hornsund, where the bedrock is garnet mica schist and marble garnet mica schist with a soil pH ranging from 6.39 to 7.21. At Hornsund we collected data from two sets of dry and mesic habitats, one of them slightly more acidic than the other. This seems to be the reason for the split in community 2, where all plots are from our mesic habitats in Hornsund, as one of the groups is negatively correlated to pH. The moss *Racomitrium lanuginosum* (character species for community 4) was shown to be acidophilic by Elvebakk (1982), which matches well with our observations, as this community was found

on the dry habitats in Hornsund. All in all, our investigations show that soil pH is influenced by bedrock, and that the distribution of plant communities is linked to pH, although we do not get exactly the same results as Elvebakk (1982).

Other environmental variables concerned, communities 1 (*Sanionia uncinata* community), 2 (*Salix polaris* community) and 4 (*Racomitrium lanuginosum* community) which were positively correlated with vegetation cover and moss depth. All three communities were found in Hornsund, which appeared weakly grazed, and where the ground was covered with a thick moss and lichen layer. The strong coastal influence, with relatively low temperatures and high air humidity, at this site is an obvious factor which would contribute to the dominance of bryophytes and lichens. As noted above, really wet habitats with water seepage were avoided. Community 4 is negatively correlated with moisture, which fits well with the community's location on dry sites. Community 3 (*Saxifraga oppositifolia* community) consists of a large group of plots, and we can see from fig. 3b that it is highly spread along axis 1, and to some degree along axis 2. The community contains 6 plots from mesic habitats, which are all placed to the right in the biplot due to their positive correlation with moisture and vegetation cover.

The factor most decisive for composition of the plant communities found in our study, is pH which in turn is dependent on bedrock composition. The effect of moss depth and vegetation cover, should however, not be overlooked, as neither should grazing and climatic conditions, which might be very important at a local scale. A thick moss cover obstructs plant establishment, both by lack of bare soil for a seedling establishment, and because of the moss cover functioning as insulation, rendering the underlying soil cold and sometimes totally frozen.

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Plant community diversity at different scales in six localities on Svalbard

Wenche Eide¹, Kari Klanderud² and Rune Tommelstad³

¹ Department of Botany, University of Bergen, Allégaten 41, N-5007 Bergen, Norway, ² Department of Biology and Nature Conservation, The Agricultural University of Norway, Postboks 5014, 1432 Ås, ³ Botanical department, NTNU, Høgskoleringen 5, 7491 Trondheim.

Abstract

Different processes control plant community diversity at different scales. To estimate community diversity at different levels in the Arctic, six localities differing in local climate, geology, and disturbance by grazers, were investigated on Svalbard. Mesic and dry habitats were sampled in each locality, and soil pH, soil nutrient status, vegetation cover, moss depth and grazing intensity were estimated to examine how diversity is related to environmental factors. Significant differences in species diversity and species richness between localities were only found when dry and mesic habitats were analysed separately. A positive relationship between species diversity and temperature conditions was only found in the mesic habitats. High soil pH, soil nutrient status, and vegetation cover are positively related to species diversity and richness at habitat level, while moss depth is negatively related. Our results indicate that biological interactions are more important for community diversity in the productive mesic habitats than on the dry ridges.

Keywords: *Diversity Species richness Shannon-Wiener Arctic Svalbard*

Introduction

Due to harsh environmental conditions, such as low temperatures, strong winds, short growing season, water limitations and low soil nutrient content, the diversity of vascular plants in the Arctic is low. Only 173 species occur in Svalbard (Elven & Elvebakk 1996). However, the cryptogam diversity is relatively high, with 373 species (Frisvoll & Elvebakk 1996). This is due to a large variation in topography and geology, as well as uneven snow distribution and the large areas manured by birds, giving the area high habitat diversity. The explanation and quantification of community diversity has been an important subject during the development of modern ecology (e.g. Pielou 1975, MacArthur 1960, Whittaker 1965), though it has been frequently asked if species diversity has any functional significance (e.g. Hurlbert 1971, May 1973, Schultz & Mooney 1993). There is general agreement that temperature is an important factor controlling diversity in alpine and arctic environments (Rannie 1986, Birks & Odland 1998, Walker 1995), but climate and diversity is most likely not simply linked (Walker 1995). To understand which factors control plant community diversity, we have to understand the processes that control diversity at different levels. Species diversity varies with abiotic (Gough *et al.* 2000) as well as biotic factors. For instance, heavy grazing/manuring from geese and reindeer influence vegetation at a local scale (e.g. Jefferies *et al.* 1994, Staaland & White. 1991), but the effect on long-term diversity in the Arctic is uncertain. Ecologists have observed that species diversity increase with increased pH, but in the Arctic, the relationship between pH and diversity is not well known. Gough *et al.* (2000) shows a stronger correlation between pH and species richness, i.e. a simple species list, than species density where species abundance is accounted for, implying that other factors may be acting at the local scale to reduce species number.

Our study is a part of a larger project, and aims at quantifying and explaining plant community diversity on Svalbard within uniform habitats (alpha diversity) as well as within a locality (gamma diversity) (Whittaker 1972), incorporating vascular plants, bryophytes and lichens. Svalbard is warmest in the central parts and colder towards the coast (Elvebakk 1997), and we expected local differences in temperature to be an important variable explaining the species richness and diversity. Soil moisture and wind are also important abiotic factors in the Arctic, and at a local scale, we expect species richness to increase along a topographic gradient with increasing soil moisture. We also expect environmental conditions such as grazing/manuring, soil nutrient content, pH, moss abundance and total vegetation cover to be important factors influencing community diversity.

We ask the following questions: How does community diversity and richness differ at different scales, i.e. between habitats and localities? How do abiotic and biotic factors influence the species diversity and richness at these localities?

Table 1. Geographic location (latitude/longitude), geology and age in million years before present (BP) of the localities investigated. * = only briefly visited.

| Locality | Latitude/ longitude | Bedrock (mill.years BP) |
|------------------------------|---|---|
| Templet | 78°23'34.5''N 16°48'14.8''E | Permian, calc (250-265) |
| Adolfbukta* | 78°39'30N 16°46'30E | Carbon/perm calc (290) |
| Pyramiden | 78°39'37.0''N 16°17'51.7''E | Devon (360-410) Site 1 calcareous Site 2 acidic |
| Hornsund | 77°00'23N 15°31'28E | Middle Proterozoic Site 1 marbel and garnet mica schist Site 2 garnet mica schist |
| Bellsund | 77°45'20.5''N 14°24'38.1''E | Carboniferous (330-360) |
| Prins Karl Forland | 78°53'43.3''N 10°28'26.8''E | Precambrium (>360) |
| Casimir Perierkammen* | 79°05'N 11°45'E | Precambrium (>360) |
| Blomstrandhalvøya | 78°57'50.8''N 12°02'47.7''E site 2: 78°58'07.2''N 12°05'23.0''E | Precambrium (>360) |

Material and methods

Study sites

Six localities were studied during the period 9-14 July 2001. The localities were chosen to include as large contrasts as possible in climate, bedrock and grazing pressure during this time frame. Additionally two localities were briefly visited. An overview of the localities is presented in Table 1.

Sampling

At each locality we selected a dry, a mesic, and, where possible, a very dry habitat of approximately 500 m² each. This gave a dataset with two fixed factors, locality and habitat. Within each fixed selected habitat we chose randomly seven plots where we analysed the vegetation by the point-frame method. The frame size was 0.5 m x 0.5 m, divided by double layer of strings into 25 cross-points. See Crawley (1997, p 497) for discussion of this method. The frequency of the vascular plant species, the bryophytes, and the lichens were recorded by noting their occurrences below each vertical projection of the cross-point. Vascular plant species that did not occur below a cross point were also noted within each frame.

To achieve a more complete impression of the flora within each locality, a vascular plant species list for each locality was made, including other habitat types. Following the system of Karlsen & Elvebakk (1996), the frequency of each species was recorded and an “Index of Thermophily” value calculated within about 1 km² for each locality. Based on the fact that plant species are temperature demanding to different degrees, as indicated from their distribution pattern, and that relatively warm sites are supposed to have a stronger contribution of “thermophilous” plants than cold sites, the index values are supposed to indicate the temperature conditions at the local scale. Index values derived from botanical data sets have shown a very high correlation with temperature data (Brosø 1997), supporting the reliability of this method. One major disadvantage with this method is that it does not compensate for lack of different habitats (in our case wet and/or bog areas), causing an underestimation of the index at some of the sites. Brosø (1997) suggested a solution to this problem, but that would require a different approach in the field than applied in this study, and different index calculations. In addition, it is likely that not all species within a locality were recorded, due to the relatively short time available. It is also important to keep in mind that this is a relatively rough estimate, and cannot be interpreted as quantitative values. The usefulness of the method, therefore, lies mainly in comparisons between localities.

Environmental data was collected either by plot, by habitat or by site. By plot we counted reindeer, geese and ptarmigan droppings, measured the depth of the moss layer in five points along the plot diagonal, inclination and aspect, depth of active layer (soil above the permafrost), and estimated the total vegetation cover. We also collected five soil samples from each habitat for pH measurements. For each soil sample pH was measured both in a solution of 0.2M KCl and in distilled water. The difference between pH in water and KCl is interpreted as an indication of the nutrient status in the soils, with a large difference indicating low level of nutrients and small difference a high level. To obtain an estimate of grazing/fertilizing, we laid out a 50 m x 4 m transect in each habitat. At more patchy localities, the transect was divided into two 25 m x 4 m transects to avoid including different habitats. The droppings were separated into “reindeer summer”, “reindeer winter” and “herbivore birds” (ptarmigan and geese) based on appearance.

To quantify the species diversity, the Shannon-Wiener diversity index (H) was used:

$$H = -\sum p_i \ln(p_i)$$

The number of hits per species were summed over the frames, and divided by the total number of possible hits, to obtain the proportional abundance pi for each species. The diversity index was used to calculate diversity at habitat (alpha) and locality (gamma) level, since gamma diversity can be considered equal to alpha diversity at a higher level of organisation (Walker 1995). In addition to the Shannon-Wiener diversity index, which incorporates both abundance and species richness, we counted the number of species within each frame, without taking abundance into account. Species richness was estimated per 0.25m² frame to obtain maximum information about the variation in the statistical analyses. In order to keep the denomination as simple as possible, species richness per frame was adjusted to number of species per m². At locality level species richness was calculated as mean number of species per m².

Analysis

SYSTAT (version 9.0 1997) was used for all statistical analyses. Pearson correlation matrices for environmental (independent) variables were performed with probability values calculated using a Bonferroni test. These results were used to select which variables to include when examining differences within habitat type among localities. Linear regressions were calculated separately for the two dependent variables, Shannon-Wiener diversity index and species richness, against the independent variables.

In performing the Analysis of Variance the first step was to look at the differences between localities, using the Shannon-Wiener index and the species richness, separately. Both species richness and the Shannon-Wiener diversity index were used as dependent variables to compare these two different ways of measuring species diversity. In the next step, a two-way ANOVA, with locality and habitats as fixed factors and species richness as the dependent variable, was performed. The results from using species diversity as the dependent variable were similar to species richness analyses, hence there was no reason for presenting both. Since species richness nowadays is the preferred method, we chose to use it in these analyses. Using the results from the correlation matrices, all possible combinations of the selected environmental variables were subsequently tested.

Variances were examined for homogeneity within residual plots and normality by exploring probability plots with normal distribution. The assumptions were met in the dataset except for soil pH, which never met the criterion of equal variance. Hence, the pH results must be interpreted with care. The reason is probably due to a relatively large difference between some of the measurements. Statistical significance means $P < 0.05$. To avoid using correlated independent variables in the regression analysis, and also to see where response and predictor variables correlated, a correlation matrix was created for each of the two habitats "dry" and "mesic". Tests for interactions between the variables are recommended for the next step, however, this was never done, due to lack of time. Since slope, inclination, and active layer seemed to have been measured inconsistently in field, they were removed from the dataset prior to the analysis. In addition, the pH measurements on mineral and organic soil were lumped together, due to large differences among people in sampling and definitions of what was organic and mineral soil, respectively. Thus, the pH measurements are now means of the two soil types.

Results

Indices of Thermophily are highest in the inner fjord localities Templet and Pyramiden (Table 2). The index for Blomstrandhalvøya further northwest is also very high. The Thermophily indices are lower in the southernmost and more oceanically localities Hornsund and Bellsund, whereas the westernmost Prins Karls Forland has the lowest Thermophily index. These

Table 2. Thermophily indices for each locality, pH (mean \pm SD) and estimates of droppings, bird, reinW (reindeer winter), ReinS (reindeer summer), and total number of droppings per m² for the habitats. * = Only briefly visited.

| | Thermophily index | Habitat | pH | Droppings (m ²) | | | |
|-----------------------|-------------------|----------|---------------|-----------------------------|-------------|-------|-------|
| | | | | Bird | ReinW Total | ReinS | |
| Templet | 30.75 | Very dry | 7.6 \pm 0.2 | - | 0.16 | 0.34 | 0.50 |
| | | Dry 1 | 7.9 \pm 0.1 | 0.18 | 0.15 | 0.105 | 0.225 |
| | | Mesic 1 | 7.2 \pm 0.1 | 1.065 | 0.16 | 0.34 | 0.50 |
| Pyramiden | 30.75 | Dry 1 | 7.3 \pm 0.1 | 0.185 | - | - | 0.185 |
| | | Mesic 1 | 7.0 \pm 0.1 | 1.095 | - | - | 1.095 |
| Adolfbukta* | 17.25 | - | - | - | - | - | - |
| Hornsund | 11.00 | Dry 1 | 5.8 \pm 0.6 | 0.11 | - | - | 0.11 |
| | | Dry 2 | 7.7 \pm 0.2 | 0.14 | - | - | 0.14 |
| | | Mesic 1 | 6.5 \pm 0.1 | 1.635 | 0.03 | 0.07 | 1.735 |
| | | Mesic 2 | 7.1 \pm 0.1 | 1.72 | 0.04 | 0.05 | 1.81 |
| Bellsund | 8.25 | Dry 1 | 5.5 \pm 0.7 | 1.025 | 0.14 | 0.64 | 1.805 |
| | | Dry 2 | 6.6 \pm 0.3 | 0.075 | 0.07 | 0.13 | 0.275 |
| | | Mesic 1 | 6.2 \pm 0.1 | 0.059 | 0.055 | 0.24 | 0.354 |
| Prins Karls Forland | 3.50 | Dry 1 | 6.8 \pm 0.3 | 0.07 | 0.005 | 0.02 | 0.095 |
| | | Mesic 1 | 6.5 \pm 0.2 | 0.19 | 0.015 | 0.01 | 0.215 |
| Blomstrand-halvøya | 26 | Very dry | 8.0 \pm 0.1 | - | - | - | - |
| | | Dry 1 | 7.3 \pm 0.2 | 0.1 | 0.02 | 0.015 | 0.135 |
| | | Dry 2 | 7.8 \pm 0.2 | 0.01 | - | - | - |
| | | Mesic 1 | 7.1 \pm 0.1 | 0.505 | 0.16 | 0.03 | 0.695 |
| | | Mesic 2 | 7.2 \pm 0.2 | 1.53 | 0.035 | 0.065 | 1.63 |
| Casimir Perierkammen* | 9.5 | - | - | - | - | - | - |

estimates correspond with the climatic conditions expected at the localities due to the geographic location. Table 2 also shows the measured pH-values, which are higher in the dry than in the mesic habitats, except for the first dry habitats in Hornsund and Bellsund.

Droppings are number of total droppings (reindeer, geese, ptarmigan) per m², and show the highest numbers at Hornsund (3.795 droppings/m²) and the lowest at Prins Karls Forland (0.310 droppings/m²).

