Snorre Henriksen

Spatial and temporal variation in herbivore resources at northern latitudes

NTNU

Innovation and Creativity

Preface

Spring 1998, I met Prof. Bernt-Erik Sæther and Ronny Aanes over a cup of coffee in the canteen at Rosenborg discussing a potential master thesis. This meeting was the start of what is now a 10 year long Svalbard story, and Bernt-Erik and Ronny have stuck with me all this time. Like a poet, Bernt-Erik has the ability to say many things with few words, which can sometimes be a challenge for the recipient of his scientific poetry. He has helped me to put things into perspective and has constantly reminded me not to write exclusively for the Society of Svalbard Reindeer Researchers. Ronny and I have had many great discussions about science as well as my special topics during the years, and he has shared many of his ideas with me. He has demonstrated a remarkable confidence in my scientific and field skills, even though I may have lost or destroyed a thing or two during my years in the field. Thanks also for shortening my life significantly due to passive smoking of your Teddy without filter at Monaco. It was Dr. Nils Are Øritsland, the former director of the Norwegian Polar Institute (NPI), who introduced us to Brøggerhalvøya and Sarsøyra in 1998, and granted us access to his "herds". Unfortunately, Nils Are is not with us anymore, but we will remember him for the great person he was and what his work has meant for us and many more.

Many persons deserve a bucket of thanks for helping me both on my thesis as well as my physical and mental well being. Some of these are "the Lost Boys" Tomas and Henrik for getting me out of the office once a week. The creative statistician Thor Harald, who never runs out of ideas of how to test things. vidaR, who never misses a detail. Ivar for his endless patience with R-questions. Brage for countless discussions and Sigrun for making life a little bit greener. In addition, thanks to the great ladies at the department; Ingunn, Lisbeth and Tove for helping me with the administrative part.

A lot of people have provided help and assistance in the field. Some of the data used in this thesis is actually based on fieldwork we did as far back as 2000, when glaciers were large, crevasses small, and the Zodiac didn't have any holes. Since then I, and my allied in the field, Brage, have received help from; Mathias Eriksson, Werner Lars Georg Johansen, Helge Skoglund, Jukka Pekka Ikonen and Morten Snøspurv. I have also had a great team of co-authors in Tromsø from whom we also got the reindeer data, satellite images and juniper samples: Dr. Torkild Tveraa, Dr. Per Fauchald, Dr. Kari Anne Bråthen, Dr. Kjell Arild Høgda and Prof. Rolf A. Ims. I would also like to

Trondheim, August 2007

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The thesis is based on five papers, which are referred to in the text by their Roman numerals:

I   Hansen BB, **Henriksen S**, Aanes R, Sæther B-E (2007) Ungulate impact on vegetation in a two-level trophic system. Polar Biology 30:549-558

II   **Henriksen S,** Aanes R, Grøtan V, Sæther B-E (manuscript) Spatial synchrony and the effects of climate on the growth of a high arctic dwarf shrub.

III   **Henriksen S**, Herfindal I, Aanes R, Sæther B-E, Høgda K-A, Tveraa T, Bråthen KA, Ims RA (manuscript) Spatio-temporal patterns and the effects of climatic variation in common juniper growth.

IV   Herfindal I, **Henriksen S**, Aanes R, Tveraa T, Sæther B-E, Høgda KA, Bråthen KA, Fauchald P, Ims RA (manuscript) Environmental variables as proxies for reindeer performance.

V   **Henriksen S**, Aanes R, Sæther B-E (manuscript) The effect of ground-icing on two high arctic plant species; an experimental study.

SUMMARY

Herbivores may affect plants directly through foraging, trampling and fertilization or indirectly through altered competitive relationships between plant species. In addition, herbivores may cause indirect interactions between species that do not compete for the same resources, but are object to grazing from a shared herbivore. A re-introduction of a large herbivore, the Svalbard reindeer (*Rangifer tarandus platyrhynchus*), was found to generate a strong trophic top-down effect on the vegetation, including a reduction in cover of mosses, vascular plants and lichens. This supports the "exploitation ecosystem hypothesis". This caused a reduction in reindeer carrying capacity K and sustained reduction in herbivore densities. Plant groups differed in the rate of recovery after the reindeer population peak, and lichens did not show any sign of recovery. Consequently, the irruption caused a shift in the composition of the vegetation.

In addition to top-down effects of herbivores on plants, plant-herbivore interactions may work through variation in foraging resources caused by variation in environmental conditions. We investigated which climatic variables were able to explain local growth of two long-lived evergreen plant species *Cassiope tetragona* and juniper (*Juniper communis*), sampled over a large geographic area at Svalbard and Finnmark (Norway), respectively. Both species responded positively to high summer temperatures. *C. tetragona* growth was also negatively related to the summer Arctic Oscillation (AO) index and number of overcast days in July. Juniper growth was positively associated with a high winter AO, September temperature and precipitation. Juniper growth was positively correlated with a rapid phenological development and high net primary production (measures derived from satellite images), growing conditions that are generally recognised to decrease nutritional value of plants as forage for ungulates. Juniper with high average growth responded more to high a winter AO/NAO, summer temperature and derived spring NDVI than plants with low average growth. We found that juniper was able to capture important environmental factors and can thus be used as a proxy for foraging conditions.

Because temporal variation in climate affects plants at both temporal and spatial scales, it may cause synchronised population growth rates among plants and subsequently ungulate populations over large distances. We analysed whether growth of

C. tetragona and juniper was correlated among localities and to what extent this correlation decreased with distance was performed. In addition, we analysed which climatic variables could be capable of generating synchronised growth. The spatial synchrony was high over large areas for *C. tetragona*. However, which climatic variable caused this synchrony was not possible to identify. The spatial correlation in juniper growth was on the other hand low and even increased slightly with increasing distance.

Body growth in ungulates is influenced by both demographic and environmental variability. The effect of demographic stochasticity is density dependent. Autumn body mass (measured as carcass weight) of semi-domesticated reindeer calves (*R. t. tarandus*) in Finnmark, northern Norway, was negatively affected by high population density. Furthermore, there was a negative relationship between calf body mass and unfavourable winter conditions (mainly through heavy snow accumulation), whereas body mass was positively associated with slow plant development during summer. Accounting for the within-herd variation in population density did not affect the relationship between environment variables and body mass to any extent. There was a negative relationship between calf body mass and juniper growth, indicating that juniper can capture environmental variation of importance for reindeer growth. Accounting for both density and juniper growth resulted in several changes in how environmental variables affected reindeer body mass, but still the general impression of negative effects of snow rich winters persisted.

Global climate is warming rapidly. One result of the change in global climate is the frequency of periods with temperature above 0°C during winter will increase in arctic regions. If above zero temperatures are combined with precipitation, this can cause formation of ground-ice or crusty, hard snow. This will directly affect forage availability for herbivores, but little is known about how it may affect plant species of importance for herbivores. We experimentally constructed ground-ice during early winter on high arctic heath vegetation to simulate the effect of an icing event on plant performance. Growth response of a small willow (*Salix polaris*) and a rush (*Luzula confusa*) was measured the following summer. Both species showed some response to icing. *S. polaris* that had been subject to experimental icing, showed increased growth later in season compared to the control groups. *L. confusa* showed a weak negative response throughout the summer to the experimental icing event.

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GENERAL INTRODUCTION

The influence of large herbivores on vegetation, ecosystem and landscape dynamics have been increasingly acknowledged (Hobbs 1996; Danell 2002; Danell et al. 2003; Rooney and Waller 2003; Côté et al. 2004). Our understanding of the importance of landscape pattern for large herbivore dynamics has also improved (Turner et al. 1994; Illius and O'Connor 2000; Walters 2001). However, at the landscape scale, herbivore-vegetation interactions can be quite complex, involving many interacting factors such as plant competition, topography, climate, disturbance regimes and biogeochemical cycles (Danell 2002). Plants have evolved under varying herbivore pressure, both in strength and duration, resulting in a range of "strategies", such as resistance or tolerance through chemical substances, in relation to herbivory. Plants' ability to develop such defence strategies may vary between species and even within species in different regions or habitats, and also depend on the availability of resources (Coley et al. 1985). It is also assumed that there is a trade-off between growth and defence (van der Meijden et al. 1988, but see Lehtilä 1996), and the limited resources available and the short growing season in arctic and alpine areas may not allow for an efficient defence (de Jong 1995; Dormann 2002). Thus, many arctic and alpine plants have a limited range of defence strategies which will influence how they are affected by grazing.

Changes in management of large ungulates have lead some populations to become very abundant, resulting from altered harvesting regimes and reduced predation since many of the large predators in Europe and North America have been drastically reduced in numbers or even become extinct (Côté et al. 2004). Introduction of species to previously uninhabited areas may also cause populations to irrupt. An irruption is characterised by a rapid increase in population numbers, followed by a crash to lower abundances and then increase to a carrying capacity K lower than peak abundance (Leopold 1943; Riney 1964; Caughley 1970, 1976; McCullough 1997; Forsyth and Caley 2006). This made researchers early last century to realize that herbivores can have negative ecosystem effects (Leopold 1933; Leopold et al. 1947). However, it has always been inherently difficult to assess the relationship between the herbivore and its resources, and the effect of variation in climate or resources may be density dependent (Sæther 1997). Traditionally, field ecologists have collected data on plants at small

spatial scales with varying methods and reliability (Kerr and Ostrovsky 2003). Alternatively, foraging resources has been classified according to the availability of vegetations types, assuming some relationship between the composition of forage species in the vegetation type and the quality and quantity of food (e.g. Skogland 1983). Furthermore, since such data often are collected only once a year, it is not suitable for identifying the most important period of plant growth for the herbivore and when the impact of herbivory on the plants is greatest. However, herbivores may exhibit large temporal and spatial variation in resources, and better ways of obtaining such data was needed. Proxies have consequently become important in the research on plant-herbivore interactions since they can provide information related to foraging conditions on finer temporal and spatial scales. In research, a proxy variable is something that may not in itself be of any great interest, but from which information regarding a variable of interest can be obtained. Even though a proxy normally can not provide information on what the herbivore eats, it can provide important information on temporal and spatial variation of the resources in general.

Herbivores are influenced by climate both directly and indirectly, where indirect effects may be mediated through altered foraging conditions (quality, quantity and availability). Even though plant response to variation in climate differ between species and functional groups, primary production is generally positively affected by an increased length of growing season and high temperatures on a short time scale (Arft et al. 1999; Callaghan et al. 2004). From a herbivore's perspective, variation in weather during the growing season primarily affects nutritional quality and the net primary productivity, i.e. the quantity, of the forage resources. However, plant quality and quantity are often negatively related when these entities are affected by the climate. Warm and dry weather causes rapid plant development and growth, resulting in reduced nutritional value at northern ranges (Bø and Hjeljord 1991; Albon and Langvatn 1992; van der Wal et al. 2000). Fluctuations in climate could be correlated over large areas (Koenig 2002), which could cause synchronised plant responses over large spatial scales (Koenig and Knops 1998), ultimately causing synchronised herbivore population growth rates (Bjørnstad et al. 1999; Lande et al. 1999). The risk of local or global population extinction is influenced by the spatial scale of synchrony (Allen et al. 1993; Bolker and Grenfell 1996; Heino et al. 1997; Palmqvist and Lundberg 1998; Engen et

al. 2002). However, plants may respond differently to variation in climate on a larger scale, e.g. due to different phenological stages, which could be caused by e.g. different altitude (Albon and Langvatn 1992; Mysterud et al. 2001a; Mårell et al. 2006), allowing herbivores to escape potentially negative effects of synchronised variation in resource levels by seasonal movements. In high arctic areas, the vegetation is often limited to lower altitudes only, but by visiting snow beds, newly emerged forage can be found even late in season.

In northern regions especially, there has been little research on herbivore resources at larger scales. The present thesis can be viewed as a natural extension of the research which has been done on the observed population dynamics in northern ungulates. The following main questions are addressed in the present thesis: What are the environmental factors explaining plant performance and can they explain synchrony in fluctuations in growth? How does variation in environmental conditions influence body mass in ungulates, and can tree-ring data be used as a proxy of foraging conditions? And finally, by what mechanism and to what extent may ungulates alter their forage resources? Results from these studies can improve our mechanistic understanding of ungulate fluctuations by including measures of plant growth. Since there is an interaction between the herbivore and its resources, the present thesis will hopefully fill a gap of knowledge, so that future studies on population dynamics can design studies to reduce the noise term by including variation in resources in the models.

MATERIAL AND METHODS

Study area

Data were collected from the high arctic archipelago Svalbard, Norway, and from Finnmark, the northernmost county of mainland Norway. The climate on Svalbard is strongly affected by the North Atlantic current, resulting in a mild and oceanic climate during winter compared to other areas of these latitudes. However, the winter climate is highly variable and periods with temperature above 0°C and rain has been recorded at all months. Finnmark is characterised by a strong coast-inland gradient, where the

interior of Finnmark has a typical continental climate; cold and dry winters and relatively warm summers. Coastal areas receive more precipitation; both in summer and in winter (see Bråthen et al. 2007 for a more detailed description).

In 1978, 15 Svalbard reindeer (*Rangifer tarandus platyrhynchus*), 9 females and 6 males, were reintroduced (Aanes et al. 2000, 2002) to Brøggerhalvøya (78°55' N, 11°50' E), an area where the reindeer had been hunted to extinction at the end of the 19th century (Lønø 1959). Three of the males were lost during the first months. The long period without any large herbivores had lead to lichen dominated vegetation, which is known to be highly preferred food for reindeer during winter (Skogland 1984) due to its high content of carbohydrates. Fieldwork for paper I was performed at Brøggerhalvøya. Field work on paper II and V was performed on central parts of Svalbard, i.e. Adventdalen, Reindalen and Colesdalen (between 78°02' - 78°16' N, 14°55' - 16°50' E), where reindeer likely have been continuously present for thousands of years. These areas are characterised by slightly higher summer temperatures and less precipitation than Brøggerhalvøya. Topographically, western Finnmark is characterised by steep hills, deep valleys and narrow fjords. In coastal Finnmark downy birch (*Betula pubescens*) are found in a narrow belt along the coast, and in valleys extending into the mountain ranges. The forest line in western parts of Finnmark is at 300-500 m a.s.l. while at has no forest (exposed sites) or a forest limit at 100-150 m a.s.l. Interior parts of Finnmark (Finnmarksvidda) have more homogenous topographic and vegetation characteristics. The juniper sampling sites in Finnmark was located in the low alpine zone which is characterised by low shrub tundra in this region (see Bråthen et al. 2007).

Study species

Two sub-species of Rangifer have been in focus in the present thesis; Svalbard reindeer and semi-domesticated reindeer (*R. t. tarandus*). Svalbard reindeer is a small-bodied wild reindeer which has evolved practically without any enemies. Polar bears extremely rarely kill reindeer (Derocher et al. 2000) and polar fox may occasionally kill calves (predation rate unknown but assumed to be low). As a result, the Svalbard reindeer is rather sedentary, does not appear in large herds and do not perform long seasonal migrations. The lack of seasonal migration may also be explained by small variation in

forage resources on a large spatial scale, and physical barriers such as glaciers, open water and mountains. They can rapidly increase their body mass during summer through deposition of fat, which is important for survival during the winter. The population at Brøggerhalvøya increased rapidly after reintroduction and peaked at about 360 animals in 1993, but a combination of an extreme climatic event and high reindeer numbers reduced the population to below 80 animals during winter 1993-94 (Aanes et al. 2000). Post-crash population sizes have ranged between 100 and 200 animals approximately (Aanes et al. 2000). Due to physical barriers, migration rates to neighbouring areas are probably low, but unknown.

Reindeer husbandry has long traditions in Norway, and reindeer in Finnmark is normally free ranging and only gathered during marking of calves, slaughter and before moving in and out of winter pastures. The data on reindeer from Finnmark were collected through the Ecosystem Finnmark project (Fauchald et al. 2004a), where reindeer numbers were counted annually in spring while the body mass of calves were obtained as carcass weight at autumn slaughtering for each herd.

Two long-lived evergreen plant species were collected for retrospective analyses of temporal and spatial variation in growth caused by variation in climate. From Svalbard, *Cassiope tetragona* (hereafter *Cassiope*) was collected. *Cassiope* is a long-lived evergreen, dwarf-shrub with circumpolar distribution that is known to live 100+ years (Rayback and Henry 2006). The plant produces two alternating sets of opposite leaves along the stem, forming four distinct rows. The leaves remain attached to the stem for 20+ years (Callaghan et al. 1989), but leaf scares can be retained over the full length of the shoot (Johnstone et al. 1997). Leaves remain green and photosynthetical active for 3-5 years. Small leaves are normally formed in the fall each year forming a wave-like pattern of leaf-lengths (Johnstone et al. 1997). Furthermore, a dark band is visible between annual growth increments (Vie 1998). *Cassiope* growth has been found to be most responsive to temperature and precipitation during summer but also to winter conditions, as well as weather during the previous year (Callaghan et al. 1989; Johnstone and Henry 1997; Vie 1998; Rayback and Henry 2005). A large scale climate index, the Arctic Oscillation, has also been shown to be correlated with *C. tetragona* growth (Aanes et al. 2002; Rayback and Henry 2005). Seventeen years of annual growth was measured from a total of 140 plants sampled at 25 localities, ranging from

coast to inland over a maximum distance of 133.5 km between localities at Brøggerhalvøya, Adventdalen, Reindalen and Colesdalen (Fig. 1). From Finnmark, common juniper (*Juniper communis*) twigs were collected during summer 2003, from an area covering the same ranges as the reindeer herds (Fig. 2). Juniper is a small dioecious coniferous tree often depressed to shrub-like forms in arctic and alpine environments. Annual growth is detectable as rings on the stem due to distinct periods of dormancy during the cold season. Juniper is, to our knowledge, not used as forage by large herbivores to any great extent in the study area. Measurements of annual growth from 114 individuals sampled at different localities from the period 1982-2002 were used.
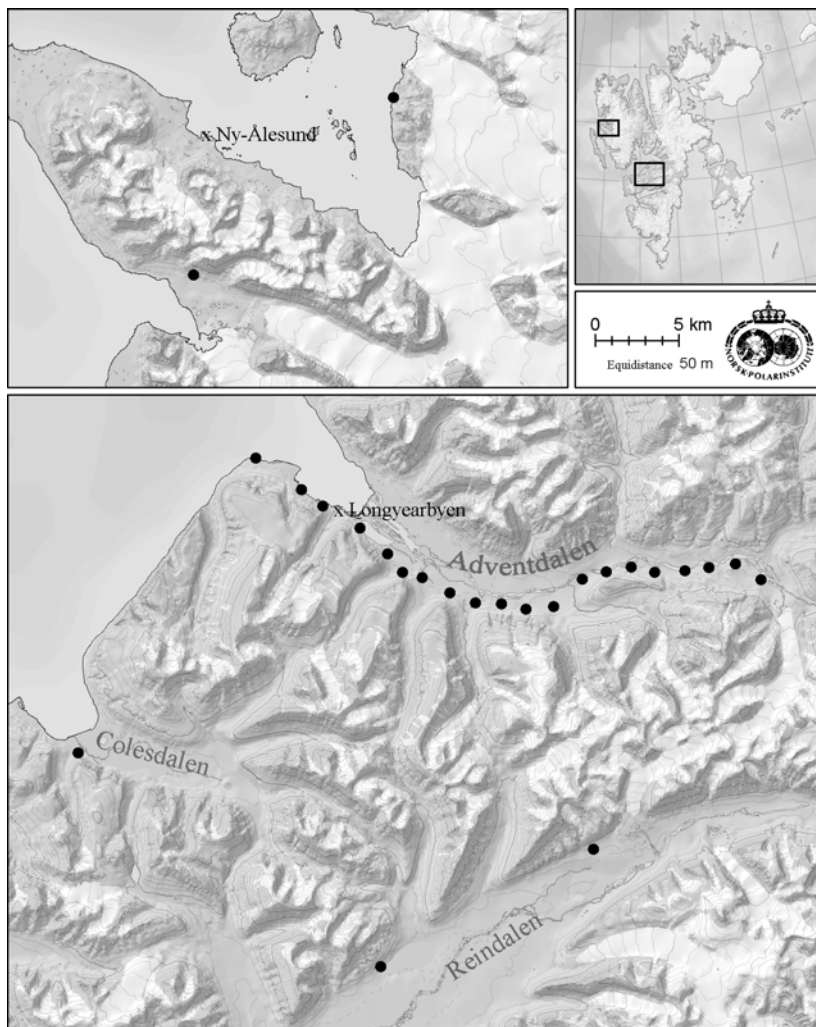

Figure 1 *Cassiope* sampling localities (dots) on Svalbard.
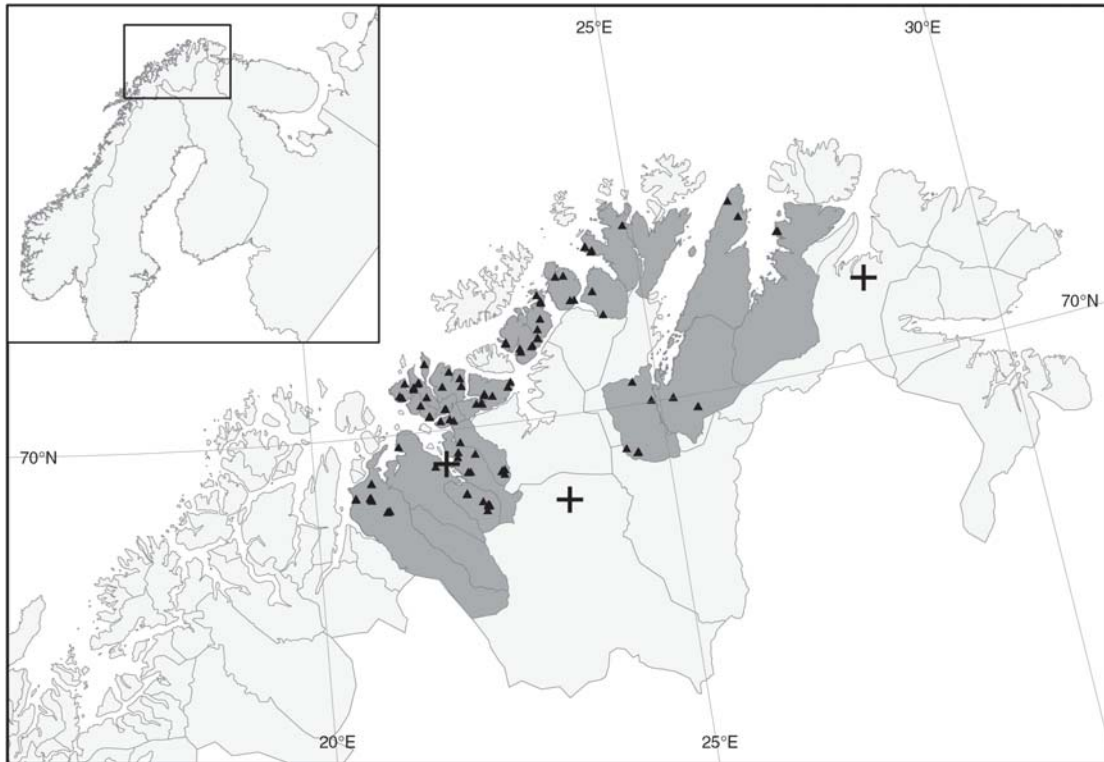
Figure 2. Localisation of the juniper samples (triangles), reindeer districts (dark grey)
and the weather stations (cross) in Finnmark, northern Norway.

Climatic data and satellite-derived indices of plant phenology

Two types of climatic data were acquired; local measurements of temperature,
precipitation, snow depth and number of overcast days, in addition to measures of large
scale climate (the North Atlantic Oscillation (NAO) and the Arctic Oscillation (AO)). In
arctic regions, the number of meteorological stations is limited, but in the study area on
Svalbard the distance between plant sampling localities and meteorological stations was
relatively short. In Finnmark, only three stations provided adequate data from the
complete period. This may affect the relationship between biological and
meteorological parameters that were compared over a relatively large spatial scale.

