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Exploring plant-ecological patterns at different spatial scales on Svalbard – introduction and summary

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Introduction

The terrestrial Arctic is often treated as a uniform biome of low biological diversity. It is true that species richness as well as the diversity of functional groups declines with increasing latitude within most organism groups (Matveyeva and Chernov 2000). However, trends in other less studied aspects of biological diversity, such as genetic diversity within species, might well turn out to be comparable to other biomes (Callaghan et al. 2004, The ACIA report 2005), at least on certain spatial scales. When exploring patterns of diversity at different levels of biological organisation it is important to consider how they vary at different scales in time and space in relation to variability of the environmental factors that affect diversity. Typical for the Arctic is the overriding role of abiotic factors in shaping the environment experienced by the organisms in most habitats, and the large topographic impact on theses factors, thereby creating large environmental heterogeneity at various spatial scales (Jónsdóttir 2005).

The Svalbard Archipelago is situated in the High Arctic, extending across the three coldest bioclimatic sub-zones (termed zones hereafter) of the Arctic, termed A, B, and C (Elvebakk 1997, CAVM Team 2003). Due to its dramatic topography, large environmental contrasts are encountered across relatively short distances, which provide an ideal situation for demonstrating and studying terrestrial ecology in a variety of arctic settings. During the summer 2005, the University Centre in Svalbard (UNIS) organised a post-graduate course in arctic plant ecology (AB-326) where the students explored spatial heterogeneity of four different plant-ecological patterns in relation to environmental variables: (1) vegetation differentiation, (2) species richness, (3) reproduction, and (4) plant tissue chemical composition of common vascular plant species. A separate scientific report was written on each of these four themes (for practical reasons there are two separate reports on reproduction) and the main findings will be summarised and discussed below. The unifying question for the project themes was whether these patterns were under stronger control of local environmental factors than of large or intermediate scale (regional) factors such as climate and bedrock. Large-scale temporal pattern, i.e. vegetation history, was also addressed in a literature survey by one of the students.

Materials and methods

Twelve students of nine different nationalities, studying at nine different universities, participated in the course. The students worked in four project groups each focusing on one of the patterns identified above after. During a seven-day cruise with MS Stockholm we visited and collected data from eight different localities in the western and northern regions of the Svalbard Archipelago, including both Spitsbergen and Nordaustlandet, thus covering all three bioclimatic zones represented on Svalbard. The localities and the study sites within each locality were chosen to reflect a wide range of climatic and edaphic conditions as well as grazing intensities by vertebrate herbivores (geese, reindeer). At each locality, two sampling sites were identified, each situated in one of two contrasting habitat types: an exposed ridge habitat and a zonal habitat which was a mesic habitat assumed to represent average bioclimatic conditions for the zone it belonged to. The size and shape of the areas sampled depended on the extent of the identified habitat.

Within the identified area of each habitat seven 50x50 cm plots were randomly chosen. Each plot was photographed using a camera with sensors for green, red and far-infrared light, which enabled calculations of NDVI. In each plot, plant community composition was quantified by the point intercept method (point framing). At 25 evenly spaced points all vertical plant hits were recorded down to the cryptogam layer (only one hit) or the bare ground if not vegetated. After that, the plot was inspected and all additional plant species present were recorded. In total, 112 plots were investigated, 14 in the Arctic Polar Desert Zone (A), 56 in the Northern Arctic tundra Zone (B) and 42 the Middle Arctic tundra Zone (C).

To reveal how sexual reproductive effort and success is affected at different spatial scales we focused specifically on the widespread *Saxifraga oppositifolia* and collected 4 flowers from each of two individuals within or close to each plot. The flowers were brought to the lab and the number of fertilised and apparently unfertilised ovules was counted (in the lab). In addition, variation in reproductive strategies and ploidy levels among all vascular plant species recorded in the plots was analysed based on literature information, primarily from Brochmann and Steen (1999).

At last, the plots were destructively harvested for the aboveground biomass of the dominating vascular plant species for chemical analyses in the lab. A range of environmental parameters were estimated in the plots, such as soil temperature, soil moisture (both in the field and in the lab), soil pH (in the lab), total vegetation cover, aspect and slope. In addition, grazing intensities by various herbivore groups were estimated for the area by counting their droppings along two 20 m transects. All students collaborated on collecting data and samples in the field and on analysing samples in the laboratory. Each project group then analysed the data appropriate to address their specific questions. More detailed method descriptions are given in the individual project reports.

Result summary and discussion

The observed and measured characteristics of the different study sites are summarised in Table 1.

We recorded a total of 214 species of vascular plants, bryophytes and lichens within the analysed vegetation plots. In accordance with the general species richness pattern on Svalbard (Elvebakk 1996), cryptogams dominated the species pool with 86 lichens and 71 bryophytes, while vascular plant species counted only 53. The species richness group (Marteinsdóttir and Arnesen) showed that both large-scale species richness (i.e. gamma diversity *sensu* Whittaker 1972) and small scale species richness (alpha-diversity) decreased continuously from bioclimatic zone A to C, while mean species richness for all species did not differ between the two habitats as we expected. Interesting patterns emerged, however, when analysing the different species groups separately: the richness of both vascular plants and bryophytes was greater in zonal habitats than on ridges, while the opposite was true for the lichens. The general hump-shaped relationship between species richness and productivity as described for vascular plants in many other ecosystems apparently does not exist on Svalbard (Waide et al. 1999, Mittelbach et al. 2001), at least not when using NDVI as a productivity measurement. These results confirmed what has been found in other high arctic areas (see overview in Waider et al. 1999), i.e. that vascular plant species richness is positively related to productivity. The species richness group had the unique opportunity to explore the richness-productivity relationship for other plant groups than vascular plants as well: no relationship emerged when all species groups were combined, bryophytes showed no particular pattern, while lichen species richness alone showed a humped-shaped relationship with productivity. When restricting the range of productivity by considering the two different habitats separately, a significant positive relationship between species richness and plant productivity emerged for all species combined in the less productive ridge habitats as well as separately for bryophytes and lichens, while no relationships were apparent in the more productive zonal habitats. We believe that these results reflect the differences in functionality among the three groups.

Plant species differ in their life histories, and such differences are expected to have a strong impact on spatial and temporal plant dynamics. Thus, a more detailed functional classification of species than used in the species richness analysis might be an important tool for understanding plant community structure and dynamics. Reproductive strategy is a crucial part of plant life history with functional implications because theory on geographic parthenogenesis (distribution of asexually reproducing organisms) suggests that asexual and sexual species do not occupy the same niches. Patterns of modes of reproduction in plants have been studied on both global and local scales; however, little work has been done on the intermediate-landscape level scale. In her report on reproduction strategies of vascular plants on Svalbard, Terra Birkigt demonstrated that there is no apparent differentiation in modes of reproduction or ploidy levels (often linked to asexuality) among habitats or bioclimatic zones, which contradicted what she expected (i.e. higher proportion of asexual species and higher ploidy levels in locations with shorter growing seasons and cooler temperatures and more sexuals and lower ploidy levels in milder locations). However, when all localities were combined the percentage of selfers was higher than the global average, indicating that plants on Svalbard tend to inbreed more than plants globally.

Even though no obvious patterns were detected in terms of mode of reproduction in Svalbard, plants relying on sexual reproduction, disregarding whether they are selfers or outcrossers, may show differences in reproductive effort and pollination success in response to environmental factors operating at various spatial scales. Accordingly, the other members of the reproduction group (Pietiläinen and Nyakatya) reported on significant differences between localities across the different bioclimatic zones in both reproductive effort and success in the widespread *Saxifraga oppositifolia*, while variation on a local scale (between habitats) was less pronounced. This species shows large variation in growth form and, interestingly, the trailing growth form which is confined to mesic habitats (including zonal) had significantly larger reproductive effort in terms of number of ovules per fruit than the compact form, the other main growth form, which is more common on ridges.

Present day arctic and alpine plant community composition often varies greatly over small scales, and especially along slopes spanning the topography/snow-cover gradient from a ridge via zonal habitats to snow beds. In addition, macroclimatic variation affects plant species pools and thus determines which species are available in the different bioclimatic zones (Elvebakk 1997). Several important abiotic and biotic variables such as soil moisture, nutrient levels (e.g. nitrogen) and herbivory (cf. Mulder 1999) are expected to be related to both micro- and macroclimatic gradients, while pH is independent of climate. By using ordination techniques the vegetation differentiation group (Speed, Møller and Sokol) demonstrated that the largest variation in plant community composition was found on a small scale, i.e. between individual plots within habitat. The measured and estimated environmental factors included in the analysis explained small proportion of the total variation (ca. 3 %). Partitioning that variation among the factors showed that soil pH was the most important factor (36%), while microclimate and large-scale differences in bioclimatic zones came second (28 and 29% of the explained variation, respectively).

In accordance with factors affecting vegetation differentiation, the pattern of chemical composition of plant tissue can be affected by various factors operating on different spatial or temporal scales including feedbacks through interactions with other trophic levels. At the global scale, C/N levels in plant tissue decrease towards higher latitudes and altitudes (Hedin 2004, McGroddy et al. 2004) but level out or increase from mid to high latitudes (Reich & Oleksyn 2004). However, there is a general lack of studies that assess plant N and C along natural climate gradients within the Arctic. The chemical composition group (Beck, Elverland and Støvern) examined how carbon and nitrogen levels in leaf tissue of four common vascular plant species were related to microclimate (bioclimatic zone), local environment (zonal vs. ridge habitat) and herbivory. Contrary to what was predicted, the C and N levels were not related to macroclimate. On a local scale, however, C/N ratios were lower in leaves from zonal habitats than ridge habitats mainly due to higher N levels. These results were interpreted such that within the Arctic, small-scale differences in plant conditions are more important for plant chemical composition than large scale climate differences. As pointed out in the report, phenological difference may also be responsible for the habitat difference: N content is known to reach maximum levels just after snowmelt, and then decrease during the season (e.g. van der Wal et al. 2000). Reindeer grazing intensity, measured as dropping density, was not correlated to low C/N relationships as predicted, while goose grazing correlated with low C/N levels. However, it was impossible to draw any conclusions about the causality of these relationships based on the data.

The history of the Svalbard vegetation is poorly known, but the published paleoecological records, as reviewed by Teija Pesiö, indicate that vegetation cover was more extensive at the "climatic optimum" during Holocene when climate was both warmer and moister than today. This makes it tempting to believe that the occurrence of present-day thermophilous plant species may be a relict from warmer periods rather than recent establishments in response to climate warming. Unfortunately, the poor resolution of the paleo-records does not allow any comparisons between past and present plant community differentiation, species richness or modes of reproduction among plant species.

Conclusions

Taken together, the message that emerges from the course projects is that the different ecological patterns studied here are not all influenced by the factors operating at the same spatial scale within the arctic biome:

1. Patterns in vegetation differentiation and plant chemical composition are influenced more strongly by local environmental factors (operating within a locality: soil pH, microclimate) than by environmental factors acting on an intermediate regional scale.
2. Species richness as well as reproduction effort and fertilisation success within a single species (*S. oppositifolia*) appear to be strongly influenced by factors operating on an intermediate, regional scale (differences between localities or bioclimatic zones).
3. Variation in mode of reproduction among vascular plant species is apparently influenced by factors operating on large, geographic scale such as climate.
4. The available paleo-records suggest that climate also strongly influences the overall vegetation cover.

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Table 1. Study sites visited during the AB-326 excursion with UNIS year 2005. Sites are Bohemiaflya (BOH), Magdalenafjorden northe side (MAG-N) and Magdalenafjorden south side (MAG-S), Forkdalen (FOR), Kinnvika (KIN), Florabukta (FLO), Biskayerhuken (BIS), Engelskbukta (ENG), and Colesdalen (COL). Habitats include both a mesic zonal habitat (Z) and a dry ridge habitat (R). Locations are given by latitudes (N) and longitudes (E) in degrees, minutes and seconds. Bioclimatic zones (A-C) are according to Elvebakk (1997). Herbivory is given as total number of droppings from goose (Gd), winter reindeer (WRd) and summer reindeer (SRd). Soil moisture, Soil pH, Soil temp., Aspect, Slope, Vegetation cover, Moss depth are given as mean values at the plot scale. N = 7 for sampled environmetal variables except for + (n = 6), ++ (n = 5), +++ (n = 4) and †(n = 3). See text for further descriptions of both field and lab-based methods used to quantify environmental parameters.

Site	Habitat	Location	Biolimatic zone	Grazing (# droppings)	Soil pH	Soil moisture (%)	Soil temp. (°C)	Aspect (°)	Slope (°)	Veg. cover (%)	Moss height (cm)	Bedrock
BOH	Z	78,24,22.6(N) 14,41,25.7(E)	C	27 Gd, 4 SRd	6.34	30.5	6.7	25.6++	2.3	56.4	0.97+	Mesozoic sandstone, with marine deposits
BOH	R	78,24,22.6(N) 14,41,25.7(E)	C	No droppings	6.49	4.7	8.6	86+	2.4	7.9	0.03+	Mesozoic sandstone
MAG-N	Z	79,5,36,16(N) 12,04,58(E)	B	61 Gd, 58 WRd, 18 SRd	5.18+	18.8	7.2	110	9.1	87.3	2.3	Precambrian gneiss
MAG-S	Z	79,33,25(N) 11,01,07(E)	B	165 Gd, 2 SRd	4.97	20.1	6.6	230	13.6	71.9	2.5	Precambrian gneiss
MAG-S	R	79,33,25(N) 11,01,07(E)	B	55 Gd, 5 WRd, 2 SRd	4.55+++	17.4	6.6	219	7.9	58	1.9	Precambrian gneiss
FOR	Z	79,31,53.3(N) 15,12,19.4(E)	B	26 Gd, 18 WRd, 8 SRd	6.12++	32.1	3.7	130	10.4	73.3+	2.19	Devonian sandstone and shale
FOR	R	79,13,49.8(N) 15,12,33.3(E)	B	26 Gd, 49 WRd, 21 SRd	6.3+	15.5	4.5	134	5.1	28.6	0.9	Devonian sandstone and shale
KIN	Z	80,03,15.9(N) 18,15,06.4(E)	A	7 WRd	7.78+	9.2+	4.0	141+	3.1	11	0	Precambrian carbonate rocks with stromatolites
KIN	R	80,03,15.2(N) 18,15,10.5(E)	A	1 WRd	7.75+++	5.1+	3.0	196+	9.1	0.8	0.04	Precambrian carbonate rocks with stromatolites
FLO	R	80,01,48.5(N) 18,41,33.7(E)	A/B	4 SRd	7.32++	6.5+	4.9	92.6++	2.9	2.7	0.57	Precambrian carbonate rocks with stromatolites

Site	Habitat	Location	Biolimatic zone	Grazing (# droppings)	Soil pH	Soil moisture (%)	Soil temp. (°C)	Aspect (°)	Slope (°)	Veg. cover (%)	Moss height (cm)	Bedrock
BIS	Z	79,50,02.3(N) 12,23,00.8(E)	B	81 Gd, 21 WRd, 3 SRd	5.84++	16.5	8.9	232	7.7	31.7		Precambrian phyllite, with transported marine deposits
BIS	R	79,50,18.9(N) 12,23,30.1(E)	B	16 Gd, 34 WRd, 8 SRd	6.17+	13.2	10.1	209	8.4	23.1	0.88+	Precambrian phyllite, but varied on a small scale
ENG	Z	78,51,16.8(N) 11,43,36.7(E)	B/C	12 Gd, 52 WRd, 28 SRd	7.28+	24.8	9.6	188+	9.3+	55+	1.06†	Precambrian metamorphosed dolomite rocks with phyllites and quartzites
ENG	R	78,51,16.0(N) 11,43,42.0(E)	B/C	1 Gd, 43 WRd, 13 SRd	7.26	17.8	9.5	194	7.4	41.9	0.93+++	Precambrian metamorphosed dolomite rocks with phyllites and quartzites
COL	Z	78,06,37.5(N) 15,03,43.9(E)	C	223 Gd, 21 WRd, 39 SRd	6.24++	30.6	7.0	207	3.9	99.6	4.83	Tertiary sandstone and shale
COL	R	78,06,36.2(N) 15,03,05.8(E)	C	5 Gd, 39 WRd, 18 SRd	5.9+	6.43	9.3	176+	5.3	37	1.65+	Tertiary sandstone and shale

Species richness of vascular plants and cryptogams in the High Arctic: no universal pattern observed in relation to primary productivity

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Abstract

The present study examined the relationship between species richness of vascular plants, bryophytes and lichens and plant productivity in the High Arctic Archipelago of Svalbard. Species richness were recorded in ridge- and zonal habitats in the three northernmost subzones of the Arctic bioclimatic zone. Primary productivity was estimated by using a digital camera with sensors for green, red, and near infrared radiation and calculation of the Normalized Difference Vegetation Index (NDVI) from the pictures. The total species richness increased towards warmer bioclimatic zones, and cryptogams made up more than two thirds of the species richness. No difference in total species richness between zonal and ridge habitats was observed. However, there were significantly higher species richness of lichens at ridges, and of bryophytes and vascular plants at zonal sites. A significant overall relationship between species richness on ridge- and zonal sites and primary productivity (NDVI) were observed for vascular plants (linear) and for lichens (unimodal/hump-shaped). No relationship was found for all species groups together. On ridges, a significant linear relationship was found for overall species richness, bryophytes, and lichens respectively. No significant relationship between species richness and primary productivity was observed in zonal habitats. The results indicate that the hump-shaped relationship between plant species richness and primary productivity does not apply to the high Arctic, and emphasize the importance of including cryptogams in ecological studies in the Arctic.

Keywords

Species richness; primary productivity; alpha diversity; High Arctic; NDVI;

Introduction

The increased focus in the last decade on loss of biodiversity due to anthropogenic impact has lead to an explosion of surveys investigating the relationship between plant species richness and primary productivity in various ecosystems. Different theories and factors like competition and facilitation have been suggested to explain the observed patterns (reviewed in Waide et al. 1999). In nature no universal pattern seems to exist, some are though more common than others (e.g. Waide et al. 1999; Mittelbach et al. 2001; Mouquet et al. 2002). For vascular plants, the hump-back relationship proposed by Grime (1973) seems to be the most frequently observed. This basic model suggests that diversity decreases when primary productivity increases beyond a certain level. This decrease in diversity has been explained by the increased interspecific competition. Linear relationship is also reported from some studies (reviewed in Waide et al. 1999; Mittelbach et al. 2001). The relationship seems to be scale dependent (e.g. Gross et al. 2000; Chase & Leibold 2002). On a local to regional scale, hump-shaped relationship is most often seen (or no relationship) but on a continental to global scale the positive linear relationship is equally or more common (Waide et al. 1999; Mittelbach et al. 2001). Most studies treating plant diversity-productivity relationships include only vascular plants when estimating the plant species diversity (Mittelbach et al. 2001). Very few take into account lichens and bryophytes (but see Bültmann and Daniels 2001), which contribute to substantially to the biodiversity in the Arctic (Murray 1992)

Although the relationship between species richness and primary productivity has been studied extensively, only a few studies on this topic have treated High Arctic ecosystems (Waide et al. 1999). Those studies show either a positive linear relationship between species richness and annual net primary productivity or no clear relationship (Waide et al. 1999; Gough et al. 2000). The Arctic is a harsh environment and the local and regional species pools of plants are limited by extreme temperature, short growing season, low nutrient availability, wind exposure, and frost disturbance (Walker 1995; Waide et al. 1999). Only about 0,4% (1500 species) of the known vascular plants of the earth are found in the Arctic (Billings 1992). The arctic cryptogam flora contains about 750 bryophytes and 1200 lichen (Murray 1992) which means that vascular plants accounts for only about 40% of the vascular-lichen-bryophyte flora. It is then not surprising that cryptogams and lichens in particular have been shown to play an important functional role in most arctic communities (Longton 1997; Matveyeva & Chernov 2000).

There is a need for more thorough investigations of the diversity of plant communities, where both cryptogams and vascular plants are taken into account and their relations to primary productivity both in High- and Low Arctic areas. Hence the aim of the present study from high arctic Svalbard is to contribute to the knowledge of relationship between biodiversity of plants and primary productivity by including cryptogams. The vascular flora of Svalbard consists of 173 species (Elven & Elvebakk 1996) compared to 373 bryophytes (Frisvoll & Elvebakk 1996) and more than 700 lichens species (A. Elvebakk, pers. comm). Svalbard reaches through the three northernmost bioclimatic subzones of the Arctic (Elvebakk 2005), i.e. from the middle arctic tundra subzone, through the northern arctic tundra subzone to the coldest arctic polar desert subzone (referred to as zones here). In all zones we investigated primary productivity and species richness of vascular plants, bryophytes, and lichens on ridges, which are low productivity habitats, and zonal habitats, which are among the more productive habitats of the Arctic tundra. Estimates of primary productivity were obtained using a handheld multi spectral camera, and calculation of Normalized Difference Vegetation Index (NDVI) from the pictures.

This study addresses how patterns in plant species richness are distributed between zonal and ridge habitats. We hypothesize higher species richness in zonal habitats than on ridges. Stress from harsh climate has been pointed out to bee one of the key factors in determining species richness in the Arctic, and such stress should be more prominent at ridges than at zonal habitats (Walker 1995, Elvebakk 1999). We also ask which patterns can be seen between species richness and primary productivity. We hypothesize a linear positive overall relationship, as facilitation has been proved to be a more prominent factor than competition in the high Arctic (Klanderud & Totland 2004). We also expect different species richness-productivity patterns for vascular plants, bryophytes, and lichens.

Methods

Study sites

Eight localities on the western and northern part of Svalbard were studied during the period 20-26 July 2005 (Fig. 1). The localities were chosen to accomplish a rich diversity in bedrock type, pH, and bioclimatic zones. On most of the localities one ridge and one zonal habitat were chosen as study sites. Our definition of ridge- and zonal habitats is in accordance with Elvebakk (1999), where a ridge is considered as a positive landform strongly exposed to wind and desiccation, and a zonal habitat is intermediate with respect to abiotic ecological factors. In Florabukta, only ridge vegetation was studied, and in Magdalenafjorden one extra zonal site on the north coast of the fiord was analysed additionally to the ridge and zonal sites on the south coast. An overview of the site and habitat conditions is shown in table 1.

Table 1. Geographic coordinate, bioclimatic zone, bedrock type, and habitat for the study sites. Bioclimatic zones according to Elvebakk (2005).