The variation in Shannon-Wiener diversity index and species richness at locality (gamma diversity) and habitat (alfa diversity) level is shown in Table 3. Both Shannon-Wiener and species richness are shown for the localities, and the estimates seem to correspond well. Templet has the highest species richness, and also a relatively high Shannon-Wiener index, whereas Blomstrandhalvøya has the lowest species number and the lowest Shannon-Wiener diversity index. Only Hornsund is an exception, with the highest Shannon-Wiener index and the second lowest species number. At habitat level, the mesic habitats have the highest species diversity at all the localities, whereas the very dry habitats have the lowest diversity (Table 3).

Table 3. Shannon-Wiener diversity indices for habitats (alpha diversity) and localities (gamma diversity). Species richness shown as mean number of species/m² for each locality.

| | Species richness | | Shannon-Wiener diversity index (H) | | | | |
|---------------------|------------------|------|------------------------------------|------|-------|-------|---------|
| | | | Very dry | Dry | Dry 2 | Mesic | Mesic 2 |
| Templet | 11.8 | 2.4 | 0.67 | 1.79 | - | 3.47 | - |
| Pyramiden | 7.7 | 2.2 | - | 0.94 | - | 2.77 | - |
| Hornsund | 6.3 | 2.86 | - | 2.3 | 1.86 | 2.5 | 2.3 |
| Bellsund | 8.8 | 2.04 | | 1.74 | 0.9 | 2.07 | - |
| Prins Karls Forland | 9.4 | 2.3 | - | 1.93 | - | 2.04 | - |
| Blomstrandhalvøya | 3.7 | 1.86 | 0.48 | 1.45 | 1.07 | 2.26 | 2.46 |

The differences between the localities, using both the Shannon-Wiener index and Species Richness, separately, showed no statistically significant difference between localities. However, two-way ANOVA, with locality and habitats as fixed factors and species richness as the dependent variable, shows a different pattern. The model as a whole comes out highly statistically significant with $p < 0.001$ and 58.7 percent of the variance in the data-set explained by these two variables (F-ratio = 19.39, df = 16, 218, n = 235). Performing a Bonferroni post-

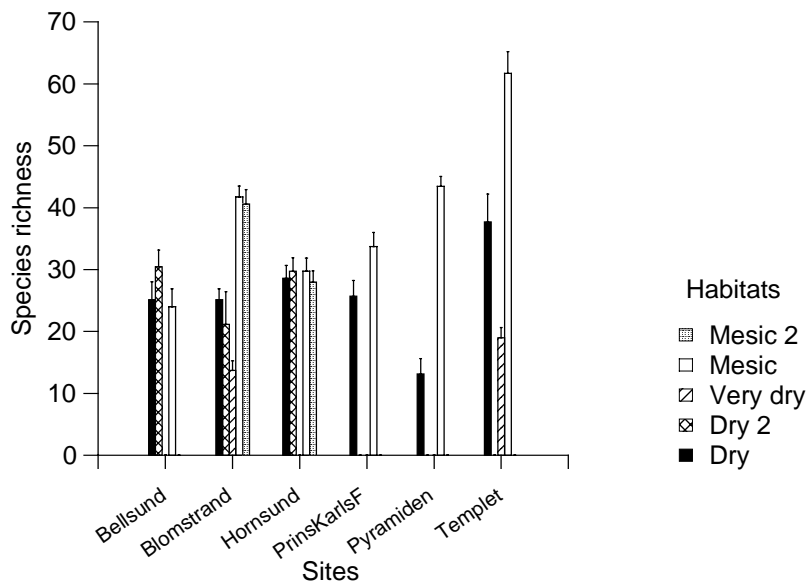


Fig. 1. Species richness at the different localities, measured as mean number of species per m² presented with standard error for (a) dry and (b) mesic habitats. When two dry localities have been investigated the locality is given “2” at the end and “3” indicates a second mesic site investigated.

significantly (at a 0.05 level) different from Bellsund, Blomstrandhalvøya and Prins Karls Forland. In addition Templet differs significantly from the second dry site at Blomstrandhalvøya, and Pyramiden differs significantly from the two dry sites in Hornsund. On the mesic sites (Fig. 1) the Bonferroni pair-wise comparisons show a significant difference between Templet and all the other sites. Pyramiden is significantly different from Bellsund and both the Hornsund sites. In addition the both Hornsund sites differ from both the Blomstrandhalvøya sites. As a result, all analyses are performed separately for dry and mesic habitats.

Table 4 shows that more of the environmental variables are significantly correlated in the mesic (b) than in the dry (a) habitats. In the dry habitats, soil pH is significantly correlated with nutrient availability (pH diff) and moss cover. Moss cover is significantly correlated with vegetation cover, whereas vegetation cover is correlated with species richness. Total amount of droppings (Droptot) is highly correlated with winter droppings from reindeer (DropW), and droppings from geese (DropG) is highly correlated with summer droppings from reindeer (DropS). In the mesic habitats (Table 4b), the response variable species richness is significantly correlated with soil pH and droppings from winter reindeer (DropW), whereas Shannon-Wiener diversity index (SW) is correlated with soil pH, nutrient availability (pHdiff), and droppings from winter reindeer (DropW). Soil pH is highly correlated with total amount of droppings (Droptot) and droppings from geese (DropG).

Vegetation cover (Cover) is significantly correlated with moss cover, total amount of droppings (Droptot), and droppings from geese (DropG), the latter also correlating with moss cover. The different kinds of droppings are highly correlated with each other. The results from all regressions performed are presented in Table 5.

Table 4. Correlation matrices for the six localities, performed separately for the “dry” (a) and “mesic” (b) habitats. All values are calculated per m². The abbreviations are as follows: pH diff = the difference of soil pH measured in water and in 0.2M KCl solution, Cover = percentage plant cover (also including lichens) in the analysed grids, SpecR = species richness, Droptot = number of ptarmigan, goose and reindeer dropping, DropG = goose droppings, DropS = summer reindeer droppings, DropW = winter reindeer droppings, SW = Shannon-Wiener diversity index, and Moss = moss depth (mm). Bonferroni probabilities are indicated when statistically significant (*^(*) P close to 0.05, * P<0.05, **p<0.01).

a)

| | Soil pH | pH diff | Cover | SpecR | Droptot | DropG | DropW | DropS | SW | Moss |
|---------|---------|---------|---------------------|-------|---------|--------|-------|-------|------|------|
| Soil pH | 1.00 | | | | | | | | | |
| pH diff | -0.59** | 1.00 | | | | | | | | |
| Cover | -0.32 | 0.20 | 1.00 | | | | | | | |
| SpecR | -0.06 | 0.05 | 0.55* | 1.00 | | | | | | |
| Droptot | -0.11 | 0.03 | -0.07 | 0.05 | 1.00 | | | | | |
| DropG | -0.43 | 0.13 | 0.12 | 0.08 | 0.42 | 1.00 | | | | |
| DropW | 0.08 | -0.04 | -0.14 | 0.01 | 0.92* | 0.03 | 1.00 | | | |
| DropS | -0.48 | 0.15 | 0.14 | 0.11 | 0.29 | 0.95** | -0.11 | 1.00 | | |
| SW | -0.15 | 0.24 | 0.41 | 0.31 | -0.42 | 0.08 | -0.48 | 0.06 | 1.00 | |
| Moss | -0.53* | 0.39 | 0.52 ^(*) | 0.22 | -0.09 | 0.07 | -0.19 | 0.04 | 0.44 | 1.00 |

b)

| | Soil pH | pH diff | Cover | SpecR | Droptot | DropG | DropW | DropS | SW | Moss |
|---------|---------|---------|--------|--------|---------|--------|--------|-------|-------|------|
| Soil pH | 1.00 | | | | | | | | | |
| pH diff | -0.35 | 1.00 | | | | | | | | |
| Cover | -0.23 | 0.13 | 1.00 | | | | | | | |
| SpecR | 0.49* | -0.42 | 0.05 | 1.00 | | | | | | |
| Droptot | 0.58** | -0.41 | -0.46* | 0.17 | 1.00 | | | | | |
| DropG | 0.55** | -0.35 | -0.49* | 0.04 | 0.97** | 1.00 | | | | |
| DropW | 0.29 | -0.07 | -0.04 | 0.56** | 0.04 | -0.16 | 1.00 | | | |
| DropS | -0.12 | -0.19 | 0.22 | 0.40 | -0.01 | -0.25 | 0.58** | 1.00 | | |
| SW | 0.48* | -0.45* | -0.05 | 0.76 | 0.42 | 0.29 | 0.50** | 0.43 | 1.00 | |
| Moss | -0.23 | 0.11 | 0.23* | -0.31 | 0.20 | 0.19** | -0.25 | 0.14 | -0.15 | 1.00 |

There is a weak tendency towards lower Shannon-Wiener indices with increasing soil pH and in the dry habitats (Fig. 2a), whereas species richness seems to have no clear pattern with increased pH (Fig. 2b). Both Shannon-Wiener and species richness increase with increased pH in the mesic habitats (Figs. 2c, d). None of the regressions are significant.

Table 5. Results from linear regressions performed on the independent variables pH, percent cover, difference between pH measured in water and in KCl (pH-difference, see methods for further details), the total number of droppings/m², and moss depth. Both the Shannon-Wiener diversity index (ShannonW) and Species richness (SpeciesR) are used as dependent variables, with n=9 and n=8, respectively. The values used are averages from each habitat. The probability values (p-value) are in bold when statistically significant, R² = squared multiple. For convenience, the corresponding figures are added on.

| Habitat | Dependent variable | Independent variable | Regression line | R ² | p-value | Corresponding figures |
|---------|--------------------|----------------------|---------------------|----------------|-------------------|-----------------------|
| Dry | SW | Soil pH | 2.871 + (-0.189)X | 0.110 | 0.383 | 2a |
| Mesic | | | -1.850 + 0.630X | 0.272 | 0.185 | 2c |
| Dry | SpeciesR | | 23.224 + 0.442X | 0.003 | 0.886 | 2b |
| Mesic | | | -100.585 + 20.200X | 0.437 | 0.074 | 2d |
| Dry | SW | Cover | 0.257 + 0.027X | 0.852 | <0.0001 | 3a |
| Mesic | | | 2.067 + 0.005X | 0.004 | 0.888 | 3c |
| Dry | SpeciesR | | 16.290 + 0.211X | 0.267 | 0.154 | 3b |
| Mesic | | | 49.984 + (-0.139)X | 0.005 | 0.867 | 3d |
| Dry | SW | pH-difference | 1.023 + 0.641X | 0.487 | 0.328 | 4a |
| Mesic | | | 3.955 + (-1.927)X | 0.662 | 0.014 | 4b |
| Dry | SpeciesR | | 32.370 + (-7.333)X | 0.094 | 0.423 | - |
| Mesic | | | 68.221 + (-39.434)X | 0.434 | 0.076 | - |
| Dry | SW | Total droppings | 1.643 + (-0.498)X | 0.065 | 0.509 | - |
| Mesic | | | 2.060 + 1.084X | 0.242 | 0.215 | 5a |
| Dry | SpeciesR | | 28.782 + (-13.625)X | 0.254 | 0.167 | - |
| Mesic | | | 32.816 + 13.296 | 0.057 | 0.569 | 5b |
| Dry | SW | Moss depth | 1.194 + 0.103X | 0.418 | 0.060 | 6a |
| Mesic | | | 2.403 + 0.004X | 0.009 | 0.823 | 6c |
| Dry | SpeciesR | | 22.106 + 1.207X | 0.301 | 0.126 | 6b |
| Mesic | | | 41.795 + (+0.253)X | 0.047 | 0.606 | 6d |

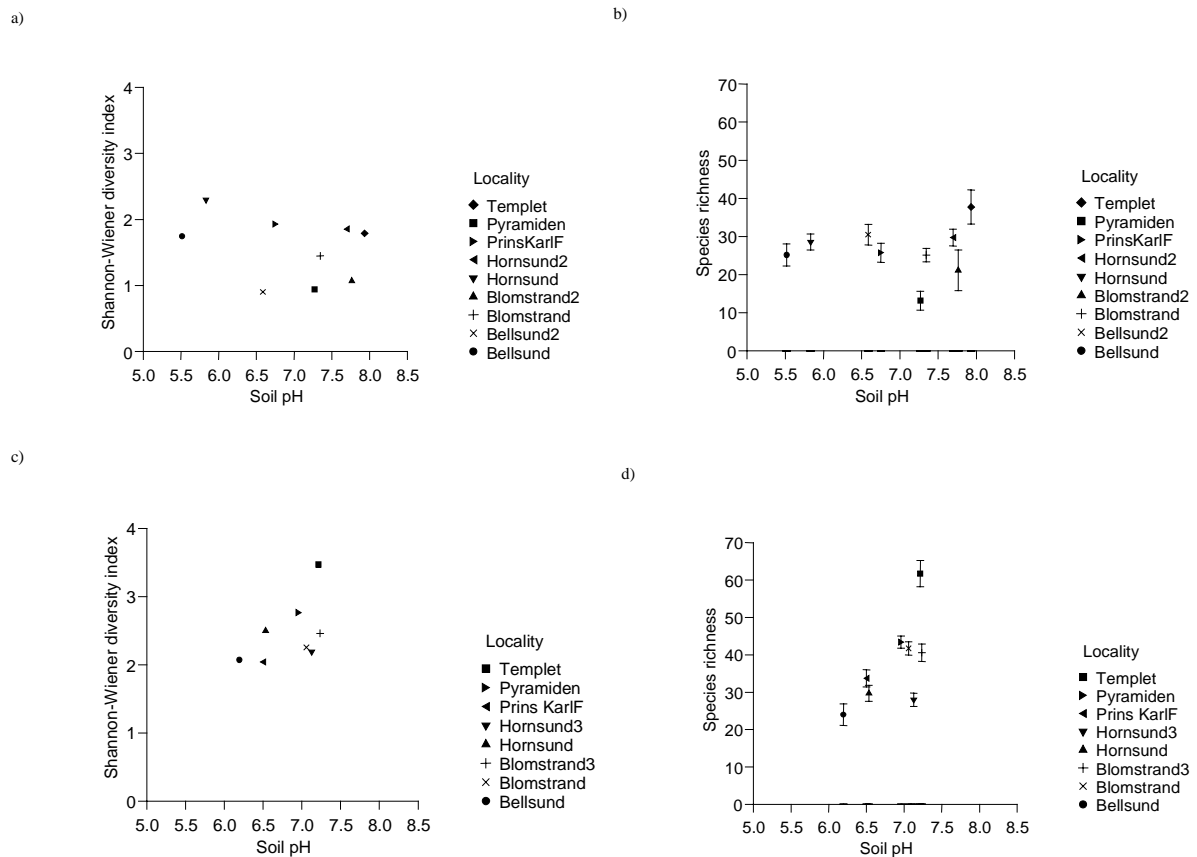


Fig. 2. The relationships between soil pH and diversity, presenting: (a) Shannon-Wiener in dry habitats, (b) Species richness (m^2) in dry habitats, (c) Shannon-Wiener in mesic habitats, and (d) Species richness (m^2) in mesic habitats. When two dry localities have been investigated the locality is given “2” at the end, and “3” indicates a second mesic site investigated.

Figure 3a shows that the Shannon-Wiener diversity index increases with increased vegetation cover in dry habitats, giving a highly significant regression. Species richness also seems to increase with increased vegetation cover (Fig. 3b), but this relationship is not significant. In the mesic habitats species richness shows a weak negative relationship with vegetation cover (Fig. 3d). The vegetation cover is clumped above 70 % in all the mesic sites, and no trends are observed for the Shannon-Wiener index (Fig. 3c).

Increased pH difference, which indicates a decrease in available nutrients, is strongly negatively related to Shannon-Wiener index in mesic habitats (Fig. 4b). No effect is observed on Shannon-Wiener in dry habitats (Fig. 4a), or on species richness in any of the habitats.