The NAO is a large scale climate phenomenon influencing temperature and
precipitation in the North-Atlantic region (Hurrell 1995), and has been widely used in
ecological research (Hurrell et al. 2003; Mysterud et al. 2003). The NAO is expressed as

an index calculated from the difference in normalized sea level pressure between Lisbon, Portugal, and Stykkisholmur, Iceland. The index may also be based on values from two other southern stations, i.e. the Azores and Gibraltar. A high positive NAO index is generally associated with relatively warm and wet winters in the northern Atlantic coastal Europe, whereas low values tend to result in cold winters with little precipitation (Hurrell 1995). The AO index reflects the mean deviation from average sea level pressure measured through the Northern Hemisphere at longitudes poleward of 20° N (Thompson and Wallace 1998). The AO and NAO are closely related and origins from the same physical entity, but the AO-index is regarded as a better predictor (at least in some areas) of weather at high latitudes (Thompson and Wallace 1998), and has proven to be a better proxy for local temperatures than NAO in the study areas (Yoccoz et al. 2004).

In paper III and IV, satellite-derived indices of plant growth and phenology, based on the annual curves of the Normalised Difference Vegetation Index (NDVI) were used. The NDVI is found to correlate highly with the photosynthetic activity (Myneni et al. 1995). The spatial resolution on the dataset was approximately 8 x 8 km^2. From the annual NDVI-curves, five variables that are expected to reflect plant growth and phenology (Reed et al. 1994; Pettorelli et al. 2005a) were calculated. Onset of spring (OS) is measured as the specific week in spring when NDVI-values reach levels corresponding to leaf burst on birch (*Betula* sp.). Peak time (PT) is the specific week in summer when the NDVI-value reaches its highest level, while Peak value (PV) is the NDVI-value at this time. Derived spring NDVI (DSN) is measured as the NDVI-value at OS minus the NDVI-value at the previous 15-day composite image, and integrated NDVI (IN) is the area below the curve from OS to onset of autumn (OA). Onset of autumn (OA) is the week number in autumn when NDVI-values drop below the corresponding NDVI-value as onset of spring. The estimates of OS and OA are highly correlated to leaf development and yellowing in downy birch (Karlsen et al. 2006).

RESULTS AND DISCUSSION

Plant-herbivore interactions (Paper I)

Irruptive ungulate populations have been reported in several cases where species have been introduced to previously uncolonised areas or where predators have been removed (Leopold 1943; Riney 1964; Caughley 1970, 1976; McCullough 1997; Forsyth and Caley 2006). Leopold (1943) defined an irruption as a rapid increase in population size that will exceed the capacity of resources to sustain the population. This generates a reduction in resources and, consequently, a decrease in K and reduced population growth rates following a population peak (McCullough 1997). Such a reduction in K owing to high grazing pressure may also be termed overgrazing, which (in a range ecology context) may be defined as when "forage species are not able to maintain themselves over time due to an excess of herbivory or related processes" (see Mysterud 2006). The concepts of irruption and overgrazing are important in studies of ungulate population dynamics, but difficulties in obtaining time series of population growth rates and plant primary production or composition have resulted in few studies considering these effects (but see Klein 1987; McLaren and Peterson 1994; Manseau et al. 1996; Olofsson et al. 2001; Côte et al. 2004).

Assessing the effects of grazing on a plant community is challenging for several reasons. For instance, herbivory does not only affect the plants consumed but also other species due to changes in competitive interactions (Pacala and Crawley 1992; Danell and Bergström 2002). Removing one plant species may promote growth of less preferred or more grazing tolerant/resistant species due to reduced competition. An even more subtle way herbivores and plants may interact is through apparent competition (Holt 1977), which is characterized as an indirect interaction among plant species that do not compete for resources but are object to grazing from a shared herbivore (Reader 1992).

An opportunity to study the effects of grazing in a simple ecosystem with only one large herbivore and no predators was offered when Svalbard reindeer were reintroduced to Brøggerhalvøya in 1978. About 100 years of reindeer absence had allowed the vegetation to recover from previous grazing (Øritsland and Alendal 1986), and was characterised by thick lichen mats (Brattbakk 1986). The introduced reindeer

population was counted annually and the vegetation was monitored at several occasions during the period 1979-2005 (Holand et al. 1981; Scheie and Grøndahl 1990; Ødegård and Ranheim 1996; Ditlefsen 2000; this study). In the study of the plant-herbivore dynamics at Brøggerhalvøya, we documented that the increase in reindeer numbers generated a rapid decline in cover of all plant groups and particularly for vascular plants and lichens. Following the reindeer population crash and apparent long-term stabilisation at lower densities, mosses recovered completely and even exceeded their original cover. In contrast, vascular plants recovered only partly, and the previously dominant lichen mats were depleted and showed no sign of recovery. This resulted in a shift in the vegetation composition from lichen dominated to a more moss dominated vegetation and suggested a long term reduction in K, as supported by the sustained reduction in herbivore numbers. This supports the "exploitation ecosystem hypothesis" (Oksanen et al. 1981) predicting top-down control of vegetation by herbivores in moderately unproductive areas, where functional predators are predicted to be absent. Further, the reindeer diet at Brøggerhalvøya seemed to change during the irruption (Ødegård and Ranheim 1996) as highly preferred species became less abundant and more grazing tolerant/resistant species increased in abundance. The shift in plant composition likely forced the animals to include larger proportions of low quality forage, such as mosses, in their diet (see Ødegård and Ranheim 1996). Such a change in diet composition may ultimately have consequences for growth and reproduction, although Svalbard reindeer are more adapted to a moss dominated diet during winter than other subspecies of *R. tarandus* (Sørmo et al. 1999). Because the reindeer population density at Brøggerhalvøya has remained relatively low following the population crash, the complete lack of lichen recovery suggests that even low herbivore pressure will permanently suppress forage lichens in this study system, probably owing to the non-migratory behaviour of Svalbard reindeer combined with the slow growth rate and negative impact of trampling on lichens (Skuncke 1958; Bayfield et al. 1981; Cooper and Wookey 2001).

Effects of climate on plant growth and reindeer body mass (Paper II, III, IV, V)

Through the research on effects of predicted global climate change, our understanding of the response of different plant species to variation in temperature, precipitation, increased nutritional levels, reduced solar radiation and UV-radiation has improved (Chapin et al. 1995; Arft et al. 1999; Callaghan et al. 2004). This has subsequently improved our understanding for how spatial and temporal variation in weather can influence herbivore populations through variation in plant primary production, and to some extent, the value of plants as forage for herbivores. However, most studies on effects of climate change have focused either on plants, using local weather variables (e.g. Callaghan et al. 1989; Chapin et al. 1995; Havström et al. 1995), or on animals, without data on plants (e.g. Smith et al. 1995; Post et al. 1997; Forchhammer et al. 1998a,b). Few studies have paid attention to how interactions between plants and herbivores will be affected by rapid climate change (but see Brown et al. 1997; Jaksic et al. 1997).

Most of the research on plant responses to climate change has focused on changes in summer climate, as this period is the growing season for plants in northern regions. However, the largest changes in climate are expected to occur during winter, resulting in shorter, warmer and wetter winters - although this general pattern includes large regional and local spatial variation, especially regarding precipitation (IPCC 2002, 2007; ACIA 2004). A shortening of winter is already visible in some areas (Høgda et al. 2001; Parmesan and Yohe 2003; Root et al. 2003). The timing of snowmelt influences the start, and consequently the length, of the plant growing season (Walsh et al. 1997; van der Wal et al. 2000; Wahren et al. 2005; Aerts et al. 2006), which may have great importance for survival, growth and reproduction of northern ungulates (Pettorelli et al. 2005b). Generally, it is expected that an earlier spring and a longer growing season would make forage of high quality available for herbivores at an earlier stage, but it would also cause a phenological shift (van der Wal et al. 2000), i.e. an earlier reduction of forage quality. However, since green plants will be available for a longer time, herbivores are expected to benefit from an extended growing season.

We found that body mass of semi-domesticated reindeer calves slaughtered in the autumn in Finnmark was related to several climatic variables. Deep snow during late

winter and early spring (April and May respectively) negatively affected calf body mass. This was likely a combined effect of increased cost of movement and reduced accessibility to forage, and an effect of delayed spring (Tveraa et al. 2003; Fauchald et al. 2004b). Similarly, the negative effect of a high winter NAO index was probably also related to the snow conditions. Increased body mass was associated with slow plant development during spring (derived spring NDVI) and a high summer NAO, possibly due to a positive effect of cold and wet summers on forage quality, which is known to cause a slow decrease in the nutritional value of plants. However, reindeer weight was not found to be related to summer temperature or precipitation. A negative relationship was found between juniper growth and reindeer weight, further emphasising the importance of forage quality rather than quantity for growth in northern ungulates (Sæther 1985; Sæther et al. 1996; Mysterud et al. 2001b; Herfindal et al. 2006).

In the study on the relationship between climate, NDVI and juniper growth (paper III), we found that the annual growth of individual juniper twigs were not affected by elevation or solar radiation. Solar radiation was measured as a function of aspect and slope from a digital elevation model, however local conditions may be affected by competition for resources such as light and nutrients from other species that can be more important than solar radiation as such. High juniper growth was associated with warm summers, and a warm and wet September. Junipers with high average growth responded positively to a high winter AO and winter NAO, while plants with a low average growth tended to be negatively influenced by high NAO and AO values during winter. Similarly, the positive effect of high summer temperature and derived spring NDVI was stronger for junipers with a high average growth compared to those with a low average growth, which could be caused by local variation in competition for resources.

The growing season is shorter on Svalbard compared to Finnmark, but still many of the same environmental factors affected *Cassiope* as juniper in Finnmark. However, we found no effects of conditions during winter and only one spring/early summer (AO-June) variable was found to influence *Cassiope* growth. *Cassiope* responded positively to high temperatures in July and August, but *Cassiope* growth was a negatively associated with summer AO, June AO, precipitation in July and number of overcast days in July. Many of these environmental variables were highly correlated though.

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However, the summer AO-index had the highest explanatory power on local *Cassiope* growth, illustrating the explanatory capabilities of a large scale index able to capture a composite measure of the weather.

The main focus of consequences of climate change has been on long term changes in average temperature and precipitation and less on stochastic extreme events. It is assumed that the number of warm spells during winter will increase in the future, a trend already apparent in Canada (Shabbar and Bonsal 2003), resulting in more frequent rain on snow events (ROS) or ground icing. These events are known to cause a direct effect on forage availability for herbivores since the ground will be covered by ice, or the snow will become hard and impenetrable, resulting in reduced herbivore population growth rates (Forchhammer and Boertman 1993; Aanes et al. 2000; Kohler and Aanes 2004). What is less clear is what these events may do to the plants. It is a well studied phenomenon in agriculture: ice formation on fields can cause loss of crops because plants experience low oxygen levels (anoxia), as well as direct frost injuries (Bertrand et al. 2003). Plants in high latitudes are highly freeze tolerant and are expected to have some resistance to anoxic conditions (Crawford et al. 1994; Phoenix and Lee 2004), but how a long period of ice encasement affects survival and growth the following summer has not been studied as far as we know. Only some anecdotal reports of reduced plant survival exists (Robinson et al. 1998), but it was only found on plants exposed to experimentally increased nutrient levels.

We simulated an icing event on Svalbard. In late November, plants were covered by a 10-15 cm ice sheet, similar to what was reported from Ny-Ålesund during the 1993-94 winter (NA Øritsland pers. comm.), and comparable to what have been measured in parts of the study area in recent years (R. Aanes and B.B. Hansen, unpublished data). The experimental icing was expected to have negative effects on plant growth the following summer and possibly a negative effect on plant survival (Phoenix and Lee 2004). This is due to the anoxic conditions which the plant is subject to, possibly forcing them to apply less efficient metabolic pathways. Surprisingly, the effect was very small, and even tended to be positive for *S. polaris* in late season, an important forage plant for Svalbard reindeer. The rush *L. confusa* displayed a weak negative response. However, only two plant species were considered in this study and research on other species and also on possible delayed effects should be conducted

before concluding that an icing event has little or no negative impact on plants. Furthermore, changes in nutritional quality of the plants after this experimental extreme weather event were not measured. Hence, if the quality of the plants were significantly reduced following an icing event it likely will affect the consumers in a negative way. However, since nutritional quality is inversely related to vegetative growth (van der Wal et al. 2000), we assumed that changes in quality relative to quantity will not be very large.

Proxies in ecological research (Paper II, III, IV)

Even though great advances have been achieved in understanding the contribution of deterministic and stochastic events on variation in animal population growth rates (Engen et al. 1998), less knowledge has been achieved on the relationship between herbivores and their resources in northern regions. Few studies have actually been able to link forage availability, quality and quantity on larger scales to population characteristic (but see Albon and Langvatn 1992). Instead, proxies of plant performance, such as NDVI (Reed et al. 1994; Myneni et al. 1995), meteorological measures or large scale climate indices (Stenseth et al. 2003; Weladji and Holand 2003), altitude (Albon and Langvatn 1992; Mysterud et al. 2001a) and tree-rings (McLaren and Peterson 1994), or a multitude of these measures (e.g. Aanes et al. 2002; Herfindal et al. 2006; Mysterud et al. 2007; Tveraa et al. 2007) have been used in population ecology studies. Hence, proxies have proven valuable in explaining population dynamics, but how some of these proxies are related to important variables for herbivores is still poorly understood.

Tree rings and dendrochronological analyses

As a plant species not selected as forage by large Scandinavian herbivores, the juniper have both advantages and disadvantages for the purpose as indicator of plant response to environmental variation. Because it is very little browsed, its performance is only to a small extent influenced by variation in herbivore densities, and may thus be a good indicator of variation in climate irrespective of grazing pressure. Further, the radial

growth provides data on growth that cannot be obtained from the selected forage species, except some deciduous tree-species (Andersen and Sæther 1996). The performance of forage species is likely to be affected by variation in grazing pressure (Bråthen and Oksanen 2001; Tømmervik et al. 2004; Bråthen et al. 2007). However, the measure of juniper radial growth as proxy for the performance of grazed plant species has less value if there are large differences between species in the response to environmental variability. Several studies indicate that the vegetation response to climate variation to a high extent is similar, at least within functional groups of plants, and particularly when looking at the direction of response to an environmental variable (Chapin et al. 1995; Kellomäki and Kolström 1994; Arft et al. 1999; Lenart et al. 2002; Post and Stenseth 1999; Callaghan et al. 2004). Further, the response seems to be valid over large distances (Kellomäki and Kolström 1994; Post and Stenseth 1999; Arft et al. 1999), and particularly within vegetation zones (Arft et al. 1999). It was found that juniper radial growth was negatively related to reindeer calf body mass in the autumn. Calf body mass was generally lower in years with high juniper growth. Because there is commonly a negative relationship between the plant performance (measured as. growth rate) and the quality of the plant as forage, these findings suggest that reindeer calf growth rate is not limited by plant quantity during summer, but rather variation in the quality of the forage. Accordingly, we conclude that using juniper as a proxy for performance of forage species of large herbivores is valid.

Meteorological data

Meteorological stations have provided high-accuracy data with high spatial resolution since the 20th century. Measures like temperature, precipitation and snow-depth are found to explain many ecological patterns. However, in most studies, one depends on weather stations already established, and these may be located far from the study area. As most weather systems depend on larger weather phenomena, like the North Atlantic Oscillation (NAO), Arctic Oscillation (AO) or El Niño Southern Oscillation (Stenseth et al. 2002), using these gives a more general picture of weather conditions within a specific month, season or year (Hallett et al. 2004, Hurrell 1995). However, the effects of these weather systems will vary spatially, e.g. by moving from coastal to continental

areas (Hurrell 1995), or with elevation and topography (Mysterud et al. 2001b). A thorough investigation of the relationship between local climate and AO/NAO was not performed. However, in Finnmark, a high winter NAO was negatively associated with snow depth in May, and summer NAO and summer temperature was positively associated. At Svalbard, AO-June was found to be positively correlated with precipitation in July and the summer AO-index (see Aanes et al. 2002) were found to be associated with cold and wet summers (results not presented). In the studies of the relationship between climate, juniper and reindeer in Finnmark, both NAO and AO were included in the analyses. Due to the high correlation between these climate indices and that they basically originate from the same physical phenomenon (Thompson and Wallace 1998), this may seem unnecessary. Still, the relationship between local climate and these indices is not fully understood, and more importantly, there may be some differences in their ability to capture environmental conditions of importance for plants and animals. This was evident since they differed to some extent in their ability to explain variation in both juniper growth as well as reindeer calf body mass in the autumn.

Satellite-derived indices

Satellite-derived phenology indices such as the NDVI have provided data on plant phenology and primary production on a temporal and spatial scale which was unheard of a few decades ago. However, the spatial resolution of those indices imposes some limitations and challenges (see Pettorelli et al. 2005a for a review). Some of these limitations are related to the fact that herbivores forage selectively, selecting plants and plant parts based on nutritional value, biomass, availability etc. (Danell and Bergström 2002). Consequently, the animal only samples a small fraction of the available biomass from which the NDVI is calculated. Knowledge about how forage plants respond relative to other plants is of great importance if the relationship between climate, plant response and herbivore forage selection, and consequently growth, survival and reproduction is to be fully understood. In addition, knowledge of animals' spatial and temporal movement and forage preferences at different times is important. In a heterogeneous landscape, such as the coastal areas of Finnmark, the spatial resolution of

the satellite images may in some cases have a limited ability to track changes in important reindeer forage resources. Furthermore, since plant species distribution and primary production can vary greatly over relatively short distances, e.g. due to increased elevation, an 8 x 8 km^2 pixel may not capture important areas or species for a selectively foraging herbivore. In Finnmark, the juniper radial growth was found to be positively related to a high derived spring NDVI, high peak values, early peak time and a high integrated NDVI. In addition, a positive relationship between the reindeer calf body mass and derived spring NDVI was found.

This concludes several strengths and drawbacks of both satellite-based environmental indices, and indices based on meteorological observations or weather systems; 1. Indices from satellite images give a high spatial resolution while meteorological observations are collected from the closest weather station, not necessarily close to the study area. Large scale weather system based indices do not have a spatial component. 2. Indices from satellite images are more direct measures of the vegetation, and give both qualitative and quantitative representation of vegetation components. Weather observations measure factors that probably affect vegetation. 3. Satellite-derived indices give little information (at least the most commonly and readily available indices) of the environmental conditions during winter, particularly extreme events. Weather indices have, to a certain degree, this ability. 4. All indices are freely available, but satellite-derived indices are not as readily available and often need some processing before they can be used. Thus, there are higher requirements for technical skills in order to use the data (Kerr and Ostrovsky 2003). 5. Dendrochronological data can be used to obtain historic records of plant performance and can function as a proxy for foraging conditions due to the ability of trees to capture a composite picture of environmental variables normally used in analyses of how the environment influence herbivores.

Climate and large scale spatial and temporal synchrony in growth (Paper II, III)

Synchronised variation in population growth rates have been found among many taxa (see Liebhold et al. 2004 for references). Even though the synchrony as such is fairly easy to demonstrate, the underlying mechanisms of synchronised variation is harder to

find and separate. Among animal populations, three main sources of synchrony have been identified: 1) correlated stochastic influence, 2) dispersal among populations and 3) trophic interactions with species that themselves exhibit synchronous fluctuations or are mobile (Bjørnstad et al. 1999; Koenig 1999; Lande et al. 1999; Liebhold et al. 2004). Correlated fluctuations in climate over large areas (Koenig 2002) could cause similarities in the noise structure of population growth rates over large areas (Ranta et al. 1998). This has been termed the "Moran effect" (Moran 1953). One assumption from the Moran effect is that environmental variables affect the local dynamics similarly over the entire geographical range. However, there could be regional variation in the impact of the same environmental variable on population dynamics (Mysterud et al. 2000; Sæther et al. 2003; Both et al. 2004; Crozier and Zabel 2006), and this will result in less synchrony in population dynamics than expected considering only the correlation in weather variables (Engen and Sæther 2005). Estimating the relative contribution of the factors causing synchrony has proven difficult, and only in resent years has the relative contribution of these factors been quantified (Engen et al. 2005; Grøtan et al. 2005; Sæther et al. 2007). Consequently, by studying plants, many of the difficulties encountered in animal studies may be overcome, or ignored, such as dispersal. But still plants may be affected by a common mobile predator which may affect the synchrony. This problem may be reduced by looking at plants normally not fed upon by any herbivores.

A major contribution to the research on synchrony in plants came from Koenig and Knops (1998), who looked at synchrony in production in large seed crops, known as mast-seeding. Spatial autocorrelation in mast-seeding was found in several species and was detectable between sites up to 2,500 km apart. They also investigated autocorrelation in tree rings and were able to find synchrony in growth at sites up to 5,000 km apart. The synchronised seed production may simply be due to spatially autocorrelated climate, but it may also have evolved as a strategy to reduce seed predation or facilitate dispersal or pollination (Norton and Kelly 1988; Koenig et al. 1994). Consequently, animal populations may have synchronised growth rates due to synchronised variation in resources over large areas, which may influence the risk of local and global extinction (Allen et al. 1993; Bolker and Grenfell 1996; Heino et al. 1997; Palmqvist and Lundberg 1998; Engen et al. 2002).

When using a proxy for studying climate effects on herbivore resources, a common problem is low spatial resolution. Non-linear effect of environmental proxies on ecological processes (Mysterud et al. 2001b) may further complicate our understanding of the relationship between climate, plants and herbivores. With this in mind, an investigation of whether synchrony in fluctuation in plant growth was present in *Cassiope* on Svalbard and which climate variables could be attributed to this synchrony was performed. The plants showed a high correlation in annual growth, even at maximum distance (133 km). Temperature in July and August, together with summer AO, explained a large amount of the local variation in annual growth. However, these variables were not able to explain a significant amount of the synchrony in plant growth. This may be due woody plants being less responsive to variation in climate than e.g. forbs (Post and Stenseth 1999). It could also be the sum of several environmental factors that synchronised *Cassiope* growth of which it was not possible to identify the responsible synchronising driver due to complex relationships between these drivers. Although we still have difficulties in identifying the mechanism leading to synchrony, synchronised variation in plant growth is nevertheless high at the scale of our study area and this could contribute to synchronise reindeer population dynamics if one assumes that other plants species have similar response to environmental variation. However, environmental stochasticity during winter is important for Svalbard reindeer population dynamics (Aanes et al. 2003), and may prevent us from finding such mechanisms. The synchrony in juniper growth in Finnmark was also investigated. Here, synchrony increased slightly (but significantly) with distance between samples, and no environmental factors with ability to synchronise plant growth could be found. This could be due to large heterogeneity in the environment at short distances.

FUTURE PROSPECTS

A central challenge in ecology is to relate variation in climate to variation in population dynamics of large herbivores (Sæther 1997). However, to improve our understanding of these relationships we need to focus on how variation in climate affects important forage plant characteristics, i.e. quality, quantity and availability. Global climate change will cause a change in these characteristics within plant species, but may also alter

competitive relationships and hence, the species composition within a plant community (Robinson et al. 1998; Callaghan et al. 2004). Consequently, herbivores in northern latitudes may experience a change in their resource base and how these factors interact need attention in future studies.

Proxies such as NAO/AO and NDVI have become widely used in ecological research (Stenseth et al. 2003; Pettorelli et al. 2005a), and have proven to be a valuable tool, but caution must be taken when a proxy is used in ecological research. A good understanding of how measures of the proxy relate to physical characteristics of importance for plants and herbivores at different temporal and spatial scales is important (Mysterud et al. 2001b; Hallett et al. 2004). Furthermore, how plants and herbivores respond to this variation is needed if we are to understand these complex relationships. Such information must subsequently be incorporated in management of ungulates.

Even though it is difficult to estimate the frequency of extreme climatic events in the future, we need to think of how an altered climate may cause new challenges for plants, animals and humans. Changes in frequency and magnitude of winter warm spells, erosion due to rapid snowmelt and river discharge, fire and insect outbreaks, in addition to altered permafrost patterns, may all pose unexpected responses. More innovative experimental studies designed for realistic climatic scenarios are needed. It is also important to have a better understanding of plants' ability to evolutionary adapt to a rapid change in climate, and possibly in herbivore pressure.