Study site (North,East)	Habitat	Bioclimatic zone	Bedrock
Bohemanflya (78°24'22.6'',14°,41'25.7'')	Zonal	C	Marine deposit
Bohemanflya (No data)	Ridge	C	Erroded sandstone
Magdalenafjorden North coast (79°05'36.16'',12°04'58.0'')	Zonal	B	Gneiss
Magdalenafjorden South coast(79°33'25.0'',11°01'07.0'')	Zonal	B	Gneiss
Magdalenafjorden South coast (No data)	Ridge	B	Gneiss
Forkdalen (79°31'53.3'',15°12'19.4'')	Zonal	C	Sandstone and shale
Forkdalen (79°31'49.8'',15°12'33.3'')	Ridge	C	Sandstone and shale
Kinnvika (80°03'15.9'',18°15'06.4'')	Zonal	A	Marble/dolomite
Kinnvika (80°03'15.2'',18°15'10.5'')	Ridge	A	Marble/dolomite
Florabukta (80°01'48.5'',18°41'33.7'')	Ridge	A	No data
Biskayerhuken (79°50'02.3'',12°23'00.8'')	Zonal	B	Phyllite with eolic marine deposits
Biskayerhuken (79°50'18.9'',12°23'30.1'')	Ridge	B	Phyllite
Engelsbukta (78°51'16.8'',11°43'36.7'')	Zonal	B/C	Alkaline soil
Engelsbukta (78°51'16.0'',11°43'42.0'')	Ridge	B/C	Alkaline soil
Colesdalen (78°06'37.5'',15°02'43.9'')	Zonal	C	Tertiary sandstone and shale
Colesdalen (78°06'36.2'',15°03'05.8'')	Ridge	C	Tertiary sandstone and shale

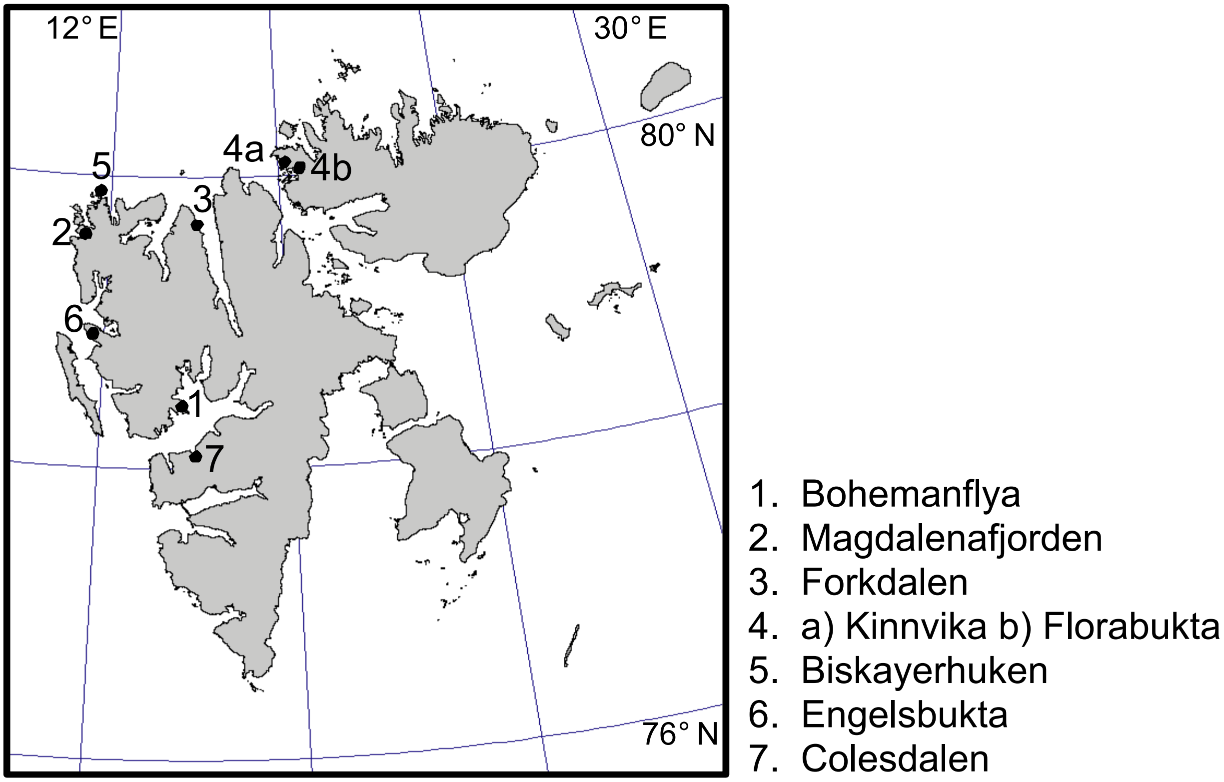

Figure 1. Map of Svalbard. The eight visited localities are marked with numbers.

Species data

Species diversity considers both species richness and the abundance of individual species. Such data can be obtained using various field methods, for example cover estimates, density or biomass. Indices based on species richness and abundance (i.e. the Shannon Wiener index) can then be calculated (Guo & Rundel 1997). Since bryophytes and lichens are difficult to assess with respect to abundance, we chose to consider species richness only, which also is a widely used estimate for diversity (Waide et al. 1999). At each site, seven 0.5 by 0.5 m quadrates were put out randomly within each habitat. The species richness was analysed by recording all vascular plants, bryophytes, and lichens within the quadrates, excluding only saxicolous crustouse lichens. Cryptogams not identified in field were collected and identified under a microscope.

Measurements of primary productivity

Several field methods exist for evaluation of primary productivity. Some studies use direct productivity values for example of the production of mass (g m^{-2} $year^{-1}$), energy (J m^{-2} $year^{-1}$) (Mittelbach et al. 2001). Others use indirect estimates of available energy and corollary surrogates for productivity such as the community standing biomass (g m^{-2}), latitude, altitude, actual evapotranspiration and average annual temperatures of the study ecosystems (Groner et al. 2003). It has been shown that distribution of diversity-productivity relationships in plant communities is not sensitive to the directness of productivity estimates (Mittelbach et al. 2001; Groner et al. 2003). A method widely used in large scale vegetation studies, is remote sensing of the reflected light from the vegetation and the calculation of the NDVI (Goward et al. 1987). Handheld units are now available for NDVI measurements on plot scale. We used a Tetracam ADC 2 camera with digital sensors in the green, red and near infrared bands to record the reflection from the same 0.5 by 0.5 m quadrates as we recorded the species richness. The NDVI was then calculated for each plot. This index is based on the typical reflection curve of active chlorophyll cells in the optical and near infrared spectrum. The curve has an intermediate reflection of green light, a typical dip in the red spectrum, and a quite high reflection of near infrared light. The NDVI transformation is computed as the ratio of the measured intensities in the red (R) and near infrared (NIR) spectral bands using the following formula:

$$\mathrm{NDVI} = (\mathrm{NIR} - \mathrm{R})/(\mathrm{NIR} + \mathrm{R})$$

The formula returns theoretical values between – 1 and 1. By examining a number of pictures, a threshold NDVI of 0.3 was set to distinguish living biomass of vascular plants, bryophytes, and lichens from bare stones, open soil, and dead litter on the ground. All pixel values lower than the threshold value was set to zero (Fig. 2). A mean NDVI for all the pixels in the plot were then calculated. The processing of pictures was carried out using the software Pixelwrench and Briv32 (Tetracam Inc. Chatsworth, CA, USA 2002) and for pixel classification IDL 6.1 (RSI. Boulder, CO, USA 1996). Three pictures were taken of each plot, and a mean of these were used as the estimate of photosynthetic productivity. The variation of mean NDVI of pictures taken of the same plot was less than 0.001.

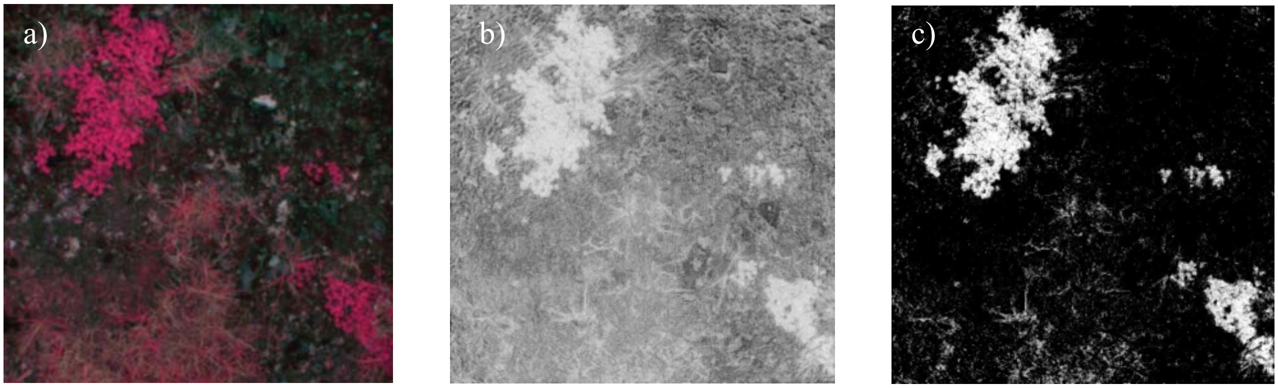

Figure 2. Processing of a green, red, NIR picture of a ridge 0.5 by 0.5 m plot: a) False colour image: Red colour represents reflectance of near infrared light, green represents red light, and blue represents green light, b) Unclassified NDVI map, c) Classified NDVI map where all pixel values below 0.3 are set to zero.

Data analysis

A linear mixed model with location as a random variable was used to analyse whether species richness was significantly different between the ridges and the zonal habitats. Relationships between species richness and productivity were analysed using mixed linear and mixed quadratic model with location as a random variable. As our species data were counts, normally known to have a Poisson distribution, we transformed the data matrix using the following formula: $\ln(n + 1)$. Statistical analyses were carried out using S-Plus® 6.2 for Windows (Insightful Corp. Seattle, WA, USA 2003).

Results

Primary productivity versus plant species richness in the high Arctic

The relationship between species richness and primary productivity varied, and different taxonomic groups showed different relationships (Fig. 3). No significant trend was observed between primary productivity and the total species richness of both ridge- and zonal habitats (Fig. 3a). However the linear- mixed model fitted the data from ridges best (df = 31, t = 2.365, p = 0.025; Fig. 3b). The same was observed for bryophytes (df = 31, t = 3.714, p < 0.001; Fig. 3c) and lichens (df = 31, t = 3.017, p = 0.005; Fig. 3d). Looking at both ridge and zonal habitat together the best fit for lichens was a quadratic mixed model (df = 34, t = 7.369, p < 0.001; Fig. 3d), but for vascular plants the linear mix model (df = 70, t = 2.117, p = 0.038; Fig. 3b). No relationship was found between species richness and primary productivity in zonal habitats (Fig. 3).

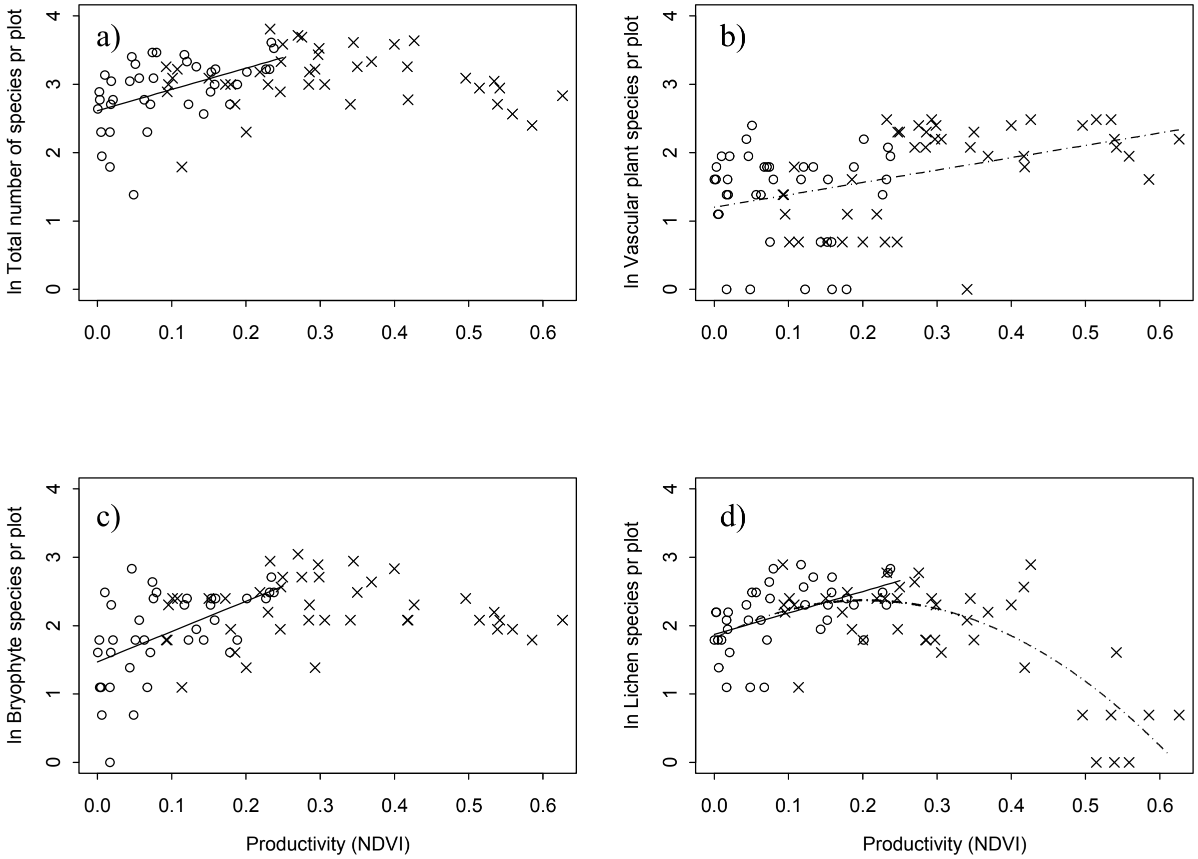

Figure 3. Scatter plot of species richness versus primary productivity. Species richness calculated from the ln of the mean number of species per site and primary productivity estimated from NDVI values. a) All species, b) Vascular plants, c) Bryophytes, d) Lichens. Circles represent the ridge habitat and x the zonal habitats. Dashed lines represent the best relationship between species richness and primary productivity for both habitat together, whole lines represent the best relationship between species richness and primary productivity on ridges.

Patterns of species richness of ridges versus zonal habitats

No significant difference in total species richness was found between zonal and ridge habitats (df = 102, t = 0.974, p = 0.333; Fig. 4a). However, zonal sites had significantly higher number of vascular plants (df = 102, t = 0.333, p = 0.974; Fig. 4b) and bryophytes (df = 102, t = 2.301, p = 0.023; Fig. 4c) and ridges had significantly more lichen species (df = 102, t = -3.497, p < 0.001; Fig. 4d).

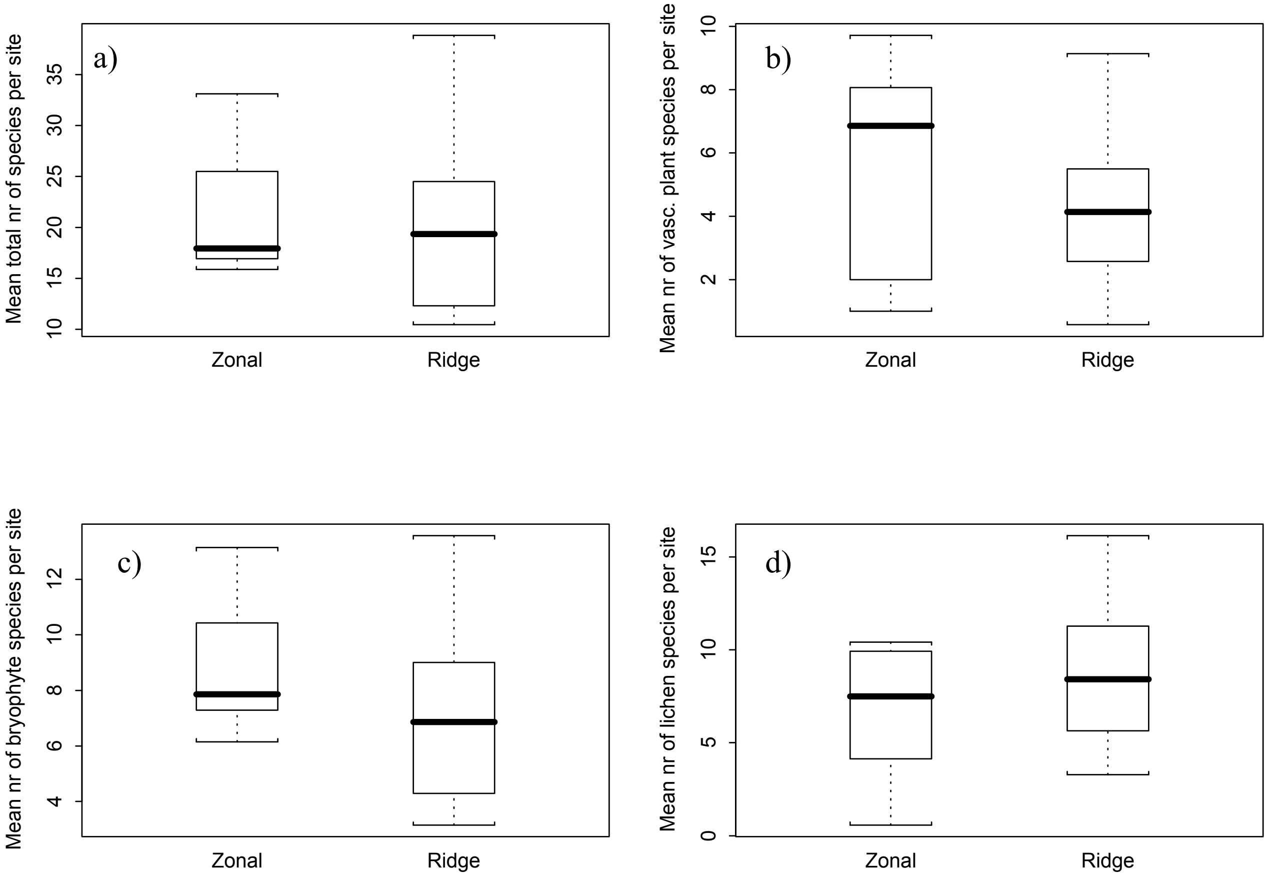

Figure 4. Comparison of species richness in ridge and zonal habitats. a) All species, b) Vascular plants, c) Lichens, d) Bryophytes. Species richness calculated from the mean number of species per site. The box represents the middle 50% of the data (from 25% in the lower hinge to 75% in the upper hinge). The line in the box is the media of the data. The upper and lower horizontal lines represent the minimum and maximum values, respectively.

Discussion

Plant species richness versus Primary productivity in the High Arctic

Several authors have stated that hump-shaped relationships should be visible when studying different community types of variable productivity (e.g. Guo & Berry 1998, Mittelbach et al. 2001), but we did not observe that pattern. Looking only at vascular plants, on both ridge- and zonal habitats, a significant fit for the linear mixed model was observed. Waide et al. (1999) collected data from surveys at arctic and alpine sites in the northern hemisphere. They found that the number of vascular plant species, and mean aboveground net primary productivity (ANPP) show a linear relationship in the High Arctic. For their low arctic sites (which by many will be considered as alpine rather than arctic) they found no relationships. Gough et al. (2000) did a thorough study at several sites and communities around Toolik Lake in low arctic Alaska. They conclude that no simple relationship exists between primary productivity (ANPP) and richness of vascular plant species. The present study is on a finer scale than Waide et al. (1999), but supports their findings of linear relationship.

Splitting the data into ridges and zonal habitats gave no significant relationship, so the linear tendency observed seems to be an overall pattern, from the low productive ridges to the more productive zonal sites. A hump-shaped relationship was observed between richness of lichen species and primary productivity. This suggests that the vascular plants, quite efficiently exclude most lichens from high productive arctic environments, which is in accordance with e.g. Cornelissen et al. (2001), Hollister et al. (2005) and Wahren et al. (2005). No significant pattern was found between bryophyte species richness and productivity, or when observing all species on both ridges and zonal habitats.

Looking at ridge- and zonal habitats separately, we found no trends in the zonal habitats. At the ridges a linear positive trend between species richness and primary productivity was significant for all species taken together, bryophytes and lichens, but not for vascular plants alone. A nursing/positive plant interaction is suggested as the main explanation for this linear relationship. The vascular plants are accounting for most of the productivity, even at ridges (Nakatsubo et al. 2005). At the most extreme ridges there are very few vascular plants, but quite a number of lichens and bryophytes between the stones and gravel. However at less exposed ridges there are more vascular plants, increasing the productivity rate. Although vascular plants are often stated to have negative effect on species diversity of cryptogams (Cornelissen et al. 2001, Hollister et al. 2005, Wahren et al. 2005), they can also act as nursing plants, when vegetation cover is sparse, and there is little competition among groups (Klanderud & Totland 2004). Callaway et al. (2002) showed in their survey of alpine plant communities that the interactions between plants were predominantly positive in communities with high abiotic stress. Klanderud and Totland (2004) studied this effect in Svalbard and found that in the shelter of the dwarf shrub *Dryas octopetala* a higher species richness of lichens and bryophyte species was observed.

Patterns of species richness of ridges versus zonal habitats

The overall species richness including all taxonomic groups (vascular plants, bryophytes and lichens) did not differ significantly between ridges and zonal habitats. Hence, the hypothesis of higher general species richness on zonal sites than ridges must be rejected for all species. However, both vascular plants and bryophytes were significantly richer in species in zonal habitats than on ridges while lichens were more species rich on ridges. Ridges are stressful habitats while zonal habitats are intermediate with respect to major ecological factors (Elvebakk 1999) which explains why bryophytes and vascular plants are more abundant there. Contrary, many lichens are adapted to exposed sites, partly because of lower competition with taller (and shading) bryophytes and vascular plants (Cornelissen et al. 2001).

Further studies

Our results show no detectable pattern between richness of vascular plants and cryptogams. Most studies treating species richness/diversity of plants and their relationship to different factors, like primary productivity use only vascular plants as representatives for the whole plant community. We suggest that such studies in the Arctic also should include cryptogams.

Conclusions

No universal pattern was observed between species richness and primary productivity. Different patterns are observed for vascular plants, bryophytes, and lichens respectively, dependent of habitat type. Our findings suggest that competition, facilitation, and wind exposure are the important factors for explaining the observed patterns. This study underlines the importance of including cryptogams in studies of arctic plant community dynamics.

Acknowledgements

This study was done as a part of an UNIS course in arctic plant ecology. We would like to thank Inga Svala Jonsdottir for planning and organizing this course as well as valuable comments and instructions in the field and during report writing. We would also like to thank Arve Elvebakk for his help in identifying bryophytes and lichens. We are very grateful to Gunnar Austrheim for his comments in field and help with statistic analysis and comments on our report. We also thank the other participants of the course for help in the field, valuable discussions, and a good moral support.

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Reproductive Strategy of Vascular Plants on Svalbard

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Abstract

Theory surrounding geographic parthenogenesis suggests that asexual and sexual species do not occupy the same niches. Patterns of geographic parthenogenesis have been observed on both global and local scales; however little work has been done on the intermediate-landscape level scale. We conducted a survey of the vascular plants in different habitat types and bioclimatic zones in Svalbard representing varying conditions of productivity. We used values from the literature to compare reproduction mode and ploidy level of the vascular plants occupying diverse conditions. We expected to observe a higher proportion of asexual species in locations with shorter growing seasons and cooler temperatures and more sexuals in milder locations. We also expected to observe a higher proportion of diploids in the milder conditions. Contrary to our expectations, we did not observe any differences in mode of reproduction or ploidy level in any of the habitat types we sampled. We did observe a higher percentage of selfers in the sites we sampled when combined for Svalbard compared to the global average, indicating that plants on Svalbard tend to inbreed more than plants globally.

Introduction

Plants and animals that reproduce asexually do not occupy the same niches as their closely related sexual relatives (Lynch, 1984). This has been observed on the global scale (Peck *et al.* 1998) and the local scale (Fox *et al.* 1996). Globally, asexuals and extreme inbreeders (selfers) occur more commonly in disturbed sites, in xeric conditions, at higher elevations and higher latitudes (Bierzychudek, 1985, Peck *et al.* 1998). This phenomenon is termed geographic parthenogenesis. On the local scale differences in the niches of asexuals and sexuals have been observed in organisms as diverse as snails and dandelions (Fox *et al.* 1996; Verduijn *et al.*, 2004). Sexual variants of *Taraxacum officinale* occurring on the northern border of their range are found sympatrically with asexuals. Verduijn *et al.* (2004) found that on this local scale, sexuals were restricted to south-facing slopes while asexuals had wider distributions (Verduijn *et al.,* 2004). Based on the observations of geographic parthenogenesis on both global scales and local scales we attempt to observe patterns in sexuality on an intermediate scale. In this study we examine the distribution of asexuals, extreme inbreeders, sexuals and species with mixed strategies on an intermediate scale of varying productivity over the island archipelago of Svalbard.