No clear pattern appears when comparing the number of droppings per m^2 with Shannon-Wiener and species richness in the dry habitats. In mesic habitats it seems the Shannon-Wiener and species richness increase with the number of droppings, to a certain extent, and then decreases (Figs. 5a, b).

There is a weak increase of Shannon-Wiener diversity index and species richness with moss depth in the dry habitats (Fig. 6a, b). In the mesic habitats, however, species richness seems to decrease, whereas Shannon-Wiener seems to increase slightly with increased moss depth (Fig. 6c, d). The regressions, however, were not significant.

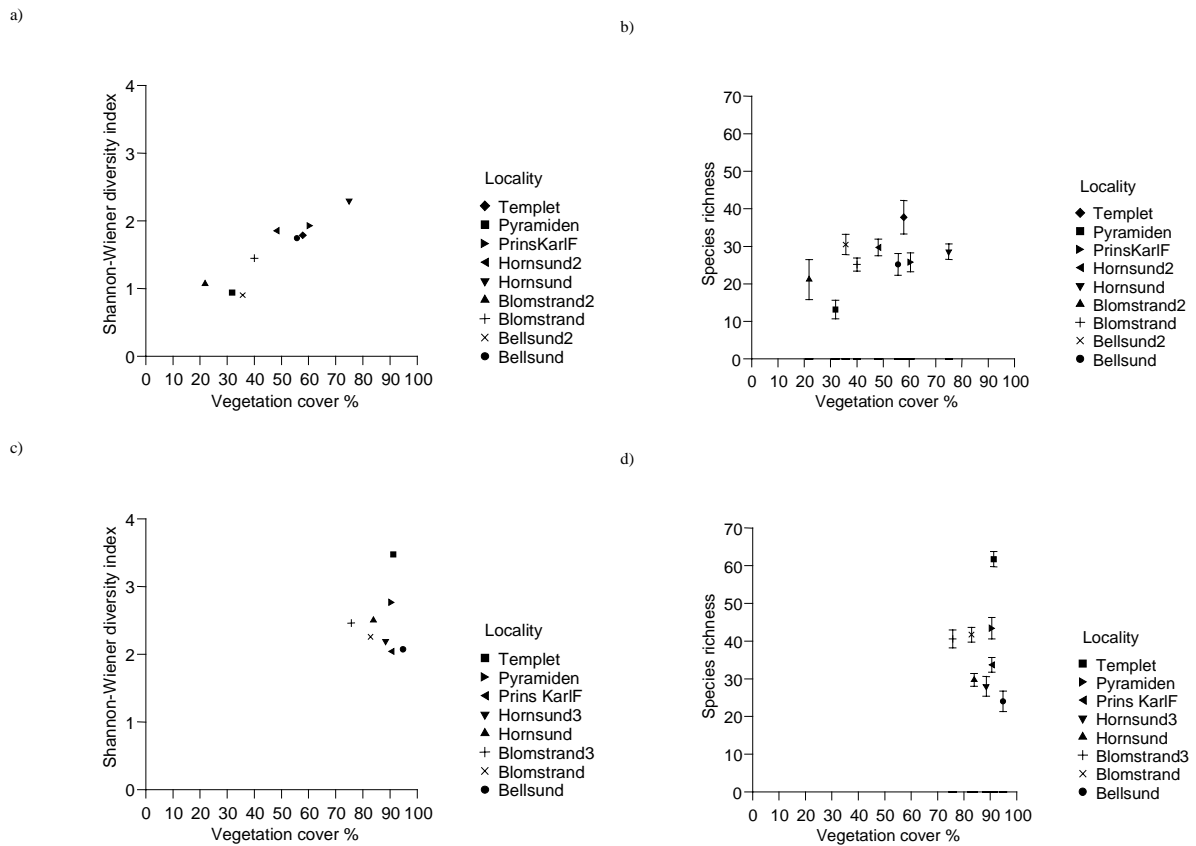


Fig. 3. The relationships between vegetation cover and diversity, showing: (a) Shannon-Wiener in dry habitats, (b) Species richness in dry habitats, (c) Shannon-Wiener in mesic habitats, (d) Species richness in mesic habitats. When two dry localities have been investigated the locality is given “2” at the end, and “3” indicates a second mesic site investigated.

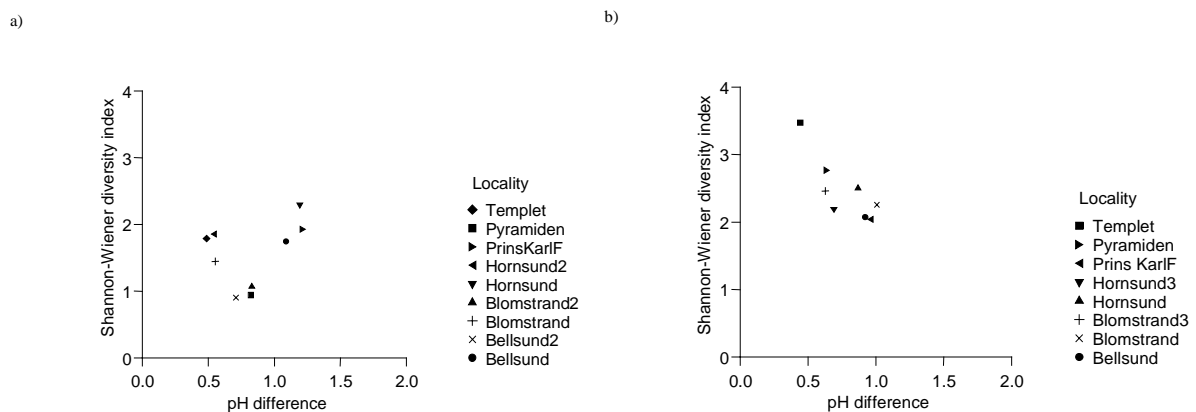


Fig. 4. The relationship between pH difference (indicating nutrient conditions) and Shannon-Wiener in (a) dry and (b) mesic habitats. When two dry localities have been investigated the locality is given “2” at the end. “3” indicates a second mesic site investigated.

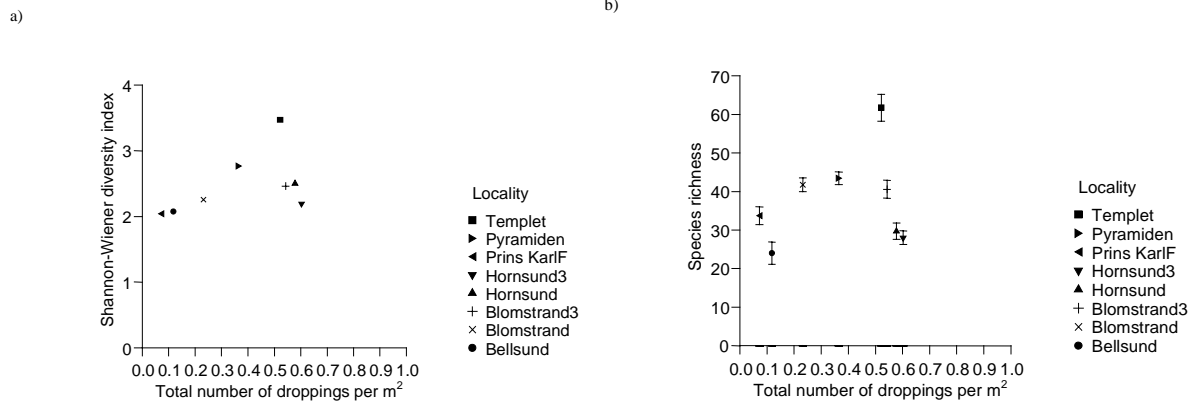


Fig. 5. The relationship between total amount of droppings per m² and (a) Shannon-Wiener and (b) Species richness in mesic habitats. When two dry localities have been investigated the locality is given “2” at the end. “3” indicates a second mesic site investigated.

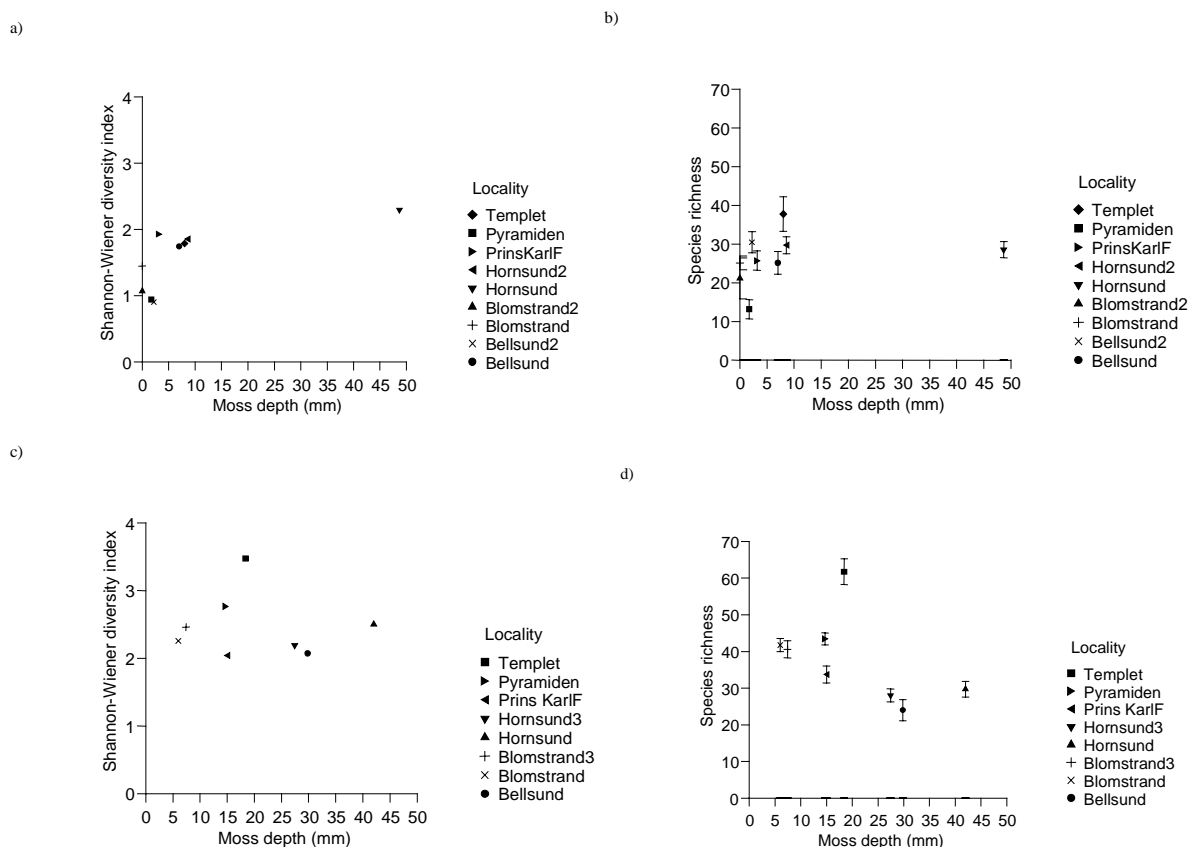


Fig. 6. The relationship between moss depth (mm) and diversity, presenting: (a) Shannon-Wiener in dry habitats, (b) Species richness in dry habitats, (c) Shannon-Wiener in mesic habitats, (d) Species richness in mesic habitats. When two dry localities have been investigated the locality is given “2” at the end, and “3” indicates a second mesic site investigated.

Table 6. Species richness used as the dependent variable for the two habitats, dry (a) and mesic (b), presenting the statistically significant models explaining the largest proportion of variance. The abbreviations used in the table are as follows; SS = sum of squares, df = degrees of freedom, MS = Mean square, R² = Squared multiple R (amount of variance explained), N = number of samples, P = probability value.

a)

| Dependent variable: Species richness | SS | df | MS | F-ratio | P | R ² | N |
|---|--------|-----|-------|---------|--------|----------------|-----|
| Locality | 17.795 | 5 | 3.559 | 69.010 | <0.000 | 0.744 | 125 |
| Error | 6.137 | 119 | 0.052 | | | | |
| Locality | 17.892 | 5 | 3.578 | 99.692 | <0.000 | 0.823 | 125 |
| Droppings (m ²) | 1.901 | 1 | 1.901 | 52.975 | <0.000 | | |
| Error | 4.236 | 118 | 0.036 | | | | |
| Locality | 12.049 | 5 | 2.410 | 52.909 | <0.000 | 0.775 | 125 |
| Moss depth (mm) | 0.763 | 1 | 0.763 | 16.744 | <0.000 | | |
| Error | 5.374 | 118 | 0.046 | | | | |
| Locality | 10.424 | 5 | 2.085 | 44.636 | <0.000 | 0.747 | 119 |
| Cover (%) | 0.533 | 1 | 0.533 | 11.415 | 0.001 | | |
| Error | 5.231 | 119 | 0.047 | | | | |
| Locality | 12.655 | 5 | 2.531 | 82.113 | <0.000 | 0.849 | 125 |
| Moss depth (mm) | 0.629 | 1 | 0.629 | 20.415 | <0.000 | | |
| Droppings (m ²) | 1.768 | 1 | 1.768 | 57.365 | <0.000 | | |
| Error | 3.606 | 117 | 0.031 | | | | |

b)

| Dependent variable: Species richness | SS | df | MS | F-ratio | P | R ² | N |
|---|--------|-----|-------|---------|--------|----------------|-----|
| Locality | 20.065 | 5 | 4.013 | 622.763 | <0.000 | 0.968 | 110 |
| Error | 0.670 | 104 | 0.006 | | | | |
| Locality | 7.490 | 5 | 1.498 | 278.348 | <0.000 | 0.975 | 53 |
| Soil pH | 0.097 | 1 | 0.097 | 18.043 | <0.000 | | |
| Error | 0.248 | 46 | 0.005 | | | | |
| Locality | 19.920 | 5 | 3.984 | 696.120 | <0.000 | 0.972 | 110 |
| Moss depth (mm) | 0.081 | 1 | 0.081 | 14.096 | <0.000 | | |
| Error | 0.589 | 103 | 0.006 | | | | |
| Locality | 7.572 | 5 | 1.514 | 413.045 | <0.000 | 0.983 | 53 |
| Soil pH | 0.079 | 1 | 0.079 | 21.431 | <0.000 | | |
| Moss depth (mm) | 0.083 | 1 | 0.083 | 22.522 | <0.000 | | |
| Error | 0.165 | 45 | 0.004 | | | | |

To investigate what combinations of environmental variables explain most of the variation in species richness, ANOVA analysis were performed separately for the habitats, with locality as a fixed factor. Based on the results from the correlation matrices, all possible combinations of the variables pH, pH-difference, percent cover, moss depth, and total numbers of droppings were performed. The significant models are presented (Table 6), showing a difference in which variables, and combinations of variables are the most important in the two habitats. Since several combinations give almost the same high amount of variance explained they are all presented. In the dry habitats, including moss depth and total number of droppings together with locality, gave the highest amount of variance explained (84.5%), whereas moss depth and soil pH together with locality explained most of the variance (98.3%) in the mesic habitats.

Discussion

Diversity can be quantified in different ways and many studies have shown that species richness alone give as useful information as diversity indices that incorporate abundance (Walker 1995). In our results the two methods most often gave the same results. However, exceptions exist, for example in Hornsund (Table 3), where the two methods show different trends. According to the Shannon-Wiener index, Hornsund has the highest species diversity, whereas the species number is the second lowest among the localities. The habitats showing the greatest diversity in Hornsund (Dry, Mesic, Mesic 2) are all densely covered with cryptogams. Thus, in this case, it seems that the Shannon-Wiener diversity index catches more of the bottom layer variation than the species richness measure does alone. This is probably because of the estimate of the frequency of the individual species, which is incorporated in the diversity index.

