

G l o b a l C h a n g e ,
H e r b i v o r y a n d
A r c t i c P l a n t s

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DECLARATION

I hereby declare that the work presented in this thesis is my own and has not been accepted in any previous application for a degree. The help given by others and all sources of information have been duly acknowledged.

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SUMMARY

Global Climate Change is predicted to have its greatest impact in terrestrial arctic ecosystems. Understanding their responses will be a first step towards extrapolating to other parts of the world. A meta-analysis of arctic field experiments, investigating effects of different components of environmental changes is presented in this thesis. It demonstrates that factors causing higher nutrient availability either directly (nutrient addition) or indirectly (soil warming), have the greatest influence on plant growth. However, despite current understanding of potential responses to altered environment, the future structure of arctic plant communities cannot be predicted with any reliability: influential factors such as intraspecific variability in susceptibility to environmental change, competition and herbivory have received too little attention. This study addresses the importance of these factors in the context of climate change, in a *Salix polaris-Luzula confusa* heath on Spitsbergen, Svalbard, 78°N

Regarding intraspecific variation, two genotypes of *Polygonum viviparum*, postulated to show differential adaptations to length of growing season, are in fact shown to be ecologically almost indistinguishable in this respect, although there are significant differences in their temperature-dependent germination rates.

The common approach to investigating competitive plant-plant interactions is shown to be inconclusive in the arctic tundra. Removal of neighbours also removes physical shelter and is thus not an appropriate way of detecting competition. However, comparison of the growth of plants in monospecific and mixed stands showed that competition does indeed occur, and that the balance between facilitation and competition can be different for different species. Experimental warming in the field led to changes in the growth of one of the two species, but not in the other, although lab experiments indicated that both plants should profit. This suggests a competitive growth suppression of *Luzula confusa* by the more responsive *Salix polaris*, evidence for the potential of plant-plant interactions to modify species responses to climate change.

As with plant-plant interactions, herbivory may also overrule the influence of climate change on plant growth. Excluding reindeer for three years led to slightly increased growth of *Salix polaris*, increased allocation to anti-herbivore defence and altered sex ratio. Simulating reindeer grazing in exclosures caused a brief increase in

phenolic defence compounds, and in the longer term slightly increased nitrogen content of the leaves, making the grazed plants more attractive to reindeer than controls. However, when plants were subject to moderate levels of experimental fertilisation, shading and warming, leaf nitrogen and carbon-based defence compounds displayed only little change. It was only when shading levels exceeded 70% that leaf nitrogen content increased and phenolics and condensed tannins decreased. These very high degrees of shading are unrealistic in terms of predictions for the arctic tundra. In a simple model incorporating competition, grazing and anti-herbivore defence, the imposition of warming and longer growing seasons had no noticeable effect on the relative abundance of defended and undefended plants. Moreover, the model gave evidence for a strong synergistic effect of grazing and competition, reducing the abundance of undefended plants at moderately high levels of grazing, while defended ones increased.

Overall, this thesis leads to the conclusion that biotic interactions (i.e. plant-plant and plant-herbivore interactions) are powerful agents in arctic terrestrial plant communities, and modify the response of plants to environmental changes. Further research into the exact mechanism of their actions are a next and necessary step towards the understanding of arctic tundra in a changing climate.

CHAPTER 1

GENERAL INTRODUCTION

There are at least three sound scientific reasons for working in arctic terrestrial ecosystems. Firstly, the Arctic is one of the simplest terrestrial ecosystems on this planet, containing only few plant species, herbivores and predators. This makes it an ideal model for investigating processes that are also occurring in more complex systems. Secondly, major parts of the Arctic are still pristine environments. Human impact is limited (although it might be locally devastating), and ecological processes are still largely natural, uninfluenced by man. Thirdly, the consequences of anthropogenic Global Climate Change are predicted to be most strongly experienced in the Arctic (Maxwell 1992; IPCC 1998). The combination of these three reasons makes the Arctic an ideal system to work in when interested in effects of environmental changes on plant life.

Direct effects of various factors associated with Global Climate Change (i.e. elevated temperature, higher nutrient availability, increased atmospheric CO₂-concentrations and UV-B radiation) have been well investigated over the last two decades. Some of these factors seem to have a dramatic impact on plant growth or reproduction, while others are seemingly less important. In CHAPTER 2, I review field experiments simulating Global Change, providing a quantitative, meta-analytical summary of plant responses. Additionally, I evaluate if the concept of plant functional types is useful for explaining and predicting differences between species' responses to environmental manipulations.

