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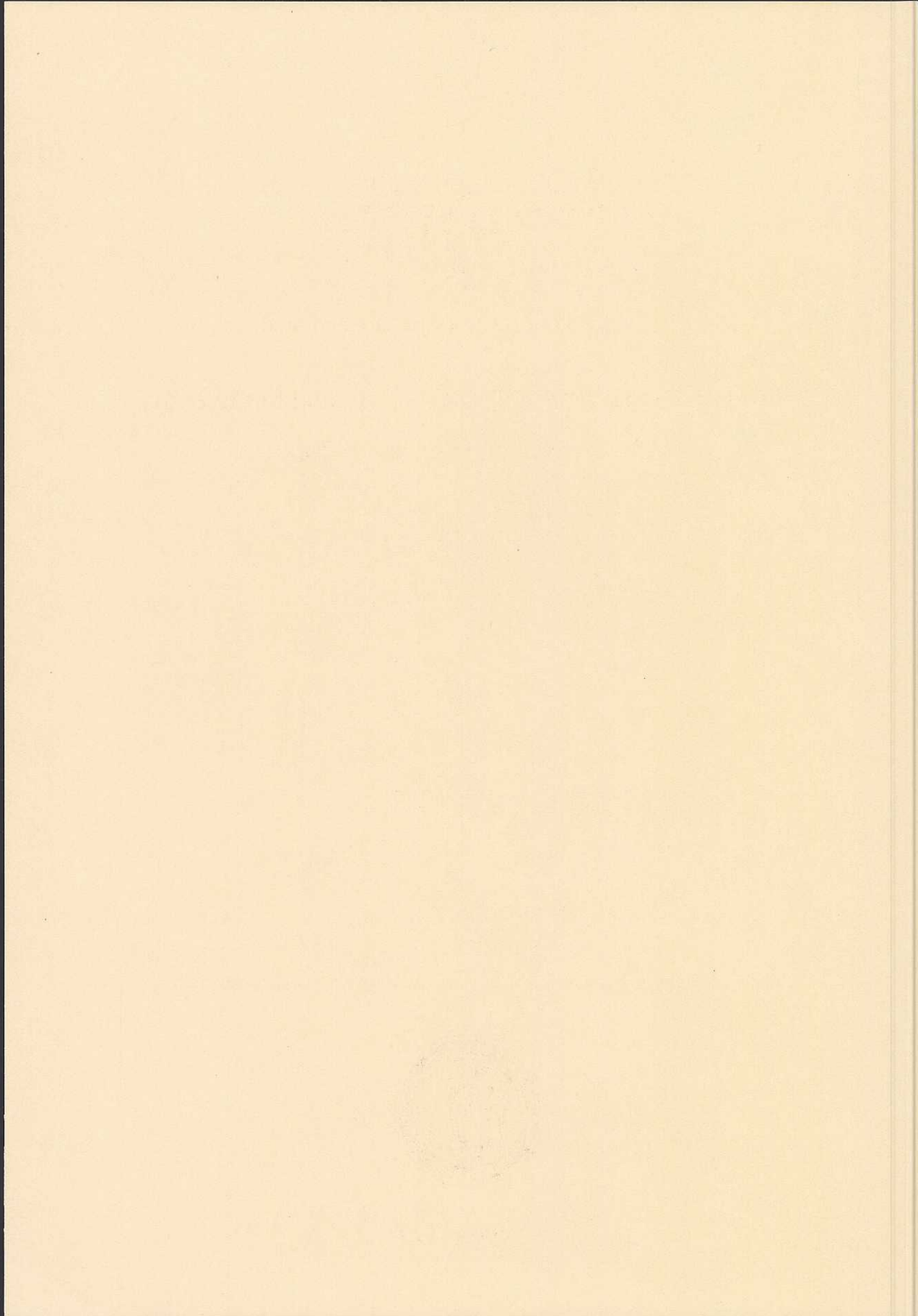
Dissertation

Climate Change: Impacts on structure and biodiversity
of subarctic plant communities

Juha M. Alatalo



Göteborg 1998



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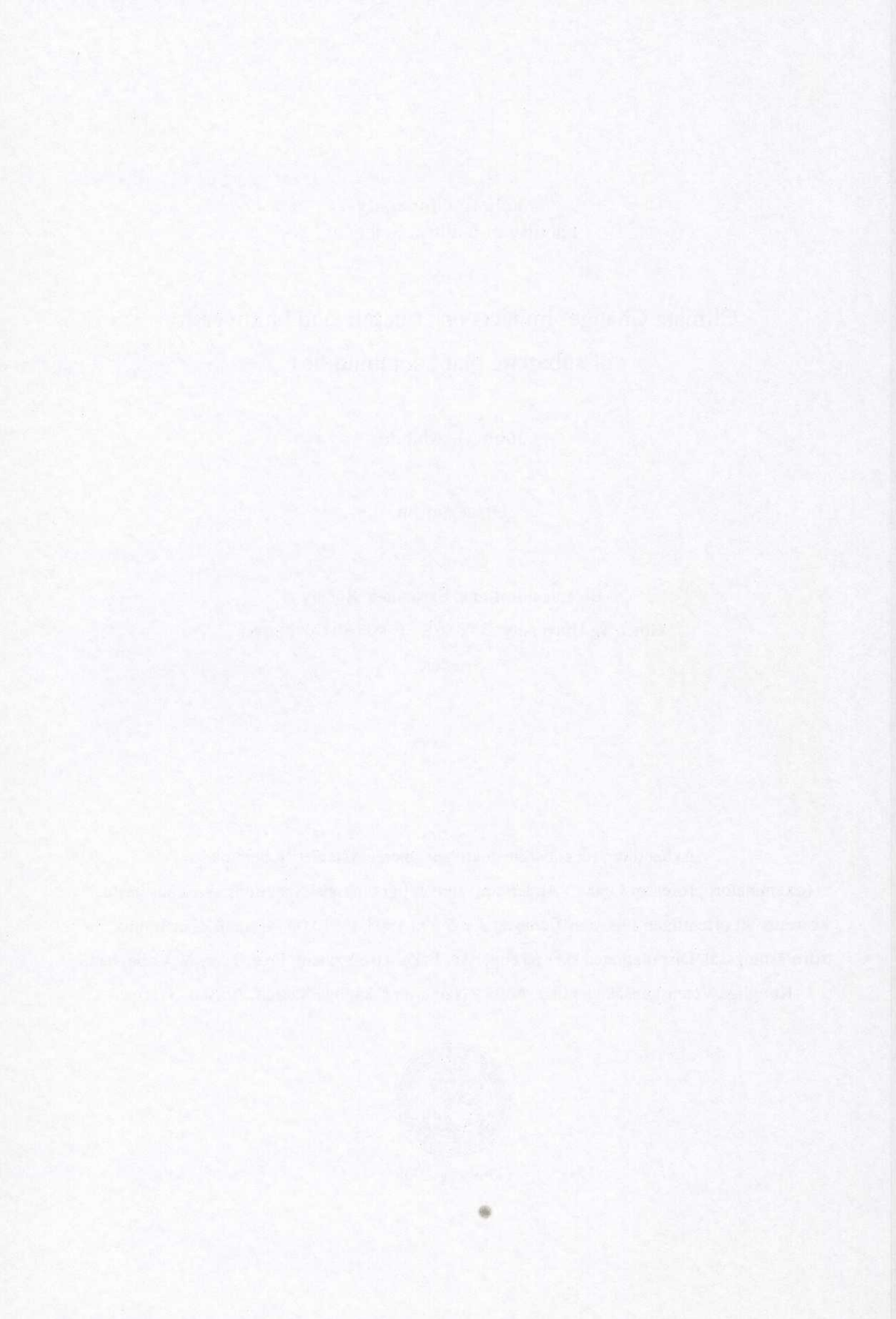
Dissertation

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Avhandling för filosofie doktorsexamen i systematisk botanik
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Kungliga Vetenskapsakademien, Abisko Naturvetenskapliga Station, Abisko, Sverige.