The Thermophily indices estimated in this study coincide well with what could be expected considering the location of the study areas. The most exposed sites have the lowest values, with the highest indices occurring in the fjords. To test these values properly, they should have been plotted against mean July temperatures for each locality, but such data were not available. Temperature is supposed to be one of the main factor controlling species richness and diversity (e.g. Rannie 1986, Körner & Larcher 1988, Dahl 1951, Birks & Odland 1999). When dry and mesic habitats are analysed together, this is not fully reflected in our results. Templet and Pyramiden, which are regarded as “very warm” localities (Table 1), have as expected, high number of species per m² and high Shannon-Wiener diversity indices. Prins Karls Forland, however, is expected to be cold/intermediate. It has the lowest Thermophily index, but the second highest number of species per m², and a relatively high Shannon-Wiener compared to the other localities. The lowest species number and the lowest Shannon-Wiener diversity index is found at Blomstrandhalvøya, which should be one of the warmest localities with the second highest Thermophily index. Hornsund and Bellsund have both low/intermediate Thermophily indices and low/intermediate species richness, whereas Hornsund has the highest Shannon-Wiener of all the localities. When dry and mesic habitats are analysed separately, there is a pattern of increasing species richness with increasing Thermophily index in the mesic habitats. In the dry habitats, no such patterns are observed. These results might indicate that factors other than temperature, for example wind and moisture, are more important for species richness in the dry habitats. Grazing might also be an important factor overruling abiotic factors, which might be indicated by the high diversity in Hornsund, where reindeer grazing is lower than on any of the other localities. Grazing is also supposed to be low at Prins Karls Forland, which also has a higher species richness and diversity than expected from the temperature conditions.

The type of habitat is important for explaining the variation in species diversity and richness, and it seems that the different environmental factors have different influences in the dry and mesic habitats. Walker (1995) found the same pattern in south and north facing slopes in Alaska. She found that biological interactions were more important on the more productive south facing slopes, whereas physical factors had a stronger control, leading to a more random distribution of the species, on the north facing slopes.

In mesic habitats both species richness and species diversity were strongly positively related with soil pH, whereas no effect is shown in the dry habitats. This suggests that other factors, such as wind, temperature, cryoturbation, less capacity to hold on to the water, etc., will be of overriding importance in dry habitats. An increase in species number with increased pH has been observed by ecologists for many years. In the Arctic, however, the relationship between species diversity/richness and pH is not well understood. However, Gough *et al.* (2000) showed that in the Alaskan tundra, pH is closely related to species richness and diversity, regardless of other factors.

The correlation matrixes show that both vegetation cover and moss depth are negatively correlated with pH in our study. The low pH values found in the marble and garnet mica schist sites in Hornsund (Table 2), which had dense cover of cryptogams, might explain this. Except for these sites and for Dry 2 in Bellsund (Table 2), which was close to the shore, and thus could be influenced by salt water, the general trend is for higher pH values in the dry habitats than in the mesic ones. This indicates that factors such as vegetation cover and soil moisture have an important influence on soil pH and in some situations override bedrock effects.

The nutrient content of the soils, estimated as the difference in the two pH measurements, was significantly correlated with species diversity in mesic habitats. The regression analysis suggest that high species diversity might be coupled to high nutrient status. There is also a significant positive relationship between vegetation cover and species richness/diversity in the dry habitats. In the mesic habitats, however, the cover values are clumped at the upper end of the scale, which makes it difficult to discover possible trends. Nevertheless, a weak decrease in both richness and diversity when cover approaches 100 %, might be seen. Such a unimodal response of species richness to vegetation cover is common in habitats with intermediate productivity (e.g. Grime 1979, García *et al.* 1993, Theodose & Bowman 1997), as species number eventually decreases as a result of increased competition. The impact of competition on plant communities in the Arctic, however, is uncertain (Gough *et al.* 2000). It is thought that competition in harsh environments, such as in the Arctic, is of minor importance (Callaghan & Emanuelsson 1985). Thus, competition might be less important on the dry ridges, where fewer species coexist, and where other factors are more likely to limit plant growth, than in the more productive mesic habitats. This is consistent with Walker (1995), and with the view that competition is more intense in productive communities (Grime 1979).

Species richness decreases with increasing moss depth in mesic habitats, whereas no trends are shown for the species diversity index, or on the dry ridges. Thus, the reduction in species number is not pronounced by any decrease of the diversity index, as the reduced species number is probably “hidden” in the diversity index due to a high evenness among the remaining species. However, the reduction in species richness might be explained by competition from mosses. Mosses are important for the nutrient flow in arctic ecosystems and

nutrient immobilisation by mosses makes the nutrients unavailable for other plant species (Longton 1997).

The amount of animal droppings is most likely too low to detect any significant effects in the dry habitats. There is a positive relationship between droppings and species richness and diversity in the mesic habitats, where the droppings are also significantly correlated with pH. The droppings in the mesic habitats are mainly from geese. These are rich in nitrogen, and experiments have shown increased plant growth by geese faeces (Bazeley & Jefferies 1989). Tolvanen & Henry (2000) also found that faeces deposited by herbivores (muskox), is an important factor affecting plant growth in nutrient limited habitats, although nutrients released from faeces are not always immediately available for vascular plants. It has been shown that nutrient enriched areas have greater vegetation cover. However, reindeer and geese may also reduce the moss cover and moss depth both through grazing and trampling. This may change the physical properties of the sites and give more space for other species (Jónsdóttir 1991, van der Wal *et al.* 2000). Such disturbed micro-sites might as well be invaded by nitrogen fixing bacteria, which also will improve conditions for plant growth. Furthermore, it is difficult to distinguish between causes and consequences, i.e. whether the mesic habitats have a high cover because of additional nutrient through dropping, less competition, or whether the animals are confined to areas with dense vegetation cover. Grazing activity effects different habitats differently. This is seen by the weak negative correlation between droppings and species richness in the dry habitats. In this habitat type the plants may be more vulnerable to damage than in mesic habitats and heavy grazing might thus reduce diversity.

As a conclusion, both species richness and species diversity indices are of value in biodiversity studies, as these two measures give different information. Different processes seem to control diversity in different habitats. The influence of soil pH and biological interactions are more pronounced in the more productive mesic habitats than on the dry ridges. High soil pH and nutrient content, as well as grazing/manuring, have are positive related to species diversity and species richness in the mesic habitats, whereas increase of moss depth has a negative influence.

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Raunkiaer life forms and plant functional types on Svalbard

Timo Kossonen¹, Lisbeth Rauff², and Åsa Lindgren³

¹Centre of Biodiversity Research, Department of Biology, University of Turku, ²Botanical Institute, Department of Physiological Ecology, University of Copenhagen, ³Department of Botany, University of Stockholm, S-10691 Stockholm

Abstract

The abundance of vascular plant, bryophyte and lichen species was investigated in six different sites along the west coast of Spitsbergen (Svalbard, Norway). Vascular plants were divided into functional types and into groups according to Raunkiaer life forms. The abundance of different groups was studied along a moisture gradient (very dry - dry - mesic) and their abundance was projected on various environmental variables. We found the biological spectrum of the Svalbard flora to be close to that found by Raunkiaer and matching what is expected in the arctic region. This study showed that the utilisation of the abundance of a specific life form was better than biological spectra for revealing small scale ecological differences such as sites comparisons within a region and habitats within a site. Chamaephytes were the most abundant life form in the most exposed very dry habitats, and hemicryptophytes were the most abundant life form in the less exposed mesic habitats. Cryptophytes were the least abundant life form in all habitats but were more abundant in mesic habitats compared to dry and very dry habitats. Bryophyte and vascular plant frequency increased towards mesic habitats, while as lichens decreased. The bryophyte layer appeared as an important factor affecting vascular plant frequencies, especially for the deciduous dwarf shrubs, but generally plant functional types revealed only a few correlations with environmental variables. Soil moisture and small-scale topography are hypothesized as the most important factors affecting (vascular plant) functional type frequencies locally.

Introduction

The variation in the dominant plant types among different habitats is striking in the Arctic and is clearly related to climate, microclimate and topography (Shaver et al. 1997). Many ecologists have attempted to use the functional differences among arctic plants in order to understand the mechanisms controlling their distribution (Shaver et al. 1997). One function of descriptions of vegetation patterns is to provide a point of departure for ecological studies (Oksanen & Virtanen 1995).

The aim of this project was to investigate the diversity in high arctic vegetation in the Svalbard archipelago in terms of their functional type and life form composition and to analyse the relationship between the abundance of these groups and different abiotic and biotic environmental factors. There are three main approaches that have been used to identify functional types and guilds; subjective, deductive and data-defined (Gitay and Noble 1997). The subjective classifications are based on observations in the ecosystem and the vegetation is divided into groups such as trees, shrubs, grasses etc. In a deductive approach, a functional classification is derived from a statement of the importance of a particular process in the functioning of an ecosystem and functional categories are then deduced from these premises. The data-defined approach uses multivariate techniques in order to seek clusters of species based on a set of characters (Gitay & Noble 1997). The three approaches can be used at different scales, and in this study we are focusing on subjective life form classification by Raunkiaer (1903) and on vascular plant functional types (Chapin et al. 1996), which utilises

the deductive and data-defined approaches. Lichens, bryophytes and vascular plants were also studied as three separate and distinct entities.

Raunkiaer life forms

The traditional classification of vascular plant species into life forms has been widely used in studies of plant geography and was first proposed by Raunkiaer in 1903. On a geographical scale life forms are usually expressed as biological spectra with the percentage number of species belonging to a particular life form as a unit. Raunkiaer (1934) showed that the biological spectrum is essentially the same in regions with broadly similar climates, and the biological spectra can therefore be used as a biological expression of climate. To be able to relate the biological spectra to a standard he defined the normal spectra from an estimated percentage of the species of the world's flora that belong to the different life forms.

The life form classification is based on the way species protect the surviving buds and shoot apices from the unfavourable season. In environments where the unfavourable season is characterised by extreme cold and exposure, hemicryptophytes, chamaephytes and cryptophytes are dominating. Hemicryptophytes form the group with most species in the Arctic. The buds are often protected by a leaf rosette, since many species belonging to the hemicryptophytes are either rosette or tussock forming. Hemicryptophytes have their surviving buds or shoot apices situated at the soil surface; while chamaephytes, the character life form of the arctic, are either cushion forming or buds are situated just above the soil surface. Cryptophytes have their surviving buds or shoot apices buried in the ground (Raunkiaer 1934.) Raunkiaer's life forms have not received as much attention in ecology as they might deserve, even though a quantification of the plants of each life form could give a meaningful ecological spectra on smaller scales with abundance per unit area as unit.

Vascular plant functional types

Another subjective approach for grouping plant species is according to growth form and/or functional types. A functional type is a non-phylogenetic classification leading to a grouping of organisms that responde in a similar way to environmental factors (Gitay and Noble 1996).

Arctic/alpine plants can be divided into prostrate woody plants, graminoids, herbaceous perennials (often rosette plants), cushion plants, geophytes, annuals, bryophytes and lichens (Körner 1999). Another common way of grouping arctic growth forms is to use the groups: grasses, sedges, deciduous shrubs, evergreen shrubs, forbs, bryophytes and lichens, eventually with subdivision into erect, prostrate or caespitose (Shaver et al. 1997; Chapin et al. 1996). These functional types have been used to describe vegetation responses to the environment and to herbivory (Chapin et al. 1996). The above-mentioned functional types are those used in the present project. Chapin et al. (1996) defined these groups by subjective classification based on experiences with the distribution along environmental gradients. A cluster analysis based on different ecological important plant traits was used on the most common species in the arctic tundra to group the species. The groups made by cluster analysis were similar to the subjective groups (Chapin et al. 1996). This indicates that the species in these groups are actually physically responding in a similar way, and are not just artificial groups.

Hypothesis

We expect to find a biological spectrum of the Svalbard flora that corresponds to the climate of the arctic region in which Svalbard is found. We expect to find a difference in the abundance of life forms according to differences in the degree of exposure, which in this study is assumed to correspond roughly to habitats with different moisture levels, and due to the variation in the degree of bud protection.

We expect the proportion of different functional types to be dependent of various environmental factors. Deciduous dwarf shrubs, forbs and grasses are expected to be more dominating in habitats with a high nutritional status (as indicated by small pH H₂O-KCl difference, see methods below) and evergreen dwarf shrubs more dominating in less nutritional habitats. Sedges and bryophytes are expected to be dominating in mesic habitats, while lichens and evergreen dwarf shrubs are expected to dominate in more dry habitats. Grazing is expected to influence the plant composition to dominance of primarily sedges, and grasses, which in the sense of Raunkiaer life forms means dominance of hemicryptophytes.

Materials and Methods

Study sites

Between the 9th and 14th of July 2001, six different localities on Svalbard, with different bedrock, grazing pressure, temperature and degree of oceanity, were visited for vegetation analysis. An overview of the site characteristics is shown in Table 1. The sites belong either to the Northern arctic-tundra zone (NATZ) or the middle arctic-tundra zone (MATZ) (table 1) (*sensu* Elvebakk, 1997).

Vegetation analysis

The vegetation was analysed by point framing, using 50x50cm frames with 25 equally distributed points. In each point, one hit from the field (phanerogam) layer and one from the bryophyte/lichen (cryptogam) layer was recorded. Plants were identified to species level for vascular plants, bryophytes, fruticose- and foliose lichens. Only the most common crustose lichens were identified. All species names are according to Elvebakk and Prestrud (1996). In each habitat 11-12 frames were analysed. In addition the total vegetation cover was also estimated.

Environmental factors

In each frame the moss depth was measured at 5 standardised points, and the depth of the active layer was measured by pressing an iron rod as deep in to the ground as possible in each frame. Soil samples were taken from the organic and mineral layer from five of the frames for pH-measurements. Soil samples were also brought to the laboratory at UNIS and sieved through a 2 mm sieve. The soil solution was extracted in both distilled water and 0.2 M KCl. Soil and extraction solution was added to plastic bottles in 1:2 v/v, shaken for 1 hour, and left to sediment for 2 hours before measuring the pH with "Portable sension™ 156 Multiparameter Meter, HACH". The pH difference in water and KCl (pH_{H₂O}-pH_{KCl}) gives an indirect estimate of the nutrient status of the soil. A low difference indicates a high soil nutrient status due to the high proportion of mineral cations bound to the soil colloids and therefore minimal ion exchange of H⁺ with K⁺.

A temperature index (T-index) of the sites based on the abundance and number of thermophilous and non-thermophilous species is used as an estimation of temperature/climate for each site (Sub report 2 AB-306 2001)(Table 1). The method is based on the fact that plants are temperature demanding to different degrees. The method is described in Karlsen and Elvebakk (1996). For further details on the calculations see "sub report 2 AB-306 2001"

Grazing pressure or manuring was estimated by counting herbivore droppings along a separate transect and also from the frames. We differentiated between old and fresh reindeer droppings, winter and summer reindeer droppings, old and fresh goose droppings and ptarmigan droppings.