As most of these studies employed an experimental approach, they were performed on a relatively small scale. They thus included only little of the ecotypic and genetic variability among and within populations, which exists as a consequence of the occurrence of steep ecological gradients (“propinquity” sensu Crawford 1997b). This variability may contribute to a higher resilience of Arctic plant species and the vulnerability extrapolated from the findings of these studies might be overestimated. However, high genetic diversity is in itself no guarantee for wide ecological amplitudes and the existence of buffering *ecotypic* variability. *Polygonum viviparum*

has been one of the species for which the propinquity concept has been invoked. In CHAPTER 3 I shall look at the distribution, biomass and germination of two genotypes of this species in the light of intraspecific variability, and if indeed there is evidence of differentiation with respect to the length of growing season.

Studies on effects of Global Climate Change in the Arctic have concerned themselves mainly with direct effects on individual plant species or groups, or effects on the total ecosystem (e.g. carbon fluxes). Biotic interactions within the plant community have generally been neglected (but see Hobbie *et al.* 1999; Jonasson 1992; Shevtsova *et al.* 1995; 1997). *Competition* among plants in arctic plant communities has been investigated by removal experiments in only three studies (Hobbie *et al.* 1999; Jonasson 1992; Shevtsova *et al.* 1997). They found more positive than negative plant-plant interactions, indicating that facilitation might be more important than competition in structuring arctic vegetation. On the other hand, dominance of *Betula nana* in plots that have been fertilised and/or warmed for over 10 years at Toolik Lake, Alaska, indicate competitive exclusion of low growing vegetation (Bret-Harte *et al.* 2001).

Apparently, there is a conflict between the observational evidence suggesting negative plant-plant interactions and the experimental assessment, hinting at positive interactions. This might be an artefact of the experimental approach: CHAPTER 4 illustrates how facilitation and competition can co-occur, and that different experimental manipulations are required to disentangle the effects of each of them. On the other hand, if competition among plants does occur and structure the community, how will Global Climate Change affect these interactions? What repercussions will any alteration of competitive balance have? With the field and a laboratory experiments described in CHAPTER 5, I address these questions, looking at the performance of two species under elevated and ambient temperatures, with and without competition.

The second neglected type of biotic interactions in the Arctic is *herbivory*. While there are dozens of studies investigating herbivore (reindeer/caribou, muskox, snowshoe hare) foraging in relation to snowmelt pattern, forage digestibility & availability (Bryant & Kuropat 1980; Klein & Bay 1991, 1994; Danell *et al.* 1994b), there are virtually no data on the responses of plant secondary compounds to either grazing or

Global Change (Gunn & Skogland 1997). Moreover, the response of arctic plants to different grazing intensities is poorly investigated (but see Chapin 1980). While the acceleration of nutrient cycling by ungulate grazing has been postulated (Bryant & Reichardt 1992), examples of the consequences of grazing exclusion are scant (Loonen & Solheim 1998; Van der Wal *et al.* 2001b). One surprising effect of reindeer exclusion on plants is the possible change of the male to female sex-ratio in dioecious species, as shown in CHAPTER 6. This chapter tests in how far differential growth rates and differences in the amount of chemical defence are able to explain the observed pattern.

One way of balancing the strong growth demand for carbon and nitrogen (due to very restrictive growing conditions) with the need to deter grazers would be to rely on inducible defence (Coley *et al.* 1985; Karban & Baldwin 1997). However, only one study has examined the induction of defence compounds by herbivores in Low Arctic woody plants (Chapin *et al.* 1985). Such data are still to be produced for the High Arctic and CHAPTER 7 shows the results of a defence induction experiment with *Salix polaris*. More specifically, it looks at the response of polar willow to simulated grazing over different time scales, from 15 minutes to one year.

The consequences of Global Climate Change in the Arctic on plant defence compounds are little known (Bryant & Reichardt 1992). It is likely that environmental changes that affect the carbon-nutrient balance of plants will have an impact on the concentrations of secondary compounds (Bryant *et al.* 1983). In CHAPTER 8 the consequences of shading, fertilisation and temperature manipulations on plant quality (leaf nitrogen, carbon based defence) are investigated in a field experiment.

However, there are few such experiments that have investigated effects of GCC on forage quality (Walsh *et al.* 1997; Van der Wal *et al.* 2000c). The extrapolation of responses of herbivore populations to alterations of both quantity and quality of their forage is therefore at present largely speculation (Gunn & Skogland 1997; Aanes *et al.* 2000; Van der Wal *et al.* 2000c). One possible way to overcome the shortage of experimental data is obviously by model simulations. For a plant species, optimal allocation to anti-herbivore defence is not only governed by grazing intensity and availability of resources, but also by competition with undefended neighbours. The relative importance of competition and herbivory is addressed by a simple model in CHAPTER 9, which also allows simulating alterations of environmental conditions, such as temperature and length of growing season.