In the Arctic, one of the most important limiting factors is the length of growing season. The short growing season restricts the amount of time the plants have to flower, transfer their pollen to another individual, pollinate, fertilize and produce a seed. The situation is made more difficult as the cold conditions inhibit the diversity of pollinators found in milder climates. Therefore vascular plants are dependent on only a few species of flies or the wind for exchanging genes between individuals. Successful fertilization by out-breeding in the Arctic is not assured. Consequently many species in the Arctic employ strategies of extreme inbreeding (autogamous reproduction), asexual reproduction (cloning) in addition to outbreeding (allogamous reproduction) and combinations of these (Brochmann & Steen, 1999).

Much research has gone into explaining geographic parthenogenesis without involving climatic constraints. Glesner and Tilman (1978) argue that asexual species do not dominate globally because they can only be successful under conditions lacking biotic interactions (eg. predation, competition or parasitism). In environments without predators or competitors, Glesner and Tilman contend that the advantages of rapid asexual reproduction allow these species to dominate. However, in the presence of biotic interactions, genetically identical individuals are vulnerable. Bierzychudek (1985) argues that the simplest explanation for the greater range extensions of asexuals is the association of asexuality with increased ploidy levels. She maintains polyploids have more genetic variability on an individual level thus they may be more physiologically and ecologically flexible and have larger ranges of tolerance than primarily sexual diploid species.

In this study we examine these ideas by surveying the vascular plants growing in areas of varying productivity. We survey plants growing in three bioclimatic vegetation zones and two different habitat types within each and compare their distribution to their mode of reproduction and ploidy.

The two habitats we examine are ridges and zonal sites. Although they occur close to each other within the same bioclimatic zone, the climatic conditions are quite different. Snow blows off and melts quickly from ridges increasing the snow free season and consequently increasing the growing season of plants growing on ridges. In zonal sites the snow stays longer, as these areas are often sheltered from the wind and/or shaded. They can be relatively productive as they have higher moisture levels. Based on this, we can hypothesize that species occurring on ridges would be sexual, as they have longer growing seasons while those growing on zonal sites would have a tendency to employ more mixed or clonal strategies.

We visited 3 different bioclimatic zone types based on the Circumpolar Arctic Vegetation Map (CAVM team 2005) on Svalbard. We visited areas in Zone A , the northern polar desert; Zone B, the northern arctic tundra; and Zone C, the middle arctic tundra. Zone A is the least productive bioclimatic zone and Zone C is the most. If the growing season length is the prime determinant of the mode of reproduction we would expect to observe sexual allogamous species in locations where the growing season is extended and strict asexual species where the growing season is the shortest. Species employing mixed strategies, or autogamous sexual reproduction would be expected in the intermediately productive areas. In zone A, in the ridge habitat we could expect sexual autogamous species and in the zonal habitat species that reproduce clonally. In Zone B, we could expect to observe species that reproduce sexually both by autogamous and allogamous strategies, and in the zonal site we could expect species with autogamous sexual and asexuals strategies. In Zone C, on the ridge we could expect sexual allogamous species and further down on the zonal site sexual autogamous species or species with mixed strategies. On a general scale we can assume that areas of higher productivity are likely to support more herbivores and have more competition therefore these predictions also agree with Glesner and Tilman (1978). Additionally, from Bierzychudek (1985) we can expect polyploids to be more widespread than diploids and asexuals to be more widespread than sexuals.

Methods

All vascular plant species were identified in seven 50cm x 50cm plots in eight sites along the northwestern coast of Spitsbergen and Nordaustlandet. The seven plots were chosen within a 20m x 20m area. The eight sites were selected to cover a range of bioclimatic zones. Two of the sites were located in Zone A, three were located in Zone B and four were located in Zone C. All sites were located near the shore on the North-west coast of Svalbard.

Species were classified as Sexual, Clonal or Mixed; the sexual species were further classified as Allogamous or Autogamous and all species were classified as Polyploid or Diploid, following Brochmann and Steen (1999). Classification data was available for most of the 51 species we observed.

Contingency tables were used to compare the occurrence of species within categories. When there was only one degree of freedom the Chi-square test was employed with Yates correction. Contingency tests were performed on the total species dataset, the species per habitat and the species per bioclimatic zone. Classifications were pooled with similar groups when more than 1/5 of the values were less than 5.

Globally, 20-25% of species self-fertilize (Takebyashi and Morrell, 2001, and references therein) and approximately 50% of vascular plants are polyploid (Ayala *et al.* 2000, Soltis & Soltis, 2000). These values were compared with the frequency of selfers and polyploids we observed on Svalbard using Chi-square tests corrected for one degree of freedom with Yates correction.

Results

Sexual reproduction was the most common mode of reproduction in the species we sampled (CHI=38.9, df= 2, P<0.01), however within the sexually reproducing species the dominant strategy was to self-pollinate (autogamous reproduction) (fig. 1).

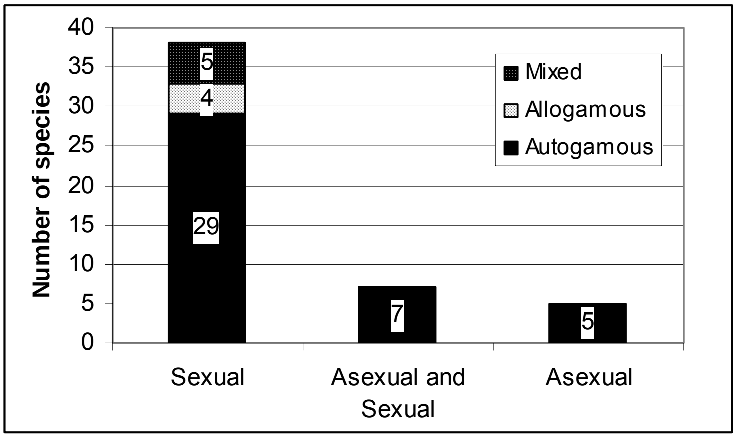

Figure 1. Number of species observed with predominantly Sexual, Mixed or Asexual reproductive strategies. Sexual reproduction can be either autogamous, allogamous or a combination of both (mixed).

More polyploid species were observed than diploid. The general pattern of ploidal level and reproductive strategy tends to fit Bierzychudek's predictions: No diploid clonal (asexual) species were observed and the majority of the strict inbreeding species were polyploid (Fig. 2). Although the sample size was low: allogamous sexual species were predominantly diploid and species employing mixed strategies occurred in equal frequencies. These differences were not statistically significant (Chi= 4.19 df =4 P=0.242 when mixed strategies pooled or Chi=2.65, df=3, P=0.448 when mixed strategies pooled and sexual autogamous pooled with asexual)

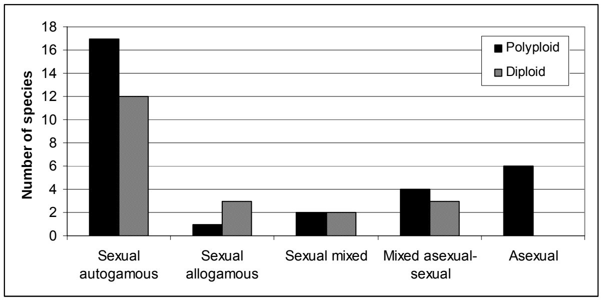

Figure 2. Frequency of species we observed, divided by reproductive strategy and ploidy level.

No differences were detected in mode of reproduction over different bioclimatic vegetation zones (Chi=4.21, df=4, P=0.38) or habitat types (Ridge or Zonal) (Chi=0.92, df=2, P=0.92) (Fig. 3).

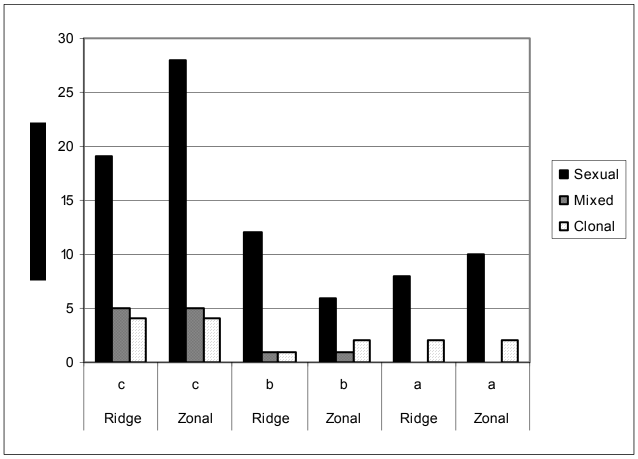

Figure 3. Reproductive strategy of observed vascular plant species over bioclimatic vegetation zone sites and by habitat type (ridge or zonal). Bioclimatic vegetation zone C is the most productive and A is the least. Sexual reproduction includes both allogamous and autogamous reproduction.

Overall, polyploids were more common than diploids, but not significantly (Chi=1.96, df=1, P=0.16 after Yates' correction for 1 df) (Fig. 4). No differences were detected between habitat types (Chi=2.56, df=2, P=0.28) or bioclimatic zones (Chi=0.02, df=1, P=0.87 after Yates' correction for 1 df).

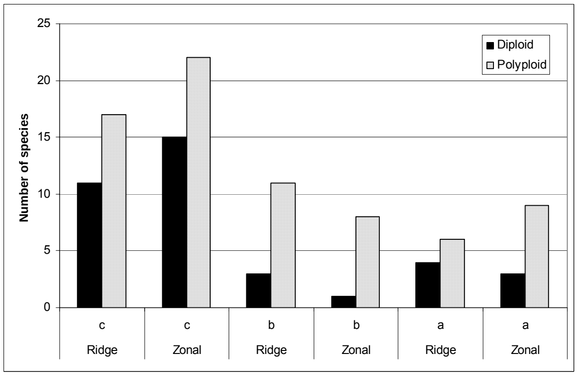

Figure 4. Number of diploid and polyploid species observed in each bioclimatic zone (C most productive and A is least) and in each habitat type.

Although no significant differences were observed between ploidy or reproductive strategy among plants in bioclimatic zones or habitat types the results for Svalbard differed significantly from the 25% selfing rate observed on a global scale (Takebashi and Morrell, 2001 and references therein) (Chi=80.8, df=1, P<0.01 after Yates' correction for 1 df). The global occurrence of polyploids is approximately 50% (Ayala *et al.* 2000, Soltis & Soltis, 2000) and this is not statistically different from the ~60% polyploidy rate we observed on Svalbard (Chi=1.96, df=1, P=0.161 after Yates' correction for 1 df).

Discussion

We did not discern any significant patterns between bioclimatic vegetation zones or habitat types and the reproductive strategy and ploidy of vascular plants. However, we did discern a general trend for the plants we surveyed on Svalbard when taken as a whole. The proportion of species that self-fertilize globally is estimated to be about 25% (Takebashi and Morrell, 2001 and references therein) whereas among the plants that we observed 90% of the sexuals self-fertilize. This significant difference agrees with the observations of geographic parthenogenesis on a global scale: plants that reproduce autogamously-extreme inbreeders-occur in higher frequencies in 'harsh' environments. However the explanation for this need not be related to lack of biotic interactions as suggested by Glesner and Tilman (1978). These plants have evolved from sexual outbreeders. In the Arctic, they simply ran out of time and/or pollinators to reproduce allogamously over the short growing season and instead evolved autogamous reproductive strategies.

Smaller scale differences between modes of reproduction and/or ploidy were not observed on the interspecific level at the landscape scale. The bioclimatic zones we sampled ranged from the relatively productive zone C, the middle arctic tundra, to the unproductive arctic polar desert found in zone A. This provided sufficient variation in productivity to alter the biotic interactions experienced by the plants growing there. In the polar desert, the plants were spatially separated and did not experience as intense competition as those growing in zone C where plants grew together tightly. An important biotic interaction for species growing in the Arctic that was not mentioned by Glesner and Tilman (1978) is facilitation. Species that have cushion growth forms can be favoured in sparsely vegetated windswept locations, and genetically identical clones adapted to a specific set of conditions could be favoured in such environments-however we did not see any evidence of this.

Bierzychudek (1985) argues that polyploids express a "hybrid vigour" associated with their high ploidy levels which allows them to endure conditions diploids cannot. We did not observe any differences in the distribution of polyploids and diploids. Although we observed a higher percentage of polyploids overall (approximately 60%) in the plants that we sampled compared to the estimated global average of 50% (Ayala *et al.* 2000, Soltis & Soltis 2000). Diploid species were ubiquitous in all bioclimatic zones, including the polar desert. We did not observe any asexual diploids. This supports Bierzychudek's hypothesis that asexuality is associated with polyploidy.

There are severe limitations to the conclusions that can be drawn from this study. The most important is that mode of reproduction and ploidy were not measured per plant in the field, but rather values from the literature were used. Many of these plants have the possibility to reproduce sexually and clonally and the most common method was the one described in the literature. It is plausible that the other method was the one employed by the plants we observed, but we were unable to identify mode of reproduction in the field. Ploidy levels were also taken from the literature and many of these were derived from studies further South in mainland Scandinavia and estimating ploidy level can be difficult as chromosomes change slightly over time. In addition to these issues, the numbers of species we observed were low with few species per category.

In general this study lends support to geographic parthenogenesis, such that sexual autogamous reproductive strategies are more common on Svalbard than further South, but no patterns can be distinguished between areas of varying productivity within Svalbard.

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On reproduction ecology and pollination success of the purple saxifrage, *Saxifraga oppositifolia*, on Svalbard.

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Abstract

We studied the reproduction ecology of an arctic plant species in relation to environmental factors at different spatial scales on Svalbard during a cruise in late July 2005. We chose *Saxifraga oppositifolia* (purple saxifrage), as our target species as it would be abundant and mostly past its flowering at our study sites during our course in late July. Samples were collected at approximately 14 sites at seven different localities.

We expected to detect differences in reproductive effort and reproductive succes in different habitats. Assuming higher outbreeding rates in early flowering populations and higher inbreeding rates in late flowering populations, we hypothesized that early flowering populations would have lower seed-ovule ratios than late flowering snowbed populations. In our material this could not be ascertained.

Compact growth form was found to be more common on dry ridges and the less compact trailing growth form in the more mesic zonal habitats. The effect of growth form was significant in the number of ovules (reproductive effort) but not in the number of seeds or the seed-ovule ratio (reproductive success).

In our present material the location of the population was the single most important and highly significant variable in the reproductive traits of *Saxifraga oppositifolia*.

keywords: arctic, reproduction, *Saxifraga oppositifolia*, seed-ovule ratio, growth form.

Introduction

Arctic plants meet many unique environmental factors that all need to be dealt with, some of which are drought, permafrost, leaching of nutrients, cryoturbation, extreme temperatures, short growing season and the persistent snow cover (Callaghan & Jonasson 1996, Walker 1995, Breckle 2002). Climatic and environmental factors are unpredictable in the arctic and allocation to reproduction in arctic areas thus forms a special challenge to plants (Stenström 1998).Temperatures have a great importance in all aspects of arctic ecosystems. Harsh winds and grazing by geese and reindeer form an added challenge (Walker 1995, Breckle 2002).

Mineral nutrient cycles are enhanced in dense cushion formed saxifrages inside which the microclimate is more favourable than in the surroundings. Cushions tend to work as nutrienttraps and greatly help the resorption of nitrogen as well as other minerals in addition to the thermal advantages (Walker 1995, Breckle 2002).

Purple saxifrage, *Saxifraga oppositifolia,* is an arctic-alpine early flowering perennial herb which is common all over Svalbard (Elvebakk & Prestrud 1996). It is an ecologically and morphologically variable species with a wide range of habitats. It flowers very soon after snowmelt (Körner 2003).

We wanted to find out whether there is a difference in reproductive effort (the total number of ovules) and the reproductive success (number of seeds, percentage of fertilized ovules) in *S. oppositifolia* between early thawing and late thawing habitats. The purple saxifrage is an early flowering and opportunistic species and it generally highly outcrossing (Gugerli 1997, Gugerli *et al.* 1999). It could be expected to be more outcrossing in early thawing than late thawing habitats due to pollinator activity. We thus expected the early flowering individuals in dry ridge habitats to have a higher percentage of fertilized ovules than populations in late thawing zonal habitats (Stenström & Molau 1992).

Materials and Methods

Study site

This study was conducted on Svalbard, an archipelago in the Arctic Ocean. It lies between latitudes 74ºN and 81ºN, and longitudes 10ºE and 35ºE. We sampled our species at six localities along the north western coast of the archipelago (Table 1).

We chose our sampling sites from the areas where the other groups of our course chose their dry (D) (ridge) and zonal (Z) sites as we concluded that it would give us a lot of data on the ecological parameters of each site. We got data of e.g. pH, soil moisture, soil temperature, vegetation cover and other species (bryophytes and vascular plants) except for Nybyen, where such data is not available.

At some localities the chosen habitats provided strong contrast in conditions for our species (e.g. Bohemaflya, Engelsbukta) while in other localities the contrast was obviously not very strong (e.g. Forkdalen, Kinnvika) did not differ enough for our purposes in terms of the seed-ovule ratio.

Study species

Purple saxifrage was chosen for this study for various reasons. First of all it is a circumpolar species and probably has the widest global distribution in the family Saxifragaceae (Mossberg & Stenberg 2003; Webb & Gornall 1989). It also has a wide ecological range in its habitats. It grows from dry to moist soils and from sea level to 3800 m a.s.l. in the Alps (Webb & Gornall 1989) often continuously along ecological gradients (Gabrielsen *et al.* 1997). It is also mentioned as the northernmost vascular plant species of the world, having been found up in northern Greenland at 83°15´ (Gjaerevoll & Rönning 1999).

Furthermore, the purple saxifrage is one of the very first plants to flower after snowmelt. Perfloration commences as soon as 4-8 days on average after snowmelt although it does have a large variation also in this respect (Stenström & Molau 1992). Finally, it is an ITEX (International Tundra Experiment) follow-up species in the Northern hemisphere.

Purple saxifrage is not endangered at the moment (Mossberg & Stenberg 2003; Stenström & Molau 1992). Climate change (e.g. the potential warming and drying of northern areas and increased UV-B radiation) can however, become a threat to this species in future (Körner 2003; Wadhams *et al,* 1996). As a shade-intolerant pioneer species it is vulnerable to competition. It will decline in its present habitats if invading and faster-growing plant species grow taller and shade it or if the plant cover in its habitat becomes overgrown (Stenström 1998; Stenström *et al*. 1997, Gugerli 1997).

Ronning (1996) has distinguished two subspecies (subsp. *reptans* and subsp. *pulvinata*) in The Flora of Svalbard, whereas other researchers have suggested other taxonomic categories, mainly morphs but also species (see for example Harding 1981; Hultén & Fries 1986; Brysting *et al*. 1996 and Webb & Gornall 1989).

According to Molau (1993) *S. oppositifolia* is a true pollen-risk strategist in all respects, meaning that it allocates strongly to very early flowering to gain sufficient time for seed maturation.

Purple saxifrage is protogynous, self-compatible, but mainly outcrossing and dependent on its pollinators, which are mainly bumblebees (*Bombus* spp.) (Stenström&Molau1992). There are, however, no bumblebees in Svalbard and the pollinating insects are probably mainly small Diptera (flies, mosquitoes, syrphids) (Stenström 1998). The pollinating insects of Svalbard have not been studied to any larger extent.

Sampling and sample analyses

At each locality, we randomly picked seven 50x50 cm plots within each habitat, a dry ridge. We aimed at sampling four flowers or fruits from each of two individual plants either within each plot or, if not precent, the two closest individuals (54 flowers in total). Due to low density at some of the sites this was not always possible thus resulting in fewer sampled individuals (Table 1). Flowers were immersed in ethanol (70vol %) in small glass jars (24x24, “Assistent”) until it was possible to further study them in the laboratory.

In the laboratory, we opened the ovary of each flower and counted the number of fertilized and unfertilized ovules under the dissecting microscope at 6.4x magnification. Fertilized ovules were fuller, rounder and often darker in colour, whereas non-fertilized ovules remained small in size and white or transparent in colour.

Statistical analyses

The statistical analyses were conducted with SAS 9.1 Software (SAS Institute, Inc 2001). Three-way analysis of variance was conducted to test the effect of population, habitat and growth form (Table 1) on number of seeds, number of ovules, seed-ovule ratios and the percentage of fertilized seeds.

Before the variance analysis (ANOVA) the data was log-transformed ($x' = \log(x+1)$) to follow normal distribution.

In addition, Pearson correlation coefficients were calculated to investigate the relationships between the reproductive variables (no.of seeds and ovules, s-o ratio, %fertilized) and the environmental variables (soil moisture, soil temperature and pH).

Results

Site, habitat and growth form effects

Population site was the only highly significant factor. The effect of the population site turned out to be very significant on all reproductive variables (Table 3).Based on our current material habitat seems to influence the number of seeds and the percent of fertilized seeds significantly. The influence of habitat can not be detected in the case of relative seed set (seed-ovule ratio) affected (Table 3).Growth form correlated with reproductive effort (the number of ovules) but not with the number of seeds (Table 3). All interaction effects were found to be non-significant (Table 3).

Environmental effects

Purple saxifrage is often said to be circumneutral in its habitats and it grows on substrates with pH from approximately 5 to as high as 8.5 (Elvebakk 1994; Arve Elvebakk, pers.comm.2005, Gugerli 1997, Webb & Gornall 1989).

In our material soil pH showed a negative correlation with seed-ovule ratio (r = -0.256, df = 92, p<0.05) and to the percent of fertilized seeds (r = -0.282, df = 89, p<0.001).

Thus, the lower the pH, the more seeds are fertilized. It could be hypothezised that there is less competition in more acidic sites which gives the shade intolerant *S. oppositifolia* an advantage in those sites. There could also be other biochemical or soil related factors in effect that would need to be studied further.

The most acidic substrate of all our study sites was found in Magdalenafjorden, which was also the only site where *S.oppositifolia* was completely lacking. The soil pH-values in Magdalenafjorden varied from 4.3 to 5.8. Those values possibly form the lower limit of pH-tolerance for *S.oppositifolia*.

Draught is a major stress factor for arctic and alpine plants and the importance of soil moisture in arctic habitats has frequently been noted (e.g. Körner 2003; Rae, 2003; Stenström 1998). Our material shows a positive correlation with soil moisture to the percent of fertilized seeds (r = 0.211, df = 104, p<0.05). The effect on the other reproductive variables is not significant.

The trailing form is usually growing on more wet environments as it is said to be more flood-tolerant (Crawford&Abbott 1994). However, both forms also occur together in the same habitats and also intermediate growth forms are abundant. At several sites (Kinnvika, Biskayerhuken, Nybyen) we observed very tight cushion forms and very trailing forms in the same habitats only about 3-5cm apart from each other. At some points it was obvious that the microhabitat (slope, exposure, soil moisture) was different, but there were nevertheless individual plants that represented different growth forms and grew side by side in habitats that appeared outwardly to be quite similar. Further research might shed some light to whether the habitats really differ, and if so, how. Plants are known to respond strongly to microclimatic variables and minute variations can have observable effects in plant structure and phenology (e.g. Rae 2003; Mook 2004).

Soil temperature (mean) was also very clearly positively correlated and had an effect on the number of seeds (r = 0.412, df=111, p<0.001) and the number of ovules (r=0.300, df=111, p<0.001).

Discussion

Based on our study, it was evident that locality significantly influences the reproductive performance, whereas the habitat and growth form affected only some reproductive traits.

We suspect that our sampling was probably some weeks too early and that a later sampling might have made it easier to detect the differences in fertilized and non-fertilized seeds (seed-ovule ratios). In a later sampling the difference might have been even more significant because it would have been easier to clearly see the difference between fertilized and unfertilized ovules. It is also possible that we were not always able to accurately determine late thawing and early thawing habitats. Moreover, the amount of flowers that we obtained was not very large for statistical analysis.