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Paper I

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Paper II

Title:

Spatial synchrony and the effects of climate on the growth of a high arctic dwarf shrub

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ABSTRACT:

We analysed a 17 year time series of annual growth from the dwarf shrub *Cassiope tetragona* from 25 locations at Svalbard, a high arctic archipelago. There was a positive association between temperature in July and annual growth at 84% of the 25 localities, while the June Arctic Oscillation index explained variation in growth at 88% of the localities, making it the best predictor of plant performance. A warm August and a dry July also affected the growth positively at many localities. Common environmental forcing acting over large distances is expected to cause synchronised growth. By modelling the separate effect of environmental stochasticity we attempted to estimate the spatial scaling of the component that is due to environmental stochasticity in the growth of *Cassiope tetragona*. The spatial synchrony in growth was high between all localities and was reduced from $\hat{\rho}_0$ = 0.691 at zero distance to $\hat{\rho}$ = 0.608 at maximum distance. The maximum distance between our sampling localities of 133 km was too short to allow us to determine the spatial scaling, by definition, of the environmental noise. Average temperature in July and August was able to explain the largest proportion of the synchrony, but not at a statistical significant level. Thus, in this study we identified the climatic drivers guiding the growth of *C. tetragona*, and found a high degree of growth synchrony spanning over the whole study area.

Keywords

INTRODUCTION

Plants in the Arctic live in a marginal environment where resources are limited in both time and space. In such an environment, small variation in climate may have large consequences for survival, growth and reproduction of the individual plant. Even though summers in the Arctic are characterized by little variation in temperature and precipitation on an absolute scale, the effect size may still be large. Small changes in temperature, precipitation or length of snow free season can consequently have large effect on plant growth (Chapin et al. 1995; Arft et al. 1999; Callaghan et al. 2004), resulting in varying foraging conditions for resident herbivores (van der Wal et al. 2000). Although plant responses to variation in climate differ between species and functional groups, most species respond positively to increased temperature (Arft et al. 1999). Hence, in arctic regions temperature and photoperiod in June, July and August are considered key environmental factors for plant performance (Johnstone and Henry 1997; Arft et al. 1999). Plant responses to variation in climate will also depend on local environmental conditions, such as soil nutrient levels, snow accumulation, water resources, interspecific competition and herbivore mediated effects (Chapin et al. 1995; Arft et al. 1999; Aerts et al. 2006).

An understanding of how temporal variation in weather is translated into biological responses at different spatial scales is important for obtaining a mechanistic understanding of spatio-temporal population patterns (Mysterud et al. 2000; Sæther et al. 2003; Both et al. 2004). Fluctuations in weather are often correlated over large areas (Koenig 2002), and this could cause correlations in population fluctuations over large areas (Ranta et al. 1998b). This effect has been called the "Moran effect" (Moran 1953). Although the theoretical prediction of the Moran effect is based on several simplifying assumptions (Ranta et al. 1998a;

Bjørnstad et al. 1999; Liebhold et al. 2004; Engen and Sæther 2005), some evidence suggests that spatial covariation in climate is an important synchronizing agent in many taxa (see Liebhold et al. 2004 and Sæther et al. 2007 for references). The spatial scaling may be measured as the distance from zero in which the temporal fluctuations in populations size, or plant growth in this case, is at a certain level. The spatial scale of synchrony in population fluctuations influences the risk of e.g. local and global extinction (Allen et al. 1993; Bolker and Grenfell 1996; Heino et al. 1997; Palmqvist and Lundberg 1998; Engen et al. 2002).

Although a large number of studies have examined spatial synchrony in animal populations, the demographic mechanisms generating this synchrony are poorly understood. Body growth is known to be an important demographic character among ungulates because larger individuals generally breed earlier, have more offspring per breeding attempt and survive for longer (Roff 1992; Stearns 1992). Because herbivores can utilize large areas where the quality, quantity and availability of forage can vary considerably both in time and space (Bø and Hjeljord 1991; van der Wal et al. 2000), knowledge of how environmental variables affect the foraging niche is essential for an understanding of herbivore population dynamics. Many studies using dendrochronological methods (e.g. Briffa et al. 1998; Macias et al. 2004) have found spatial correlation in plant growth assumed to be caused by similar environmental forcing. However, few studies have quantified the contribution of different climate variables to the spatial correlation (Dietz and Arx 2005).

Our study had three main objectives: First we wanted identify which climatic covariates explained local *Cassiope tetragona* (hereafter *Cassiope*) growth. Secondly, we wanted to estimate whether plant growth was correlated among localities and to what extent this correlation decreased with distance. In addition we

wanted to check whether influential covariates could explain correlated growth among localities. Due to its long lived nature and annual growth increments *Cassiope* is probably the only species in high arctic regions suited for constructing chronologies of annual growth. It is sensitive to variation in summer temperature (Nams and Freedman 1987; Johnstone and Henry 1997; Rayback and Henry 2005), and it is not eaten by any herbivores due to its low nutritional value and high content of flavonoids (Denford and Karas 1975) and plant phenols (Harborne and Williams 1973). Our approach involved fitting time series of annual growth increments (AGIs) from *Cassiope* to a stochastic model that includes environmental covariates (e.g. climatic variables). This enable us to estimate the contribution of different covariates to the synchrony of fluctuations in growth (Engen et al. 2005). We hence examined whether spatial heterogeneity in the contribution of different environmental variables to local plant growth can explain a proportion of the spatial synchrony in growth rates.

MATERIAL AND METHODS:

Study sites

We collected *Cassiope* from three valleys in the central area of Svalbard (Adventdalen, Reindalen and Colesdalen) and two localities (Brøggerhalvøya and Ossian Sars) on the north-west coast of Svalbard (Fig. 1). The three valleys are of varying length but all run from the sea in west and ends in the interior of Nordenskiöldland in east. The length of the valleys Adventdalen, Reindalen and Colesdalen are about 32 km, 42 km and 12 km respectively. At the northernmost sampling sites, Brøggerhalvøya and Ossian Sars, close to the small research settlement Ny-Ålesund, glaciers and sea create isolated land masses. Hence, no

long valleys creating a potential coast inland gradient exists. These sampling sites are therefore close to the sea (approx. 1.5 km and 0.1 km respectively).

Plant sampling

The plants were sampled during summer 2003 in areas with as similar slope and aspect as possible within and between valleys. Nonetheless, the topography and rivers made some areas inaccessible. We thus sampled *Cassiope* in valleys with different topographic aspects. Shoots were collected within plots with the same slope and aspect as the more general area, avoiding e.g. small depressions which could result in different microclimate. The elevations increases from the sea to the interior of the valleys, so the altitude of our sampling locations was 41 m a.s.l. in Colesdalen, Engelskbukta 45 m, Ossian Sars 9 m and ranged from 4 m to 147 m a.s.l. in Adventdalen, 41 m to 121 m a.s.l. in Reindalen. Shoots were collected from an area of ca. 10 x 10 m^2. Only one shoot was taken from each plant to avoid pseudoreplication. Long shoots with few side branches were selected and stored in paper bags and subsequently frozen upon arrival at the field station (maximum three days after sampling).

Measurement of *Cassiope*

We used plants from 25 localities (Fig. 1) from which we were able to measure minimum 17 years of growth. In the models, we only included AGIs from the period 1985-2001. Growth from 2003, the year of sampling was not used. Neither did we include growth from 2002 since plants collected early in 2003 appeared to have short AGI in 2002 relative to plants collected later in 2003. The elongation observed in plants collected later in 2003 was not likely caused by an effect of the climate in 2003

since resource translocation out of current years growth (i.e. from 2003 in our case), was not found in *Cassiope* by Nams and Freedman (1987). The leaves stay green for 3-5 years and some stem elongation could occur at one year old parts of the stem.

AGIs were measured using a stereomicroscope with micrometer eyepiece resulting in an accuracy of about ± 0.06 mm. Annual growth was found using a combination of patterns of internode lengths (see Johnstone et al. 1997 for a detailed description), leaf lengths (Callaghan et al. 1989) and the presence of dark band on the stem indicating end of growing season (Vie 1998). We assumed that short internode length and small leaves indicated the end of each year's growth (Johnstone et al. 1997). We also checked adjacent leaf rows for this indicator since this not always was present on each row, each year. By applying all these method, the error in identification of AGIs was probably small. Annual stem elongation was calculated as the sum of internode lengths within the year's growth. The total length of the chronologies was often limited by the scares becoming vague where the shoot became covered by moss or soil. Annual average stem growth of the plants collected was 6.82 mm ± 2.62 (mean ± SD).

Environmental data

Svalbard is an arctic semi-desert and the weather at central parts is characterised by little precipitation and slightly warmer summers than at the north-western locality; Ny-Ålesund, Brøggerhalvøya. Meteorological stations are located at Longyearbyen and Svea at the central part of Svalbard and at Ny-Ålesund on the north-west Svalbard. At Ny-Ålesund the climate is more oceanic, typically with colder and wetter summers. In June, July, August, and often September, the average temperature is above zero degrees. No meteorological station are located in Colesdalen or Reindalen, so we

used the closest (Longyearbyen meteorological station which is located ca. 22 km away from Colesdalen and Svea meteorological station which is located ca. 20 km from Reindalen). There was no significant temporal trend in either temperature or precipitation ($F_{1,16}$ <1.593, P > 0.224) at either meteorological station during the study period. We also included a large scale climate index, the Arctic Oscillation (AO) (Thompson and Wallace 1998), which is considered to be a better predictor of local weather at high latitudes (Thompson and Wallace 1998; Aanes et al. 2002; Yoccoz et al. 2002) compared to the more commonly used North Atlantic Oscillation (NAO) (Hurrell 1995).

At all *Cassiope* locations we calculated an index of incoming solar radiation on the basis of a digital elevation model (DEM) (©Norwegian Polar Institute), using Arc/Info workstation version 8.3 (ESRI 2004). The incoming solar radiation index has values from 0 to 255, where aspect and slope, in addition to shadows from mountains, affect the value. Thus, a spot facing directly against the sun (perpendicular in slope and aspect), will have a value of 255, while a spot covered in shadow will achieve a value of 0. The altitude and azimuth of the sun was calculated relative to one location (Longyearbyen) for every 10 days in June, July and August, starting on 1st June with one value for every second hour of the day. Using this we could calculate the index of solar radiation for each of the 25 *Cassiope* locations for 120 points in time from June through August. The aspect and slope was calculated based on four 20 x 20 m^2 pixels from the DEM centred around the *Cassiope* locations. All index values below 10 were set equal to zero and we summed the number of points in time during the summer where the locations had a potential for receiving sun.

Estimation of parameters

Local growth

We tested if there was any significant delayed growth response using an autocorrelation function (Royama 1992). This was done by evaluating the residual correlation in *Cassiope* growth in year *t* with growth in year *t+1* when controlling for AO-June year *t*, the local climate covariate explaining observed variation in growth at most localities. We found a delayed growth response at only one locality and we thus assume no significant delayed growth response and that the main factor influencing growth is variation in environmental conditions. Hence, to test to what extent the environmental variables were able to explain variations in growth we fitted a linear model with mean AGI for each locality as response and climate as explanatory variable at each location. To allow for straightforward comparisons among localities, we standardised the growth within each locality before fitting the model. Environmental variables included in the model were: monthly averages of local precipitation and temperature from May to September, last date with ground snow, length of growing season (number of days with temperature above 0 °C), number of overcast days as well as average summer temperature and precipitation (June-August and July-August) in addition to a seasonal AO-index (three month intervals starting in December), an annual AO-summer index (AOS) calculated from monthly values from June through September (see Aanes et al. 2002) and monthly AO values.

Spatial synchrony

The estimation of spatial synchrony was based on standardised growth measurements. Following Engen and co-workers (Engen et al. 2005; Grøtan et al.

2005; Sæther et al. 2006; Sæther et al. 2007), the contribution of different environmental variables to synchrony was estimated using standardised residuals after fitting the model with various environmental variables as covariates at each location. We used a parametric model for the spatial autocorrelation of the form

$$\rho(z) = corr[U(w), U(w+z)] = \rho_0 + \rho_\beta z \qquad \text{(eqn. 1)}$$

where U(w) and U(w+z) are standardised residuals obtained by fitting local models at localities with a distance z apart. ρ_0 is the correlation as distance approaches zero and ρ_β represents the change in correlation with distance. For the given parameters (ρ_0, ρ_β) we have a complete description of the multivariate normal distribution each year. The complete likelihood is found by adding the log likelihood contributions for each year. This function is maximised numerically to give estimates of (ρ_0, ρ_β). The sampling properties for the estimates are found by parametric bootstrapping (Efron and Tibshirani 1993; Lillegård et al. 2005). Significant differences in (ρ_0, ρ_β) based on including different covariates were tested for by examining whether 0 was included in the appropriate lower and upper quantiles of the distribution of differences between bootstrap distributions.

RESULTS

Effects of climate on *Cassiope* growth

There was very little variation in amount of sun received at the *Cassiope* locations. All north facing locations had a potential for receiving sun at 103-114 of 120 points in time between 1st June to 29th August, whereas the four south/west facing locations

(Brøggerhalvøya, Ossian Sars and the two locations in Reindalen) received slightly less (78-95) because of mountain shadows during the night when the sun's position was at low altitudes from north. As a consequence, average growth at each location was not related to incoming solar radiation ($F_{1,24} = 0.084$, $P = 0.77$).

Examining linear models of *Cassiope* growth at each locality, several covariates explained a significant amount of variation in growth. June AO-index explained the observed variation in *Cassiope* growth at the largest number of localities since a high June AO was associated with reduced growth at 88% of the localities (Tab. 1), in addition AO-July and AO-September both explained growth at 40% of the localities. Temperature in July was positively associated with annual growth at 84% of the localities (Tab. 1) and number of overcast days was negatively associated with growth at 64% of the localities, whereas clouds in June and August only affected growth significantly at four and zero localities, respectively. Furthermore, temperature in August was positively associated with growth at 80% of the localities and precipitation in July negatively affected growth at 64% of the localities (Tab. 1). Neither temperature nor precipitation (except for at one locality) in June affected the growth, and we found correlation between temperature and precipitation in May and growth at only two and zero localities respectively. Furthermore, length of growing season and time of snowmelt was correlated with *Cassiope* growth at zero and two localities respectively. Plants from the north-western locality, Ossian Sars, did not respond to any of the summer covariates, except AO-June, despite of a relatively large sample size (n = 10).

Spatial synchrony in *Cassiope* growth

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The estimate of spatial synchrony in growth between populations at zero distance was $\hat{\rho}_0$ = 0.691 [0.489, 0.817] (mean and 95% confidence interval). Parametric bootstrap distributions of the intercept ρ_0 and slope ρ_β are shown in Fig. 2. The spatial autocorrelation in annual growth decreased with increasing distance between localities but was high within the spatial range of our study area and the slope was not significantly different from zero ρ_β < -0.001 [-0.002, < 0.001]. Hence estimating the spatial scaling, by definition (Lande et al. 1999), was not possible. This showed a common environmental noise operating over the whole study area. The covariate that explained the highest proportion of the spatial scale of synchrony was average temperature in July-August (Fig. 3 and 4). However, the estimate of the scaling at zero distance ρ_0 = 0.511 [0.292, 0.683] and the slope ρ_β = -0.002 [-0.004, > -0.001] was not significantly different from the model without any covariates as 0 was included in the appropriate lower and upper quantiles of the distribution of differences between bootstrap distributions (intercept [-0.449, 0.078], slope [-0.004, 0.001]). Fitting temperature in July to the spatial autocorrelation model resulted in an estimate of $\hat{\rho}_0$ = 0.561 [0.351, 0.715] and ρ_β = -0.001 [-0.004, <0.001], which was not significantly different from the model without covariates. Several other covariates explained similar amounts of spatial scaling (Tab. 2), but none of these were able to explain a significant amount of the spatial correlation.

DISCUSSION

We found that *Cassiope* growth was positively affected by high temperatures, particularly in July and the negative effect of precipitation is caused by a negative association with temperature. No single environmental variable reduced the synchrony of the residual variation in plant growth significantly indicating that no

single environmental variable could be attributed to the observed synchrony in growth of *Cassiope*. Nonetheless, we were able to quantify a high synchrony in *Cassiope* growth over the whole study area whereas the spatial scale of the synchrony could not be estimated.

We chose primarily to examine the environmental effect on *Cassiope* growth on a monthly basis rather than seasonal measures of e.g. temperature because this would enable us to identify variables which have similar impact on plant growth over large areas as well as measures with potentially opposing effect between localities, which could have a desynchronising effect (Engen and Sæther 2005). If some measures of local weather or regional climate, e.g. the AO-index, have nonlinear or non-monotonic relationship with local climate (Mysterud et al. 2001), this could cause different growth response at different localities and potentially desynchronised growth. We found that *Cassiope* growth was positively affected by high July temperatures at 84% of the localities and little precipitation in July was associated with high growth at 64% of the localities (Tab. 1). Since temperature and not water is assumed to be limiting for growth during most summers (Welker et al. 2005; but see Bliss 1977), a strong negative correlation between temperature and precipitation at two meteorological stations in July (r < -0.496, P < 0.014) and a marginally non-significant result for Ny-Ålesund (r = -0.315, P = 0.069) explains this pattern in dry climate. Water is normally not limiting for growth because runoff from melting snow provide sufficient amounts of water and the amount of precipitation during summer is usually so small that it will not cause flooding or other direct negative effects on plant growth. The number of overcast days in July were also important (significant at 76% of the localities) most likely resulting from the strong negative correlation with July temperature at Longyearbyen and Svea (r > -0.687, P < 0.002). Due to the

correlation it is not possible to test whether there is an interaction between these two variables but looking at the coefficients and r-square values (Tab. 1), temperature appears to be more important than solar radiation. Temperature in August explained similar amounts of variation in *Cassiope* growth as temperature in July, but since growth is expected to cease in mid August most years (Nams and Freedman 1987), this could simply be due to the high correlation between July and August temperature ($r > 0.515$, $P < 0.004$). Consequently, average temperature in July and August explained a similar fraction of *Cassiope* growth as temperature in July (i.e. 80% of the localities). The only environmental variable able to describe growth conditions for *Cassiope* in early summer was AO-June (88% of the localities). Hallett et al. (2004) also found that large-scale climate indices may explain a larger part of ecological processes than local climate and accounted this to measures of local climate failing to capture complex associations between weather and ecological processes. Looking at the relationship between June AO values and weather in June within our study period, we found that AO was not significantly correlated with temperature ($r < 0.18$, $P > 0.49$) or precipitation ($r < 0.34$, $P > 0.20$). June-AO was however at all three meteorological stations positively correlated with precipitation in July ($r > 0.50$, $P < 0.05$) and negatively, but not significantly correlated with temperature in July ($r < -0.22$, $P < 0.39$). In other words, a high June-AO resulted in a rainy and possibly colder July (see Aanes et al. 2002). We have not tested whether this delayed local response to the AO is a general pattern for this period and region of the Arctic or of a more incidental nature. The summer AO index (AOS) as described by Aanes et al. (2002) was found to have a strong negative effect on *Cassiope* growth at Brøggerhalvøya (Aanes et al. 2002). They found that high AOS values were associated with colder, cloudier and wetter weather conditions causing reduced plant

growth. Contrary to what Aanes et al. (2002) found, we found no strong effect of AOS at the two north-western localities (P > 0.06). This could be related to the summer 2000 which was the coldest within the study period and the growth was accordingly reduced. This made identification of AGIs difficult and may have resulted in misplacement of AGIs.

An important contribution to a mechanistic understanding of how climate affects *Cassiope* growth came from Nams and Freedman (1987) who analysed the within season growth and development of *Cassiope* on Ellesmere Island in Arctic Canada. They found that plants responded rapidly after snow melt, measured as frequency of bud burst, but shoot elongation was compressed to a 50 day period starting in late June. Growth rates peaked in mid July and rapidly decreased before completely ceasing in mid August even though the snow free season lasted 65-80 days (Nams and Freedman 1987). This strategy may provide insurance against the effects of an unpredictable growing season. Several studies have found a positive effect of temperatures in late winter or early growing season on *Cassiope* and other arctic plants (Callaghan et al. 1989; Havström et al. 1995; Johnstone and Henry 1997; Rayback and Henry 2005). The mechanism behind this is however less clear. Some have suggested that weather in April and May to cause tissue desiccation by wind and damage to apical meristems from abrasion by ice particles (Callaghan et al. 1989). Because *Cassiope* do not grow at exposed places, this could only happen in years with very little snow. It is more likely that climate during late winter or spring has an effect on the conditions during the growing season, e.g. through an effect on length on growing season, which could cause e.g. precipitation in May (e.g. Callaghan et al. 1989; Johnstone and Henry 1997), or temperature during winter (Rayback and Henry 2005), to be correlated with growth.

In this study we wanted to relate fluctuations in AGIs of *Cassiope* to variation in local and regional climate variables and then analyze how these variables contributed to the spatial scaling of the synchrony in growth. If environmental variables are able to synchronise plant growth over large distances, these variables may also be important in explaining synchrony in herbivore populations. However, we found no single environmental variable explaining a significant proportion of the observed synchrony in growth of *Cassiope* (Tab. 2). After accounting for average temperature in July-August, a large fraction the synchrony in plant growth was still unexplained (Fig. 4), thus there are probably other synchronizing factors, some of which could be unmeasured autocorrelated environmental variables. We did not have any sampling localities at intermediate distances (42 – 102 km), and only two localities sampled at distances >102 km from other sampling localities (Fig. 1). The growth characteristics of these plants will hence affect the scaling of the synchrony. However, we have no reason to assume that these plants not are representative for this area, or that this area has a climate very different from what we should expect relative to the climate of the central area. Even though AO-June was able to explain local growth (Tab. 1) it was not the primary cause of the observed synchrony. This can be due to differences in how large scales indices such as AO translates into local conditions as shown by Mysterud et al. (2001), i.e. a high AO may result in snowfall at high elevation while the precipitation falls as rain at sea level. A similar pattern as was found in this study was found in Norwegian roe deer (*Capreolus capreolus*) populations where the NAO was positively related to population growth rates in 94.7% of the populations but did not significantly affect the pattern of synchrony among populations (Grøtan et al. 2005; but see Hallett et al. 2004).

If the pattern of temperature covariation we observed within Adventdalen in July 2004 and 2005, based on information from 18 temperature loggers placed along same route as we sampled *Cassiope* (S. Henriksen unpublished) were representative for the study period, we should have expected a larger synchronising effect of summer temperature. A general pattern that emerged was a notable decrease in temperature from the coast to the interior of Adventdalen during most months, except during July and August. The average number of days with temperatures above zero degrees in 2004 and 2005 was 124 close to the coast, while 33.2 km further east, this was reduced to 106 days. If we assume the plants can be photosynthetical active at all temperatures above zero degrees (which is unlikely), this result in a growing season 2.5 weeks longer at the coast. Hence the plants are at different phenological stages when the important July temperature affects the plants, and the growth response may consequently differ. Variation in length of growing season may also result in differences in resource allocation. High temperatures and long summers may cause the plants to produce flowers and seed on expense of vegetative growth (Callaghan et al. 1989) while plants in colder environments, i.e. inland, are less likely to reproduce and hence can allocate more to growth. The time series of temperature data is too short to calculate the scaling in temperature, but we can use this to see how the local temperature affects the growth of *Cassiope* at the sampling localities closest to the temperature loggers. By plotting all pairwise absolute differences in temperature between temperature loggers for each month against all pairwise correlations in growth between locations, we found that correlation in growth decreased significantly with increasing difference in temperature between localities in April-June ($p < 0.007$). Even though plant growth does not initiate before the ground thaws in mid June, some have suggested that

weather in April and May to cause tissue desiccation by wind and damage to apical meristems from abrasion by ice particles (Callaghan et al. 1989). However, it could simply reflect differences in length of growing season or timing of start of growing season since temperatures in July and August vary little along Adventdalen and thus have little potential to explain variation in growth.

