Global Change, Herbivory and Arctic Plants

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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.

Carsten F. Dormann
Aberdeen, June 2001.

Co-operations:

Chapter 3: The transect used for snowmelt and soil water content data was established by Steve D. Albon and Richard Harding, Centre for Ecology & Hydrology. Data on snowmelt and soil water content were collected by people acknowledged in that chapter.

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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: influencial 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, 78ºN

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 CO_2-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 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

Fig. 2 Svalbard is largely covered by glaciers.

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, prostate 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 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. 3 Reindeer bucks grazing in an *Eriophorum* swamp.

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-shaved, 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 lusher 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 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 Glacous 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).

CHAPTER 2

CLIMATE CHANGE IN THE ARCTIC: USING PLANT FUNCTIONAL TYPES IN A META-ANALYSIS OF FIELD EXPERIMENTS[1]

Abstract The effects of global climate change are predicted to be strongest in the Arctic. This, as well as the suitability of tundra as a simple model ecosystem, has led to many field experiments investigating consequences of simulated environmental change. On the basis of 36 experiments reviewed here, minor light attenuation by clouds, small changes in precipitation, as well as increases in UV-B radiation and atmospheric CO_2-concentrations will not affect arctic plants in the short term. Temperature elevation, increases in nutrient availability and major decreases in light availability, however, will cause an immediate plant growth response, and in addition alter nutrient cycling, possibly creating positive feedback on plant biomass. The driver of future change in arctic vegetation is likely to be increased nutrient availability, arising from, e.g. temperature-induced increases in mineralisation.

Arctic plant species differ widely in their response to environmental manipulations. The concept of plant functional types (PFT) as suggested by Chapin *et al.* (1996) for the Arctic was used to investigate differences in response to treatments. Whilst classification into PFTs may be useful in some respects, it proved generally unsatisfactory for generalisation of responses and predictions of effects. Nevertheless, a few generalisations and consistent differences between PFTs could be detected. Responses to fertilisation were by far the strongest, particularly in grasses. With respect to elevated temperature, deciduous and evergreen shrubs were most responsive. Future studies should focus on interactive effects of treatments, investigate long-term responses to manipulations, and incorporate interactions with other trophic levels. With respect to plant functional types, a new approach, which

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[1] together with Sarah J. Woodin (accepted by *Functional Ecology*, subject to revision)

groups species according to their response to environmental manipulations is advocated.

INTRODUCTION

The climatic effects of global change are expected to be most pronounced in the Arctic (Maxwell & Barrie 1989; 1992; IPCC 1990; 1998; Cattle & Crossley 1995). Many experiments have investigated the potential responses of this biome to environmental change (Henry & Molau 1997). They have generally focussed on plant responses, with some accounts of soil processes (Nadelhoffer *et al.* 1991; Jonasson *et al.* 1993; 1999; Robinson *et al.* 1995; Hobbie 1996) and invertebrates (Strathdee & Bale 1993; Hodkinson *et al.* 1998). Ecosystem processes have also been studied (Billings *et al.* 1983; 1984; Oechel *et al.* 1994; 1998), but detailed investigation of plant growth linking plant and ecosystems are rarely included in such studies (but see Hobbie & Chapin 1998b; Shaver *et al.* 1998). An integrated understanding of how the whole arctic biome will alter with climate change is still lacking (Callaghan *et al.* 1992; 1995; Reynolds & Leadley 1992). This review attempts to distil generalisations about the response of arctic plants to environmental manipulations, to aid the development of a comprehensive framework.

To predict the changes to vegetation that might occur within the Arctic, it is essential to understand the mechanisms and pathways of plant response to altered environmental conditions. Physiological aspects of responses to temperature, CO_2, UV-B, etc. are well understood (Bazzaz 1990; Taulavuori *et al.* 1998) but our knowledge of how these act in concert and how they affect the performance of different species in the field, is poor. It is this knowledge, however, that is needed to estimate climate change effects on other trophic levels (e.g. soil micro-organisms or herbivores) and to predict ecosystem functioning by means of mechanistic modelling (Reynolds & Leadley 1992).

Global Climate Change: Models and Predictions

For the Arctic, consistent predictions from transient-CO_2-increase-GCMs for the middle of this century have been made. These are:

- Winter temperature to increase by c. 5-10°C (IPCC 1998), but summer air temperature will probably be elevated by only 1-5°C (Cattle & Crossley 1995; Rowntree 1997).

- Winter and summer precipitation to increase by c. 0.25 to 5 mm·d^{-1}, but may be locally less than at present, e.g. on the Taimyr Peninsula (Rowntree 1997). Such variability will to result in more dry days in much of the Canadian and Alaskan Arctic, but more precipitation-days in Greenland and over the Arctic Sea. Soil moisture will decrease, as it is more determined by temperature-dependent evapotranspiration than by rainfall (Rowntree 1997).

However these predictions are still plagued with uncertainties: cloud-radiation interactions blur the picture, and different assumptions about their effect can influence the predicted temperature rise; ocean-atmosphere coupling is modelled on too coarse a scale; and the effects of aerosols, potentially resulting in radiative forcing, are only poorly understood (IPCC 1990; Rowntree 1997).

During the past few decades, environmental conditions have changed in arctic regions (Chapman & Walsh 1993; Serreze *et al.* 2000), and increased vegetation growth as well as northwards migration of the tree line have been predicted (Emanuel *et al.* 1985; Epstein *et al.* 2000). Over the last 40 years temperatures have risen by 0.2 to 0.3 °C, but locally trends exceed 0.5 °C per decade (Serreze *et al.* 2000). Moreover, snow cover area has declined by c. 10% since 1972, and precipitation (rain and snow) in Northern Canada have increased by 20% over the last 40 years (Serreze *et al.* 2000). There are, however, insufficient data to find trends in cloud cover in arctic regions.

Despite the fact that the concentration of ozone depleting substances in the atmosphere is no longer increasing, ozone depletion in the Arctic has become more severe in recent years, and is predicted to intensify over the next two decades (e.g. Shindell *et al.* 1998). This is because the stratosphere is cooling due to ozone loss and tropospheric warming. Maximum thinning of the ozone layer above the Arctic typically develops in early spring (e.g. > 70% O_3 loss in March 2000, Sinnhuber *et al.* 2000), when the combination of snow cover and weak irradiance largely protects terrestrial ecosystems from potential UV-B damage. Despite subsequent atmospheric mixing, the persistence of air from the polar vortex (Fairlie *et al.* 1999), and summer O_3 destruction driven by NO_x chemistry (Pierce *et al.* 1999), decrease mean amounts of O_3 in the air column in late spring and summer. The potential for increased exposure to UV-B in the Arctic exists, and satellite imagery suggests that exposure has increased as O_3 has decreased since the late 1970s (Madronich *et al.* 1998;

Searles *et al.* 2001). However, prediction of future trends in UV-B exposure is confounded by the effects of pollutants within the troposphere, and the uncertainties associated with prediction of future patterns of cloud amount and type (Madronich *et al.* 1998).

Plant Functional Types

Experiments at different geographic locations within a biome inevitably involve different plant species. To generalise and to incorporate plant responses into vegetation process models it is not necessary, however, to distinguish the responses of each species. Instead, the concept of plant functional types (PFT) can be used, with a PFT defined as a grouping of species sharing the same response to a perturbation (Gitay & Noble 1997). PFTs do not necessarily include groups equivalent to taxonomical, physiognomical or morphological classifications (Gitay & Noble 1997; Hobbs 1997), but often do (Chapin *et al.* 1996; Diaz & Cabido 1997; Shaver *et al.* 1997). This is because a PFT might represent the strategy by which different species have adapted over evolutionary time to the major abiotic or biotic constraints (e.g. Diaz & Cabido 1997).

For arctic environments, Chapin *et al.* (1996) followed a different approach to PFT-classification, based on a cluster analysis of plant traits such as leaf longevity, typical soil moisture and photosynthetic rate. Their aim was to predict plant effects on ecosystems. The result was a dichotomous key, which first splits vascular and non-vascular plants, then splits the vascular into woody and herbaceous groups. Woody plants are then separated into evergreen and deciduous, and the herbaceous species are differentiated into aerenchymous (sedges and rushes) and non-aerenchymous species (grasses and herbs).

In this review, we use the concept of plant functional types to integrate findings from Arctic field studies which have manipulated important factors in climate change-scenarios. Specifically, we ask 1.) What are the patterns of response of plants to different climate change factors in manipulative field experiments?, and 2.) Does the concept of plant functional types provide a useful and justified generalisation of plant responses? Although a meta-analysis for temperature elevation experiments within the International Tundra Experiment (ITEX) project was performed recently (Arft *et* *al.* 1999), this is the first systematic analysis incorporating a range of environmental manipulations.

METHODS

The Database

This review includes Arctic field studies north of the polar circle, published before 2001, in which abiotic components of expected climate change were manipulated, such as cloudiness (shading), atmospheric CO_2 concentration, nutrient availability (fertilisation), soil water availability (watering), temperature and UV-B. Fertilisation is by far the most commonly manipulated factor in Arctic field experiments, and so only those in which fertilisation was considered in combination with at least one other factor were included. The only exception was the study of Shaver & Chapin (1986), which includes data on grasses which were otherwise poorly represented amongst the experiments reviewed. Some studies had to be excluded: Hartley *et al.* (1999) and Starr *et al.* (2000) reported from soil warming experiments, where treatments were unfortunately confounded with air warming and season length manipulations, respectively. Shirazi *et al.* (1998) and Phoenix *et al.* (2000) had to be excluded because they manipulated disturbed vegetation. In total, 41 articles, reporting 36 separate experiments, form the database for analysis (Table 1).

We included data for all species (or genera or species groups), years and treatments reported in the original papers, but excluded those manipulations which have no direct bearing on climate change (neighbour removal, clipping). Only main factors were included in the database, as no interaction was reported in more than five studies, with the exception of the temperature × fertilisation interaction. Combining the six experiments that manipulated fertilisation and temperature provided no evidence for any overall pattern of interaction (data not shown).

Most experiments measured more than one response variable. We selected those most commonly assessed and assigned them to one of five groups: biomass, leaf, reproductive, physiological and chemistry measurements (details of grouping are given in the appendix). Not all data given in an article could be incorporated: The root:shoot ratio, for example, was not included into the biomass-group, as it reflects *relative* rather than *absolute* change. Cover data (e.g. Robinson *et al.* 1998), ecosystem parameters (e.g. Shaver *et al.* 1998) and other measurements *per plot* were not used, and the leaf-group only includes parameters relating to individual leaves, and not to leaf number or total leaf biomass. Clearly, not all parameters within a designated group would necessarily be expected to show the same directional responses to any particular environmental perturbation. In fact, in two instances in the physiology response group, within one species and treatment, one parameter showed opposite responses to others (Baddeley *et al.* 1994; Wookey *et al.* 1995). The inclusion of these parameters had no effect on the overall results, as shown by the results of both eliminating and inverting the sign of these data points.

Averaging over all response variables within each group yielded one value per response group per species, treatment, year and experiment. This means, for example, that a study reporting the aboveground biomass and photosynthetic responses of four species to two treatments over 4 years generated a total of 2 x 4 x 2 x 4 = 64 data-points.

Responses of species to treatments were recalculated from data presented in tables and graphs to make the different species and treatments comparable. The value in the meta-analysis database (X) was calculated as:

$$X = \log_{10}\left(\frac{\text{average value of response variable for treatment}}{\text{average value of response variable for control}} \cdot 100\%\right)$$

This transformed absolute into relative (% of control) values, correcting for size differences between species. Where data for a treatment were not given, because they were not significant (e.g. Chapin & Shaver 1985 for elevated temperature), a value of 100% (= no change) was entered for analysis. We followed the approach recommended by Hedges *et al.* (1999) and $\log_{10}$-transformed the ratio for all analyses.

For analysis of treatment effects on PFTs, only biomass and leaf-nitrogen content were used, as no other response variables provided sufficient data.

Statistical analysis

Although it would have been desirable to follow a strict meta-analytical approach (i.e. expressing effects as multiples of standard deviations: Gurevitch *et al.* 1992; Gurevitch & Hedges 1993, 1999; Arft *et al.* 1999; Goldberg *et al.* 1999), we regarded this as inappropriate for two reasons. Firstly, too few articles reported sample size, sums of squares, F-values or alike, making it impossible to extract estimates of sample variation. In some cases, where results were not significant, not even the treatment effect on the mean was reported. Also, most experiments were factorial designs including two or more treatments, and the measures of variance presented often did not represent the variance of the main effect. To exclude all such articles from analysis would have made the sample size vanishingly small. Secondly, we found the software (MetaWin 2, Sinauer Assoc., Sunderland, MA, USA) used in recent meta-analyses (Goldberg & Novoplansky 1997; Gurevitch *et al.* 2000; Searles *et al.* 2001) unable to take account of the complicated structure of the data (especially nesting and non-linear repeated measurements). Its usage would thus have led to a bias towards sites/studies with many factors and/or species investigated.

We incorporated data points from different years as repeated measurements. Because few studies reported data from more than two years, a linear repeated measurement structure could not be applied (SAS Institute Inc. 1989). *Duration* was thus nested within *site* to account for multiple measurements within one experiment (which is equivalent to a repeated measurement with an unspecified covariance matrix). Latitude, elevation, average annual temperature and average July temperature, number of replicates and number of subsamples were considered as covariates. The different treatment manipulations were nested within *site*, while the species reported from an experiment were nested within treatment.

The data set was analysed using the MIXED procedure of SAS (SAS Institute Inc. 1989). Denominator degrees of freedom were calculated using the Satterthwaite option. After the full model was tested (covariates entered first), it was simplified by stepwise removal of interactions and covariates, with a removal threshold of $P = 0.1$ (Crawley 1993). This procedure eliminated all covariates, leaving only main effects in the model.

Residuals were tested for assumptions of ANOVA, namely that the transformed data were normally distributed and groups had homogeneous variances (Sokal & Rohlf 1995). Post-hoc comparisons were performed using Tukey’s honest significant difference test (Sokal & Rohlf 1995; SAS Institute Inc. 1989). Error bars represent standard errors of means according to the output of the statistical model and are thus corrected for blocking and repeated measurements.

Table 1 Summary of experimental factors manipulated. Often more than one study reported from one site. Comments refer to shortcomings of the experiment discussed in the papers.

factor	# of sites	prediction	level of treatment	studies	comments
CO_2	2	700 PPM*[1]	680 PPM	1-3	
fertilisation	14	0-5 gm^{-2} y^{-1}*[2]	1-25 gm^{-2} y^{-1}	4-27	often too high doses; often NPK-combinations
light availability	8	–10-20%*[3]	–50%	6-13, 15-27	very uncertain prediction of cloud cover
UV-B	2	5% depletion*[4]	15% depletion	3, 28-30	spring peak higher, uncertain predictions
warming	23	2-5°C	2-5°C	6-12, 15-26, 31-41	greenhouses (for critique see Kennedy 1995; Marion *et al.* 1997), summer only
watering	5	+10-25%y^{-1} *[3]	10-60% (summer)	4, 13-19, 41	watering as fertiliser application control excluded

*[1] IPCC (1990)

*[2] Nadelhoffer *et al.* (1991)

*[3] IPCC (1998)

*[4] Madronich *et al.* (1998)

1: Tissue & Oechel (1987); 2: Moorhead & Linkins (1997); 3: Gwynn-Jones *et al.* (1997); 4: Henry *et al.* (1986); 5: Shaver & Chapin (1986); 6: Chapin & Shaver (1985); 7: Shaver *et al.* (1986); 8: Chapin *et al.* (1986b); 9: Chapin *et al.* (1995b); 10: Chapin & Shaver (1996); 11: Shaver *et al.* (1998); 12: Molau & Shaver (1997); 13: McGraw (1985); 14: Karlsson (1985); 15: Wookey *et al.* (1995); 16: Parsons *et al.* (1994); 17: Parsons *et al.* (1995); 18: Potter *et al.* (1995); 19: Press *et al.* (1998); 20: Havström *et al.* (1993); 21: Michelsen *et al.* (1996a); 22: Graglia *et al.* (1997); 23: Jonasson *et al.* (1999); 24: Wookey *et al.* (1993); 25: Wookey *et al.* (1994); 26: Welker *et al.* (1993); 27: Baddeley *et al.* (1994); 28: Johanson *et al.* (1995); 29: Taulavouri *et al.* (1998); 30: Gehrke (1999); 31: Stenström *et al.* (1997); 32: Jones *et al.* (1997); 33: Hobbie & Chapin (1998a); 34: Hobbie *et al.* (1999); 35: Hobbie & Chapin (1998b); 36: Mølgaard & Christensen (1997); 37: Welker *et al.* (1997); 38: Alatalo & Totland (1997); 39: Stenström & Jónsdóttir (1997); 40: Molau (1997); 41: Shevtsova *et al.* (1997)

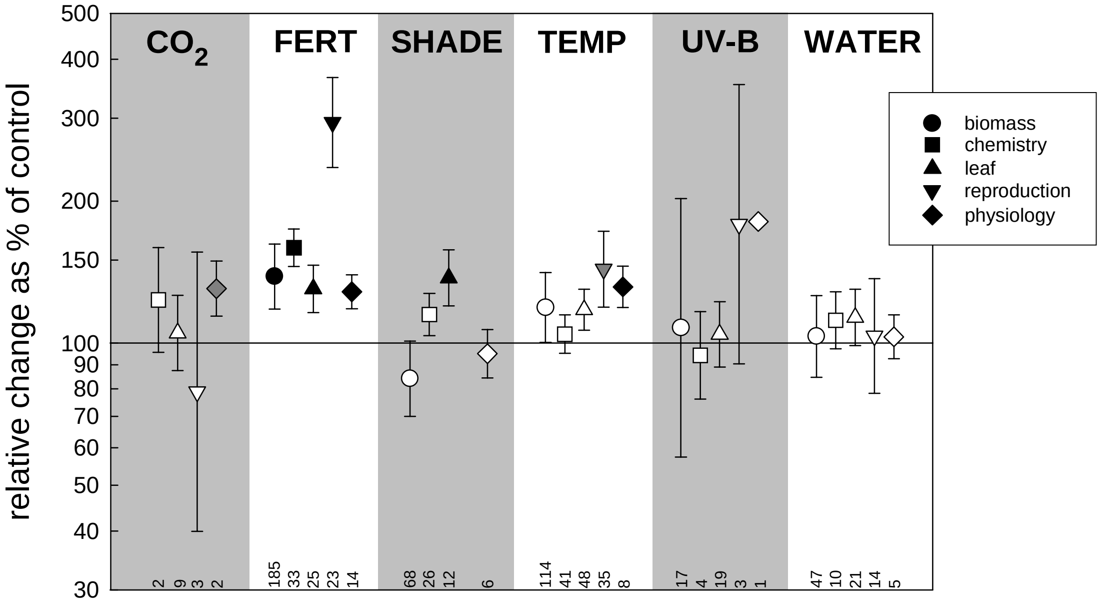

Fig. 1 Response of plants to environmental perturbations. Values are means ± standard error, depicted as % of untreated controls. Black and grey symbols indicate that means differ significantly from 100% ($P < 0.05$ and $0.1 > P > 0.05$, respectively; two-tailed t-test). Treatments are: elevated CO_2, fertilisation (FERT), light attenuation (SHADE), elevated temperature (TEMP), elevated UV-B radiation and irrigation (WATER). Note that y-axis is scaled logarithmically. Numbers at the bottom refer to corrected sample size (df + 1).

RESULTS

Treatment effects

Fertilisation

Biomass in fertilised plots was on average 141% of controls, with a similar magnitude of response in leaf measures (135% of controls; Fig. 1). Element concentrations in leaves and physiological parameters responded more strongly, to 162% of controls, and physiological parameters increased to 151% of controls. The dramatic boost in reproductive measures (294% of controls) indicates nutrient limitation of reproduction through seeds or bulbils in the Arctic. Factorial application of nitrogen and phosphorus identified phosphorus to be the limiting factor to reproduction in most cases (Henry *et al.* 1986; Shaver & Chapin 1986).

PFTs differed in their biomass response to fertilisation (Table 2), with grasses profiting significantly and no other PFT showing any statistically detectable response (Fig. 2). Grass biomass increased more than 15-fold (Parsons *et al.* 1995; Shaver &

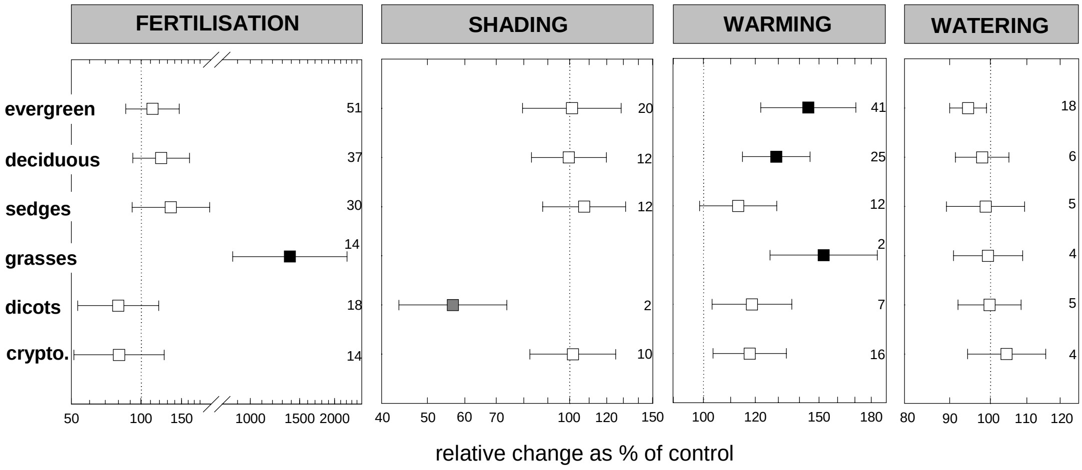

Fig. 2 Biomass response of plant functional types (PFT) to a) fertilisation, b) shading, c) elevated temperature and d) irrigation as % of untreated controls (see also statistical results, Table 2). Solid symbols indicate that means differ significantly from 100% (two-tailed t-test on $\log_{10}$-transformed data). Response of grasses to fertilisation differs from all other PFTs (Tukey's hsd, $P < 0.05$); response of dicotyledons to shading is almost significantly different from the other PFTs (Tukey's hsd, $P = 0.094$). Note differences in scaling and that the x-axis is scaled logarithmically. Numbers refer to sample size.

Chapin 1986). Overall, this resulted in the biomass of the total vegetation being on average 193 ± 134% of control plots (n = 13).

Temperature

Elevated temperature caused significant increases in reproduction and physiology (144% and 132% of controls, respectively; Fig. 1), but the other parameters were unaffected. These data provide no evidence for significantly increased growth or dilution of soluble cell compounds due to increase in biomass, as might have been expected.

Cryptogams, dicotyledons and sedges were unaffected by elevated temperature (Fig. 2). Warmer temperatures resulted in significantly increased biomass of deciduous and evergreen shrubs

Table 2 Statistical results of the differences between plant functional types in terms of above-ground biomass in the different treatment (see Fig. 2). For no manipulations was a co-variate (latitude, elevation, mean annual temperature, mean July temperature, duration, replication) or co-variate interaction significant below the threshold of $P < 0.1$, to be incorporated in the final model.

treatment	**NDF**	**DDF**	**F**	***P***
fertilisation	5	25	4.94	0.0018
shading	5	43	2.00	0.0981
warming	5	93	2.28	0.0424
watering	5	31	0.15	0.9960

and grasses, but they were still of similar magnitude as the other PFTs.

Shading

Leaf measures increased significantly in shaded plots and chemical parameters tended to increase (to 138% and 115%, respectively; Fig. 1), but there was no significant effect of shading on biomass. No data on the effect of shading on reproductive performance were found, and no other reported measurements showed any significant response.

Dicotyledons were negatively affected by shading, but none of the other PFTs, among which grasses were not represented, showed a significant biomass response to shading (Fig. 2). Also, there were no significant differences in response between PFTs (Table 2). The above-ground biomass of the total vegetation did not suffer significantly under the manipulations (73 ± 28% of controls; n = 9).

Elevated CO_2

The few data points available indicate a significant increase in physiological process rates in response to elevated CO_2 (130% of controls; Fig. 1). There was no overall effect of CO_2 on leaf, chemistry or reproductive parameters, and no biomass data were available. The lack of data prevented analysis of PFT responses to CO_2, and indeed prevents a reasonable assessment of long-term impacts of elevated CO_2 on arctic vegetation.

UV-B

The impact of UV-B on plant performance has been addressed in only two field experiments (Table 1). In them, UV-B had no significant influence on biomass, leaf, chemical or reproductive measurements, but increased physiological parameters (132% of control; Fig. 1). Overall, plants responded to the increased radiation by protecting their leaves by increased concentrations of UV-B and radical absorbing substances (Taulavuori *et al.* 1998) without any further manifestations on their performance.

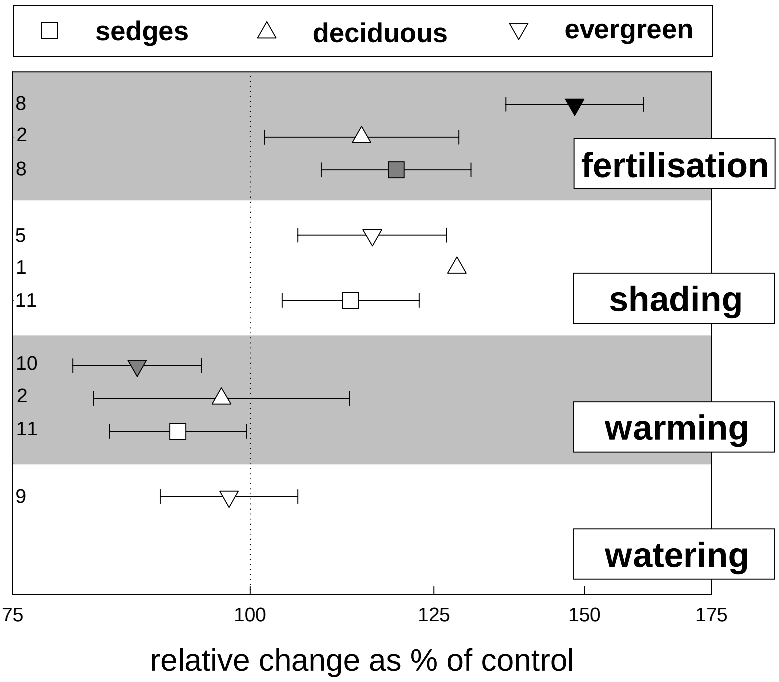

Fig. 3 Nitrogen content in leaves of three PFTs in the different treatments (see also statistical results in Table 3). Black and grey symbols indicate means differ significantly from 100% ($P < 0.05$ and $0.1 > P > 0.05$, respectively; two-tailed t-test). Symbols without error bars are represented by one value only (numbers refer to corrected sample size). Note that x-axis is scaled logarithmically.

Watering

Irrigation did not affect any of the response groups (Fig. 1). This is mainly due to the fact that some studies did not give data, but stated the non-significance of watering, which resulted in many 100% points in this analysis. PFTs showed no significant difference in their responsiveness (Table 2, Fig. 2). Evergreen shrubs tended to show a negative biomass response, but too few data points for almost all PFTs prevent a more sensitive analysis.

Effects of manipulations on leaf-nitrogen concentration

Although there were far fewer data than for biomass, leaf-nitrogen concentration was the second response variable with enough data points to justify separate analysis for individual PFTs (Table 3). Three PFTs, sedges, deciduous and evergreen shrubs, qualified for analysis, although deciduous shrub responses to shading were represented by only one data point. Generally, there is an increase in tissue nitrogen in fertilised and shaded plots, a decrease in warmed plots, and, for the only PFT

Table 3 Statistical results of the analysis of nitrogen content of leaves (see Fig. 3).

effect	NDF	DDF	F	*P*
experimental factor	3	13	12.80	0.0004
plant functional type	2	8	0.25	0.7874
interaction	4	34	2.60	0.0535

represented, no change in watered plots (Fig. 3). It is interesting that although no overall impact of temperature manipulations on the chemical response group were found (Fig. 1), leaf nitrogen concentrations were decreased in both sedges and evergreen shrubs (Fig. 3).