Table 1. Overview of site characteristics. ¹⁾Middle arctic tundra zone, with a mean temperature of the warmest month of 5-7°C ²⁾Northern arctic tundra zone, with a mean temperature of the warmest month of 5-7°C (Elvebakk 1997) ³⁾ Temperature index, (Sub report 2, AB-306 2001)

| Site | Sub site | Longitude | Latitude | Date | Bedrock | Biogeographical zone | Tindex ₃₎ | Grazing | Habitats |
|--------------------|----------|----------------------|----------------|----------|---|----------------------|----------------------|-------------------|--------------------------|
| Templet | | 16°48'14.8'' E | 78°23'34.522 N | 07-09-01 | Permian, calciculous | MATZ ¹⁾ | 30.75 | High | Very dry Dry Mesic |
| Pyramiden | | 16°17'51.7'' E | 78°39'37.0'' N | 07-10-01 | Carboniferous | MATZ | 30.75 | Low | Dry Mesic |
| Hornsund | 1. | 15°31'28E | 77°00'23N | 07-11-01 | Middle Proteozoic, Marble Garnet mica schists | NATZ ²⁾ | 11 | Low | Dry/Mesic |
| | 2. | | | | Middle Proteozoic, Garnet mica schists. | | | | |
| Bellsund | | 14°24'38.1''E | 77°45'20.5''N | 07-12-01 | Carboniferous | MATZ | 8.25 | Extremely high | 2xDry Mesic |
| Prins Karl Forland | | 10°28'26.8''E | 78°53'43.3''N | 07-13-01 | Precambrium | NATZ | 3.5 | Low | Dry Mesic |
| Blomstrandhalvøya | 1. | 12°02'47.7''E | 78°57'50.8''N | 07-14-01 | Precambrium | MATZ | 26 | Low | Dry/Mesic |
| | 2. | 12°02'05.23.0'' E | 78°58'07.2''N | | | | | | |

Data analysis

Each vascular plant species was assigned to one of the five Raunkiaer life-form groups (Raunkiaer 1934) and one of the functional types (Chapin et al. 1996) (appendix 1). All bryophyte species (liverworts, acrocarps and pleurocarps) were clustered into one group (appendix 2), and lichen species were placed in three groups: fruticose, foliose and crustose lichens (appendix 3). The Raunkiaer biological spectrum for Svalbard based on this study was found by calculating the number of vascular species belonging to each life form as a percentage of the total number of vascular species found in this study. This was also done for each site*habitat using an equal number of frames from each site. This gives only one value per site, which doesn't allow any statistical analysis, but makes it possible to use the data qualitatively. The abundance of a life form/functional type is calculated as the number of hits of species belonging to the specific life form or functional type in question in a frame. This is the primary unit used in all statistical analysis.

Statistical comparisons of Life forms were made with sites, sub sites, habitats and site*habitats effects. Means were compared by bonferroni-adjusted t-test on Significant ANOVA F-test using the SAS General Linear Models procedure. Linear regressions of life forms were made using SPSS regression procedures. Statistical analyses of the functional groups were made using the SPSS (v. 10). The differences in the frequencies of functional types between and within habitats were examined using a one-way ANOVA. Since the frequency data did not show homogeneity of variance we used Tamhane's T2 post hoc test to examine the means and for the same reason we used Spearman's rho in calculating the correlation coefficients. For canonical analysis (redundancy analysis, RDA) we used the CANOCO (v. 4.0) program. In RDA we used data only from the dry and mesic habitats, as there were only three very dry habitats presented, compared to six from both dry and mesic habitats.

Results

Environmental data

The environmental data is shown in table 2 as mean values for all habitats at all sites. The depth of the active layer varied from about 0.2 to almost 0.6 meters. Bird droppings were present in almost every habitat investigated, but reindeer droppings were slightly less frequent, and lacking from several habitats. The pH-values are, with a few exceptions, relatively high

Raunkiaer life forms

The biological spectrum found in this study was mainly in agreement with the results found by Raunkiaer (1934), but differed in some ways. We found a smaller proportion of the species belonging to chamaephytes but a higher proportion to cryptophytes and hemicryptophytes than that found by Raunkiaer (figure 1).

Table 2. Environmental data. Mean values for all sites and habitats. PKF= Prins Karls Forland. ¹⁾1=very dry, 2=dry, 3=mesic. ²⁾Tindex (see report 2)

| Site | Habitat ¹⁾ | T-index ²⁾ | Mossdepht (cm) | Active layer(cm) | Bird droppings (no/m ²) | reindropwin (no/m ²) | reindropsum (no/m ²) | Droppings total (no/m ²) | pHorgH2O | pHorgKCl | pHminH2O | pHminKCl | pHorgdiff | pHmindiff |
|-------------------|-----------------------|-----------------------|-------------------|---------------------|---|-------------------------------------|-------------------------------------|---|----------|----------|----------|----------|-----------|-----------|
| Templet | 2 | 30.75 | 0.27 | 32.8 | 0.18 | 0.15 | 0.105 | 0.435 | | | 7.93 | 7.45 | | 0.48 |
| Templet | 1 | 30.75 | 0.06 | 23.8 | 0 | 0.145 | 0.015 | 0.16 | | | 7.66 | 6.85 | | 0.81 |
| Templet | 3 | 30.75 | 1.74 | 39.9 | 1.065 | 0.16 | 0.34 | 1.565 | 7.21 | 6.78 | 7.23 | 6.71 | 0.43 | 0.52 |
| Pyramiden | 2 | 30.75 | 0.17 | 25.7 | 0.185 | 0 | 0 | 0.185 | 6.96 | 6.48 | 7.33 | 6.44 | 0.48 | 0.89 |
| Pyramiden | 3 | 30.75 | 1.47 | 57.1 | 1.095 | 0 | 0 | 1.095 | 7.01 | 6.39 | 6.87 | 6.21 | 0.62 | 0.66 |
| Hornsund | 2 | 11 | 4.87 | 25 | 0.11 | 0 | 0 | 0.11 | 5.83 | 4.64 | | | 1.19 | |
| Hornsund | 2 | 11 | 3.00 | 22 | 0.14 | 0 | 0 | 0.14 | 7.44 | 6.87 | 7.96 | 7.44 | 0.57 | 0.52 |
| Hornsund | 3 | 11 | 4.20 | 55 | 1.635 | 0.03 | 0.07 | 1.735 | 6.13 | 6.17 | 6.61 | 5.65 | -0.04 | 0.96 |
| Hornsund | 3 | 11 | 3.52 | 45.9 | 1.72 | 0.04 | 0.05 | 1.81 | 7.18 | 6.43 | 7.07 | 6.45 | 0.75 | 0.62 |
| Bellsund | 2 | 8.25 | 0.70 | 16.4 | 1.025 | 0.14 | 0.64 | 1.805 | 4.8 | 3.51 | 6.85 | 6.33 | 1.29 | 0.52 |
| Bellsund | 1 | 8.25 | 0.55 | 21.5 | 0.075 | 0.07 | 0.13 | 0.275 | 6.39 | 6.04 | 6.64 | 5.4 | 0.35 | 1.24 |
| Bellsund | 3 | 8.25 | 2.56 | 34 | 0.59 | 0.055 | 0.24 | 0.885 | 6.16 | 5.32 | 6.24 | 5.23 | 0.84 | 1.01 |
| PKF | 2 | 3.5 | 0.31 | 22.7 | 0.07 | 0.005 | 0.02 | 0.095 | 6.75 | 5.58 | 6.77 | 5.57 | 1.17 | 1.2 |
| PKF | 3 | 3.5 | 1.50 | 25 | 0.19 | 0.015 | 0.01 | 0.215 | 6.63 | 5.76 | 5.86 | 4.44 | 0.87 | 1.42 |
| Blomstrandhalvøya | 2 | 26 | 0 | 29 | 0.1 | 0.02 | 0.015 | 0.135 | 6.72 | 6.59 | 7.55 | 6.93 | 0.13 | 0.62 |
| Blomstrandhalvøya | 2 | 26 | 0 | 30 | 0.01 | 0 | 0 | 0.01 | 7.7 | 6.77 | 7.78 | 7.016 | 0.93 | 0.764 |
| Blomstrandhalvøya | 1 | 26 | 0 | 25 | 0.005 | 0 | 0 | 0.005 | | | 7.99 | 7.31 | | 0.68 |
| Blomstrandhalvøya | 3 | 26 | 0.60 | 28.4 | 0.505 | 0.16 | 0.03 | 0.695 | 7.01 | 5.93 | 7.13 | 6.29 | 1.08 | 0.84 |
| Blomstrandhalvøya | 3 | 26 | 0.74 | 52 | 1.53 | 0.035 | 0.065 | 1.63 | 7.29 | 6.48 | 7.3 | 6.45 | 0.81 | 0.85 |

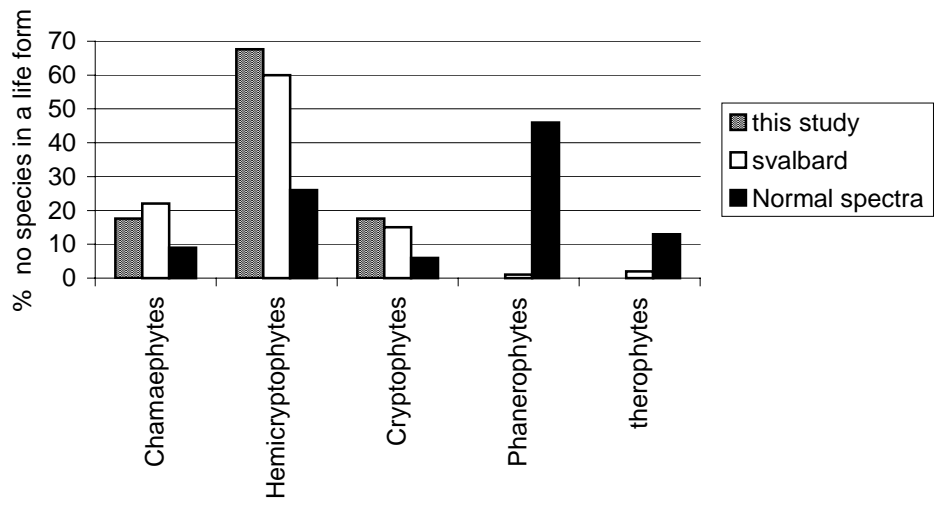


Figure 1. Biological spectra found in this study, the biological spectra in Svalbard found by Raunkiaer (1934) and the normal spectra of the world's flora.

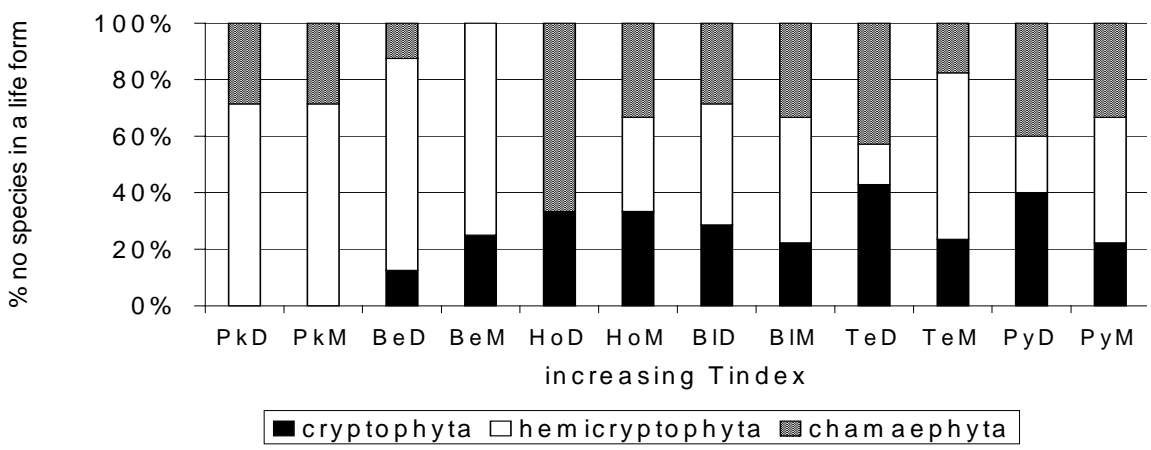


Figure 2. The biological spectrum in all sites and habitats sorted with increasing temperature index. Pk= Prins Karls Forland, Be= Bellsund, Ho=Hornsund, Bl= Blomstrandhalvøya, Te=Templet, Py= Pyramiden, D=dry, M=mesic

In this study no phanerophytes and therophytes were recorded. Compared to the normal spectrum, chamaephytes, cryptophytes and hemicryptophytes had a higher presence in the biological spectrum and phanerophytes and therophytes had a low presence (Figure 1). The contribution of chamaephytes, hemicryptophytes and cryptophytes in Svalbard showed to be at least twice the percentage found in the normal spectrum (Figure 1). The biological spectrum in each habitat and each site is shown in figure 2. Sites were sorted according to Temperature index. Cryptophytes were absent from the coldest site and the percentage of cryptophyte species increased only weakly along the T-index gradient.

The abundance (number of hits per frame) of life forms in the different sites is shown in figures 3 and 4. Cryptophytes were more abundant in Templet compared to Hornsund, Bellsund, PKF and Blomstrand. Hemicryptophytes were more abundant in Bellsund compared to all other sites and Chamaephytes were more abundant in Pyramiden and Blomstrand compared to all other sites (figure 3). In Hornsund, Bellsund and Prins Karls Forland hemicryptophytes were the most abundant life form compared to the other life forms; while in Blomstrand Chamaephytes is the most abundant life form (figure 4).

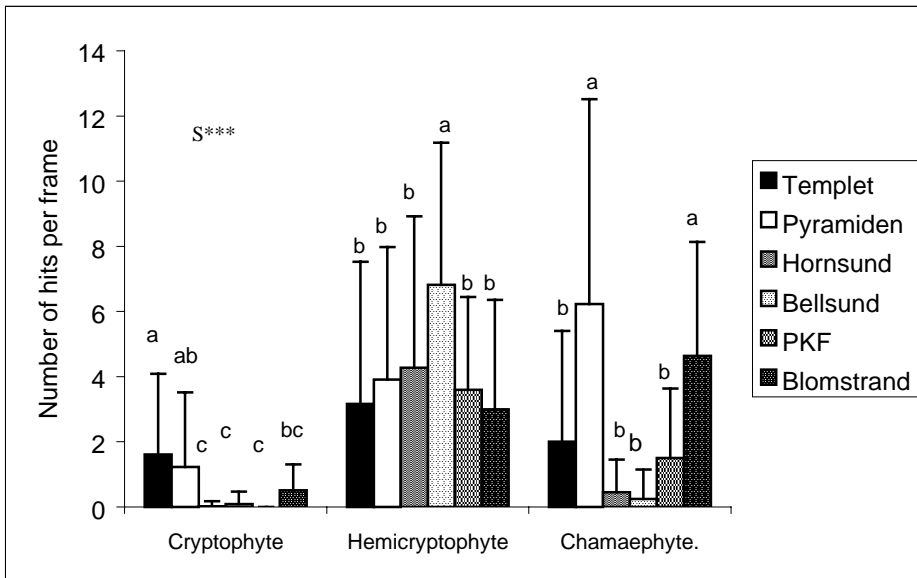


Figure 3. Comparison of abundance of life forms at different sites (Mean \pm std.dev.). Results of ANOVA with significant effect of site (S). Significant differences between individual sites (tested by bonferroni-adjusted t-test) are indicated by different letters ($P < 0.05$).

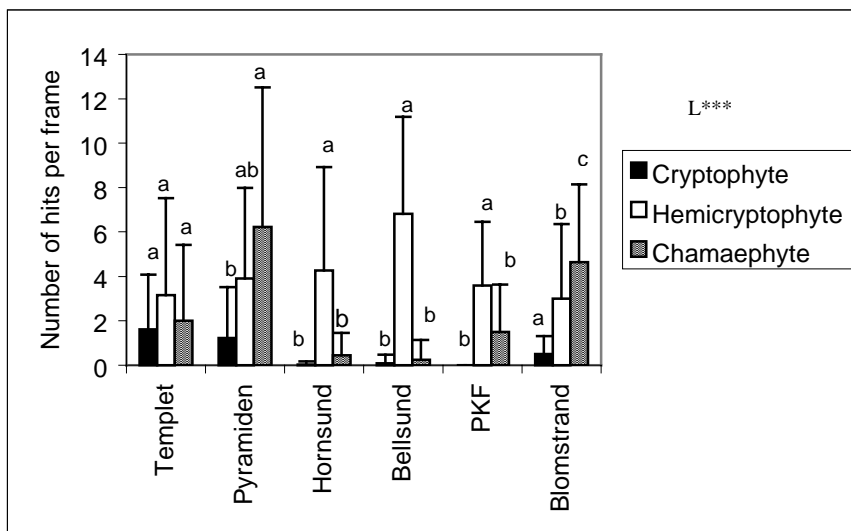


Figure 4. Comparison of life form abundance within sites (mean \pm std.dev.). Results of ANOVA with significant effect of life form (L). Significant differences between individual life forms (tested by Bonferroni-adjusted t-test) are indicated by different letters ($P < 0.05$).