Acknowledgement

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Table 1. For each location we calculated the relationship between relevant covariates and *Cassiope* growth using a linear model. AO is the Arctic Oscillation index in June (AO-June) and June through September (AOS) respectively. Numbers in bold indicate a significant relationship. Localities A1-A22 are in Adventdalen, B30 and B31 on Brøggerhalvøya and Ossian Sars respectively, C40 is Colesdalen and R51 and R52 are Reindalen (see Fig. 1).

lok	n	AO-June		AOS		Temperature July		Temperature August		Precipitation July		Overcast days in July	
		coef	r^2	coef	r^2	coef	r^2	coef	r^2	coef	r^2	coef	r^2
A1	**27**	**-1.28**	**0.65**	**-2.48**	**0.65**	**0.70**	**0.44**	**0.74**	**0.43**	**-0.06**	**0.48**	**-0.14**	**0.46**
A2	3	**-0.89**	**0.31**	-1.26	0.17	0.43	0.17	0.45	0.16	**-0.05**	**0.35**	**-0.11**	**0.26**
A3	3	**-1.18**	**0.55**	**-2.19**	**0.51**	0.41	0.15	**0.56**	**0.25**	**-0.05**	**0.33**	-0.09	0.17
A4	3	**-1.10**	**0.48**	**-2.05**	**0.45**	**0.66**	**0.39**	**0.71**	**0.40**	**-0.06**	**0.43**	**-0.11**	**0.30**
A5	4	**-1.22**	**0.58**	**-1.90**	**0.38**	**0.60**	**0.33**	**0.74**	**0.44**	**-0.05**	**0.29**	**-0.13**	**0.40**
A6	3	**-0.94**	**0.35**	**-1.99**	**0.42**	**0.52**	**0.24**	**0.75**	**0.45**	-0.04	0.19	**-0.10**	**0.25**
A7	2	**-0.98**	**0.38**	**-2.02**	**0.43**	**0.66**	**0.40**	**0.73**	**0.43**	**-0.05**	**0.35**	**-0.13**	**0.36**
A8	2	**-0.89**	**0.31**	**-2.04**	**0.44**	**0.60**	**0.32**	0.27	0.06	-0.03	0.15	**-0.12**	**0.32**
A9	3	**-0.81**	**0.26**	**-1.48**	**0.23**	**0.72**	**0.47**	**0.71**	**0.40**	-0.03	0.11	**-0.11**	**0.26**
A10	3	-0.74	0.21	**-1.93**	**0.40**	**0.79**	**0.56**	**0.75**	**0.45**	-0.04	0.21	**-0.12**	**0.31**
A11	3	-0.60	0.14	-1.26	0.17	**0.52**	**0.25**	**0.78**	**0.49**	-0.04	0.19	-0.08	0.16
A12	8	**-1.00**	**0.39**	**-2.05**	**0.45**	**0.59**	**0.32**	**0.71**	**0.41**	**-0.04**	**0.24**	**-0.11**	**0.25**
A13	2	**-0.80**	**0.25**	**-1.75**	**0.33**	**0.54**	**0.26**	**0.78**	**0.49**	-0.03	0.13	**-0.11**	**0.28**
A14	3	**-0.77**	**0.24**	**-1.62**	**0.28**	**0.61**	**0.33**	**0.81**	**0.53**	-0.04	0.25	**-0.11**	**0.28**
A15	4	**-1.19**	**0.56**	**-2.13**	**0.48**	**0.53**	**0.25**	**0.56**	**0.25**	**-0.05**	**0.29**	**-0.11**	**0.30**
A16	3	-0.69	0.19	-1.27	0.17	0.50	0.23	**0.67**	**0.36**	-0.03	0.16	-0.07	0.12
A17	3	**-1.11**	**0.48**	**-1.97**	**0.41**	**0.61**	**0.34**	**0.79**	**0.50**	**-0.05**	**0.30**	**-0.10**	**0.25**
A18	4	**-1.02**	**0.41**	**-2.19**	**0.51**	**0.74**	**0.49**	**0.62**	**0.31**	**-0.05**	**0.33**	**-0.14**	**0.42**
A19	3	**-1.04**	**0.42**	**-2.31**	**0.57**	**0.59**	**0.31**	**0.59**	**0.27**	**-0.06**	**0.52**	**-0.13**	**0.38**
A20	18	**-0.93**	**0.34**	**-1.90**	**0.38**	**0.62**	**0.35**	**0.68**	**0.37**	**-0.04**	**0.24**	**-0.11**	**0.28**
B30	4	**-0.93**	**0.34**	-1.35	0.19	**0.58**	**0.24**	**0.60**	**0.44**	**-0.03**	**0.27**	0.00	0.00
B31	10	**-0.89**	**0.31**	-1.41	0.21	0.14	0.01	0.41	0.17	-0.02	0.08	0.01	0.00
C40	9	**-0.86**	**0.29**	**-1.66**	**0.29**	**0.74**	**0.50**	**0.82**	**0.54**	-0.04	0.21	**-0.10**	**0.23**
R51	9	**-1.15**	**0.52**	**-2.36**	**0.59**	**1.14**	**0.62**	0.63	0.19	**-0.07**	**0.38**	**-0.13**	**0.45**
R52	4	**-1.28**	**0.64**	**-2.06**	**0.45**	**0.87**	**0.36**	0.56	0.15	**-0.08**	**0.46**	**-0.10**	**0.30**
Weigthed average		-1.03	0.43	-1.97	0.43	0.63	0.36	0.67	0.36	-0.05	0.30	-0.10	0.30
% sig. localities		88%		80%		84%		80%		64%		76%	

Table 2. Intercepts ($\hat{\rho}_0$) and slopes (ρ_β) with 95% CI for the six best covariates and the total synchrony from the parametric bootstrap function. AOS is the Arctic Oscillation summer index (June-September) as described by Aanes et al. 2002.

Covariate	$\hat{\rho}_0$	ρ_β
Total (no covariates)	0.691 [0.489, 0.817]	-0.0005 [-0.0019, 0.0004]
Temperature June	0.701 [0.510, 0.821]	-0.0002 [-0.0012, 0.0020]
Temperature July	0.561 [0.351, 0.715]	-0.0012 [-0.0035, 0.0003]
Temperature August	0.544 [0.334, 0.716]	-0.0018 [-0.0041, -0.0012]
Temperature July- August	0.511 [0.292, 0.683]	-0.0019 [-0.0044, -0.0002]
Precipitation July	0.600 [0.388, 0.759]	-0.0018 [-0.0042, -0.0002]
AOS	0.598 [0.400, 0.760]	-0.0011 [-0.0030, 0.0004]

Figure legends:

Fig. 1. Localisation of the *Cassiope* samples (dots), with increasing numbers from east to west in Adventdalen (see Table 1), and two of the weather stations (x).

Fig. 2. The distribution of bootstrap replicates of the intercept and slope respectively from the model without any covariates

Fig. 3. The distribution of bootstrap replicates of the intercept and slope respectively from the model with temperature in July-August as covariate

Fig. 4. The correlation in the fluctuations of annual *Cassiope* growth on Svalbard due to environmental covariation ρ_e as a function of distance (solid black line) with 0.025 and 0.975 quantiles (dashed). Red lines denote the spatial autocorrelation in residuals that remain after accounting for the effect of temperature in July-August (solid red line) with 0.025 and 0.975 quantiles (dotted red)

Fig. 1
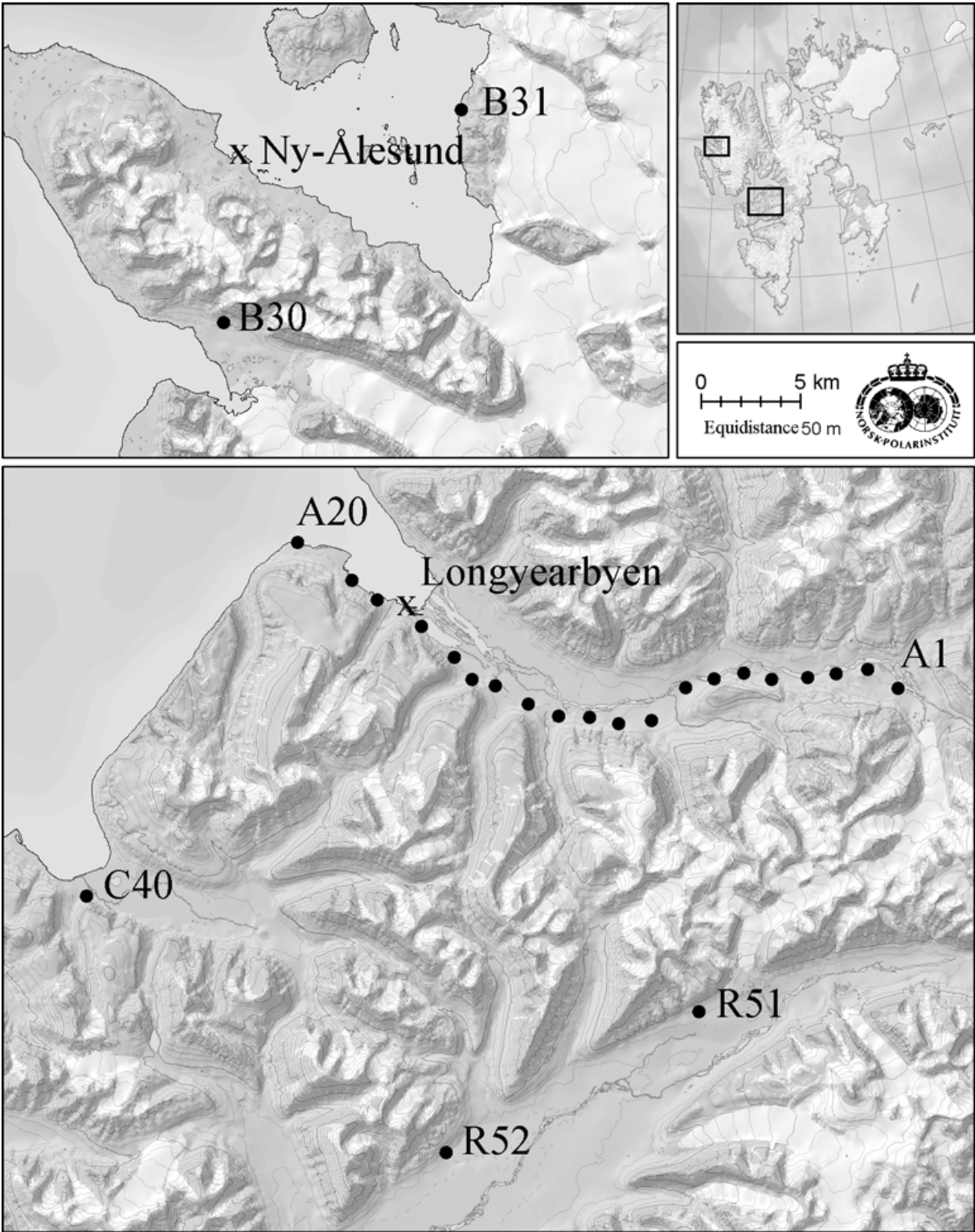
Fig. 2
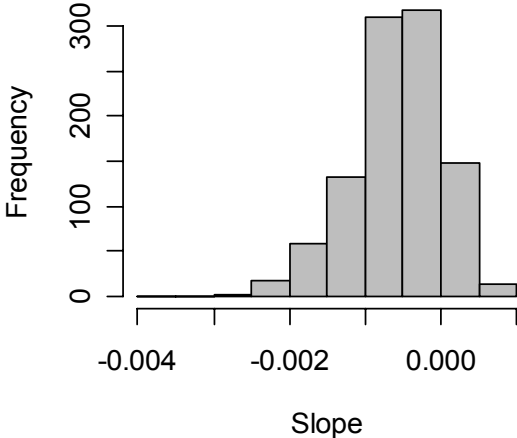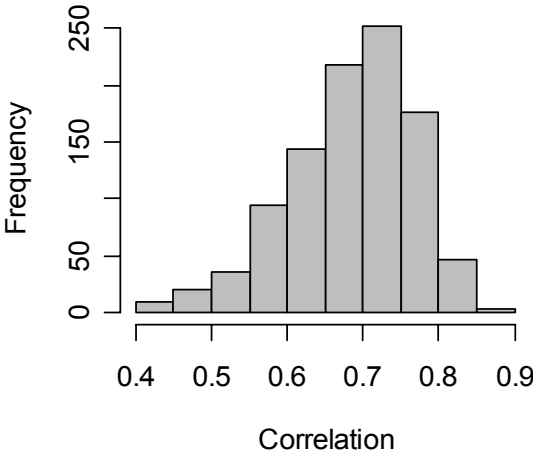
Fig. 3
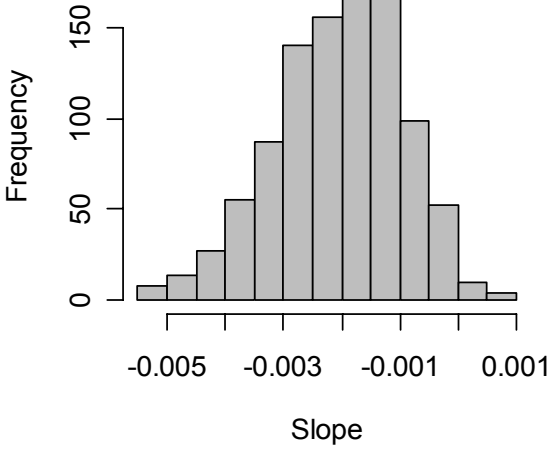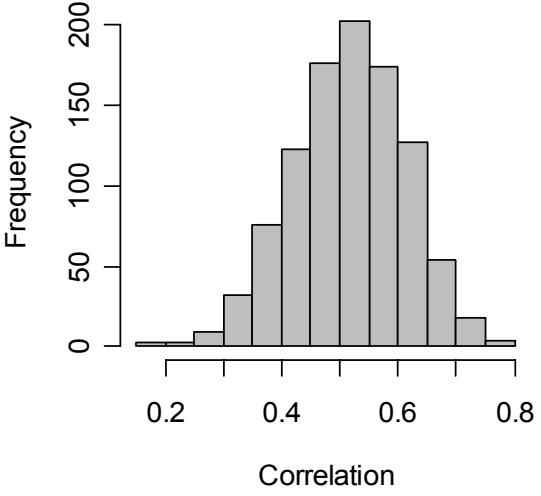
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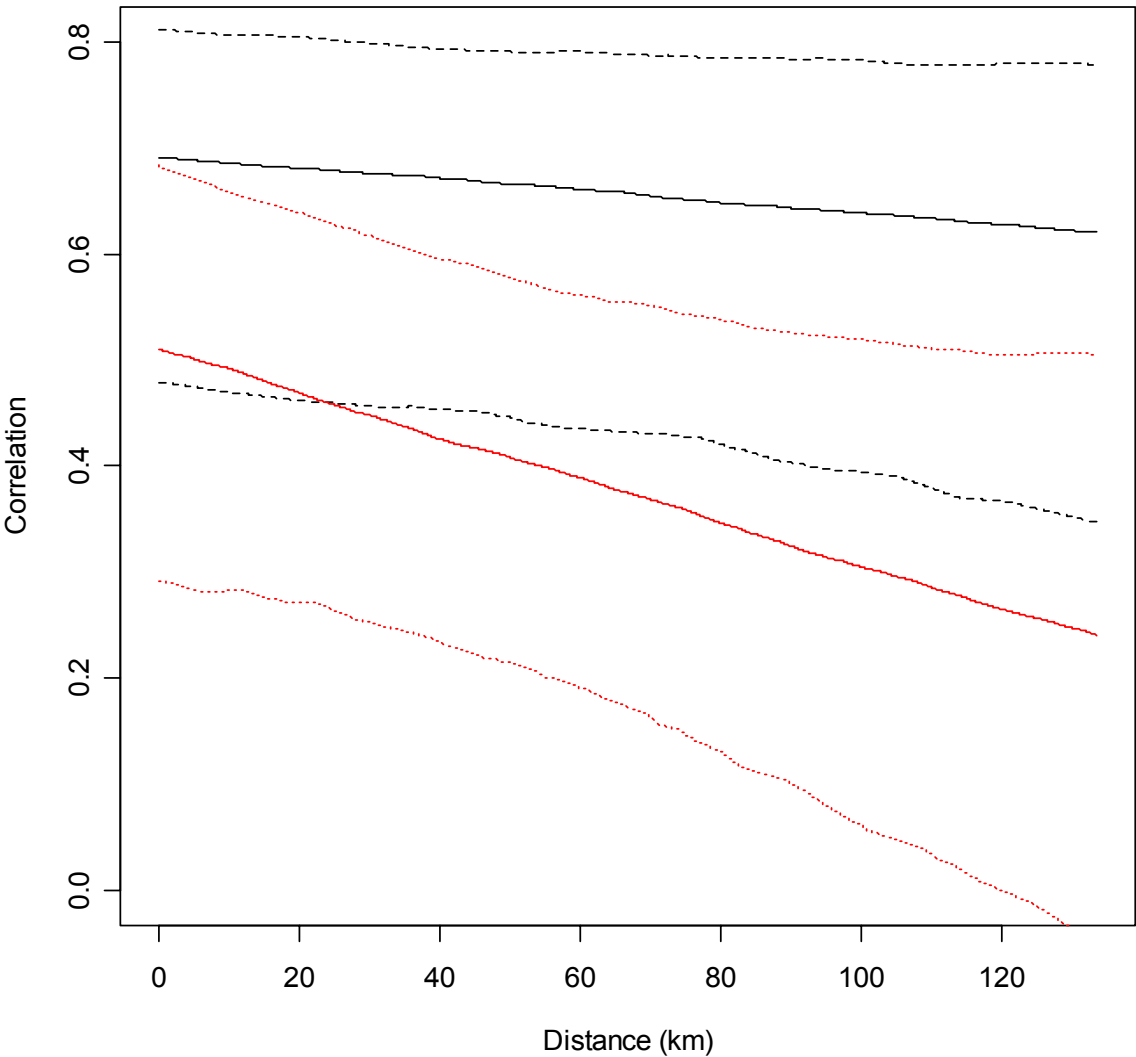
Paper III

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Spatio-temporal patterns and the effects of climatic variation in common juniper growth

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Abstract

We analysed the annual radial growth of juniper in relation to environmental variation obtained from local and regional climate measures, as well as environmental phenology obtained from annual NDVI-curves based on satellite images. Juniper growth was high during warm and dry summers, and in years when the plant phenology increased rapidly during spring. Furthermore, juniper growth was high following winters with a high value of the Arctic Oscillation (AO) index. Individuals with high average growth were more correlated with derived spring NDVI and responded more to high values of winter AO and North Atlantic Oscillation (NAO) index, and to high summer temperatures, compared to plants with low average growth. Spatial synchrony in the annual growth was found to be low and even increased slightly with increasing distance. In the context of predicting environmental variation that relates to foraging conditions for herbivores, juniper radial growth capture much of the variation that a variety of more commonly used variables do, and may therefore be suitable for analyses of environmental variability on herbivore performance.

Introduction

Understanding how variation in climate affects ecological processes has become imperative with the prospects of rapid climatic change (Stenseth et al. 2002). How measures of climate, such as large scale climate indices, relate to local variation in weather depend on geographical location creating potential for spatial heterogeneity in ecological responses (Liebhold et al. 2004). Plant response to climate change and natural variation in weather may in turn vary greatly at different scales due to local conditions modifying the response through e.g. neighbour effects, herbivores and parasites (Callaghan et al. 2004), creating a heterogeneous environment where plant growth characteristics vary spatially and temporally. Although plant species may respond individually to environmental variation (Callaghan et al. 2004), the growth generally relates to climate by being temperature and nutrient limited in their northern boundary (Arft et al. 1999; Callaghan et al. 2004; Aerts et al. 2006) and precipitation limited at their southern boundary (Garcia et al. 2000). However, from a temperate herbivore perspective the nutritional values of plants, i.e. the quality, rather than quantity or accessibility, is often more important for foraging behaviour and ecology (White 1983; Sæther and Andersen 1990; Bø and Hjeljord 1991; Lenart et al. 2002). High plant growth associated with warm weather is likely to cause a reduction in nutrient levels in the tissue, making the plants less suitable as forage (Deinum 1984; Bø and Hjeljord 1991; Chapin et al. 1995; Lenart et al. 2002). Consequently, in order to gain knowledge on how the variation in resources may influence important life history trait and population dynamics of herbivores, we need information on how plants respond to variation in climate and how local conditions may

modify this relationship. However, due to potentially large effects of high herbivore densities on forage plants (Bråthen et al. 2007), care should be taken if forage plants are used in such analyses.

Because direct measures of plant growth characteristics or herbivore forage conditions are rarely available on a regional scale, few studies have been able to quantify the relationship between climate and characteristics of forage plants (but see Bø and Hjeljord 1991; Post and Stenseth 1999). As a result, studies on environmental effects on large herbivore often rely on indirect or proxy measurements of environmental condition, such as average monthly temperature or precipitations, assuming to reflect important environmental conditions for plant growth. Moreover, temporal variation in climate is often correlated over large areas (Koenig 2002), causing synchronised variation in plant growth (Koenig and Knops 1998), life history traits (Sæther et al. 2007) or ungulate population dynamics (Grøtan et al. 2005). Consequently, studies on temporal variation in plant characteristics should be conducted over large areas. One method to obtain time-series of plant activity is through tree-ring analysis (e.g. Koenig and Knops 1998; Liang et al. 2005). The applicability of tree-ring records as indicators of past plant growth and how climate affect plant performance, is related to a relatively easy sampling, that they can be precisely dated, and that they may contain a highly resolved climate response (Briffa et al. 1990; Böhm et al. 2001; Frank and Esper 2005).

Another source of plant performance measure at a large geographical scale is vegetation indices derived from satellite images. Satellite images can provide measures that relate directly to vegetation activity and biomass, such

as the Normalised Difference Vegetation Index (NDVI) (Reed et al. 1994; Myneni et al. 1995; Kerr and Ostrovsky 2003; Pettorelli et al. 2005b).

In this paper we have two objectives: First, we examine whether temporal variation in local as well as regional climate variables explain annual variation in common juniper (*Juniperus communis*) tree ring growth. Second, we estimate the spatial synchrony in juniper growth and whether climate can act as synchronizing agent.

Methods

ENVIRONMENTAL DATA

We used information on environmental conditions from three different sources. First, we used local weather observations from three meteorological stations covering the study area (Fig. 1). We used the monthly mean from these three stations to assign weather data (i.e. temperatures, precipitation, and snow-depth, Table 1) that represented the study area. To represent all juniper locations we averaged the data from the three meteorological stations. Correlation in both precipitation and temperature during summer was high between the three meteorological stations (Fig. 1) during the study period (summer temperature r > 0.822, P < 0.001, summer precipitation r > 0.550, P < 0.010).

Second, we obtained two large-scale climate indices, the North Atlantic Oscillation (NAO; Hurrell 1995) and the Arctic Oscillation (AO; Thompson and Wallace 1998). The AO is a natural cycle in the Northern Hemisphere (Thompson and Wallace 1998), and the NAO may be viewed as a signature of the AO in the Atlantic sector (Overland and Adams 2001). The AO is

recognised as a better indicator of local weather at these latitudes compared to the NAO (Yoccoz et al, 2002). The NAO/AO phenomenon is described extensively in the literature (Hurrell 1995; Hurrell and van Loon 1997; Stenseth et al. 2003; Hallett 2004) and we will not discuss their physical properties here. It may appear confusing to focus on both the AO and the NAO as they represent the same physical phenomena. However, previous studies have shown that either can explain local weather and/or biological parameters at northern latitudes. We thus chose to show the relationships to local climate and juniper growth from both the AO and the NAO.

High values of both NAO and AO are related to higher than normal surface pressures south of 55° N combined with a broad region of anomalously low pressures throughout the Arctic and sub-Arctic (Hurrell et al. 2003). During winter this generally leads to increased levels of precipitation and relatively warm temperatures in the northern Europe (Hurrell 1995). The relationship between summer climate and NAO/AO is less studied. However, the positive phase of the AO have been found to be correlated with increased precipitation and reduced temperatures on Svalbard (Aanes et al. 2002). NAO- and AO-values were retrieved from http://www.cgd.ucar.edu/cas/jhurrell/indices.html (read 1. June 2005) and http://horizon.atmos.colostate.edu/ao/ (read 14. November 2005), respectively.