Duration of experiments

One reason for our present poor understanding of plant responses to climate change is the generally short duration of field experiments. Chapin *et al.* (1995b) stated that the short-term (3 years) responses generally differ from long-term (9 years) responses. Therefore we incorporated *duration* as a covariate in the statistical model, but it was never significant ($P > 0.1$). This does not say that long-term effects are the same as short-term effects, only that the database was insufficient to detect a change in effects.

Effects of latitude and altitude

Effects of latitude and altitude or their interaction were not detectable in biomass responses to any manipulations. In the Low Arctic, vegetation occurs over a wide altitudinal range and at altitudes above 1000 m the biomass response to warming treatments increased markedly (from c. 120% of controls to c. 260%). However all these data are from one area (near Abisko, Sweden), and site -specific effects can not be disentangled from an altitudinal effect.

DISCUSSION

The response of plants to environmental manipulations differed greatly within and between the response groups and factors manipulated (Fig. 1). Despite the huge scatter in the data, a response group was significantly ($P < 0.1$) affected by a treatment in 9 out of 28 cases. Fertilisation increased the parameters in all five response groups assessed, but most noticeably so in reproductive measures (294% of control). Elevated temperature significantly increased the mean reproduction and physiology responses (135% of controls). Shading led to a small but significant increase in leaf parameters (to 140% of controls), but biomass was not significantly affected. Elevated CO_2 and increased UV-B caused a significant increase in physiological parameters, but did not significantly influence any other response group. Watering had no significant effect on any response group assessed.

Fertilisation

Reports on fertilisation experiments in the Arctic are abundant, but as their variance shows, the results are not straightforward. The general trend of fertilisation stimulating to plant growth is complicated by the reduced performance of some species. Though experimental evidence is still lacking (Hobbie *et al.* 1999), this growth suppression can be attributed to shading by taller plants (McGraw & Chapin 1989; Mulder & Ruess 1998; Chapin *et al.* 1995a; Havström *et al.* 1993; but see Jonasson 1992). Individually, higher plants generally respond to fertilisation with increases in all measured parameters, including nitrogen accumulation (Chapin *et al.* 1986b; Shaver *et al.* 1998) through photosynthesis (Oberbauer *et al.* 1986) and to colonisation efficiency (Klokk & Rönning 1987), and total vegetation biomass is increased. Thus nutrient availability is most likely to be the main factor limiting higher plant processes in arctic ecosystems.

Temperature

Though it has been argued that increasing shrub biomass and cover competitively reduces the performance of other members of the community, Hobbie *et al.* (1999; 1998a) and Shevtsova *et al.* (1997) found only few negative responses to selective plant removal. They concluded that it is not competition that prevents some other PFTs responding to elevated temperature in the short term (Hobbie *et al.* 1999). Overall, we found no change in the total biomass of the vegetation (125 ± 23% of controls; $n = 50$).

Generally, plant physiological processes have a Q_{10} of approximately 2 (i.e. a 100% increase in process rate over 10 °C). With temperature manipulations of +4 °C in the field we would expect to see approximately 40% increases in physiological parameters, and the mean increase of 44% (Fig. 1) was exactly as expected. So other factors, such as nutrient availability or product inhibition, seem not to limit physiological responses to temperature. Biomass, leaf and chemical responses do not parallel the trend in physiological measures. This is because soil temperature was generally not as much elevated as air temperature. Nutrient uptake could not have been increased greatly by the treatment (Atkin & Cummins 1994). Kummerow & Ellis (1984) showed however, that low air temperature limited growth in the sedges *Carex bigelowii* and *Eriophorum vaginatum* much more than did low soil temperature.

Arft *et al.* (1999) reported a general trend of stronger vegetative responses to elevated temperature in the Low Arctic and reproductive responses in the High Arctic. As this distinction was not made in our analysis (due to the few studies that assessed reproduction in the High Arctic), we cannot judge whether the similarity in reproductive and leaf parameter responses seen in our study opposes their findings or, more likely, is the result of pooling data from the Low and High Arctic.

Shading

Plant species react idiosyncratically to shading (Chapin & Shaver 1985; Shaver *et al.* 1998). A frequent response is leaf and/or internode elongation, which is commonly interpreted as an attempt to escape the zone of shading (Grime 1979). Such elongation may be outweighed by a reduction in leaf width or thickness, but none of the studies assessed both parameters simultaneously. Shading tends to cause nutrient accumulation in leaves, as growth is often reduced due to limited availability of assimilates, while nutrient uptake is maintained (Chapin & Shaver 1996). Light reduction of about 60% corresponds with that experienced by understorey plants in boreal forests (Michelsen *et al.* 1996a), while reduction due to increased cloudiness will probably be less severe. However, as shading effects might accumulate over time, a conservative, i.e. storage-based growth form with long-lived leaves may eventually gain relative profit from these conditions.

Elevated CO_2

Those field data which are available suggest that impacts of elevated CO_2 may be limited. An increase in tiller production in *Eriophorum* was not related to higher leaf growth rate, nor did the leaf area differ between CO_2 treatments (Tissue & Oechel 1987). Transpiration and CO_2 uptake were not significantly affected, although root and soil enzyme activities can increase in elevated CO_2 (Moorhead & Linkins 1997). Thus elevated CO_2 will not necessarily translate into increased biomass, as plants can acclimatise to a new CO_2 environment within weeks (Tissue & Oechel 1987).

Similar evidence comes from laboratory experiments in which Oberbauer *et al.* (1986) found no effects of CO_2 on biomass, despite a positive effect on photosynthesis. They also showed, for three plant species, that responses to elevated CO_2 were not nutrient limited. Sonesson *et al.* (1992) found that the moss *Hylocomium splendens* responded strongly to a doubling of atmospheric CO_2 concentration, with a doubling of its net rate of light saturated photosynthesis. Lichens, on the other hand, showed hardly any response to elevated CO_2 (Sonesson *et al.* 1995). It has been argued that the CO_2 concentrations encountered by all arctic plants in the field are generally above ambient, due to the plants proximity to CO_2 generated by soil respiration, and therefore, CO_2 is not limiting to their growth (Crawford 1989, p. 159; Sonesson *et al.* 1992). This does not dismiss the importance of CO_2 as an ecological factor. Evidence is accumulating, at the ecosystem level, that elevated CO_2 concentrations increase carbon translocation into arctic soils (Billings *et al.* 1983; Grulke *et al.* 1990). However, it has been convincingly argued that this is only a short term effect (Oechel *et al.* 1994), while more subtle changes may occur over a longer time scale (Oechel *et al.* 1997).

UV-B

Some plants seem able to make use of the high energy input for photosynthesis (Gwynn-Jones & Johanson 1996; Björn *et al.* 1997), but UV-B radiation is usually associated with negative effects such as photooxidative damage, enzyme-destruction by radicals and reduced growth due to higher allocation to protective structures and molecules (Taulavuori *et al.* 1998). Like CO_2, there are too few data points from field experiments on UV-B radiation to enable extrapolation. Laboratory studies provide clear evidence that UV-B radiation can influence plant growth (Sonesson *et al.* 1995; Sonesson *et al.* 1996; Gwynn-Jones *et al.* 1997; Gwynn-Jones & Johanson 1996). However, a reduction in biomass of two subarctic grasses was not evident at high, but rather at intermediate UV-B doses (Gwynn-Jones & Johanson 1996). Reduced biomass was ascribed to the costs of producing UV-B absorbing compounds. The recent meta-analysis of UV-B studies by Searles *et al.* (2001) also conclude that UV-B radiation primarily causes increases in the concentration of UV-B absorbing substances, but only modest levels of growth reduction. In contrast to this, the bryophyte *Hylocomium splendens* showed strong impairment of biomass production under increased UV-B (c. 50% of control, Sonesson *et al.* 1996), while lichens were again hardly affected (Sonesson *et al.* 1995).

Water

Despite frequent claims of potential water limitation of plant growth (Billings 1987; Gold & Bliss 1995; Hodkinson *et al.* 1999; Bliss & Gold 1999), only very few positive responses to watering occur in our dataset. Negative responses were at least as common (e.g. Welker *et al.* 1993), despite the fact that only dry vegetation types were chosen for irrigation treatments.

Soil moisture is regularly reported to influence the distribution of Arctic plants (Kincheloe & Stehn 1991; Bliss *et al.* 1994; Walker *et al.* 1994), however, the relationship is not straightforward. Rainfall affected the number of leaves of *Cassiope tetragona* in the European Arctic negatively (Callaghan *et al.* 1989), but had no such effect in Eastern Canada (Johnstone & Henry 1997). The timing of precipitation seems crucial, as it might affect photosynthesis only in the drier late season (Enquist & Ebersole 1994). Oberbauer & Miller (1982) provide evidence that several tundra species profit from waterlogged soils, in contrast to which Oechel *et al.* (1998) found a lower water table to slightly increase primary production. Water movements in the soil, increasing nutrient availability and productivity (Chapin *et al.* 1988), further complicate the picture. No clear-cut view on the present or future role of water in arctic ecosystems has yet emerged (Kane 1997).

Effects of manipulations on leaf-nitrogen concentration

Nitrogen accumulated in the leaves of plants in fertilised and in shaded plots can presumably not be used for growth due to limitation by temperature and/or assimilates. Decreases in the leaf nitrogen concentration of plants in warmed plots are likely because temperature manipulations affect air temperature more than soil temperature (Hobbie & Chapin 1998b). Thus, photosynthesis and carbon assimilation are likely to increase more than N-uptake, and nitrogen will be diluted by increased growth. Indeed, this is supported by the observed overall responses of physiological parameters (135%) to elevated temperature (Fig. 1).

Duration of experiments

Only two sites (Toolik Lake, Alaska, and Abisko, Sweden) provided data exceeding three years. A comparison of the experiments of these two sites is given by Shaver and Jonasson (1999), who conclude that factors affecting the carbon and/or nitrogen cycle will in the longer term affect plant growth. Especially shading effects took more than 6 years to cause a marked decline in vegetation biomass.

In a meta-analysis of the International Tundra Experiment (ITEX), Arft *et al.* (1999) reported a transient response of plants to warming in experiments of four years duration. Woody plants showed a positive vegetative growth response in the first two years that was not maintained thereafter. Herbaceous plants, on the other hand, demonstrated a sustained increase in their reproductive effort, but without any apparent increase in their reproductive success. As only few data were available for the fourth year of the experiments, one has to be cautious with the interpretation of the ITEX meta-analysis findings. Moreover, four years can still be considered a short duration for arctic plant communities.

Effects of latitude and altitude

Arft *et al.* (1999) also report a greater response of vegetative measures to temperature elevation in the Low Arctic, and of reproductive measures in the High Arctic. As only biomass measures were used in the present analysis, our data cannot corroborate their statements, but rather indicate that it is not only the Low vs. High Arctic distinction which is important, but also the effect of altitude at any given site within the Arctic.

Plant Functional Types

The enormous variation depicted in Fig. 1 is not surprising, as the data represent plants of various morphological and taxonomical groups, from deciduous trees to lichens. The concept of plant functional types proposed for the Arctic (Chapin *et al.* 1996) suggests a dichotomous splitting of plant species. We tested this concept using the biomass-group responses.

As Fig. 2 illustrates, there are generally few differences between PFTs in their responses to individual treatments. The significant effect of PFT in fertilisation treatments (Table 2) is due to the strong responsiveness of grasses compared to the absence of response in all other PFTs (Fig. 2). Similarly, the negative biomass response of one PFT (dicots) to shading caused a marginal significance of PFT. Responses to warming are significantly related to PFT, with three PFTs showing similar, positive responses and three showing no response (Tab 1, Fig 2). All PFTs showed a similar lack of response to watering.

Looking at patterns of PFT biomass response across all treatments, the only response of dicots was a negative one to shading, the absence of positive responses to other factors perhaps being due to the rosette form of many arctic dicots, in which an increase in leaf numbers/size would lead to self-shading. Neither sedges nor cryptogams responded to any treatment, both evergreen and deciduous shrubs showed a positive response to warming only, and grasses responded positively to both warming and fertilisation (Fig. 2). The response of grasses to fertilisation was the strongest response observed. Shaver *et al.* (1997) attribute this to the modular organisation of graminoids, and argue that the higher tissue turnover enables them to respond more rapidly to environmental manipulations than other PFTs. This is not supported by the temperature data, however, which show deciduous and evergreen shrubs to be as responsive as grasses to elevated temperature. Also, cryptogams showed no obvious response to any kind of perturbation.

Thus, while there is a theoretical argument in favour of separation into plant functional types (Chapin 1993; Gitay & Noble 1997; Hobbs 1997), within our data only one separation is really distinct: grasses exhibit an extraordinary biomass response to improvement in nutrient availability (Fig. 2). The support previously given to PFT groupings (Chapin *et al.* 1996; Arft *et al.* 1999) can thus only partly be corroborated here (see also Press *et al.* 1998). This may be because species' morphological features (growth form) and physiological characteristics are not strongly linked; similar morphotypes may have different physiological responsiveness, and *vice versa*. For example, the physiological characteristic of high tissue turnover rate is common to two different morphotypes, deciduous shrubs and grasses (Chapin & Shaver 1996). On the other hand, species with very responsive and conservative growth characteristics can occur not only within the same morphotype, but also within the same family or genus (see, e.g., McGraw & Chapin 1989). Thus a morphotype-based PFT classification may not be the best for predicting responses to environmental change. A desirable next step would be the creation of a PFT classification primarily based on species' responses to various environmental manipulations (e.g. Dyer *et al.* 2001). This would clarify whether responsiveness to, say, fertilisation was correlated with responsiveness to other factors, for example elevated CO_2.

Gaps in our knowledge

Of the different factors contributing to the changes in the arctic, CO_2, and UV-B are the most expensive and difficult to study, and likely interactions between, for example, CO_2 and fertilisation or temperature (Oechel *et al.* 1994) have not been assessed at all. There is still doubt as to whether UV-B exposure will increase in the Arctic, as increasing cloudiness might off-set this trend. But CO_2 concentration is certainly increasing (Maxwell 1992) and this should perhaps become the focus of closer investigation, not simply to measure biomass responses, but also to assess changes in plant physiology and forage quality. On the other hand, it could be argued that CO_2 studies are less important, because they have commonly shown acclimation of photosynthesis to elevated CO_2 (Bazzaz 1990), and thus expected ecological consequences for the whole vegetation would be small.

Even for some commonly investigated factors such as fertilisation or irrigation, experiments have sometimes not been performed appropriately. Nitrogen additions have exceeded natural levels by up to two orders of magnitude and might have caused damage to the species. These extremely high loads might also increase plants' vulnerability to sudden temperature changes, due to loss in hardiness. Watering experiments generally suffer from infrequent applications. Recruitment in dry sites is probably limited by dry soil (Billings 1987; Gold & Bliss 1995), but we are aware of only one relevant study assessing germination rate or seedling establishment (Wookey *et al.* 1995).

One prediction of global circulation models (GCMs) is that the growing season in the Arctic will be longer in future (Maxwell 1992). Differences in season length can cause profound differences in morphology and productivity of species (Crawford & Smith 1997). However, we know of only three experimental studies addressing this effect: Walsh *et al.* (1997) measured carbon and nitrogen content of caribou forage, but did not publish biomass data, while the short-term experiment of Van der Wal *et al.* (2000c) showed that differences in snowmelt timing affected patch choice by reindeer, but did not affect above-ground biomass by the end of the season. Starr *et al.* (2000) could show physiological and phenological responses, but did not assess biomass. As Galen & Stanton (1993) showed in alpine systems, advanced snowmelt can have strong (mostly positive) impacts on the cover of different species, while delay to the start of the growing season was generally without short-term effect (Galen & Stanton 1995). Research in this direction should be encouraged.

The experiments that form the basis for this meta-analysis commonly investigated impacts of components of global climate change on plants and vegetation *per se*, but only recently have interactions among plants come into focus (Jonasson 1992; Hobbie *et al.* 1999; Shevtsova *et al.* 1995). Interactions with herbivores are still poorly understood (Gunn & Skogland 1997; Harrington *et al.* 1999; Van der Wal *et al.* 2000c), as are effects on mycorrhiza and other intertrophic relationships (Michelsen *et al.* 1996b).

CONCLUSIONS

On the basis of the experiments reviewed it appears that, of all the components of environmental change considered, the driver for future change in arctic vegetation is likely to be increased nutrient availability, which could both affect the performance of individuals and recruitment to their populations. Minor changes in precipitation, increases in UV-B radiation and increased atmospheric CO_2-concentrations will have little effect on arctic plants in the short term. Temperature elevation, increases in nutrient availability and major decreases in light availability, however, will cause immediate plant growth responses, and in addition alter nutrient cycling. In the case of increased nutrients and/or temperature, effects on nutrient cycling may create positive feedbacks on plant biomass (Hobbie 1996, 1995).

There is wide variation in the responses of arctic plant species to environmental manipulations. Whilst classification into plant functional types may be useful in some respects (e.g. correlation of plant morphology with environmental gradients: Diaz & Cabido 1997), we suggest that it is generally unsatisfying for generalisation of responses to, and predictions of effects of, environmental change. In the absence of a better classification system, it may be that analysis at the species level is still the most realistic option.

The short duration of the experiment used here (generally less than five years) is a major obstacle to predict the future course of vegetational development in a changing climate. Additionally, of the many gaps in our understanding of ecological processes related to responses of plants and vegetation to a changing climate, the investigation of changes in biotic interactions across all trophic levels seems to be the most urgent and intricate challenge.

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CHAPTER 3

NO EVIDENCE FOR ADAPTATION OF TWO POLYGONUM VIVIPARUM GENOTYPES TO LENGTH OF GROWING SEASON: ABUNDANCE, BIOMASS AND GERMINATION[1]

Abstract The high degree of habitat heterogeneity and fragmentation in arctic ecosystems may support a high genotypic and ecotypic variability. This may buffer the survival of plant species threatened by global climate change, in particular in the Arctic where temperature increases are expected to be greatest. Here, we assessed if two genotypes of *Polygonum viviparum* (characterised by different colours of their bulbils), i) differ in their abundance along a snowmelt gradient, ii) if their biomass allocation pattern are influenced differentially by environmental variables, and iii) if the temperature dependency of bulbil germination differs between genotypes. We found slight differences in the effect of timing of snowmelt on abundance of the genotypes, which seem to have little ecological relevance. Total plant biomass and biomass allocation to the different plant compartments was similar for both genotypes and was negatively correlated with soil water content. Bulbil germination was assessed over a temperature range from 2 to 25°C and results indicate an earlier (maximum of five days) germination of one genotype, but final germination (> 80%) and germination rate were similar for both types. Germination was weakly temperature dependent, with faster germination at higher temperatures. *Polygonum viviparum* bulbils clearly did not germinate as would be expected by the constant thermal time concept for agricultural seeds, as they were able to compensate for low temperatures. Overall our results could provide no convincing evidence for genotypic variability in *Polygonum vivipa-*

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[1] together with Sarah J. Woodin and Steve D. Albon (submitted to Ecography)

rum being of ecological relevance with respect to anticipated climate change in the Arctic.

INTRODUCTION

The observed rate of global warming has been greatest in the Arctic (Serreze *et al.* 2000) and the general circulation models predict this will continue (IPCC 1990, 1998; Maxwell 1992). The potential consequences for plants and vegetation are immense, and the question of whether the changes anticipated will lead to the extinction of plants characteristic to this severe environment has caused some concern (Chapin & Körner 1994). It has been argued, however, that spatial heterogeniety at a very small scale (proximity of very different habitats within a metre), a natural feature of arctic vegetation, has given rise to high ecotypic variation within species, each ecotype being adapted to slightly different set of environmental conditions (Crawford *et al.* 1993; Crawford 1997a, b). This might allow plant species to survive vegetational change by changes in the relative abundance of these ecotypes.

So far, evidence for differences in important ecological properties within a arctic species is circumstantial: higher maximum photosynthesis seems to compensate for a shorter growing season in *Saxifraga oppositifolia* (Crawford *et al.* 1995), and along a gradient of season length some species (*Polygonum viviparum*, *Saxifraga oppositifolia*) differ in their morphology (Crawford *et al.* 1993; Crawford & Smith 1997). *Dryas octopetala* significantly reduces its allocation to the gynoecium in sites with a shorter growing season (Wada 1999). On the other hand, it has recently been shown that seeds from different altitudes in the Andes differ in their stratification requirements, as well as their percentage of maximum germination (Cavieres & Arroyo 2000).

Polygonum viviparum is a widespread arctic-alpine species, common to periglacial regions of the northern hemisphere. Vegetative reproduction, a feature of many arctic plants (Billings 1987), occurs via bulbils, i.e. seed-analogue structures produced on the flowering stalk (Law *et al.* 1983). In the Arctic, production of mature fruits is a very rare event (Law *et al.* 1983; Söyrinki 1989), and for populations in the Alps it was shown that there is a trade-off between the production of flowers and bulbils (Law *et al.* 1983), which shifts with increasing altitude in favour of bulbils (Bauert 1993). The bulbils are pre-formed as long as four years before emergence (Diggle 1997). They ripen over the summer and usually become dispersed in late summer or early autumn. Occasionally, bulbils germinate on the flowering stalk (“vivipary”), but this has been observed only very sporadically in the population investigated here (CFD, personal observation). Germination apparently takes place in the next spring, growth in the first year relies mainly on stored starch, as by late August only the cotyledons have emerged (personal observation). Around 10% of the bulbils germinate successfully (range 0 - 63%; CFD, unpublished data), especially in very moist places.

Individuals of *Polygonum viviparum* differ in the colour of the bulbils. It can range from light to dark red, pale yellow to dark brown and even green and purple bulbils have been reported (Bauert 1993; Crawford & Smith 1997). Bulbil colour is a genetically determined trait (Bauert 1996), which means that differences in success and distribution of bulbil colours has direct implications for the genetic structure and diversity of the *Polygonum viviparum* population at a given site. It has been suggested (Crawford & Smith 1997) that the genotypes represented by different bulbil colours are adapted to differences in season length, with individual with red bulbils being more abundant on short-season low-shore sites, while brown ones dominate in long-season ridge sites.

The present study assesses 1.) whether different genotypes of *Polygonum viviparum* show differences in their distribution with respect to environmental variables, and 2.) whether temperature dependency of germination correlates with the distribution of the genotypes.

METHODS

Site and species description

Field work was carried out in Semmeldalen, Svalbard (78ºN 15ºE). This innerfjord valley harbours a variety of vegetation types, from dry, unvegetated schist humps, over a dry peat *Salix polaris*-heath, to wet, graminoid rich communities and waterlogged *Eriophorum scheuchzeri*-swamps (for details see Rønning 1996, 1967).

Polygonum viviparum occurs in almost all of these communities, except for the extremely wet and extremely dry ones. Its cover rarely exceeds 1%, but occasionally one can find over 100 individuals per m^2. Most individuals of *Polygonum viviparum* at this site produce red bulbils (c. 85%), but brown (c. 15%), pale-yellow and purple bulbils (each < 1%) can also be encountered.

Survey

In August 1999 40 permanent plots were established in Semmeldalen, representing points on various environmental gradients (soil water content, season length, slope, exposure, aspect). Volumetric soil water content was measured with a soil conductivity insertion probe (SCIP, CEH Wallingford, UK) at four subsamples per site on 26 July 2000. Season length was estimated on a five point scale based on the duration of snowlie. Slope and aspect were measured with a compass and inclinometer, respectively. Exposure was estimated on a five point scale from raised above the surrounding area (5) to trough position (1). This was applied both at the scale of 4 m^2 and 100 m^2 (small scale relevant to individual, larger scale relevant to plant community structure). At each site two *Polygonum viviparum* plants was excavated, one with red and one with brown bulbils. As both red and brown plants did not always occur at each site, sample sizes are less than 40. Plants were sorted into rhizome, seeds and leaves plus flower stalk, and pre-dried at 40°C for one week. After transport back to the lab, samples were re-dried at 70°C for 24 hours and weighed to the nearest 0.1 mg.

Snowmelt transect

A 520 m long transect was established in May 1999, to assess patterns of snowmelt and hydrological conditions over a range of vegetation types and topographic positions. The transect consisted of three parallel lines, 40 m apart, with an aluminium pole every 40 m. During spring 2000, the transect was monitored every other day to assess when poles became snowfree. Subsequently volumetric soil water content was measured with the SCIP at four points around the pole at least biweekly throughout the summer, until mid August 2000. For each of the 45 poles the date when it became snowfree and soil water content data for the summer are available (S.D. Albon, unpublished results).

On the 25 July 2000 *Polygonum viviparum* individuals with red and brown were counted in a 4 m^2 circle around each pole. Some (< 5%) *Polygonum viviparum* inflorescences were infested by a fungus and the colour of their bulbils could not be determined.

Germination test

Bulbils of *Polygonum viviparum* were collected in a dry *Salix polaris*-heath in Semmeldalen, Svalbard, in the first week of August 1999. They were manually stripped from plants with either brown or red bulbils, stored in plastic bags and kept frozen (-12°C) until the start of the germination experiment.

The germination test was carried out using a temperature gradient plate (Grant Instruments Inc., U.K.). This was set to a temperature range from 1 to 26°C, with 14 temperature steps of approximately 2°C. The aluminium gradient plate was cleaned with bleach (20%) prior to the experiment. Two layers of paper kitchen towel were placed on the plate and sprinkled with distilled water until saturated. Onto this, a plastic grid of 14 by 14 cells was placed to reduce airflow and to compartmentalise the bulbils. Above the plate, two greenhouse lights provided continuous illumination (c. 250 µmol $\text{m}^{-2}\,\text{s}^{-1}$). The exact temperature in the germination cells was measured with a Squirrel temperature data logger (Skye Instruments, UK). These deviated from the set temperature by +1°C at the low end to -1°C at the high end. The realised temperature range thus was 2 to 25°C.

On 1 May 2000 (the beginning of the growing season), 25 randomly picked bulbils were put into each of the cells across the whole temperature gradient, in the middle six rows of the grid, with alternating rows of brown and red bulbils. This resulted in three replicates per temperature and colour. Another set of 25 bulbils of each colour was weighed wet, dried and re-weighed to assess possible size differences between the colours. The results indicate that there was no difference in dry or fresh weight between red and brown bulbils, but red bulbils had significantly higher water content than brown ones (Table 1). Germination seemed to be independent of bulbil size (personal observation, Gugerli 1997).

All bulbils were checked for signs of germination every morning for one month. The bulbils are cone-shaped, and the radicle generally emerges at the bottom end, being visible even before emergence as a white dot in the aperture of the bulbils. Emergence of the radicle was scored as successful germination and the germinated bulbil was removed from the plate. The red bulbils deviated from this germination pattern: in about half of them the radicle emerged through the side of the bulbil, rather than through

Table 1 Initial fresh and dry weights (mg) and water content (in % fresh weight) of *Polygonum viviparum* bulbils, with standard errors and one-way ANOVA statistics. N=25 per colour.

	red	brown	F	*P*
fresh	3.00 ± 0.25	3.34 ± 0.25	0.91	0.344
dry	1.15 ± 0.10	1.38 ± 0.11	2.30	0.136
% H_2O	62.4 ± 0.66	58.8 ± 0.49	13.45	0.001

Table 2 Comparison of *Polygonum viviparum* with brown (N = 33) and red (N = 36) bulbils. Data given are means for dry weight, standard error and Kruskal-Wallis statistics.

	brown	red	H	*P*
total weight [mg]	146.5 ± 13.2	161.0 ± 12.0	2.50	0.114
leaves & stalks [mg]	31.5 ± 3.11	33.9 ± 2.79	0.41	0.475
rhizome [mg]	85.7 ± 8.23	99.3 ± 8.07	3.08	0.079
seed weight [mg]	29.3 ± 3.59	27.8 ± 2.88	0.01	0.923
number of seeds	23.0 ± 1.63	23.1 ± 1.93	0.20	0.652

the bottom aperture. This was hardly ever observed in the brown bulbils.