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Botanical Institute, Systematic Botany, Göteborg University, Box 461, SE-405 30 GÖTEBORG, Sweden.

ABSTRACT

This thesis concerns the effects of the anticipated climate change on a circumpolar cushion plant *Silene acaulis*, and on two common types of subarctic plant communities. The predicted changes in climate over the next 50 years are expected to be particularly large in arctic and subarctic regions. Earlier studies has mainly aimed at responses of single species, particularly vascular plants. In order to better understand the possible responses of subarctic-alpine plant communities. Manipulative field experiments was applied on different scales: detailed study of reproductive and vegetative responses of a common circumpolar plant species (*Silene acaulis*), and effects on biodiversity, structure, biomass, and reproduction, of two contrasting plant communities (rich meadow and poor heath, respectively, including non-vascular plant species).

The results show that *S. acaulis* may respond positively in reproductive terms to an increase of its temperature regime, and that both temperature and nutrient treatments had positive effects on vegetative characters. The result of main importance is that there can be considerable variation of responses, in time, and space, of individual plants species to environmental perturbations at various scales in a seemingly homogenous vegetation community. Thus, individual plants respond differently depending on their physical environment and genotype. This is probably caused by differentiated competition occurring at spatial scale (depending on neighbour plants), whereas the variation in time is probably a chaotic effect due to unpredictable weather conditions among years.

The studies at the plant community level shows that responses to environmental manipulations may vary both among functional plant groups, as well as within functional groups among plant communities. Consequently competition success may shift among functional plant groups depending on the vegetative structure of the plant community. Further, bryophytes tended to respond in negative manner whereas lichens responded in neutral or positive manner, the responses depending on the vegetative structure of the vascular plant community. This may cause considerable changes in biodiversity and vegetation structure of subarctic-alpine plant communities in the future.

Key words: *Silene acaulis*, subarctic, alpine, climate change, tundra, plant communities, plant functional types, biodiversity, vegetation structure, biomass, reproduction, vegetative, plant competition, plant responses, plasticity.

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- I. Alatalo, JM. and Totland, Ø. 1997. Response to simulated climatic change in an alpine and subarctic pollen-risk strategist, *Silene acaulis*. *Global Change Biology* 3 (Suppl. 1): 74-79.
- II. Alatalo, JM. and Molau, U. (submitted). Variation in time and space of vegetative responses to induced environmental change in a circumpolar cushion plant, *Silene acaulis*.
- III. Molau, U. and Alatalo, JM. 1998. Responses of subarctic-alpine plant communities to simulated environmental change: Biodiversity of bryophytes, lichens, and vascular plants. *Ambio* (in press).
- IV. Alatalo, JM and Molau, U. (manuscript). Responses of two contrasting subarctic-alpine plant communities to simulated environmental change: Structure, biomass, and reproduction.

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CLIMATE CHANGE: IMPACTS ON STRUCTURE AND BIODIVERSITY OF SUBARCTIC PLANT COMMUNITIES.

Background

Large anthropogenic emissions of "greenhouse gases" are thought to induce changes in our climate over the next 50 years, the changes expected to be particularly large and occur first in arctic and sub-arctic regions (Mitchell et al. 1990, Maxwell 1992). The background to this thesis can be found in the interest to study the effects of climate change on arctic ecosystems.

Although the largest increase is thought to occur during the winter period (Chapman and Walsh 1993), the climate changes might still influence the period available for growth of plants either by initiating earlier snow-melt, or/and by delaying the start of permanent snow-cover (Molau 1995, 1997a). Furthermore, an increase of summer temperature, even though small, can have major impacts on individual plant species and communities. This follows the logic that Arctic regions are characterised by their cold environment (Polunin 1951), and plant growth and reproduction often being a limiting by heat (Billings and Mooney 1968, Saville 1972, Jonasson et al. 1996) and short growing periods (Kudo 1991). Therefore, an increase of the plants temperature regime, or prolonging the growing period, should have positive impact on many species. Except for these more direct effects, climate change, or maybe better termed environmental change, will probably increase the amount of nutrients available, through the indirect effects an increased temperature is thought to have on decomposition and nutrient mineralisation (Swift et al. 1979). However, experimental studies have not given direct evidence for the idea (Nadelhoffer et al. 1991, Jonasson et al. 1993, Robinson et al. 1995, Vourlitis and Oechel 1997). There is also a direct increase of atmospheric nitrogen (N) and phosphorus (P) from anthropogenic sources (Neffel et al. 1985, Van Cleve et al. 1990). The "fertilising" of the tundra is thought to have large impact on the structure of the plant communities since most tundra ecosystems are nutrient limited, and the greatest responses are often found to nutrient addition (Chapin and Shaver 1985, Henry et al. 1986, Wookey et al. 1993, Chapin et al. 1995).

Expecting responses in plant species, the following questions may be asked: will all plant species respond in the same manner? If not, are there differences among functional plant groups? Will individual species respond in the same manner along latitudes or altitudes? How will whole plant communities respond in terms of structure and biodiversity? What is determining the response of plants/communities?

It was soon clear that "no" was the answer of the first question: not all plant species respond in the same manner to the experimental treatments simulating climate change. Instead responses to temperature and fertiliser treatments were shown to be highly individualistic (Chapin and Shaver 1985, Henry et al. 1986, Henry and Molau 1997). Almost the whole array of possible responses have been reported: species responding in positive manner in vegetative characters (*Calamagrostis lapponica*, Parsons et al. 1995), negative responses in vegetative characters (bryophytes, lichens, Press et al. 1998), indifferent vegetative responses (*Ledum palustre*, Suzuki and Kudo 1997, *Saxifraga oppositifolia*, Henry and Molau 1997 and reference therein), positive reproductive responses (*Papaver radicum*, Mølgaard and Christensen 1997, *Ranunculus nivalis*, Molau 1997b, *Silene acaulis*, Alatalo and Totland 1997), indifferent reproductive responses (*Saxifraga oppositifolia*, Stenström et al. 1997), and contrasting reproductive and vegetative responses (*Polygonum viviparum*, Wookey et al. 1994).

Noting that species differed in responses, and that the species could usefully be grouped into functional groups, Chapin et al. (1996) stated a specific hypothesis of responses of functional plant groups in a climate change scenario. Deciduous dwarf shrubs were hypothesised to increase in upland tundra, and evergreen dwarf shrubs to decline.