As a third source of information about environmental conditions, we used environmental phenology derived from the annual NDVI-curve (Reed et al. 1994; Pettorelli et al. 2005b). The annual NDVI-curves were obtained from the GIMMS dataset based on satellite images from the AVHRR sensor

onboard the NOAA satellites (Tucker et al. 2001; Zhou et al. 2001). NDVI is based on the difference in absorbed radiation from red and near infrared radiation, and is found to closely correlate with photosynthetic activity and primary production (Myneni et al. 1995; Schloss et al. 1999). The GIMMS dataset contains 15-days maximum values of NDVI on a spatial resolution of 8 * 8 km^2 (Zhou et al. 2001). Typically at the Northern Hemisphere, the NDVI-values will rise rapidly during spring to a peak level at early summer, and decrease during late summer and autumn (Tucker 1986). Based on this curve, a set of ecological relevant variables can be calculated (Reed et al. 1994; Pettorelli et al. 2005b). We calculated the following variables describing environmental phenology (see Fig. 2 in Garel et al. 2006): onset of spring, derived spring NDVI (a measure on the speed of plant progression during spring), peak value, peak time, integrated NDVI (a measure of the foliage net primary production) (Table 1). For details regarding the calibration of NDVI-values in order to determine the onset of spring, see Karlsen et al. (2006). The variables were calculated annually on a pixel level.

JUNIPER DATA

Common juniper is a small dioecious coniferous tree often depressed to shrub-like forms in arctic and alpine environments. Annual growth is detectable as rings on the stem due to distinct periods of dormancy during the cold season. During the summer 2003, living stems were sampled from a total of 362 locations, mainly from the coastal areas of western Finnmark, Norway (Fig. 1). All locations were situated in the low alpine vegetation zone, i.e. above the forest line. For a more thorough description of sampling locations

see Bråthen et al. (2007). The personnel sampled the thickest part of the stem from an individual juniper at each location after which the stem sections were frozen. Annual growth was measured as width of the tree-ring (μm) with a precision of 1.0 μm, using a Leica stereomicroscope with a digital camera and on-screen measuring system (Leica Qwin Image processing and Analysis software version 2.3a). We selected the thickest part of the cross-section for measurement to minimise the risk of overlooking the narrowest rings. Stems which had scars or where rings were undistinguishable were excluded (n=248), and we thus had 114 locations available for the analyses. Length of growth time series varied from 15 to 32 years, with the last complete ring in all samples corresponding to 2002. Juniper has previously been found to reliably capture environmental variability (Böhm et al. 2005; Macias et al. 2004; Frank and Esper 2005).

Values of environmental phenology were assigned to each juniper location using the annual means of the 3*3 pixels surrounding the location, such that each juniper location was assigned the mean value of environmental phenology of the nine closest pixels from the GIMMS dataset. We excluded pixels that had a large proportion of its coverage in ocean. For all locations, we extracted the elevation and an index of incoming solar radiation. The index for incoming solar radiation was calculated for each juniper location on the basis of a digital elevation model, using the HILLSHADE command in Arc/Info workstation version 8.3 (ESRI 2004). The incoming solar radiation index has values from 0 to 255, where the aspect and slope, in addition to shadows from mountains, affect the value. Thus, a spot facing directly against the sun (perpendicular in slope and aspect), will have a value of 255, while a spot

covered in shadow will achieve a value of 0. Aspect and slope of the sun was set to 180° and 43°, respectively, corresponding to sun position at 12.00 local time, 20. June at 22°68'E, 70°12'N (i.e. mean longitude and latitude for the juniper locations).

STATISTICAL ANALYSES

Because the data on environmental phenology were available for 1982 - 2002, we used this as the study period in all analyses. Due to the rather high collinearity between some of the environmental variables (Table 2), we choose a univariate approach to estimate the effect of environmental variation on juniper growth.

We first analysed if the average radial growth W on each juniper location was influenced by the elevation or the incoming solar radiation at the location, with linear regression models.

We analysed the effect of the environmental variables on the annual variation in juniper growth with a univariate linear mixed model for each environmental variable (Table 1) and with juniper sample id as random factor. The estimation was done with restricted maximum likelihood (REML), and the significance, as well as the effect sizes of the environmental variable on the juniper growth was calculated based on 10000 draws from the posterior distribution of the parameters using function `mcmcsamp` in package `coda` (Plummer et al. 2007). A parameter was considered statistically significant if the 95 % confidence interval (CI) from the resampling did not include zero. Moreover, we wanted to explore if the effect of environmental conditions were influenced by the average radial growth during the study period for each

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juniper sample. This was done by including average juniper growth at the location in interaction with the environmental variable, retaining the main effect of both. We ranked models using AIC_C-values based on the maximum-likelihood estimate of log-likelihood values (Burnham and Anderson 2002). However, parameter estimates and their uncertainty from the best models were based on REML, following the procedure for the univariate modelling. The mixed models were fitted using the function `lmer` in the `lme4` package (Bates and Sarkar 2006) developed for R (R Development Core Team 2006).

SPATIAL SYNCHRONY

The spatial analysis is, following Engen et al. (2005), based on studying the residuals obtained from fitting the model to time series observations at times t at each location j,

$$R_{i,t}(j) = W_{i,t+1}(j) - \mathrm{E}\left[W_{i,t}(j) \mid W_{i,t-1}(j), u_{i,t}(j)\right], \qquad \text{(eq. 1)}$$

where E denotes the expected growth based on estimated parameters and u_i is covariate i. Each locality specific set of residuals, $R_i(j)$, were standardized to mean 0 and unit variance prior to further analysis. The candidate synchronizing mechanism in this study is clearly spatial autocorrelation in the environmental noise, which generally decreases with distance (Koenig 2002). To test whether the correlation in residuals decreases with distance, we model the correlation ρ in residuals as a linear regression against distance z

$$\rho(z) = \mathrm{corr}\left[R, R(w+z)\right] = \rho_0 + \gamma z \qquad \text{(eq. 2)}$$

, where ρ_0 is the correlation as distance z approaches zero.

An alternative specification of the correlation structure of residuals could be a distance independent correlation of residuals

$$\rho(z) = \text{corr}\left[R, R(w+z)\right] = \rho \quad \text{(eq. 3)}$$

Data were available over partly overlapping time periods. However, each year represents a realisation of a multivariate normal distribution with parameters describing the correlation structure as given in equations 2 and 3. The complete likelihood is found by adding together the log likelihood contributions for each year. By numerical maximisation we can obtain estimates of the parameters describing the spatial structure in residuals (see Engen et al. (2005) for further details).

The sampling properties of the estimated parameters were found by parametric bootstrapping (Efron and Tibshirani 1993) of the residuals from the multinormal models defined by eqs. 2 and 3 and the distance matrix. Calculations of the likelihood and simulations of the multinormal distributions were done by the functions `dmvnorm` and `rmvnorm` respectively in package `mvtnorm` (Genz et al. 2004) using R (R Development Core Team 2006).

To compare models, we must test whether the parameters differ among models. This is done by examining whether 0 is included in the 95 % confidence interval of the distribution of differences between the two bootstrap distributions (Grøtan et al. 2005, Sæther et al. 2007). To test whether the regression coefficient γ in eq. 2 was significantly different from 0, we

performed Monte Carlo simulations by simulating new datasets under the 0-hypothesis and examined whether the parameter estimate based on the data were included in the 95 % confidence interval of the parameter obtained by simulating under the 0-hypothesis.

Results

The mean radial growth in juniper during 1982 - 2002 was 185 ± 99 µm (mean ± SD), with lowest growth in 1983 (128 ± 62 µm), and highest growth in 1998 (256 ± 134 µm). There was an overall increase in the growth from 1982 - 2002, with approximately 35 ± 8.5 µm pr. decade ($F_{1,19}$ = 17.56, P < 0.001). The average radial growth in juniper was not related to local variation in elevation ($F_{1,112}$ = 0.086, P = 0.770) or in incoming solar radiation ($F_{1,112}$ = 1.19, P = 0.277). Peak value ($F_{1,19}$ = 2.57, P = 0.019) and integrated NDVI ($F_{1,19}$ = 8.39, P = 0.009) increased during the study period whereas onset of spring, peak time and derived spring NDVI did not show any significant trend during the study period (all P > 0.29). Furthermore, summers became warmer during the study period ($F_{1,19}$ = 5.75, P = 0.027). None of the other weather observations showed significant temporal trends (all P > 0.09).

THE RELATIONSHIP BETWEEN THE ENVIRONMENTAL VARIABLES AND JUNIPER GROWTH

Juniper radial growth was positively related to the winter AO index, average temperatures during summer as well as average temperatures and precipitation during September. Similarly rapid growth was also found in years

with high derived spring NDVI, high peak value, early peak time and a high integrated NDVI (Table 3).

However, the effect of winter AO, winter NAO, high summer temperature and derived spring NDVI was dependent on the average growth of the juniper. The positive effect of a high AO and NAO as well as a high summer temperature and derived spring NDVI was stronger for junipers with a high average growth compared to those with a low average growth (Table 4, Fig. 2).

SPATIAL SYNCHRONY IN JUNIPER GROWTH

The estimates based on a linear model of correlation in residuals against distance (eq. 2) resulted in estimates of the correlation at zero distance $\hat{\rho}_0$ = 0.092 [0.053, 0.137] (figures in brackets denote the 95% confidence interval). Furthermore, the spatial synchrony in growth increased significantly with the distance between the localities (Fig. 3, $\hat{\gamma}$ = 0.012 [0.005, 0.018]. By using residuals after including environmental covariates, the estimates were not significantly different between models without covariate and with covariate. Assuming a constant correlation independent of distance (eq. 3) between localities resulted in an estimate of $\hat{\rho}$ = 0.098 [0.057, 0.141], illustrating a common environmental influence on the growth. By including derived spring NDVI as a covariate (i.e. the covariate which explained the larges fraction of the synchrony) the estimate was $\hat{\rho}$ = 0.083 [0.042, 0.123]. The difference in estimates was not significant.

Discussion

We have demonstrated that environmental conditions, as measured by local weather observations, large scale climatic variation and environmental phenology derived from satellite images influence annual variation in the growth of the common juniper. We also found low spatial correlation in juniper growth throughout the study area, which increased with increasing distance (Fig. 3).

Juniper radial growth was larger in warm summers and in warm and wet Septembers (Table 3). This is in accordance to the results that have been found elsewhere (Böhm et al. 2001; Frank and Esper 2005). This supports the importance of temperature, for growth of plants in northern regions (Macias et al. 2004; Chapin and Shaver 1985; Myneni et al. 1997; Callaghan et al. 2004). High temperatures cause rapid phenological developments that in turn affect the nutritional value of plants as forage, e.g. measured as protein content (Deinum 1984; Bø and Hjeljord 1991; Chapin et al. 1995; Lenart et al. 2002). This is supported by the fact that juniper radial growth was positively related to high derived spring NDVI (fast plant development in spring), early peak time of vegetation development and a high peak value (i.e. maximum photosynthetic activity) and a high integrated NDVI (high plant primary production). Although plant species may vary in their response to variation in weather (Chapin et al. 1995), this response is probably general for the majority of other plants as well, since NDVI values indicating favourable growth conditions were related to high growth in juniper. Average summer temperature increased during the study period, and both integrated NDVI and juniper growth showed similar trends indicating that summer temperature is the main environmental driver of

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plant growth in these areas. The positive effect of a warm September on juniper growth is probably related to an extended growth season. However, the cues for cessation of growth may also be related to photoperiod (Aerts et al. 2006) which may vary over short distances when the days become short and sun is low. The positive effect of precipitation in September, which is normally a relatively cold and wet month, may be related to night temperature dropping below zero degrees on clear days with little or no clouds. Low temperatures are assumed to be one of several triggers for initiating winter dormancy (Aerts et al. 2006).

Several studies have been able to find a relationship between measures of large scale winter climate indices, such as NAO, and plant growth (Post and Stenseth 1999; Welker et al. 2005). We were also able to find that juniper was positively related to winter AO (Table 3). Juniper takes the form of a shrub at these latitudes and is probably protected from adverse weather conditions during winter by a snow cover. We therefore believe that the effect of winter AO and NAO mainly is related to the depth of the snow cover and hence start of the growing season. Because high values of the NAO and AO are associated with increased temperatures and precipitation during winter (Stenseth et al. 2003; Fauchald et al. 2004), this may result in precipitation falling as rain at the coast while as snow further inland or at higher altitudes causing large heterogeneity in snow depth at high values of the NAO and AO. Such a relationship between local climate variables and AO may explain why we found that the AO index was a better predictor of local conditions on the juniper locations than locally measured snow depth (Table 3) (Mysterud et al. 2001; Pettorelli et al. 2005a).

We used the average snow depth in April and May measured at the three meteorological stations (Fig. 1), because snow depth is assumed to affect the timing of the spring green up (Aerts et al. 2006). However neither snow depth nor the timing of onset of spring was correlated with juniper growth even though May snow depth was correlated with onset of spring (Table 2). Large local variation in snow depth within the study area (Fauchald et al. 2004, appendix 2) and few meteorological stations within the sampling area may have prevented us from revealing the true relationship between snow depth and plant growth conditions relevant for juniper, e.g. length of snow free season. In addition, April snow depth may simply not be a good indicator of spring conditions because more snow may fall after this point and the rate of snowmelt may vary between years. It may also be that juniper radial growth is not sensitive to the onset of spring as measured here (i.e. NDVI) as conifers become photosynthetic active before deciduous trees. It is important to be aware that birch (*Betula pubescens*) is very common in Fennoscandia and contributes largely to the values of the NDVI (Karlsen et al. 2006).

We found no significant relationship between juniper radial growth to elevation or solar radiation at the sample location. Several factors may account for this. Firstly, because all juniper stems were sampled in the low alpine zone, i.e. above the tree limit, the expected effect of elevation on radial growth may be confounded by the gradient in the tree limit from coast to inland. The tree limit increase with distance from the coast, and thus, the locations also increase in elevation. Secondly, the measure of incoming solar

radiation may not truly reflect the microclimate at the juniper locations during the growing season.

How juniper related to some of the environmental variables also depended on their overall performance. Plants with low average growth showed weaker response to variation in some climate variables than plants with a high average growth (Fig. 2). This can indicate that slow growing plants are limited by some other factors e.g. resulting from spatial variation in competition for resources such as light or nutrients. Furthermore, geographical location may influence how the climate and other physical parameters, such as solar radiation translate into local conditions. Winter AO and NAO as well as summer temperature and derived spring NDVI caused the largest difference in response between plants with high and low average growth. Clearly favourable growth conditions both during spring and summer creates possibilities for plants which are not strongly limited by e.g. competition to respond with increased growth.

We found a rather small but significant correlation in growth of juniper among the localities, indicating common environmental noise operating at large distances. Derived spring NDVI was the single covariate that explained the largest fraction of synchrony, but this covariate did not significantly change the estimated parameters in the spatial model. Probably the observed spatial correlation in growth is due to the influence of several climatic variables. We found a small but significant increase in correlation in juniper growth with increasing distance (Fig 3) and this represent the reverse trend to what could be expected based on other studies (Bjørnstad et al. 1999; Koenig 1999; Koenig 2002; Grøtan et al. 2005). This may be caused by spatial

heterogeneity in local growth conditions, clearly illustrated from the lack of correlation between incoming solar radiation and local growth. Another explanation could be that the increase in correlation is due a tendency to obtain samples from very different habitat types by chance when distance among sampling sites are low.

There are several examples of indices of large-scale climatic measures, such as the NAO, outperforming local meteorological measures in explaining ecological processes (Post and Stenseth 1999; Mysterud et al. 2003; Stenseth et al. 2003; Hallett et al. 2004) due to their ability to reduce a complex picture of e.g. precipitation and temperature into "packages of weather" (Stenseth et al. 2003). However, a smaller meridional extent and reduced variability of annular modes during summer time (Ogi et al. 2004) may reduce their applicability in describing summer conditions. When using indices for estimating how herbivores are influenced by climate through plants, the density of herbivores causes variation in grazing pressure (Manseau et al. 1996; Eilertsen et al. 2000; Bråthen and Oksanen 2001; Tømmervik et al. 2004). This is likely to affect the performance of the preferred plants, e.g. through reduced growth (Tømmervik et al. 2004; Persson et al. 2005; Guillet and Bergström 2006; Bråthen et al. 2007), which can confound the interpretation of the relationship between climate and plant performance. Juniper or other species not fed upon by ungulates will not be affected by variation in ungulate densities to a large extent. There are also some pitfalls when using a plant such as the juniper for interpreting the relationship between climate and plant growth. Firstly, the growth response of the plant may be age dependent (Carrer and Urbani 2004), and unless the

shape of the age dependent growth curve and the age of the plants are known, the accuracy of the predictions may be reduced. Secondly, growth conditions for the individual juniper may change during its lifetime as a result of e.g. altered competition for resources. However, these problems can be reduced by increasing the sample size and by using plants of similar age. However, juniper radial growth capture much of the environmental variation that other more commonly used variables do, and may therefore be suitable for analyses of environmental variability on herbivore performance. This study also illustrates the need for verification of these indices ability to reflect local conditions in a spatially heterogeneous landscape (Karlsen et al. 2006). Satellite based indices has the advantage of having higher spatial resolution than e.g. the NAO index, but NDVI values can vary with vegetation type, nutrient conditions, soil background and illumination conditions (Karlsen et al. 2006). Consequently, caution must be taken when a resolution of 64 km^2 is applied to a highly heterogeneous landscape. Future studies will have the opportunity to use data with higher spatial resolution (e.g. the MODIS dataset, Huete et al. 2002), which likely will give a more accurate correlation between juniper, as well as other plants, and NDVI.

Council of Norway (programmes LANDSKAP, BIOMANGFOLD and

NORKLIMA), and the Directorate for Nature Management.

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Tables

Table 1. Environmental variables used in the analyses of juniper radial growth, and their abbreviations in parentheses. "Regional" refers to a variable being calculated for the entire region, whereas "local" means that the value of the variable is calculated for each juniper location (Fig. 1).

Explanatory parameter	Description
Onset of spring (OS)	Week number in spring when the NDVI-value represents birch leaf burst. Local
Integrated NDVI (IN)	Sum of the NDVI-values during the growing season. Local
Peak value (PV)	The NDVI-value at peak time. Local
Peak time (PT)	Week number in summer when the NDVI-value reaches its highest value. Local
Derived spring NDVI (DSN)	The NDVI-value at onset of spring minus the NDVI-value the previous 15-days maximum composite image. Local
Winter NAO (W-NAO)	Average annual value of the North Atlantic Oscillation index from December - March. Regional
Winter AO (W-AO)	Average annual value of the Arctic Oscillation index from December - March. Regional
Summer NAO (S-NAO)	Average annual value of the North Atlantic Oscillation index from June - August. Regional
Summer AO (S-AO)	Average annual value of the Arctic Oscillation index from June - August. Regional
April snow-depth (April SD)	Average snow depth in April. Regional
May snow-depth (May SD)	Average snow depth in May. Regional
Summer temperature (Summer T)	Average temperature (°C) during June, July and August. Regional
Summer precipitation (Summer P)	Sum of precipitation (mm) during June, July and August. Regional
September temperature (September T)	Average temperature (°C) during September. Regional
September precipitation (September P)	Sum of precipitation (mm) during September. Regional

Table 2. Correlation matrix between the environmental variables (Table 1) between the years. Above the diagonal is given the r-values, below the corresponding p-values. N = 21 years for all correlations, Sept = September.

	OS	IN	PV	PT	DSN	W-NAO	W-AO	S-NAO	S-AO	April SD	May SD	Summer T	Summer P	Sept T	Sept P
OS		-0.593	-0.104	0.713	-0.207	-0.232	-0.133	-0.228	-0.365	0.331	0.602	-0.450	-0.380	-0.107	0.275
IN	0.005		0.755	-0.191	0.357	0.020	0.159	0.063	0.180	0.103	-0.078	0.718	0.028	0.120	-0.310
PV	0.653	<0.001		0.149	0.301	-0.332	-0.102	0.160	-0.017	0.257	0.220	0.632	-0.325	-0.056	-0.096
PT	<0.001	0.407	0.519		-0.456	-0.009	0.148	-0.450	-0.060	0.105	0.366	-0.231	-0.432	-0.165	-0.058
DSN	0.369	0.112	0.185	0.038		0.037	-0.063	0.048	-0.181	0.146	-0.013	0.437	-0.111	0.066	0.244
W-NAO	0.312	0.829	0.149	0.970	0.873		0.807	0.056	0.271	-0.265	-0.441	-0.027	0.026	0.033	-0.220
W-AO	0.565	0.492	0.661	0.523	0.787	<0.001		0.154	0.141	-0.040	-0.272	0.187	0.029	0.126	-0.112
S-NAO	0.320	0.786	0.489	0.847	0.835	0.811	0.504		0.576	-0.350	-0.334	0.475	-0.232	0.045	0.096
S-AO	0.103	0.436	0.943	0.795	0.432	0.234	0.541	0.006		-0.444	-0.329	0.307	0.089	0.134	-0.032
April SD	0.143	0.657	0.261	0.652	0.527	0.246	0.863	0.120	0.044		0.779	0.002	-0.148	0.129	-0.026
May SD	0.004	0.738	0.372	0.103	0.955	0.045	0.233	0.139	0.146	<0.001		-0.171	-0.290	0.047	0.063
Summer T	0.040	<0.001	0.002	0.314	0.048	0.907	0.418	0.029	0.176	0.994	0.460		-0.022	0.258	0.118
Summer P	0.089	0.905	0.150	0.051	0.633	0.910	0.901	0.312	0.701	0.532	0.203	0.925		0.313	0.021
Sept T	0.643	0.604	0.811	0.475	0.777	0.888	0.586	0.847	0.563	0.536	0.840	0.260	0.166		0.028
Sept P	0.228	0.172	0.679	0.804	0.287	0.339	0.630	0.680	0.889	0.912	0.787	0.610	0.929	0.905	

Table 3. Parameter estimates and 95% confidence interval for the effect of environmental variables (Table 1) on juniper radial growth (µm). Bold indicates that the 95 % confidence interval does not include zero.

Environmental variable	Estimate	95% CI
Winter NAO	0.569	-0.993; 2,135
Winter AO	**5,120**	**2,149; 8,185**
Summer NAO	-0,159	-2,980; 2,669
Summer AO	-2,191	-11,453; 7,178
April snow depth	0,277	-0.002; 0.552
May snow depth	-0.127	-0.454; 0.199
Summer temperature	**17,620**	**13,182; 21,976**
Summer precipitation	0.003	-0.075; 0.082
September temperature	**3,781**	**1,423; 6,159**
September precipitation	**0.189**	**0.006; 0.366**
Onset of spring	-1.589	-3,877; 0.591
Derived spring NDVI	**412,245**	**210,244; 608,766**
Peak value	**270,654**	**177,979; 365,108**
Peak time	**-2,660**	**-5,029; -0,234**
Integrated NDVI	**23,892**	**15,781; 32,393**

Table 4. The best (ΔAIC < 2) environmental models including interaction between environmental variables (Env, see Table 1) and mean growth at the location (Gr). An X indicates that the variable was included in the candidate model

Environmental variable (i)	Env_i	Gr	$Env_i * Gr$	ΔAICc	AICc-weight
Winter NAO	X	X	X	0,00	0,809
Winter AO	X	X	X	0,00	0,985
Summer NAO		X		0,00	0,621
	X	X		1,99	0,229
Summer AO		X		0,00	0,629
	X	X		1,77	0,260
April snow depth	X	X		0,00	0,266
		X		1,82	0,227
May snow depth		X		0,00	0,510
	X	X		1,42	0,251
	X	X	X	1,51	0,239
Summer temperature	X	X	X	0,00	1,000
Summer precipitation		X		0,00	0,632
September temperature	X	X		0,00	0,570
	X	X	X	0,61	0,421
September precipitation	X	X		0,00	0,582
	X	X	X	1,61	0,261
Onset of spring		X		0,00	0,421
	X	X		0,27	0,366
	X	X	X	1,36	0,213
Derived spring NDVI	X	X	X	0,00	0,754
Peak value	X	X		0,00	0,676
	X	X	X	1,68	0,292
Peak time	X	X		0,00	0,609
	X	X	X	1,87	0,238
Integrated NDVI	X	X		0,00	0,655
	X	X	X	1,62	0,342

Figure legends

Figure 1. Localisation of the juniper samples (triangles) and the weather

stations (cross) in Finnmark, northern Norway.