Statistical analysis

Survey data were analysed using Generalised Linear Mixed Models, with bulbil colour nested within site and site as a random factor (SAS Institute Inc. 1989). As the best fitting regression model for the effect of soil water content on total biomass of *Polygonum viviparum* along the survey sites was an exponential function, both biomass and soil water content data were ln-transformed.

Cumulative germination was calculated for each cell separately and regressed against the non-linear logistic function ($y = a / (1 + (x/x_0)^b)$), using the SigmaPlot (Jandel Scientific Software, San Rafael, California) regression module. The maximum germination coefficient a was constrained to be equal or less than 100%. x_0 represents time to half-maximal germination, and $-b$ is the slope in x_0.

Weighed germination coefficients (using 1/*coefficient of variance* as weight) for each cell were than compared for red and brown bulbils using a Generalised Linear Mixed Model with bulbil colour as fixed effect, temperature as covariate, and block (pairing adjacent rows with red and brown bulbils together) as random factor. The initial model also contained the temperature × colour interaction, and was simplified by excluding all terms which were not significant at $P < 0.1$ (Crawley 1993). For all tests the response variables showed no significant divergence from either a normal distribution or homogeneity of variance.

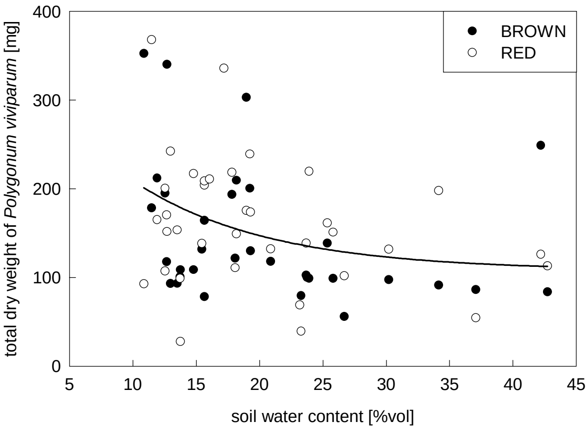

Fig. 1 Total biomass of *Polygonum viviparum* as a function of soil water content. Dry weights of brown and red *Polygonum viviparum* did not differ, the regression line (biomass = 107.8 + 260.6 · $e^{-0.094 \cdot x}$; $F_{1,\ 31}$ = 5.38, $P < 0.05$, $R^2 = 0.177$) represents both bulbil colours.

Thermal time (in degree-days) was calculated as cell temperature·x_0, as neither optimal nor maximal germination temperature were reached, and the calculation according to Garcia-Huidobro *et al.* (1982) were therefore not applicable.

RESULTS

Survey: biomass allocation and environmental gradients

Polygonum viviparum plants with brown bulbils did not differ significantly in their biomass, or its allocation, from those with red bulbils (Table 2). Rhizomes made up c. 60% of the total biomass of bulbil-bearing plants, with the other 40% being evenly split between leaves and bulbils.

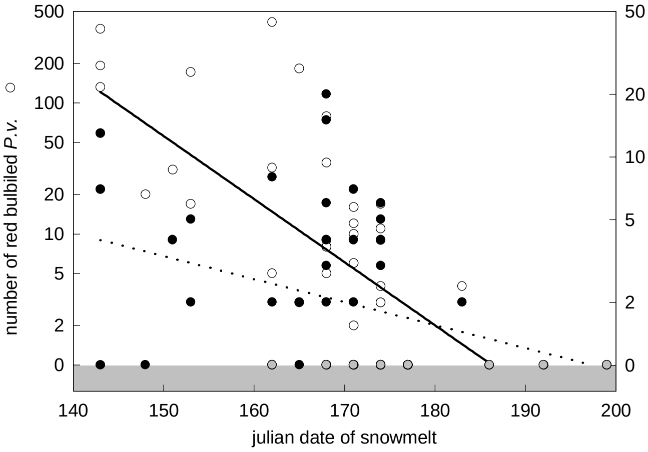

Fig. 2 Number of *Polygonum viviparum* of the two colour varieties per m^2 (log-scale) along a snowmelt gradient. Julian day on x-axis refers to time when plot became snowfree. Note difference in scaling. Regression of log(x+1)-transformed data for red: y = 8.970 – 0.048 x ($F_{1,\ 43}$ = 42.41, $P < 0.001$, $R^2 = 0.49$) and for brown: y = 2.181 – 0.011 x ($F_{1,\ 43}$ = 5.28, $P < 0.05$, R^2 = 0.09).

Of the parameters assessed at the survey sites (slope, aspect, soil water content, exposure, season length), the weight of *Polygonum viviparum* was significantly related only to soil water content ($F_{1,\ 29}$ = 5.38, $P <$ 0.05; Fig. 1). However, no difference between bulbil colours could be detected ($F_{1,\ 29}$ = 0.15, P = 0.69), nor was there an interaction between bulbil colour and soil water content ($F_{1,\ 29}$ = 0.25, P = 0.62).

Snowmelt transect

Table 3 Summary of statistical test of differences in the number of *Polygonum viviparum* occurring along a snowmelt gradient. Colour refers to differences between *Polygonum viviparum* with red and brown bulbils. Data were $\log_{10}$-transformed prior to analysis.

Effect	**df**	**F**	***P***
Snowmelt	1	32.55	0.0001
Colour	1	33.05	0.0001
Interaction	1	28.75	0.0001
Residual	42		

The abundance of the two bulbil colours of *Polygonum viviparum* differed significantly with respect to timing of snowmelt. Plants with red bulbils showed a strong negative correlation with Julian date of snowmelt, while that for brown bulbils was rather weak (Figure 2; Table 3). *Polygonum viviparum* individuals with red bulbils decrease from c. 150 ind. m^{-2} at very early snowmelt (Julian Date of c. 145) to 0 at a snowmelt date of early July (Julian date of c. 185). *Polygonum viviparum* with brown bulbils did not occur in areas of late snowmelt either. The percentage red decreased significantly with Julian day from c. 96% to 59% (arcsine-square root-transformed data: $F_{1, 31} = 4.25$, $P < 0.05$, $R^2 = 0.092$; regression equation for untransformed data: %red = 248 - 1.05·Julian day), indicating that the *relative* abundance of one genotype compared to the other is influenced by the timing of snowmelt. However, red *Polygonum viviparum* were always c. 20 times more abundant than brown ones, thus no shift in *dominance* was observed.

The density of the two colour varieties showed no significant difference in relation to soil water content on these sites (soil water content: $F_{1, 43} = 0.75$, $P = 0.391$; soil water content × colour $F_{1, 43} = 2.85$, $P = 0.099$), although soil water content and snowmelt were weakly correlated ($F_{1, 44} = 3.56$, $P = 0.066$, $r = 0.276$). That is to say that there was no relationship between density and soil water content for either colour and no significant interaction between colour and soil water content. Moreover, no relationship between percentage red and soil water content was detected ($P > 0.29$).

Germination test

Polygonum viviparum showed surprisingly little sensitivity to environmental temperature: bulbils germinated at all temperatures (2-25°C). Germination was rapid and almost complete for both bulbil colours (Fig. 3). The onset of germination was faster and (as germination rate was the same for both bulbil varieties) x_0-values was signifi-

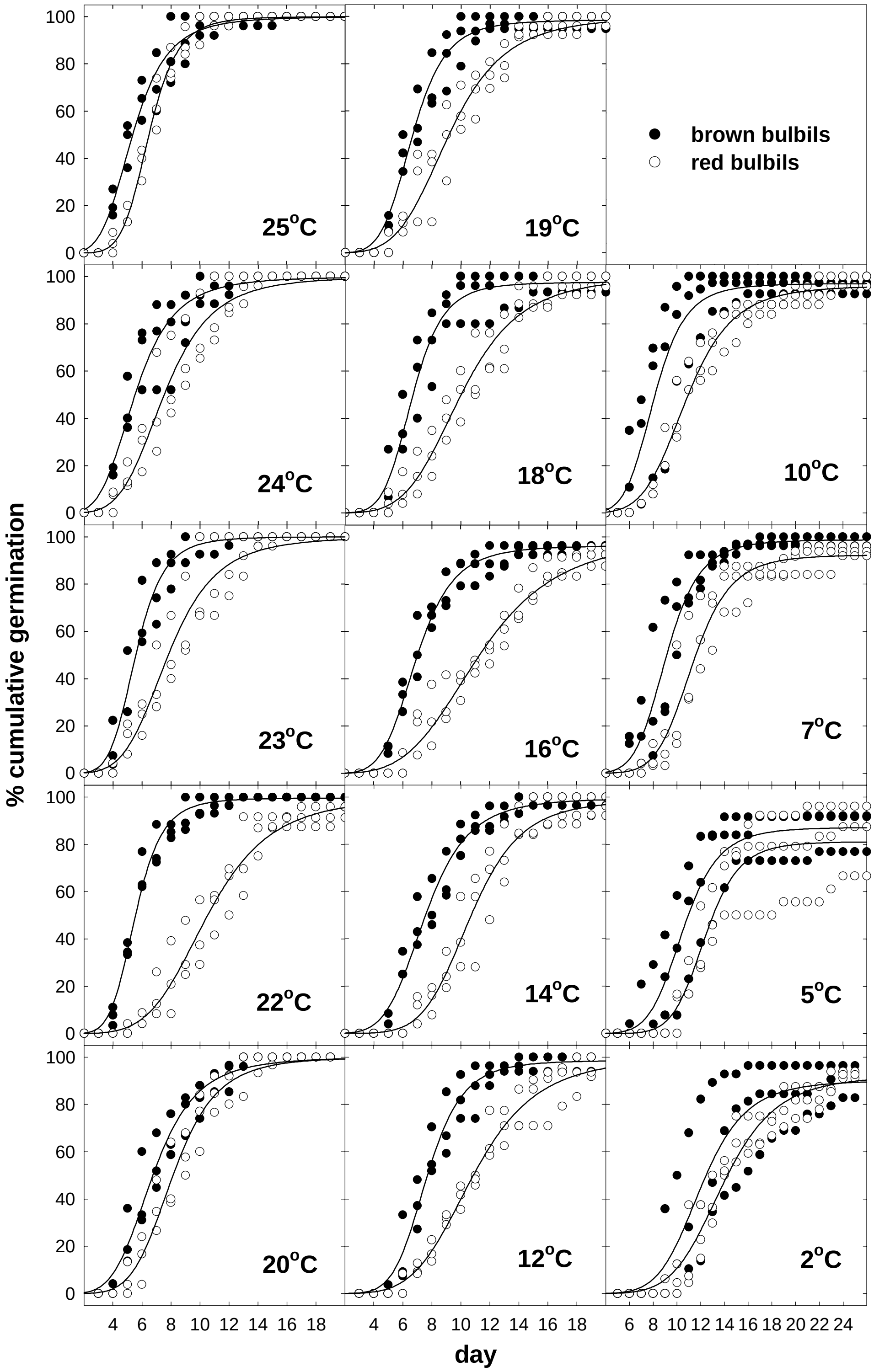

Fig. 3 Cumulative germination of red and brown bulbils at different temperature. A logistic regression function was fitted to the data of each experimental plot: germination=$a/(1+(\text{day}/x_0)^b)$. For regression coefficients see Fig. 4.

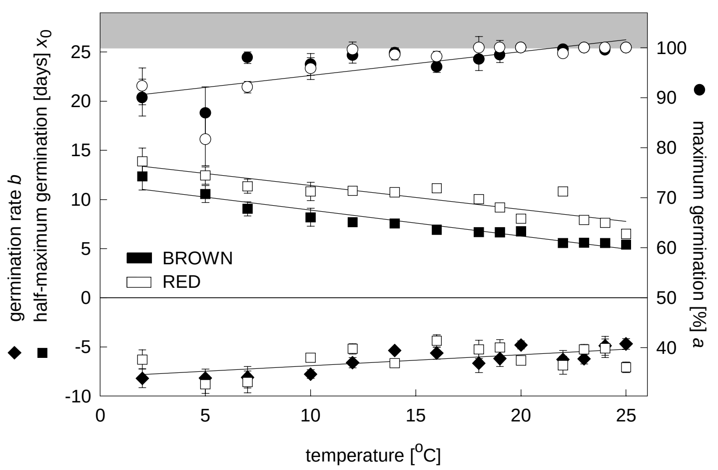

Fig. 4 Regression parameters for the different temperatures. Data from red and brown bulbils were indistinguishable for maximum germination (a) and germination rate ($-b$), but differed significantly for time to half-maximum germination (x_0). Regressions depicted are: $a = 89.94 + 0.436 \cdot \text{temperature}$; $b = -7.29 + 0.083 \cdot \text{temperature}$; $x_0(\text{brown}) = 10.79 - 0.24 \cdot \text{temperature}$ and $x_0(\text{red}) = 13.80 - 0.27 \cdot \text{temperature}$. See Table 4 for statistical analysis of parameters.

cantly lower for brown bulbils than for red (Fig. 4; Table 5). The maximal difference of c. 5 days occurred at temperatures of 12 to 19°C and was minimal at both low and high temperatures (Fig. 3 & 4).

Maximum germination of red and brown bulbils alike was slightly lower at low temperatures, but still very high (90% at 2°C; Figures 3 & 4). Once germination started, rates (b) were similar for both bulbil colours, but again dependent on temperature (Figure 4; Table 4). Increasing temperature from 2°C to 10°C accelerates the onset of germination and increases the maximum germination with little impact on germination rate (Figs. 3 & 4). From 12°C to 25°C x_0 decreases more slowly and

Table 4 Statistical results from the analysis of germination regression coefficients (Fig. 4) for red and brown bulbils. †, ** and *** refer to $P < 0.1$, 0.01 and 0.001, respectively. Effects not given and interaction of colour and temperature were not significant at $P > 0.1$ and hence removed from the model.

parameter	Effect	df	MS	F	R^2
	Block	2	4.295	5.98**	0.08
final germination (a)	temperature	1	47.800	66.54***	0.42
	error	80	0.718		
	block	2	1.0807	2.73 †	0.08
slope (b)	temperature	1	6.0946	15.42***	0.15
	error	80	0.3953		
	block	2	87.91	24.15***	0.08
time to half-maximal	temperature	1	1123.82	308.74***	0.52
germination (x_0)	colour	1	569.65	156.49***	0.26
	Error	80	3.64		

maximum germination remains constant, while the germination rate fluctuates inconsistently. As the error bars in Fig. 4 indicate, time half-maximum germination (x_0) and maximum germination varies more between replicates at low than at higher temperatures. No such pattern is apparent for *b*.

DISCUSSION

With respect to germination requirements, arctic-alpine plants are exceptionally tolerant to low temperature (Söyrinki 1941). However, even these plants hardly germinate below 5°C (Mooney & Billings 1961; Sayers & Ward 1966), and out of 12 high arctic species tested by Bell and Bliss (1980) only three ruderals (*Oxyria digyna*, *Phippsia algida* and *Saxifraga cernua*) germinated below 5°C. As the microclimate in the shelter of the vegetation deviates from the ambient air temperature, this low germination ability at very low temperature might not be limiting recruitment, however. With respect to maximal germination, arctic-alpine plants seem to fall into one of two categories: either they germinated most fully, or hardly at all (Bliss 1958). Interestingly, *Polygonum viviparum* was described as a poorly germinating species (4-10%, Bliss 1958), in contrast to our findings, although it is unclear if this study was performed on bulbils or the very rare seeds. Our study indicates that germination can occur at temperatures close to freezing, and that maximum germination is very high and decreases little with temperature (Fig. 4). Indeed the temperature dependency of all germination parameters, but especially for x_0, is very low: increasing temperature by a factor of 12 only halves the time to half-maximum germination (Fig. 4). This clearly demonstrates the adaptation of *Polygonum viviparum* bulbils to low germination temperatures in its arctic-alpine habitat.

Ecotypes adapted to different season lengths?

Overall, we found no convincing evidence for the adaptation of different genotypes of *Polygonum viviparum* to differences in season length as hypothesised by Crawford and Smith (1997). In our study area the red type of *Polygonum viviparum* always was far more abundant than the brown type, yet a decrease in its dominance along the snowmelt gradient could be detected. The dominance of the red over the brown genotype is not based on any of the parameter we measured, but might be e.g. related to differential susceptibility to rust (as shown for interspecific differences in the Polygonaceae by Hatcher *et al.* 1994).

The biomass performance of both genotypes of *Polygonum viviparum* was similar, weakly related to soil water content, with a preference shown by both types to drier sites. However, we did detect a difference in response to a gradient in snowmelt, i.e. differences in season length, which indicates less tolerance of shorter seasons in *Polygonum viviparum* with red bulbils. However, beyond a threshold date of snowmelt (Julian date 185; i.e. 4 July) no *Polygonum viviparum* of either bulbil colour could be found. Thus, both genotypes have the same minimum season length requirements, and, beyond this, the different dependencies on season length has no impact on the total weight, but only on the abundance of *Polygonum viviparum* generally.

Along an environmental gradient, there was no difference in biomass allocation between *Polygonum viviparum* with red and brown bulbils. We thus have to conclude that the ecological difference with respect to snowmelt cannot be corroborated by the survey data.

Germination characteristics of the two bulbil colours are consistent with the field findings, in as much as slight differences between genotypes could be detected, but their ecological relevance in the field is doubtful. Brown bulbils emerged a few days earlier than the red, but total germination (*a*) and germination rate (*b*) were identical (Fig. 4). This leaves the problem of the very different abundances of the two bulbil colours. Red dominates brown by an order of magnitude (Fig. 2). However, we could detect no characteristic that made this genotype more successful than the brown one. One obvious reason is that the genes coding for bulbil colour are not coupled to those providing ecological benefits. Alternatively, the high genetic diversity of *Polygonum viviparum* in the Arctic (Bauert 1996) and in alpine areas (Diggle *et al.* 1998) is not adequately represented by bulbil colour. While we cannot reject the idea that environmental change will have limited effects in the High Arctic because ecotypic variation, and thus adaptational potential, is very high, we found no support for the idea of Crawford and Smith (1993) that *Polygonum viviparum* bulbil colours reflect this ecological preadaptation.

The base temperature and thermal time problem

In plants adapted to cold climate it is of particular interest to know the minimum temperature requirements for germination (base temperature T_b) and the temperature·time required for, say, 50% germination (thermal time 50% Tt_{50}). The concept of thermal time assumes that a constant temperature sum is needed for seeds to germinate, thus temperature·time to germination = constant. How useful is this concept for the bulbil germination of *Polygonum viviparum*?

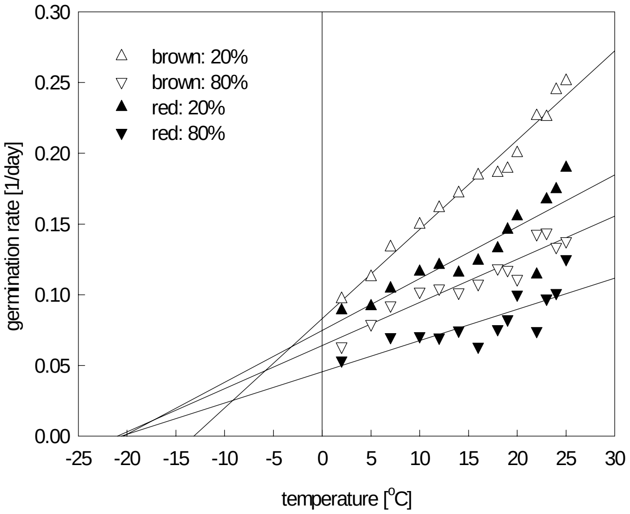

Fig. 5 Germination rate as a function of temperature. Only 20th and 80th germination percentile rates are depicted (average of three replicates). Brown and red bulbils differed significantly in slope (see Table 4 for analysis of 50th percentile). Linear regression is extended to x-axis to estimate base temperature.

The common approach to determining base temperature (T_b) is to regress germination rate (= 1/time required for x% of the seeds to germinate) against temperature (Angus *et al.* 1981; Garcia-Huidobro *et al.* 1982). Doing this for various percentiles of germination all regressions should share the same x-axis intercept, the base temperature (e.g. Pritchard & Manger 1990). With our data set, this approach yielded no satisfactory result: data points did not lie on a straight line (Fig. 5; Table 5). More importantly, however, the base temperature extrapolated from this approach was about -20°C, which is obviously unrealistic. The approach should be carried out on a "clean" data set, from which low or high temperatures, at which germination times deviate from the assumed relation, are deleted (Angus *et al.* 1981; Moot *et al.* 2000). However, there is no apparent break in the data for *Polygonum viviparum*, either at high or low temperatures (Fig. 5).

As Figure 6 shows, thermal time is proportional to temperature (at least up to c. 18°C), indicating that less thermal time is required for germination at low temperatures. This assumes an 0 °C as base temperature, which is ecologically sound. Using

Table 5 Comparison of two alternative ways to calculate base temperature (lowest temperature where germination could occur). 1. Regression of germination rate (until 50%: $1/Tt_{50}$) against temperature (see Fig. 5) and 2. thermal time (until 50% germination (Tt_{50}) against germination (see Fig. 6). The table shows regression parameters for the two approaches as well as the derived base temperature (T_b) and thermal time for 50% germination (Tt_{50}). *** indicates a significance level of $P < 0.001$. Assuming temperature independent germination would yield a slope of 7.47 ± 0.33 (SE) for brown and 10.19 ± 0.32 for red bulbils (calculated as grand mean of x_0 for all temperatures; N = 42). Notice how marginally the regression for red bulbils deviates from this null model, indicating extremely weak temperature dependence of x_0.

		regression parameters					**derived**	
	colour	**intercept**	**slope**	**df**	**F**	**R²**	**Tb [°C]**	**Tt50 [°Cd]**
1/Tt50%	brown	0.0765	0.0043	40	195.1***	0.830	-17.79	232.55
	red	0.0634	0.0026	40	67.0***	0.626	-24.38	384.61
Tt50%	brown	21.19	5.71	28[1]	413.4***	0.937	-1.04	-[3]
	red	10.37	9.93	21[2]	791.9***	0.973	-3.71	-[3]

[1] only data < 20°C used

[2] only data < 18°C used

[3] temperature dependent, see regression parameters

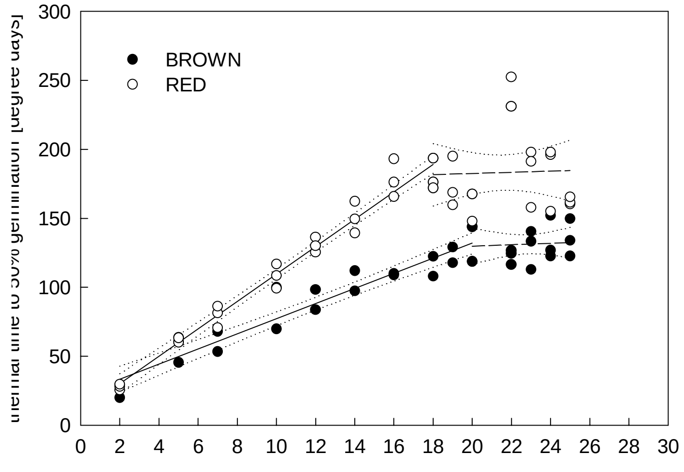

Fig. 6 Thermal time accumulated until 50% germination, comparing red and brown bulbils. Fitting a continuous function to the data always led to unacceptably high deviation from the obviously linear relation in the temperature range from 2 to 18°C (or 20°C for the brown bulbils). For regression parameters see Table 4. Dotted lines are 95% confidence limits. Dashed lines are not significant ($P > 0.8$).

the unrealistic –20 °C from the method described previously, thermal time would indeed be almost constant, but the base temperature would not relate to reality. Extrapolating the lines in Fig. 6 to the x-axis yields a base temperature of c. -2°C (Table 5), which is much more reasonable.

It can thus be concluded that the thermal time concept can not be readily applied to plants growing in very cold climates, as they seem to be able to compensate for the lack of warmth at low temperatures (see also Heide 1992). This hints at the adaptation of the enzymes involved in germination (e.g. α-amylase to break down the starch) to very low temperatures, being little influenced by the low temperatures of this experiment (notice shallow slopes in Fig. 4). The linear relationship between thermal time and germination temperature (Fig. 6) would then be a consequence of the greater variability of temperature (varies 12-fold) compared to x_0 (varies 2-fold). The results thus support the evidence provided by Heide (1992) of almost temperature independent germination below a threshold temperature of c. 20°C.

ACKNOWLEDGEMENTS

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CHAPTER 4

FACILITATION AND COMPETITION IN THE HIGH ARCTIC: THE IMPORTANCE OF EXPERIMENTAL APPROACH[1]

Abstract In the last decade, plant ecologist have focussed more on the occurrence of positive plant-plant interactions than ever before. Especially in severe environments, such as the Arctic, species removal experiments tended to find facilitative rather than competitive effects, casting doubt on the importance of competition under extreme growing conditions. Two approaches to measure plant-plant interactions presented here reveal that competition affects plant growth even in the High Arctic. The comparison of *Luzula confusa* and *Salix polaris* in pure and mixed stands indicates a pronounced reduction in growth in mixed stands. This could not be detected in a removal experiments, which inevitable also altered site microclimate. Causes and implications are discussed using a conceptual model derived from that of Brooker & Callaghan (1998).

INTRODUCTION

Perennial plants living in severe environments have adapted to unpredictable resource availability, disturbances and physical limitations of growth. They are, by definition, stress-tolerant (sensu Grime 1979) and commonly show features of resource storage to buffer environmental fluctuations (Chapin *et al.* 1990). For example, succulent desert plants grow self-sustained on water and nutrients acquired during periods of plenty, with greatly reduced root growth during the intervening "dormant" period (Larcher

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[1] submitted to Acta Oecologica

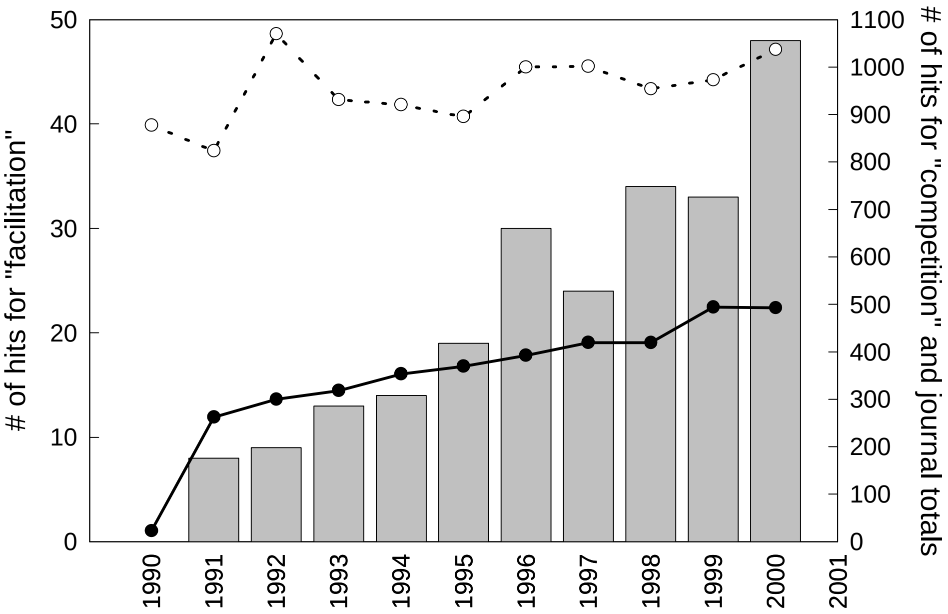

Fig. 1 Web of Science search hits on the terms: ((“positive interactions” OR facilitation) AND plant)), shown as bars, ((“negative interactions” OR competition) AND plant)) in filled points and total publications of *American Naturalist*, *Ecology*, *Journal of Ecology*, *Oecologia* and *Oikos*, shown as open points, from 1990 to 2000.

1995). Thus periods of plant competition are seemingly restricted in such environments. Examples like this gave rise to the idea that (interspecific) competition is less intense in ecosystems with low productivity (Grime 1979). Indeed in these systems *beneficial* effects of neighbours were postulated and detected (e.g. nurse plants: Callaway 1992; Barnes & Archer 1999; associational refuge: Hay 1986; Mulder & Ruess 1998; physical amelioration: Bertness & Shumway 1993; Bertness & Hacker 1994).