Looking at responses of whole plant communities to environmental manipulations, there are to my knowledge only a few studies on the subject at present in the Arctic (Chapin et al. 1995, Robinson et al. 1997, Press et al. 1998). This is particularly true if one counts the cryptogamic species as a part of the plant community. The studies that exist, have shown that after an initial dominance of graminoids in Alaskan tundra, the long-term response went in the favour of deciduous dwarf shrubs (Chapin et al. 1995). Bryophytes declined in Alaskan wet tundra (Chapin et al. 1995), and in a subarctic dwarf shrub heath (Press et al. 1998), but increased in a high arctic polar semi-desert (Robinson et al. 1997), whereas lichen biomass was reported to decline in the subarctic dwarf shrub heath (Press et al. 1998). Including bryophytes in studies on effect of climate change on arctic ecosystems may be important for several reasons, important food resource for invertebrates (Gerson 1982) and vertebrates (Longton 1984), and as being important for primary production (Oechel and Sveinbjörnsson 1978, Webber, 1978, Longton 1982) and nutrient cycling (Longton 1984).

Admitting the complexity of the story of climate change and its possible impacts on terrestrial ecosystems, this study can contribute to a better understanding of the possible responses of arctic plant communities to climate change

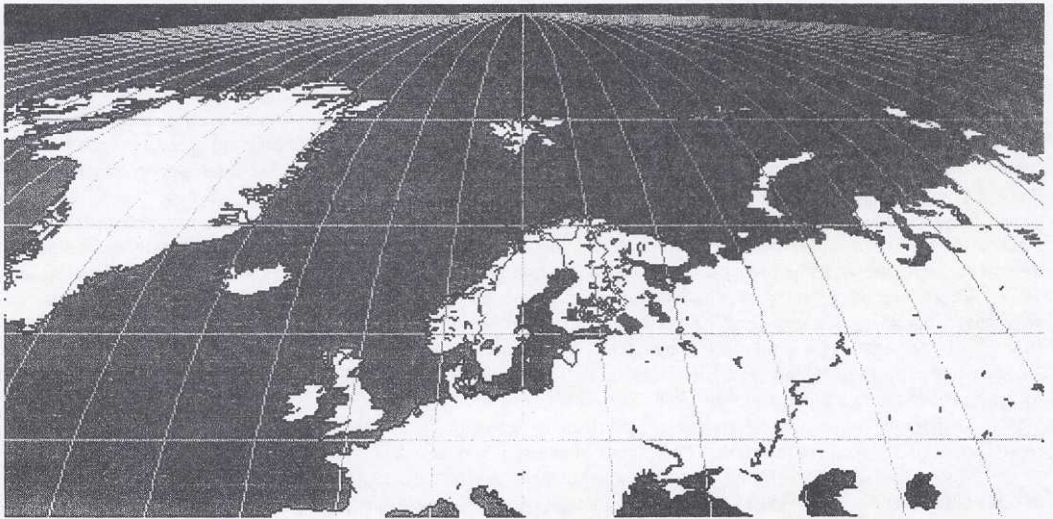
scenarios. This thesis will firstly examine the responses of a common circumpolar cushion plant, *Silene acaulis*, found in alpine through high arctic environments: in terms of reproductive responses (study I), and in the variation of vegetative responses in time and space (study II). Thereafter I address the responses of two contrasting subarctic-alpine plant communities: a rich meadow and a poor heath community, to factorial manipulations of temperature and fertiliser treatments, specifically in terms of biodiversity (study III), structure, biomass, and reproduction (study IV).

Methods and materials

Field site and plant communities

The field work mainly conducted in northernmost Sweden at the Latnjajaure Field Station (Fig. 1.) in the valley of Latnjavagge, 68°21'N, 18°21'E, at 1000 m elevation. The valley is covered by snow for most of the year, and the climate is classified as subarctic-alpine (Polunin 1951, Alatalo & Molau 1995) with a mean annual temperature of -2.2 to -2.7°C (data from 1993–96). The experiment was set up in a rich meadow community with continuous vegetation cover on calcareous rocks, and in a poor heath community with sparse vegetation cover on an acid glacial moraine ridge (Molau and Alatalo 1998). However, part of the study (I) was conducted at Mt. Sandalsnut, Finse, Hardangervidda, southwest Norway (60°37'N, 7°32'E).

Figure 1. Map over northern Europe and Scandinavia, showing the approximate location of the Latnjajaure Field Station, northern Sweden.



Experimental design

While study (I) only simulated an increase of temperature, the following studies (II-IV) also incorporated the anticipated increase of available nutrients. The experiment of studies III -IV, consisted of four replicate blocks, two in the rich meadow, two in the poor heath. Study II was only conducted in the rich meadow (with two replicate blocks). A fully factorial design of two components of environmental manipulations was employed: increased temperature (T) by Open Top Chambers (hereafter OTCs, Fig. 2, for detailed information on the construction of OTCs, see Marion et al. 1997), and fertiliser treatment (F), with two replicate plots per treatment combination and four control plots in each block. Thus there was a total of 20 plots in each habitat: 8 control plots and 4 plots for each of the (T, F and TF) treatments. Within each block, ten 1x1m plots were distributed systematically in a grid, the different treatments randomised among the plots in the autumn of 1994.

All plots were mapped using a point frame for the first time in July 1995, and the respective treatments were implemented immediately after mapping (see Walker 1996). Fruit number was calculated in end of season each year. In the subsequent seasons, fertiliser (5 g N and 5 g P per m^2 ; see Chapin et al. 1995, diluted in 10 l of water), was

added a few days after melt-out of the plots. Ambient temperature was recorded at standard shaded screen level (200 cm above ground), whereas temperature on ground level within experimental plots was recorded by a Delta T™ logger in the poor heath, and by Tinytags™ in the rich meadow. The OTCs were left on the plots throughout the winter, and thus prolonged the growing season in the T plots by 1–2 weeks (Molau and Alatalo 1998).

Table 1. Effect of OTCs on microclimate on ground level in the rich meadow and poor heath communities, and ambient temperature at standard screen level, at Latnjajaure, northern Sweden. Mean temperature in °C for each month in all cases. Reprinted from Molau and Alatalo 1998. OTC (Open Top Chambers), Ctr (control).

Rich meadow community									
Year	June		July		August		Mean June-August		Mean difference
	Ctr	OTC	Ctr	OTC	Ctr	OTC	Ctr	OTC	
1996	6.7	8.3	10.2	11.6	11.5	13.2	9.0	10.6	1.6
1997	8.1	11.0	12.3	14.7	8.2	9.6	9.1	11.4	2.3

Poor heath community									
Year	June		July		August		Mean June-August		Mean difference
	Ctr	OTC	Ctr	OTC	Ctr	OTC	Ctr	OTC	
1996	6.8	7.5	10.5	11.1	10.6	11.1	9.2	9.9	0.7
1997	8.0	10.5	12.5	15.1	8.6	9.3	9.1	11.2	2.1

Ambient temperature				
Year	June		July	August
1995	4.4		5.9	5.3
1996	3.2		7.4	9.9
1997	5.3		9.9	8.9

The results

Inter-annual climate variation, and effect of Open Top Chambers on microclimate

The OTCs increased temperature at the field surface from 0.5 to 2.6 °C, depending on year and month (Table 1, for detailed information on the performance of OTCs at other sites, see Marion et al. 1997). However, the natural inter-annual ambient summer temperature variation was even larger, with monthly mean temperatures varying strongly among years, from 3.2 to 5.3 °C in June, from 5.9 to 9.9 °C in July, and from 5.3 to 9.9 °C in August (Table 1). 1995 was the coolest year, while 1997 was the warmest; Latnjavagge was thus experiencing a short-term, gradual "climate warming" from 1995 to 1997. Furthermore, the summer of 1997 was exceptionally warm, the warmest on record since 1937 at the nearby weather station of Katterjåkk (SMHI). The 1996 also being a very "good" summer at these latitudes, the combination of those two subsequent good summers must be seen as an extreme event.