Figure 2. The effect of the environmental variables (Table 1) on juniper

growth, in relation to the mean growth of each juniper, based on the

model selection in Table 4. Solid line is the effect on juniper individuals

with large annual growth, dashed indicates medium annual growth while

dotted line represents individuals with small annual growth. Thin lines

represent 95 % confidence interval of the fitted thick lines.

Figure 3. The correlation in juniper growth in relation to distance for a model

without a covariate. The solid line denotes the 50% quantile of the

bootstrap distribution of ρ (eq. 2). The dashed lines are the 5% and 95%

quantiles. Dots are correlation in residuals between each pair of juniper

locations

Figure 1.
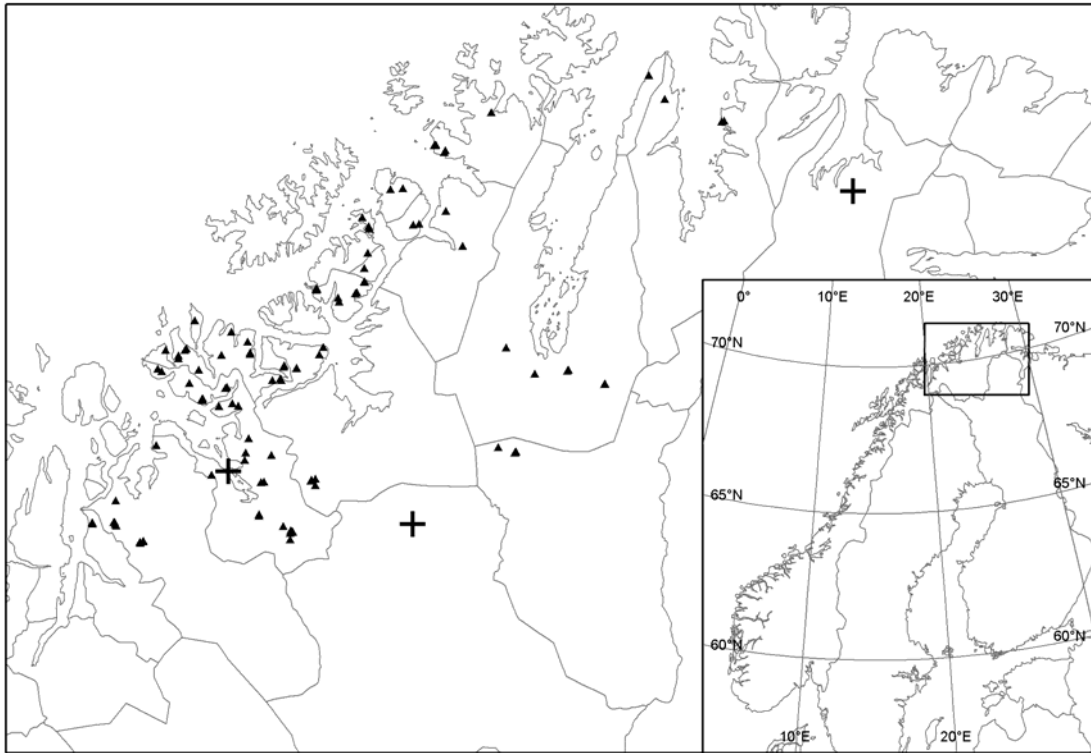
Figure 2.
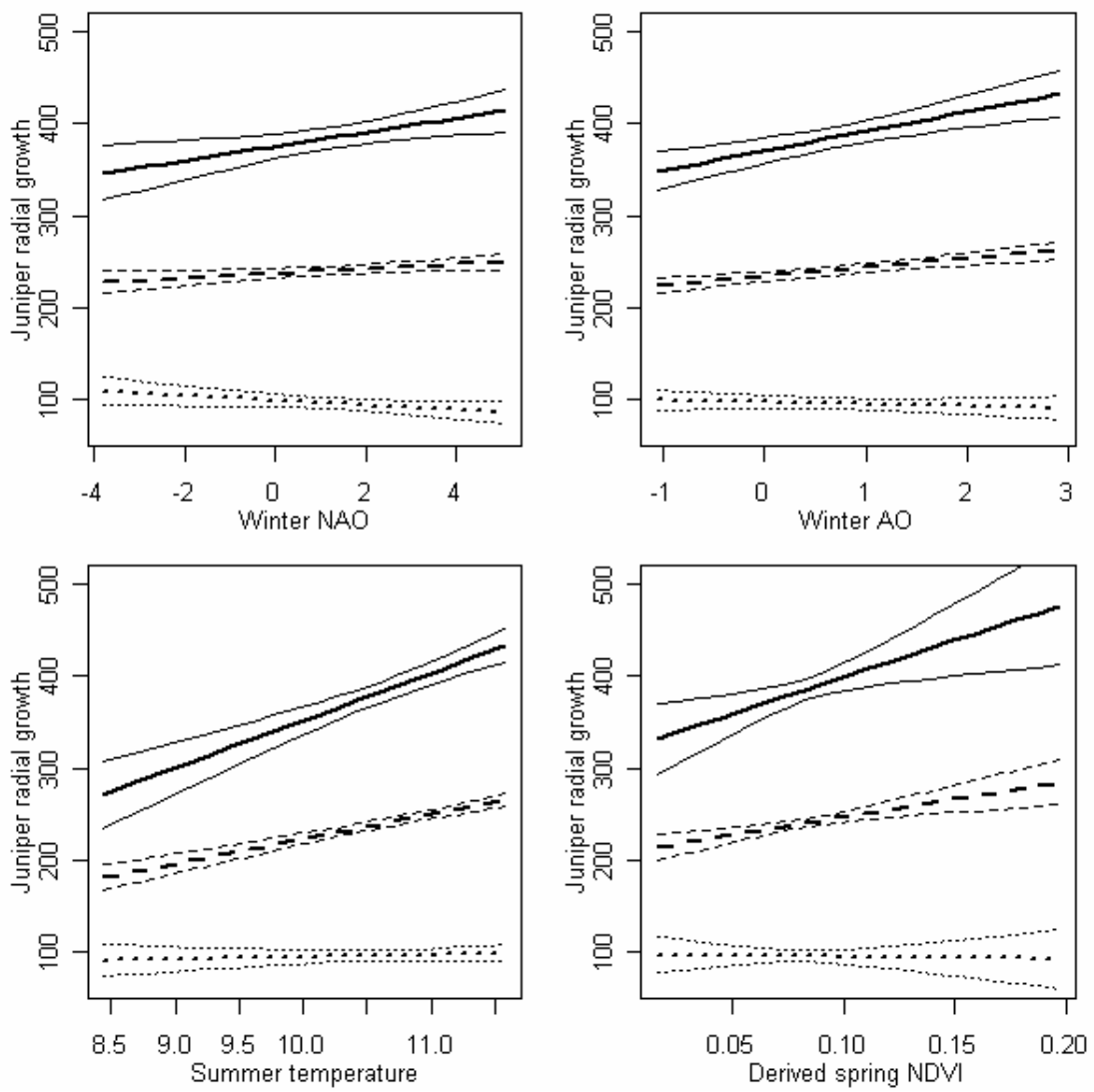
Figure 3.
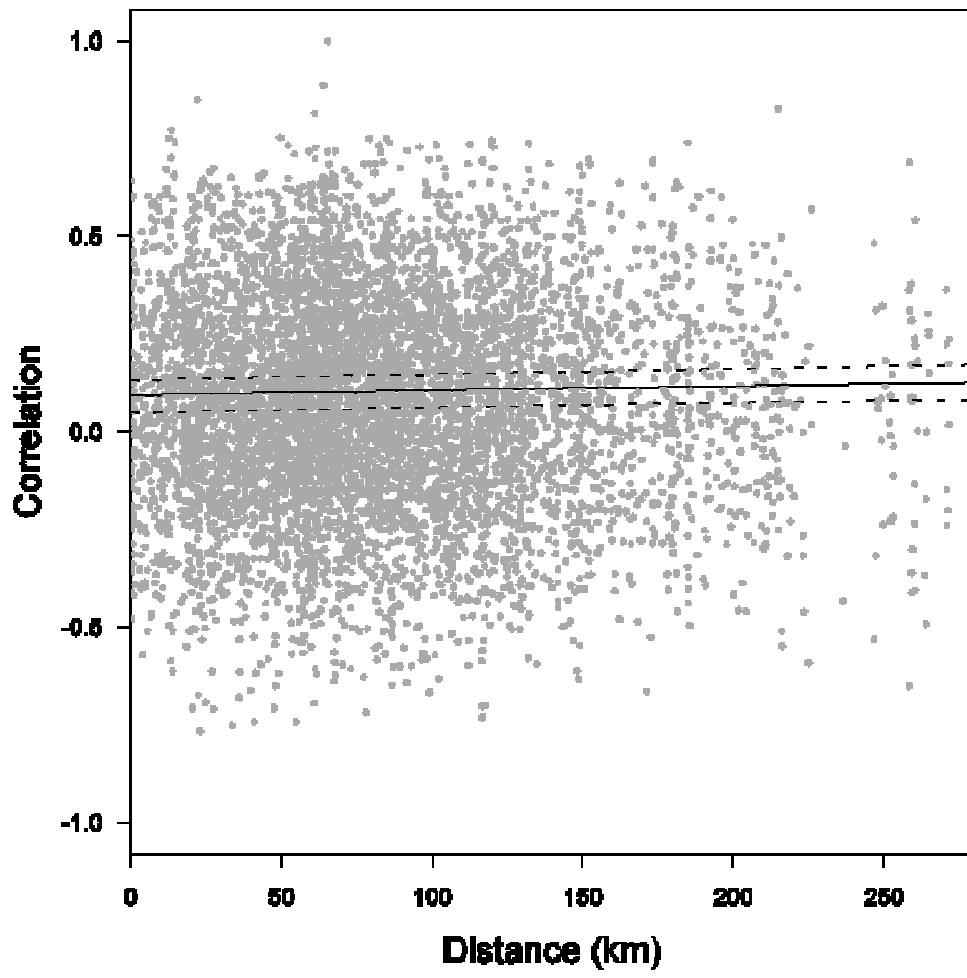
Paper IV

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Environmental variables as proxies for reindeer performance

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Abstract

The effect of environmental variation on ungulate life history traits often operates through mechanisms related to quantity, quality and accessibility of their forage, that is, their foraging niche. In general, it is assumed a negative relationship between plant performance (measured e.g. by growth) and their value as forage for herbivores. A variety of environmental variables have been used to explain the mechanisms between the environment and ungulates. However, few of them are based on direct measurements of plants. Here, we relate the body mass of reindeer calves to environmental variation measured from large-scale climate indices, meteorological observations, satellite-derived indices of plant phenology, as well as plant performance as measured by juniper radial growth. Furthermore, we account for the effect of population density on the body mass. The calf body mass was negatively related to within-herd population density. Furthermore, the autumn body mass was negatively related to low values of winter NAO, high snow-depths in April and May, a fast plant development in spring, high values of summer NAO, high levels of precipitation in September, and high juniper growth. The effect of most of the environmental variables remained after accounting for the density effect. However, accounting also for juniper growth, several of the environmental variables changed with respect to their relationship to calf body mass, while juniper growth was little affected. These results indicates that variation in reindeer body mass is to a large extent related to variation in the quality of their forage in spring and summer, and that juniper radial growth well capture the environmental mechanisms between climate and forage that create the variation in reindeer body mass.

Introduction

The role of environmental variation on life history traits and population dynamics in ungulates has for a long time been subject of interest (Sæther 1997). Body mass has been recognised as one of the first life history traits that is influenced by environmental conditions, particularly at young ages (Sæther 1997, Lindström 1999, Mysterud 2006), and variation in body mass among cohorts can have lasting effects for the population performance and growth rate (Mysterud et al. 2002, Solberg et al. 2004).

The environmental effects on ungulate populations can be separated into direct effects, e.g. temperature stress or energetic costs of movement in deep snow, and indirect effects, e.g. increased level of insect harassment (Hagemoen & Reimers 2002) or through the influence on forage conditions (Post & Stenseth 1999). In particular the influence of variation in forage conditions has been paid attention when explaining temporal and spatial variation in life history traits and population dynamics. The foraging niche of ungulates can be divided into quantity, quality and accessibility of the plants (White 1983, Andersen & Sæther 1992), and variation in one or several of these components will influence life history traits, and evidently also population dynamics. Several studies have linked the variation in life history traits in ungulates to environmental variation assuming that the mechanism operates through the foraging conditions (e.g. Sæther 1985, Langvatn et al. 1996, Post & Stenseth 1999, Mysterud et al. 2001a, Solberg et al. 2004, Herfindal et al. 2006). In temperate and northern ungulates, where winter and summer are contrasting in the amount of food available, special focus has been paid on the role of winter vs. summer conditions on both life history traits and population dynamics (Sæther 1997, Aanes et al. 2002, Tveraa et al. 2007). Because the main period of body growth and development in temperate and

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northern ungulates is during spring and early summer (Klein 1970), variation in foraging conditions in this period is often found to be most important for variation in life history traits like body mass (Bø & Hjeljord 1991, Langvatn et al. 1996, Sæther et al. 1996, Herfindal et al. 2006). However, the pattern is not unambiguous; the influence of environmental variation on a population depends not only on the species (e.g. Mysterud et al. 2001a), but also on the characteristics of the populations (Herfindal et al. 2006), or habitat characteristics (Skogland 1983, 1985, Mysterud et al. 2001b).

In the search of direct and indirect environmental effects on ungulates life history traits, a variety of variables have been used. Most common is climatic measures like temperature and precipitation, giving environmental information on a more local scale, and large-scale climate indices like the North Atlantic Oscillation (NAO, Hurrel 1995) and El Niño Southern Oscillation (ENSO, Chavez et al. 1999). Common for these variables is a rather poor spatial resolution, and that most of the effects on ungulates are indirect, e.g. through the effect on foraging conditions. Recently, satellite images have proven to perform well by giving information of resource availability in ungulate studies, and such data can provide information about environmental variation at a fine spatial scale (Kerr & Ostrovsky 2003). Providing indices of vegetation activity, satellite images give a more direct link between foraging conditions and ungulate performance. Nevertheless, ground measures of plant activity are desired in order to calibrate the vegetation activity indices to best calculate the plant activity measures (Reed et al. 1994, Karlsen et al. 2006). Furthermore, at temperate and arctic regions, such data gives little information about winter foraging conditions. An obvious source of plant performance data is direct measures the plants that constitute the forage. Several studies support a negative

relationship between the plant performance (i.e. measured as growth) and its value as forage for ungulates (Deinum 1984, Chapin et al. 1995, Bø & Hjeljord 1999, Lenart et al. 2002). Accordingly, variation in plant performance can give indications about the availability of high-quality forage for ungulates. However, apart from being very resource demanding, time series can be hard to get for the preferred foraging plants during summer because these often are annual plants or leave few growth patterns that can be related to performance. Furthermore, because there can be close links between ungulate density and plant performance due to variation in grazing pressure (Danell et al. 1985, Bergström & Danell 1987, Persson et al. 2005), the growth pattern in preferred forage plants can contain a substantial degree of noise that is not related to environmental conditions. This can be overcome by choosing plants that are little or not grazed by ungulates, but still show the same performance signature in relation to environmental conditions as plant species that are more preferred as forage.

Here our aim is to explore the importance of environmental variation, particularly related to variation in foraging conditions, on a life history trait (calf body mass in autumn) in a northern ungulate, the semi-domestic reindeer (*Rangifer tarandus*). The calf body mass can be influenced through pre- and post-natal maternal investment, through foraging conditions during summer, or through other mechanisms like insect harassment. We use environmental variables obtained from meteorological observations, derived from satellite images, as well as the variation in juniper (*Juniper communis*) radial growth, to obtain time series about the environmental variation that overlap with the time series of calf body mass.

We expect body mass in autumn to be positively associated to environmental variation that relates to high access to winter forage and high quality of the summer forage. Moreover, we predict that by accounting for population density, the ability of

the environmental variables to explain body mass variation will be influenced if the

environmental variable is related to density-dependent mechanisms. Finally, by

accounting for the juniper growth when evaluating the other environmental variables,

we investigate to what extent juniper growth is able to capture the environmental

variation that is explained by meteorological data and satellite derived vegetation

indices, and thus the value of juniper growth as a proxy for environmental variation at

these latitudes.

Methods

REINDEER DATA

Mean reindeer calf body mass and number of individuals within each district was

collected annually from 20 reindeer districts in western Finnmark, Norway (Fig. 1),

from 1984 - 2002, by the Reindeer Husbandry Administration and the reindeer

owners (Fauchald et al. 2004). The reindeer are kept on joint grazing areas at the

interior part of Finnmark during winter, where the climate is cold and dry, favouring

availability to lichen which is the preferred winter forage (Fauchald et al. 2004).

During summer the herds are separated and graze in the coastal districts (Fig. 1). The

body mass was measured as carcass weight (the body mass of the individual minus

head, skin, metapodials, bleedable blood and viscera), and was measured in late

autumn before the reindeer herds were moved to their winter grazing areas. The

population size in a grazing district was estimated as the total number of animals in

the spring before calving. Population size was ln-transformed. The variation in

density (number of individuals / km^2) among the populations depends on the size of

the reindeer management districts, which include varying degree of suitable reindeer

area. Thus, the variation in between-herd population density would not yield

interpretable information. However, because we included reindeer herd as random

factor in our analysis (see Statistical analysis below), we account for the among-herd

variation in population density, and observe the within-herd effect of variation in

population density. Accordingly, the term population density refers to variation in

population size within each herd, and not among them.

ENVIRONMENTAL DATA

A wide range of environmental variables have been used to infer the influence of

climate on ungulates. The link between the environment and the ungulate can be

direct, e.g. increased energy demands in extreme temperatures or cost of locomotion

in deep snow, or work through pathways. Example of the latter can be the influence

of climate on plant quantity and quality as forage for herbivores, and level of stress

due to parasites and insect harassment in warm weather. In order to capture these

different pathways, we used several measures of environmental variation.

As large-scale measures of climate variation, we used the North Atlantic

Oscillation index (NAO; Hurrell 1995) and the Arctic Oscillation index (AO;

Thompson & Wallace 1998), where the AO in general is found to be a better indicator

of local weather at higher latitudes compared to the NAO (Thompson & Wallace

1998, Yoccoz et al. 2002). High values of both winter-NAO and winter-AO are

related to high levels of precipitation and relatively warm winters in the northern

Europe, while low NAO and AO values indicate dry and cold winters (Hurrell 1995).

AO and NAO are positively correlated with precipitation at these latitudes during

winter (Yoccoz et al. 2002), but the winter precipitation will mostly come as snow

even in warm winters, and the AO is positively related to snow depth at most

locations within the study area (Fauchal et al. 2004, see also Mysterud et al. 2001a).

The relationship between summer AO/NAO and local weather has been less studied, but Henriksen et al. (in prep.) found a positive correlation between summer temperature and summer NAO. Aanes et al. (2002) found on the other hand that a high AO was associated with increased precipitation and cloudiness on Svalbard. Even though the NAO and AO originates from the same physical entity, and some regard them as inseparable (Rogers & McHugh 2002, but see Thompson & Wallace 1998) we chose to include both in the analyses because their ability to explain local weather and biological phenomenon in these latitudes is not extensively studied. NAO- and AO-values were retrieved from http://www.cgd.ucar.edu/cas/jhurrell/indices.html (read 1. June 2005) and http://horizon.atmos.colostate.edu/ao/ (read 14. November 2005), respectively.

In addition, we used local weather observations from three meteorological stations covering the study area (Fig. 1), averaged to get measures for the entire study area. We obtained monthly means of temperature, snow depth and the sum of precipitation.

We had two sources of plant performance in the study area. Firstly, based on the annual Normalised Difference Vegetation Index (NDVI)-curve from the GIMMS-dataset (Tucker et al. 2001), we calculated five indices of plant phenology; Onset of spring, derived spring NDVI, peak value, peak time, and integrated NDVI (Table 1). The NDVI is an index of the relationship between reflected visible red (VR) and near infra red (NIR) radiation from the ground ($NDVI = (NIR - VR)/(NIR + VR)$) and is found to represent the greenness of the vegetation, or the photosynthetic activity (Myneni et al. 1995). For details regarding the variables, see Table 1, and regarding the calibration of the threshold values for onset of spring and onset of autumn, see Karlsen et al. (2006), and for general information about the phenology variables, see

Reed et al. (1994) and Pettorelli et al. (2005a). The spatial resolution of the GIMMS-dataset is 8 x 8 km^2, and phenology variables were calculated annually for each pixel in the data set. To get annual values for each herd district, we averaged the annual values for pixels that fell inside the border for the herding districts.

Finally, we had information about plant performance through juniper radial growth during the study period. The juniper growth was estimated by measuring, to the closest 1.0 μm, the increment in annual tree-rings from stems sampled from 114 locations covering the study area. For details regarding the juniper data and its relation to the environment, see Henriksen et al. (in prep.). Because the number of juniper samples from each reindeer district varied considerably, we used the annual mean of standardised time series of juniper growth, thus we had one time-series of juniper growth for the study area. This averaging can be justified because of the very low spatial correlation in the growth pattern of juniper in the study area (Henriksen et al. in prep.).

STATISTICAL ANALYSES

Because the environmental variables (Env$_i$, Table 1) is expected to be highly correlated (Henriksen et al. in prep.), we included only one at a time as explanatory variables, that is, a univariate approach regarding the environmental variables. We accounted for the within-herd dependencies in body mass by including herd as a random variable in a mixed linear model approach. By estimating the autocorrelation in carcass mass in each herd locality we found significant positive autocorrelation at lag 1 in only 4 of 20 time series, and significant negative in 1 time series. Thus, we do not consider temporal autocorrelation in the time series to be influential in the

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analyses. Regarding density-dependence on the body mass, we only considered the direct effect on the calf body mass, i.e. the effect of N_t on W_t, where t is year.

We first ran univariate models to investigate the effect of each explanatory variable on the body mass. Second, we retained population density in the model, and included the environmental variables one by one, to examine whether the variation in body mass operates through population density directly, or through environmental effects that also cause density to vary. Finally, we also included juniper growth in the model, in order to see to what extent environmental variables were able to give additional information about environmental effects on reindeer calf body mass. Although the juniper growth is closely related to some of the environmental variables (Henriksen et al. in prep.), and co-linearity between explanatory variables is generally not recommended in multiple regression models (Mitchell-Olds & Shaw 1987), we believe the robustness of the linear mixed models to be adequate to handle this. Nevertheless, the inclusion of juniper growth would give an indication of to what extent the environmental variables are able to explain the variation in reindeer body mass after including a direct measure of plant performance, although the parameter estimates of the environmental effects may be unreliable.

All mixed models were fitted with restricted maximum likelihood estimates. The distribution of the parameter estimates in such models is likely to not be symmetric, and thus, a resampling technique (e.g. 10,000 Markov chain Monte Carlo simulations) from the posterior distribution of the parameter estimates can be used to obtain e.g. confidence intervals. We considered a parameter to be significant if the 95% confidence interval from the resampling not included zero.

Results

The mean calf carcass mass was 17.43 kg (2.45 SD), but this varied between years from 15.54 kg in 1984 to 20.96 kg in 2002. Moreover, there were variation in the calf carcass mass among the reindeer herds, ranging from 14.76 kg to 19.46 kg (mean values during the study period). At the same time, some herds experienced three-fold variation in the population size. In most herds, the population size decreased during the study period, and the average herd size was 4755 individuals. There was a negative relationship between population density and the calf carcass mass at the within-herd level (Fig. 2a).