Over the last decade studies investigating positive interactions among plants have increased dramatically (Fig. 1), leaving little doubt of their generality and importance (Holmgren *et al.* 1997; Kareiva & Bertness 1997; Bertness 1998), and rather questioning the assumed importance of *competition*. Tilman (1988), Oksanen (1990) and more recently Körner (1999) argued that the few resources available are under strong demand and plants adapted to these harsh environments can exploit them efficiently - leading to (nutrient) competition even in the arctic tundra. Moreover, modelling approaches have indicated that while the *intensity* of competition (compared to performance in monospecific stands, Weldon & Slauson 1986) might be lower in harsh environments, its *importance* (relative to other factors) might still be very high indeed (Chesson & Huntly 1997): plants are living closer to the brink of existence, and even slight decreases in resource availability may thus have very strong effects.

Competition experiments in the Arctic have generally found negative effects of neighbour removal (Jonasson 1992; Shevtsova *et al.* 1995; 1997; Hobbie *et al.* 1999), indicating the importance of facilitation compared with competition (Carlsson & Callaghan 1991; Callaway & Walker 1997; Holmgren *et al.* 1997; Brooker & Callaghan 1998). For example the removal of *Betula nana* led to a decreased abundance of *Vaccinium myrtillus* (Jonasson 1992), and similarly the growth of *Empetrum nigrum* was impeded after the removal of *Vaccinium myrtillus* (Shevtsova *et al.* 1995). Interactions between removal and water and warming treatments (Shevtsova *et al.* 1997) indicated that the mechanism of facilitation was by alteration of the microclimate.

One reason why some neighbour removal experiments in the Arctic have failed to detect competition might be that they inevitably manipulate facilitation, and examine only the net outcome of interactions, not isolating either competition or facilitation. Removal of neighbours will lead to a higher exposure to the physical stress of the environment (e.g. lower temperature, soil drying, Brooker & Callaghan 1998). To investigate whether this masks effects of competitive interactions, we compared two approaches to the study of competition: firstly, the removal of the competitor and secondly, a comparison of plant performance in pure and mixed stands. Plants growing with neighbours experience amelioration of the environment, but the performance also depends on neighbour identity (i.e. intra- vs. interspecific competition). As our findings indicate, different approaches should be employed simultaneously to gain a fuller understanding of plant-plant interactions.

METHODS

The study was carried out in Semmeldalen (77.90 °N 15.20 °E), a valley c. 20 km south of Longyearbyen, Svalbard, in a *Salix polaris*-heath (Rønning 1996). The dominant plant type in terms of cover are bryophytes (mostly > 60%; in our sites dominated by the liverwort *Ptilidium ciliare* and mosses *Polytrichum* spp. and *Drepanocladus uncinatus*), while *Luzula confusa* (c. 10%) and *Salix polaris* (c. 20%) are the main vascular plants. Lichens and bare soil (peat) cover is usually less then 10%. The *Salix polaris*-heath occupies slightly elevated ground and the soil dries out rapidly over the course of the growing season. Nutrient availability is low and there is also evidence for water limitation (Van der Graaf 1999). Summer air temperatures average between

5 and 10 °C, with soil temperatures c. 2 °C at 5 cm depth (unpublished data). The vegetation is grazed heavily by reindeer.

1. Neighbour removal experiment

This experiment was set up in August 1998 as a species removal experiment, nested within a factorial ± nitrogen by ± phosphorus fertilisation experiment (four treatment combinations, five replicates, resulting in 20 independent removal subplots per species). Within each fertiliser treatment one subplot of 50 cm × 50 cm was cleared of *Luzula confusa*, one was cleared of *Salix polaris* and a third one left as control. For *Luzula*, leaves and shootbases were removed (resulting in no re-growth), whilst for *Salix* a less complete removal of stems was repeated twice per year. Data presented are averaged over the fertilisation treatments as there were no significant treatment effects other than the effect of phosphorus on *Salix*, and in this case only the phosphorus-free plots are used for analysis.

2. Comparision of growth in pure and mixed stands

Plots were established in June 1999 at the onset of the growing season. They (N = 15; 60 cm diameter) each comprised a dense stand of *Luzula*, a dense stand of *Salix* and a mixture of both.

Harvest and Statistical analysis

On 1-5 August 2000, after two seasons, five shoots of each species were randomly sampled above-ground from each subplot. These five shoots were sorted into live and dead leaves (*Luzula*) or leaves and stem (*Salix*), dried at c. 45 °C and weighed. Stems of the five *Salix* per subplot were frozen and transported back to the lab. Their growth over the last three years was analysed retrospectively, using the stem length increments, which were transformed into biomass growth CHAPTER 6).

For both experiments, subsamples within subplots were averaged. The model structure accounted for the nesting of competition plots within fertilisation treatments (experiment 1 only) and for blocking. Data were $\log_{10}$-transformed to successfully meet assumptions of ANOVA and analysed with the MIXED procedure of SAS (SAS Institute Inc. 1989).

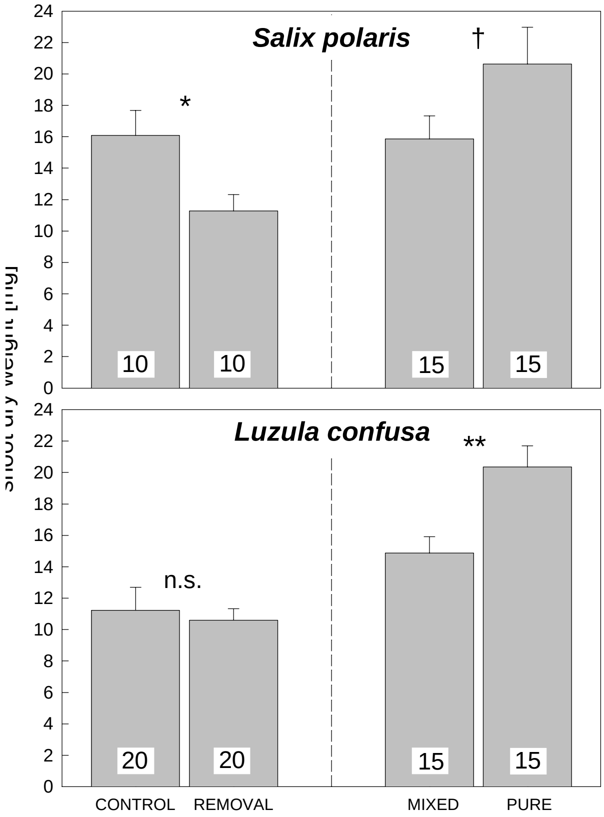

Figure 2 Shoot biomass of *Salix polaris* (upper panel) and *Luzula confusa* (lower panel) in untreated controls and after two seasons without interspecific competition (left half) and growing unmanipulated in mixed and pure stands (right half). Error bars depict standard errors. †, * and ** refer to $P < 0.1$, 0.05 and 0.01, respectively. Numbers indicate level of replication.

RESULTS

The removal of *Luzula* led to a 30% decrease in *Salix* shoot weight ($F_{1,\,18} = 6.41$, $P < 0.05$; Fig. 2), indicating facilitation. On the other hand, *Salix* performed slightly better in pure stands than in mixed ($F_{1,\,28} = 3.75$, $P = 0.0731$; block: $F_{14,\,29} = 2.10$, $P = 0.0881$) suggesting interspecific competition.

For *Luzula*, the results are very different: *Salix* removal had no effect on shoot biomass ($F_{1,\,37} = 0.05$, $P = 0.8238$), while plants performed significantly better in pure than in mixed stands ($F_{1,\,28} = 10.24$, $P < 0.01$), which indicates competitive interactions without facilitative effects of neighbours (Fig. 2).

DISCUSSION

Our results demonstrate clearly the effect of experimental approach on the detection of competition in a severe environment. The classical removal experiment (Aarssen & Epp 1990) would lead to the conclusion that there is no competition among the plant species investigated (due to the negative response of *Salix polaris* and the lack of response of *Luzula confusa*). Hence, a facilitative relationship rather than one of competition would be concluded. However, both species perform better under intra- than interspecific competition, indicating that competition is of some importance.

One recent synthesis (Brooker & Callaghan 1998) provides a framework for explaining the occurrence of both facilitation and competition, focussing especially on harshness of the physical environment, leaving aside biotic harshness (Bertness 1998).

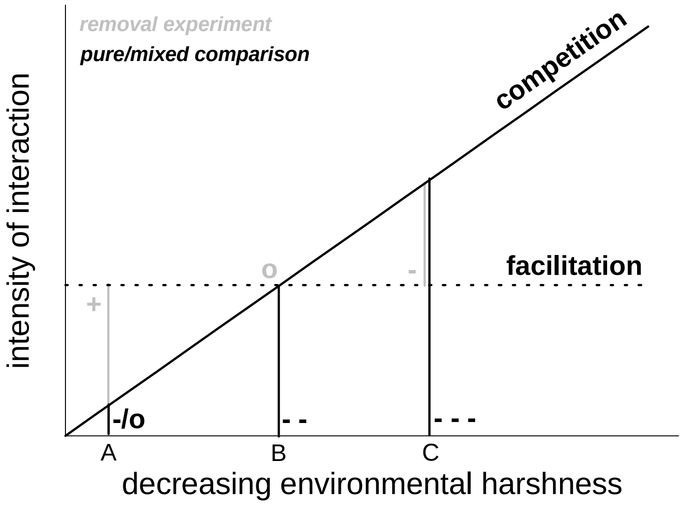

Figure 3 Intensity of faciltation and competition along a gradient of decreasing environmental harshness adapted from Brooker & Callaghan (1998) to represent the intensity rather than the importance of interactions. The observed net outcome of the two types of interactions is illustrated for three points: in A, facilitation overweighs competition, leading to a *negative* effect of neighbour removal (grey vertical lines and symbols, indicating positive (+), neutral (o) or negative (–) net effects). In B, both interactions cancel each other out and in C competition is dominant over facilitation, leading to *positive* effects of neighbour removal. Comparing the performance in mixed and pure stands (black vertical lines and symbols) leads to different conclusions, however. As facilitation is acting in both stands, only competition effects are detected. Assuming that interspecific competition is stronger than intraspecific, plant performance should be lower in mixed stands over the entire gradient, with the difference to pure stands increasing with decreasing environmental harshness.

Figure 3 is a modified representation of this concept. Its main assumptions are: the intensity of facilitation is constant along a gradient of environmental harshness, while the intensity of competition increases. Thus the *net* outcome of plant-plant interactions changes along the gradient. In a low productivity environment (point A), facilitation is more important than competition, the net interaction is facilitative, and neighbour removal would have negative effects on the performance of the target plant. At decreased severity, competition and facilitation are equal (point B), and even further on (point C) competition dominates, leading to positive performance of the target plant in response to neighbour removal.

With respect to figure 3, *Salix* represents the situation at A, with removal having a negative effect, but competition still being evident. *Luzula*, on the other hand, represents the situation at B, with removal of competitors having no effect as facilitation and competition cancel each other out, while interspecific competition is very apparent in the comparison of stands (Fig. 2). This means that two plant species within the same community might experience their environment differently, in this case possibly because of a better environmental adaptation of *Luzula*.

Two assumptions of the concept have to be regarded with caution: firstly, competition intensity might not increase as the environment becomes more benign, but stay constant or even decrease (Goldberg *et al.* 1999). And secondly, depending on the mechanism, facilitation intensity may also not be constant along the environmental gradient. However, a constant intensity of facilitation seems a reasonable null model (Brooker & Callaghan 1998), and also the increase in competitive intensity along a productivity gradient with standing crop below 350 g m^{-2} seems plausible (Belcher *et al.* 1995; Bonser & Reader 1995; Dormann *et al.* 2000).

There is, however, an alternative explanation to the pattern depicted in figure 2. A stronger intra- than interspecific facilitiation would also lead to an increased performance of *Salix* in pure stands compared to controls, as there are more *Salix*-plants facilitating each other. Still the performance would be reduced with the removal of *Luzula*, as this species still provided *some* facilitation. For *Luzula*, this mechanism would be the same: asymmetric facilitation, with a high facilitative value of *Luzula* and a low one for *Salix*. The concept of intra- versus interspecific competition is much more a commonplace than the same idea for facilitation, but the latter might be equally valid.

The mechanism of facilitation in our study is unknown. Amelioration of the physical environment (e.g. reduced wind stress) as described for most facilitation studies (see Brooker & Callaghan 1998) is a possibility, but protection of *Salix* from reindeer grazing by the dead leaves of *Luzula* is also plausible (Van der Wal *et al.* 2000c).

The growth of Arctic plants is generally nutrient limited (Shaver & Chapin 1980; 1986; Chapin *et al.* 1986c; Henry *et al.* 1986; Parsons *et al.* 1994). Thus, it is likely that in addition to facilitation, *Salix* and *Luzula* are also competing for soil resources, probably nitrogen and/or phosphorus (Shaver & Chapin 1986; Baddeley *et al.* 1994). However, the factorial fertilisation experiment, of which the removal experiment is a subset, found no consistent increases in biomass with nitrogen or phosphorus addition (*Salix* showed a marginally significant response to phosphorus). We could thus not identify with any certainty the limiting resource.

In conclusion: as both competition and facilitation are possibly acting, both will structure the community. Disregarding facilitative interactions in the experimental design can lead to misconceptions about forces shaping communities in harsh environments. Thinning experiments would make the removal of a co-occurring species comparable to that of the target species and thus allow testing the assumption of equality of facilitation by different species (asymmetry of facilitation) and the greater intensity of inter- compared to intraspecific competition.

ACKNOWLEDGEMENTS

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CHAPTER 5

COMPETITION IN A CHANGING ENVIRONMENT: A CASE STUDY FROM THE HIGH ARCTIC[1]

Abstract Competition among plants in extreme environments such as the High Arctic has often been described as unimportant, or non-existent. Environmental factors have been suggested to overrule any negative plant-plant interactions. Few studies have actually addressed this issue in the Arctic experimentally, and those that did found little evidence for competition. Species interactions will presumably become more important in the future, as Global Climate Change takes effect on arctic terrestrial ecosystems.

We investigated plant-plant interactions in the High Arctic, following the growth of the wood rush *Luzula confusa* and the dwarf willow *Salix polaris* under conditions of intra- and inter-specific competition, and under elevated temperature treatment, over two growing seasons. Our findings indicate that competition is acting in the natural vegetation, and that warming will alter the balance of interactions in favour of *Salix polaris*, probably due to increased nitrogen availability in warmed plots. To aid understanding of the mechanisms of competition, a controlled environment growth experiment was conducted, manipulating competition, temperature and nutrient availability. The mechanism of competition is unclear, but *Salix* is more responsive to nutrient availability than *Luzula*. Also, while *Luzula* showed a positive response to higher temperature in the laboratory, its performance was actually reduced by interspecific competition in the warmed plots in the field. The consequences of altered

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[1] together with René van der Wal & Sarah J. Woodin (submitted to Journal of Ecology)

competitive balance, and the role of herbivores in influencing plant competition, are discussed in the light of our findings.

INTRODUCTION

Polar regions will be most affected by anthropogenic climate changes (IPCC 1990; Serreze *et al.* 2000). In particular, atmospheric warming due to increasing greenhouse gas emissions is predicted to be most pronounced in the Arctic and Antarctic (IPCC 1998). Arctic terrestrial ecosystems, particularly the vegetation, have been frequently found to respond strongly to experimental perturbations simulating environmental change (for review see Dormann & Woodin 2001; CHAPTER 2). Long-term field experiments on the effects of elevated summer temperature (Chapin *et al.* 1995b) and the indirect consequences of warming (e.g. higher soil mineralisation rates and thus increased nutrient availability, Nadelhoffer *et al.* 1991) have demonstrated major changes in plant species composition (Chapin *et al.* 1995b; Chapin & Körner 1995; Shaver *et al.* 1996; Press *et al.* 1998).

What are the causes of changes in plant species abundance and performance? To date the majority of studies point to individualistic responses of species to environmental perturbations (Chapin & Shaver 1985; Press *et al.* 1998; Dormann & Woodin 2001), rather than competitive displacement, although change in competitive balance is in general one of the best investigated processes underlying changes in vegetation composition (Glenn-Lewin & van der Maarel 1992). In fact, the occurrence of competition among neighbours at high latitudes has been disputed on the basis of theoretical arguments (Grime 1979) and empirical findings: the few competition experiments in the Arctic have rarely found positive effects of neighbour removal, but often negative ones (Jonasson 1992; Shevtsova *et al.* 1997; Hobbie *et al.* 1999), indicating the importance of facilitation over competition (Carlsson & Callaghan 1991; Callaway & Walker 1997; Holmgren *et al.* 1997; Brooker & Callaghan 1998; but see CHAPTER 4). On the other hand Tilman (1988), Oksanen (1990) and, more recently, Körner (1999) reject the idea of competition-free environments. They argue that in harsh environments the few resources available are under strong demand and plants adapted to these environments can exploit them efficiently, leading to (nutrient) competition even in the Arctic tundra. Modelling approaches have indicated that while the *intensity* of competition (sensu Weldon & Slauson 1986) might be lower in harsh environments, its *importance* might still be high (Chesson & Huntly 1997). For plants living close to the brink of survival, any, albeit slight, decrease in resource availability through competition may have strong effects. Moreover, as changes in the Arctic climate result in more favourable conditions for plant growth (longer seasons, higher temperatures, increased nutrient availability), the intensity of competition might be expected to increase.

Competition experiments in the High Arctic are difficult to perform, as the neighbour removal approach favoured in temperate systems (Aarssen & Epp 1990) has potentially serious shortcomings. Brooker & Callaghan (1998) argued that neighbours can facilitate the growth of the target plant, by ameliorating the harshness of the environment (e.g. reduction in wind stress). The removal of neighbours would thereby not only reduce competitive interactions, but also eliminate positive plant interactions. A resulting net-negative effect of neighbour removal does not necessarily indicate the absence of competition in a closed canopy, but the overriding effects of facilitation (CHAPTER 4). This study investigates specifically three main questions: 1. Is competition occurring between two dominant species of High Arctic tundra vegetation? 2. How does warming affect the intensity of interaction between the two species? and 3. What resources do the species compete for? Given the problems of studying competition in an extreme environment, this investigation follows the natural growth of plants in pure and mixed stands in the field, thus overcoming the limitations of a removal experiment. A lower performance of a species in mixed stands compared to pure stands is taken to indicate the occurrence of inter-specific competition. To aid interpretation of the mechanisms of effect of warming, comparison is made between a field temperature manipulation experiment and a controlled environment study in which both temperature and nutrient supply are manipulated.

METHODS

1. Field experiment

Experimental set-up

The study was carried out in Semmeldalen (77.90 °N 15.20 °E), a valley c. 20 km south of Longyearbyen, Svalbard. 15 pairs of plots (60 cm diameter) each of which comprised a dense stand of *Luzula*, a dense stand of *Salix* and a mixture of both were carefully selected in a representative patch of *Salix polaris*-heath (Rønning 1996), within an overall area of c. 100 by 20 m. The experiment consisted of warmed plots and controls, randomly assigned to the paired plots. The whole site was enclosed by an electric fence to prevent disturbance by reindeer.

The 15 treatment plots were subjected to warming over most of the 1999 growing season, from 16.6.1999, i.e. about ten days after snowmelt, to 29.8.1999, and over the whole snow-free period in 2000 until harvest (13.6.2000 - 3.8.2000). Greenhouses of a modified “cloche” type (Strathdee & Bale 1993) were used to raise air temperature. They consisted of an open cylinder (∅ 57 cm, height 45 cm) made of a sheet of transparent plastic, with a thin, optically neutral polyester gauze as a roof. While the gauze allowed gas exchange with the surrounding air, and rain to reach the plots, it did retain warm air in the greenhouse by preventing convection to the surrounding atmosphere (Strathdee & Bale 1993). This design avoids the problems of closed constructions as discussed by Kennedy (1995). Air temperature at vegetation level was measured with three RS temperature loggers per treatment at hourly intervals.

The relatively tall structure of the greenhouses prevented the gauze from shading the plot, as the sun was never high enough. Light intensity in the greenhouses (measured using microvolt integators fitted with a PAR quantum sensor, ΔT, Cambridge, U.K.) was reduced by 11 ± 3%. This is very little, compared to the c. 50% (1100 vs. 500 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) difference between sun and overcast sky, and slightly less than the reductions induced by greenhouses of other designs (Chapin *et al.* 1995b; Michelsen *et al.* 1996a).

The soil around all plots was trenched to about 20 cm depth with a knife to let the greenhouse rim into the soil to prevent entry of cold air, as well as to sever connections of plants within the plot to plants outside. As the soil closed immediately, no noticeable gap remained. All measurements were performed inside the circle, allowing a 10 cm buffer strip around the perimeter. It could be argued that trenching might cause an increase in below-ground senescence, increasing mineralisation rate and thus plant performance. However, soil nitrogen concentrations and growth rates measured in trenched control plots were very similar to those measured in untrenched plots nearby (data not shown).

Soil water content was measured four times during the 1999 season and twice in 2000, using a soil conductivity insertion probe (SCIP, CEH Wallingford, U.K.). To avoid disturbing the plots more than necessary, measurements were only taken in the pure stands. Values obtained were transformed into soil water content using a previously established relationship (Rob Rose, CEH Wallingford, U.K., unpublished data).

Ion exchange membranes were used to assess treatment impacts on nutrient availability, following the method of Weih (1998). Cation and anion exchange membranes (BDH, U.K., #55164 and #55165, respectively) were cut into pieces (1 × 6 cm), with a plastic thread run through the membrane for easier recovery in the field, and membranes were stored until use in 2M NaCl in 0.1M HCl. In the field (23.6.1999 and 21.7.2000, respectively), a pair of membranes was inserted into a c. 5 cm deep slit in the soil cut with a knife at an angle of 45° to the surface. The slit was closed again, and membranes stayed in place until recovery (28.8.1999 and 1.8.2000, respectively). To assess differences between species stands, pairs of membranes were placed in stands of both *Salix* and *Luzula*. At recovery, the membranes were separately transferred into small tubes filled with distilled water. The tubes were stored cool until further processing in the lab. There, ions were extracted from individual membranes with 20 ml 2 M NaCl in 0.1 M HCl by shaking for two hours. Samples were then analysed with a FIA-Star autoanalyser (FIA, Norway) for NH_4^+- and NO_3^--nitrogen. For the analysis of NO_3^--nitrogen it was necessary to neutralise the HCl of the sample by adding equivalent amounts of NaOH to the carrier solution. Without an extensive test series under field conditions it is not possible to translate the N-concentrations on the membrane into actual nitrogen availability to the plants, but this still provides a valid integrative measure of the relative availability of nitrogen in the different stands and treatments (Weih 1998).

Growth measurements

Within each greenhouse and control plot three randomly chosen individuals of each species were marked in both pure and mixed stands. In the first treatment year the responses of *Luzula* and *Salix* plants were assessed by measurement of the length of each leaf and branch, respectively, of marked individuals at the beginning (16.6.1999) and at the end (29.8.1999) of the growing season. Plants sampled from the plots at the beginning and end of the experiment were measured (leaf and branch length), dried for 7 days at c. 45 °C and weighed. These data allowed transformation of the length measurements taken within the experiment into above-ground biomass. In the second treatment year, too few of the tags from 1999 were re-discovered to enable repeat length measurements. Thus on 1-3 August 2000 the experiment was terminated by destructive above-ground biomass harvest of five plants of each species from both pure and mixed stands within each plot. *Luzula* was sorted into dead and live leaves, *Salix* into live leaves and stem, and material (except *Salix* stems) was dried for 7 days at c. 45°C and weighed. *Salix* stems were frozen and transported back to the laboratory where the part of the stem grown during the last two years was severed with a razor blade, dried and weighed. Additionally, a patch of pure stand of each species (10 cm × 10 cm) was harvested destructively to enable extrapolation from individual shoots to the whole stand. The number of ramets/shoots in that square was counted. Plant cover for *Luzula*, *Salix*, other vascular plants, mosses and lichens was estimated by eye for each plot. Cover estimates and biomass data from the 10 cm × 10 cm samples were used to calculate the average biomass of *Luzula* and *Salix* per m^2 for this vegetation type.

Statistical analysis

For the growth analysis (1999) and the final harvest (2000), replicate plants were averaged for each stand type (pure, mixed) within each plot. Years were analysed separately because diffferent measurement methods were used, hence any between year difference would be confounded with growth assessment method. The model structure accounted for the nesting of stand types within warming treatments and for blocking. Data were $\log_{10}$-transformed to successfully meet assumptions of ANOVA and analysed employing the MIXED procedure of SAS (SAS Institute Inc. 1989). Initial biomass was used as a covariate. Error bars depict standard error of the mean for untransformed data.

2. Phytotron experiment

Experimental set-up

Salix polaris and *Luzula confusa* were collected at the site of the field experiment (2-3 September 1999) as cuttings and whole plants, respectively, and kept wrapped in wet tissue paper in plastic bags in a refrigerator unit during transport back to the laboratory. There, all plants were kept in a freezer at –7°C for 8 weeks to simulate winter situations, after which they were transplanted into plastic pots (∅ 7.5 cm, height 7.5 cm) filled with a 90:10 v/v mixture of sand and peat, placed on individual saucers. The competition treatment was realised by transplanting four individuals into each pot, two of each species, while the competition-free pots contained four plants of the same species (substitutive design, Gibson *et al.* 1999). During the four week initial phase of the experiment , all pots were kept at 12°C and received weekly addition of 1/100th Hoagland solution (Hendry & Grime 1993) to enhance establishment of the transplants. On 2-4 December 1999 dead plants (24%) were replaced and the experimental treatments were started.

The three competition treatments (*Luzula* monoculture, *Salix* monoculture and *Luzula*/*Salix* mixture) were maintained at two temperatures (7.5 and 13.5°C) and two levels of nutrient availability (1/10th Hoagland solution (high nutrients) and 1/100th Hoagland solution (low nutrients)). Throughout the experiment pots were watered three times a week by addition of distilled water to the saucers. Nutrient treatments were applied once a week with the distilled water (65 ml per pot).

Ten replicates of each competition x nutrient treatment combination (3 species mixtures × 2 nutrient levels) were placed in two phytotrons (Sanyo, USA), one at each temperature. Pots were arranged in a block design and, to reduce within- and between-chamber effects, pots were shuffled within each chamber weekly, and plants and temperature regimes were swapped between chambers every other week. Relative humidity was maintained at 67 ± 2 % (S.D.) and photosynthetic active radiation at the level of the leaves was 370 μmolphoton$\cdot$m$^{-2}\cdot$s^{-1}. Data loggers (RS logger #13467, Radio Supply, UK; with internal sensor, wrapped in tin foil to eliminate direct warming by the lights, recording at half-hourly intervals; resolution ± 0.5°C) placed at the level of the pots indicated that the temperatures achieved were 7.5 ± 2.19°C (S.D.) for the cold and 13.5 ± 1.7°C for the warm treatments. Thus, the realised temperature difference between treatments was 6°C.

Soil moisture in the pots was measured gravimetrically on an additional set of pots without plants. It decreased between watering events from c. 21 to 13% soil dry weight, which was due to the high evaporation of water caused by the high-light environment. The differences in soil moisture between temperature treatments, however, were marginal compared to the fluctuations within the temperature treatments (soil moisture of pots before/after watering: warm = 21.5 ± 0.3% / 5.8 ± 0.7% soil dry weight; cold = 19.2 ± 0.1% / 3.3 ± 0.4%).