SUMMARY OF PAPERS

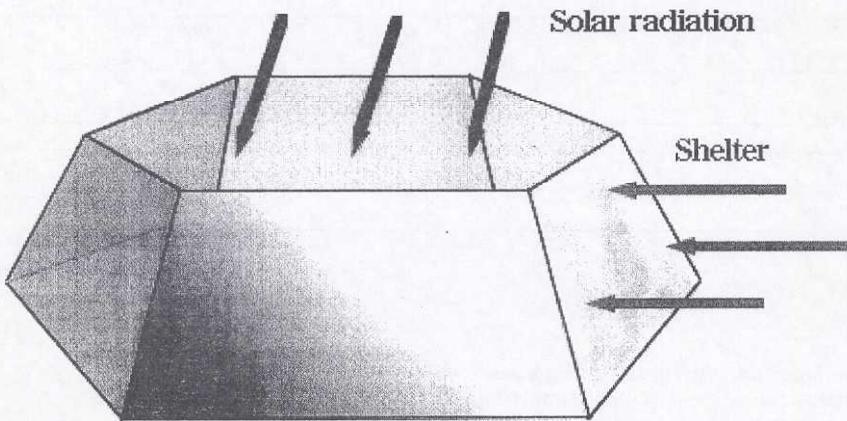
*Paper I. Reproductive responses of *Silene acaulis* to simulated climate change.*

From the background of Molau (1993) presenting a hypothesis that the reproductive responses of arctic and alpine plant species to climate warming, should depend on the species flowering time. By classifying arctic and alpine plant species into "pollen-risking" and "seed-risking" strategies, depending on their flowering phenology, it was then hypothesised that a climate warming could alter the seed pool in alpine and arctic areas. Late-flowering seed-risk strategists were hypothesised to increase their seed production over time due to a prolonged vegetation period, whereas early-flowering pollen-risk strategists was not thought to increase their seed production to the same extent (Molau 1993). The first study aimed to examine a potential effect of climate warming on the flowering phenology and

reproduction of a common circumpolar cushion plant, *Silene acaulis*. A early-flowering species that could be classified as a pollen-risk strategist according to the classification of Molau (1993). In order to do so, experimental temperature enhancement (by using OTCs, Fig. 2) was applied to two populations (a subarctic-alpine site and a more southern alpine site), where the experiment was run for two and one years, respectively.

The two year temperature enhancement at the sub-arctic site had a marked effect on the flowering phenology. Cushions inside the OTC started flowering substantially earlier than control cushions. Both the male and female phases developed faster in the OTCs, and maturation of capsules occurred earlier. The cushions also responded positive in reproductive terms and produced more mature seeds and had a higher seed/ovule ratio. After one year temperature enhancement at the alpine site there was a weak trend for earlier flowering, but there were no significant difference in seed production or seed/ovule ratio. From this it was concluded that the hypothesis of Molau (1993) did not hold true in general sense, and that early flowering "pollen-risk" strategist also had a potential to increase their seed production if the anticipated climate change would come true.

Figure 2. Open Top Chamber (OTC), the standard "passive" ITEX device used for increasing temperature in the experiments simulating climate change. Temperature increase obtained by a combination of shelter and "greenhouse effect" (the outward-bouncing long-wave radiation reflecting against the sides, thus trapping the heat). The material used is transparent polycarbonate (construction by Urban Nordenhäll). Ground surface area is ca 1m². © Ulf Molau.



Paper II. Variation in time and space of vegetative responses of *Silene acaulis* to simulated environmental change.

Most studies on potential effects of climate change on arctic ecosystems having aimed at vegetative responses of either graminoids or dwarf shrubs (e.g. Carlsson and Callaghan 1994, Parsons et al. 1994, 1995, Chapin et al. 1995, but see Molau 1996) it felt natural to start looking at other functional plant groups. Further, knowing of no study emphasising on the small scale spatial variation of plants in response to "climate change experiment", and my resources being limited for studies on "large scale variation". This study aimed specifically on the small scale variation within a seemingly homogenous vegetation community, of vegetative responses (stem elongation, leaf length, and leaf width) of the cushion plant *Silene acaulis*, to two components of environmental manipulations (temperature and fertiliser). This was conducted among years, blocks, and plots, in a factorial design. The results showing that there was a significant interaction among all factors studied. It was shown that the vegetative growth responses of individual plant species do not only depend on the temperature and nutrient regime they are experiencing, the responses also depend on what time, and geographical scale they are measured in. Thus, individual plants respond differently depending on their physical environment and genotype. This is probably caused by differentiated competition occurring at spatial scale (depending on neighbour plants), whereas the variation in time is

probably a chaotic effect due to unpredictable weather conditions among years, inter-annual climatic variation being more unpredictable in the Arctic than at lower latitudes (Ferguson and Messier 1996).

Papers III & IV. Responses of two contrasting subarctic-alpine plant communities to simulated environmental change: Structure, biomass, reproduction, and biodiversity of bryophytes, lichens, and vascular plants.

Having studied the responses of individual species, and at the same time realising from the growing number of studies, that extrapolation from individual species responses to community responses, was not without problems. In fact, it could easily lead to erroneous conclusions. Therefore a long-term project was started with the objective of studying both short-term, and long-term responses, of two contrasting subarctic-alpine plant communities, a rich meadow, and a poor heath, respectively. Especially, we were interested in the responses in terms of biodiversity, a subject that had not received any major interest (at that time). Furthermore, we were also interested in the development of the vegetative structure of the plant communities since we thought it might be influencing the responses of the "bottom layer", especially the cryptogamic component of the plant community. The cryptogamic community being a subject that had largely been ignored by the scientific community working on climate change (but see Chapin and Shaver 1985, Potter et al. 1995, Robinson et al. 1997, Press et al. 1998), even though their relative importance increases towards polar areas (Vitt and Pakarinen 1977, Wiegolaski et al. 1981). The general pattern of vegetative

Table 2. General tendencies (not always significant) of vegetative responses as relative change of the rich meadow and poor heath communities. Abbreviations as follow: negative change (-), no change (0), positive change (+), within parenthesis = week tendency, rich meadow (R), poor heath (P), cover (%), species diversity (Div.), mean height (H), and biomass (M), canopy layer (CL), bottom layer (BL), mosses, lichens, evergreen dwarf shrubs (Ev.gr.), deciduous dwarf shrubs (Dec.), Graminoids (Gram.), herbs (Herb), cushion plants (Cushion). Treatments: Ctr (control), T (temperature), F (fertiliser), and TF (combined temperature and fertiliser treatment). Data from studies III and IV, Latnjaure, northern Sweden.