Several of the environmental variables had significant effect on the calf carcass mass in autumn, not accounting for density effects. There were negative relationships between the calf carcass mass and winter NAO, April and May snow depths, September precipitation, derived spring NDVI, and juniper radial growth, while the carcass mass was positively associated with summer NAO (Table 2). Accounting for the within-herd variation in population density, the effect of winter NAO became non-significant at alpha = 5 % level (Table 2), while there were a negative relationship between September temperature and the carcass mass (Table 2). The other relationships did not change considerably. In all models, the effect of population size was significantly negative, with effect size similar or slightly stronger than for the model with population size alone (Fig. 2). Accounting for both population density and juniper growth gave several changes in the environmental effects. Both population density and juniper growth did not change considerably in their effect size or confidence interval in these models. The effect of winter NAO remained non-significant, while the effect of winter AO now became significant (Table 2). Furthermore, there was a positive relationship between summer temperature and body mass, and peak value and body mass (Table 2). However, the effect of September

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temperature and derived spring NDVI became non-significant after accounting for both population density and juniper growth (Table 2). Several other environmental variables changed effect size, particularly onset of spring and integrated NDVI (Table 2), however, the effect was not significant at the 5 % level.

Discussion

The role of population density and environmental stochasticity variation on life history traits has been studied within most taxa where suitable data exist. In herbivores, the role of density-independent effects is to a large extent related to quantity, quality and accessibility of forage (Klein 1970). However, density effects are expected to operate through food-limitation, and can be hard to disentangle from the density-independent effects. We found both high density-effects on reindeer calf body mass (Fig. 2a), effects of plant performance (Fig. 2b) and of environmental conditions (Table 2) that can be related to the foraging niche of the reindeer, but also caused by other mechanisms.

During winter, the reindeer in the study area share joint grazing area on the interior (southern) part of Finnmark county (Fauchald et al. 2004). In these areas, cold and dry climate usually ensures little snow and good conditions to forage on lichens, the main food resource during winter for reindeer in the study area (Fauchald et al. 2004). A high AO/NAO during winters is recognised with high level of precipitation in the study area, while the AO has proven better at explaining variation in temperature (Yoccoz et al. 2002), which will decrease the accessibility to lichens by increasing the snow depths and the energetic costs of cratering for lichen (Collins & Smith 1991, Weladji & Holand 2003). The negative influence of snow depths in April and May on the carcass mass is most likely a consequence of the same mechanisms,

but may also relate to when reindeer can start forage on fresh vegetation in spring.
However, we found no significant effect of onset of spring, as estimated from the
annual NDVI curve. The effect of April and May snow depths is therefore most likely
related to harsh winter conditions.

The importance of plant growing conditions in spring and early summer for
ungulate performance (Klein 1970) is supported by the negative relationship between
body mass and derived spring NDVI, and summer NAO. The derived spring NDVI
indicates the speed of plant development. A slow plant development can give access
to plants of higher quality for a longer time, because young and newly emerged
vegetation has higher nutritional value and digestibility than old and rapidly growing
vegetation (Albon and Langvatn 1992). Summer weather can have great impact on
plants quality as forage (Deinum 1984, Bø & Hjeljord 1991, Lenart et al. 2002), and
is pointed as one of the main factor for body mass variation in autumn in ungulates
(moose; Sæther et al. 1996, Hjeljord & Histøl 1999, Solberg et al. 2004, Herfindal et
al. 2006, red deer; Langvatn & Albon 1986, Albon & Langvatn 1992, Langvatn et al.
1996, Mysterud et al. 2001a, Pettorelli et al. 2005b, reindeer; Lenart et al. 2002,
Pettorelli et al. 2005c). The effect of summer NAO can also relate to the level of
insect harassment, e.g. parasitism by the warble fly (*Hypoderma tarandi*) and nose bot
fly (*Cephenemyia trompe*). The activity of these insects is found to increase with
temperature during summer (Hagemoen & Reimers 2002), and have negative impact
on the body mass in the study area (Fauchald et al. 2007). We did not find significant
effect of summer temperature and precipitation on the calf body mass, even after
accounting for population density (Table 2). However, the effect of summer NAO on
calf body mass remained significant, suggesting that such large-scale variables are

able to catch more of the weather signature that influence ungulates, e.g. through forage conditions compared to local climate measures (Hallet et al. 2004).

Henriksen et al. (in prep.) found a strong relationship between September weather and juniper performance. If reindeer body mass relates to plant performance, this should be visualised by effects of September weather. The significant negative relationship between reindeer body mass and September precipitation, as well as temperature after accounting for population density (Table 2), indicates that autumn conditions can be more important than previously expected for northern ungulates. Profitable conditions at this season can increase the period with access to high-quality forage, and low temperatures combined with little precipitation seems to not benefit the plant performance as measured as radial growth (Henriksen et al. in prep.), while such conditions was beneficial for reindeer body mass (Table 2). This finding further emphasise the contrasting effect of environmental conditions on plants and herbivores. This opposite response to environmental conditions was even more evident by the negative association between juniper growth and reindeer body mass (Fig. 2b).

Juniper radial growth performed well in explaining the annual variation in reindeer body mass, even after accounting for density effects (Table 2, Fig. 2b). The growth of juniper most likely capture the environmental variation that relates to the entire vegetation growing season, and is in this context better suited to predict variation in life history traits as a consequence of the general foraging conditions during summer than several of the other variables. Nevertheless, juniper radial growth was highly related to spring conditions (Henriksen et al. in prep.), and indeed, the relationship between derived spring NDVI and reindeer body mass became non-significant after accounting for juniper radial growth (Table 2). Furthermore, the relationship between body mass and summer temperature and peak value (maximum

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biomass productivity) became significantly positive after accounting for the effect of juniper growth (Table 2). Juniper growth, on the other hand, was more or less un-affected in terms of effect size and significance by the other environmental variables. Accordingly, the quality of juniper as a proxy for environmental conditions influencing ungulates through foraging conditions lies in the ability to capture the sum of environmental factors that influence the plants' suitability as forage, as well as not being foraged upon and thus unaffected by density-variation in ungulate populations. An advantageous future approach would be to examine the correlation between common juniper growth and the growth of important forage plants for reindeer in this ecosystem.

Acknowledgements

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Tables

Table 1. Environmental variables (Env$_i$) used in the analyses of reindeer calf carcass mass in autumn.

Explanatory parameter	Description
Onset of spring (OS)	Week number in spring when the NDVI-value represents birch leaf burst. Local
Integrated NDVI (IN)	Sum of the NDVI-values during the growing season. Local
Peak value (PV)	The NDVI-value at peak time. Local
Peak time (PT)	Week number in summer when the NDVI-value reaches its highest value. Local
Derived spring NDVI (DSN)	The NDVI-value at onset of spring minus the NDVI-value the previous 15-days maximum composite image. Local
Winter NAO (W-NAO)	Average annual value of the North Atlantic Oscillation index from December - March. Regional
Winter AO (W-AO)	Average annual value of the Arctic Oscillation index from December - March. Regional
Summer NAO (S-NAO)	Average annual value of the North Atlantic Oscillation index from June - August. Regional
Summer AO (S-AO)	Average annual value of the Arctic Oscillation index from June - August. Regional
April snow-depth (April SD)	Average snow depth in April. Regional
May snow-depth (May SD)	Average snow depth in May. Regional
Summer temperature (Summer T)	Average temperature (°C) during June, July and August. Regional
Summer precipitation (Summer P)	Sum of precipitation (mm) during June, July and August. Regional
September temperature (September T)	Average temperature (°C) during September. Regional
September precipitation (September P)	Sum of precipitation (mm) during September. Regional

Table 2. Parameter estimates and 95% confidence interval for the effect of population density and environmental variables (Table 1) on reindeer calf carcass mass (kg) in autumn. Bold indicates that the 95 % confidence interval does not include zero.

Environmental variable	Univariate models		Account for population density		Account for population density and juniper growth	
	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI
Population density	**-1.591**	**-2.426; -0.830**	-	-	-	-
Winter NAO	**-0.119**	**-0.225; -0.014**	-0.073	-0.176; 0.030	-0.015	-0.116; 0.087
Winter AO	0.035	-0.167; 0.232	0.053	-0.140; 0.244	**0.201**	**0.013; 0.380**
Summer NAO	**0.384**	**0.197; 0.574**	**0.384**	**0.204; 0.563**	**0.426**	**0.254; 0.593**
Summer AO	0.547	-0.098; 1.167	0.427	-0.177; 1.032	0.526	-0.032; 1.089
April snow depth	**-0.022**	**-0.041; -0.002**	**-0.024**	**-0.043; -0.005**	**-0.028**	**-0.045; -0.010**
May snow depth	**-0.033**	**-0.054; -0.011**	**-0.035**	**-0.057; -0.014**	**-0.048**	**-0.067; -0.028**
Summer temperature	0.078	-0.235; 0.397	0.004	-0.303; 0.304	**0.368**	**0.055; 0.672**
Summer precipitation	0.004	-0.002; 0.009	0.001	-0.005; 0.006	-0.001	-0.006; 0.004
September temperature	-0.134	-0.297; 0.028	**-0.213**	**-0.373; -0.054**	-0.147	-0.302; 0.006
September precipitation	**-0.016**	**-0.029; -0.003**	**-0.018**	**-0.030; -0.005**	**-0.013**	**-0.025; -0.001**
Onset of spring	-0.095	-0.263; 0.070	-0.095	-0.249; 0.064	-0.142	-0.293; 0.009
Derived spring NDVI	**-22.697**	**-37.314; -8.048**	**-18.489**	**-32.889; -4.363**	-8.485	-23.100; 5.445
Peak value	4.560	-2.665; 11.738	6.438	-0.639; 13.266	**11.701**	**4.504; 18.739**
Peak time	0.048	-0.133; 0.225	0.061	-0.111; 0.231	0.048	-0.114; 0.211
Integrated NDVI	-0.004	-0.698; 0.696	0.088	-0.606; 0.754	0.677	-0.011; 1.345
Juniper growth	**-15.998**	**-24.540; -7.743**	**-23.375**	**-31.903; -15.551**	-	-

Figures

Figure 1. Localisation of the reindeer herds grazing area (dark grey areas) and the

weather stations (crosses) in Finnmark, northern Norway.

Figure 2. The relationship between population size (a) and juniper radial growth

accounting for the effect of population size (b) on calf carcass mass in autumn in

semi-domestic reindeer in northern Norway.

Figure 1.
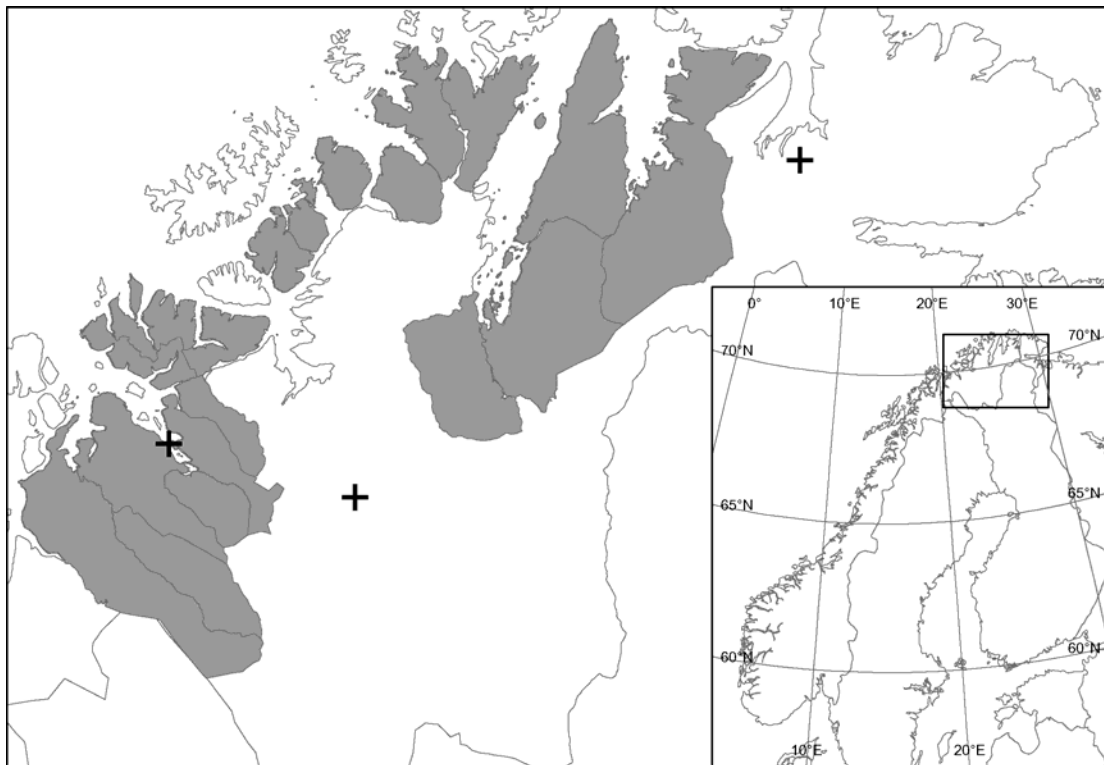
Figure 2.
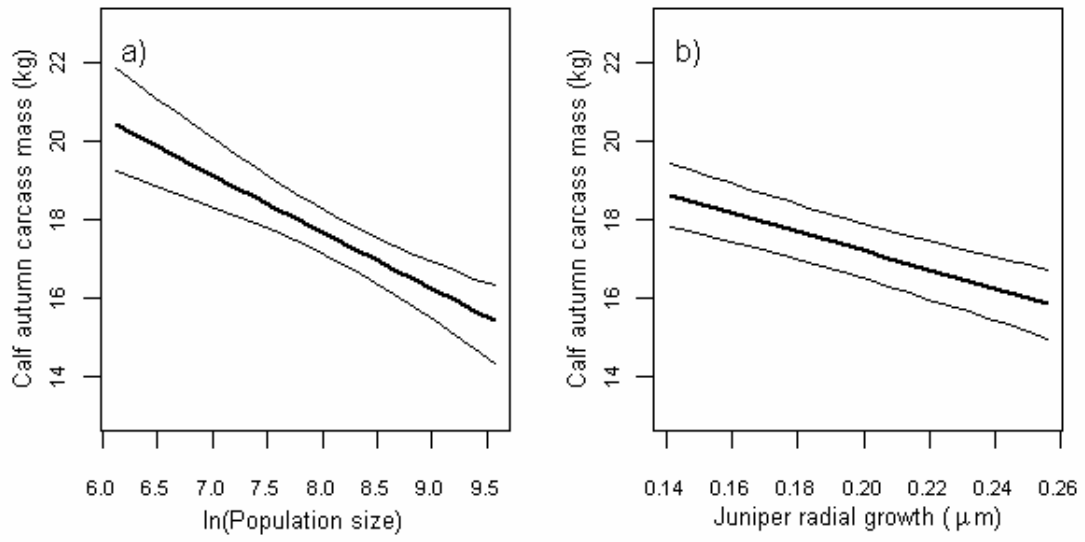
Paper V

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The effect of ground-icing on two high arctic plant species; an experimental study

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Keywords:

Ground-icing, High Arctic, Svalbard, Environmental stochasticity, Climate effects on plants, plant response, Salix polaris, Luzula confusa,

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Abstract:

The future Arctic climate will be warmer, more variable and contain more frequent extreme climatic events. One potentially dramatic effect on Arctic ecosystems resulting from a changing climate will be an increased frequency of ice directly on the ground during winter caused by freezing rain. We have investigated the effect of ground-ice on two common plant species (*Salix polaris* and *Luzula confusa*) that are important as forage for the resident Svalbard reindeer (*Rangifer tarandus platyrhynchus*). Ground-icing will produce anoxic conditions for the plants, which may increase the respirational costs due to a switch to more costly metabolic pathways and may also cause direct frost injuries and death. Such icing events are also known to cause increase in the mortality rates of reindeer because it causes inaccessibility to the food plants. We compared plots in which a thick ice layer directly on top of the vegetation was constructed before any major snowfall in late November with un-manipulated control plots. We found that *Salix* leaves from iced plots became heavier and larger in autumn than leaves from control plots. However, the difference in leaf weight between experimental groups (treatment and control) was minor and may not be a result of the experimental treatment. Furthermore, *Salix* leafs from iced plots were longer than leafs from un-iced plants at all measuring periods. There was a tendency for reduced growth of the rush *Luzula* throughout the season. However, based on model selection we can not conclude with certainty that this in *Luzula* was caused by the experimental icing. On the other hand, an increased mortality or drastically reduced growth as expected from general theory did not occur in these two species.

Introduction

Warming of the climate system is unequivocal (IPCC 2007) and the rate of climate change is predicted to be highest in high Arctic areas (IPCC 2001, 2002, 2007; ACIA 2004). Many experiments have been conducted to evaluate the effects of climate change on plant growth, reproduction and distribution (see Arft et al. 1999; Phoenix and Lee 2004) mainly by manipulating temperature and precipitation during the growth season. The predicted changes in climate are expected to be largest during winter, with an increase in winter temperature of 0.4-0.7°C per decade over land areas (ACIA 2004). So far, only a handful studies (Walsh et al. 1997; van der Wal et al. 2000; Wahren et al. 2005) have considered the effect of changing winter climate on the plant performance, and the focus has mainly been on the effect of altered length of growing season due to increased precipitation as snow or increased temperature and earlier spring.

One of the important conclusions from the General Circulation Models is that increased winter temperature will result in more frequent ground icing and rain-on-snow (ROS) events, a trend that is already apparent in the Canadian Arctic (Shabbar and Bonsal 2003; Hanesiak and Wang 2005). Both these events are characterised by rain during winter on frozen or snow-covered ground. Such rainfall during winter has important consequences for arctic herbivores because it causes increased mortality (e.g. musk ox (*Ovibus moschateus*) (Forchhammer and Boertman 1993); Svalbard reindeer (*Rangifer tarandus platyrhynchus*) (Aanes et al. 2000; Kohler and Aanes 2004) due to reduced accessibility to important food resources. Furthermore, invertebrates such as *Collembola* have been shown to be negatively affected through reduced survival during an icing event (Coulson et al. 2000).

Arctic feeding ranges for herbivores are characterised by extremely short growing seasons during summer. Hence, the timing of snow melt is important for the timing of onset of spring. In fact, snow manipulation experiments from Svalbard (van der Wal et al. 2000) as well as other high arctic ranges (e.g. Walsh et al. 1997; Wahren et al. 2005) have demonstrated that an earlier onset of spring will cause a phenological shift, i.e. earlier senescence and thus reduced quality. In contrast, the total plant biomass throughout the season will increase. Small changes in both quality and quantity of forage resources may therefore add up to large effects on critical demographic traits of the herbivores, i.e. "the multiplier effect" (sensu White 1983). For instance, variation in the quality of the food plant may effect the body growth of the young females that in turn may affect the age of maturity (Sæther 1997). Thus, reduction in the quality of important food plants due to seasonal carry-over effect of icing may therefore potentially have important consequences for the demography of large herbivores.

Ground-ice is formed when freezing rain falls on ground colder than 0°C. It is characterised by a solid sheet of ice directly on the vegetation which can result in an oxygen deficiency for the plants and increasing CO_2 levels (Rakitina 1970). Such O_2 deficiency is expected to cause a significant metabolic shift for the plants, thus the use of carbon (C) is accelerated (Bertrand et al. 2001). Furthermore, anaerobic respiration could cause the accumulation of potentially phytotoxic end-products. Ultimately, oxygen deficiency can affect winter survival and spring regrowth (Bertrand et al. 2003). However, low metabolic rates can prevent the accumulation of potentially phytotoxic metabolites and possibly maintenance of sufficient level of C reserves to sustain cold acclimation and spring regrowth (Bertrand et al 2003). Despite this information, little is known about the effects on plant growth from ground-

ice events in the arctic. Some information exists from Svalbard where Robinson et al. (1998) found that *Dryas octopetala*, subject to experimental fertilizing, was injured during a natural icing event due to delayed frost hardening

Our objective was to assess the effect of ground-icing occurring early in winter on the growth of two important forage plants (*Luzula confusa* and *Salix polaris*) for the wild Svalbard reindeer, the only large herbivore in the area. Based on the empirical evidence described above, we expected that the icing event would have a negative effect on plant growth measured through length and weight of leaves.

Methods

Study area

The experiment was located to Adventdalen (78°12'N, 15°50'E) Svalbard, Norway. Adventdalen is a large east-west oriented valley, characterised by a growing season of 6-9 weeks and little precipitation (190 mm annually, measured at Longyearbyen Airport which is situated at the Adventdalen outlet). The prevailing wind directions are from east and west, partly caused by the topography's channelling effect, causing little snow to accumulate during winter. Experimental plots were located at an almost flat *Luzula* heatland with a uniform physical character (e.g. slope, aspect and moisture level). This vegetation type covers about 3% of the vegetated area of Adventdalen (Brattbakk 1986). However, the two dominating species of this vegetation type, the dwarf willow *Salix polaris* (hereafter called *Salix*) and the rush *Luzula confusa* (hereafter called *Luzula*) is found throughout most vegetation types and especially the first is considered to be important forage plant for reindeer (Staaland et al.1991; van der Wal et al. 2000). *Luzula* is probably less preferred during the growth period, but is an important forage plant during winter (Bjørkvoll

2006). Associated species of the Luzula heat vegetation type are some grasses and a few dicots (e.g. *Pedicularis dasyantha* and *Polygonum viviparum*).

Experimental manipulation

In mid July 2003, we randomly outlined plots within the Luzula heatland. Within the plots we counted the number of leafs of *Salix* and *Luzula* within a 15 x 15 cm^2 area that constituted the centre of the experimental plot. There was no initial difference between plots in density of leaves of *Salix* or *Luzula* in plots later exposed to different treatments (F < 1.06, P > 0.30). To construct the ice layer, wooden frames which were 60 x 60 cm^2 and 15 cm high, were placed out in late November 2003. Three potential ground-icing events were recorded at the local meteorological station before we experimentally induced ground-icing, one in October and two in November (a total of 6.9 mm precipitation). The amount of natural icing was measured in all plots before any treatment was initiated. The amount of precipitation was sufficient to cover 6% (range 0 – 58%) of the ground with ice from natural icing process, the average thickness was 4 mm (±4 mm).

Furthermore, crusty ice and snow covered 50% of the ground-within plots, with an average thickness of 15 mm (SD = ±10 mm). This snow was penetrable to water. We then applied cold tap water to the plots within the treatment group. Initially it was sprinkled on gently (simulating a natural rainfall), not to disrupt the plants or the soil. When a ice layer of a few centimetres covered all plants, the water was poured on at a faster rate. This was repeated until all boxes were filled with water. Due to small hummocks, the depth of the ice layer varied slightly (mean 10.8 cm SD = ±3.03) measured at two points inside each plot. This measure was achieved by letting to thin wooden sticks of known length becoming encased by the ice. The amount of

water that we applied was similar to the record high precipitation during November and December in 1993 at Ny-Ålesund (287 mm) (Førland et al. 1997). This rainfall resulted in thick ground-ice and massive reindeer die-offs and emigration from the area (Aanes et al. 2000; Kohler and Aanes 2004).

We also measured snow and ice conditions at five places within 60 randomly selected plots not included in the experiment expected to representative for uniced control plots. The ground-ice (mean 1.6 cm, SD = ±1.6) and snow cover (8.2 cm, SD = ±3.7) was similar to the experimental plots. All snow and ice had disappeared before the first bud break in *Salix* and before the current years green leaves of the *Luzula* appeared in iced as well as control plots. The ground had thawed to a depth of 8-10 cm at the onset of green-up.

Measuring plant response

In 2004 we measured leaf lengths of *Salix* and *Luzula* inside each plot of both experimental groups (control and treatment) for 40 and 20 individual leafs, respectively, in the centre of the plot demarked with small wooden sticks summer 2003 (15 x 15 cm^2). The number of plots where leaf length (Salix and Luzula) were measured each month in the field were 15 and 10 for control and experimental plots respectively. We measured Salix leaf weight from 7 control plots and 6 treatment plots sampled each of the three months. The area in which measurements of 40 *Salix* leaves were achieved was marked and leaves were measured within the same area at three occasions during summer 2004, once each period: 25-30 June, 15-18 July, 12-18 August. *Luzula* were less common and were measured within a larger predetermined area (40 x 20 cm^2). In each plot and each period we also sampled 40 *Salix* and 20 *Luzula* leaves outside the area for repeated measurements by clipping

all leaves within a predetermined area within the experimental plot. However, the number of clipped Luzula leaves were in many plots small, consequently the number of plots with sufficient number of leaves were too small to test the effects of experimental treatment on Luzula leaf weight. A minimum distance of 30 cm between destructive samples was maintained to reduce the effect of this treatment. These leaves were stored in paper bags, frozen and subsequently dried at 70°C for 24 hours before measuring length and weight. Length was measured using a digital slide calliper to the nearest 0.01 mm. Weight was measured on a Sartorius MC210S to an accuracy of 0.01 mg.