Grazing impact

Saxifraga oppositifolia is an important and preferred fodder plant to some Svalbard vertebrates (Elvebakk & Prestrud 1996) and the grazing pressure by geese (*Anser* sp., *Branta* spp.) and Svalbard reindeer *(Rangifer tarandus platyrhynchus)* was obvious in all our study sites where the purple saxifrage was found (Table 1). It was strongest in Magdalenafjorden and Colesbukta where we found no *S. oppositifolia*. In the former site this was probably due to the acidic soil and at Colesbukta the vegetation cover was possibly too closed for a pioneer plant species, which is not a good competitor (Stenström 1998). Geese are also reported to forage on *S.oppositifolia* fruits (Piroznikov 1993) and the snow bunting (*Plectrophenax nivalis*) eats S. *oppositifolia* fruits (Stenström 1998).

The grazing pressure by reindeer in Nordaustlandet (Kinnvika study-site) is of special interest. The Nordaustlandet reindeer differs from the mainland Svalbard reindeer and has a different metabolism and different grazing patterns from those of the mainland Svalbard (Ståland & Punsvik 1979). Nordaustlandet reindeer moves mainly singly or in pairs and 5- 45% of its rumen content can consist of *S.oppositifolia.* In Kinnvika area it does not consume mosses or lichens at all. As the area is quite windy snow is soon blown away and the reindeer has access to *S. oppositifolia* throughout the year (Ståland & Punsvik 1979).

At the time of our study (July 2005) the grazing pressure was not noticeable at Kinnvika, and mainly some old winter faeces was found at the site. However, the reindeer populations fluctuate, and *S. oppositifolia* is known to need at least two good growing seasons to be able to achieve good or maximum reproductive success (Stenström 1998).

Pollination

It was interesting to note that four of the plants we studied in Kinnvika (our northernmost stop at 80ºN) and three plants of the still flowering population in Nybyen had mosquitoes inside their flowers when opened under the dissecting microscope. All of these plants had some fertilized flowers and some which were not (yet?) fertilized and some which were still flowering. It is tempting to assume that the mosquitoes were present on these flowers as pollinators, possibly seeking places to rest or hide in, or eating the pollen. The diet of many adult male mosquitoes consists of plant pollen. One single pollination event is sufficient to reach full seed set in *S. oppositifolia* (Stenström & Molau 1992).

Clonality and genetics

Piroznikov (1993) has observed that *S. oppositifolia* reproduces by rooting of small side shoots that have been separated from the mother plant. Stenström and Molau (1992) have found, however, that vegetative propagation is uncommon in *S.oppositifolia*, so perhaps this would additionally be an interesting question for further studies. Clonal reproduction of vascular plants is especially prominent in mesic and wet habitats (Jónsdóttir, unpubl.) and trailing forms of *S.oppositifolia* that seem to root from their side shoots are clearly more common in mesic habitats.

When the trailing form flowered, our subjective observation was that it had fuller capsules (bigger seed size?) more fertilized seeds/capsule and the plants had less dead flowers on them. We did not have an opportunity to research this aspect in more detail during this course, but it would be an interesting question to look into at some later opportunity.

Our general field observations support the view that the morphological variation in *S.oppositifolia* is continuous along ecological gradients rather than two distinct types (Brysting *et al.* 1996). Several morphological traits seem to vary more or less independently of each other, e.g. the general growth form of the plant (compact- intermediate-trailing), flower colour (all shades from very dark pink to white) and flower size (large-intermediate-small), petal form (pointed- intermediate-rounded) and petal overlapping (from much to none) and phenology (early-intermediate-late).

There is probably ample gene flow between most of these different forms and different populations and it will be studied further in subsequent genetic analyses. Samples for further DNA analyses were obtained from all of the sites of this study.

The concern for species survival has greatly increased during recent years with intensifying human interference and consequential habitat destruction. In the arctic areas this means particularly changes in the climate and increase in UV-B radiation due to changes in the ozone layer (Wadhams et al. 1996; Körner 2003).

Genomics technologies have been focused on research on biotechnology or human health until now but they can provide tools for addressing many ecological questions as well (Frankham *et al*. 2004)

Functionally important molecular variation can be studied with modern laboratory techniques by using neutral genetic markers (such as microsatellites) which can help us identify the genomic regions that are under selection and thus related to adaptation.

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Table 1. Description of the sampling localities and sites along the west and north coast of Svalbard.

Site name (date of visit)	Habitat (number of plants sampled)	**Field observations, grazing effects**
BOHEMAFLYA (20.07.2005)	Dry (12) Zonal (12)	some flowers, no grazing
FORKDALEN (22.07.2005)	Dry (14) Zonal (16)	some grazing
KINNVIKA (23.07.2005)	Dry (15) Zonal (15)	some flowers & pollinators(mosquitoes) still many flowers,
FLORABUKTA (23.07.2005)	Dry (14)	still some flowers very little grazing
BISKAYERHUKEN (24.07.2005)	Dry (10)	still some flowers, the species was not found in the zonal habitat
ENGELSKBUKTA (25.07.2005	Dry (14) Zonal (14)	still flowering on the very late habitats some grazing
NYBYEN (01.08.2005)	Wet (10) Dry (10)	many flowers & pollinators (mosq.) some flowers, some grazing

Table 2. Reproductive traits (mean ±SD) of *Saxifraga oppositifolia* when grouped by locality, habitat and growth form.

Grouping			N	no.seeds	no.ovules	s/o ratio	tot. ovules	%fertilized
Location	1.	Bohemaflya(BOH)	23	18.0 ±15.9	69.2±26.1	0.36±0.49	87.1±22.7	21.0±17.1
	2.	Forkdalen (FOR)	24	25.1±12.4	31.5±12.7	1.34±2.48	56.6±16.2	43.8±17.9
	3.	Kinnvika (KIN)	17	26.2±19.6	79.0±35.9	0.34±0.27	105.2±48.4	23.2±13.3
	4.	Florabukta (FLO)	13	27.2±16.8	31.2±17.9	1.13±0.89	54.0±26.0	45.4±21.9
	5.	Biskayerhuken(BIS)	18	132.8±59.8	91.7±42.7	0.78±1.18	224.4±69.1	58.3±15.2
	6.	Engelskbukta (ENG)	23	62.0±69.2	90.4±60.1	0.57±0.45	152.4±111.5	35.6±16.8
	7.	Nybyen (NYB)	10	15.7±16.2	62.4±32.8	0.27±0.21	78.1±44.5	19.4±12.5
Habitat		dry (D)	92	44.2±55.3	63.8±38.6	0.88±0.52	106.8±76.4	35.2±22.1
		zonal (Z)	36	47.9±53.0	71.6±53.2	0.76±0.63	119.4±93.6	37.2±18.8
Growth form		compact (co)	86	46.9±56.0	61.0±40.0	1.02±1.56	106.6±78.6	38.5±21.9
		trailing (tr)	29	45.6±56.7	79.7±48.3	0.51±0.56	125.2±91.6	30.3±18.9
		intermediate (int)	13	33.7±39.3	68.5±47.7	0.49±0.39	102.2±78.0	28.8±17.6

Table 3. The results of three-way ANOVA of the reproductive variables of *Saxifraga oppositifolia* with population, habitat and growth form as factors showing F values, (degrees of freedom) and significance levels for each factor and their interactions; ns = not significant.

Factor	**No. seeds**	**No. ovules**	**Seed-ovule ratio**	**Total ovules**	**% fertilized**
Population (P)	14.188 (6,105) p<0.001	11.437 (6,105) p<0.001	22.951 (6,105) p<0.001	46.605 (6,106) p<0.001	37.716 (6,102) p<0.001
Habitat (H)	11.541 (1,105) p<0.001	0.515 (1,105) n.s	2.005 (1,105) n.s	2.952 (1,106) n.s	32.828 (1,102) p<0.001
Growth form (G)	2.647 (2,105) ns	1.490 (2,105) n.s	2.132 (2,105) n.s	0.259 (2,106) n.s	0.048 (2,102) n.s
P x H	1.135 (4,105) ns	3.278 (4,105) p<0.05	1.685 (4,105) n.s	0.628 (4,106) n.s	19.609 (4,102 n.s
P x G	0.880 (6,105) ns	2.040 (6,105) n.s	1.609 (6,105) n.s	0.026 (6,106) n.s	0.243 (6,102) n.s
H x G	1.158 (2.105) ns	2.135 (2,105) n.s	0.529 (2,105) n.s	0.113 (2,106) n.s	0.243 (2,102) n.s
P x H x G	0.413 (1.105) ns	0.550 (1,105) n.s	0.028 (1,105) n.s	0.038 (1,106) n.s	0.089 (1,102) n.s

Spatial scale and environmental drivers of vegetation differentiation on Svalbard

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Abstract

Determinants of vegetation differentiation on different spatial scales were analysed in order to assess the level of variance between arctic plant communities. Variance was partitioned between different groups of variables to test and establish the relative importance of pH, microclimate, bioclimatic zone and herbivory in controlling community structure on a landscape scale. Vegetative biomass and species compositions were assessed using the point intercept method, along with environmental data from ridge (exposed and dry) and zonal (sheltered and mesic) habitats at seven localities in Svalbard. Vascular plants, bryophytes and lichens were studied. Detrended correspondence analysis (DCA) was used to identify key factors associated with the community structure of plots. Variance partitioning was used to assess the relative variation of different groups of drivers. Most variance was found to be between plots (i.e. at a small scale), as together habitat and location explained less than 10% of the total variance. pH was found to be the single most important factor controlling community composition, but grouped microclimatic variables explained a greater proportion of variance in the zonal habitats than in the ridge habitats. Herbivory was found to be associated with the same relative proportion of variance to abiotic drivers in both habitats, but causation of vegetation differentiation can not be implied. The findings from this study suggest that community structure is determined on a localised scale in the arctic.

Keywords: *pH; microclimate; bioclimatic zones, herbivory; community ordination, variance partitioning*

Introduction

Arctic plant communities are similar to all biomic systems in terms of community organisation principles, despite existing in extreme environments (Walker 1995). Abiotic conditions are frequently assumed to be drivers of vegetation differentiation through differential effects on the competitive power of species with contrasting requirements (Breckle 2002). Within stressful environments however, the relative importance of competition declines (Calloway et al. 2002) and the importance of herbivory and abiotic impacts on individual plants and species within the community increases (Mulder 1999). Many of the factors controlling vegetation differentiation in both arctic and other terrestrial environments act upon different scales. Therefore spatial scale is an important issue in the determination of plant community structure.

Spatial scale is fundamental in ecology at the species level (Hartley and Kunin 2003) and at the community level (Harte et al. 2005). Species ranges are limited by the effects of environmental factors on population dynamic processes (Gaston 1990), and as communities are comprised of a collection of populations environmental factors are often assumed to be responsible for community differentiation (e.g. Graae et al. 2004). Even large scale biogeographic patterns such as range limitation may have a small scale basis. For example the model of Carter & Prince (1981) demonstrates range limitation controlled by localised patch colonisation and extinction rates. In a similar mode, vegetation differentiation (that is the difference in vegetation community composition) could have foundations on many different scales, for example, through controls of species' arrival (large scale impacts on the species pool) or survival (smaller scale impacts on competitiveness and viability).

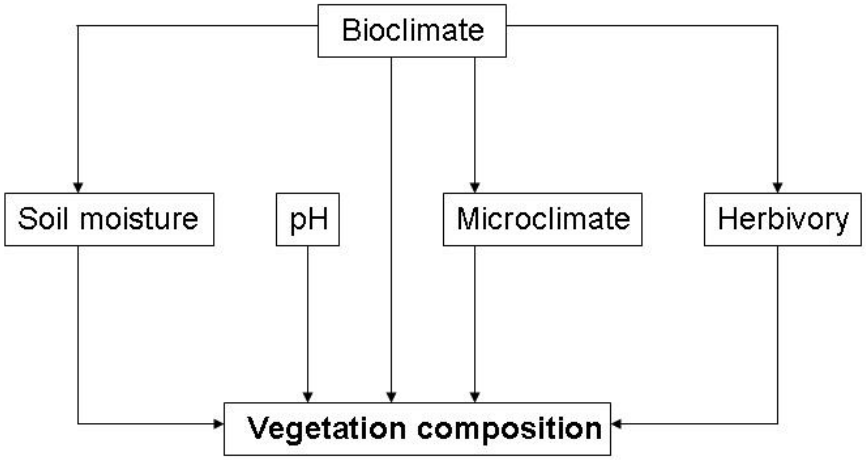


Figure 1. Conceptual model demonstrating selected drivers of vegetation differentiation examined in this study. Note that bioclimatic zone acts upon a different level to the other drivers.

Climatic conditions (bioclimatic zones and microclimate), substrate pH and herbivory are often discussed as key factors in spatial vegetative community differentiation (Figure 1 ; see e.g. Gough et al. 2000, CAVM Team 2003, van der Wal et al. 2004). Soil pH is an important determinant of the regional species pool in northern regions and explains the majority of the variation in species richness in these zones (Gough et al. 2000; van der Welle et al. 2003). In general, calcareous soils tend to support richer communities than acidic soils, potentially due to restricted rates of nitrification at low pHs (tundra communities are often nutrient limited e.g. Shaver et al. 1992), but both arctic acidophilic and basophilic species exist (Elvebakk 1982). Soil pH can vary over short distances within tundra ecosystems with bedrock, soil aging (associated with decreases in pH) and biotic influences such as bryophyte acidification (van der Welle 2003). Amongst communities, pH can explain a significant amount of variation, but at smaller scales other local factors may increase in importance (Gough et al. 2000).

At the local scale, microclimate is assumed to be a crucial variable in vegetative differentiation (Rae 2003). Microclimate (often assessed through microtopography) controls abiotic soil variables such as soil temperature and moisture and also incipient radiation, and indirectly, the timing of snow melt. Rae (2003) found that radiation load was the primary factor affecting species composition in Svalbard plant communities, with soil moisture also being important. However, the influence of climate on a larger scale is likely to impact on the regional species pool, thus controlling community composition. The zonation of arctic plant communities in terms of climate, community composition and dominance has provided the basis for a bioclimatic zone classification of vegetative communities in Svalbard (Elvebakk 1997) thus it may be expected that community composition will vary with bioclimatic zone.

Biotic as well as abiotic factors may be involved in vegetation differentiation. Reindeer (*Rangifer tarandus* ssp. *platyrhynchus*) and geese (*Anser brachyrhynchus* and *Branta leucopsis*) are the primary herbivores on Svalbard. Herbivory could conceptually be a driver of community differentiation due to grazer discrimination for different functional groups or species. There is evidence for discrimination between forage stands of differing qualities and quantities (van der Wal et al. 2000). Staaland & Punsvik (1980) analysed the diet of Svalbard reindeer and found that grasses, sedges and dwarf shrubs were preferred whilst bryophytes were less prominent features of the diet; although this study was spatially and temporally limited to summer in Nordaustlandet, it is clear that dietry preferences in reindeer do occur although these vary seasonally (Odasz-Albrigtsen 1999; Tyler & Øritsland 1999). Mosses and herbs however, form a greater part of the diet of geese (Alsos et al. 1998). Herbivory (including grazing and trampling) has also been shown to affect the balance between different functional groups within a community due to changes in moss depth caused by herbivores impacting on soil temperature, to the benefit of vascular plants (van der Wal & Brooker 2004). Manuring is also an effect of herbivory and this has the potential to influence plant communities (van der Wal et al. 2004) through changing the rates of nutrient cycling, forms of nutrient sinks and also creating heterogenic spatial distributions of nutrients.

Through a vegetation survey of seven sites on Svalbard, in which two meso-topographically differentiated habitats were studied in terms of vegetation community composition, biomass and environmental factors the following hypotheses were tested:

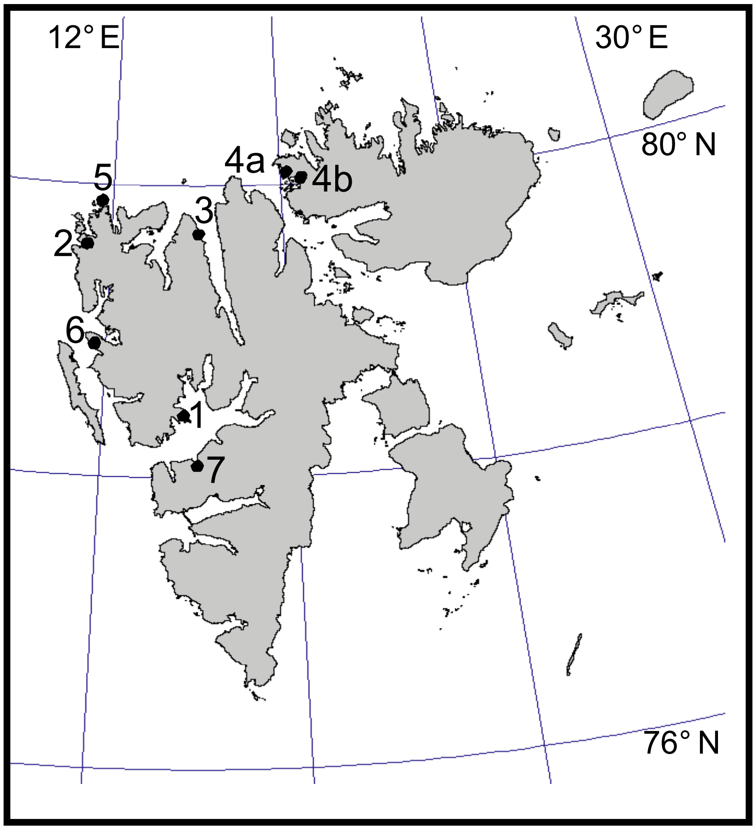
- First, that as environmental differentiation can occur on both small and large scales with large scale biogeographic patterns often having a small scale basis; and that in this study habitats were selected within sites to be meso-topographically differentiated; it was hypothesized that there would be greater variance between communities at the habitat level than at the higher spatial scale level of site.
- Secondly, that as arctic bioclimatic sub-zones are classified on the basis of vegetation type in addition to climate (Elvebakk 1997), it was hypothesized that they would explain a

greater proportion of variance between communities than other environmental variables, despite being measured on a larger scale.

- The relative proportion of variance explained by microclimate and pH was also investigated to test the assumption that pH would be a more important factor in vegetative differentiation as it operates on a larger scale and more directly on the regional species pool, (Strum et al. 2001), thus affecting the potential for colonisation in communities exhibiting prevalent clonal reproduction (Peck et al. 1998).
- Finally, due to the potential for direct bidirectional feedbacks between plant communities and herbivory level (Crawley 1997a) notably through herbivore discrimination, it was also hypothesized that herbivory would account for less variance between communities than abiotic conditions. Testing of this was incorporated within the design through inclusion of herbivore density assessment.

Methods

Study areas and sampling



1. Bohemanflya
2. Magdalenafjorden
3. Forkdalen
4. a) Kinnvika b) Florabukta
5. Biskayarhuken
6. Engelskbukta
7. Colesdalen

Figure 2. Map of study sites on Svalbard

Sampling was undertaken along the western and northern coasts of the island of Spitsbergen and on the west of Nordaustlandet between 20th and 26th July 2005 (see Figure 1). At seven sites paired zonal (those habitats ecologically intermediate between ridge and snow-bed habitats

(Elvebakk 1999) and ridge habitats were selected with an additional zonal site at Magdalenafjorden and an additional ridge site at Florabukta, to give a total of 18 individual plant communities (within a nested design). Seven plots were sampled in each habitat. The sites were selected to give a range of bioclimatic sub-zones (sensu Elvebakk 1997) from A – C (referred to as zones hereafter) and the habitats were selected as being representative within the site. Plots were positioned randomly within the limits of each habitat.

The point intercept method (see Jonasson 1988; Bråthen & Hagberg 2004) was utilised to assess biomass within each plot. 50cm x 50cm frames were used with 25 intercept points projected using bi-layered perpendicular strings. Each intercept point was separated from the adjacent by 10cm on each axis. Every vascular intercept was recorded at every point, along with a maximum of one intercept for each of litter, standing dead biomass or cryptogrammic interception. Bare ground was recorded where rock, rock crustose lichens or soil were the only intercept at a point. All vascular plants, bryophytes and lichens (with the exception of rock crustose lichens) were recorded to species level where possible, otherwise to genus level (following Lid & Lid (2005) for vascular plants; Frisvoll and Elvebakk (1996) for bryophytes and Santesson et al. (2004) and Elvebakk & Hertel (1996) for lichens). Vegetation cover was estimated excluding crustose lichens.

Soil temperature was assed within the plots by averaging two readings at 5cm below the soil surface taken with a handheld probe. Soil moisture was assessed using a Delta-T HH2 unit and a ML2x theta probe. An average of between two and four readings was taken (depending on the substrate's affinity for probing). The slope and aspect of the plots was assessed using an inclinometer. An aspect index was calculated as the deviation from an assumed optimum of 225° {=Absolute value of 225° - Aspect°} (e.g. Austrheim et al. 1999). Herbivory was estimated by counting the number of droppings of geese and reindeer (summer and winter separately) along two 25m long transects, each 2m wide, within each habitat. Top-soil samples were taken for pH analysis in the laboratory. Samples were sieved to 2mm and dissolved in deionised water. After shaking for 45mins and sedimenting for 12hrs the pH was assessed using a Hanna pH meter.

Data analysis

A data matrix was compiled using both number of hits per species and environmental data (listed in Appendix A). Bare ground was included as a species in the analysis to limit the variance in the matrix and to ensure that all plots contained species data (see Lepš & Šmilauer 2003). Species were coded by functional group. If the total number of interceptions within a plot was below 25 the remainder were assumed to be bare ground. Any missing values in the environmental section of the matrix were in-filled using habitat averages for that site. The data was exported to CANOCO for Windows 4.5 (ter Braak 2004) using CanoImp. As the intercept data are counts, all species data were log transformed within CANOCO (see ter Braak & Šmilauer 1998). Rare species were down-weighted in the analysis to avoid disproportionate effects. A slope/aspect interaction index was calculated within Canoco as the product of the two variables. Bioclimatic zone, although categorical was included as a quantitative variable for the purpose of CCA due to the requirements of the program analysis (ter Braak & Šmilauer 1998).In all statistical analyses alpha was taken as 0.05.

Unimodal models were used throughout the analyses as initial unconstrained detrended correspondence analyses (DCAs) showed that the longest gradient approached 4. The DCA was used to primarily visualise the data. Further ordinations used canonical correspondence analyses (CCAs), constrained by the environmental data set, to extract key factors in vegetation differentiation. A hierarchical analysis was performed to extract the variance explained at the different levels of the experimental design (site and habitat) using unrestricted CCAs.

Partitioning of variance between different explanatory variables (and groups of associated variables) was carried out following Økland (2003). The unique and shared variance components were calculated for different specified groups, having first checked all variables to be included in the groupings for significance. Where two groups existed {A|B} (the effect of A when the variance explained solely by B was extracted by taking it as a covariable) and {B|A} were initially calculated followed by {A∩B} (the shared variance of A and B) as {AUB} – {A|B} – {B|A} (where AUB is the total variance explained by A and B). Variance was partitioned between both microclimate and pH, and between herbivory and abiotic drivers in the different habitats. The herbivore variance was partitioned into goose and reindeer effects for both vascular plant and bryophyte functional groups. A three way partitioning of variance (see Økland (2003) for protocol) between microclimate, bioclimatic zone and pH was performed on the total undivided data set.