Fig 1. Geographical location of Svalbard with respect to Europe & Russia.

Any thesis trying to assess consequences of Global Climate Change in the High Arctic must remain a patchwork. Partly because some major avenues of research have already been followed up and provide a reasonable understanding of parts of the system (see review in CHAPTER 2), and partly because some gaps in our knowledge are too extensive to be filled in by one three-year enterprise. By addressing the various different questions outlined above, I hope

not only to fill in some of these gaps but also to give some ideas as to which research questions seem scientifically desirable next steps.

THE ARCTIC ECOSYSTEM ON SVALBARD

The High Arctic on Svalbard (Fig. 1) is a very young and 'immature' ecosystem. Most areas are periglacial, i.e. less than a kilometre distance from permanent snow and ice. Glaciers still cover over 80% of Svalbard (Fig. 2). In the (less than) 8000 years since the end of full glaciation, extremely low temperatures (yearly average of -5°C), heavy erosion events every spring/summer due to meltwater run-off and instability of tundra



Fig. 2 Svalbard is largely covered by glaciers.

permafrost (cryoturbation) have prevented the formation of soils in all but a few valley bottoms. And only on these peaty and boggy soils is plant production dominated by vascular plants. Ridges and polar deserts, sand flats and gravel slopes are either completely barren or exhibit infrequent moss

patches. Bryophytes, which dominate most vegetation types in terms of cover, are not further considered here, not because they are not important, but rather because their ecosystem function is still unclear (Longton 1988; Oechel & Van Cleve 1986): by keeping water even in their dead remains, they produce swamps where it is wet anyway, and their drought tolerance keeps them alive in dry places. In how far they actually alter their environment, enabling and disabling the establishment of vascular plants, remains to be seen (Van der Wal & Brooker, in prep.).

Due to the undeveloped soil, the shallow weathered mineral horizon and the impeded decomposition of dead plant material, nutrient availability is extremely low in the Arctic, and nitrogen the factor limiting plant growth (Chapin & Shaver 1985; Shaver *et al.* 1986; Wookey *et al.* 1994). Additionally, plant production is low as a consequence of a short growing season and low air and soil temperatures (e.g. Chapin 1983; Kummerow & Ellis 1984; Billings 1987). Vascular plants have become adapted to these conditions, depending more on storage and internal recycling of nutrient and reserves than their temperate congeners (Chapin *et al.* 1980; 1986a), using clonal growth as the main form of reproduction and obviously by a multitude of other structural adaptations (short, prostrate growth, low leaf turnover, solar tracking by flowers, etc.).

So have animals. Winter fur, relying on internal (reindeer/caribou, muskox) or external (arctic fox) storage over the winter or deterministic reproductive timing are specific adaptations to the Arctic. Additionally, herbivores (in the case of Svalbard mainly the Svalbard reindeer and different geese species) are optimising their food intake with respect to the usage of different plant communities through the season, and



Fig. 3 Reindeer bucks grazing in an *Eriophorum* swamp.

of plants within these communities (Stahl & Loonen 1998; Van der Wal *et al.* 2000c). They are following the "green wave" of maximum new biomass from the snow-free ridges in spring to the



Fig. 4 View over Semmeldalen towards the Van Mijenfjorden in the South.

summer-dry *Salix polaris*-heath and further to the late snow-free graminoid "pastures". Grazing pressure differs between plant species, time of the season, valleys and years, as the size of reindeer populations seems to be more regulated by icing events in winter and parasite intake in summer than plant production (Audun Stien, pers.comm., Irvine *et al.* 1999; Tyler & Øritsland 1999).

SITE DESCRIPTION

The field experiments were carried out in a valley system on the high arctic island West-Spitsbergen, Svalbard (78°N 5°E). The main study site was located in Semmeldalen (Fig. 4), c. 15 km north of the Van Mijenfjorden, and c. 20 km south of the capital Longyearbyen. As there is no human settlement in the area, the valley system can be described as pristine, though winter activities and travelling by snow scooter do cause disturbance to animals as well as soil and plants.

The shape of the valley indicates its origin was caused by glacial forces, leaving a U-shaped, straight valley reaching from the pass to Colesdalen at c. 250 m a.s.l. down to the coast of the Van Meijenfjorden at sea level. The length of the valley is c. 25 km. Near the sea, it opens into a river delta, where clayey sediments and constant waterlogging support a vegetation very different from the upper part of the valley.