The phytotron experiment was harvested after three months (1-5.3.2000). The soil was carefully transferred into a set of sieves (1 mm and 0.5 mm mesh size) and

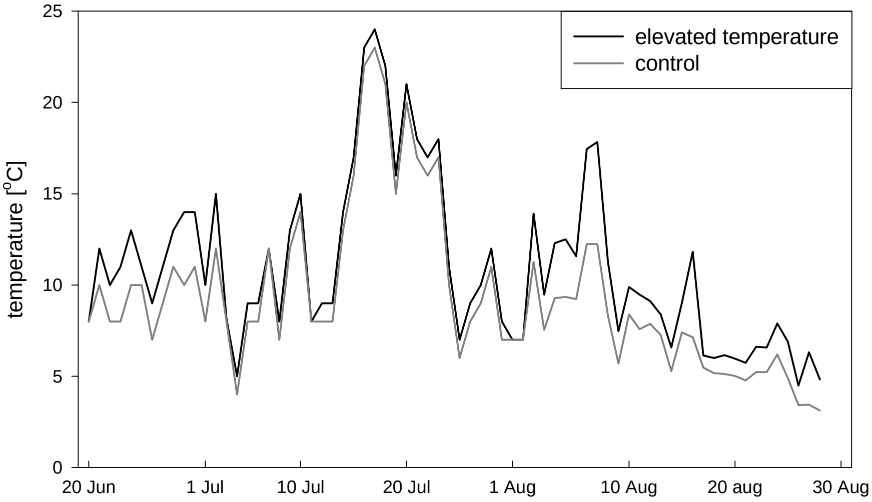

Fig. 1 Field experiment: Temperature during the experimental period of 1999 in the greenhouses (black line) compared to ambient (grey line). Lines are smoothed from 24 hour averages based on hourly readings (N = 3).

rinsed until roots disentangled. *Luzula* plants were divided into roots, rhizome, shoot bases, and live leaves, while dead leaves were discarded. *Salix* plants were divided into roots, stem and leaves only, keeping the occasional inflorescences separate as well. All plant parts were washed, bagged, dried at 70 °C for 48 hours, and weighed to the nearest 0.01 mg.

Statistical analysis

Logistic regression showed that plant mortality was not significantly ($P > 0.05$) related to any of the experimental factors, and we thus assumed no distortion of plant biomass data by mortality. For the statistical analysis, data for average dry weight of a species per pot were $\log_{10}$-transformed to meet assumptions of General Linear Models (homoscedasticity and normal distribution of residuals). The models contained a block factor as random effect, temperature, competition and fertilisation as fixed effects, and the interactions between the fixed effects. The full model was tested and then stepwise simplified with a threshold level of $P < 0.1$ (Crawley 1993).

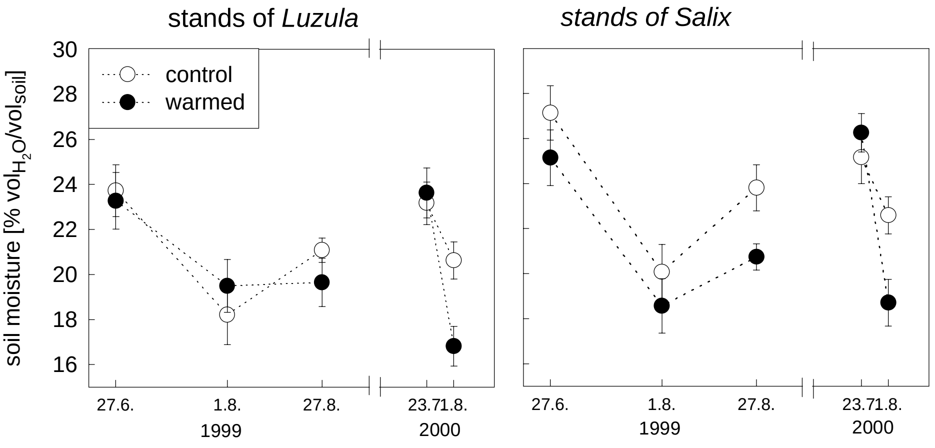

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Fig. 2 Field experiment: Soil moisture in the pure stands of *Luzula* (left) and *Salix* (right) and temperature conditions of the experiment (N = 15). Filled symbols represent elevated temperature treatment, open symbols controls.

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water content between stands of *Luzula* and *Salix* ($P > 0.1$), but dramatic changes between sampling dates (Fig. 2; $F_{4,\,112} = 16.80$, $P < 0.0001$).

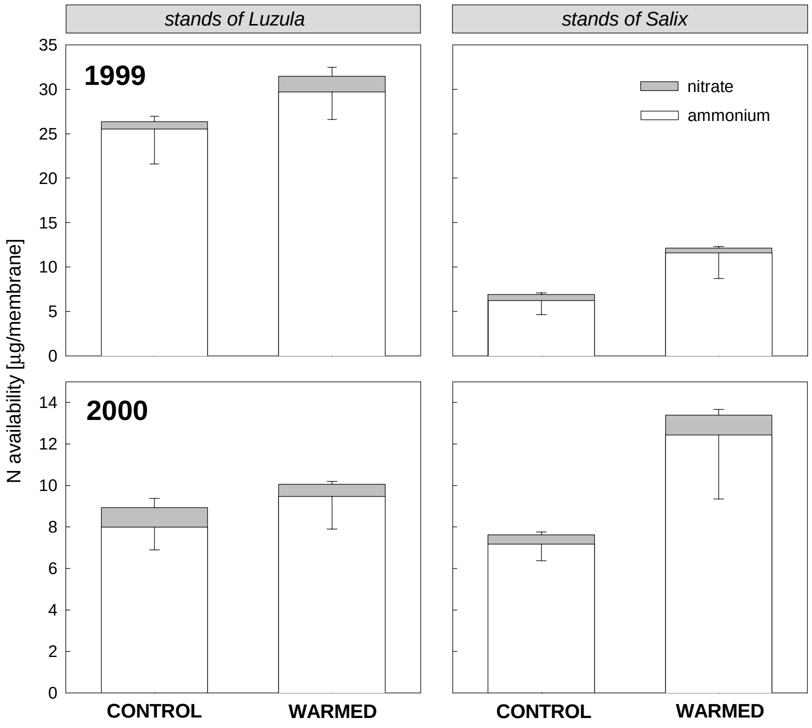

Fig. 3 Field experiment: Cumulative nitrogen availability in the pure stands of *Luzula* (left) and *Salix* (right) and temperature conditions (N = 15). Error bars are –1SE for ammonium (white) and +1SE for nitrate (grey).

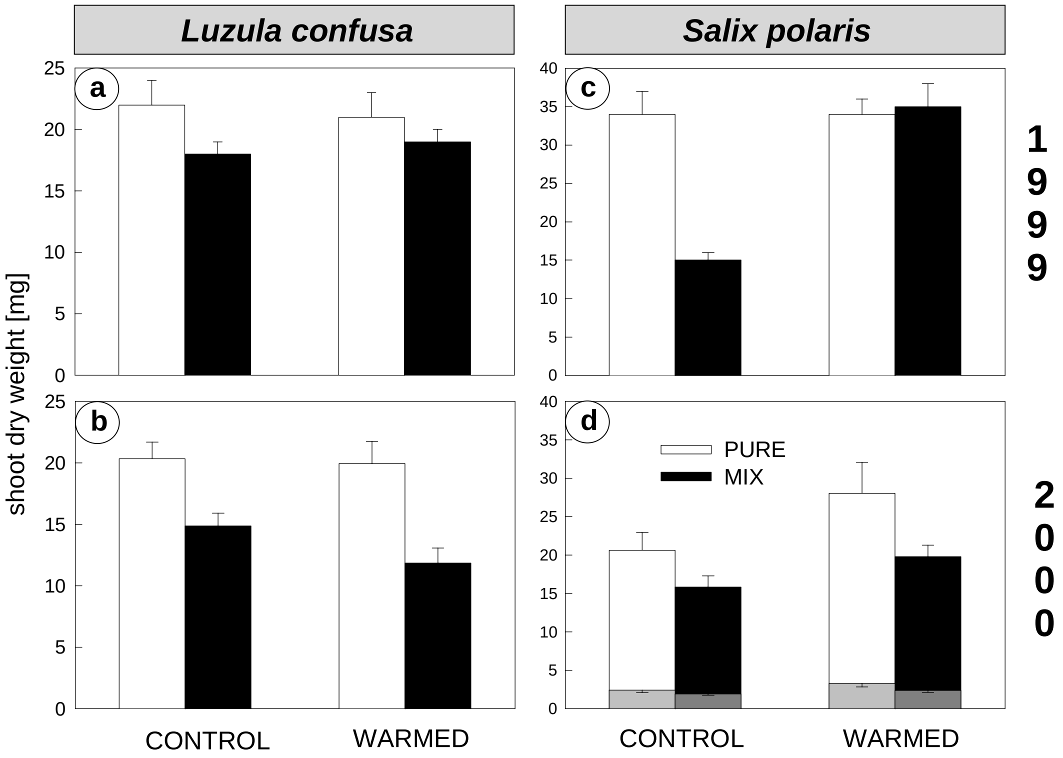

Fig. 4 Field experiment: Current years above-ground growth per shoot of *Luzula confusa* (a, b) and *Salix polaris* (c, d) in pure (white) and mixed stands (black), after one (a, c) and two (b, d) season of elevated temperature, compared to controls (N = 15). Shading indicates biomass of stems. Error bars represent +1 SE.

In 1999, ion exchange membranes were in the soil for three months, while in 2000 they were employed for three weeks during the warmest period of the summer only. Accordingly total nitrogen absorbed on the membranes differed by a factor of three between the years in *Luzula* stands (Fig. 3). NO_3^--nitrogen comprised less than 1% of the total N, and did not differ between stands (or treatments) in either year ($P >$ 0.35 in all cases). Effects of stand and treatment on absorbed nitrogen were consistent in both years, as there were no significant interactions of year with either factor ($P >$ 0.2).

Nitrogen availability differed greatly between stands and treatments. At ambient temperature in 1999, ion exchange membranes in *Luzula* stands contained more than four times the amount of NH_4^+ than those in *Salix* stands (Fig. 3; $F_{1,\ 32} =$ 48.57 $P < 0.0001$). In 2000 there was no such discrepancy ($F_{1,32} = 0.05$, $P = 0.819$), suggesting that the greater amounts of NH_4^+ in the *Luzula* stands are available earlier and/or later in the season, when membranes were not in place in 2000. Warming increased the availability of NH_4^+ (Fig. 3), but nitrogen availability in the soil was too

Table 1 Field experiment: Statistical analysis of effects of temperature (ambient vs. elevated) and stand type (pure vs. mixed) on biomass of *Luzula confusa* and *Salix polaris*.

		Luzula confusa			***Salix polaris***		
	source	**ddf/ndf**	**F**	**P**	**ddf/ndf**	**F**	**P**
1999	initial length	1/28	93.89	0.0001	1/27	66.47	0.0001
	temperature	1/14	2.64	0.1265	1/14	54.19	0.0001
	stand type	1/28	2.83	0.1037	1/27	30.89	0.0001
	interaction	--	--	--	1/27	21.01	0.0001
2000	temperature	1/14	4.39	0.0547	1/14	5.99	0.0282
	stand type	1/28	56.17	0.0001	1/29	9.99	0.0037
	interaction	1/28	3.78	0.0619	--	--	--

heterogeneous to yield a significant difference between treatments ($F_{1,\,14} = 2.09$ and 2.42, *P* = 0.167 and 0.142 for 1999 and 2000, respectively). Relative effects of warming on nitrogen availability to plants were, however, much more pronounced in the *Salix* stands (+ 86% and + 34% for 1999 and 2000, respectively) than in those of *Luzula* (+ 16% and + 19%; Fig. 3).

Treatment effects on plant growth

In 1999, shoot growth of *Luzula confusa* was only marginally less in mixed than in pure stands, and showed no detectable response to elevated temperature (Fig. 4a, Table 1). In contrast, the next year *Luzula* shoot biomass was significantly reduced in mixed stands, and there was a tendency for this to be more pronounced in warmed plots (Fig. 4b, Table 1).

Above-ground biomass of *Salix polaris* at ambient temperature was strongly reduced in the presence of *Luzula confusa* in 1999. However, under elevated temperature, this difference completely disappeared, suggesting a release from competition (Fig 4c, Table 1). The following year *Salix* biomass was again lower in mixed stands, this time irrespective of temperature (Fig. 4d, Table 1). There was also a positive response to warming which tended to be greater in pure stands (+ c. 40%) than in mixed (+ c. 25%) . Overall, temperature effects were slightly stronger than competition effects (Table 1).

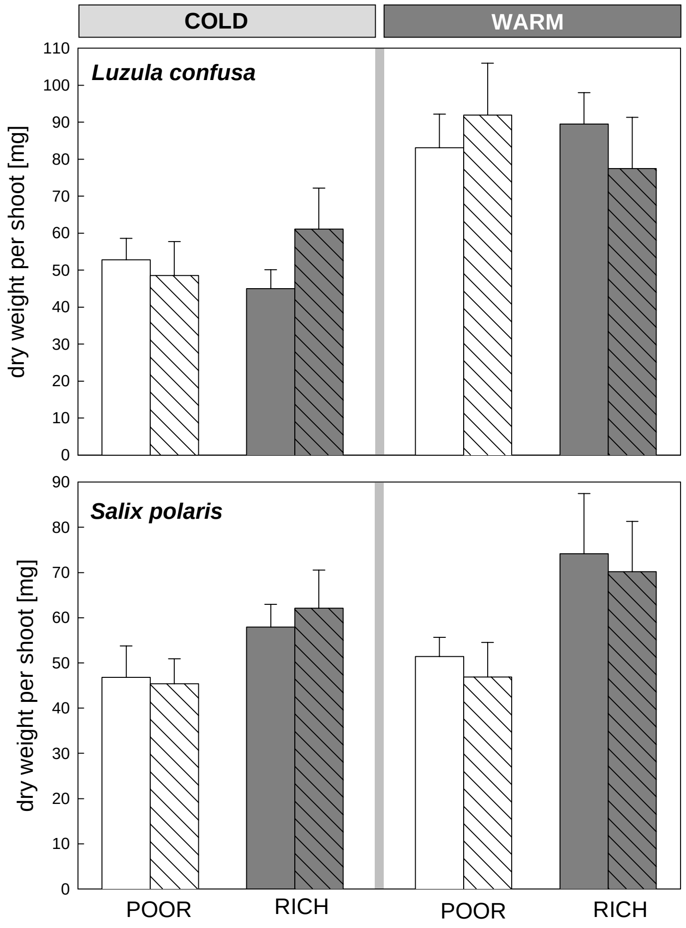

Fig. 5 Phytotron experiment: Total dry weight of *Luzula* and *Salix* plants under cold and warm conditions. “Poor” and “rich” under the graph refer to nutrient availability. Hatched bars represent data from plants growing under competition. Error bars depict +1 standard error of the mean.

Relative contributions to vascular biomass

Warming did not affect the numbers of plant shoots per 100 cm^2 (*Luzula*: control 42 ± 4.7, warmed 42 ± 2.6; *Salix*: control 48 ± 4.9, warmed 50 ± 4.0). Total above-ground biomass of vascular plants (i.e. essentially *Luzula* and *Salix*, as other species were only represented at very low biomass) increased due to warming from 421 ± 52 g m^{-2} to 482 ± 58 g m^{-2}. The percentage contribution of *Luzula* decreased from 36 ± 6% to 28 ± 3%, while that of *Salix* increased accordingly from 64 ± 6% to 72 ± 3%.

Table 3 Phytotron experiment: Statistical results (F-values) for effect of treatments on total biomass and biomass allocation to plant parts for *Luzula* and *Salix* (Table 2). Flowering occurred too rarely to allow analysis. N = 74 and 80 for *Luzula* and *Salix*, respectively. †, *, ** and *** refer to P <0.1, < 0.05, < 0.01 and < 0.001, respectively, while ^{ns} indicates non significant effects. × indicates interactions of t (temperature), f (fertilisation) and/or c (competition). -- indicates factors not included in the statistical model.

	temperature		**fertilisation**		**others**
	Luzula	*Salix*	*Luzula*	*Salix*	*Salix*
total	39.64***	1.19^{ns}	0.70^{ns}	10.24**	
leaves	47.65***	0.01^{ns}	1.64^{ns}	3.39 †	t×c*; t×f×c*
shoot base	12.70***	--	2.15^{ns}	--	
rhizome/stem	12.70***	0.43^{ns}	0.01^{ns}	5.76 *	
roots	42.31***	24.49***	1.16^{ns}	9.14**	competition†

Phytotron experiment

The two species differed strikingly in their response to experimental treatments: total biomass of *Luzula* was affected only by temperature, while that of *Salix* responded only to fertilisation (Fig. 5, Table 2). Temperature significantly increased the growth of leaves, shoot bases, rhizomes and roots of *Luzula*, but only enhanced root growth of *Salix* (Tables 2 and 3). Fertilisation, on the other hand, had no significant effect on any parameter measured in *Luzula*, while it significantly increased the weight of stems and roots in *Sali*x.

Competition had very little effect on either species, the only main effect being a marginally significant reduction in *Salix* root biomass (Table 3). *Salix* leaves showed complex treatment responses. There were no effects of warming or competition in low nutrient conditions. However with high nutrient supply, leaves at low temperature grew better in mixed stands, while leaves at high temperature grew better in pure stands (significant competition × fertilisation × temperature interaction: Table 3).

Table 2 Phytotron experiment: Average dry weight of the different plant parts according to treatment ± 1 SE for *Luzula confusa* and *Salix polaris*. Flowers occurred at maximum once per treatment combination, thus no errors are given.

temperature	**COLD**				**WARM**			
nutrient	**POOR**		**RICH**		**POOR**		**RICH**	
competition	**pure**	**mixed**	**pure**	**mixed**	**pure**	**mixed**	**pure**	**mixed**
Luzula confusa								
flowers	0	0	0.85	0	0	0	1.5	0
leaves	7.8 ± 1.11	6.5 ± 1.13	7.2 ± 0.66	9.1 ± 1.41	13.7 ± 1.97	15.1 ± 2.64	16.3 ± 1.61	10.0 ± 2.01
shoot bases	1.4 ± 0.14	1.8 ± 0.28	1.6 ± 0.19	1.9 ± 0.36	2.07 ± 0.23	1.9 ± 0.26	2.2 ± 0.17	3.3 ± 0.46
rhizome	21.9 ± 2.76	22.6 ± 4.44	16.3 ± 2.76	26.1 ± 5.08	28.9 ± 3.46	28.6 ± 4.42	26.8 ± 2.74	35.9 ± 4.71
roots	21.6 ± 3.04	17.6 ± 3.83	19.1 ± 2.04	24 ± 5.53	38.4 ± 4.16	46.2 ± 7.62	42.7 ± 5.08	33.1 ± 9.98
Salix polaris								
flowers	0.3	0.13	0	1.5	0	0.52	1.1	0.94
leaves	3.9 ± 0.54	3.9 ± 0.58	3.6 ± 0.36	7.6 ± 2.2	4.0 ± 0.64	3.8 ± 0.91	8.3 ± 1.77	3.8 ± 0.87
stem	36.4 ± 6.00	36.8 ± 4.47	46.4 ± 4.47	41.2 ± 5.87	33.6 ± 2.72	32.0 ± 6.83	39.0 ± 6.06	53.0 ± 9.94
roots	6.3 ± 1.14	5.0 ± 1.3	8.0 ± 0.88	11.8 ± 3.28	13.8 ± 1.97	10.6 ± 1.37	25.7 ± 5.34	12.5 ± 2.71

DISCUSSION

Does competition occur between dominant species of High Arctic tundra?

Our data show reduced performance of both *Salix polaris* and *Luzula confusa* in the presence of the other species. Competition between the two species is thus clearly detectable, and is of relatively high intensity, reducing shoot biomass of both *Salix* and *Luzula* by c. 25% (at ambient temperature, averaged across years). This demonstrates that the harsh environment does not preclude the occurrence of interspecific competition, as also suggested by Oksanen (1990) and Theodose & Bowman (1997). In the phytotron experiment such competitive interactions were not observed, most likely due to the planting density being rather low.

Few other arctic field experiments have shown evidence for competition, but they are exceptions. Reducing competition by clipping neighbours increased bulb and root mass of *Triglochin palustris* (Mulder & Ruess 1998), hinting at competitive suppression of growth in this sub-arctic salt marsh. Also, in a transplantation experiment of boreal trees into tundra habitats two species (*Betula papyrifera* and *Picea glauca*) had significantly greater growth in the reduced competition treatment (Hobbie & Chapin 1998a). However, the majority of arctic studies that employ the classical neighbour removal approach (Aarssen & Epp 1990) have failed to detect competition consistently. Jonasson (1992) found no significant increase in any species following the removal of the dominant species in three vegetation types, suggesting that "… competition from them was not a major limiting factor to the growth of co-occuring species" (p. 420). Similarly, in the Alaskan Arctic, no vascular species (except *Ledum palustre*, which is particularly sensitive to light competition) increased aboveground biomass in response to removal of any of four dominant species (Hobbie *et al.* 1999). In the Scandinavian Sub-Arctic *Empetrum nigrum* did respond positively to removal of *Vaccinium vitis-idaea*, but *Vaccinium* suffered from the removal of *Empetrum* (Shevtsova *et al.* 1997). It was suggested that *Vaccinium* dominated the competition for light, but *Empetrum* created a moister and warmer microclimate, favouring *Vaccinium.* The communities in these three studies were more species-rich than our *Luzula-Salix* heath, which may cause competition to be diffuse, rather than species specific (Hobbie *et al.* 1999). However, in a sub-arctic dune system of comparable structural simplicity to our heath, removal of the nitrogen-fixing Fabaceae *Lathyrus japonicus* resulted in no change in the biomass of the grass *Elymus mollis*, and vice versa (Houle 1998).

Following the argument of Brooker & Callaghan (1998) this apparent lack of positive responses to species removal may be due to the balance between facilitation and competition which occurs in extreme environments. Removal of neighbours also removes physical shelter, which is regarded as being very important in the Arctic (Carlsson & Callaghan 1991). However, our comparison of growth of species in pure and mixed stands supports the notion of Theodose & Bowman (1997) that "… competition can be an important force structuring plant communities in an extreme environment." (p. 109). As long as a certain level of protection is provided by neighbours, whether they be conspecifics or other species, competition for resources also operates. Decreased protection (as in a removal experiment) may reduce the performance of a plant such that it is unable to respond positively to resources made available by the removal of its neighbour. Further experiments on competition in the Arctic should take this into account, and develop approaches that allow comparison of different neighbour densities without alteration of the level of physical protection.

It should be noted that the site of our investigation is intensively grazed by reindeer, which were excluded from the experiment. It is unclear, how far grazing would alter the observed competitive (and facilitative) interactions between *Luzula* and *Salix*. Work by Mulder & Ruess (1998) in a low-arctic salt marsh indicates that the subdominant species might profit from the grazing of its neighbours, but, if the herbivore is positively selecting it, competitive effects would be enhanced (see also Huisman *et al.* 1999). Both *Luzula* and *Salix* are extensively grazed over winter and early spring, after which the use of *Luzula* rapidly drops over the course of the growing season, but *Salix* remains an important food item throughout the summer (Van der Wal *et al.* 2000c). Thus, the losses due to grazing are likely to be far greater for *Salix*, and it has been shown to suffer 40% reduction in leaf biomass in response grazing in the previous year (Skarpe & Van der Wal 2001). In contrast, simulated winter grazing of *Luzula* did not influence its performance during the growing season (R. van der Wal, unpublished data). Thus grazing might be expected to shift the competitive balance observed in this study observed in favour of *Luzula*.

How does warming affect the interaction between the two species?

Elevated temperature in the field had a dual effect on the microsite conditions, increasing both air temperature and soil nitrogen availability. In the phytotron experiment the plants demonstrated strong, species specific responses to both these factors, with *Luzula* profiting from higher temperatures, and *Salix* from increased nutrient availability. The individualistic nature of plant species' responses to environmental manipulations is a recurrent theme in global change ecology(Chapin & Shaver 1985; Press *et al.* 1998; Dormann & Woodin 2001), which makes it difficult to distil generalisations.

The responses of *Luzula* and *Salix* in the field differed from those expected on the basis of the results of the phytotron experiment. Predictions were of an increase in biomass for both species, *Luzula* profiting from warming, and *Salix* from the accompanying higher nutrient availability. However, only *Salix* significantly increased in biomass. A similar discrepancy was observed by McGraw & Chapin (1989), when, in the laboratory, two *Eriophorum* species responded similarly to nutrient enrichment, whilst in the field the species adapted to the respective site outcompeted the other. It is difficult to explain the complete lack of response of *Luzula* to warming in the field. The temperature difference between treatments in the field was less than half of that in the phytotrons, and thus possibly not sufficient to produce analogous effects. However, a trend in the same direction might have been expected, while in fact the opposite was observed. Another possibility is that *Salix* suppresses the response of *Luzula* to warming. There is some evidence that the reduced growth of *Luzula* in mixed stands, seen in the second year of the experiment, is greater at elevated temperature. This possibly results from the warming-induced stimulation of *Salix* in the mixed stands the previous year. However, competition cannot explain the lack of response of *Luzula* in pure stands to warming, and the conclusion must be that some factor other than temperature is limiting to the shoot growth of *Luzula* in the field.

Salix polaris clearly gains the most benefit from elevated temperature in the field, probably through the increase in nutrient availability in warmed soil. *Salix* is also apparently able to suppress the growth of its competitor. Thus continued stimulation of the growth of individual *Salix* shoots by increased temperature would cause an eventual decline of *Luzula*, which may be accelerated if branching of *Salix* shoots also increases. Grazing could prevent *Salix* from outcompeting *Luzula* in warmer climate, and be responsible for persistent co-dominance of the two species in this high-Arctic system.

However, the take-over of arctic vegetation by shrubs and eventually trees fits the predictions derived from climate warming models (Emanuel *et al.* 1985; Starfield & Chapin 1996; Epstein *et al.* 2000) as well as long-term experimental evidence (Chapin *et al.* 1995b; Shaver & Chapin 1995; Press *et al.* 1998).

What resources are *Salix* and *Luzula* competing for?

We cannot provide a clear answer to this question. Light competition is unlikely, because the density of vegetation is very low, and the occurrence of shading is presumably scant. In dense stands of *Luzula* the removal of dead *Luzula* leaves increased light availability at ground level from 64 ± 2% of incident PAR to 85 ± 1%, a 25% relative increase (data not shown). However, a light availability of 64% is still very high and in a field shading experiment a light availability of only 47% did not significantly affect growth of either species over a two year period (CHAPTER 8).

It has been frequently shown that Arctic plants are nutrient rather than temperature limited (Chapin & Shaver 1985; Shaver *et al.* 1986; Wookey *et al.* 1994; Chapin *et al.* 1995b; Wookey *et al.* 1995; Chapin & Shaver 1996; Shaver *et al.* 1998; Jonasson *et al.* 1999; but see Parsons *et al.* 1994; Michelsen *et al.* 1996a; Graglia *et al.* 1997). It is thus likely that competition among plants would be for soil nutrients, most likely nitrogen and/or phosphorus. In this study nitrogen availability was increased considerably by elevated temperature (Fig. 3). In the phytotron experiment only *Salix* responded to nutrients. The increased growth of *Salix* in the field could be simply a warming-induced fertilisation effect, from which *Luzula* does not benefit. This would explain the better performance of *Salix* than *Luzula* in response to warming.

As nutrient availability is higher in stands of *Luzula*, why then is *Salix* biomass in control plots lower there? Possibly *Luzula* preempts nutrients from *Salix* (mixed controls in Fig. 4d), but is unable to transform this into growth, due to other limitations. Alternatively, one could speculate that *Salix* is more flexible in its response, while *Luzula* follows a conservative growth pattern. In the longer term *Salix* would thus be favoured, as it could make use of nutrient flushes within that season, thereby outgrowing *Luzula* (see data on biomass in pure stands).

In the face of climatic change, confirmation both of the mechanisms behind, and the trajectory of changes within, the competitive balance of plant communities are urgently needed. Controlled environment growth experiments may not provide reliable predictors of plant interactions in the field. Further field research of plant competition in harsh environments should embrace different approaches to avoid the pitfalls of a facilitation-competition trade-off situation, as negative interactions are important even in one of the most extreme environments, and may dictate vegetation response to climate change.