Results

Data exploration

A total of 210 species were identified within the point frames, of which 100 were recorded by interception and thus included in the analyses (species listed in Appendix A). DCA identified a total inertia (variance in species data) within the entire data set of 4.334. The amount of variance explained by the dominant axes within the DCA ordination are shown in Table 1, for the species data set and the species/environment relationships (where environmental variables were included passively in an indirect ordination and thus not affecting the axial positions). Figure 3 shows a biplot of a DCA of the entire data set. Bioclimatic zone, pH and herbivory are apparent as key vectors and the biomass of the different functional groups (total interceptions) within the community is also apparent as a key factor associated with community differentiation. Goose herbivory is strongly associated with bryophyte biomass whilst reindeer herbivory is closely associated with vascular plant biomass. Soil moisture appears to be more important than soil temperature in explaining community variation.

Table 1. Results from DCA of total data set and data set split by habitat type, showing the total inertia of the data, and the variance explained by the first axis and cumulatively by the first four axes

Data Set	Total Inertia	% Variation in species matrix explained by:		% Variation in species-environment matrix explained by:	
		First Axis	First Four Axes	First Axis	First Four Axes
Total	4.334	12	27.7	25.8	45.9
Zonal	4.379	11.9	29.6	20.9	33.6
Ridge	3.201	17	35.7	26.8	40.5

Hierarchical analyses of community variation

The variance explained by the different spatial levels was extracted from the total species data set within a CCA. At the site level a low but significant proportion of the total variance was explained (2.6%: F = 2.918, P = 0.002), whilst at the habitat level a slighter higher proportion of the total variance was explained (3.3%) which was also significant (F=3.646, P = 0.002). However, the remainder of the variance was explained residually (i.e. between plots; 94.1%). The data set was thus split by habitat so analyses could be performed specific to each habitat. DCAs of the contrasting habitats (Figure 4) identified differing inertia in the different habitats. There was more variance within the zonal communities than the ridge communities (inertia = 4.379 and 3.201 respectively) and a larger proportion of the variance was explained by the primary DCA axes within the ridge than zonal habitats (Table 1).

The DCA ordinations (Figure 4) show that pH was a key factor associated with vegetation differentiation in both habitat types, as was herbivory. Bioclimatic zone and soil moisture were key factors within the zonal habitat only. Reindeer herbivory was still associated with vascular plant biomass, but the strong association of goose herbivory with bryophyte biomass was only apparent within the zonal habitats. A similar proportion of variance was explained by site in both habitat types. In the zonal habitat, site explained 4.8% of the variation and in the ridge habitat, site explained 4.6% of the variance (with respective P values of 0.002 and 0.006).

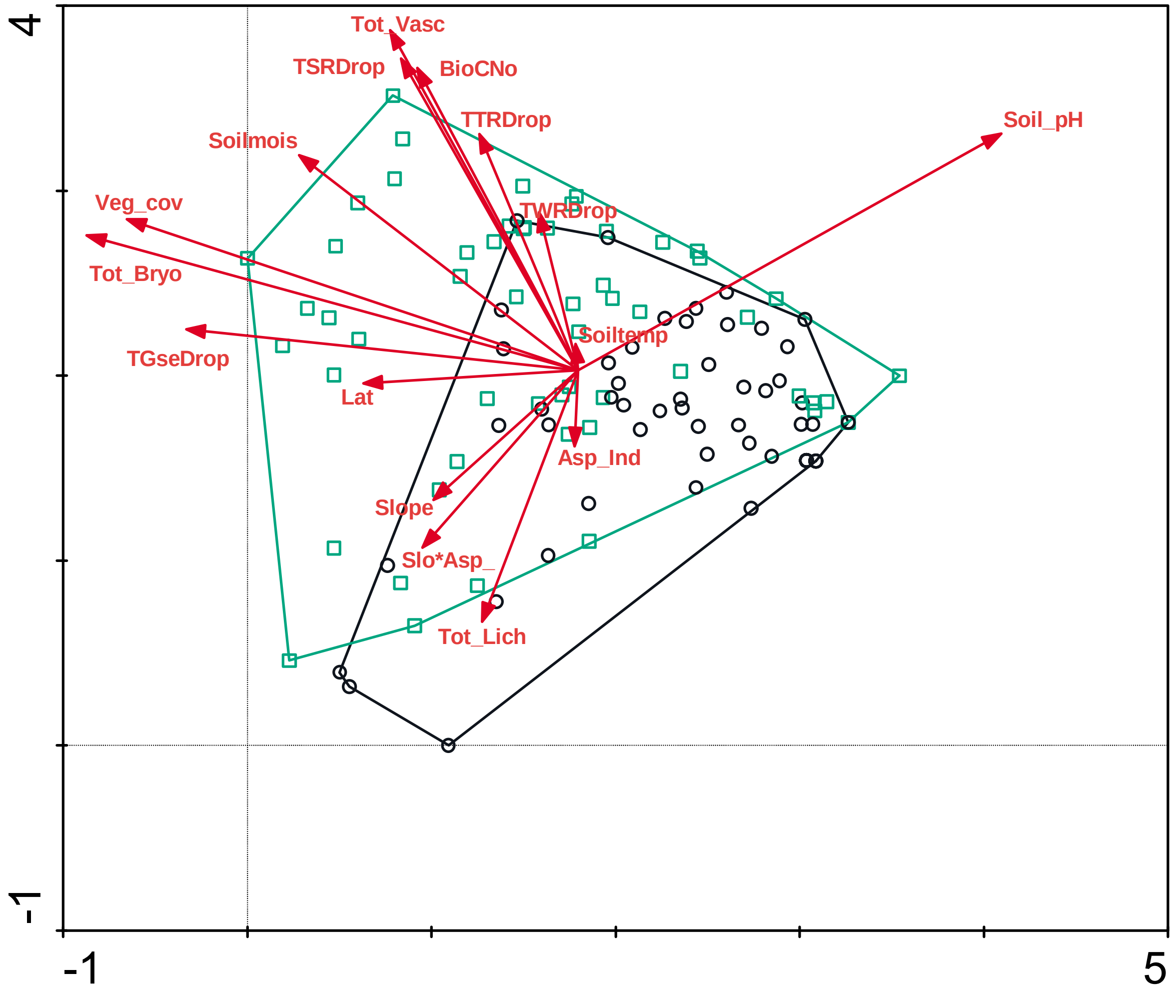


Figure 3. DCA ordination of all sites and habitats, showing the first two axes. Squares are plots in the zonal habitat and circles in the ridge habitats. Arrows represent environmental factors overlaid onto the unconstrained ordination to visualise associations with community differentiation. Asp_Ind = aspect index, BioCNo = bioclimatic zone number, Lat = latitude, Slo*Asp = slope/aspect index interaction, Slope = slope, Soilmois = soil moisture, Soiltemp = soil temperature, soil_pH = soil pH, TGseDrop = transect goose droppings, TWRDrop = transect winther reindeer droppings, TSRDrop = transect summer reindeer droppings, TTRDrop = Total transect reindeer droppings, Tot_Bryo = total number of bryophytes, Tot_Lich = total number of lichens, Tot_ Vasc = total number of vascular plants, Veg_cov = vegetation cover.

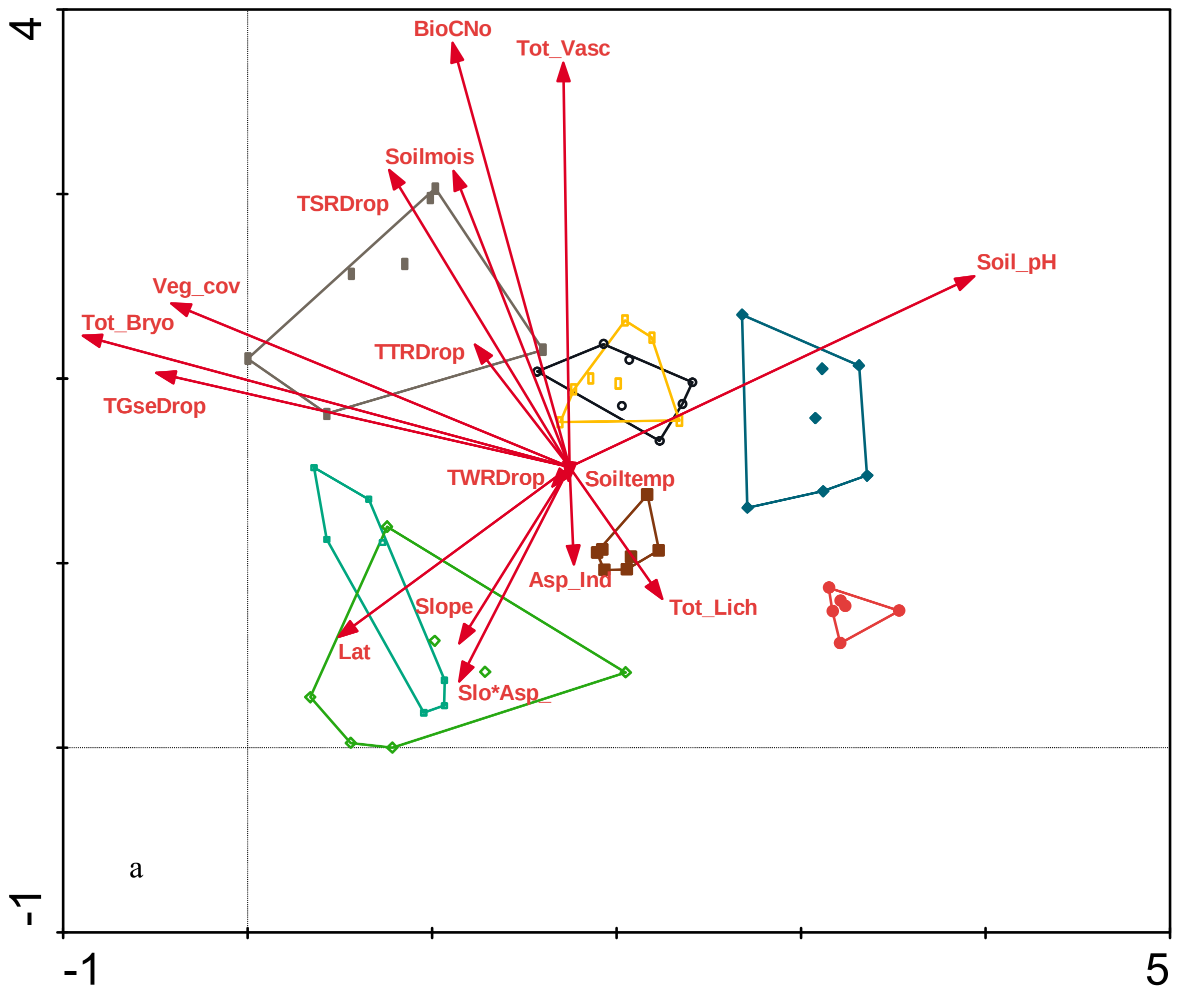


Figure 4a. Legend on next page

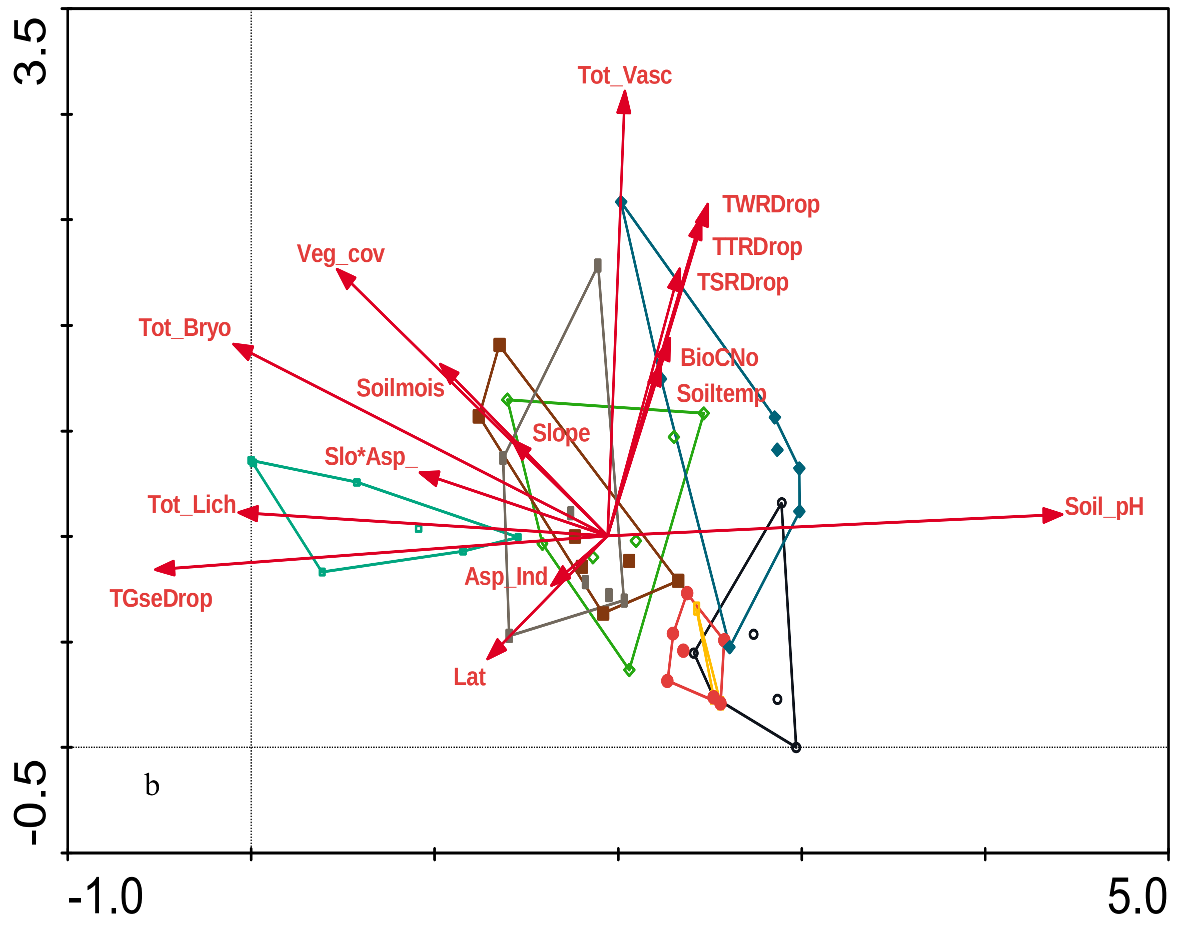


Figure 4b. Unconstrained DCA ordinations (first two axes)of plots in a) zonal (previous page) and b) ridge habitats. The different groupings refer to different sites. Overlaid environmental factors are shown by arrows. Asp_Ind = aspect index, BioCNo = bioclimatic zone number, Lat = latitude, Slo*Asp = slope/aspect index interaction, Slope = slope, Soilmois = soil moisture, Soiltemp = soil temperature, soil_pH = soil pH, TGseDrop = transect goose droppings, TWRDrop = transect winther reindeer droppings, TSRDrop = transect summer reindeer droppings, TTRDrop = Total transect reindeer droppings, Tot_Bryo = total number of bryophytes, Tot_Lich = total number of lichens, Tot_ Vasc = total number of vascular plants, Veg_cov = vegetation cover.

Variance partitioning

The three-way partitioning of variance for the entire data set, taking pH, microclimate and bioclimatic zone as groups showed that pH explained over 36% of the variance explained by the three groups (51.2% of the total). Microclimate and bioclimatic zone explained 30% and 28.2%

respectively. The shared variance component between pH and microclimate amounted to 7.1% but none of the other shared components explained over 1% (Figure 5).

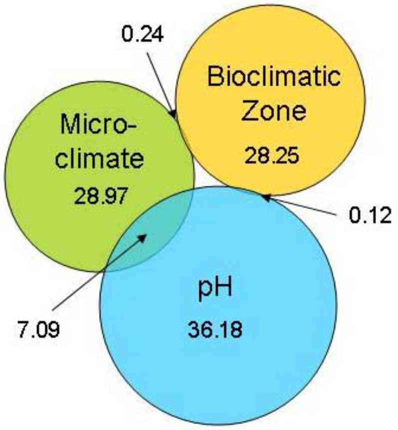
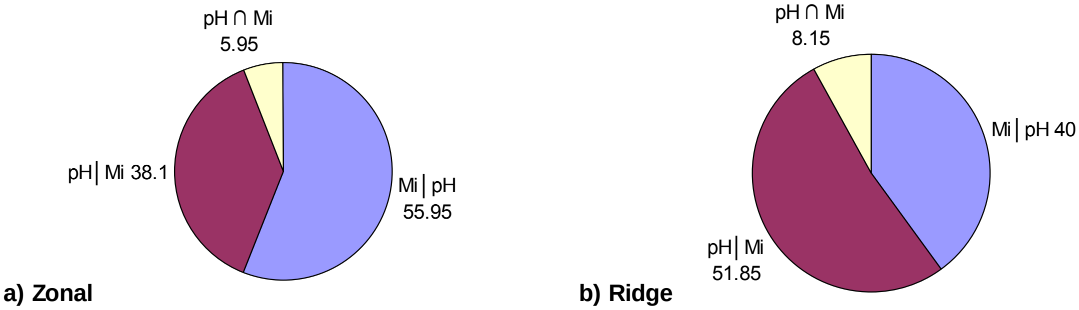


Figure 5. Venn diagram showing three way partitioning of variance between pH, microclimate and bioclimatic zone. Numbers refer to the relative variance explained by that factor/group. Shared variances are shown by the overlapping sectors. There was no shared variance between all three groups. 51.2% of the total variance in community composition was explained by these three groups.

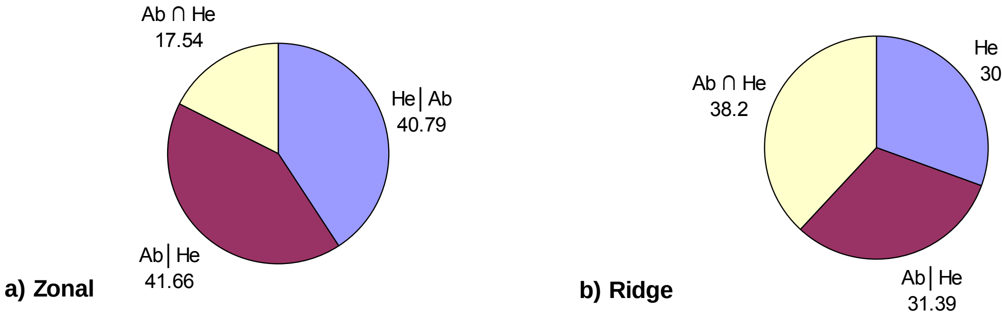
In the ridge habitats over half of the variance explained was due to pH (Figure 6a) whilst within the zonal habitats, microclimate explained more of the variance than pH (Figure 6b). For both habitats the shared variance component was a minor contributor to the total explained variance. However, almost 80% of variance was left unexplained in each habitat by these two groups alone. When variance was partitioned between herbivory and abiotic drivers no difference in the relative importance of the driver groups was observed between habitats (Figure 7). However, the shared component explained double the relative variance in the ridge than in the zonal habitats and more variance was left unexplained in the zonal habitat by herbivory and abiotic drivers.

Partitioning of the variance explained by different types of herbivory on different vegetative functional groups revealed that reindeer grazing was responsible for more variance in community composition than goose grazing in both bryophytes and vascular plants (Figure 8). However, within bryophytes, the shared variance of both goose and reindeer grazing was the dominant component in association with community composition whilst it was the least important factor within the vascular community. In addition, a greater proportion of the total variance in bryophyte community composition was explained by herbivory than in the vascular plant community.



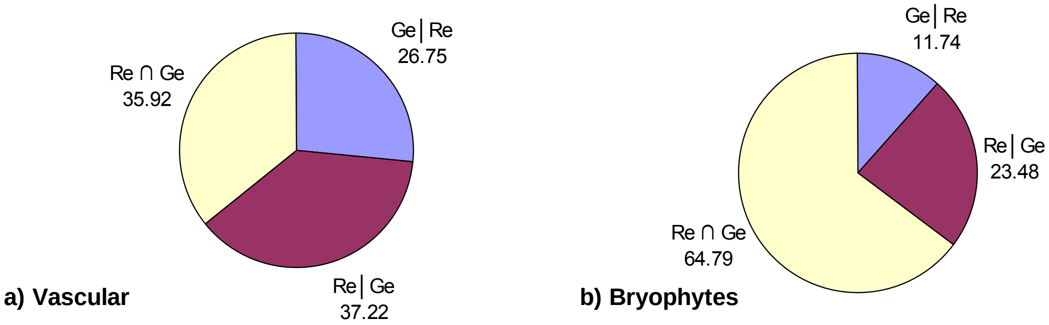
a) Zonal **b) Ridge**

Figure 6. Pie charts showing the relative variance explained by pH, microclimate (Mi) and the shared variance (pH ∩ Mi) in a) zonal habitats and b) ridge habitats where the combined effect explained 20.3% of the total variance in both habitats.



a) Zonal **b) Ridge**

Figure 7. Pie charts showing the relative variance explained by herbivory (He) and abiotic (Ab) drivers as well as the shared variance component (He ∩ Ab). a) zonal habitat, the combined effect explained 19.5% of the total variance in that habitat b) ridge habitats where the combined effect explained: 27.8% of the total variance in those habitats.



a) Vascular **b) Bryophytes**

Figure 8. Pie charts showing the relative variance explained by reindeer herbivory (Re) and goose herbivory (Ge) as well as the shared variance component (He ∩ Ab). a) vascular plant (all herbivory explained 10% of the total variance in the functional group). a b) bryophyte (all herbivory explained 28.4% of the total variance in the bryophyte community).

Discussion

Community variation at different scales

There was a high degree of variation between communities observed in this study. Hierarchal analyses showed that neither site nor habitat levels of the study design explained a large proportion of the variance in communities. It was hypothesized that habitat difference would explain more variation than geographic location and although this was true, the majority of the variation was below these levels of spatial scale and thus at a lower level than hypothesised. This suggests that determinants of community structure act at a lower level than habitat or act upon spatially heterogonous communities. There was a higher variation between communities in the zonal habitat than in the ridge habitats (in terms of the total inertia and the proportion of variance explained by the dominant axes in ordinations) and there was no difference between habitats in the amount of variance explained by location. This implies that communities were more variable between plots within the zonal habitat. It is conceivable that small scale differences in canopy architecture and biomass may impact upon community differentiation (Crawley 1997b) on a scale below habitat; potentially leading to higher variation in zonal habitat communities as deciduous shrubs (those dominant in terms of canopy structure) had a greater biomass in those habitats (data not shown).

Drivers of vegetation differentiation

Microclimate, pH and bioclimatic zone

The three way partitioning of variance between microclimate, pH and bioclimatic zone did not identify bioclimatic zone as the strongest driver of vegetation differentiation, as was hypothesised. Bioclimatic zone was in fact found to be the least important of the three selected driver groups. However, bioclimatic zone still appeared to be a key factor in the community ordinations, notably in the zonal habitats where there was a strong correlation with the second DCA axis. It is perhaps not surprising that bioclimatic zone correlated most strongly with community variance in the zonal habitats than the ridge habitat and for the vascular component of the community than for the bryophytes as it is the vascular flora of zonal habitats which is used for bioclimatic classification (Elvebakk 1997). The finding that less variance was explained by bioclimatic zone than expected may be due to the fact that a variety of locations with different characteristics were included within each bioclimatic zone, or that bioclimatic zone does not act on the same scale upon which community composition is controlled.

It was hypothesised that pH would explain a greater proportion of the variance in community structure than microclimate due to pH having a greater impact on regional species pools. This was shown to be the case for the entire data set and more strongly in the ridge habitats than zonal habitats. In fact pH had the single greatest explanatory effect in the total data set, although microclimate explained a greater proportion of the relative variance in the zonal habitats. The importance of pH is likely to be due to the presence or absence of acidophilic or basophilic species (Elvebakk 1982) and its importance in community ordinations is not rare (Gough et al. 2000, Sturm et al. 2001). However, why microclimate should be more important than pH in zonal sites is less clear. It is possible that the increased biological activity and biomass in zonal sites has a buffering effect on the realised pH, for example through reducing exposure to weathering activity which would decrease the relative importance of pH (the different degrees of exposure of the two meso-topographies between habitats may also have the same effect). Alternatively there may be more variation in microclimate in the zonal habitats due to the contrasting topographic nature of the habitat classifications. As Gould et al. (2002) stated, topographic control is manifested as variation in dominant moisture regimes among differing landscape terrain units. The correlation between microclimate and pH is not well investigated, thus further studies are required.