Study III	Canopy %		Bottom %		Moss %		Lichen %		Moss no.		Lichen no.		Div. BL		Div. CL	
	R	P	R	P	R	P	R	P	R	P	R	P	R	P	R	P
Ctr	+	0	0	+	0	0	0	+	-	-	-	-	-	0	0	0
T	-	+	+	+	0	0	+	+	-	+	+	+	-	+	-	0
F	+	+	0	+	-	0	+	+	-	-	+	+	+	+	-	+
TF	+	+	0	-	-	-	0	0	-	0	+	0	0	+	-	+

Study IV	Canopy %		Ev. gr. %		Dec. %		Gram. %		Herb %		Cushion %		Moss %		Lichen %	
	R	P	R	P	R	P	R	P	R	P	R	P	R	P	R	P
Ctr	+	(+)	0	+	+	(+)	+	-	+	-	(+)	-	0	0	0	+
T	-	+	+	+	+	0	0	+	-	-	+	0	0	+	+	+
F	+	+	-	+	-	-	+	+	+	+	-	-	0	+	+	+
TF	+	+	(-)	+	0	-	+	+	+	-	+	-	-	0	(+)	

Study IV	Canopy H		Ev. gr. H		Dec. H		Gram. H		Herb H	
	R	P	R	P	R	P	R	P	R	P
Ctr	+	0	+	0	+	0	(+)	0	+	-
T	0	+	+	+	+	+	+	+	(+)	-
F	+	+	+	+	+	+	+	+	+	+
TF	+	+	+	+	+	+	+	+	+	0

Study IV	Canopy M		Ev. gr. M		Dec. M		Gram. M		Herb M		Cushion M		Moss M		Lichen M	
	R	P	R	P	R	P	R	P	R	P	R	P	R	P	R	P
Ctr	+	(+)	+	0	+	(+)	(+)	-	+	+	-	+	+	+	+	+
T	+	+	+	+	+	+	+	+	+	+	+	(-)	0	+	+	+
F	+	+	0	+	-	(+)	+	+	+	+	+	-	(-)	+	+	+
TF	+	+	+	+	(+)	+	+	+	+	+	+	-	-	0	+	+

responses can be viewed in Table 2. The most striking result being that the vascular plant community generally responded in a positive manner with an increase in complexity of the structure, the cryptogamic community differed in its responses. Mosses generally being negatively affected by all treatments, whereas lichens responded in a neutral or positive manner. Especially, the negative trend of mosses was most pronounced in the rich meadow community. Interestingly the vascular plant community seemed to respond more in terms of canopy height than canopy cover. Thus, the vascular plant species responded by increasing their mean height. When looking at the reproductive responses, another clear pattern appears. In the rich meadow the reproductive responses were largest to temperature during the first year, whereas the responses were larger to fertiliser in the second and third treatment year (Fig. 3). The only significant treatment effect on reproduction in the poor heath was on graminoids, responding to fertiliser in the second and third year.

Discussion

It is now clear that vegetation communities will not move "en bloc" along northward gradients following a climate change (Molau 1997a). Instead the new plant communities of the Alpine and Arctic will be formed by a mixture of already existing species, and invading species (Billings and Peterson 1992, Chapin and Körner 1995). Among the factors that probably will have the largest effect on the species composition are the differences in responses among already present species to a changing environment (Razhivin 1995, Molau 1996). Phenotypic plasticity, as well as genetic recombination, will probably be important for a species' future (Wookey et al. 1993, Parsons et al. 1994). Furthermore most of the stress from climate change will be on already existing individuals, this since most of the arctic plants are long-lived with life-spans covering centuries not being unusual (Molau 1993, 1997c). Thus, the individuals we see today, will also be the ones that will have to cope with the changes in the environment. Moving the thought another step, it becomes clear that the studies we are conducting are therefore actually being imposed on those very individuals whose future we are trying to predict, making it a rather unique situation. Therefore, while the experiments not being perfect simulations of the expected changes, they can anyhow give some insight of limiting factors, and response patterns of plants to these factors. Below follows a short discussion concerning the results of studies I - IV, focusing on responses of the different functional plant groups.

Responses of the moss and lichen communities

Chapin et al (1995), found that mosses neither increased in species number nor in cover in response to temperature enhancement in Alaskan tundra, while lichens increased both in species number and cover. Press et al. (1998) found a decline in abundance of both mosses and lichens in response to temperature enhancement in a sub-alpine shrub heath community at Abisko. The rich meadow community at Latnjajaure responded similarly to the results of Chapin et al. (1995): temperature enhancement increased bottom layer cover in the rich meadow, while species diversity of the bottom layer decreased. Lichens increased in both cover and species number, while mosses remained unaffected. The poor heath community responded differently; both cover and species diversity index increased in response to temperature enhancement. Mosses and lichens both increased the number of species; moss cover did not change while lichen cover increased. Thus, the increase in bottom layer cover caused by temperature enhancement in the rich meadow and poor heath communities was due to an increase of lichen cover, while mosses were not able to increase their cover in neither community.

Chapin et al. (1995) and Robinson et al (1997), found an increase of mosses in response to fertiliser in Alaskan tussock tundra, and high arctic semi-desert, respectively. However, Press et al. (1998) report a decline of both mosses and lichens in response to nutrient addition. Fertiliser treatment increased the species diversity of the bottom layer in both communities at Latnjajaure, as well as total bottom layer cover in the poor heath, but not in the rich meadow community. There was decline in the number of moss species in both of the communities at Latnjajaure, and moss cover decreased in the rich meadow but not in the poor heath community. The decrease in mosses was supplemented by an increase in number of lichen species and cover in both communities. Further there was a significant nutrient effect on moss biomass, biomass decreasing in all treatments and most pronounced in the fertiliser treatments in the rich meadow community.

The results are partly consistent with the results from the Alaskan moist tussock tundra, where there was no short term effect of combined temperature and fertiliser treatment on non-vascular plants, but with a drastic decline in the long term (Chapin et al. 1995). At Latnjajaure the combined temperature and fertiliser treatment had no effect on the species diversity index of the bottom layer in the rich meadow, but increased species diversity in the poor heath community. However, total bottom layer cover of the rich meadow decreased due a decrease in moss cover, while the lichen cover remained stable. In the poor heath moss cover declined similarly, but was supplemented by an increase of lichen cover, the total bottom layer cover thus remaining intact.