Data analyses

We fitted global linear mixed effect model using maximum likelihood with experimental treatment as fixed effect together with month and day number within month to allow for different slopes within different months. In addition, we included the identification number of the plots as random factor to account for sampling location. Within each plot we outlined an area defined as a subplot from which we made the destructive sampling. Subplot within plots was included as random factor to account for different sampling location within plots in different months. Subplot was nested within plots in the models. As response we used log-transformed weights of individual leaves and log-length of leaves from the field measurements. AIC_C was calculated based on the log-likelihood estimates from the `lmer` function in R-package `Matrix` (Bates and Maechler 2006). The models were compared using a likelihood ratio test. All analyses were done in R 2.4.1 for Windows (R Development Core Team 2006). We selected the most parsimonious model according to AIC_C (Akaike Information Criterion corrected) (Burnham and Anderson 2002) and we

computed Akaike weights (w) to compare the relative performance of models rather than only their absolute AIC$_C$ value. Weights can be interpreted as the probability that a model is the best model given the data at hand and the set of models. We determined a weighted average of parameter estimates $\left(\hat{\bar{\theta}}_i\right)$ by model averaging (Burnham and Anderson 2002) where the covariate of interest is evaluated in terms of the Akaike weights of the models in which the target covariate occurs. Thus, we calculated model-averaged estimates as:

$$\hat{\bar{\theta}} = \sum_{i=1}^{R} w_i \hat{\theta}_i \qquad \text{Eqn. 1}$$

where i is a unique candidate model containing the variable of interest.

We constructed 95% confidence intervals for each model-averaged covariate coefficient using model coefficient standard errors (Burnham and Anderson 2002) calculated as the square root of the variance:

$$v\hat{a}r\left(\hat{\bar{\theta}}\right) = \sum_{i=1}^{R} w_i \left[v\hat{a}r\left(\hat{\theta}_i \big| g_i\right) + \left(\hat{\theta}_i - \hat{\bar{\theta}}_i\right)^2 \right] \qquad \text{Eqn. 2}$$

The resulting confidence intervals conservatively incorporate model uncertainty and provide a less biased evaluation the covariate effects.

Results

Considering weight of *Salix* leaves, the two most parsimonious models included treatment indicating a positive effect of icing on leaf weight. They also included an interaction between day-number within month and month (Tab 1), which is explained by a rapid growth in June while there were no measurable growth during the period plants were collected in July and August. The best model also included a month-treatment interaction caused by the plants in iced plots which grew faster than plants

in control plots late in season (Figure 1). However, there were no difference between the three best models ($\Delta AIC_C < 2$) for leaf weight and we can hence not exclude the possibility of no effect of treatment since the model including only month and day were amongst these (Tab 1). In addition, the model averaged confidence interval (CI) of treatment included zero (Tab 2) indicating weak or no effect of treatment. Field measurements of *Salix* length gave similar results (Tab 1), with two exceptions. First, length of *Salix* leaves measured in field subjected to experimental icing was found to be slightly longer than plants from control plots in all months (Figure 1). This was not an effect of different relationship between length and weight for different treatments, since there was no interaction between log length and treatment (anova: F=0.613, p=0.542). Second, the best model without treatment had a $\Delta AIC_C = 2.53$, strongly indicating that treatment had an effect. The model averaged CI of treatment did however include zero (Tab 2).

For *Luzula* the icing appeared to cause a negative effect throughout the season (Figure 1) possibly caused by a delayed start of growth season, an effect the plants appeared unable to compensate for. This was also reflected in the model selection, where the best model included only main effects of time (month and day) and treatment (Tab 1). However, the model including only time (month and day) was not much poorer ($\Delta AIC_C < 2$), and we can not conclude that this difference was caused by the icing alone. Also, the modelled averaged estimate of CI for treatment did include zero (Tab. 2).

Discussion

In this study we have demonstrated that two arctic plants, important as forage for a large ungulate, showed small responses in growth patterns to an experimentally

extreme winter with heavy ground-icing. The results from field measurements of *Salix* length and measurements of leaf weight from the dried plant material appeared to give slightly contrasting results regarding early season growth. Considering *Salix* leaf weight, no difference in phenological development between treatments was found early in the season while an increased growth was found at the end of the growing season in plants subjected to experimental treatment. Length of *Salix* leaves measured in the field was longer for plants exposed to ground-ice in all months (Figure 1). Consequently we can not conclude that icing caused an earlier spring green up. However, considering leaf length, the two best models included treatment, strongly indicating a positive effect of icing. The apparent difference in response in length and weight may be due to leaves becoming thinner when the growing season is short (Kudo 1996; Kudo et al. 1999), i.e. leaf mass per leaf area decreases, however we found no indication of this.

Luzula displayed a negative response to being exposed to ground-ice. This pattern was consistent throughout the growing season although slightly more pronounced early in the season. However, the model selection did not suggest substantial evidence for an effect of experimental treatment since the model without treatment had a $\Delta AIC_C < 2$ (Burnham and Anderson 2002) (Tab 1). Our results appears similar to what van der Wal and co-workers (2000) observed in plots with delayed snowmelt in a nearby area. Plants subjected to a late spring in their study were unable to compensate for this and remained smaller than plants subjected to an early spring. The overall effects of a severe icing incident on summer grazing conditions may appear to be minor for reindeer. However, since we have not measured the effect of icing on nutritional quality, we only can assume that the plants experienced a "phenological shift" as described in a comparable study (van der Wal

et al. 2000), i.e. nutritional quality decreases with time after snowmelt. The natural ROS events in March and April may have caused hypoxic conditions within control plots, thereby reducing the apparent difference between controls and experimental plots. We did not attempt to measure survival in 2004 since all experimentally iced plots had a lush cover of Salix leafs. Salix is a creeping dwarf shrub with underground branches or runners. If an individual, or parts of an individual, died this would have been visible as dead branches and open areas without any green leaves. Tagging of individual plants was not feasible, but still we are convinced that the survival of plants were not affected. Luzula tufts consist of both dead and live leaves. We did not attempt to measure live to dead ratio, but no tufts appeared to have died. The difference in response between Salix and Luzula to the icing may be due to different life-history strategies. The overall conclusion that neither growth nor survival of these plants are heavily affected by icing is still valid. The wooden frames used to construct the ice layer were removed some time after the snow and ice had melted but before green leaves appeared which should not cause a marked effect on plant growth even early in season.

A warmer climate may result in more frequent ground-icing and/or ROS events, inducing anoxia, i.e. deprivation of oxygen for plants. Until now, the research on effects of anoxia and ROS has mainly been directed towards agricultural plants, plants that through breeding programs may have lost adaptations for coping with these extremes. One study has been performed on Svalbard where it was found that the unlikely event of anoxia during summer, which may result from flooding, had surprisingly little effects on arctic plants (Crawford et al. 1994). However, the response of green leafs and photosynthetical active plants to anoxia may not be comparable to winter dormant plants. Generally the effect of ground-icing or ROS on

arctic plants is poorly understood even though many experiments (mainly by changing temperature and precipitation patterns during summer) have been performed to predict the effects of climate change in the Arctic. The ability of these experiments to mimic natural processes has been questioned (Phoenix and Lee 2004). This mainly results from the fact that the experimentally induced changes are abrupt and the whole spectre of changes caused by climate change are difficult to predict and even harder to replicate. Our experiment on the other hand, replicates an abrupt change in weather. Nonetheless, this experiment may not reflect how plants respond to repeated winters with ground-icing or any possible carry over effects to the next growing season, such as reduced biomass or nutritional quality. One characteristic feature of many high arctic regions is the lack of deep soil which may explain the relatively small effect on growth from ground-icing. Plants grow in well drained gravel and sand substrates which in combination with little precipitation results in low soil moisture levels during winter and hence air filled pores in the soil (Cary and Mayland 1972). An above ground-ice layer may therefore have a relatively smaller effect on O_2 levels below ground. And since large amounts of the live biomass of arctic plants is below ground, the effect of ground-icing may be restricted to above ground plant parts and transport through roots and stems may be sufficient for survival of above ground components. Our experimental plots were relatively small (60 x 60 cm^2) and diffusion from the surroundings may have increased the soil O_2 levels even further reducing the potential negative effect of ground-icing. However, this remains an open question. In addition, the reduced O_2-levels may have caused slightly reduced metabolic rates, and consequently, iced plants may have conserved resources during the winter.

The consequences of ground-icing and ROS on plants in Arctic regions have been considered in theory before (Phoenix and Lee 2004), but so far only predictions and no field studies have been made as far as we know (see Crawford 2003 for a recent review). Phoenix and Lee (2004) considered these two events in their review paper on plant perturbation experiments in arctic regions. They speculated that depletion of carbohydrates due to respiration may reduce plants ability to survive repeated ice-encasements, and therefore this respiration could also reduce anoxia tolerance in Arctic species. However, most winter rainfalls are normally of short duration, one or two days, and may therefore not be of sufficient length to result in increased respiration (Lund and Livingstone 1999).

Arctic ungulates dependent upon a relatively steady supply of food throughout the year and may in light of the predictions from GCMs face uncertain future prospect under a new climatic regime with periods of very high mortality from direct effect of ground-icing or ROS (i.e. locked pastures). The effect is already apparent and is most likely an important contributor to the western Queen Elisabeth Peary caribou (*Rangifer tarandus pearyi*) population decreasing to a historic low level due to several years with severe snow conditions in combination with icing (Miller and Gunn 2003). Shabbar and Bonsal (2003) accordingly found an increase in the frequency of winter warm spells in Canada, confirming the predictions from the IPCC report of increased temperature and frequency of these extreme events. The lack of research on effects of variable winter weather on Arctic plants has left researchers to speculate about the future for the animals that depends upon them. We have in this study found that the direct effects on some plants are relatively small and the indirect effects on herbivores from ground-icing will not extend beyond the direct effect inflicted during the winter assuming our findings are general for most plant species, under the

assumption of no delayed effects or changes in nutritional values. Other species or plant communities may possibly respond more negatively which will further strengthen the negative effect experienced by reindeer. On the other hand, arctic plants are adapted to their environment and it should not be to surprising that they may appear to cope relatively well to extreme weather events (Crawford and Abbott 1994). Such events has happened through history although they may be more common in the future.

It is well documented that heavy icing may result in strong negative impact on herbivore populations with increased mortality and migration (Aanes et al. 2002; Kohler and Aanes 2004). If such winters also affect the quantity or quality during the following summer of plant species not included in this study, the herbivores will even more affected through a double twist of negative effects. From Svalbard, several instances of heavy icing have been reported (Lønø 1959; Alendal and Byrkjedal 1974; Larsen 1976; Reimers 1977; 1982; 1983; Tyler 1987; Øritsland 1998; Aanes et al. 2002; Kohler and Aanes 2004) with large impact on the reindeer population size, but this also regularly occurs in other coastal areas of the Arctic such as Greenland (Forchhammer and Boertmann 1993) and Arctic Canada (Parker et al. 1975). But since it is mainly the youngest and oldest individuals and to some extent, adult males, that die during these events, the population can rapidly increase to its former size. Small populations on the other hand will be more vulnerable to such stochastic events since the effect of demographic stochasticity comes into effect, with the possibility of local extinctions. However, the probability of a female giving birth to a calf is dependent of her body mass, hence a hard winter will temporarily reduce the recruitment rate (Solberg et al. 2001).

Further studies should look into the physiological aspect of anoxia tolerance during winter in arctic plants, long term effect of single events as well as consequences of repeated icing event in subsequent years. In addition the effect on nutritional quality from a reindeer's point of view should be considered for these situations.

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Table 1. The best models from the model selection of multiple linear mixed models of the three data sets. "Salix weight" is the log leaf weight of dried Salix leaves. The best model has an AIC_C of 2625.3. "Salix length" is the models with log-transformed leaf length of Salix measured in the field as response. The best model has an AIC_C of 1093.2. "Luzula length" is field measurements of log leaf length of Luzula. The best model has an AIC_C of 2100.4. K refers to the number of estimated parameters, not including the individual groups, but considering random effects as one estimated parameter. Abbreviation: M = month (June, July, August), D = day within month, T = treatment (control and icing).

Model	ΔAIC_C	w_i	K
Salix weight			
M+D+T + M:T + M:D	0	0.34	11
M+D+T + M:D	0.5	0.26	9
M+D + M:D	1.1	0.19	8
M+D+T + M:T	3.3	0.06	9
M+D+T	4.2	0.04	7
M+D+T + M:T + M:D + M:T:D	4.8	0.03	14
Salix length			
M+T	0	0.46	6
M+D+T	1.98	0.17	7
M	2.53	0.13	5
M+D+T + M:D	3.27	0.09	9
M+T + M:T	3.86	0.07	8
M+D+T + M:T	5.84	0.03	9
Luzula lenght			
M+D+T	0	0.321	7
M+D + M:D	1.84	0.128	8
M+D+T + M:T	1.91	0.123	8
D+M+T + M:D	2.24	0.105	9
M	2.63	0.086	9
M+T	3.44	0.057	5

Table 2. Weighted average of parameter estimates (WAPE) and confidence intervals for all coefficients for all three data sets. 95% Confidence intervals with lower confidence level (LCL) and upper confidence level (UCL) shown in bold do not contain zero. Intercept is day one of treatment one (control) in month six (June). Abbreviations: D = day within month, T = treatment, M6 = June, M7 = July, M8 = August, : indicates interaction

Parameter	Salix weight			Salix lenght			Luzula lenght		
	WAPE	LCI	UCI	WAPE	LCI	UCI	WAPE	LCI	UCI
Intercept	4.301	**3.762**	**4.839**	6.123	**6.027**	**6.220**	7.500	**1.221**	**13.780**
D	0.157	**0.028**	**0.264**	0.007	-0.008	0.022	0.065	-0.101	0.212
T	0.053	-0.222	0.329	0.114	**0.005**	**0.223**	-0.139	-0.573	0.295
M7	0.799	**0.240**	**1.359**	0.148	**0.099**	**0.197**	0.163	-1.098	1.423
M8	0.796	**0.251**	**1.340**	0.213	**0.154**	**0.271**	0.210	-0.951	1.372
M7:T	0.067	-0.895	1.029	-0.013	-0.146	0.120	0.100	-0.167	0.367
M8:T	0.275	-0.646	1.195	-0.011	-0.102	0.080	0.075	-0.217	0.367
M7:D	-0.147	-0.213	0.273	0.001	-0.029	0.031	0.027	-0.274	0.328
M8:D	-0.133	-0.151	0.392	0.083	-0.411	0.576	-0.015	-0.210	0.179
M6:T:D	0.003	-0.036	0.042	<0.001	-0.006	0.006	0.001	-0.035	0.033
M7:T:D	-0.010	-0.067	0.047	0.002	-0.016	0.020	0.002	-0.179	0.176
M8:T:D	-0.002	-0.020	0.016	0.001	-0.005	0.006	0.001	-0.432	0.433

Figure captions:

Figure 1. Boxplot of median weight of individual *Salix* leaves, median length (mm) of live Salix leaves and median length (mm) of live *Luzula* leaves respectively, within treatments and periods. The bottom and the top of the box show the 25 and 75 percentiles respectively, whiskers indicate ±1.5 interquartile. Dark grey = controls, light grey = experimental treatment.

Fig 1
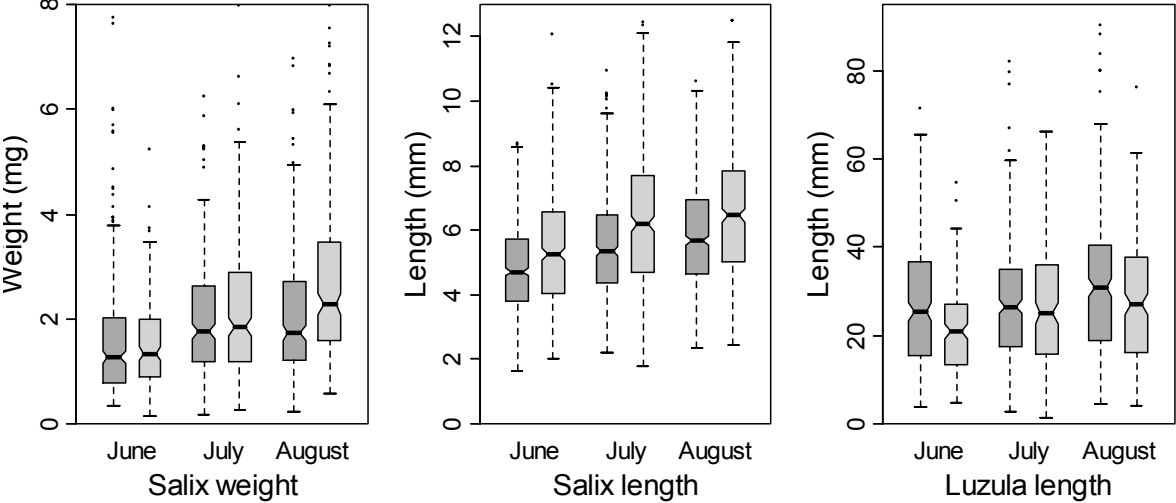
Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos. Zoology	Breeding events of birds in relation to spring temperature and environmental phenology.
1978	Egil Sakshaug	Dr.philos Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos. Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake.
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos. Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation.
1984	Eivin Røskaft	Dr. philos. Zoology	Sociobiological studies of the rook *Corvus frugilegus*.
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exosed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos. Zoology	Biochemical genetic studies in fish.
1985	John Solem	Dr. philos. Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains.
1985	Randi E. Reinertsen	Dr. philos. Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds.
1986	Bernt-Erik Sæther	Dr. philos. Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach.
1986	Torleif Holthe	Dr. philos. Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna.
1987	Helene Lampe	Dr. scient. Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires.
1987	Olav Hogstad	Dr. philos. Zoology	Winter survival strategies of the Willow tit *Parus montanus*.

1987	Jarle Inge Holten	Dr. philos Bothany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway
1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987	Bjørn Åge Tømmerås	Dr. scient. Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction.
1988	Hans Christian Pedersen	Dr. philos. Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care.
1988	Tor G. Heggberget	Dr. philos. Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure.
1988	Marianne V. Nielsen	Dr. scient. Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*).
1988	Ole Kristian Berg	Dr. scient. Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.).
1989	John W. Jensen	Dr. philos. Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth.
1989	Helga J. Vivås	Dr. scient. Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*.
1989	Reidar Andersen	Dr. scient. Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation.
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture,
1990	Bengt Finstad	Dr. scient. Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season.
1990	Hege Johannesen	Dr. scient. Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung.
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos. Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmion (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams.
1990	Tor Jørgen Almaas	Dr. scient. Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues.
1990	Magne Husby	Dr. scient. Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*.
1991	Tor Kvam	Dr. scient. Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway.
1991	Jan Henning L'Abêe Lund	Dr. philos. Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular.
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants

1991	Trond Nordtug	Dr. scient. Zoology	Reflctometric studies of photomechanical adaptation in superposition eyes of arthropods.
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway
1991	Odd Terje Sandlund	Dr. philos. Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism.
1991	Nina Jonsson	Dr. philos.	Aspects of migration and spawning in salmonids.
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient. Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher.
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient. Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos. Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks.
1992	Arne Vollan Aarset	Dr. philos. Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient. Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient. Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels ans some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient. Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient. Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Bothany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient. Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek.
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient. Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*.
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994	Inga Elise Bruteig	Dr. scient Bothany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers

1994 Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses
1994 Morten Bakken	Dr. scient. Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*.
1994 Arne Moksnes	Dr. philos. Zoology	Host adaptations towards brood parasitism by the Cockoo.
1994 Solveig Bakken	Dr. scient Bothany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply
1995 Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions.
1995 Hanne Christensen	Dr. scient. Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*.
1995 Svein Håkon Lorentsen	Dr. scient. Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition.
1995 Chris Jørgen Jensen	Dr. scient. Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995 Martha Kold Bakkevig	Dr. scient. Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport.
1995 Vidar Moen	Dr. scient. Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations.
1995 Hans Haavardsholm Blom	Dr. philos Bothany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden.
1996 Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae.
1996 Ola Ugedal	Dr. scient. Zoology	Radiocesium turnover in freshwater fishes
1996 Ingibjørg Einarsdottir	Dr. scient. Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines.
1996 Christina M. S. Pereira	Dr. scient. Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation.
1996 Jan Fredrik Børseth	Dr. scient. Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics.
1996 Gunnar Henriksen	Dr. scient. Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region.
1997 Gunvor Øie	Dr. scient Bothany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae.
1997 Håkon Holien	Dr. scient Botany	Studies of lichens in spurce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters.
1997 Ole Reitan	Dr. scient. Zoology	Responses of birds to habitat disturbance due to damming.
1997 Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture.

1997 Per Gustav Thingstad	Dr. scient. Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher.
1997 Torgeir Nygård	Dr. scient. Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors.
1997 Signe Nybø	Dr. scient. Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway.
1997 Atle Wibe	Dr. scient. Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry.
1997 Rolv Lundheim	Dr. scient. Zoology	Adaptive and incidental biological ice nucleators.
1997 Arild Magne Landa	Dr. scient. Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation.
1997 Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*.
1997 Jarle Tufto	Dr. scient. Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997 Trygve Hesthagen	Dr. philos. Zoology	Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997 Trygve Sigholt	Dr. philos. Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997 Jan Østnes	Dr. scient. Zoology	Cold sensation in adult and neonate birds
1998 Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins.
1998 Thor Harald Ringsby	Dr. scient. Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998 Erling Johan Solberg	Dr. scient. Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998 Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity.
1998 Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro.
1998 Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach.
1998 Bente Gunnveig Berg	Dr. scient. Zoology	Encoding of pheromone information in two related moth species
1999 Kristian Overskaug	Dr. scient. Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999 Hans Kristen Stenøien	Dr. scient Bothany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)

Year	Name	Degree / Subject	Title
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway.
1999	Ingvar Stenberg	Dr. scient. Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis.
1999	Trina Falck Galloway	Dr. scient. Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Torbjørn Forseth	Dr. scient. Zoology	Bioenergetics in ecological and life history studies of fishes.
1999	Marianne Giæver	Dr. scient. Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*.
1999	Ingrid Bysveen Mjølnerød	Dr. scient. Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos. Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient. Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient. Zoology	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat (*Luscinia s. svecica*)
1999	Gunnbjørn Bremset	Dr. scient. Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient. Zoology	Host spesificity as parameter in estimates of arhrophod species richness
1999	Sonja Andersen	Dr. scient Bothany	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen, I	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient. Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient. Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos. Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard

2000	Pål A. Olsvik	Dr. scient. Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient. Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient. Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species
2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forset systems
2001	Ingebrigt Uglem	Dr. scient. Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient. Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient. Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient. Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr.philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and
2002	Henrik Jensen	Dr. scient Biology	Causes and consequenses of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr.scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr.scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*

2003	David Alexander Rae	Dr.scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr.scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr.scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo Salar* L.) parr and smolt
2004	Torkild Bakken	Dr.scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004	Ingar Pareliussen	Dr.scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr.scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr.scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr.scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*).
2004	Lene Østby	Dr.scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr.scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr.scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr.scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr.scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr.scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr.scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	PhD Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr.scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr.scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations.
2005	Christian Westad	Dr.scient Biology	Motor control of the upper trapezius

2005	Lasse Mork Olsen	PhD Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	PhD Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	PhD Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Ander Gravbrøt Finstad	PhD Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	PhD Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr.scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation
2006	Kari Mette Murvoll	PhD Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr.scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	Phd Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr.philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr.scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	PhD Biology	Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	PhD Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	phD Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	phD Biology	Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania
2006	Anna Maria Billing	phD Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	phD Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	phD Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	phD Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	phD Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	phD Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	phD Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation

2007	Kari Jørgensen	phD Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	phD Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, */Mamestra Brassicae/* L. (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	phD Biology	Spatial and temporal variation in herbivore resources at northern latitudes