Herbivory

Herbivory was a key factor in community composition; in both habitat types it explained a similar proportion of community variance as explained by abiotic factors (including microclimate, soil moisture and pH), although it was hypothesised that it would explain less. Additionally, reindeer herbivory was associated with vascular plant biomass in both habitat types whilst goose herbivory was strongly correlated with bryophyte biomass in the zonal habitat; yet variance partitioning suggested that reindeer herbivory was more important in controlling the community composition of both functional groups than goose herbivory, potentially due to higher impacts of other aspects of herbivory by reindeer, such as fertilization.

The associations of herbivory with communities consisting of high biomass of certain functional groups could be due to herbivore dietary selection (for geese see Alsos et al 1998, Bazeley & Jefferies 1997 and Gauthier et al. 2004; reindeer see Staaland & Punsvik 1980, Odasz-Albrigtsen 1999, Olofsson et al. 2002, Wegener et al. 1992, Wegener & Odasz-Albrigtsen 1998). Alternatively, the associations of herbivory with functional groups biomass may be an outcome of herbivory. For example, van der Wal et al. (2004) found that the effects of reindeer herbivory impact on functional group composition of communities through increased nutrient levels leading to increase in graminoid abundance. Geese prefer forage with high nutrient quality and will generally select vascular plants over bryophytes unless high quality food is at low levels. Female breeding geese particularly are less likely to leave nesting areas in search of higher quality food (Alsos et al. 1998). Changes in functional group composition and canopy structure of the community in response to herbivory may also be responsible for the observation of a greater variance in bryophyte community composition being explained by herbivory than the composition of the vascular plant community.

The study design utilised and the community ordinations cannot imply causation of environmental variables on species composition, only association. Therefore it is unclear whether herbivory is a determinant of vegetation differentiation, or its presence is a result of different community compositions (see van der Wal et al. 2001). Thus it is clear that the hypothesis of abiotic conditions being more important than herbivory in vegetation differentiation cannot reliably be tested using this design. Further research (possibly using manipulation studies) into whether herbivores primarily act as determinants of arctic vegetation differentiation or respond to community structure would prove interesting. This could expand into looking at lichens as an additional functional group. van der Wal et al. 2001 investigated the relationship between reindeer and the abundance of lichens on Spitsbergen and found that it depends on the growth form of the lichens. Fruticose lichen abundance was negatively associeated with reindeer densities whereas foliose lichens appeared to indirectly benefit from the reindeer, although again causation cannot be implied as the study is based on correlation patterns. Additionally in a meta-analytical study of a range of manipulation experiments, Cornelissen et al.(2001) found that lichen decline is a function of increasing vascular plant biomass. The direct and indirect effects of herbivory on lichens thus require thorough investigation to produce a comprehensive view of community differentiation in response to environmental drivers.

Study design

This study involved assessing environmental variables at different scales to each other and also in some cases on different scales to the species data. This should not be a major problem as different factors operate on different levels. For example herbivory acts on a scale large than the 50cm plots assessed for community composition. However, community assembly is a function of processes at a larger scale than on which it was assessed – the species present at a location are a sub-sample from the regional species pool (Begon et al. 1996). Additionally, some factors are assessed on a different timescale to that in which they operate, for example soil temperature and moisture were assessed at a single time (as no long term data was available) whilst the annual averages or extremes are more likely to be crucial in determining community composition. The assessment of herbivory was through transect counts of droppings, however the number of droppings does not necessarily imply herbivore activity. Nevertheless, at high densities dropping counts are the best instantaneous estimate of herbivore activity.

Due to the nature of the study design there is some unbalance in terms of the distribution of the different environmental variables quantified. For example some extremes of pH and microclimate were encountered at some sites whereas only three bioclimatic zones were visited. This may have some effect on the variance partitioning results due to the differing ranges of the different factors. A stratified design may prove to be more suited to such investigations. Other factors not considered within this study also may have a key impact upon the community composition. Biotic effects such as competition and the presence of keystone or dominating species may impact upon the vegetation community. Facilitation has been shown to be an important aspect of plant communities in harsh environments (Calloway et al. 2002).

Conclusions

Most variance between Svalbard plant communities was found to be at a small scale (i.e. within habitats/between plots). This implies that the level of determination of vegetation differentiation is at a local scale or acts upon locally heterogeneous communities, determining competitiveness and survival. Consistent with this, bioclimatic zone was found to explain a lesser proportion of variance between communities than pH and microclimatic effects; however, it was still identified as a key factor in vegetation differentiation, especially in zonal habitats. Bioclimatic zone was also well correlated with vascular plant biomass. pH was the single most important variable in explaining community variance although in zonal habitats, the grouped microclimatic factors were more important. Further research into the importance of pH in determining community structure at the landscape scale is required.

Herbivory was found to be associated with different community types, and explained the same relative amount of inter-community variance as abiotic factors in both habitat types. However, herbivore causation of vegetation differentiation cannot be implied, as herbivory may also be a response to vegetation type. Additionally, reindeer grazing was found to be associated with high vascular plant biomass whilst goose grazing was associated with bryophyte biomass, although reindeer grazing was explained the most variance in both vascular and bryophyte functional groups.

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Appendix A

Species list

Species	**Hits**
Abietinella abietina	2
Abietinella sp.	2
Alectoria nigricans	4
Anastrophyllum minutum	2
Andreaea rupestris	1
Aulacomnium turgidum	10
Barbilophozia sp.	1
Bistorta vivipara	39
Brachythecium sp.	1
Bryocaulon divergens	1
Bryum sp.	3
Bryum pseudotriquetrum	2
Caloplaca cinnemomea	1
Cardamine belldiflora	1
Carex fuliginosa ssp. misandra	22
Carex rupestris	14
Cassiope tetragona	105
Cerastium arcticum	8
Cetraria aculeata	6
Cetraria sp.	3
Cetraria islandica	16
Cetrariella delisei	39
Cetrariella fastigiata	2
Cladonia coccifera	4
Cladonia gracilis	2
Cladonia macroceras	1
Cladonia macrophylla	1
Cladonia mitis	23
Cladonia uncialis	3
Cladonia sp.	5
Cochlearia groenlandica	3
Conostomum tetragonum	1
Dicranum sp.	69
Dicranella sp.	17
Ditrichum flexicaule	6
Distichium sp.	6
Draba corymbosa	1
Draba oxycarpa	1
Draba subcapitata	1
Dryas octopetala	170
Encalypta rhaptocarpa	1
Equisetum arvense	1
Equisetum variegatum	16
Flavocetraria cucullata	1
Flavocetraria nivalis	34
Hylocomium splendens	7
Hypnum bambergeri	10
Lecanora epibryon	14
Lecidea ramulosa	4
Lepraria incana	1
Leciophysma finmarkicum	42
Leptogium sp.	1
Lopadium pezizoideum	1
Lophozia sp.	2
Luzula confusa	100
Luzula nivalis	3
Minuartia rubella	1
Mycobilimbia sp.	4
Mycobilimbia lobulata	1
Ochrolechia frigida	207
Ochrolechia grimmiae	12
Ochrolechia sp.	3
Oncophorus wahlenbergii	2
Oxyria digyna	7
Papaver dahliana	4
Pedicularis hirsuta	3
Physconia muscigena	4
Poa arctica	24
Pohlia cruda	7
Pohlia nutans	3
Polytrichastrum alpinum	54
Polytrichum juniperinum	21
Polytrichum piliferum	5

Polytrichum sp.	3
Potentilla hyparctica	3
Psoroma hypnorum	4
Pseudeohebe pubescens	8
Ptilidium cilare	109
Puccinellia vahliana	1
Racomitrium canescens	6
Racomitrium lanuginosum	27
Rinodina sp.	3
Rinodina milvina	1
Salix polaris	173
Salix reticulata	2
Sanionia uncinata	159
Saxifraga aiziodes	5
Saxifraga oppositifolia	41
Saxifraga rivularis	1
Schistidium apocarpum	11
Schistidium sp.	1
Silene acaulis	4
Sphaerophorus globosus	4
Stellaria longipes	9
Stereocaulon alpinum	10
Stereocaulon sp.	5
Syntrichia ruralis	5
Tetralophozia setiformis	18
Timmia austriaca	3
Tomentypmum nitens	55

Environmental variables included within data analyses

Locality (categorical with seven sites visited)
Habitat (categorical with two levels; zonal and ridge)
Soil temp. (mean °C)
Soil moisture (mean %vol)
Veg. cover (%)
Slope (° inclination)
Aspect Index (=ABS(225°-aspect°)
Aspect Slope Interaction (interaction function between two above variables within Canoco)
Soil pH - surface soil
Bioclimatic zone
Latitude
Transect Geese Droppings (count)
Transect Winter Reindeer Droppings (count)
Transect Summer Reindeer Droppings (count)
Transect Total Reindeer Droppings (count)

Variables included in microclimate grouping

Soil temp. (mean °C)

Slope (° inclination)

Aspect Index (=ABS(225°-aspect°)

Aspect Slope Interaction (interaction function between two above variables within Canoco)

Variables included in abiotic grouping

Soil temp. (mean °C)

Soil moisture (mean %vol)

Slope (° inclination)

Aspect Index (=ABS(225°-aspect°)

Aspect Slope Interaction (interaction function between two above variables within Canoco)

Soil pH - surface soil

Bioclimatic zone

Latitude

Variables included in herbivory grouping

Transect count of Goose Droppings

Transect count of winter Reindeer Droppings

Transect count of Summer Reindeer Droppings

Transect count of Total Reindeer Droppings

Local environmental and grazing gradients outweigh macroclimatic factors in controlling carbon and nitrogen levels in arctic plants

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Abstract

While responses of nitrogen (N) and carbon (C) concentrations in arctic plants to environmental change scenarios have been experimentally studied, the general pattern of how natural concentrations of C and N in plants vary through the Arctic is still poorly understood. Here, we present an analysis of C and N levels in above ground tissue of *Salix polaris, Dryas octopetala, Saxifraga oppositifolia*, and *Luzula confusa* in ridge and zonal habitats along a macroclimatic gradient on Svalbard ranging from 78°06' N to 80°03'N. Plant material was collected at eight localites in the middle of the growing season along with local environmental data on soil characteristics (pH, moisture, loss on ignition, temperature), and grazing intensity. We differentiated between the macroclimates at the different localities, using the two principal components in the environmental data that were least correlated with differences at a local scale, i.e. between the zonal and the ridge habitats. Linear regression of the C and N concentrations in the plant material against the principal components revealed no correlations between macroclimate and N and C in the plants. However, C/N ratios were higher in ridge than in zonal habitats, though only in *L. confusa* this was related to an increase in N. Further, we detected no correlation between reindeer grazing intensity on the nutrient status on the four species, while goose herbivory was related to high levels of Nitrogen in the plant tissue. This indicates that local environmental gradients related to the length of the growing season and wetness play a larger role than macroclimatic gradients in mediating the C and N contents in above ground tissue of arctic plants.

Introduction

Most climate models predict a pronounced climate change in arctic regions with summer temperatures over land increasing between 4 and 7.5°C and winter precipitation by 5 to 80 % by the year 2080 (ACIA 2004; McCarthy et al. 2001). As the physical environment controls plant establishment and growth, as well as soil processes in the arctic, environmental change could alter ecosystem structure in the arctic tundra (Billings 1987; Press et al. 1998). In particular, nutrient cycling or the movement of chemical elements such as carbon (C), nitrogen (N) and phosphorous (P) through the system is likely to undergo modification. As nutrient cycling encompasses the movement and reuse of nutrients as they pass through several different biotic and abiotic ecosystem components, small changes in nutrient cycles could have cascading effects on other ecosystem processes (Mack et al. 2004; Weintraub & Schimel 2003; 2005).

Carbon is the main structural element in all living tissue, while N is crucial in cells for the synthesis of proteins and metabolic processes involved in the transfer of energy. Hence, higher N tissue concentrations increase plant growth (Evans 1989). The ratio of carbon to nitrogen (C/N) in tissue is therefore negatively correlated with the rate of ecosystem nutrient cycling through photosynthesis, primary production, leaf litter and soil organic matter decomposition (Shaver et al. 1992). Furthermore, C/N is very a useful estimate of the quality of plant parts as forage from a herbivore perspective (van der Wal et al. 2000).

One could expect to observe higher C/N in little productive habitats with slow nutrient turnover rates; this would imply that the Arctic displays higher C/N ratios than biomes further South. Moreover, C/N ratios would then be higher in the more northern and harsh arctic regions than in the milder ones. Similar responses would be expected to local environmental gradients, caused by climate, topography, and biotic interactions. As plants with lower C/N present forage of higher quality, a positive correlation between grazing intensity and vegetation C/N is expected.

However, at a global scale, N levels in plant tissue increase towards higher latitudes and altitudes (Hedin 2004; McGroddy et al. 2004) except for evergreen woody species in which they are constant (Körner 1989). Consequently, C/N ratios are expected to decline rather than increase with latitude. Laboratory experiments indicate that the higher N concentrations in colder climates are necessary to compensate for the lower efficiency of N-rich enzymes at low temperatures (Körner 1999; Tjoelker et al. 1999; Weih & Karlsson 2001; Woods et al. 2003). Reich & Oleksyn (2004) also found that leaf N increased from the tropics to the drier mid-altitudes and believed this effect to be temperature related. From mid to high latitudes however, N concentrations levelled out or decreased, which the authors accounted to effects of low temperature on decomposition and soil processes resulting in limited availability of N. None of these studies included data from arctic regions. Kudo et al. (2001), Tolvanen, et al. (2004) and van Wijk (2005) however, compared leaf N mass at one or more arctic sites with subarctic sites. While Tolvanen et al. (2004) found no significant differences between leaf N in plants at a sub arctic and an arctic site, Kudo et al (2001) found an increase in N at the colder sites with shorter growing season (they compared an arctic with two sub arctic sites). Welker et al. (2003) investigated N together with $\delta^{13}C$ and $\delta^{15}N$ in three different *Carex* species in the Eurasian coastal arctic. They found that the total leaf N content responded to an environmental gradient as leaf N was highest where the temperatures were colder.

Nitrogen is the major limiting element in dry and mesic arctic tundra (Shaver and Chapin 1995), and the effects of temperature, nutrient addition, and herbivory on plant C and N in arctic plants has been assessed experimentally. Welker et al. (1997) showed that *Dryas octopetala* leaf N was significantly lowered under increased temperatures. Combined warming and snow manipulation to a deeper snow cover however, caused an increase of as much as 25 % in leaf N in a dry tundra (Welker et al. 2005), with deciduous shrubs and graminoids having almost identical leaf N content. A warming experiment in arctic Canada on five different arctic plant species showed that in the woody species warming decreased the N concentration and increased the C/N ratio, whereas the N concentrations in the investigated forb and sedge species were not affected (Tolvanen & Henry 2001). Leaf N concentrations also differed between developmental stages, being highest early in the season. Similarly, the C/N ratios and nitrogen content in *Luzula confusa* and *Salix polaris*, decreased and increased, respectively, after snow melt van der Wal et al. (2000). Jónsdóttir et al. (in press) further showed that the response of N concentrations in *Carex bigelowii* depends on developmental stages as well as tissue types. Overall, N in aboveground tissue was reduced by warming, whereas belowground storage organs showed no response late in the season.

Tolvanen et al. (2004) investigated the resource allocation in *Oxyria digyna* and *Eriophorum angustifolium* in sub arctic Sweden and high arctic Canada in response to simulated and natural grazing. *E. angustifolium* showed no clear response in N concentration, across habitats or phenological stages. Caterpillar herbivory however increased the N concentration in *O. digyna*. In another simulated grazing experiment, demonstrated that N concentrations in *S. polaris* were not affected by summer browsing, but resources were allocated to compensatory growth in the following year (Skarpe & van der Wal 2002).

As indicated above, more studies are needed to assess plant nitrogen and carbon concentrations in plants along natural climate gradients within the Arctic. Such studies would add to the understanding of global patterns of C and N , including the arctic tundra. In addition they would make it possible to relate to the finding of experimental studies the observed trends in the nutrient status and production of arctic plants. Here, we investigate the natural variation in carbon and nitrogen contents in four selected arctic plants species, *Salix polaris* Wahlenb.*, Saxifraga oppositifolia* L.*, Dryas octopetala* L. and *Luzula confusa* (Hartm.) Lindeb. The reason for choosing these four species was mainly that they all are widely distributed on Svalbard, and that we expected to find all or some in most of the localities and habitats visited during fieldwork.

More specifically, we aim to differentiate between the effects of macroclimate, the local environment, and herbivory on C and N levels in arctic plants. We test the hypothesis that C/N ratios in above ground biomass of plants are constant across Arctic bioclimatic subzones on Svalbard. In addition, we investigate whether local variation in C/N can be observed among different habitat types. Finally, we test the hypothesis that local C/N ratios are negatively correlated with herbivore activity, more specifically grazing by reindeer and geese.

Material and Methods

Study localities and sampling

Seven different localities situated along the northwestern coast of Spitsbergen and on Nordaustlandet were investigated (Fig. 1, Table 1). The localities cover three arctic bioclimatic subzones (see description of zones below). At each locality we selected two approximately 20 × 20 m areas that were representative of two different habitats, namely zonal and ridge habitats. The zonal habitats are more moist and less exposed to wind and low temperatures during winter than the ridge habitats, due to a greater snow cover during winter. In each area, we sampled plant material from seven randomly chosen 50 × 50 cm plots, giving a total of 112 plots (Table 2). The localities are described in more detail in table 1.

Bioclimatic zones

Elvebakk (1999) divides the Arctic in six different subzones (referred to as zones herafter), based on climatic and botanic criteria, e.g. mid July mean temperature, bedrock maps, vegetation maps and records. The zones are the cold Arctic Polar Desert zone, or subzone A (T_{July} 1-2,5 °C), the intermediate Northern Arctic Tundra zone, or subzone B (T_{July} 2,5-4 °C), the Middle Arctic Tundra zone, or subzone C (T_{July} 4-6 °C), Southern Arctic Tundra zone, or subzone D (T_{July} 6-8 °C), Arctic Shrub Tundra, or subzone E (T_{July} 8-10 °C) and Northern Boreal Heathlands, or subzone F (T_{July} 8/9-10 °C). According to Elvebakk (2005) Svalbard can be divided in tree of the bioclimatic zones, subzones A, B, and C. In this paper we use the bioclimatic subzones to constitute an estimate of macroclimate in the statistical analysis. Zone A represents Artic Polar Desert zone, B represents Northern Arctic Tundra zone, BC representing a zone in the transition between Northern Arctic

Tundra zone and Middle Arctic Tundra zone (Elvebakk, pers.com.) and C represents Middle Arctic Tundra zone.

Focal species

Salix polaris Wahlenb. is a low, creeping shrub with long shoots which grow subterranean or in moss carpets. It grows in large, highly branching stands, on a range of soils and habitats, including gravel, moss tundra, and snow beds. It is common throughout Svalbard (Lid & Lid 2005; Rønning 1996) and much browsed by reindeer (Skarpe & van der Wal 2002).

Dryas octopetala L. is a low, evergreen dwarf shrub which grows in compact, flat cushions. It grows on exposed ridges and at other areas that are not or sparsely covered by snow during winter, especially on calcareous substrates. It is common throughout Svalbard (Rønning 1996).

Saxifraga oppositifolia L. forms mats or tufts and has often creeping branches. It grows both in dry and moist places, on open gravel, and in dense vegetation. It is widespread and common throughout Svalbard (Lid & Lid 2005; Rønning 1996). The flowers of *S. oppositifolia* are grazed by reindeer (Staaland 1983) and by barnacle geese during the incubation period (Alsos et al. 1998).

Luzula confusa (Hartm.) Lindeb. is a graminoid growing in loose tufts in dry tundra localities, in early snow beds and on exposed ridges. *L. confusa* is widespread and common throughout Svalbard (Lid & Lid 2005; Rønning 1996). It is also a major compound of the reindeer diet during summer.

Nitrogen and carbon content in green tissue

Green leaves were collected from each of the four focal species in the 112 plots, if they were present. The leaf harvest was performed between 20-26 July, which is believed to be the middle of the growing season on Svalbard. The leaves were temporarily stored in bags at a dry place on board the cruise vessel and dried at 70°C for 24 hours after return to the lab. Once dry, the plant samples were carefully grinded into a fine powder using a ball mill, and dried again at 70°C for another 24 hours. After the samples had cooled down in desiccators, they were weighted on a Mettler MT5 digital balance with an accuracy of 0.001 mg, rolled in 5 x 9 mm tin capsules and stored in an Elisa plate cell before analysis in an elemental analyzer EA 1110, CHNS-O. The ideal weight for each sample was 5.0 ± 0.2 mg. For calibration and control during the C/N analysis several standards of methionine were also added in each C/N run: 1.0 ± 0.2 mg, 3.0 ± 0.2 mg, 4.0 ± 0.2 mg, 5.0 ± 0.2 mg and 6.0 ± 0.2 mg, respectively. After each 12th sample an addition al 5 ± 0.2 mg standards was added. Also a bypass (empty space) and a blank (empty capsule) were added in the beginning of each run.

Soil temperature and soil moisture

Soil temperature was measured with a digital thermometer and a probe in two diagonal corners of each plot, 5 cm deep in the soil. The mean of the two measurements was used. Soil moisture was measured using a thetaprobe soil moisture sensor. At places where the soil was deep enough, measurements were taken in each of the four corners of a plot. Soil moisture was then calculated as the mean sum of the 2 to 4 moisture readings in each plot.

Soil pH, loss on ignition and loss of water

In each of the 112 plots, soil samples were collected from the upper 3 - 5 cm in the soil layer for investigation of pH, available water content (Loss Of Water by weight, LOW), and soil organic content (Loss On Ignition, LOI). The samples were packed into airtight plastic bags in the field, marked and stored in a cool place until analysis. In the lab the samples were passed through sieves with a mesh size of 2.0 mm. A small part of each sample was used to determine soil pH. The remainder was weighed and reweighed after drying for 24 hours at 105°C to evaporate the water in the sample and estimate LOW. After calculating LOW, small sub samples were weighted and ignited in an oven at 500°C. The remaining ash was cooled down before weighing and LOI was calculated as the weight loss.

For the pH samples de-ionised water was added to a volume of soil up to the double soil+water volum. The samples were shaken for 45 minutes and set to sediment for 12 hours, before measuring pH.

Estimation of grazing intensity by dropping counts

In each habitat we randomly placed two transects of 25 m. Reindeer and goose droppings within a distance of one meter from each side of the transect were counted and served as an estimation of the grazing intensity by the respective herbivores.

Statistical analyses

Structure within the environmental data

We used principal component analysis (PCA) to detect the main gradients among the environmental variables. Within the space delimited by the environmental variables, PCA identifies the perpendicular axes that show a maximum of the variation in the data. This is done in a step-by-step manner so that the first axes, the first principal component, account for the major part of the variation in the data.

The environmental variables were scaled to unit variance in order to eliminate the effect of the different measurement scales of the variables on the PCA result. The dataset contained one categorical variable, namely the bioclimatic zone variable, with four categories. It was given a weight equal to that of the continuous variables in the analysis by converting it to 4 dummy variables and rescaling them so that their variances added up to 1. Practically, this rescaling consisted of setting non-zero observations in the dummy variables to E, whereby.

$$E = \sqrt{\frac{1}{\sum_{i=1}^{5} \mathrm{var}(Z_i)}} \qquad (1)$$

and Z refers to the dummy variables in 1/0 format.