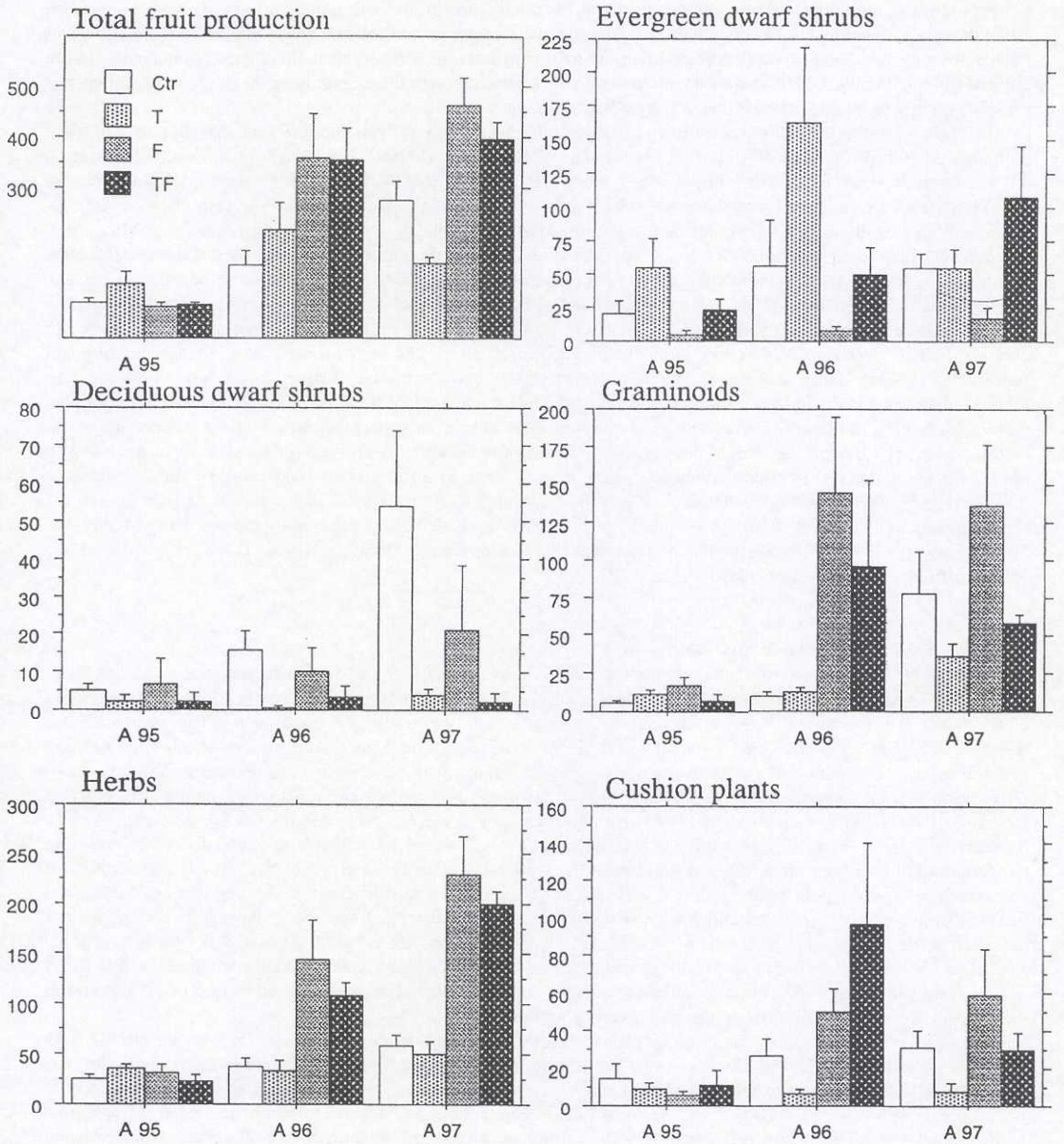


Figure 3. Fruit production of the total vascular plant community, of evergreen dwarf shrubs, deciduous dwarf shrubs, graminoids, herbs, and cushion plants, of the rich meadow community, at Latnjajaure, northern Sweden, 1995 - 1997. Treatments: Control (Ctr), temperature (T), fertiliser (F), and combined temperature and fertiliser (TF). Error bars ± 1 S.E. Redrawn from data from study IV.

A significant interaction among fertiliser and temperature on lichens in both communities caused the results to differ somewhat from those of Press et al. (1998) who found that lichen biomass decreased dramatically to temperature and nutrient treatments alone, in a nearby sub-alpine shrub heath community at Abisko. In the rich meadow at Latnjajaure, the lichens slightly decreased their cover in control and the combined temperature and nutrient treatment, whereas temperature and nutrient treatment alone increased lichen abundance dramatically. In the poor heath community, lichen abundance increased in all treatments with the largest increase in the temperature and fertiliser treatments alone, lichen biomass responding in similar way.

The contrasting results obtained from different studies probably reflects the different structures of the plant communities (Chapin et al. 1995: moist tussock tundra; Robinson et al. 1997: high arctic polar desert; Press et al. 1998: sub-arctic shrub heath (open birch forest); study III and IV in this thesis: sub-arctic alpine rich meadow and poor heath above tree-line). Particularly, vascular plants, when abundant, may constrain the responses of the non-vascular plants. In the high arctic polar desert, and the sparsely vegetated poor heath community (above tree-line), non-vascular plants respond forcefully to nutrient treatments, while in the more densely vegetated shrub heath (below tree-line) and rich meadow communities, the overall responses of non-vascular plants tend to be negative or neutral. It is important to note that the decrease in cover and species number of the bottom layer at Latnjajaure mainly occurred due to a decline in mosses, while there were no negative effect on lichens to experimental treatments. In contrast, lichen cover increased in all treatments, in both communities, and most pronounced in the temperature and fertiliser treatments. Thus, in general for alpine communities above tree-line, lichens might have a potential to increase their abundance in response to climate change while mosses might decrease. Climate change in mid-alpine regions is thought to cause a major decline of mosses, thus lichens may become the dominant component of the bottom layer even though they might not actually increase in abundance. A decrease of mosses might have severe impact on the arctic invertebrate community, since mosses serve as an important food resource for invertebrates (Gerson 1982). The impact on vertebrates is less clear although they are known to be important food source for vertebrates as well (Longton 1984). A decline in moss cover in areas that are dominated by mosses may also increase the seed germination and establishment of seedlings of vascular plants (During and Van Tooren 1990, Jónsdóttir 1991), and nutrient availability (Jónsdóttir et al. 1995).

Responses of the vascular plant community

In our study the canopy cover of both communities increased by the fertiliser and combined temperature and fertiliser treatments. Temperature enhancement alone had a positive effect on the cover of the poor heath community but no effect in the rich meadow. These results may be compared with the results obtained from a five year study on responses of plant abundance and biodiversity to fertiliser treatments at high alpine Rocky mountains, Colorado (Theodose and Bowman 1997). Species diversity of vascular plants was shown to increase following N+P fertilisation in a high alpine dry meadow, whereas N+P fertilisation decreased species diversity in a wet meadow at the same site (Theodose and Bowman 1997). In our study, species diversity of the poor heath also increased by fertiliser, and the combined temperature and fertiliser treatments, while the control plots and the plots receiving temperature enhancement alone showed no change. This probably reflects the effect of the initially low number of vascular species of the poor heath community. Even though graminoids was the functional group that had the highest increase in abundance, there was still plenty of room for other vascular plant species to expand. However, species diversity in the rich meadow community decreased in all treatments except the control plots; this is in line with the studies of Chapin et al. (1995) and Theodose and Bowman (1997). The mechanism is that graminoids respond very aggressively with a large increase in abundance, whereas other species that can not respond as fast as the graminoids are over-grown, and the initially high species diversity index declines.

Looking at mean canopy height, our results differed somewhat from the study of Press et al. (1998), who report an increase of canopy height of a dwarf shrub heath in a subalpine birch forest to temperature, fertiliser, and the combined temperature and fertiliser treatments. In our study the mean canopy height increased dramatically in both communities by the fertiliser and the combined temperature and fertiliser treatments, while temperature treatment had no effect in the rich meadow and a strong positive effect in the poor heath community. However, control plots (who experienced a "natural" increase of temperature among the years) increased their canopy height substantially in the rich meadow, but did not change in the poor heath community. Biomass increased significant by the fertiliser and temperature treatments in both communities, this is in contrast to Press et al. (1998) who got no treatment effect on total biomass of a dwarf shrub heath in a sub-alpine birch forest, the lack of response of biomass thought to be an effect of faster turnover of plant material (Press et al. 1998).