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CHAPTER 6

INDUCED DEFENCE IN A HIGH-ARCTIC DWARF SHRUB (*SALIX POLARIS*)[1]

Abstract Plants severely restricted in their growth by constraints of the abiotic environment face the dilemma of having to allocate precious resources and assimilates to anti-herbivore defence. One way to overcome this is by relying on inducible defences, which increase the resistance to grazing on later occasions. While this has been described for sub-tropical and boreal plant species, no test of inducible defence has been carried out in the High Arctic. Here, we report the effect of simulated grazing on *Salix polaris* on Svalbard, 78°N. We assessed nitrogen, carbon and phenolic concentrations of leaves at seven time intervals after clipping: 15 minutes, 1, 4 and 24 hours, and 7, 30 and 365 days. After correcting for seasonal trends in the nitrogen data, a short decrease after 1 hour was detectable, which disappeared again at longer time intervals. Phenolic compounds increased within 15 minutes and were also significantly higher than controls after 1 day, but after a week or longer no difference was detectable. Reindeer used plots clipped in the previous year significantly more than controls. Plots with a clipping level of 50% received more bites than controls, while the scatter was too big to detect this pattern for the 100% clipping.

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[1] together with Christina Skarpe

INTRODUCTION

For plants to avoid herbivory is generally costly, and will be favoured by natural selection only when the cost for prevention is less than the cost of the herbivory that is prevented (CHAPTER 9, Feeny 1976; Rhoades 1979; Coley *et al.* 1985; Grubb 1992). Plant traits that have been suggested to reduce herbivory include chemical and structural defence (Palo *et al.* 1992; Gowda 1996), low or unbalanced nutrient content (Moran & Hamilton 1980) and a growth form that reduces availability (Milchunas & Lauenroth 1993). Considering the cost for such measures, an ability to vary the effort over time in relation to the actual risk for attack, would seem appropriate. The existence of such strategies is indicated by the many reports of short- or long term herbivory-induced defence in plants from different taxonomic groups and in different environments (Karban & Baldwin 1997, and references therein). Plant responses to herbivory may include both fast growth to compensate for loss of biomass and the development of means to prevent further damage (Maschinsky & Whitham 1989; Noy-Meir 1993; Järemo *et al.* 1996). In plants expressing both types of responses, a temporal differentiation in resource allocation to defence and to compensatory growth would be expected.

Plants may undergo a sequence of chemical and structural changes after being wounded. Some changes may reflect physiological processes without relation to the herbivore, others may have an effect as defence against pathogens entering the wounded tissue (Enyedi *et al.* 1992) and/or against repeated attack by herbivores (Edwards *et al.* 1986; Bryant *et al.* 1991b). Rapidly induced responses may affect the individual animal that caused the initial damage or others foraging in the same group, whereas long-term responses may act by reducing the population of the herbivore (Bryant 1981; Haukioja 1990). Contrary to costly defence or avoidance strategies, plant responses aiming to compensate for herbivory and maximize competitive ability includes fast growth, high nitrogen content and low allocation to defences, all traits that increases palatability of the plant and the risk for herbivory (Danell *et al.* 1994a; Järemo *et al.* 1996). Thus, a plant that has suffered browsing by a large herbivore, is in a trade-off situation on when to allocate resources to minimise costs to further herbivory and when to use resources for compensatory growth and accept a larger risk for repeated herbivory.

We studied the temporal variation of responses following simulated browsing by reindeer on the high-arctic shrub *Salix polaris* in Spitsbergen, Svalbard. Particularly we asked: Does plant content of phenolics and/or nitrogen differ between a grazed and an ungrazed plant, and, if so, what is the variation over time? The breakdown of one exclosure allowed us to also investigate if reindeer prefer to feed on plants that were grazed the previous year compared to previously ungrazed plants.

METHODS

Study system

The study was carried out in Semmeldalen, 77^{o}90'N, 15^{o}20'E, on Nordenskjølds land, Spitsbergen, Svalbard. The area is a wide valley covered by polar desert and high-arctic tundra, dominated by heath with *Luzula confusa* (Hartm.) Lindeb. and *Salix polaris* Wahlenberg. The valley has a fairly stationary population of reindeer at a density of ca. 12 animals per km^{2} (Audun Stien, personal communication), which is high for Svalbard. Reindeer are the only mammalian herbivores in the area.

Salix polaris is common throughout Spitsbergen and occurs in most habitats except wet bogs and polar desert (Rønning 1996). It is a deciduous dwarfshrub with subterranous creeping stems and branches, and often has only shoot tips and leaves showing above ground. *Salix polaris* is an important food plant for reindeer (Staaland 1985, Christina Skarpe unpublished), particularily early in summer (Halle 2000) and probably during winter (Christina Skarpe, unpublished), when animals are cratering for food under the snow.

Field methods

The study used two exclosures, that have been set up in 1996, and that have not been accessible for reindeer for two full years prior to the extablishment of this experiment. Two hundred plots measuring 20 × 20 cm with at least 20 % cover of *Salix polaris* were selected in each of the two exclosures, allowing 20 replicates per treatment per exclosure. There was at least 1 m between adjacent plots. Plots were numbered, and randomly allocated to different treatments.

In June and July 1999, 50 % of the leaves (i.e. every other leaf) from each shoot in each plot were hand picked. Care was taken not to damage the apical bud, which nevertheless happened occasionally. After a predetermined time, the remaining leaves were picked for analysis. Time intervals between simulated herbivory and leaf sampling for analysis were 15 minutes, 1 hour, 4 hours, 24 hours, 7 days, 30 days and 1 year. For times up to 4 hours, the leaves initially removed from the plot were used as control. For longer times, control plots, which previously had not any leaves removed, were harvested. Four simulated herbivory scenarios were used to study the response one year after defoliation: 100 % of the leaves were picked early in the season (9-10 July 1999) or late (30-31 July 1999), or 50 % of the leaves were picked early (2-3 July 1999) or late (29 July 1999). From these plots, and from untouched control plots, all leaves were harvested 5-17 July 2000. Leaves were dried in open paper bags at c. 40 ºC in the field cabin, and re-dried (24 hours at 70 ºC) prior to grinding.

Reindeer broke into one of the two exclosures probably in late autumn 1999, and when field work was resumed in July 2000, there was much evidence of foraging by reindeer earlier in the summer. Thus, for the 1 year treatments only samples from the undisturbed exclosure were used. As there had been no grazing for the previous two years in the trespassed exclosure, it was possible to investigate whether reindeer had used the treated plots differently from the surrounding vegetation. Plots were dug out, and analysed for signs of browsing (branches bitten off).

Laboratory methods

Samples were ground in a ball mill and analysed colourimetrically for phenolic compounds following the recommendations of Hagerman (1998): phenolics were determined using the modified Prussian blue assay and are expressed as percentage dry weight on the basis of tannic acid equivalents. Additionally, samples were analysed for total carbon and nitrogen using a CNS autoanalyser (Fisons, U.K.).

Statistical methods

Log_{10}-transformded data on phenolics, carbon and nitrogen concentrations were analysed by General Linear Modelling, using block as random factor, Julian day and (Julian day)^2 as covariates to correct for temporal trends within the season, and simulated herbivory, time before sampling and their interaction as fixed effects. Data were normally distributed and displayed homogenous variances. Tukey's honest significant difference post-hoc test was used to compare treatment groups.

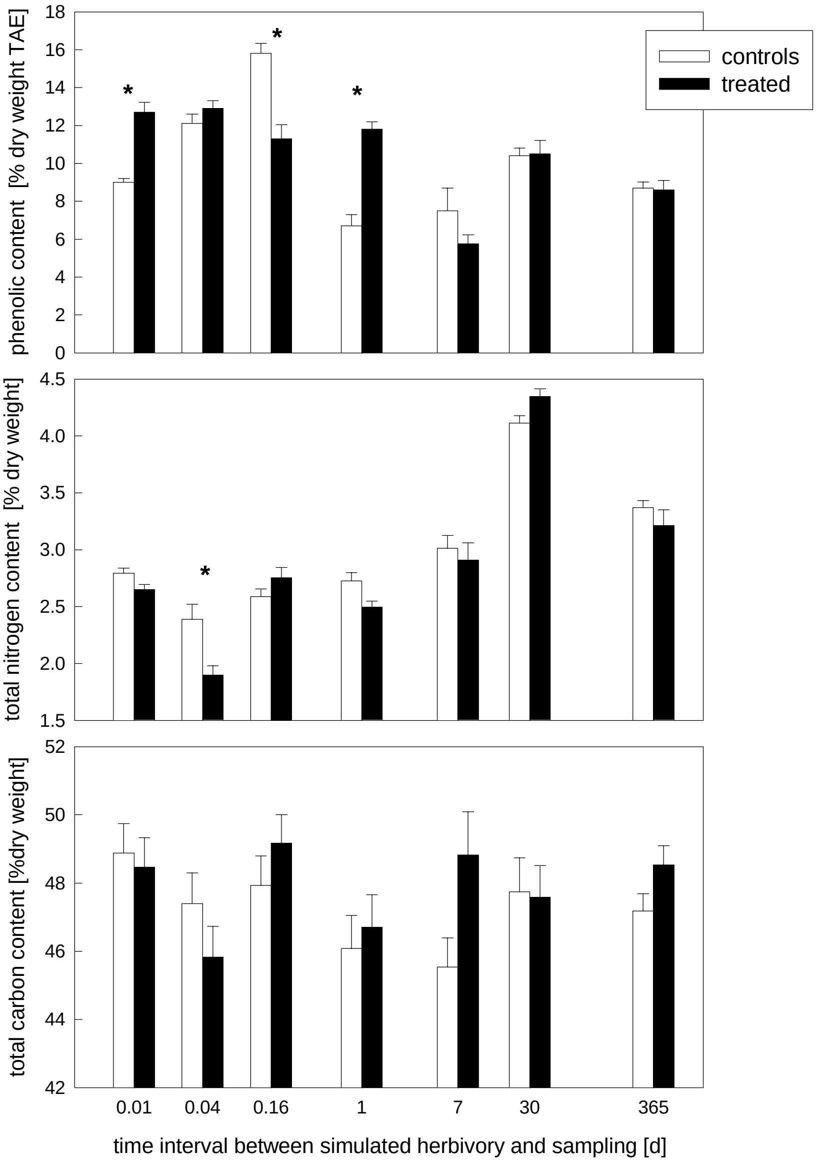

Fig. 1 Total phenolic (in tannic acid equivalents, TAE), adjusted nitrogen and carbon content of *Salix polaris* leaves at different intervals after simulated grazing (black bars) compared to controls (white). Note that time axis is on log$_{10}$-scale. Asterisks indicate significant difference between simulated grazing and control (Tukey's hsd).

RESULTS

Leaf quality after simulated grazing: 15 minutes to 1 year

Total phenolic concentrations were significantly increased only 15 minutes after leaf removal. This difference vanished after one hour, and was curiously reversed after four hours. 24 hours after simulated herbivory, phenolic concentrations were higher than in controls again, but at even longer time periods, no further differences could

Table 1 Statistical analysis of the effects of picking and interval to sampling on nitrogen, carbon and phenolic content of leaves ($N_{adjusted} = N_{observed} - N_{predicted}$ + grand mean over all $N_{observed}$).

		Nitrogen (adjusted)			Carbon			Phenolics		
source	**DF**	**MS**	**F**	***P***	**MS**	**F**	***P***	**MS**	**F**	***P***
block	1	0.0025	1.39	0.240	0.0000	0.08	0.781	0.0202	3.62	0.060
picking	1	0.0023	1.30	0.256	0.0012	2.41	0.124	0.0168	3.00	0.086
interval	6	0.0616	34.38	0.000	0.0030	5.84	0.000	0.1640	29.29	0.000
interaction	6	0.0095	5.32	0.000	0.0006	1.17	0.325	0.0908	16.22	0.000
Error	123	0.0018			0.0005			0.0056		

be detected. The striking differences between controls of different sampling times are not explained by seasonal variation (no significance of Julian date of sampling as co-variate: Table 1). In the leaf removal plots, phenolics show a slow but steady decline with re-sampling interval. As it is the variation in the controls that leads to significant differences after 15 minutes and 4 hours, these results have to be treated carefully. The difference between controls was also almost double that of effects of simulated herbivory (Fig. 1).

For nitrogen content of the leaves, a temporal trend was detectable in the data (Julian day: $F_{1,\,121} = 4.15$, $P < 0.05$; Julian day squared: $F_{1,\,121} = 4.76$, $P < 0.05$). A quadratic equation was fitted ($N_{predicted} = 0.6618 \cdot$ Julian day $-0.00189 \cdot$ Julian day squared – 54.5) and data were corrected for the temporal trend for further analysis and are depicted in Fig. 1. Nitrogen concentrations were influenced by simulated herbivory and sampling interval, indicated by a significant interaction in Table 1. After correction for sampling date, nitrogen concentration of leaves in both picked and control plots increased with interval of re-sampling in 1999, but was low again in 2000 (Fig. 1). Only after four hours is there a significant decrease in leaves of picked vs. control plants. At all other time intervals no effect of simulated grazing was apparent.

Despite c. 3% variation in total carbon concentrations (45.8 to 49%: Fig. 1), they were always similar in leaves of picked and unpicked plants (Table 1). Due to higher variance in the data, carbon showed no detectable trend over re-sampling interval. After one day, the carbon concentrations were significantly lower than after 15 minutes and 4 hours. After one week has passed between leaf removal and sampling, carbon levels were again undistinguishable from initial values.

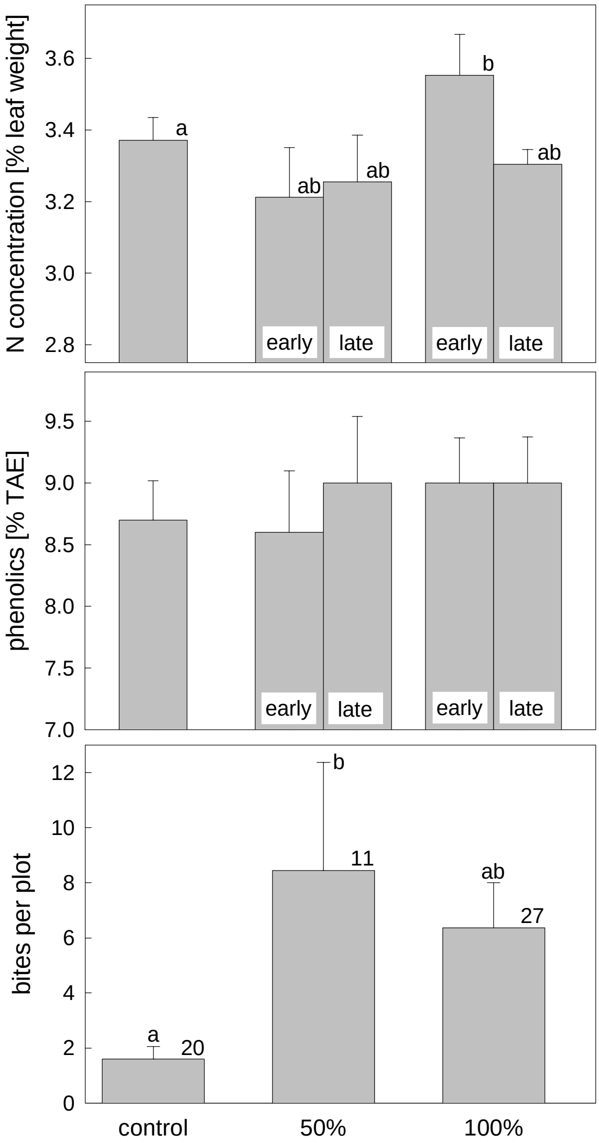

Fig. 2 Comparison of total nitrogen and phenolic concentrations, and reindeer usage of experimental plots one year after simulated grazing. 50% and 100% refer to half and full leaf removal, respectively, while "early" and "late" refer to timing of leaf removal within the season. For the assessment of reindeer feeding preferences, data from the similar early and late leaf removals were pooled to increase sample size. Error bars show standard errors, and numbers on the bars indicate sample size (N = 10 where those are not given). Bars sharing the same letter are not significantly different (i.e. $P > 0.05$).

Leaf quality and reindeer preferences after one year

Of the four leaf removal treatments (50 and 100%, both picked early and late in the season) only the 100% early showed a significant difference in nitrogen concentrations from the control (Tukey's hsd: T = 3.692, $P < 0.01$), yielding a significant effect of leaf removal on nitrogen concentration ($F_{4,\,53} = 3.47$, $P < 0.05$; Fig. 2). Picking effects were not significant for carbon concentrations ($F_{4,\,53}$ = 2.21, P = 0.081; mean = 49.1 ± 1.28 standard deviation, N = 59), but not for phenolics ($F_{4,\,53}$ = 0.29, P = 0.885; mean = 8.81 ± 1.40 SD, N = 59).

There were more bites from reindeer in the plots with 50% of leaves removed the previous season than in control plots and plots with 100% of leaves removed, there was a tendency for the latter to have more bites than unpicked controls.

DISCUSSION

In this study, we found a 40 % increase in content of phenolics 15 minutes after treatment, a decrease after 4 hours and an increase again after 24 hours. After longer times, even a year, there was no change in phenolic content. The pattern shows a quick and dynamic response, probably involving different processes. The first increase in phenolics after only 15 minutes is most likely a result of transfer of preformed compounds and/or activation of precursors (Karban & Baldwin 1997). There are records of induced plant responses only seconds after damage (Fowler & Lawton 1985; Karban & Baldwin 1997). Hay & Brown (1992) record significantly higher content of polyphenolics and condensed tannins in leaves of *Acacia nigrescens* 20 minutes after simulated browsing compared to controls. We found no longer-term increase in phenolics, contrary to many studies of chemical defence in *Salix* and other deciduous trees (Chapin *et al.* 1980; Bryant 1981; Bryant *et al.* 1994). In these studies *Salix* usually constituted a rare resource, likely to be defended (Grubb 1992), while *Salix polaris* is common on Svalbard, in fact the most abundant vascular plant species in this vegetation type. In addition, the majority of these studies were concerned with responses to winter browsing of twigs. Although a variety of phenolic compounds occur in *Salix*, most of them reach high concentrations in bark rather than leaves (Palo 1984). Over years, however, there might be a *negative* cumulative effect of grazing on phenolics due to imbalanced source-sink relationships, as can be seen by the *increase* in defence compounds with the exclusion of reindeer after three years (CHAPTER 7).

Nitrogen content of “grazed” plants decreased significantly one hour after treatment, at a time when there was no response in phenolics. Withdrawal of nitrogen from remaining leaves following browsing could be a way for the plant to protect an expensive resource and/or invest in compensatory growth, e. g. in buds for new leaves or shoots. Withdrawal of N from remaining leaves may also be a means to deter herbivores by offering a less nutritious browse (Moran & Hamilton 1980). From seven days and up to a year after the treatment, there was no response of N content to leaf removal, contrary to many findings of a long-term increase in N following natural or simulated browsing (Du Toit *et al.* 1990; Danell *et al.* 1994a) and in *Salix polaris* on Svalbard (Skarpe & Van der Wal 2001).

The tendency to increased browsing on plants clipped a year before also suggests that resources are allocated to growth, possibly enhancing nutrient content, even if we found no significant increase in N content, at the expense of defences. Such re-browsing is frequently recorded (Bergström *et al.* 2000).

Our results show a short-term response in *Salix polaris*, including changes in the content of phenolic compounds and nitrogen within a day from leaf removal. Thereafter there is little change in phenolics, and in the following season there are indications of resource allocation to growth rather than defence. However, our results must be interpreted cautiously, as the effects of simulated herbivory were less than differences between controls.

ACKNOWLEDGEMENT

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CHAPTER 7

SEX-RATIO IN WILLOW REVISITED: CONSEQUENCES OF HERBIVORE EXCLUSION[1]

Abstract For a long time dioecious plants have been a model system for understanding the interaction between plants and herbivores. Differences in growth rate and, consequently, investment in defence between sexes may lead to skewed sex ratios due to differential herbivory. In this study, we tried to evaluate the applicability of this idea to Polar Willow (*Salix polaris*), which in the study site displays a female-biased sex ratio. Excluding reindeer for three years led to an increased abundance of male flowers in one of two vegetation types investigated. Growth rates differed only slightly between the sexes, with females investing more into inflorescences. The concentration of chemical defence compounds (phenolics and condensed tannins) did not differ between sexes. On the basis of these findings, the idea that growth rate dependent herbivory caused the unbalanced sex ratio in *Salix polaris* has to be rejected. Possibly an interaction of niche differentiation between male and female willows in combination with reindeer grazing produced the observed female-biased sex ratio, but the exact mechanism remains unclear**.**

INTRODUCTION

A biased sex-ratio in dioecious plants has been reported for various species in various environments (Crawford & Balfour 1990; Dupont & Kato 1999; Hjältén 1992;

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[1] together with Christina Skarpe

Nichols-Orians *et al.* 1993; Freeman *et al.* 1976; Lloyd & Webb 1977). Commonly, sex-ratios are male-biased, but female-bias occurs too often to be called an exception (Lloyd & Webb 1977; Opler & Bawa 1978; Dupont & Kato 1999; Williams 1995). Even within a genus, sex-ratios can shift from extreme female- to male-bias (Dupont & Kato 1999).

In willows (*Salix* spp.), female-biased sex-ratios have been described from a wide range of habitats and geographical regions (further examples in Åhman 1997; for review of northern willows see Crawford & Balfour 1990). Differential herbivory has often been invoked to explain this phenomenon (Danell *et al.* 1985; Danell *et al.* 1991; Elmqvist *et al.* 1988; Elmqvist *et al.* 1991; Boecklen *et al.* 1990; Hjältén & Palo 1992; Hjältén 1992). This theory is attractive as it can be deduced from a set of defence theory concepts: female plants have higher reproductive costs *per gamete* (as eggs are bigger than pollen) and have to bear the costs of seed set (Silvertown & Lovett Doust 1994). They are therefore likely to have higher total reproductive costs. These lead to retarded growth, which in turn favours higher investment into anti-herbivore defence (Coley *et al.* 1985; De Jong 1995). Thus, male plants are less well defended than females and hence are preferred by herbivores (Hjältén & Palo 1992).

Support for the idea that differential herbivory causes a female-biased sex ratio in *Salix* ssp. is so far purely descriptive (Danell *et al.* 1991; Elmqvist *et al.* 1988; Boecklen *et al.* 1990). Here, we provide a test of the hypothesis that exclusion of reindeer (*Rangifer tarandus platyrhynchus*) will cause a change in the sex ratio of *Salix polaris* (polar willow). Moreover, we test, if 1. female *Salix* show higher allocation of biomass to reproductive tissue, 2. female *Salix* grow faster than male, and 3. female plants are better defended against herbivores than males.

METHODS

Study Area

The study was carried out in Semmeldalen (77°90N 15°20E), a valley c. 20 km south of Longyearbyen, Svalbard. This and the neighbouring valleys host a population of c. 500 Svalbard reindeer (*Rangifer tarandus platyrhynchus*), which has been closely monitored since 1994 (Irvine *et al.* 1999). Grazing pressure is among the highest in all of Svalbard (Van der Wal & Brooker 2001). Apart from a small number of ptarmigan

(*Lagopus mutus*) and pink-footed geese (*Anser brachyrhynchus*), reindeer are the only vertebrate herbivore in the system.

Two vegetation types are used most intensively by foraging reindeer during the summer: the dry heath (dominated by *Luzula confusa*, *Salix polaris* and the bryophytes *Aulacomnium turgidum*, *Drepanocladus uncinatus* and *Ptilidium ciliare*) and the wetter graminoid dominated communities (*Festuca cryophila*, *Poa* spp., *Salix polaris*, and various bryophytes, for data on soil moisture see Van der Wal *et al.* 2000b). The heath has a thick layer of peat, causing a very soft and dry upper soil horizon, and the graminoid sites have shallow soil, with waterlogged clay on layers of undrained schist. The vegetation cover is lower in the graminoid sites (54 ± 12%, compared to 95 ± 3% in the heath).

Exclosures and Sampling

In July 1997, half way through the growing season, three permanent exclosures (20 × 30 m with 1.5 m high fences) were erected in each of the two vegetation types (heath and graminoid) to prevent grazing by reindeer. The exclosure treatment was randomly assigned to one plot of a matched pair, the other serving as control. *Salix polaris* is the dominant plant species with cover values between 30 and 65% in all sites.

During 24 to 27 July 2000, the sex ratio of *Salix polaris* was assessed in all exclosures and controls. As *Salix* spreads vegetatively (as well as by seed) and its cover is relatively high, a dense system of rhizomes and stems is formed, and it is impossible to distinguish individuals. Therefore 200-300 10x10cm quadrats were placed randomly in each exclosure and control. In each quadrat, the number of male and female inflorescences was counted. Quadrats without any *Salix* were ignored. As many quadrats contained no flowers at all, enough quadrats were assessed to yield at least 40 sexed quadrats per treatment. Male and female inflorescences were in their prime at the time of recording. Their size (c. 0.8 cm in diameter) and scarcity made them very apparent, and a recorded sex bias due to different detection rates can therefore be excluded.

To estimate annual growth of *Salix* c. 20 above-ground branches of *Salix polaris* of each sex were randomly sampled in every treatment. Leaves were separated from the rest of the plant. Stems and flowers were bagged and frozen until used for retrospective growth analysis later (see below). Leaf area for both sexes was assessed using a portable leaf area meter (CI-202; CID Inc., Vancouver, Washington State, USA): 30 leaves were placed together on the measuring surface and scanned five times to yield a stable area estimate.

All leaves were subsequently dried at c. 45°C for seven days and stored for further analysis. Plants were re-dried at 65°C for 24 hours and weighed to the nearest 0.01 milligram. Samples were then ground in a ball mill and analysed colourimetrically for phenolic compounds and tannins following the recommendations of Hagerman (1998): phenolics were determined using the modified Prussian blue assay and are expressed as percentage dry weight on the basis of tannic acid equivalents. Tannins were analysed by employing the acid butanol method, expressing the content as % dry weight on the basis of quebracho equivalents (Hagerman & Butler 1989).

Retrospective Analysis of *Salix polaris* growth

Each year's growth in *Salix polaris* ends in a terminal bud and usually one or two side buds. As the stem grows out of one of the side buds in the next year (all Salix species grow sympodially, Raven 1992), annual segments can be recognised by those bud scars, which encircle the stem.

This was used to measure the length of annual stem growth increments for the current year (= C) and previous years (C-1 … C-6). Stems that showed signs of having been grazed in any of the previous six years were excluded from retrospective analysis. Thus, only five of the c. 20 stems harvested per replicate could actually be used as subsamples.

Current year's production is not only utilised for the growth of this year's segment, but also thickens the segments of previous years. For this reason the total length of stem growth increments per year rather than the volume or the weight of the annual growth increments was used in the statistical analysis. Using total length of all growth increments per branch also takes account of differences in branching pattern (which might be the difference between sexes Sakai & Burris 1985).

Statistics

The analysis of the percentage of quadrats with female plants (per number of plots containing either sex) was performed using the GLIMMIX macro in SAS (SAS Institute Inc. 1989). The module allows the analysis of binomial data from experiments with fixed (vegetation type and exclosure) and random effects (block,

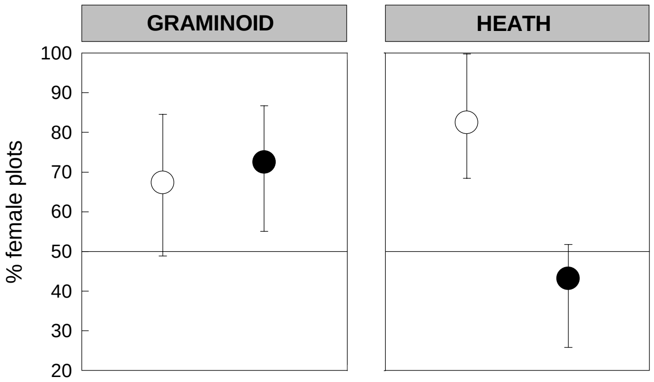

Fig. 1 Sex ratio as percentage of female *Salix polaris* in the two vegetation types in exclosures (●) and grazed controls (○).

quadrat) and nesting (block was nested in vegetation type and quadrat in exclosure). The model used a logit link, i.e. logit(p) = ln(p/(1–p)), where p = proportion of female. Denominator degrees of freedom were computed using the Satterthwaite option.