Carbon and nitrogen concentrations

We tested if the environmental variables could account for the variation in the carbon (C) and nitrogen (N) content of the four investigated species. The bioclimatic zones constitute an estimate of macroclimate. Plant samples, analyzed for C and N content, were few and unevenly spread among bioclimatic zones (A: n = 12, B: n = 19, BC: 11, C: n = 35). Due to these small sample sizes tests for statistical significance need to be interpreted with care. The response variables, concentrations of C and N and C/N ratios, in different bioclimatic zones were assessed using analysis of variance (ANOVA). If the ANOVA indicated statistically significant effects, we investigated the pattern further using Tukey Honest Significance Differences test (Tukey test), with adjustment for sample size. The Tukey test assesses pairwise differences between the mean values of the response variable for different levels of factor variables and uses the studentized range statistic to test for significance. In practice, it consists of comparing mean levels of C or N content, or C/N ratio, for all pairs of bioclimatic zones.

Because of the paucity of data from different bioclimatic zones, we used PCA axes as descriptors of the environmental conditions that separate the bioclimatic zones and used them to assess and test trends in carbon and nitrogen concentrations along large scale bioclimatic gradients. We used linear regression with PCA axes as predictor variables and C or N content, or C/N ratio as response variable. To test the performance of the models we used backward selection, based on Akaike Information Criterion (AIC, Akaike 1973). We developed linear mixed effects models (lme), both for the individual species and after pooling the species. In the latter case the species were treated as random effects,.

The effects of the two habitats with distinct topographical characteristics, ridges and zonal habitats, on C and N were tested using ANOVA with the biochemical characteristics as response variables and the habitats as grouping factors. When considering data for all species jointly, we used a lme's so the differences in response between species could be accounted for.

Using the data on droppings we estimated the influence of grazing pressure on carbon and nitrogen content using lme's with the grazing data as fixed predictor variables and species and habitat as nested random effects. The inclusion of random effects in the models, allows us to estimate the variation attributed to the grazing gradient, whilst compensating for variation due to differences between species and habitats.

All statistical analysis was performed with the software R (http://www.r-project.org/), with the libraries MASS (Venables & Ripley 2002) and nlme (Pinheiro & Bates 2000) enabled.

Results

Structure within the environmental data

The main variation in the environmental dataset is related to soil pH, and the intercorrelated variables Loss on ignition LOI, Loss of water LOW, and soil moisture (Fig. 2). These variables define the first axis produced by the PCA and account for 46 % of the variance in the data. The second and third axes jointly explain a further 35 % of the variance. The second axis is mainly a function of soil temperature, whereas the third axis is most correlated with soil moisture. The different bioclimatic zones can be characterized by the *in situ* observed environmental data (Fig. 2). The localities visited in Zone A, tended to be cold, and have basic soils with low water and carbon content. The localities in Zone B, tended to be warmest with mostly neutral to acidic soils. Overall, the more northern bioclimatic zones displayed lower soil temperature and soil moisture levels than the more southern zones (ANOVA for soil temperature, $F = 40.9$, $df = 107$, $p < 0.001$, ANOVA for soil moisture, $F = 8.8$, $df = 107$, $p < 0.001$).

Ridges and zonal habitats are well distinguished by the first axis of the PCA (Fig. 2), as ridges score higher on the axis than zonal habitats (ANOVA, $F = 33.8$, $df =110$, $p<0.0001$). On the second and third axis, the positions of ridges and zonal habitats differs much less than on the first axis, although they too are statistically different (for PC1, $F = 34.3$, $df = 109$, $p < 0.0001$; for PC2, $F = 7.3$, $p < 0.01$, for PC3, $F = 6.6$, $p < 0.05$, for all axes $df = 109$).

Effects of macroclimatic gradient on carbon and nitrogen levels

There is a trend towards higher C concentrations in more southerly bioclimatic zones (ANOVA, $F = 3.0$, $df = 73$, $p < 0.05$, Fig. 3). Pair wise comparisons of the bioclimatic zones show that this trend can be attributed the difference between C concentrations in zone A and C ($p_{Tukey} < 0.05$ for zone A vs. zone C, $p_{Tukey} > 0.05$ for all other pairs).

The first PCA axis is strongly correlated with the habitat types, whereas the second and third axes were only weakly correlated with it. The second and third PCA axes (PC2 and PC3) were therefore used to test how C and N concentrations are related to environmental gradients that are only marginally related to the differences between ridges and zonal habitats. The backward selection of linear models including PC2 and PC3, and the interaction between the two as predictor variables, and C yielded no models that performed better than the intercept-only models.

Effects of local environment and grazing on carbon and nitrogen levels

Carbon to nitrogen ratios are lower in plant material from zonal habitat than from ridge habitats (lme, t-statistic = -2.6, df = 72, $p = 0.01$, Fig. 4). This is caused by a higher nitrogen content in zonal than ridge habitat, which outweighs a small and less clear difference in carbon content (lme for nitrogen, t-statistic = 3.16, $p = 0.002$; lme for carbon, t-statistic = 1.0, $p = 0.32$; df = 72 for both models). *S. polaris* displays a similar pattern, with a higher nitrogen levels causing lower C/N in zonal habitats than ridge habitats (ANOVA for C/N, $F = 5.4$, $p = 0.028$; for nitrogen, $F = 6.7$, $p = 0.015$, for carbon, $F = 0.421$, $p = 0.52$; df = 28 for all tests). Also in *S. oppositifolia* and *D. octopetala*, both carbon and nitrogen concentrations were greater in zonal habitats, but sample sizes were too small for statistical evaluation (n = 18, and 13, respectively). The 17 samples of *L. confusa* followed the pattern of lower C/N in zonal habitats. However, this appeared to be linked to both lower carbon concentration and higher N concentration in zonal habitats than ridge habitats.

Reindeer grazing did not appear to influence the contents and ratio of carbon and nitrogen in the plant tissue. The only statistically significant response was a small increase in carbon content with increase in grazing pressure (lme parameter estimate = 0.014 ± 0.0059, t-statistic = 2.3, df = 68, $p = 0.03$).

Goose grazing, on the other hand was negatively correlated with C / N (lme parameter estimate = -0.031 ± 0.012, t-statistic = -2.7, df = 68, $p < 0.01$). The correlation was the direct effect of greater levels of nitrogen (lme parameter estimate 0.0025 ± 0.00091, t-statistic = 2.7, df = 68, $p < 0.01$) in more heavily grazed areas. Due to the low sample sizes, this effect could not be traced back to the different species.

Discussion

Our findings support the hypothesis that nitrogen levels in above ground plant tissue do not increase from the middle to the high Arctic in Svalbard. This was observed by Reich & Oleksyn (2004) in a global data set although they did not include any plant material collected at latitudes greater than 69° (Reich & Oleksyn 2005). We found an indication of higher carbon concentrations in arctic plant leaves towards colder arctic bioclimatic zones. However, this did not result in any detectable trends in C/N across the zones. Moreover, the use of principal components of the environmental data in our models did not detect any effect of the main observed environmental gradients (excluding the difference between habitats) on carbon and nitrogen. These gradients were dominated by soil temperature and soil moisture. Both variables are known to vary at small spatial scales and soil temperatures are additionally affected by weather conditions (Kang et al. 2000). Hence, there is a risk that the PCA axes are also influenced by microclimatic gradients. On the other hand, the axes as well as the soil characteristics that defined them correlated very well with the bioclimatic zones, and therefore appear to represent macroclimate rather than microclimate.

In plants growing in zonal habitats we found generally lower C/N ratios than in plants growing on ridges. In the three shrubs, *S. polaris*, *S. oppositifolia* and *D. octopetala*; this was due to higher levels of nitrogen in the zonal habitat overshadowing the slightly higher carbon levels. The lower C/N ratios in the graminoid *L. confusa*, was due to a lower carbon amount in combination with higher nitrogen amounts. Van der Wal et al. (2000) found that the nitrogen content in both *L. confusa* and *S. polaris* was highest early in the summer just after snowmelt, and then it decreased during the season as the biomass increased. This was also true for five different species investigated in arctic Canada (*Dryas integrifolia*, *Salix arctica*, *Cassiope tetragona*, *Oxyria digyna* and *Carex stans*) (Tolvanen & Henry 2001). Welker et al. (1997) found the exact same trends in *D. octopetala* and also stated that there was a greater seasonal difference in N than in C. According to Tolvanen and Henry (2001) and Chapin (1980) this decreasing pattern is common for plants in temperate and high latitude areas and is caused by an increase of structural material in plants that causes the N concentration to decline late in the season. The importance of local topographic variability for the timing of snow melt in the Arctic and thus the start of the growing season can cause a patchy assembly of plants in different phenological stages (Billings & Bliss 1959; Kudo 1991; van der Wal et al. 2000). Such spatial heterogeneity in phenological development can result in spatial differences in nitrogen concentrations of plants. As ridges become snow free earlier, plants could commence growth earlier than in zonal habitats, resulting in an earlier decline of nitrogen levels.

Reindeer and geese are the main vertebrate grazers on Svalbard and may potentially manipulate the vegetation structure. They do this through selective grazing, trampling, and manuring and also inducing the production of secondary compounds or other defence substances in plants that potentially prevent herbivory (Alsos et al. 1998, Stark et al. 2003; van der Wal et al. 2004). In the species studied here, reindeer grazing did not appear to influence the contents and ratio of carbon and nitrogen in the plant tissue. Skarpe & van der Wal (2002) observed a similar lack of variation in *S. polaris* leaf N across a simulated grazing gradient. They concluded that *S. polaris* allocated resources to increasing leaf biomass the following year, rather than producing N-based anti herbivore compounds as a defence against grazing,. We did not measure leaf biomass and cannot discriminate the responses of the different species. Nevertheless, a similar process as that suggested by Skarpe & van der Wal (2002) might be at work for the all species in this study, as all are known to be grazed (Bråten & Odasz-Albrigtsen 2000; Cooper and Wookey 2003).

Geese primarily exploit vegetation with high levels of nitrogen and primary production (van der Graaf et al. 2004). This behaviour feeds back on them, as presence of geese in itself can increase biomass and the concentration of nitrogen in it by speeding up the nutrient flow through the system. (Bazeley and Jefferies 1985). Goose grazing can also lead to higher nitrogen concentrations in plant shoots and leaves, because grazed plants produce more tissue and young tissue has lower C/N ratios than older tissue (Ouellet 1994). The activity of geese appears to interact with the distribution of high quality forage, while the strength of the interactions remains difficult to quantify. The relationship between the intensity of goose herbivory and the levels of nitrogen in plant tissue as found in this study, suggest that the goose plant interaction might be a key factor in the nutrient cycling of arctic tundra on Svalbard. Svalbard is a breeding ground for Barnacle geese (*Branta leucopsis*), Pink-footed geese (*Anser brachyrhynchus*), and Brent geese (*Branta bernicla hrota*) but densities are low compared to other high arctic regions. The growth of goose populations has caused large disturbances in regions of low arctic Canada. Our results indicate that the nutrient cycling on Svalbard too might be sensitive to changing grazing pressure.

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Table 1. Geographic coordinates, bioclimatic zones and bedrock type for the eight localities and their habitats.

Locality	**Habitat**	**Coordinates** (degrees, minutes, seconds)		**Bioclimatic zone**	**Bedrock type**
BOH	Z	78,24,22.6(N)	14,41,25.7(E)	C	Marine deposits, possibly calcareous
BOH	R	NC	NC	C	Strongly eroded sandstone
MAG-N	Z	79,5,36.16(N)	12,04,58(E)	B	Gneiss
MAG-S	Z	79,33,25(N)	11,01,07(E)	B	Gneiss
MAG-S	R	NC	NC	B	Gneiss
FOR	Z	79,31,53.3(N)	15,12,19.4(E)	B	Sandstone and Eifelian shale
FOR	R	79,13,49.8(N)	15,12,33.3(E)	B	Sandstone and Eifelian shale
KIN	Z	80,03,15.9(N)	18,15,06.4(E)	B	Calcareous with some marble/dolomite
KIN	R	80,03,15.2(N)	18,15,10.5(E)	A	Calcareous with some marble/dolomite
FLO	R	80,01,48.5(N)	18,41,33.7(E)	B	NE
BIS	Z	79,50,02.3(N)	12,23,00.8(E)	B	Phyllitic, windtransported marine deposits
BIS	R	79,50,18.9(N)	12,23,30.1(E)	B	Phyllitic but varied on a small scale
ENG	Z	78,51,16.8(N)	11,43,36.7(E)	C	Alkaline soil
ENG	R	78,51,16.0(N)	11,43,42.0(E)	C	Alkaline soil
COL	Z	78,06,37.5(N)	15,03,43.9(E)	C	NE
COL	R	78,06,36.2(N)	15,03,05.8(E)	C	NE

BOH=Bohemanflya, MAG=Magdalenafjorden, FOR=Forkdalen, KIN=Kinnvika, FLO=Florabukta, BIS=Biskayerhuken, ENG=Engelskbukta, COL=Colesdalen. Z=Zonal site and R=Ridge site. NC=No coordinates. Bioclimatic zones (A-C) are according to Elvebakk (2005, in press).

Table 2. Sampling of leaf tissue for analysis of carbon and nitrogen concentrations in four species across two different habitats and three arctic bioclimatic zones and one intermediate.

Species	*Salix polaris*	*Dryas octopetala*	*Saxifraga oppositifolia*	*Luzula confusa*
Total no. of samples	30	18	13	17
Samples per habitat (ridge/zonal)	14 / 16	9 / 9	9 / 4	8 / 9
Samples per bioclimatic zone (A/B/B-C/C)	1 / 9 / 3 / 17	3 / 0 / 6 / 8	8 / 1 / 2 / 2	0 / 9 / 0 / 8

Figures

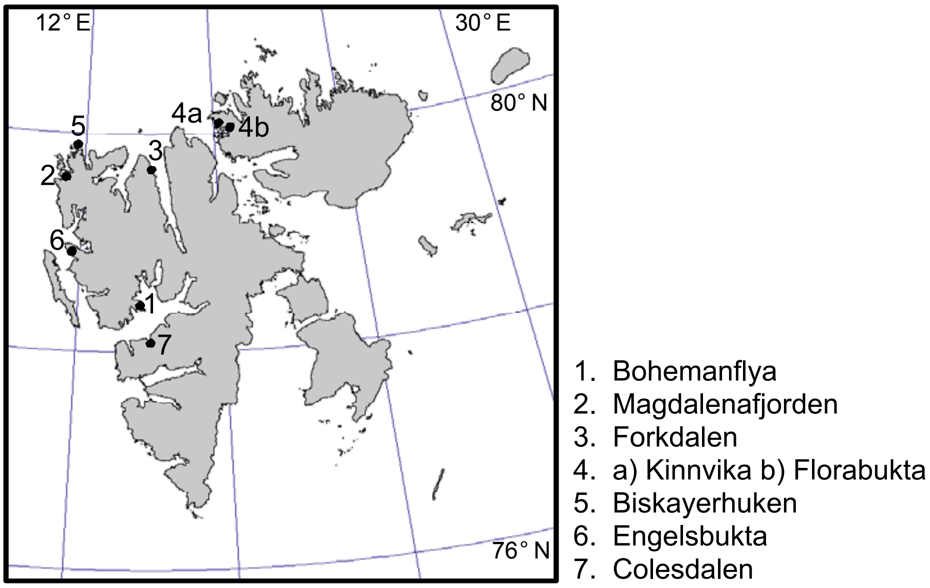

Figure 1. Map of Svalbard and the investigated localities.

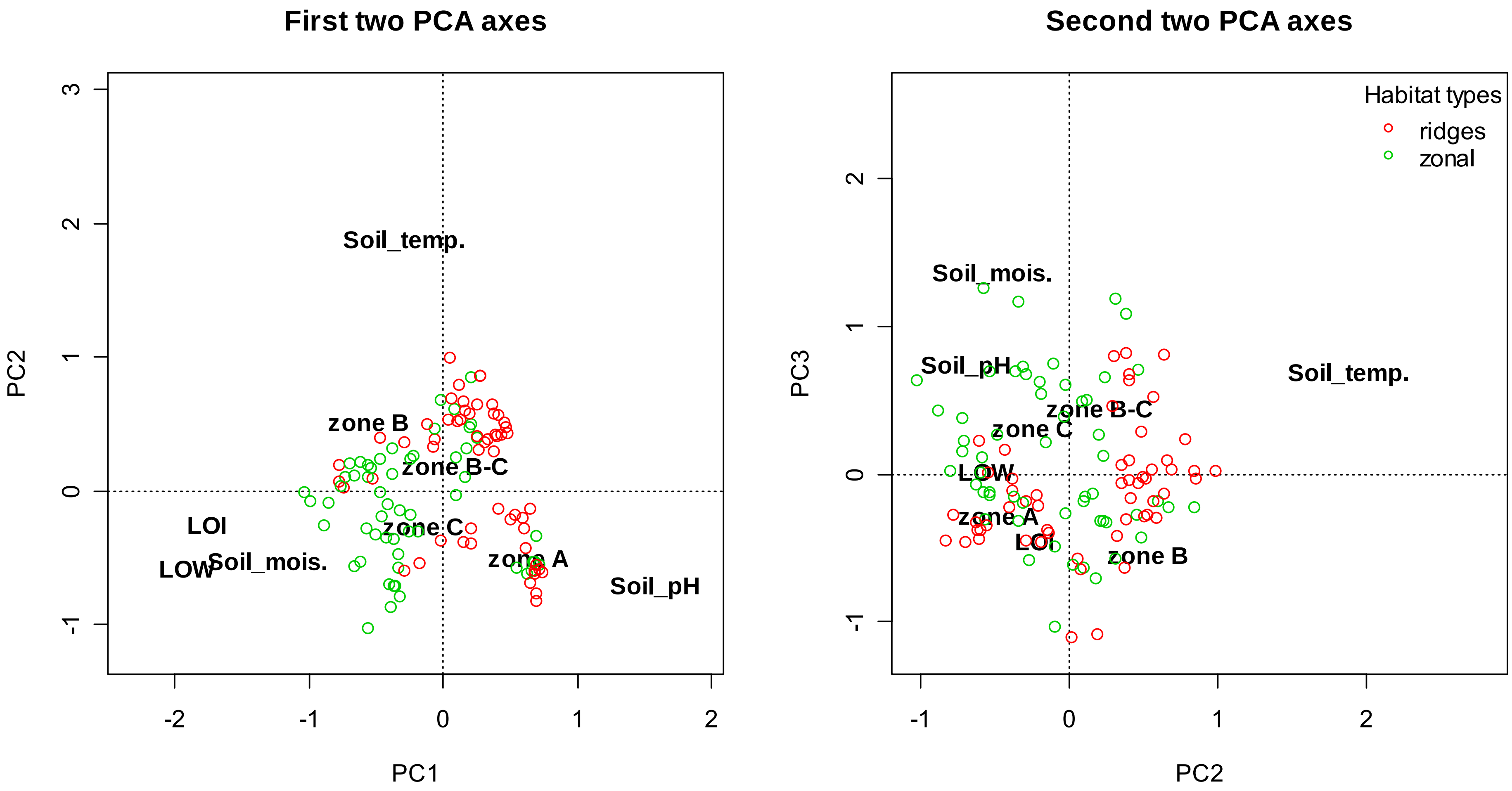

Figure 2. Biplots of the first three axis (PC1, PC2, and PC3) produced by a Principal Components Analysis of environmental variables. Analyzed vegetation plots are represented as circles. Zones A, B, B-C and C indicate arctic bioclimatic zones. (Soil_temp = soil temperature, Soil_mois = soil moisture, LOI = loss on ignition, LOW = loss on water)

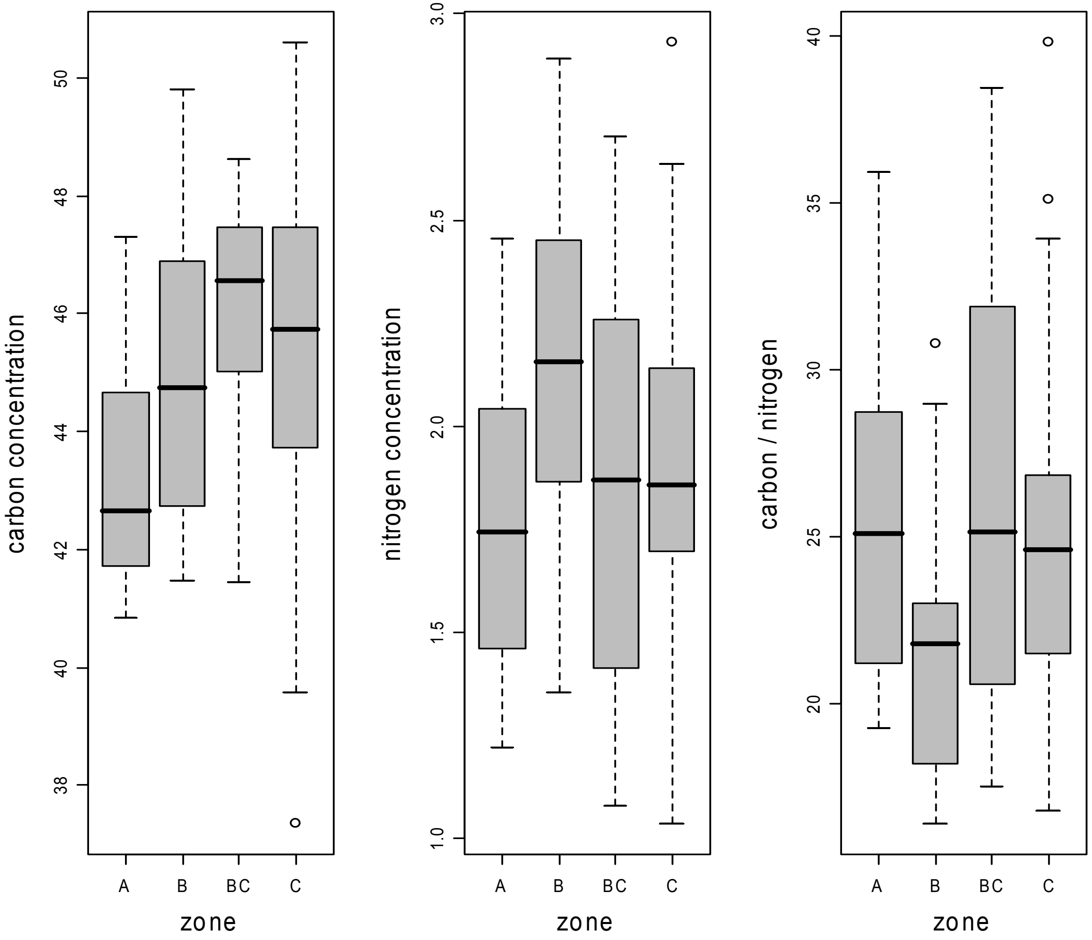

Figure 3. Trends in carbon, nitrogen, and C/N in plant leaves of *Salix polaris, Saxifraga oppositifolia, Dryas octopetala, and Luzula confusa* from 3 different arctic bioclimatic zones and an intermediate zone. The plots show the median and the boxes extend from the 25 % quartile to the 75 % quartile. The whiskers extend to the most extreme data point no more than 1.5 times the interquartile range from the box.