Evergreen dwarf shrubs

Chapin et al. (1996) hypothesised that evergreen dwarf shrubs should decline in areas with trees and deciduous shrubs as a consequence of competition for light. Instead our results are more consistent with those of Press et al. (1998), who did not find any significant changes in abundance of dwarf shrubs in a sub-alpine birch forest; I did not find any significant effect on abundance of evergreen dwarf shrubs in neither the rich meadow nor poor heath community. However, cover of evergreen dwarf shrubs tended to decline in the fertiliser treatments in the rich meadow community. In the poor heath there was a significant temperature effect on plant height; mean plant height of evergreen shrubs increased in all treatments except the control. Even though there was no significant treatment effect, biomass of evergreen shrubs increased substantially in all treatments, with the smallest increase in control plots and the most pronounced in the temperature treatment. Most of this effect was, however, brought about by species with their main distribution in boreal lowland, not the tundra specialist which remained low-responding (Molau and Alatalo unpublished). Similarly, while there was no significant treatment effect on height or biomass, they increased in all treatments in the rich meadow. Height and biomass responses differed, however, the height and biomass responding most to temperature versus fertiliser, respectively. This is partly consistent with other studies in European Arctic (Havström et al. 1993, Parsons et al. 1994, Press et al. 1998), and North American arctic areas (Chapin et al. 1995). Havström et al. (1993), found that the evergreen dwarf shrubs *Cassiope tetragona* responded to temperature in a nearby subarctic fellfield, and in a high arctic heath, whereas fertiliser increased growth in a subarctic tree-line heath. Press et al. (1998) report an increase of shrub biomass to temperature enhancement, but not to fertiliser, while Parsons et al. (1994) found significant effects of both temperature and fertiliser treatments on above-ground biomass of four dwarf shrubs (*Empetrum hermaphroditum*, *Vaccinium vitis-idaea*, *V. uliginosum*, and *V. myrtillus*), both studies conducted in subarctic tree-line heaths. In their long term study (9 years), Chapin et al. (1995) found that short-term responses were poor predictors of long term responses. Further, temperature enhanced shrub production, whereas fertiliser was shown to reduce growth of evergreen shrubs (Chapin et al. 1995). The lack of responses to fertiliser Press et al. (1998) saw as support for the notion that not all temperature responses are nutrient mediated as has been suggested by Chapin et al. (1992). Instead they argue that direct effects of temperature are important in both subarctic and arctic plant communities where it can influence allometric and developmental processes (Press et al. 1998).

The significant effect of year on fruit production of evergreen dwarf shrubs in the rich meadow probably reflects the exceptionally warm summers of 1996 and 1997, the inter annual climate warming being of greater magnitude than the experimental temperature manipulation (Molau and Alatalo 1998). In both these years the evergreen dwarf shrubs were able to dramatically increase their fruit production compared to 1995, a rather cold year. However, no such trends were found in the poor heath community. Havström (1995) found that fertiliser had a small but significant effect on flower production of two subarctic populations of *Cassiope tetragona*, but an increase in shading caused dramatic drop in flower production. Thus, he concluded that climate change would probably have negative effect on the sexual reproduction of *Cassiope tetragona*. Similarly, there was a significant but confusing treatment effect on fruit production of evergreen shrubs in the rich meadow community, treatment effect varying among years. Wookey et al. (1993) found temperature affecting seed-set of *Dryas octopetala* at a high arctic site, and fertiliser affecting fruit production of *Empetrum hermaphroditum* at a subarctic site. It was hypothesised that the responses may differ since plants are profiliating from different strategies, clonal versus reproductive spread in the Subarctic and High Arctic, respectively. Climate warming may thus be particularly important in the High Arctic, where colonisation of bare ground may occur from seed-set, and where genetic recombination may be needed. Whereas plants would benefit more in fitness from increase of vegetative growth in the subarctic areas where the canopy is more or less closed (Wookey et al. 1993).

Deciduous dwarf shrubs

In contrast to the hypothesis of Chapin et al. (1996), predicting that deciduous dwarf shrubs should increase their abundance in upland tundra, and results from North American Arctic (Chapin et al. 1995), I found that fertiliser treatment significantly decreased cover of deciduous dwarf shrubs in both the rich meadow and the poor heath communities. Part of this decrease is caused by the increase in graminoids over-topping the dwarf shrubs and becoming the intercept at sampling point. However, while there was no significant temperature effect on deciduous dwarfs, plots subjected to temperature enhancement, and control plots, increased the abundance of deciduous dwarf shrubs in both communities, most pronounced in the rich meadow. Further, temperature and fertiliser both significantly increased plant height in the poor heath, but not in the rich meadow community, whereas temperature only had a significant effect on biomass in the poor heath community. These confusing results give support to the

notion that direct effects of temperature may be important in subarctic plant communities (Press et al. 1998). Further the results may reflect the impact of vegetative structure of the plant communities. Poor heath communities might be more responsive to temperature treatments than rich meadows, since the continuous canopy of a rich meadow may isolate against solar radiation. The relative sensitivity of dwarf shrubs in the Arctic may also be environment dependent (Jonasson et al. 1996). Where temperature may stimulate growth to a greater degree than nutrient at higher latitudes or altitudes, where plants are growing closer to their lower temperature limits (Havström et al. 1993, Press et al. 1998). Another possible reason may be due to a delay in responses of deciduous dwarf shrubs as has been shown in Alaskan tundra (Chapin et al. 1995), where after an initial dominance by graminoids, the dominance switched towards deciduous dwarfs shrubs after nine years of perturbations (Chapin et al. 1995).

While I found no significant treatment effect on fruit production in neither plant community, it tended to increase among years in both the control (with increasing ambient temperature) and the fertiliser treatments of the rich meadow community. The lack of responses in the treatments using OTCs may be an unwanted side effect, OTCs probably limiting the amount of pollen available, especially for wind pollinated species as *Salix* sp. and *Betula nana* (Jones et al. 1997).

Graminoids

Parsons et al. (1995) reported that temperature and especially fertiliser treatment, caused increase in biomass and height of the dominant grass *Calamagrostis lapponica* in a subarctic heath community in northern Sweden. Similarly, Press et al. (1998) reports that the response of *C. lapponica* exceeded that of all other species at a dwarf shrub heath in a sub-alpine birch forest. While I have not analysed the data on species level, *C. lapponica* do exist in both the poor heath and rich meadow communities subject to this study, and is the dominant graminoid in the poor heath. In a five year study on plant abundance and biodiversity of alpine tundra communities in Colorado, it was found that grasses increased in abundance to fertilising both in a dry meadow and wet meadow, whereas sedges only in the wet meadow (Theodose and Bowman 1997). I found a significant effect on abundance of graminoids in the poor heath but not in the rich meadow community. In accordance with Press et al (1998), I found a dramatic fertiliser effect on plant height and biomass of graminoids in both communities, and a temperature effect in the poor heath community. The biomass of graminoids increasing by a factor of over 40 in the poor heath. *Calamagrostis lapponica* has further been shown to sustain its response over long periods (reference in Press et al. 1998), and may thus not decline as has other graminoids in Alaskan tundra. Alaskan long-time studies of effects of temperature and fertiliser treatments on tundra ecosystems have shown that after an initial domination of graminoids, deciduous shrubs tend to make a "come-back" and become dominant (Chapin et al. 1995). If this holds true in the Scandinavian mountains, we may expect a time with increase in abundance of graminoids which will enhance the food supply for herbivores, like reindeer and rodents, before shrubs slowly will take over, resulting in a decline of food supply for the herbivores in the long run.