Measurements of cumulative weight since the erection of the exclosure (stems of C-2, C-1 and C, as well as leaves and inflorescences), leaf and flower weights, leaf characters and levels of secondary defence compounds were analysed using the MIXED procedure of SAS, with the same nesting structure as described above (subsampled branches instead of quadrats, and using stem weight in C-4 as covariate). All measurements were $\log_{10}$-transformed to comply with assumptions of ANOVA (Sokal & Rohlf 1995).

The length of annual stem growth increments was also analysed with the MIXED procedure, but as a repeated measurement (unspecified covariance matrix) for the years 1994 to 2000, with exclosure effects introduced into the model for the data from 1998 onwards. Errors indicated throughout the paper refer to standard error of the mean.

RESULTS

Exclosure effects on sex ratio

The sex ratio in *Salix polaris* was markedly female biased, with an average of 70% female in controls. Exclusion of reindeer caused an even sex ratio of flowers in the heath, but had no

Table 1 Statistical results of the effects of vegetation type and exclosure on the sex-ratio of *Salix polaris*.

effect	NDF	DDF	F	P
vegetation type	1	5	0.04	0.8502
exclosure	1	5	4.78	0.0749
interaction	1	5	10.48	0.0407

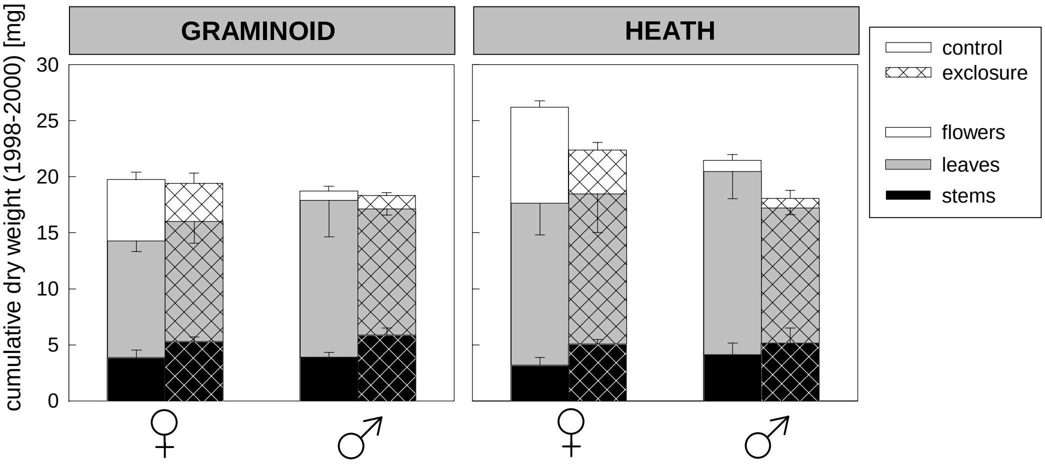

Fig. 2 Cumulative biomass since the erection of exclosures in 1998 for male and female *Salix polaris* in the two vegetation types. Stems (1998-2000) are in black, leaves (2000 only) in grey, and flowers (2000 only) in white.

effect in the graminoid community (Fig. 1, Table 1).

Exclosure effects on reproductive allocation

Female plants invested more into reproductive tissue than males ($F_{1,\ 12} = 66.55$, $P < 0.001$; Fig. 2). In controls, flower biomass per branch was eight times that of males, whilst in exclosures it was four times as much (sex × exclosure: $F_{1,\ 14} = 6.78$, $P < 0.05$).

Both the average number of flowers per current years's growth and the weight of the individual flower was higher for females (Table 4). Flower weight was neither related to the total weight of stem or this years stem growth nor to the weight of leaves ($P > 0.5$).

Table 2 Statistical results for cumulative biomass since reindeer exclusion (1998-2000), using the weight of the annual growth increment in 1996 as covariate.

Effect	NDF	DDF	F	*P*
weight 1996	1	101	27.92	0.0001
vegetation type	1	4	1.30	0.3145
exclosure	1	6	4.78	0.0719
sex	1	117	6.80	0.0103

Exclosure effects on growth

Cumulative biomass and leaf characteristics

Cumulative biomass of 1998-2000 differed significantly between sexes

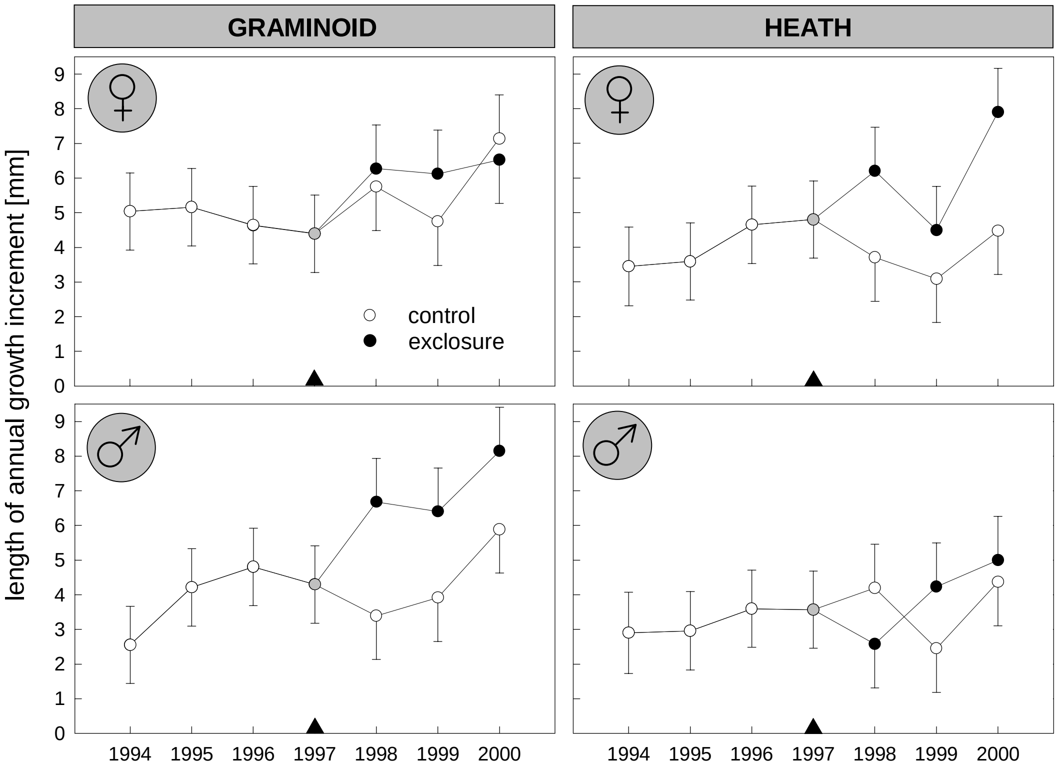

Fig. 3 Length of annual growth increments (1994 - 2000) for the two vegetation types and sexes. Exclosures were erected in 1997 (triangle).

(Fig. 2, Table 2); the total weight of females being slightly higher than that of males. Exclosures reduced total biomass in both sexes, but this effect was only marginally significant (Table 2, Fig. 2).

No difference between sexes with respect to total leaf biomass could be detected (Fig. 2). Reindeer exclusion reduced leaf biomass marginally ($F_{1,\,6} = 4.87$, $P = 0.0724$). The number of leaves per branch did not differ between sexes, treatments or vegetation types (1.62 ± 0.031; N = 24). The average weight of an individual leaf was significantly affected by the interaction of sex and exclosure. This is due to leaves of male *Salix polaris* inside the exclosures being lighter than outside (Table 4). No main effect of vegetation type, sex or exclosure was detectable ($P > 0.15$ for all factors).

Leaf area per leaf differed between sexes, with female leaves being bigger than male leaves. Sexes responded differently to the exclosures, in that the exclusion of reindeer caused an increase in the leaf area of female plants, but a decrease in male plants (Table 4). There were no detectable differences between vegetation types. Leaf area ratio was similar for both sexes, irrespective of vegetation type and exclosure ($0.126 \pm 0.004\ \mathrm{cm^2 \cdot mg^{-1}}$, N = 24, $P > 0.16$ for all factors).

Table 3 Statistical results from the analysis of the length of annual growth increments. Data were $\log_{10}$-transformed prior to analysis.

Source	**NDF**	**DDF**	**F**	***P***
vegetation type	1	1	1.12	0.5744
exclosure	1	169	10.72	0.0013
sex	1	10	1.37	0.2692
year	6	225	4.89	0.0001
vegetation type × sex	1	9	0.27	0.6160
vegetation type × exclosure	1	262	0.28	0.5974
sex×exclosure	1	275	0.19	0.6657
vegetation type × sex × exclosure	1	262	2.98	0.0855

Retrospective growth analysis

The annual stem growth (i.e. length of annual growth increment) did not differ consistently between sexes (Table 3). There were pronounced interannual variations, which were common to both sexes in both vegetation types (Fig. 3). Reindeer exclusion led to significantly longer annual growth increments (Table 3, Fig. 3). The marginally significant three-way-interaction of vegetation type, sex and exclosure (Table 3) indicates the tendency of females to profit from herbivore exclusion in the heath, but of males to profit in the graminoid community.

A preliminary attempt to relate variations in annual stem growth to summer temperature or summer precipitation revealed no significant pattern.

Exclosure effects on defence

The phenolic content of *Salix polaris* leaves did not differ between sexes ($P > 0.42$). It was significantly higher in exclosures than in controls (exclosure: 11.29 ± 0.39 %dry weight; control: 10.26 ± 0.25 %; $F_{1, 6} = 6.33$, $P < 0.05$; Fig. 4). No difference related to vegetation type could be detected ($P > 0.35$).

Condensed tannin and phenolic content were significantly positively correlated (Pearson correlation coefficient $r = 0.598$, $P < 0.05$). However, concentrations of condensed tannins did not differ significantly between sexes, exclosure/control or vegetation types (12.99 ± 0.33 %dry weight; $P > 0.26$; Fig. 4). Following the computation of Cohen (1969) and the tables in Zar (1996), the minimal detectable

Table 4 Leaf and flower characteristics of male and female *Salix polaris* in the two vegetation types inside and outside the exclosures (± standard error). Differences due to vegetation type was never significant, and the statistics given refer to the pooled data for graminoid and heath. When main effects or interactions are not indicated, they were not significant. * and ** refer to $P < 0.05$ and $P < 0.01$, respectively.

		control		**exclosure**		**statistics**
		female	male	female	male	
leaf mass [mg/leaf]	*graminoids*	3.056 ± 0.085	3.838 ± 0.770	3.490 ± 0.229	2.788 ± 0.300	
	heath	4.038 ± 0.766	3.986 ± 0.413	3.737 ± 0.085	2.750 ± 0.137	sex × exclosure: $F_{1, 10} = 6.34$*
leaf area [cm^2]	*graminoids*	0.381 ± 0.039	0.410 ± 0.065	0.472 ± 0.041	0.371 ± 0.046	sex: $F_{1, 10} = 5.00$*
	heath	0.471 ± 0.080	0.488 ± 0.065	0.516 ± 0.042	0.344 ± 0.030	sex × exclosure: $F_{1, 10} = 9.71$**
# flowers[1]	*graminoids*	0.424 ± 0.024	0.322 ± 0.108	0.538 ± 0.142	0.311 ± 0.059	
	heath	0.511 ± 0.059	0.333 ± 0.139	0.503 ± 0.072	0.244 ± 0.124	sex: $F_{1, 11} = 13.84$**
flower dry weight [mg]	*graminoids*	0.907 ± 0.249	1.544 ± 0.026	0.539 ± 0.089	1.324 ± 0.203	
	heath	2.084 ± 0.584	0.835 ± 0.255	0.835 ± 0.255	1.902 ± 0.146	sex: $F_{1, 11} = 7.85$*

[1] per current year's growth

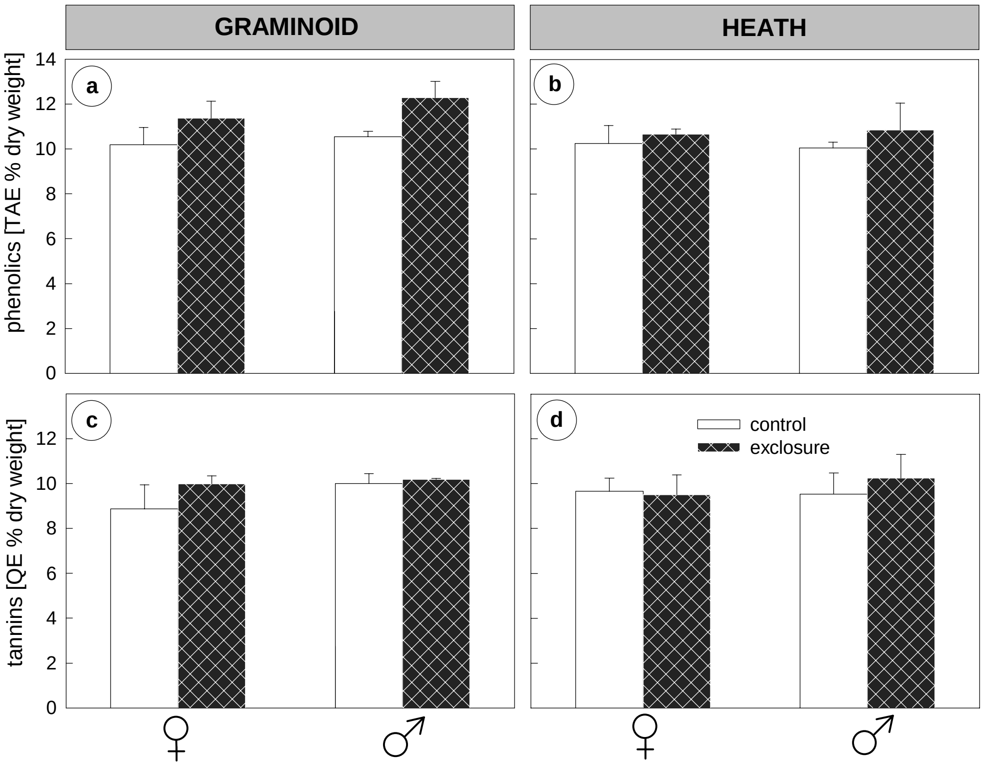

Fig. 4 Defence characteristics of *Salix polaris* leaves: Total phenolics in tannic acid equivalents (TAE; a and b) and condensed tannins in quebracho equivalents (QE; c and d) for the two sexes and vegetation types.

difference at $P = 0.05$ for condensed tannins would have been 1.2 %dry weight, i.e. about twice the maximal difference measured (Fig. 4). The sensitivity of the analysis being this high it is safe to assume that sexes did not differ in the defence types assessed.

DISCUSSION

Our results are only partly consistent with the hypothesis that the female biased sex ratio in willows is caused by herbivory. In one vegetation type (heath) the sex ratio of flowers changed in favour of the male sex, while in the other (graminoid) it did not. Female plants of *Salix polaris* showed a higher allocation of biomass to reproduction, consistent with expectations. Nevertheless female plants had significantly higher biomass than males. Considering only vegetative growth, no difference between sexes could detected. Also the last point of the chain of explanations had to be rejected in our study: no difference in phenolic or tannin content of leaves could be found. Thus while the sex ratio in reindeer exclosures changed according to the prediction of the hypothesis, the mechanism behind this remains obscure.

Growth, defence and herbivory in *Salix*

The seven *Salix* species, for which growth and defence or herbivory have been assessed in relation to gender (*Salix myrsinifolia-phylicifolia*: Danell *et al.* 1985, 1991, Elmqvist *et al.* 1988; *Salix cinerea*: Alliende 1989; *Salix lasiolepis*: Price *et al.* 1989, Boecklen *et al.* 1990; *Salix rigida*: Elmqvist *et al.* 1991; *Salix sericea*: Nichols-Orians *et al.* 1993; *Salix viminalis*: Åhman 1997; *Salix polaris*: this study) show no consistent gender-related pattern (Åhman 1997). In two species (*S. rigida* and *S. lasiolepis*) females grew slower than males and were better defended. In three species (*S. cinerea, S. myrsinifolia-phylicifolia* and *S. sericea*) no growth difference was detected, but nonetheless females were better defended. In *S. viminalis* neither growth nor herbivory intensity were different between sexes, and in our study females grew better, but were as well defended as males. Thus, overall there seems to be a tendency for female *Salix* to be better defended than males (5 out of 7 species; Palo 1984), but not to grow more slowly (2 out of 7).

The idea that slower growing plants should be defended better than faster growing ones was derived from a comparison of tropical tree species (Coley *et al.* 1985; Coley 1987), but on theoretical grounds the idea has also been extended to within species comparisons (e.g. De Jong 1995). Growth differences between male and female plants are generally much smaller than between species, and thus it is not surprising that so far it has proved difficult to show that gender-related differences in defence actually cause a reduction of herbivory on the slower growing sex (for a successful example see Jing & Coley 1990).

Another problem lies in the fact that a difference in defence investment might not lead to differences in herbivory experienced. Boecklen *et al.* (1994) could show that different herbivores show different patterns in plant usage, the sum of which does not relate to plant sex, while defence investment does (Boecklen *et al.* 1990). With only one herbivore in the system investigated here, this is of little implication.

Ecophysiological differences between sexes

Biased sex ratios may be caused by differential drought or salinity tolerance (Freeman *et al.* 1976), photosynthesis or water use efficiency (Dawson & Bliss 1989; Crawford & Balfour 1983; Jones *et al.* 1999), pH or phosphate preferences (Cox 1981). These examples stem from studies of distribution pattern along environmental gradients, however the mechanisms behind biased sex ratios remain unclear.

For many dioecious species a spatial segregation of the sexes has been described: along an ecological gradient female plants were often found at the more benign end (e.g. Freeman *et al.* 1976; Cox 1981). Dawson & Bliss (1989) describe male *Salix arctica* to be more flexible in their water use and seemingly adapted to drier microsites than female plants, which have a higher water use efficiency. For the same species, Jones *et al.* (1999) report gender- and habitat-specific responses to simulated environmental change. However quite often no ecological cause for a bias in sex ratio can be found (Dupont & Kato 1999; Williams 1995). No such research has yet been carried out on *Salix polaris*, but Crawford & Balfour (1983) report a higher range of leaf resistance for female plants, concluding that females are trying to reduce water losses more than males (Retuerto *et al.* 2000).

One ecological argument for niche separation between sexes is founded on resource limitation of reproduction for female plants and female flower-limitation of reproduction for male (Silvertown & Lovett Doust 1994). Natural selection might thus favour females with a competitive dominance over males, leading to higher female abundance in resource-rich sites (Freeman *et al.* 1976; Crawford & Balfour 1983). On the other hand this could mean that under common conditions growth might be the same for both sexes, and their response to (simulated) herbivory might not differ (Houle 1999).

In this study male and female *Salix polaris* co-occured at the same sites, at least at the scale of the exclosure (20 × 30 m). At the scale of the sampling quadrat (0.1 × 0.1 m), however, the sexes were separated: only 27 out of 498 quadrats (5.4 %) in which the sex of *Salix polaris* was assessed contained flowers of both sexes. There was no detectable pattern of spatial segregation with respect to exclosures and vegetation type. If spatial segregation of the sexes is also true on larger scales, this would be evidence for intersexual competition, with females plants displacing the subdominant males. As it is uncertain which area is covered by a single individual plant, spatial segregation at the very small scale cannot be ascribed solely to niche separation between the sexes, but is confounded by individual size.

Causes of female biased sex ratio in *Salix polaris*

In contrast to most other *Salix* species, the female bias in sex ratio of *S. polaris* seen in this study could be explained by the higher productivity (i.e. total above-ground biomass produced) of female plants, which again might be caused by a microsite separation between the sexes. That the higher biomass productivity is entirely used for reproduction (Fig. 2), supports the idea that females occupy more benign sites in order to match their additional cost of reproduction (“Jack-the-Sprat-effect”: Cox 1981).

Nevertheless herbivory is apparently important for creating or maintaining the female-biased sex ratio, otherwise there would not be any exclosure effect. However, this effect is confined to the dry heath sites, and some sort of indirect herbivore control seems to influence the abundance of male and female flowers in the heath (Väre *et al.* 1996). On the other hand, grazing pressure in the graminoid community is also lower than in the heath (Christina Skarpe, personal observation), and an effect of herbivore exclusion might become apparent in the longer term.

Surprisingly, the exclosures in the heath (and to a lesser extend in the graminoid community as well) led to lower inflorescence biomass compared to controls. This was probably caused by the increase in stem length, which diverted the assimilates from the flowers. The increase in stem length, then, might be interpreted as a response to taller growing surrounding vegetation (mosses in particular), over which *Salix polaris* has to position its leaves. A reduced inflorescence biomass might hence be a result of competition for light in a denser and taller ungrazed and untrampled vegetation.

The role of defence compounds in this context remains unclear. The significant *increase* in phenolic content in the exclosures suggests that defense is a constitutive character of *Salix polaris*. According to Bryant and Reichardt (1992), herbivory on slow growing species leads to a carbon limitation of growth. Roots still take up nitrogen, but as leaf area is reduced, carbon is in short supply. As phenolics and proteins compete for the same precursor (Jones & Hartley 1999), phenolic production is reduced in favour of proteins and hence leaf growth. Inside exclosures nitrogen will be limiting, leading to the production of secondary compounds in an overflow reaction (Hartley & Jones 1997).

That *Salix polaris* has such high phenolic and condensed tannin contents is indicative of their importance for the plant. While phenolics also serve as UV-B absorbants and protectors against fungal infections, tannins seem to function primarily as grazing deterrents (Harborne 1991; Zucker 1983). To our knowledge no specialist herbivorous insect exists on Svalbard, so that the defence can be assume to be directed towards reindeer.

An alternative explanation to the observed pattern is a differential response of male and female plants to the cessation of grazing, leading to an increase in flowering in males, but not in females. This would, however, not explain the skewed sex ratio in the controls, or the difference in response in the two vegetation types. Moreover, Houlé (1999) found no evidence for differential response of sexes to defoliation treatments.

Conclusion

The hypothesis that the female-biased sex ratio of *Salix polaris* is caused by herbivory was supported in one vegetation type, but refuted for the other. Moreover, the mechanism of growth rate dependent defence was not applicable, and therefore the link between sex and preference to reindeer remains obscure. The different results for the two vegetation types indicate that abiotic environmental factors such as soil moisture or nutrient availability might play a role as well.

ACKNOWLEDGEMENT

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CHAPTER 8

CONSEQUENCES OF MANIPULATIONS IN CARBON AND NITROGEN SUPPLY FOR CONCENTRATION OF ANTI-HERBIVORE DEFENCE COMPOUNDS IN *SALIX POLARIS*

Abstract The concentration of carbon-based anti-herbivore defence compounds is key to herbivore utilisation of forage. Production of phenolics and condensed tannins in boreal woody plants are known to reduce grazing pressure. Their production depends, among others, on the availability of nutrient resources, especially nitrogen, relative to the availability of assimilates. The carbon-nutrient balance hypothesis (Bryant *et al.* 1983) predicts a decrease in the concentration of carbon-based defence compounds with increased availability of nutrients. In a High Arctic heath, I manipulated the carbon-nitrogen balance of Polar Willow (*Salix polaris*) in a factorial, multi-level fertilising and shading experiment. Additionally, other plots were subject to elevated temperature. After two years, shading and, to a lesser extend, fertilisation had caused an increase in nitrogen concentrations of the leaves, which were highly and negatively correlated with lower phenolic and condensed tannin concentrations. Elevated temperature caused no such effects, but increased growth significantly, while shading reduced shoot biomass, and fertilisation had no detectable effect. These results are consistent with the CNB-hypothesis. It is unlikely, however, that environmental changes due to Global Climate Change will have a major impact on defence chemistry, as very high shading (> 70%) and fertilisation levels (> 1.5 $g \cdot m^{-2} \cdot y^{-1}$) were needed to produce significant deviations from controls.

INTRODUCTION

The consequences of Global Climate Change are predicted to be especially pronounced in the Arctic (Intergovernmental Panel on Climate Change 1990; 1998), specifically elevated temperatures by several degrees and increases in cloudiness and precipitation. In various field experiments it has been shown that warming, increased nutrient availability and light attenuation will affect plant growth (reviewed in Dormann & Woodin 2001). Much less is known about the consequences of environmental changes on plant chemistry. In particular with respect to substances important to herbivores, such as nitrogen and grazing deterrents like phenolics and tannins, our ecological understanding is poor. Chapin *et al.* (1986a) have been able to show how nitrogen and sugar fractions of tundra plants vary across the season, and Laine & Henttonen (1987) have tried to relate interannual differences in microtine density to weather-induced differences in phenolic and nitrogen content of blueberry (*Vaccinium vitis-idaea*). Data on the effects of environmental manipulations on defence chemistry are virtually absent for the High Arctic, however (for an exception see Van der Wal *et al.* 2000c).

The anti-herbivore defence of woody arctic plants is generally carbon-based (Bryant & Kuropat 1980; Bryant *et al.* 1991b), probably because nitrogen is the limiting nutrient in these systems (Shaver & Chapin 1986) and nitrogen-based defence is thus too costly (Chapin 1989). It has been proposed (Bryant *et al.* 1983) that growth limitations due to low nutrient availability lead to a relative surplus of assimilates, which is then invested into carbon-based defence as a “carbon overflow” mechanism (for a review see Hartley & Jones 1997). Consequently, major changes in the balance of carbon and nutrient would lead to changes in the amount of carbon-based defence (Bryant *et al.* 1983).

Global climate change will influence carbon assimilation (e.g. shading due to increased cloud cover) and nutrient supply (e.g. fertilisation through increased mineralisation in warmed soils, Nadelhoffer *et al.* 1991). Consequently both shading and fertilisation should increase the availability of the limiting nutrient nitrogen relative to carbon, but decrease carbon-based secondary compounds. However, elevated air temperature may lead to an increase in carbon assimilation, as photosynthesis of arctic plants is sensitive even to small increases in air temperature (Larcher 1995), while it may also increase nutrient mineralisation, therefore providing more nitrogen to the plant. The net effect on defence chemistry will depend on the relative magnitude of the environmental changes and the foliar chemistry responses to them.

This study investigates the consequences of the manipulation of light, nutrient availability and temperature on the concentrations of nitrogen, phenolics and condensed tannins in the leaves of *Salix polaris*. By varying shade and fertilisation at four levels in a factorial design, a whole range of different carbon-nitrogen ratios is created, enabling an estimation of the sensitivity of anti-herbivore defence in *Salix polaris* to changes in the environmental factors manipulated. The experiment also allows us to discuss various defence allocation hypotheses differing in their predictions of the effects of carbon-nitrogen imbalances.

METHODS

The study was carried out in Semmeldalen, Svalbard (77.90 °N 15.20 °E), a valley c. 20 km south of Longyearbyen, Svalbard. All experimental plots were situated in a representative patch of *Salix polaris*-heath (Rønning 1996), over an area of c. 100 by 50 m. The whole site was enclosed by an electric fence to prevent disturbance by reindeer.

Shading × fertilisation experiment

Plots of 0.5 by 1m were established in early June 1999. Treatments consisted of a full-factorial combination of four levels of fertiliser (0, 0.5, 1.5 and 5 gN m^{-2} a^{-1}) and four levels of shading (0, 53, 72 and 83%). Each treatment was replicated three times, and replicates were arranged in a randomised block design. The fertiliser (ammonium nitrate, dissolved in 2 l of water per plot) was applied in rain on five occasions during the growing seasons of 1999 and 2000. Shading was attained by placing a wire-based shading frame with one, two or three layers of optically neutral greenhouse shading cloth (B&Q, U.K.) over the plot, reducing both direct and diffuse radiation into the plots.