Fig. 5 *Luzula confusa* and *Salix polaris* (leaf size approx. 10 mm).

The sides of the valley are rather steep and covered by vegetation up to a height of about 150 m a.s.l.. There, the erosion of coarse, dark grey shale by snow and water prevents the establishment of higher plants, though on higher elevation plateaus the complete set of plants found at the valley bottom are still present.

In the valley, a river drains the melting snowfields up on the slopes into the sea. Its transport volume fluctuates significantly during the season, and with every new year's snowmelt rearranges the course of its waters. The river banks are either gravel and silt deposits or, on the opposite side, erosion cliffs of c. 50 cm height. As other streams and rivers are joining from the sides, the actual area influenced by the central river is very high, and the disturbance caused by its forces affects c. one third of the area of the valley bottom. The other two-thirds split about evenly into wet swamps and drains, drier grass- and heathland, and topographically exposed ridges.

THE VEGETATION

Most of my work has been carried out in a vegetation type called *Salix polaris*-heath (subtype of the *Luzula confusa*-heath, Rønning 1996). Dominant vascular species are *Luzula confusa* (Fig. 5), *Salix polaris*, *Poa arctica*, *Pedicularis dasyantha*, *Alopecurus borealis*, *Polygonum viviparum*, while *Ptilidium ciliare*, *Dicranum* spp., *Drepanocladus uncinatus* (= *Sanionia uncinata*), *Hylocomium splendens*, *Polytrichum* spp. and *Pohlia* spp. are the main bryophytes. Lichens are poorly represented, due to the high grazing pressure (*Peltigera malcea*, *Stereocaulon* spec., very few *Cladonia* spp.). This vegetation has a moderate snow cover in winter, and the peaty top soil dries out over the summer. As the *Salix polaris*-heath becomes snowfree early in the season, grazing pressure by reindeer is very high in spring (June), but decreases as reindeer shift to the lush grass communities later in the season.

FOCUS PLANT SPECIES

Luzula confusa (Hartm.) Lindeb. (Northern Woodrush, syn.: *Luzula arcuata* (Wahlenb.) subsp. *confusa* (Lindeb.)), Juncaceae, on Svalbard is a wide-spread and common species of dry sites, particularly in the innerfjord areas. It grows in loose tufts, where most biomass is last year's standing dead leaves. It spreads by clonal growth as well as by seeds (Rønning 1996).

Salix polaris Wahlenb. (Polar Willow), Salicaceae, is another common and widespread species on Svalbard. It is a small, prostrate growing deciduous shrub, with creeping stolons in the moss and substrate layer. Due to extensive clonal growth it forms a web of root, rhizome, stolon and stems in the upper soil, from where branches extend aboveground. Plants are dioecious with fixed sex expression. In contrast to many temperate willows, catkins of *Salix polaris* appear after the leaves, flowering usually end of June to late July, with fruiting occurring from early July onwards. Seed ripen in fluffy "greenhouses" made from hair produced in the flower. They also aid wind dispersal. Germination percentages are unknown but likely to be very low, as willows have rapidly degrading seeds. Establishment from cuttings however can be successful to a high degree.

Polygonum viviparum is described in more detail in CHAPTER 3.

THE ANIMALS OF SEMMELDALEN

The Svalbard Reindeer (*Rangifer tarandus platyrhynchus*) is the only mammal herbivore on Svalbard. In Semmeldalen, some Pink-footed Geese (*Branta brachyrhynchus*), Svalbard Ptarmigan (*Lagopus mutus*) and Snowbuntings (*Plectrophenax nivalis*) also feed on plants, but they are not supposed to have an impact on the vegetation outside their highly fertilised nesting sites. No predator controls reindeer numbers, except for reindeer culled for feeding and scientific purposes (less than 5 % of the population). Arctic Fox (*Alopex lagopus*), Arctic Skua (*Stercorarius longicaudus*) and Glaucous Gull (*Larus hyperboreus*) fill the scavenger niche in this system, but are not a common sight.

Reindeer numbers in the Semmeldalen area have been closely monitored since 1994 (Langvatn *et al.* 1999), and aerial counts from the helicopter provide data for the whole of West-Spitsbergen since 1979 (Tyler & Øritsland 1999). At present, there are about 5000 individuals on the whole of Svalbard, and c. 500 individuals in the valley-

system that incorporates Semmeldalen. The strong fluctuations in reindeer numbers have initiated research into its causes, focussing both on endoparasitic nematodes (Irvine *et al.* 1999) and direct or indirect effects of weather (Tyler & Øritsland 1999; Van der Wal *et al.* 2000c; Van der Graaf 1999).