Similar to Parsons et al. (1995) who found a significant fertiliser effect on flowering of *C. lapponica*, I found a significant treatment effect on number of flowering stalks in both communities. However, in contrast to Parsons et al (1995), I found no significant differences among treatments during the first year of treatment, but in the second and third year of the experiment the graminoids responded vigorously to nutrient addition. This can either reflect that flower buds are initiated the year before, a common feature to many arctic species (Sørensen 1941), or it may be due to delayed nutrient cycling within the plant.

Herbs and cushion plants

Vegetative characters of the cushion plant *Silene acaulis* has been shown to respond positively to both temperature and fertiliser treatments (Study II), and reproductive characters, as phenology phases developed earlier, and seed production increased significantly, in response to temperature enhancement (Study I). Similarly, the herbs *Ranunculus nivalis* (Molau 1997b), and *Papaver radicatum* (Mølgaard and Christensen 1997) have been shown to respond positively in both vegetative and reproductive terms to temperature enhancement, with the reproductive response of *R. nivalis* increasing among experimental years (Molau 1997b). From study II in this thesis, it was shown that the vegetative growth responses of individual plant species do not only depend on the temperature and nutrient regime they are experiencing, the responses also depend on what time, and geographical scale they are measured in. Thus, individual plants respond differently depending on their physical environment and genotype. This is probably caused by differentiated competition occurring at spatial scale (depending on neighbour plants), whereas the variation in time is probably a chaotic effect due to unpredictable weather conditions among years, inter-annual climatic variation being more unpredictable in the Arctic than at lower latitudes (Ferguson and Messier 1996). When looking at herbs and cushion plants as groups, the results can be compared with those of Theodose and Bowman (1997). In a five year study on plant abundance and species diversity of a resource-poor dry meadow and a resource-rich wet

meadow, they found that herbs increased to fertiliser treatment in the poor heath, whereas they were unaffected in the wet meadow. Wookey et al. (1994), however, found reproductive and vegetative responses to differ, the reproductive performance of *Polygonum viviparum* increasing significantly in a high arctic semi-desert (Svalbard), while there was no significant response in vegetative variables to an increase in mean temperature during the growing season. I found no fertiliser or temperature effect on abundance or biomass of cushion plants or herbs in study IV, but a significant fertiliser effect on mean height of herbs in the rich meadow community (the data not permitting analyses of herbs or cushion plants in the poor heath community). In contrast, both herbs and cushion plants showed significant treatment responses in terms of fruit production. Similar to the graminoids, the reproductive responses of both groups were expressed in the second and third year of experiment, and were more pronounced in the fertiliser treatments.

Summary of conclusions

1 Study I has shown that the hypothesis of Molau (1993) does not hold true in general sense and that flowering phenology can not be used as a predictor of reproductive responses of arctic plants to climate change. The late-flowering seed-risk strategists were hypothesised to increase their seed production over time due to a prolonged vegetation period, whereas early-flowering pollen-risk strategists was not thought to increase their seed production to the same extent (Molau 1993). Instead it was shown that early flowering "pollen-risk" strategist also had a potential to increase their seed production if the anticipated climate change would come true.

2 Study II has shown that the vegetative responses of individual plant species do not only depend on the temperature and nutrient regime they are experiencing, the responses also depend on what time, and geographical scale they are measured in. Thus, individual plants respond differently depending on their physical environment and genotype. This is probably caused by differentiated competition occurring at spatial scale (depending on neighbour plants), whereas the variation in time is probably a chaotic effect due to unpredictable weather conditions among years, inter-annual climatic variation being more unpredictable in the Arctic than at lower latitudes.

3 Study III and IV has shown that the vegetative structure of plant communities will change due to variation in vegetative responses both among functional plant groups, as well as within groups among plant communities. Fertiliser had negative effect on cover of evergreen dwarf shrubs, deciduous dwarf shrubs, and of bryophytes, in the rich meadow. Fertiliser had a negative effect on cover of deciduous dwarf shrubs and a positive effect on graminoids, in the poor heath. Mean canopy height and mean height of graminoids and herbs, increased in response to fertiliser treatment in the rich meadow. Temperature and fertiliser both increased mean canopy height, mean height of deciduous dwarf shrubs and of graminoids in the poor heath. Temperature alone increased height of evergreen dwarf shrubs in the poor heath. Total above-ground biomass increased in the temperature and fertiliser treatments, while biomass of graminoids was stimulated by the fertiliser treatment alone in both communities. Fertiliser treatment had negative effect on biomass of bryophytes in both communities. The overall effect of temperature and fertiliser treatments was an increased competition for light when the canopy gets more complex.

4 Study III and IV has shown that climate change will cause shifts in the dominance of bottom layer species. The difference in responses of cryptogamic species among plant communities is hypothesised to be caused by initial differences of the vascular plant cover. In the rich meadow communities, the canopy is well developed due to domination of vascular plants, and the bottom layer community only makes up a smaller part of the community in terms of biomass. The poor heath community, on the other hand, has a discontinuous vascular plant canopy, and is dominated by cryptogamic species. When the vascular plants increased their abundance even further in the rich meadow community to almost totally close the canopy due to the experimental treatments, the bottom layer was negatively affected in terms of either species diversity or cover. In the poor heath community where the canopy remained discontinuous to a greater extent even after experimental treatments, no negative responses were detected in the bottom layer community. The bottom layer species responded either positively or neutral in terms of species diversity and cover. Therefore it seems likely that the vascular plant cover is limiting the growth potential of the bottom layer species through competition over photosynthesis, nutrients, and space. Thus the responses of cryptogamic community to climate change can be either positive or negative terms of either species diversity or cover, the response to be determined by the structure of the vascular plant community. In both communities bryophytes are thought to be more vulnerable to climate change than lichens.

5 Study III further shows that there are no correlation between species number, or species diversity index, of canopy layer and bottom layer in neither community. In the rich meadow the species diversity index of the canopy was more or less constant while the species diversity index of the bottom layer varied a lot. In contrast, the poor heath showed the opposite pattern, species diversity index of the bottom layer being more or less constant while the species diversity index of the canopy layer varied. To conclude, this means that there are no ways to use any particular "key" species group for assessing total biodiversity in alpine communities; instead a "community system approach" must be used when addressing these kind of questions.

6 Study IV shows that the reproductive responses in the rich meadow were largest to temperature during the first year, whereas the responses were larger to fertiliser in the second and third treatment year. The only significant treatment effect in the poor heath was on graminoids, responding to fertiliser in the second and third year. It can be assumed that temperature may have larger short-term effect on reproduction of arctic and alpine plants than nutrients, whereas nutrients may have larger long term effect. This since climatic variables are known to vary among years in arctic and alpine areas, whereas the nutrient conditions are more or less stable among years. Thus, natural selection should favour those arctic and alpine plants species being able to respond quickly to enhanced temperature conditions. However, many plant species have been shown to be resource limited for their reproduction, therefore an increase of nutrient level may have major impact on reproduction in the long-term. This is partly supported by our results when looking at the total fruit production that was largest in the temperature treatment in the first year, whereas it was largest in the nutrient treatments in the second and third year.

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