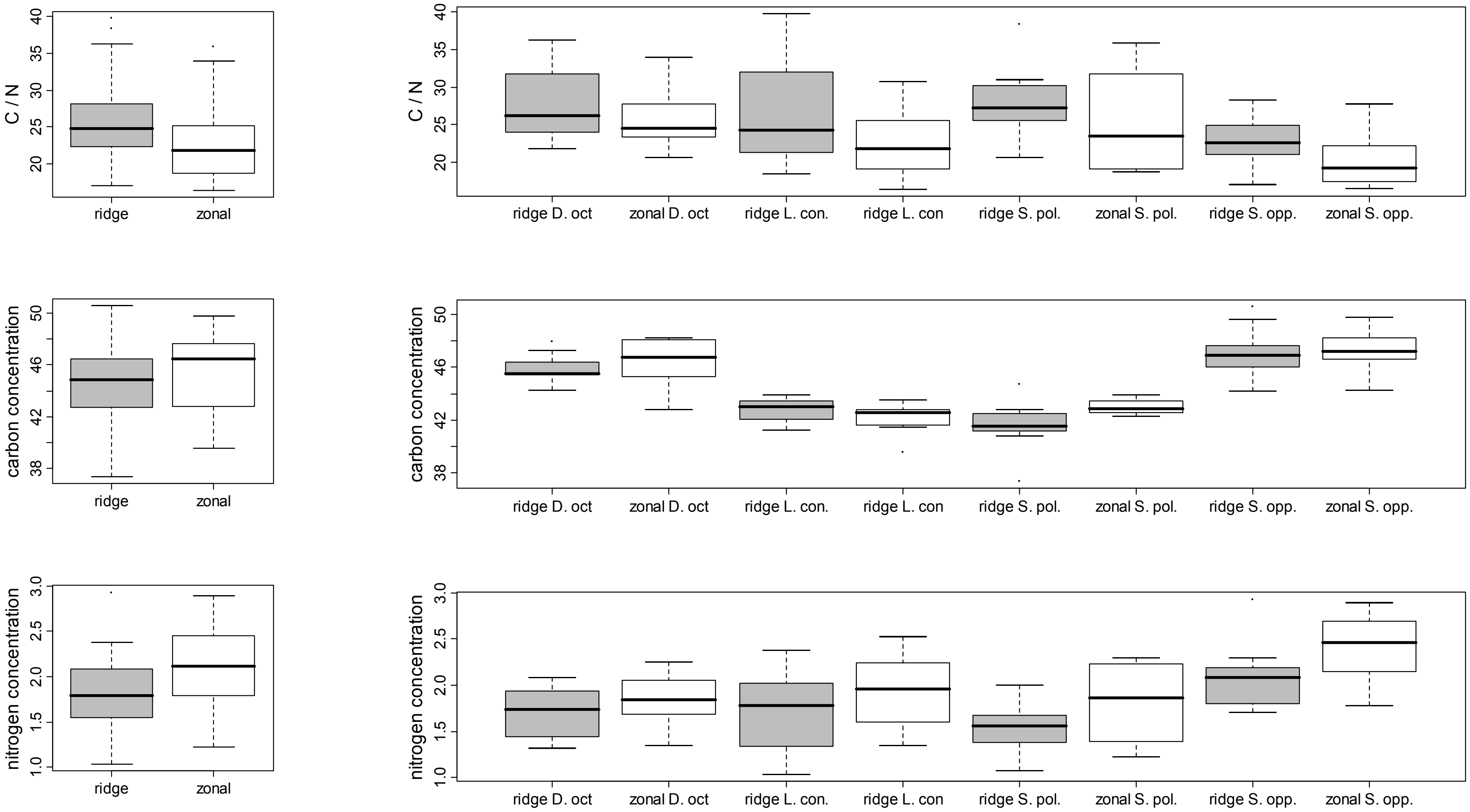

Figure 4. Carbon, and nitrogen and C/N in plant leaves from four plant species, *Salix polaris, Saxifraga oppositifolia, Dryas octopetala, and Luzula confusa* from ridge and zonal habitats. All concentrations are expressed in % dry weight. The whiskers extend to the most extreme data point no more than 1.5 times the interquartile range from the box.

An overview of the vegetation history of Svalbard

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Abstract

This study concentrates vegetation history of Svalbard during Holocene time. The emphasis has been on studies made by fossil records, pollen or macrofossil analysis. It was found that when the glaciers retreated quickly as a result of warmer climate in early Holocene vegetation spread over to freed landscape. Vegetation was more extensive during "climatic optimum" when climate was warmer and moister. With climatic deterioration during Subatlantic cooling in northern hemisphere vegetation became sparser and rather similar than the vegetation of today. It is possible that due to global warming distribution of different species shifts and current thermophilous plants get an opportunity to spread more widely.

Keywords: Svalbard, vegetation history, pollen analysis, macrofossils, Holocene, climatic change

Introduction

Svalbard is a remotely situated archipelago in the High Arctic between longitudes 10° and 35° E and latitudes 74° and 81° N. During Quaternary time it has experienced dramatic changes in climate. It has undergone several glaciations and interglacial cycles. Those many dramatic large-scale climatic changes have caused big changes in the distribution of plants (Stebbins 1985). Even during Holocene, in the interglacial after last Weichselian glaciations, there were noticeable changes in climate and thereby in vegetation (Svendsen & Mangerud 1997).

According to Rønning (1996) the present day vegetation in Svalbard is a rich and diverse realm of flowering plants in relation to its latitude. About 60 % of the archipelago is covered by glaciers and only approximately 13 % of the no-glaciated land-areas are covered by vegetation (Hisdal 1985). The climate is relatively warm because a branch of the Gulf Stream extends along the west coast of the largest island, Spitsbergen. The most fertile areas are in the inner fjord-regions in the Spitsbergen, where more than 75 % of all the vascular plant species in Svalbard are found. Some plant species are restricted to only limited areas of Svalbard, while other species are obviously limited by suitable environments. In addition to climatic variability, factors such as soil chemistry, nutrient availability, exposure and drainage affect the type of vegetation in an area (Elvebakk 1994). There are several different vegetation types according on in which kind of environment plants are growing.

It is important to know vegetation history because many processes which are important in understanding modern ecosystem composition, structure and dynamics operate over long period of time, and thus cannot be studied within a single human life (Birks & Birks 1980). Reconstructions of past communities enable comparisons to be made with ecosystems from other periods of time, so that possible causes and mechanisms of biological change within a time can be sought. Palaeoecological knowledge can provide a basis for the formulation of ecosystem models.

The purpose of this paper is to give an overview of what is known about the vegetation history of Svalbard. The emphasis is on published studies based on pollen analysis or macrofossil analysis and the time scale is limited to the Holocene period. There have been substantial climatic changes since last glaciations and for understanding responses to present day climate changes it is of interest to understand how those changes affected the vegetation. When we know something about how changes in the environment changed the vegetation in the past, it is possible to predict how present day changes in climate may change vegetation.

Present day vegetation is assumed to reflect past plant communities. Present plant communities are combinations of the species which has been able to disperse to the remote island. Also, those species which are present in contemporary plant communities have been capable survive long periods in a harsh environment. Species, which has not been able to do that, have been selected out at an early stage of the vegetation development. Although, we still have a few species as relicts from the warmer periods, they are only able to grow in the most favourable sites of Svalbard.

How to study vegetation history

Past vegetation can be studied by palaeoecological methods (Birks & Birks 1980). Palaeoecological studies aim at reconstructing the past ecosystems and relationships between past organisms and the environment they lived. However, past ecosystems cannot be studied directly. Most of the organisms do not leave readily any fossils so the studies are limited to organisms whose fossils are found. Not all fossils that are preserved and recovered in one place can directly tell what kind of vegetation has been living in. It can be that found fossil has been transported from different area and time and so it hasn't been part of the reconstructed community. Other organisms don’t leave preserved fossils and so they cannot be traced back to communities. Also, the abundance of pollen or macrofossils do not directly mirror the abundance of plants, because plants produce different amount of pollen and some plant remains are more preservable than other. All these aspects need to be considered when interpreting palaeoecological records.

Pollen analysis is widely used technique to reconstruct Quaternary environments (Birks & Birks 1980). Pollen is usually the most abundant fossil preserved in Quaternary sediments. The taxonomy of pollen grains is relatively well known and major types are readily identifiable. Pollen grains are usually easily counted under the light microscope. Pollens produced by plants are mixed more or less uniformly in atmosphere and deposited universally as a "pollen rain". So, pollen assemblages can be compared in different points with assumption that they represent different space and time. Recovered pollen grains usually originate from an assemblage of plants which originally grew together in the vegetation at the local and regional scale.

Vegetation history can be also reconstructed by using macrofossil analysis (Birks & Birks 1980). Macrofossils are plant remains seen by naked eyes. Most frequently have been used fruits, seeds, and megaspores, because they are well preserved. Also other parts such as wood, leaves, rhizomes etc. can be used. Moss remains are usually characteristics and are well preserved. Due to relatively big size of macrofossils they are not transported far away from their origin and though macrofossils can be used to reconstruct local vegetation.

What is the origin of vegetation on Svalbard?

Have there been glacial refugia on Svalbard?

During last glaciations Svalbard was almost completely ice-covered (Landvik et al. 1998). Even the ice sheet extended to the self edge on west and north of Svalbard and covered all coastal lowland and only small areas where some mountains penetrated the Late Weichselian ice sheet were ice free as nunataks. As the vegetation was wiped out during the glaciations, contemporary vegetation is the result of the development since the retreat of ice sheet. Whether some ice free areas, nunataks, provided refugia for plants to survive over the ice age, cannot be answered easily.

Molecular evidences have been used to track locations of glacial refugia (Abbot & Brochmann 2003). The assumption is that genetic diversity of present-day populations of species is higher in areas that were refugia during last ice age than in the areas which were deglaciated (Hewitt 1996; Comes & Kadereit 1998; Widmer & Lexer 2001). When a previously glaciated area is recolonized, only a sub-sample of the full genetic diversity of the source population will be introduced into the area. During the colonization process introduced genetic diversity will still decrease due to frequent founder effects and genetic drift. However, the situation may be more complicated: if formerly glaciated region is now a contact zone between migrants from different refugia, high level of genetic diversity is expected. Also, if plants have survived in small glacial refugia, they have also experienced drastic reduction in diversity because of genetic drift (Widmer & Lexer 2001).

Patterns in recent distribution of some plant species have been used as an evidence for their place of origin (Abbot & Brochmann 2003). However, it still must be bore in mind that phylogeographical evidence provides only an indication of where glacial refugia were located. There are many geophytographical evidences that plants may have survived *in situ* in Svalbard (Dahl 1987). There are some species which occur in Scandinavia and Svalbard but not in the Central European mountains, i.e. in the region which has been traditionally regarded as a glacial refugia region. That provides an evidence that there has been some refugias in otherwise glaciated area.

Because many arctic plants are not equipped with any special adaptations for long-distance dispersal, *in situ* survival is needed to explain distribution of plants (Dahl 1963). The Svalbard archipelago is so remotely situated that Hadac (1963) and Rønning (1963) suggested that most of the plants are probably glacial survivors. Today under the current climatic conditions some plant species can grow only in most favourable places. Still, they included also those species for glacier survivors. These plant species are not so probably able to survive under conditions experienced in nunataks.

Tabula rasa – Are plants able to migrate over the ocean?

Glacial survival is not always needed to explain distribution of plants (Nordal 1987). Some species are known to be dispersed over long distances even though they usually disperse only on a local scale (Abbot & Brochmann 2003). Also, some molecular evidences prove for long distance dispersal, even over the barriers such as Atlantic which have been though to be insurmountable. For example even though *Saxifraga oppositifolia* is a "short distance-disperser", it has been proved to disperse across the Atlantic (Abbott et al. 2000). Similarly, although Svalbard is situated very remotely from the mainland, there is not any reason why dispersal would not have taken place there as well.

There are only a few endemics in Northern Atlantic area, including Svalbard (Brochmann et al. 2003). None of them is a taxonomically or geographically isolated "paleoendemic" of presumambly old age. All the endemics are typical neoendemics occurring in several regions. This demonstrates that the Quaternary glaciations seriously constrained the possibilities for local plant evolution. Thereby the North Atlantic is inhabited by a typically young flora. There are three endemics (*Potentilla insularis*, *Saxifraga svalbardensis* and *Puccinellia svalbardensis*) in Svalbard. Two of those (*Potentilla insularis* and *Saxifraga svalbardensis*) are asexual and probably of recent hybrid origin (Brochmann et al. 1998; Steen et al. 2000; Brochmann & Håpnes 2001). The third one (*Puccinellia svalbardensis*) is possible conspecific with a more widespread species (Brochmann et al. 1998).

Today the majority of the true arctic plant species are hybrids. The post-Weichselian flora of Svalbard has relatively low species richness, but those species represent considerable genetic diversity (Brochmann & Steen 1999). Most of the species are polyploid. This means that present-day species are inherited from a much larger stock of diploid ancestral species. Consequently, when these species colonized previously glaciated areas, highly fixed-heterozygots in duplicated genomes ensured that genetic diversity was maintained through periods of extreme inbreeding and bottlenecks. This is an advantage for example when a deglaciated area is colonized by a single long-distance dispersed seed and the established population unavoidably is reproducing by selfing.

Vegetation history of Svalbard

Palaeoecological studies on Svalbard

Hyvärinen (1972) studied climate change during early Holocene in Svalbard. His study was based on pollen analysis of five lake sediment cores from northern Svalbard, Nordaustlandet and Bjørnøya. The oldest organic material was dated to between 10 000 and 11 000 BP which indicates that ice free areas with some kind of vegetation existed along the coasts already at that time. The early pollen spectra is similar to the recent ones. A warmer period between 9000 and 2000 BP is indicated by higher abundance of tree pollens. When coniferous and mixed forest in northern Europe in early Holocene spread, the amount of pollen from tree species increased in the atmosphere and was transported up to the High Arctic with winds. After the climatic optimum the amount of tree pollens declined. The amount of non-arboreal pollen (NAP) increased, suggesting a more extensive plant cover. As the study sites were spread among climatically different parts of the Svalbard archipelago, a synchronous vegetational optimum of all these different sites suggest a general climatic amelioration. The peak of the Post-Glacial Warm Period wad dater around 5000 BP which falls in the late Atlantic-Subboreal period, indicating that the early part of the Post-Glacial Warm Period (i.e. 9000-5000 BC), was more favourable than the later part (5000-2000 BC). At one studied site the increase of Ericales pollen suggests that *Cassiope*-heaths probably became more wide-spread at that time.

Two sub-fossil peat layers dated between 7900 and 3800 BP were found unexpectedly in Rosenbergdalen, Edgeøya (van der Knaap 1989). Today, peat layers are absent and the vegetation is sparse in the area. This shows that peat mires and more densely vegetated debris slopes were present during this period, suggesting warmer or moister climate than today. Also at this site higher long-distance pollen brought in by air masses, probably from Scandinavia was abundant, indicating warmer climate. Both pollen and plant macrofossils were studied in the peat samples. Van der Knapp (1989) found that the vascular plant vegetation around the sampling area was rather stable with only minor changes in it during the studied period. The dominant moss species, however, changed several times. Beyens & Chardez (1987) studied testate amoebae, unicellular microscopic protozoa which live in abundance on the surface of most peat bogs, in the same area. Testate amoebae are sensitive indicators of hydrological conditions in peat land and by studying them it was able to find out the wetness of the mosses during growth. It was found that there has been abrupt hydrological change from rather moist but unstable conditions to rather dry conditions.

Also droppings of reindeer embedded in sub-fossil peat samples in Edgeøya were studied by pollen analysis (van der Knaap 1989). Because reindeer consume the local vegetation, pollen is found more concentrated with less long-distance pollen in faecal pellets than in surrounding peat layers. In the faecal pellets un-manured tundra vegetation was better represented than in surrounding peat samples. Today there is bird-cliff vegetation in present close by, but that didn't show up in sub-fossil faecal pellets. Van der Knaap (1989) concluded that either there had not been any bird-cliff vegetation before or that un-manured tundra vegetation was so much better developed in the past days that it has been enough to feed the reindeer and they did not need to feed on manured bird-cliff vegetation.

Van det Knapp (1988) also studied the vegetation history from two skua-mounds of the Arctic Skua (*Stercorarius parasiticus*) in eastern Spitsbergen and northern Edgeøya. Skua-mounds are peaty hillocks that Arctic Skuas use for surveying their territory. Peat formation on those small bogs depends on manuring of birds. Van der Knaap (1988) traced vegetation history 4500 years back. He concluded that the prevailing climate was arctic during at least the past 4500 years. The fluctuations in the pollen abundance of dominant vascular plant species he interpreted in terms of fluctuating intensities of manuring by Arctic Skuas. He found some evidences that there had been twice a climatic change towards cooler conditions. The earlier one was a major climatic shift and the later one minor climatic change. The vegetation changed from a heavily to a moderately manured vegetation. He did not date those climatic changes in his work but gave an estimate that possible date for a major climatic shift was in the beginning of the Subatlantic period about 2400 BP when there was general cooling in the northern hemisphere.

Van der Knaap (1991) studied the more recent climate and vegetation history from four peat sections in South Spitsbergen and West Edgeøya and Barentsøya. The sections were dated to cover approximately the last 300−1300 years in between 22 cm and 40 cm deep peat layers. The pollen assemblage was fairly homogenous throughout. One of the sections showed that it had been rich in vascular plant species but progressively impoverished to relatively poor in species similar to the vegetation of today. This is probably due to expansion of mires which resulted in a decrease in nutrient availability. Overall van der Knaap (1991) concluded in his study that the past vascular plant vegetation has been relatively constant throughout the recorded period and similar to that today.

Birks (1991) reconstructed Holocene vegetation and climate history in west Spitsbergen, Skardtjørna, using macrofossil analysis. The basal sediment was dated to 8100 BP. All the fossil taxa are represented in the flora of Svalbard today, but not all of them occur at the west coast today. The oldest sediments had greatest macrofossil concentrations and number of taxa and the youngest sediments had low concentration of macrofossils and low number of taxa. That indicates that in general the flora has become slightly poorer. The sequence shows the evidence for gradual climatic cooling between 4000 and 2500 BP. The open sparse vegetation with much bare ground similar today has existed since about 2500 BP. Birks (1991) concluded that the composition of the vegetation around the study area has not changed substantially since 8000 BP but the vegetation cover has decreased.

Conclusion

Burrowed peat layers in Rosenbergdalen, Edgeøya, indicate that climate was warmer and moister in the period when they were formed, because today there is not such bog formation on those areas (van der Knaap 1989). The pollens of flowering plants were more abundant during warmer Subatlantic period indicating more extensive vegetation (Hyvärinen 1972). Also, pollens from *Ranunculus sulphureus*, *Oxyria digyna* and some occasional fern spores indicate more humid conditions because these species are growing in moist habitats today (Hyvärinen 1972; Rønning 1996).

The same result was found in the study made by macrofossil analysis. Birks (1991) macrofossil study indicates climatic deterioration between 4000 and 2500 BP. Before that vegetation was more extensive but after that vegetation became more sparse starting to repsesent the vegetation of today. Also, van der Knaap's (1988, 1991) studies indicates, that the vegetation in eastern part of Spitsbergen and in northern Edgeøya during the last 300 AD − 4500 BP was rather similar to the vegetation of today. The evidences for Subatlantic cooling in northern hemisphere about 2400 BP was traced in one of the studies (van der Knaap 1988).

Svendsen & Mangerud (1997) came to similar conclusion on regarding the climatic history from their study of glacial and climatic variations in Holocene in Svalbard. They found out that ice melted quickly away after climate started to warm up around 10 000 BP. The following 6000 years were warm as "climatic optimum". Climate started to cool again 4400−4000 BP and existing glaciers started to expand. The temperature was coldest during the "Little Ice Age" 1400−1800 AD. However, the "Little Ice Age" was not directly traced by palaeoecologial studies. Van der Knaap's (1988) study showed two deteriorations in climatic from 4500 to present. He estimated that the first major one was the cooling happened on the beginning of Subatlantic but as the samples weren't dated, it cannot surely said what climatic changes they were reflecting.

Discussion

One problem in palaeoecological studies in the High Arctic is that it is hard to find suitable peat layers (van der Knaap 1988). Peat depositions are scarce and they can be hard to detect. Also, permafrost makes it difficult to penetrate under unfrozen top layer. Also suitable lakes for sediment coring are spares. When suitable relatively undisturbed peat or lake bottom sediment is found, the recovered pollen amount can be still very low. The vegetation is sparse in high arctic and produced pollen is minimal due to scarcity of vegetation (van der Knaap 1990). Many plants are sterile or reproduce viviparously. Even if there is not fossil evidences that some plant species has been growing in the area, it does not mean, that it has not been present there (Birks & Birks 1980). The fossil of that species can be absent even it has been growing in studied area.

Differences in pollen amounts in different layers in peat or sediment cores may not be entirely due to differences in the local vegetation but also reflect different distances from the sites to source plants in similar vegetation (van der Knaap 1991). The highest concentration of pollens is around the source plants and the concentration drops within the distance from the source (van der Knaap 1990). Also, changes in peat lands hydrology may effect the composition of species that produced pollen.

Different plants species produce different amount of pollen. So, the abundance of a plant species is not directly correlated with the abundance of pollen (Birks & Birks 1980, van der Knaap 1990). The difference between plant species, in the amount of produced pollen depends on different things, such as whether the plant species is insect, wind of self pollinated (Birks & Birks 1980). Usually, wind pollinated plants produce large quantities of pollen to ensure pollination. Insect pollinated plants produce less pollen and cleistogamous plants only a very low amount of pollen. Thus, when reconstructing the past vegetation these specific differences must be born in mind and usually it is not possible to reconstruct an accurate population size for individual species.

Also, the dispersal distance of pollen varies a lot among species (Birks & Birks 1980). Some pollen, such as pollen of some crops, don't disperse much out of the area at all and on the contrary for example pollens of *Pinus* can be commonly found in the sediments of high arctic, thousands of kilometres out from its origin. There have been done some calibrations of how much pollen some species produce but those calibrations are site specific and not applicable from one place to another. It is understandable that the same species can produce different amount of pollen depending on what kind of environment it lives in.

The advantage for studies made by macrofossil analysis compared to pollen analysis is that macrofossils can be often recognized for more precise taxonomic level (Birks & Birks 1980). Often pollen grains can be recognized only for generic or family level which makes inferences broader and less precise. Some plant species, such as *Dryas octopetala*, produce just a little quantity of pollen but leaves identifiable macrofossils. Also, plants species which have very fragile pollen (such as *Juncus* and *Luzula*) are preserved as macrofossils.

Macrofossil analysis is most valuable when reconstructing the wetland and aquatic habitat communities and environments (Birks & Birks 1980). On the other hand, pollen analysis is better for constructing upland vegetation. Macrofossils are not usually transported far from their origin. With pollen analysis regional vegetation can be reconstructed but macrofossils are representative only for local vegetation. Macrofossils and pollen are often complementary and combining these two fossils analysis can provide more complete picture of the past vegetation.

Several different methods need to be combined to get a more realistic idea about the origin of the present day distribution of plants. When molecular studies have been applied, rather than traditional phytogeographical studies, it has been found that species may have different phytogeographical histories even if they have similar geographical distribution in today (Abbott & Brochmann 2003).

Palaeoecological studies show that vegetation in Arctic has changed due changes in the climate. Now we are living through an expected warming in Arctic. This may cause changes in plant distribution and shift in the abundance of different species. ITEX (International Tundra Experiment), which studies impacts of long-term experimental warming and climate variability on tundra ecosystems, aims at determining the responses of selected tundra plant species and vegetation to global warming (Jónsdottir 2004). It has been found that particularly herbaceous plants growing in warmer conditions have improved their growth. Also reproduction effort has increased especially in high arctic areas. Moreover, in a longer time perspective, shrubs deciduous shrubs will increase in abundance. Some species in Svalbard are living only in the most favourable conditions in limited areas (Elvebakk 1994). These species (such as *Betula nana*, *Hierochloë alpine* and *Vaccinium uliginosum* ssp. *microphyllum*) are thermophilous and require relatively warm and sheltered growing conditions. If growth conditions became more favourable generally on Svalbard, it is possible that distribution of those plants increase.

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