There was no significant difference between the two sub-sites in Blomstrandhalvoya according to cryptophyte and hemicryptophyte abundance, but chamaephytes were significantly more abundant in sub-site 1 (mean=5,68) compared to sub-site 2 (mean=3,90) (Result of ANOVA with significant effect of sub site $P=0.0289$). In Hornsund chamaephytes were significantly more abundant in sub-site 2 (mean=0,864) compared to sub site 1 (mean=0.0455) (Result of ANOVA with significant sub site effect $P=0.0063$). Hemi- and cryptophytes abundances were not different between sub sites.

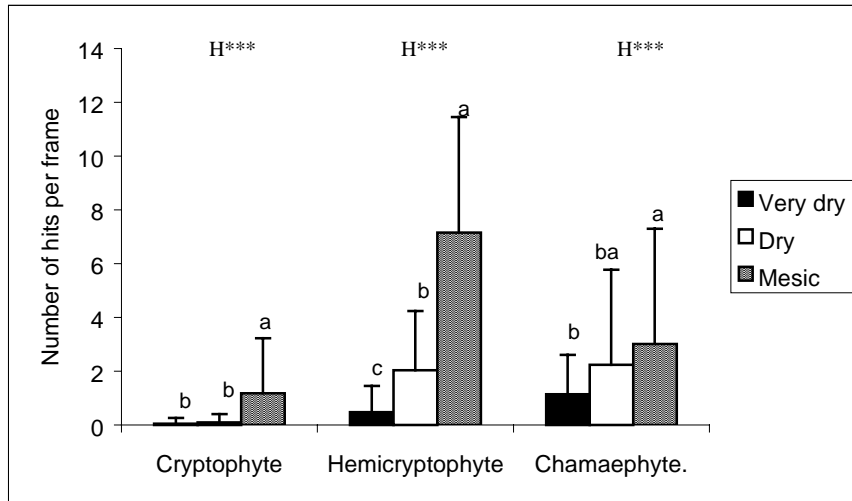


Figure 5. comparison of abundance of life forms among habitats (Mean \pm std.dev.). Results of ANOVA with significant effect of Habitat (H). Significant differences between individual habitats tested by Bonferroni-adjusted t-test are indicated by different letters ($P < 0.05$).

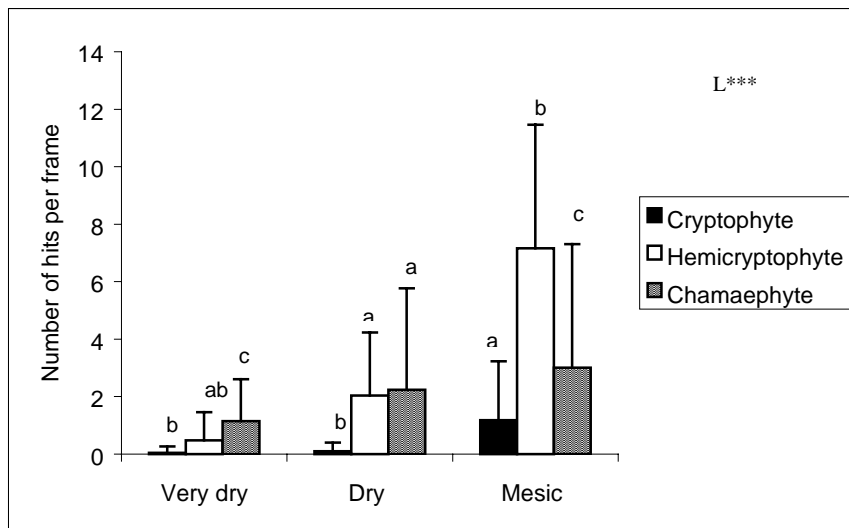


Figure 6. Comparison of life form abundance within habitats (mean \pm std.dev.) Results of ANOVA with significant effect of life form (L). Significant differences between individual life forms tested by Bonferroni-adjusted t-test are indicated by different letters ($P < 0.05$).

The abundance of all three life forms increased towards more mesic habitats (figure 5). But the dominating life form changed with habitat. Cryptophytes were least abundant in all three habitats, while Chamaephytes were most abundant in very dry sites, chamaephytes and hemicryptophytes

were equal but significantly more abundant than cryptophytes in dry sites and hemicryptophytes were the most abundant in mesic sites (figure 6).

Table 3 Comparison of life form abundance between habitats for each site individually (Mean±std.dev), N stated in brackets. The results of two-way ANOVA with Site and Habitat as factors. Hemicryptophyte: $R^2=0,565$, site ***, habitat ***, site*habitat *; Cryptophyte: $R^2=0,585$, site ***, habitat ***, site*habitat ***; Chamaephyte $R^2=0,481$, site ***, habitat **, site*habitat *** (* $P<0,05$; ** $P<0,01$; *** $P<0,001$). Difference at the 0.05 significance level between individual habitats in each site tested by Bonferroni adjusted t-test is indicated by different letters in the table. n.d.= no data

| Hemicryptophytes | | | |
|------------------|-------------------|---------------------|------------------------|
| Site | Very dry | Dry | Mesic |
| Templet | 0,00± 0,00 (12) a | 1,33± 1,30 (12) a | 8,17± 4,11 (12) b *** |
| Pyramiden | n.d. | 0,64± 1,80 (11) a | 7,18± 2,82 (11) b *** |
| Hornsund | n.d. | 1,68± 2,38 (22) a | 6,86± 4,95 (22) b *** |
| Bellsund | n.d. | 4,27± 1,93 (22) a | 11,91± 3,21 (11) b *** |
| PKF | n.d. | 2,27± 1,56 (11) a | 4,91± 3,30 (11) b * |
| Blomstrand | 1,11± 1,27 (9) a | 1,14± 1,49 (22) a | 5,64± 3,55 (22) b *** |
| Cryptophytes | | | |
| Site | Very dry | Dry | Mesic |
| Templet | 0,00± 0,00 (12) a | 0,42± 0,51 (12) a | 4,42± 2,50 (12) b *** |
| Pyramiden | n.d. | 0,09± 0,30 (11) a | 2,84± 2,84 (11) b *** |
| Hornsund | n.d. | 0,00± 0,00 (22) a | 0,05± 0,21 (22) a |
| Bellsund | n.d. | 0,00± 0,00 (22) a | 0,27± 0,65 (11) a |
| PKF | n.d. | 0,00± 0,00 (11) a | 0,00± 0,00 (11) a |
| Blomstrand | 0,11± 0,33 (9) a | 0,18± 0,39 (22) a | 1,00± 0,96 (22) b ** |
| Chamaephytes | | | |
| Site | Very dry | Dry | Mesic |
| Templet | 0,92± 1,44 (12) a | 4,17± 4,88 (12) b** | 0,92± 1,83 (12) a |
| Pyramiden | n.d. | 4,55± 6,82 (11) a | 7,91± 5,50 (11) b ** |
| Hornsund | n.d. | 0,50± 0,74 (22) a | 0,41± 1,22 (22) a |
| Bellsund | n.d. | 0,36± 1,09 (22) a | 0,00± 0,00 (11) a |
| PKF | n.d. | 2,36± 2,73 (11) a | 0,64± 0,67 (11) a |
| Blomstrand | 1,44± 1,51 (9) a | 3,59± 2,30 (22) a | 7,00± 3,57 (22) b *** |

Hemicryptophytes were also increasing towards mesic habitats when each site was analysed separately. In the case of cryptophytes this trend was seen in Templet, Pyramiden and Blomstrandhalvøya and in the case of chamaephytes in Pyramiden and Blomstrand only (table 4).

The results of the regression analysis on life forms in relation to environmental data are shown in Table 4. Cryptophytes correlated positively with the depth of active layer in dry sites. Cryptophytes showed positive correlation to winter droppings of reindeer in both dry and mesic sites.

Hemicryptophytes (in dry sites) and cryptophytes (in mesic sites) were positively correlated to

summer droppings of reindeer, while chamaephytes (in dry sites) showed a negative correlation. Cryptophytes showed negative correlation to bird droppings in mesic sites (table 4).

Table 4 Results of regression analysis of lifeform abundance in relation to environmental factors. R = Pearsons correlation coefficient, R² = R-square of regression, P= significance level of regression, N= number of samples.

| Very dry | Cryptophytes | | | | Hemicryptophytes | | | | Chamaephytes | | | |
|----------------|--------------|----------------|-----------|----|------------------|----------------|---------|----|--------------|----------------|---------|----|
| | R | R ² | P | N | R | R ² | P | N | R | R ² | P | N |
| moss depth | -0.083 | 0.007 | 0.787 | 13 | -0.083 | 0.007 | 0.787 | 13 | 0.178 | 0.032 | 0.567 | 13 |
| plant cover | -0.269 | 0.072 | 0.374 | 13 | 0.094 | 0.009 | 0.759 | 13 | 0.109 | 0.012 | 0.724 | 13 |
| active layer | 0.068 | 0.005 | 0.825 | 13 | 0.068 | 0.005 | 0.825 | 13 | 0.194 | 0.038 | 0.524 | 13 |
| Dry | Cryptophytes | | | | Hemicryptophytes | | | | Chamaephytes | | | |
| | R | R ² | P | N | R | R ² | P | N | R | R ² | P | N |
| moss depth | -0.117 | 0.014 | 0.355 | 64 | -0.123 | 0.015 | 0.334 | 64 | -0.226 | 0.051 | 0.072 | 64 |
| plant cover | 0.138 | 0.019 | 0.277 | 64 | 0.145 | 0.021 | 0.252 | 64 | 0.184 | 0.034 | 0.146 | 64 |
| active layer | 0.341 | 0.102 | 0.006** | 64 | -0.111 | 0.012 | 0.385 | 64 | 0.112 | 0.013 | 0.379 | 64 |
| bird droppings | -0.046 | 0.002 | 0.732 | 57 | -0.072 | 0.005 | 0.595 | 57 | -0.082 | 0.007 | 0.546 | 57 |
| reindropwin | 0.418 | 0.151 | 0.011* | 36 | 0.158 | 0.025 | 0.359 | 36 | -0.026 | 0.001 | 0.882 | 36 |
| reindropsum | -0.115 | 0.013 | 0.505 | 36 | 0.454 | 0.206 | 0.005** | 36 | -0.416 | 0.173 | 0.012* | 36 |
| pHminH2O | 0.136 | 0.018 | 0.536 | 23 | -0.245 | 0.06 | 0.26 | 23 | -0.019 | 0 | 0.932 | 23 |
| pHminKCl | 0.208 | 0.043 | 0.379 | 20 | -0.249 | 0.062 | 0.289 | 20 | 0.005 | 0 | 0.984 | 20 |
| pHmindiff | -0.467 | 0.218 | 0.068 | 16 | 0.334 | 0.112 | 0.206 | 16 | -0.113 | 0.013 | 0.676 | 16 |
| pHorgH2O | 0.102 | 0.01 | 0.698 | 16 | -0.068 | 0.005 | 0.797 | 17 | 0.396 | 0.157 | 0.115 | 17 |
| pHorgKCl | 0.518 | 0.268 | 0.482 | 4 | 0.997 | 0.994 | 0.003** | 4 | 0.598 | 0.358 | 0.402 | 4 |
| pHorgdiff | -0.609 | 0.371 | 0.391 | 4 | -0.996 | 0.991 | 0.004** | 4 | -0.683 | 0.466 | 0.317 | 4 |
| Mesic | Cryptophytes | | | | Hemicryptophytes | | | | Chamaephytes | | | |
| | R | R ² | P | N | R | R ² | P | N | R | R ² | P | N |
| moss depth | -0.213 | 0.045 | 0.111 | 57 | 0.301 | 0.091 | 0.023* | 57 | -0.389 | 0.136 | 0.364 | 57 |
| plant cover | 0.275 | 0.075 | 0.039* | 57 | 0.21 | 0.044 | 0.118 | 57 | -0.195 | 0.038 | 0.006* | 57 |
| active layer | 0.254 | 0.064 | 0.059 | 56 | 0.129 | 0.017 | 0.342 | 56 | 0.239 | 0.057 | 0.085 | 56 |
| bird droppings | -0.558 | 0.312 | 0.007** | 22 | -0.058 | 0.003 | 0.796 | 22 | -0.441 | 0.195 | 0.317 | 22 |
| reindropwin | 0.549 | 0.302 | <0.000*** | 50 | 0.053 | 0.003 | 0.715 | 50 | 0.298 | 0.089 | 0.123 | 50 |
| reindropsum | 0.602 | 0.362 | <0.000*** | 50 | 0.269 | 0.073 | 0.059 | 50 | -0.282 | 0.08 | 0.076 | 50 |
| pHminH2O | 0.209 | 0.044 | 0.405 | 18 | -0.485 | 0.236 | 0.041* | 18 | 0.429 | 0.184 | 0.047* | 18 |
| pHminKCl | 0.098 | 0.01 | 0.691 | 19 | -0.413 | 0.17 | 0.079 | 19 | 0.367 | 0.134 | 0.035* | 19 |
| pHmindiff | -0.036 | 0.001 | 0.889 | 18 | 0.17 | 0.029 | 0.5 | 18 | -0.25 | 0.063 | 0.040* | 18 |
| pHorgH2O | 0.249 | 0.062 | 0.169 | 32 | -0.175 | 0.031 | 0.338 | 32 | 0.309 | 0.095 | 0.076 | 32 |
| pHorgKCl | -0.152 | 0.023 | 0.676 | 10 | 0.311 | 0.097 | 0.382 | 10 | -0.791 | 0.626 | 0.145 | 10 |
| pHorgdiff | -0.02 | 0 | 0.96 | 9 | -0.463 | 0.214 | 0.21 | 9 | 0.344 | 0.119 | 0.003** | 9 |

Functional groups

The difference in the occurrence pattern of lichens compared to bryophytes and vascular plants is evident in figures 7 and 9. Lichen frequency decreased markedly towards mesic habitats; whereas bryophytes and vascular plant frequencies showed significant increases. Bryophyte frequency and vascular plant frequencies increased steadily towards mesic habitats. Lichen and vascular plants dominated in very dry habitats (figure 9) and in mesic habitats vascular plants and bryophytes dominated over lichens. In dry habitats all three groups occurred evenly.

All five vascular plant groups showed similar trends as vascular plants in general – i.e. their frequency increased towards more mesic habitats (figure 8). In the very dry habitats there were no significant differences in frequencies between the five groups (figure 10). In dry habitats the frequencies varied and only forbs established a significantly larger proportion than grasses. In the mesic habitats grasses formed a statistically smaller proportion of vascular plant frequency, whereas the frequencies of the four other groups were within the same magnitude (as they were also in dry habitats).

The correlation matrix (Table 5) should be interpreted with care. It was primarily used as an indicator of significant environmental variables in selecting environmental variables for Correspondence Analysis and as the sites and habitats were chosen by more or less subjective methods the p-values should not suggest implicit suggestion.

Bryophyte frequency and the height of the bryophyte layer (moss depth) appeared to be linked with the frequency of deciduous dwarf shrubs. Except for the nearly significant negative correlation with frequency of evergreen dwarf shrubs there were no other correlations between moss depth and groups. The total vegetative cover is not an independent environmental variable but the correlations indicate that forbs, bryophytes and possibly grasses are essentially the groups that are more frequent when the vegetative cover is high. High lichen frequency correlated with a shallow active layer.

Between the two grazing pressure / manuring indicators there were some differences. The number of bird droppings correlated with bryophyte frequency, but the number of reindeer droppings correlated with the grass frequency. The calculated nutrient statuses proved to have no correlations with the groups other than a positive correlation with lichen frequency, indicating high lichen frequency when the nutrient status of the organic layer is low.

Frequencies of three functional groups

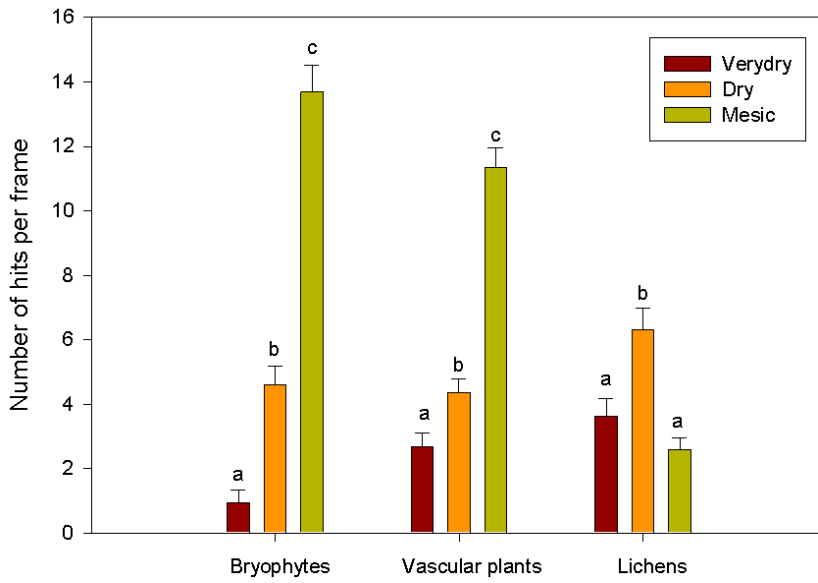


Figure 7. The average number of group individuals seized by one frame with 25 possible ‘points’. Different letters indicate significant differences. Error bar present S.E. of mean.

Vascular plant functional group frequencies

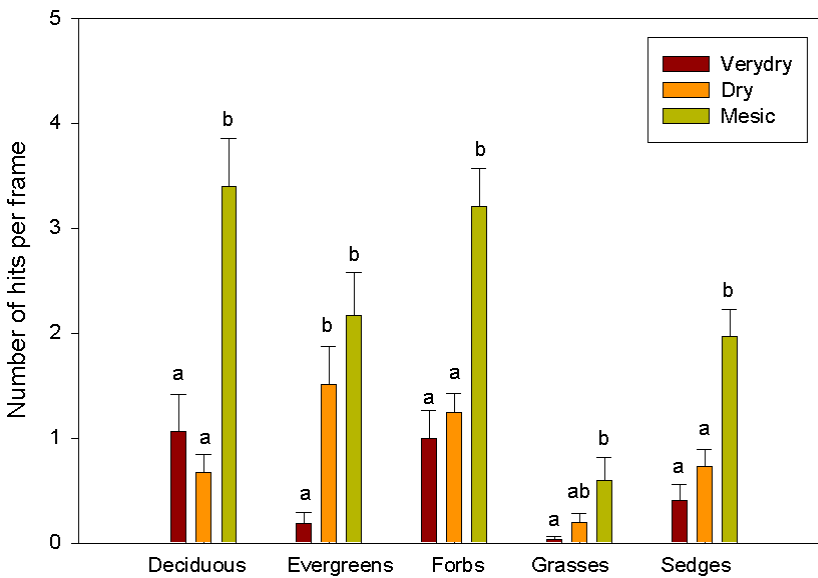


Figure 8. The average number of group individuals seized by one frame with 25 possible ‘points’. Different letters indicate significant differences. Error bar present S.E. of mean.

Comparison within habitat - bryophytes, vascular plants and lichens

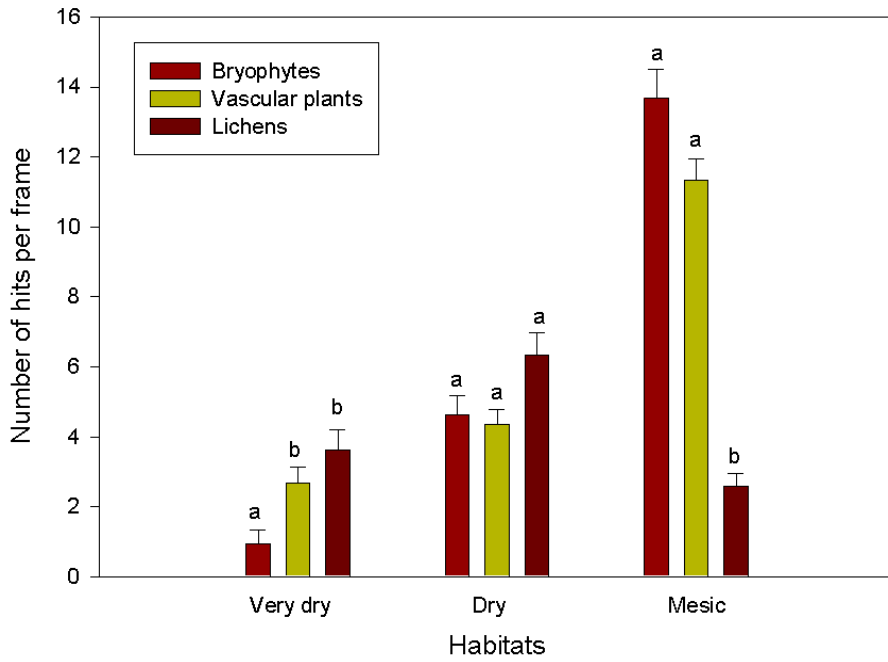


Figure 9. Same values as in Figure 7, but the focus is on differences within habitats. Different letters indicate significant differences. Error bar present S.E. of mean.

Comparison within habitats - vascular plant functional groups

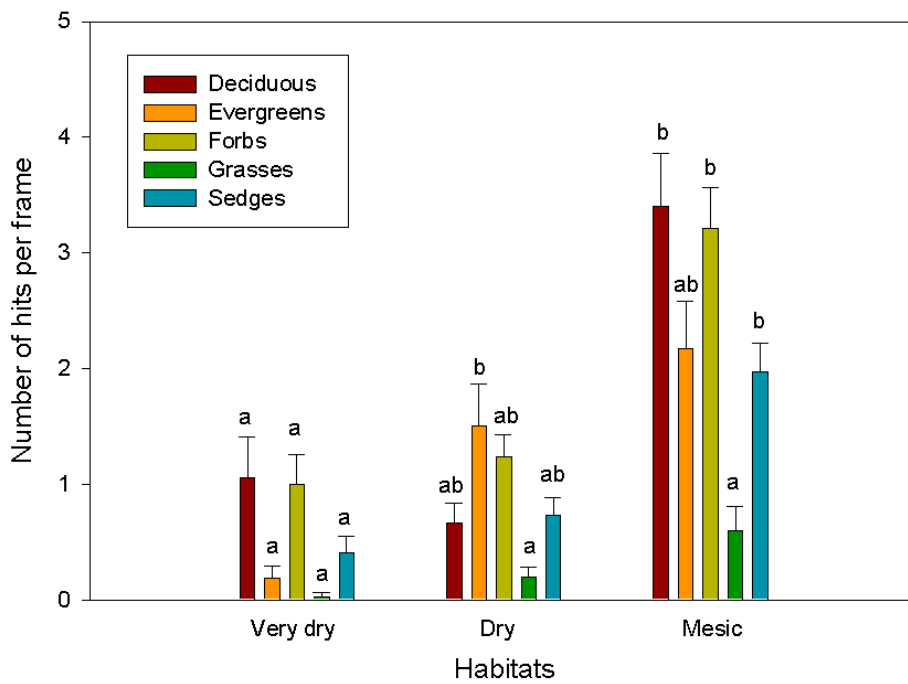


Figure 10. Same values as in Figures 8, but the focus is on differences within habitats. Different letters indicate significant differences. Error bar present S.E. of mean.

Table 5. Spearman's rho. The correlation is based on mean values using data only from dry and mesic habitats. N = 12 in all cases.

| | Deciduous | Evergreen | Forbs | Grasses | Sedges | Lichens | Bryophytes |
|-----------------|-----------|-----------|-------|---------|--------|----------|------------|
| Spearman's rho | | | | | | | |
| Lichens | -0.63* | -0.46 | -0.23 | 0.00 | -0.46 | 1.00 | |
| Bryophytes | 0.61* | -0.40 | 0.09 | 0.40 | -0.03 | -0.49 | 1.00 |
| Moss depth | 0.66* | -0.54(*) | -0.11 | 0.18 | -0.01 | -0.15 | 0.77** |
| Cover total (%) | 0.36 | -0.01 | 0.66* | 0.52 | 0.16 | -0.53 | 0.78** |
| Active layer | 0.50 | 0.54(*) | 0.51 | -0.29 | 0.34 | -0.77** | 0.39 |
| Dropping bird | 0.49 | 0.10 | 0.22 | 0.03 | 0.41 | -0.64* | 0.72** |
| Droppings rein | 0.43 | -0.34 | -0.15 | 0.59* | 0.09 | -0.27 | 0.46 |
| Dropping total | 0.51 | 0.00 | 0.00 | 0.13 | 0.41 | -0.54(*) | 0.64* |
| NUTMIN | -0.48 | -0.17 | 0.23 | 0.26 | -0.18 | 0.19 | 0.06 |
| NUTORG | -0.40 | -0.32 | -0.17 | 0.13 | 0.29 | 0.57* | -0.21 |

* Correlation is significant at the .05 level (2-tailed).

** Correlation is significant at the .01 level (2-tailed).

Although the first two axes in RDA only explain two-thirds of the variance of the group data, some trends are clearly visible (Figure 11, Table 6). The already noted correlation between deciduous dwarf shrubs and bryophytes is clear. Evergreen frequency in contrast appeared to increase towards low bryophyte layer. Grasses, reindeer droppings and bryophyte layer were interestingly increasing in the same direction. Although bryophyte frequency appears as an important factor in the ecosystem under study, the analysis suggests forb and sedge frequencies to be neutral to bryophyte frequency. Also based on this analysis it seems clear that lichens are (unsurprisingly) different from all the other groups in their requirements for optimum habitat.

Discussion

Raunkiaer life forms

Biological spectra

A reason for the discrepancy between the biological spectrum in this study and that found by Raunkiaer, is that this study only covers 36 vascular plant species of a total species number of 173 vascular plant species in Svalbard (Elvebakk and Prestrud, 1996). Raunkiaer's spectrum

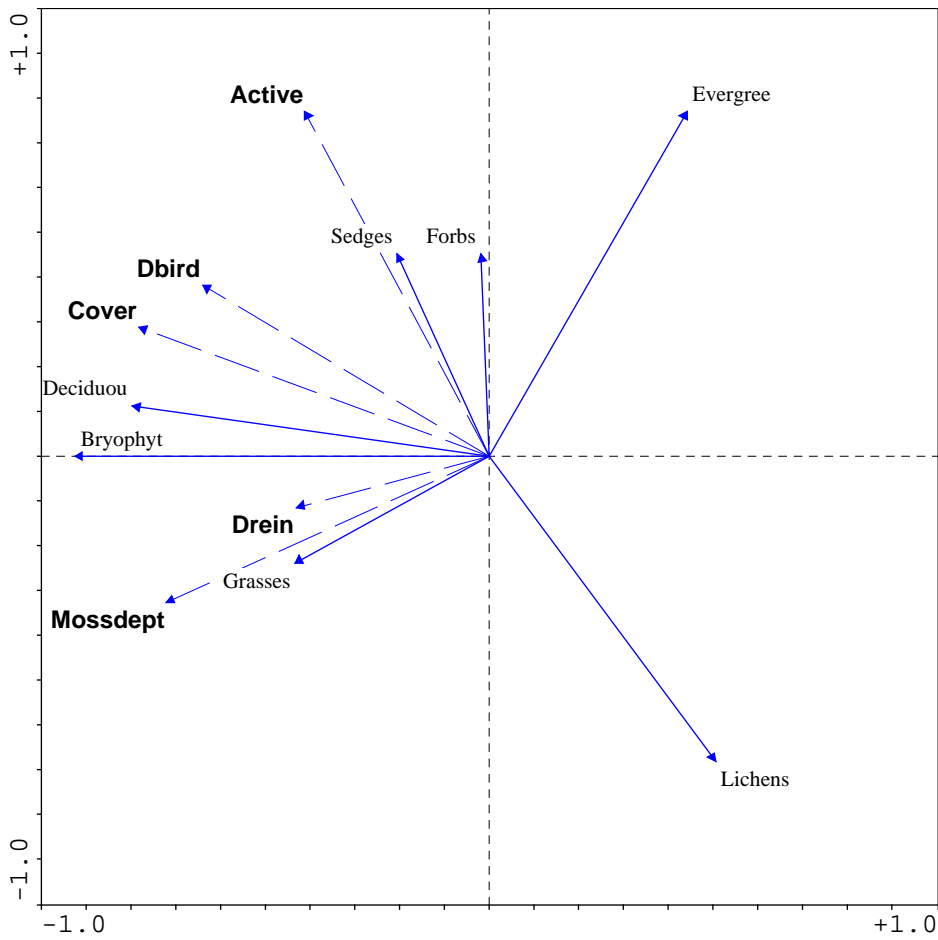


Figure 11. The RDA biplot with the first two axes. Dashed vectors describe environmental variables and solid lines functional groups.

Table 6.

Summary of the Redundancy Analysis (RDA)

| (Canonical) axes | 1 | 2 | 3 | 4 | Total variance |
|----------------------------------|-------|-------|-------|-------|----------------|
| Eigenvalues | 0.578 | 0.091 | 0.055 | 0.006 | |
| Species-environment correlations | 0.921 | 0.776 | 0.76 | 0.593 | |
| Cumulative percentage variance | | | | | |
| of species data | 57.8 | 66.9 | 72.4 | 73 | |
| of species-environment relation | 78.8 | 91.2 | 98.7 | 99.6 | |

was based on 110 species. It is very questionable if the phanerophyte species, *Betula nana*, Raunkiaer monitored should be considered as a phanerophyte at all, since *Betula nana* appears in a very prostrate growth form in Svalbard compared to the growth form it appears in on the main land. The species is very rare in Svalbard and is only observed in the inner parts of Isfjorden (Rønning 1996). The therophytes or annuals are also rare in Svalbard (*Euphrasia frigida*) or confined to specific habitats (*Koenigia islandica*). This explains why phanerophytes and therophytes were not observed in this study.

The discrepancy of the biological spectrum of the Svalbard flora from the normal spectrum of the world flora reflects the regional climate of Svalbard.

Raunkiaer (1934) found that the biological spectrum changes from temperate areas towards the north. The percentage of phanerophytes and therophytes decrease until they finally disappear. The proportion of cryptophytes stays more or less constant but it is absent from the most extreme north, because the High Arctic soil with permafrost does not protect sub-terranean buds. Hemicryptophytes form the biggest group and are roughly twice as frequent throughout the Arctic as they are on a global scale. Finally, chamaephytes increase on approaching higher latitudes: at the 10°C June isotherm the percentage of chamaephytes exceeds the normal spectra (10%), and at the 4,5°C June isotherm the percentage is twice the normal spectra (20%) (Raunkiaer 1934). This results in the Arctic being the region where the chamaephytes are most abundant and Raunkiaer (1934) set the southern limit of the Arctic zone at the 20% chamaephyte biochore. The increasing biological spectrum of chamaephytes approaching north can be explained by the fact that snow protects the buds from cold desiccating winds and mechanical wind injuries acting from above in winter and from injuries due to frost heaving and soil freezing from below. In addition, surviving buds of chamaephytes are protected by dead leaf bases, and are often cushion forming and so protected from harsh climate below and above (Crawley 1997). The leaves absorb solar energy while shading and insulation by the above ground parts result in slow soil temperature rise (Raunkiaer 1934). Because the cushion traps warm air the temperature within a cushion can rise to several degrees above the surrounding air temperature. It also protects the plants from desiccation during summer time (Pielou 1994). These adaptations make the chances of surviving both the harsh summer and winter conditions better. According to Raunkiaer 22% of the species in Svalbard are chamaephytes, which places Svalbard in the Arctic climate zone. The result of this study (18 % chamaephytes) is just below Raunkiaer's limit of the Arctic climate zone. That may be due to the small number of species monitored as mentioned above. The flora of the six sites investigated is not sufficient to represent the total flora of the Svalbard region. We only recorded 21% of the species in Svalbard at sites confined to the west coast of Svalbard and therefore lacked the more harsh localities on the north east coasts. However, compared to the normal spectrum the percentage of chamaephytes was high.

The differences in biological spectra site to site is on a much smaller scale than comparing climate regions of the world and should therefore be done with caution. The total lack of cryptophytes in Prins Karls Forland (PKF) and the weak decreasing trend with falling temperature is in accordance with the Raunkiaer theory that cryptophytes should disappear in the harshest climates. PKF had the lowest temperature index (3.5) of the 6 sites (sub report 2) and a very high degree of oceanicity. That this is not a latitudinal effect can be illustrated by observing the higher cryptophyte spectrum of

Blomstrandhalvøya, which is situated a little north of PKF but has a temperature index of 28 and has a much smaller degree of oceanity due to its placement in Kongsfjorden. We found differences on an even smaller scale between dry and mesic habitats. However, a life-form spectrum based on number of species and not their abundance is not a very ecological approach, and we find it therefore more appropriate to measure differences at this scale by abundances.

Site effects

In Hornsund, Bellsund and PKF hemicryptophyte were the most abundant life form and these sites also had the three lowest temperature indexes (table 2).

In Pyramiden and Blomstrand chamaephytes were the most abundant life forms and these sites also had the highest and the second highest temperature indexes. This trend was not observed when we compared biological spectra. It shows that the biological spectrum does not reveal differences in the dominant species on smaller scales because in these cases the abundance of a life form and not the number of species in a life form seemed to change with temperature. A small number of chamaephyte species appear to dominate in some warmer localities in a region with an otherwise overall cold arctic climate.

Habitat effects

Chamaephytes were found to be the most abundant life form in very dry habitats (significant) and possibly also in dry habitats (not significant). This can be explained by the fact that most chamaephytes are better protected against desiccation, both during summer- and wintertime, than the other life forms (for further explanation see paragraphs above). They are therefore more dominating on dry habitats that are thought to be more exposed with less snow cover (subjective observations on the habitats) than most mesic habitats. This shows another pattern in the distribution of life forms when you look on differences at a smaller scale. There seems to be another distribution than that which is evident when the sites are observed only as a hole. The chamaephyte dominance in the warmer sites that we first revealed may actually be an effect of utilisation of the dry habitats in these sites. This means that when you look at life form distribution within Svalbard, habitat differences due to different micro topography etc. might serve as a more important constraint than latitudinal or site differences.

Hemicryptophytes, on the other hand, were most dominant in mesic habitats, but when we looked at the site effects we also found hemicryptophyte domination in cold sites. An explanation could be that the otherwise less protected hemicryptophytes, adapt to the cold environment by utilising a niche in the ecosystem that is in the relatively well protected mesic habitats.

The cryptophytes were more abundant in mesic habitats compared to dry and very dry habitats. If our assumption that mesic habitats are the less exposed habitats with the highest snow cover, then mesic habitats offer a more favourable environment for the cryptophytes which are less protected from freezing injuries due to frost heavings in the soil than the other life forms. This fits very well with the positive correlation of cryptophyte abundance with active layer. In a site with a deep active layer the buds have better shelter than in habitats with shallow soils and where the permafrost layer is very close to the surface during summer.

Since life forms are based on the way species are protected against harsh conditions, better measurements of the actually winter/spring conditions would be of great value to this kind of study. Actually, measurements of snow depth or estimations drawn from careful small scale topographic investigation and meteorological data such as wind directions, wind speed and precipitation, could be useful in supporting the conclusions drawn from this study.

Grazing

The indirect method used for estimating the grazing effect makes it difficult to elucidate whether we are dealing with a fertilisation or a herbivorous effect. The hemicryptophytes, which represent the major group of grazing-tolerant graminoids, were positively correlated to the number of summer reindeer droppings (in dry habitats), but so were also the cryptophytes (in mesic habitats). It seems that in these cases the net effect of the reindeer grazing is positive in the sense of abundance. These life forms may be better protected from the grazing due to low placed buds and meristems and the fertilisation effect may overcome the deleterious effects. The positive correlation of cryptophytes to winter reindeer droppings may support that hypothesis that we are dealing with a fertilising effect in this case. In the case of Chamaephytes, which on one hand showed a negative correlation to summer reindeer droppings, the deleterious effect may be dominating. On the other hand the negative correlation of cryptophytes to bird droppings shows the complexity of this issue, but this may be explained by the grubbing behaviour by e.g. geese.

Functional groups

The nature of this study was first of all explorative and it was not designed to answer any *specific* questions concerning the interactions between different functional groups or interactions between plants and environmental variables affecting their frequency. However, based on our results, some general patterns and trends are clearly visible. As expected, the lichen frequency was at its highest in drier habitats, but all vascular plants and bryophytes clearly increased towards mesic habitats and no group preferred dry habitats to mesic. The soil humidity or moisture was one of the most important single factors acting on functional group frequencies and composition (Figures 7-10). The lack or excess of water apparently controls the abundance of the three large functional groups, especially the abundance of bryophytes.

The decrease of lichens towards mesic habitats is possibly a result of two factors: first, the photosynthesis of green algae in lichens declines gradually when the water content of the thallus increases above 150% of its dry weight. (Nash III, 1996), and secondly, the slow-growing *Ochrolechia*-type lichens dominating in dry barren soil find less room in mesic habitats already dominated by faster-growing bryophytes.

Although the method of approximating the nutrient status of the soil was indisputably elementary, its low importance was an interesting result, added to the fact that there were no significant differences in the status between the dry and mesic habitats (results not shown).

The occurrence of deciduous dwarf shrubs, or *Salix polaris* as the solitary member of this group, is clearly intertwined with bryophyte abundance. Its large ligneous parts below surface perhaps benefit from the shelter provided by bryophytes.

The overall scarce abundance of vascular plants at the study sites makes evaluation of diversity in terms functional groups. Especially in very dry and dry habitats the variation in the frequencies is high and statistical differences between sub-groups are hard to prove. A more thorough study on functional groups demands for an approach where large areas could be surveyed fast but effectively, while taking into account the importance of small-scale topographical variation not covered in this study.

Conclusion

We found a biological spectrum of the Svalbard flora close to that found by Raunkiaer and close to what would be expected in the Arctic, given the limitations in time and space of this project. This study showed that the utilisation of the abundance of a specific life form was a better tool than biological spectra to reveal small scale ecological differences such as differences in environmental variables and topography within and between sites. Chamaephytes were the most abundant life form in the most exposed very dry habitats at warmer sites and hemicryptophytes were the most abundant life form in the less exposed mesic habitats, especially at colder sites. Cryptophytes were the least abundant life form in all habitats but were most abundant in mesic habitats.

The vascular plant functional groups described here have clear responses to environmental factors when studied on a large scale (Chapin et al. 1996) In this study we were only able to reveal some small trends and possible responses. The general moisture preferences of evergreen dwarf shrubs, sedges, bryophytes and lichens were in accord with the hypothesis, but actually only lichens preferred dry habitats to mesic. Our results did not support the expectations concerning preferences for different nutrient status. A functional type and a particular growth form are in essence an outcome of all the possible factors affecting an individual. This might explain the weak responses seen when relating groups to one environmental variable. This should be contrasted to Raunkiaer's classification, which mainly reflects adaptations to survive the climatically adverse periods.

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Appendix 1 Grouping of vascular plants into life-forms and functional types.

| | Functional type | Life form |
|--|------------------------|------------------|
| <i>Cassiope tetragona</i> | Evergreen dwarf shrubs | Chaemaephytes |
| <i>Cerastium alpinum</i> | Forbs | Chaemaephytes |
| <i>Cerastium nigrescens ssp arcticum</i> | Forbs | Chaemaephytes |
| <i>Dryas octopetala</i> | Evergreen dwarf shrubs | Chaemaephytes |
| <i>Saxifraga oppositifolia</i> | <i>Forbs</i> | Chaemaephytes |
| <i>Silene acaulis</i> | Forbs | Chaemaephytes |
| <i>Bistorta vivipara</i> | Forbs | Cryptophytes |
| <i>Equisetum arvense ssp. boreale</i> | Forbs | Cryptophytes |
| <i>Equisetum scirpoides</i> | Forbs | Cryptophytes |
| <i>Equisetum variegatum</i> | Forbs | Cryptophytes |
| <i>Salix polaris</i> | Deciduous dwarf shrubs | Hemicryptophytes |
| <i>Alopecurus borealis</i> | Grass | Hemicryptophytes |
| <i>Carex fuliginosa misandra</i> | Sedges | Hemicryptophytes |
| <i>Carex maritima</i> | Sedges | Hemicryptophytes |
| <i>Carex nardina</i> | Sedges | Hemicryptophytes |
| <i>Carex rupestris</i> | Sedges | Hemicryptophytes |
| <i>Cochlearia groenlandica</i> | Forbs | Hemicryptophytes |
| <i>Draba corymbosa</i> | Forbs | Hemicryptophytes |
| <i>Draba daurica</i> | Forbs | Hemicryptophytes |
| <i>Festuca baffinensis</i> | Grass | Hemicryptophytes |
| <i>Festuca rubra ssp arctica</i> | Grass | Hemicryptophytes |
| <i>Luzula arctica</i> | Sedges | Hemicryptophytes |
| <i>Luzula arcuata ssp confusa</i> | Sedges | Hemicryptophytes |
| <i>Luzula congesta</i> | Sedges | Hemicryptophytes |
| <i>Oxyria digyna</i> | Forbs | Hemicryptophytes |
| <i>Pedicularis hirsuta</i> | Forbs | Hemicryptophytes |
| <i>Phippsia algida</i> | Grass | Hemicryptophytes |
| <i>Poa arctica</i> | Grass | Hemicryptophytes |
| <i>Poa species</i> | Grass | Hemicryptophytes |
| <i>Saxifraga cespitosa</i> | Forbs | Hemicryptophytes |
| <i>Saxifraga hirculus</i> | Forbs | Hemicryptophytes |
| <i>Saxifraga hyperborea</i> | Forbs | Hemicryptophytes |
| <i>Stellaria longipes</i> | Forbs | Hemicryptophytes |
| <i>Silene uralensis ssp arctica</i> | Forbs | Hemicryptophytes |

Appendix 3 Groupings of cryptogam species: lichens

| Species name | Functional type | Sub groups |
|-------------------------------|------------------------|-------------------|
| <i>Lopadium species</i> | Lichen | Crustose |
| <i>Ochrolechia frigida</i> | Lichen | Crustose |
| <i>Ochrolechia species</i> | Lichen | Crustose |
| <i>Rinodina species</i> | Lichen | Crustose |
| <i>Brodoa oroarctica</i> | Lichen | Fruticose |
| <i>Cetraria ericetorum</i> | Lichen | Fruticose |
| <i>Cetraria islandica</i> | Lichen | Fruticose |
| <i>Flavocetraria nivalis</i> | Lichen | Fruticose |
| <i>Cetraria species</i> | Lichen | Fruticose |
| <i>Cetrariella delisei</i> | Lichen | Fruticose |
| <i>Cetrariella species</i> | Lichen | Fruticose |
| <i>Cladonia arbuscula</i> | Lichen | Fruticose |
| <i>Cladonia crispata</i> | Lichen | Fruticose |
| <i>Cladonia gracilis</i> | Lichen | Fruticose |
| <i>Cladonia macrophylla</i> | Lichen | Fruticose |
| <i>Cladonia pocillum</i> | Lichen | Fruticose |
| <i>Cladonia species</i> | Lichen | Fruticose |
| <i>Cladonia uncialis</i> | Lichen | Fruticose |
| <i>Collema ceraniscum</i> | Lichen | Fruticose |
| <i>Lecidea species</i> | Lichen | Fruticose |
| <i>Parmelia species</i> | Lichen | Fruticose |
| <i>Sphaerophorus fragilis</i> | Lichen | Fruticose |
| <i>Sphaerophorus globosus</i> | Lichen | Fruticose |
| <i>Sphaerophorus species</i> | Lichen | Fruticose |
| <i>Stereocaulon alpinum</i> | Lichen | Fruticose |
| <i>Stereocaulon species</i> | Lichen | Fruticose |
| <i>Thamnolia vermicularis</i> | Lichen | Fruticose |
| <i>Peltigera canina</i> | Lichen | Foliose |
| <i>Physconia muscigena</i> | Lichen | Foliose |
| <i>Physconia species</i> | Lichen | Foliose |

Appendix 2 Groupings of cryptogam species: bryophytes

| Species name | Functional type |
|------------------------------------|------------------------|
| <i>Andreaea species</i> | Bryophyte |
| <i>Aneura pinguis</i> | Bryophyte |
| <i>Aulacomnium palustre</i> | Bryophyte |
| <i>Aulacomnium turgidum</i> | Bryophyte |
| <i>Barbilophozia species</i> | Bryophyte |
| <i>Barbula species</i> | Bryophyte |
| <i>Blepharostoma species</i> | Bryophyte |
| <i>Bryum argenteum</i> | Bryophyte |
| <i>Bryum species</i> | Bryophyte |
| <i>Campylium stellatum</i> | Bryophyte |
| <i>Catoscopium nigratum</i> | Bryophyte |
| <i>Cinclidium stygium</i> | Bryophyte |
| <i>Cyrtomnium hymenophylloides</i> | Bryophyte |
| <i>Dicranum scoparium</i> | Bryophyte |
| <i>Dicranum species</i> | Bryophyte |
| <i>Distichium capillaceum</i> | Bryophyte |
| <i>Distichium inclinatum</i> | Bryophyte |
| <i>Ditrichum flexicaule</i> | Bryophyte |
| <i>Ditrichum species</i> | Bryophyte |
| <i>Encalypta alpina</i> | Bryophyte |
| <i>Encalypta rhaptocarpa</i> | Bryophyte |
| <i>Ephebe species</i> | Bryophyte |
| <i>Hylocomium species</i> | Bryophyte |
| <i>Hylocomium splendens</i> | Bryophyte |
| <i>Meesia uliginosa</i> | Bryophyte |
| <i>Oncophorus wahlenbergii</i> | Bryophyte |
| <i>Orthothecium chryseon</i> | Bryophyte |
| <i>Pleurozium schreberi</i> | Bryophyte |
| <i>Pohlia species</i> | Bryophyte |
| <i>Polytrichastrum alpinum</i> | Bryophyte |
| <i>Polytrichum hyperboreum</i> | Bryophyte |
| <i>Ptilidium ciliare</i> | Bryophyte |
| <i>Racomitrium lanuginosum</i> | Bryophyte |
| <i>Racomitrium microcarpon</i> | Bryophyte |
| <i>Sanionia species</i> | Bryophyte |
| <i>Sanionia uncinata</i> | Bryophyte |
| <i>Schistidium apocarpum</i> | Bryophyte |
| <i>Scorpidium cossonii</i> | Bryophyte |
| <i>Timmia austriaca</i> | Bryophyte |
| <i>Tomentypnum nitens</i> | Bryophyte |
| <i>Tortella species</i> | Bryophyte |
| <i>Syntrichia ruralis</i> | Bryophyte |