Light availability under the shading frames was measured with a deltaT microvolt integrator fitted with a PAR photosensor (deltaT, Cambridge, U.K.). Air temperature at soil level was recorded with a RS temperature data logger (Radio Supply, U.K.), recording hourly over the whole experimental period. Soil water content was measured with a soil conductivity insertion probe (SCIP, CEH Wallingford, U.K.) on 15.6., 28.6., 1.8. and 27.8.1999, and 28.7.2000.

At the end of each season all shoots from a 25 × 25 cm square were counted and harvested from each treatment plot for determination of *Salix polaris* leaf biomass. Dead leaves were manually sorted and discarded, green leaves were counted, shoots and leaves were dried at c. 45ºC for one week, transported back into the lab and re-dried before weighing. Leaves were then ground and analysed for total carbon and nitrogen using a CNS autoanalyser (Fisons, U.K.). Phenolic content of leaves were measured following the modified Prussian blue assay using tannic acid as standard and condensed tannins by the acid butanol method using purified quebracho tannin as standard (Hagerman 1998).

Elevated air temperature experiment

15 pairs of plots (60 cm diameter) were carefully selected. The experiment consisted of warmed plots and controls, randomly assigned to the paired plots. Treatment plots were subjected to warming over most of the growing season in 1999, beginning on the 16.6.1999, i.e. about ten days after snowmelt, to 29.8.1999, and over the whole snowfree period in 2000 from 14.6.2000 until harvest (1.8.2000). Greenhouses of a modified “cloche” type (Strathdee & Bale 1993) were used to raise air temperature. They consisted of an open cylinder (∅ 57 cm, height 45 cm) made of a sheet of transparent plastic, with a thin, optically neutral polyester gauze as a roof. For further details see chapter 5. Leaf material was sampled only in 2000 and treated the same way as mentioned above.

Statistical Analysis

All data were analysed with the GLM procedure of SAS (SAS Institute Inc. 1989), using block as random factor and treatments fixed effects. To separate treatment from year effects, years were analysed separately for the shading-fertilisation experiment. The interaction of shading and fertilisation was never significant at $P < 0.1$ and thus removed from the statistical model. Shoot biomass was used as a covariate to correct for concentration or dilution effects of reduced or increased growth, respectively (Koricheva 1999).

Table 1 Environmental variable responses to shading. Temperature measurements are not replicated, values in brackets are standard deviation over the experimental period, degreedays are number of days above 0ºC. Soil water content (% water content) is given with standard errors in brackets (N = 12, due to pooling of fertilisation treatments). There is a significant effect of shading on soil water content ($F_{3, 218} = 3.75$, $P < 0.05$), which is also dependent on the date of measure (interaction: $F_{12, 218} = 12.18$, $P < 0.001$).

	shade	**0%**	**53%**	**72%**	**83%**
Temperature	mean	8.9 (5.9)	9.1 (5.0)	7.6 (4.5)	7.6 (4.6)
	degreedays	629	660	554	552
Soil	15.6.1999	23.3 (1.06)	24.4 (1.47)	26.8 (1.44)	26.6 (0.99)
water	28.6.1999	27.7 (1.45)	27.5 (1.62)	28.5 (0.79)	27.8 (0.66)
content	1.8.1999	18.6 (1.32)	18.0 (1.01)	18.7 (0.92)	18.8 (0.59)
	27.8.1999	19.6 (1.37)	19.5 (1.21)	20.3 (0.86)	20.0 (0.84)
	28.7.2000	20.2 (1.16)	23.1 (0.87)	23.7 (0.63)	25.1 (1.37)

RESULTS

Environmental parameters

Temperatures were altered by shading cloth (Table 1). Both 73 and 82% shading plots were c. 1.3°C cooler than ambient, while the 53% shading treatment caused slight warming. This led to a cumulative temperature difference in degreedays compared to control of +5% for the 53% shading and –12% for the 72 and 83% shading treatments. Shading treatments differed only little in soil water content on any of the four dates (Table 1). An effect of shading on soil water content was detectable, but more pronounced on wet days (Table 1). It was however lower than the variability over time. Fertilisation had no detectable effect on soil water content.

Air temperature in the greenhouses was on average 2.3°C higher than in controls (11.8 °C vs. 9.5 °C; $F_{1, 3288} = 103.2$, $P < 0.0001$). Soil water content at sampling date was significantly lower under elevated temperature (18.7 ± 2.00 %vol vs. 22.6 ± 1.78 %vol; $F_{1, 28} = 8.64$, $P < 0.01$).

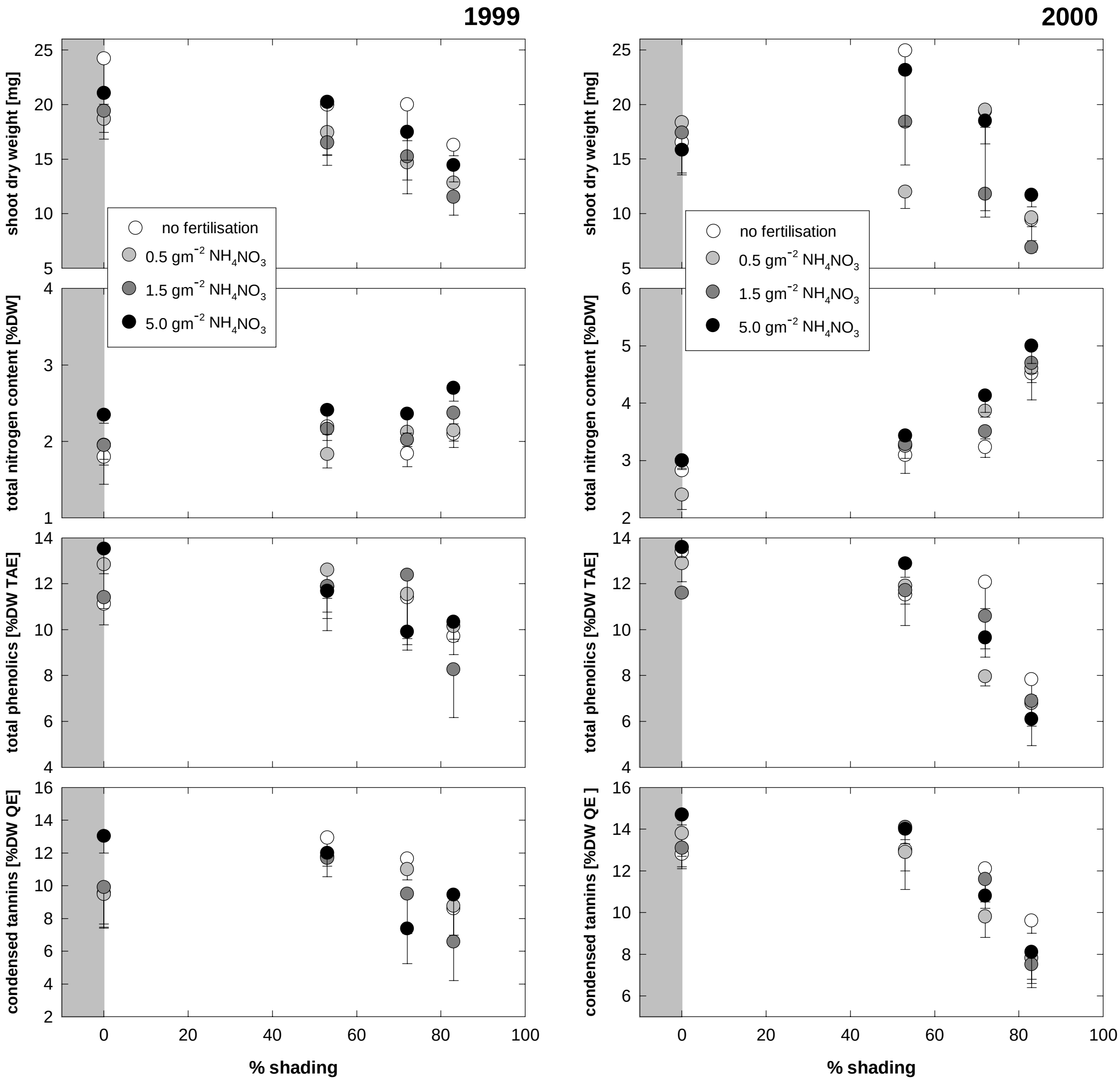

Fig. 1 Shoot biomass, leaf nitrogen, phenolic and condensed tannin content of *Salix polaris* in the four shading treatments in a) 1999 and b) 2000. Shading of points indicates level of fertilisation. Error bars indicate –1 SE.

Shading × fertilisation experiment

Shoot biomass

Above-ground shoot biomass was significantly reduced in shaded treatments in both years (Fig. 1, Table 2). However, this decrease becomes apparent only at the highest level of shading. Fertilisation surprisingly had a transient negative effect on shoot biomass in the first season (Fig. 1a), which disappeared in the second (Fig. 1b, Table 2).

Table 2 Statistial results of treatment effects on shoot biomass, nitrogen content and phenolic and condensed tannin content of *Salix polaris*.

			Shoot biomass			**Nitrogen**			**Phenolics**			**Condensed tannins**		
	factor	**df**	**MS**	**F**	***P***	**MS**	**F**	***P***	**MS**	**F**	***P***	**MS**	**F**	***P***
1999	block	2	65.96	5.40	0.009	1.098	5.40	0.039	28.56	4.83	0.040	43.99	8.41	0.006
	biomass	1	--	--	--	0.603	4.23	0.022	10.66	2.11	0.136	4.29	0.80	0.458
	shading	3	106.46	8.72	0.000	1.312	9.21	0.000	16.75	3.31	0.031	5.91	1.10	0.361
	fertilisation	3	53.22	4.36	0.010	0.088	0.61	0.610	0.71	0.14	0.936	3.85	0.72	0.548
	error	38	12.21			0.143			5.06			5.37		
2000	block	2	133.08	5.16	0.010	6.240	21.75	0.004	76.11	26.62	0.000	34.12	12.77	0.006
	biomass	1	--	--	--	1.233	8.88	0.001	5.23	2.10	0.136	9.23	5.61	0.007
	shading	3	235.40	9.14	0.000	5.240	37.74	0.000	56.36	22.65	0.000	25.20	15.31	0.000
	fertilisation	3	41.00	1.59	0.207	0.509	3.67	0.020	4.11	1.65	0.193	0.72	0.44	0.726
	error	38	25.77			0.139			2.49			1.65		

Nitrogen and carbon content of leaves

Nitrogen content of leaves was significantly correlated with shoot biomass, both in 1999 and in 2000 (r = –0.305, $P < 0.05$ and r = –0.447, $P < 0.001$; Pearson correlation), indicating that some leaves had a lower N-content simply because they were heavier (dilution by growth). To correct for this (Koricheva 1999), shoot weight was used as covariate in the analysis (see Table 2).

Salix polaris exhibited a significant increase in nitrogen content in response to shading in both years (Table 2). However, in 1999 this increase can only be observed at the highest level of shading, while in 2000 it is a pervasive trend, leading up to a 100% increase in leaf-N in fertilised plus shaded plots (Fig. 1). In 2000 the fertilisation treatment also caused a significant increase in leaf nitrogen content (Fig. 1b, Table 2). Leaf nitrogen levels were higher in 2000 due to differences in phenological stage at the date of sampling. This took place a week earlier, and the season began about one week later, resulting in a phenological difference between the 1999 and 2000 sampling of almost two weeks.

Leaf carbon content was less responsive than leaf nitrogen: only in the second year was shading significant ($F_{3,\ 39} = 4.76$, $P < 0.01$), while fertilisation was never significant. The actual difference between shaded and control plots was very small, however (control: 47.1 ± 0.36%; 85% shading: 46.1 ± 0.32%).

Defence chemistry

Levels of anti-herbivore defence were generally high, with phenolics at c. 14 %dry weight tannic acid equivalents (TAE) and condensed tannins at c. 13 %dry weight quebracho equivalents (QE). As for nitrogen, phenolic and condensed tannin concentrations were significantly but positively correlated with shoot biomass in both years, and shoot biomass was used as covariate in the statistical analysis (Table 2).

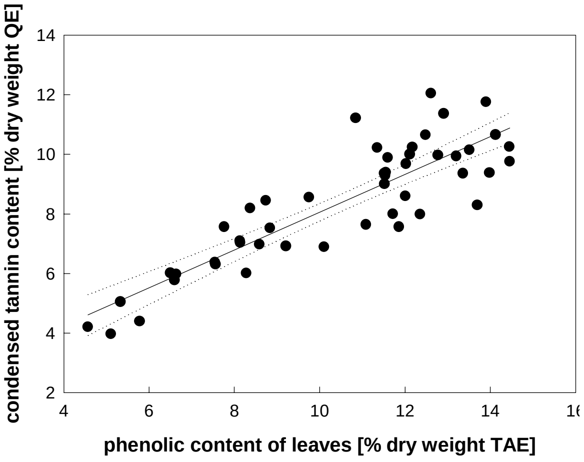

Fig. 2 Correlation plot of phenolic and condensed tannin content in 2000. Regression equation for the indicated line (and 95% confidence limits) is $y = 1.708 + 0.635 \cdot x$, $R^2 =$

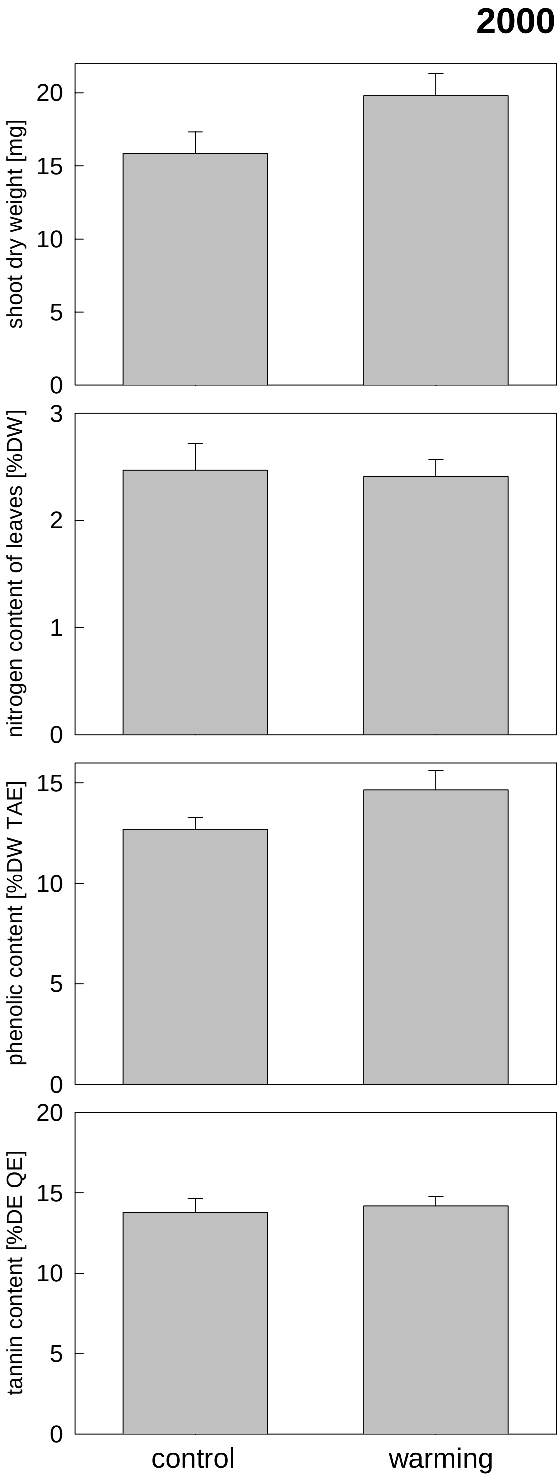

Fig. 3 Effect of elevated air temperature on shoot biomass, leaf nitrogen, phenolic and condensed tannin content of *Salix polaris*.

Phenolic concentrations showed too much treatment-independent variation in 1999 to detect significant effects of shading or fertilisation, although the highest level of shading seems to cause a decrease (Fig. 1). In 2000, this became much clearer, and the effect of shading was consistent over all treatment levels (Fig. 1; Table 2), indicating an over-proportional reduction of phenolics with increasing shading. It reduced levels of phenolics to a miniumum of 50% of controls. Fertilisation had no detectable impact in either of the two years (Table 2).

The concentration of condensed tannins followed much the same pattern as phenolics (Fig. 1). However here the shading effect is significant for both years (Table 2). Again, fertilisation was without consistent effect.

The similarity between the responses of phenolics and condensed tannins is reflected in a very high correlation for 2000 (r = 0.871, $P < 0.001$; Fig. 2), while this correlation was not apparent in 1999 (r = 0.149, $P = 0.322$).

Elevated air temperature experiment

Shoots in the warmed plots grew significantly heavier than in controls (F1, 14 = 5.99, $P < 0.05$; Fig. 3). However, nitrogen, carbon, phenolic and tannin content of leaves (Fig. 3) were not significantly altered by the manipulation of air temperature ($P > 0.56$ for all comparisons). Here, no significant correlation between shoot weight and chemical properties could be detected ($P > 0.42$ for all co-variate regressions), indicating that growth was not causing a dilution of either nitrogen or defence compounds.

DISCUSSION

As predicted by the CNB-hypothesis (Bryant *et al.* 1983), carbon-based defence compounds decreased as a function of nitrogen content (Fig. 4). Manipulating shading and fertilisation increased nitrogen concentrations in *Salix polaris*, leaves. Shoot biomass explained some of the variation in defence concentrations, but nitrogen content was much more important (on average 20% of variance in defence explained by shoot weight and 60% by N content; as both factors were correlated [$r = -0.447$, $P < 0.001$, i.e. lighter shoot have higher N content] nitrogen content as covariate reduced the importance of shoot weight to a non significant level when both factors were included). The low light availability presumably led to a carbon limitation of growth, which the plants tried to compensate by a higher amount of assimilation-linked proteins (such as RubisCO) in their leaves (Bryant *et al.* 1983). It has been shown that a higher leaf nitrogen concentration is correlated with a higher photosynthesis (Field & Mooney 1986; Price *et al.* 1989; Baddeley *et al.* 1994). This explains the increased N content of the leaves with shading. As for the decrease in the concentration of defence compounds, the CNB hypothesis suggests a higher priority for allocation of newly assimilated carbon to leaf growth to overcome the carbon limitation than for defence. On the other hand, since defence concentrations of both compound groups measured here stay constant over a wide range of light conditions, *Salix polaris* appears able to buffer much of the treatment perturbation. Moreover, fertilisation could not cause any change in the defence concentrations, despite a significant effect on growth in the first and nitrogen content in the second season. This hints again at a high buffering capacity, a high priority of maintaining the high defence levels or a high level of carbon surplus.

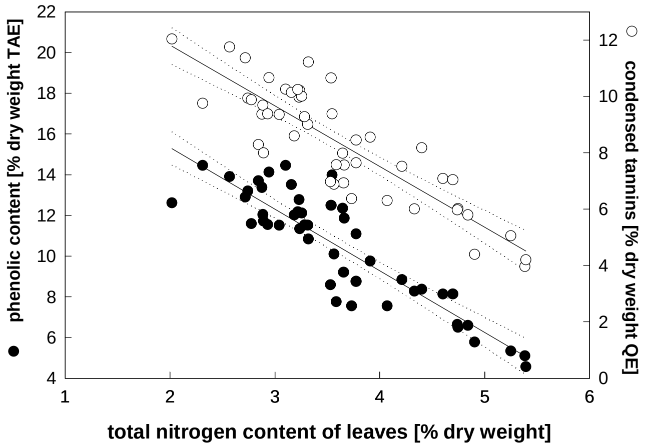

Fig. 4 Correlation of phenolic and condensed tannin content on leaf nitrogen content in 2000. Regression equation for the indicated line (and 95% confidence limits) is $y = 21.41 - 3.03 \cdot x$, $R^2 = 0.791$ for phenolics and $y = 16.12 - 2.15 \cdot x$, $R^2 = 0.749$ for condensed tannins.

A test of hypotheses

In this study I measured concentrations of two groups of carbon-based secondary compounds, both common and widespread in woody plants (Harborne 1991; Zucker 1983). Although both groups are extremely heterogeneous and consist of many different compounds, assessing their response to treatment conditions is a useful way of understanding defence allocation. Firstly, because sometimes the decrease in one type of phenolic is compensated by the increase in another type (Hartley & Jones 1997), individual phenolic glycoside concentrations do not indicate the net effect. This is even more true for species where not all types of compounds are known. Secondly, this same compensatory mechanism might also be acting across classes of defence types (e.g. tannins, phenolics, terpenoids) and thus measurements of more than one substance class is required. Thirdly, phenolics and condensed tannins belong to the best-investigated defence compound classes, and the comparison with other studies may thus lead to further generalisations.

The high correlation between the responses of phenolics and condensed tannins suggests that the mechanism governing their production may use the same clues. This was predicted by the protein-competition-models (Jones & Hartley 1999), as condensed tannins, phenolics and many proteins share the amino acid phenylalanine as precursor.

Tests of the carbon/nutrient balance hypothesis (reviewed in Herms & Mattson 1992; Hartley & Jones 1997; Koricheva *et al.* 1998) have shown the following pattern: different ways of manipulating CNB (fertilisation, shading, elevated CO_2) lead to different consequences (e.g. hardly any effects of drought, Koricheva *et al.* 1998). Moreover, different secondary compounds also respond differently, with monoterpenes being generally unresponsive, while data on condensed tannins and phenolics often support the CNB hypothesis. Our results do not support the conclusion that "plants of extremely low nutrient environments tend to be unresponsive", compared to fast growing species (Hartley & Jones 1997, p. 307). This could be due to an insufficient range of experimental conditions in previous experiments, which did not include the intensity leading to significant changes in our study (see Fig. 2).

With respect to the manipulation of light availability and fertilisation, most recent studies lend support to the CNB, despite its intellectually unsatisfactory lack of foundation in plant physiology (Hamilton *et al.* 2001). The increase in phenolics and condensed tannins with light intensity led Mole *et al.* (1988) to suggest an overflow mechanism for the production of carbon-based defence. For arroyo willow (*Salix lasiolepis*) fertilisation effects followed the predictions of the CNB hypothesis(Price *et al.* 1989). Both fertilisation and shading treatments caused an increase in nitrogen and decrease in phenolics and tannins in Sitka spruce (*Picea sitchensis*), but had no significant effect on nitrogen ($P = 0.07$), phenolics and lignin in heather (*Calluna vulgaris*) (Hartley *et al.* 1995; but see Iason & Hester 1993). Gebauer *et al.* (1998) report a significant decrease in phenolics and tannins with higher level of fertilisation loblolly pine (*Pinus taeda*), but provide no data on nitrogen content. Low light intensities significantly affected leaf concentrations of nitrogen, condensed tannins and phenolics in quaking aspen (*Populus tremuloides*) (Hemming & Lindroth 1999). Moreover, concentrations of condensed tannins correlated with nitrogen content, but not with that of phenolic glycosides. This study is also the only I am aware of that found synergistic effects of shading and fertilisation on any defence compound, in this case condensed tannins (Hemming & Lindroth 1999). That these changes in defence chemistry also translate into preference by herbivores is shown in the example of moose (*Alces alces*) grazing shaded and fertilised Scots pine more than controls (Edenius 1993) or Orkney vole (*Microtus arvensis orcadensis*) consuming preferably treated Sitka spruce (Hartley *et al.* 1995; see also Bryant & Kuropat 1980; Bryant *et al.* 1991b). Overall, our study provides further support for the carbon-nutrient balance hypothesis, as do most studies that manipulated light and/or nitrogen availability (but see Hamilton *et al.* 2001).

Global Climate Change and anti-herbivore defence

Our data provide a first and crude estimate for the impact of some environmental changes on plant anti-grazing chemistry. Although these experiments ran only for two years, cautious extrapolations can be attempted. In this context the resilience of *Salix polaris* growth and leaf chemistry to fertilisation and, somewhat less, shading are remarkable: growth and N content, phenolics and condensed tannins only decreased noticeably in the extreme shade (Fig. 2). No difference in leaf chemistry could be detected in the warming experiment, despite a significant growth response. This indicates that for *Salix polaris* it is unlikely that the projected climate changes will lead to any major change in anti-herbivore compounds or N concentration. For its herbivores this probably means a slightly increased food supply due to the increased growth under warmer conditions.

In how far these conclusions are valid for other woody species remains to be seen. Moreover, the slow growth and high reliance on storage (Chapin *et al.* 1990; Grime & Campbell 1991; Iwasa 1997) of arctic plants will buffer minor climatic effects for probably some years. Consequently I can not anticipate the major implications of altered defence chemistry due to climate change for herbivore population dynamics in the High Arctic.

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CHAPTER 9

OPTIMAL ALLOCATION TO ANTI-HERBIVORE DEFENCE: IMPORTANCE OF GRAZING PRESSURE AND COMPETITION AND THE CONSEQUENCES OF CLIMATE CHANGE

Abstract Optimal levels of anti-herbivore defence are determined not only by grazing pressure on the target plant, but also by the efficiency of the defence and by competitive interactions with neighbours. In the High Arctic on Svalbard, grazing by reindeer can be modelled without plant-to-herbivore-feedback, as reindeer population sizes are not correlated with plant growth. On the other hand, growing conditions are extreme: a short season and low temperatures inhibit optimal growth. Therefore, it is possible to model the cost and benefit of anti-herbivore defence on the competitive balance between plant species in this system. Here, I assess how the optimum allocation to defence varies in relation to grazing intensity, defence efficiency and global climate change. The model, based on a Lotka-Volterra-type competition and temperature-dependent growth indicates that competition is of considerable importance even in extreme environments. Herbivory mediates displacement of the defended plant by releasing it from competition. This process is more pronounced under high grazing pressure than under low. In other words, competition potentially magnifies the effect of herbivory. Interestingly, elevated temperatures and longer growing season have no qualitative impact on these processes, as it is especially the dominant defended plant that profits.

INTRODUCTION

Allocation of resources to anti-herbivore defence has been predicted to depend predominantly on grazing intensity, life expectancy of the consumed organ (usually the leaf), growth rate of the plant and availability of nutrients (Coley *et al.* 1985; Bryant *et al.* 1983; Herms & Mattson 1992). As pointed out by Loreau & de Mazancourt (1999), under competition the ability to exploit resources becomes much more important, especially in resource-poor environments. De Jong (1995) argued that fast growing species have no benefit from investment into anti-herbivore defence, unless grazing pressure is very high.

This study adds to these two studies a model assessing the relative importance of competition for two competing plant types, one defended, the other not, in the specific context of a terrestrial high arctic ecosystem. The reasons for restricting the approach to this extreme environment only has various reasons: 1. The optimisation of resource allocation is of vital importance for survival. Any assimilate invested into defence cannot be used for surviving the eight months long winter, soil movement, anoxic conditions etc. 2. This study ties in with other work carried out in the same system, that tries to unravel the interactions between reindeer population dynamics, parasites, vegetation and climate (Irvine *et al.* 1999; Langvatn *et al.* 1999; Van der Wal *et al.* 2000c; 2000b). 3. The arctic tundra is a very simple grazing system, in the specific case of Svalbard having only one ungulate herbivore (reindeer), the population of which fluctuates independently of plant productivity (Tyler & Øritsland 1999; see also Lee *et al.* 2000). 4. The High Arctic is predicted to experience the greatest increase in temperature due to climate change. The impact of these changes on plant performance in respect to grazing and competition are virtually unknown (but see Dormann *et al.* 2001).

The model presented addresses three specific questions:

- How are direct and indirect costs and benefits of anti-herbivore defence related to grazing intensity, i.e. when is the competitive disadvantage of slower growth rate of defended plants outweighed by the benefit of reduced grazing?
- How does the relative intensity of competition scale to that of herbivory along a grazing frequency gradient?

- How do climatic warming, longer growing seasons and higher nutrient availability affect the competitive balance of defended and undefended plant types?

METHODS

Model assumptions

The model investigates the outcome of competition between two types of plant species, differing only in their anti-herbivore strategies (and the implications of that), but not in apparency to the herbivore (e.g. as for the co-occurring cyanogenic and non-cyanogenic forms of bracken *Pteridium aquilinum*; Cooper-Driver & Swain 1976). The plants grow in a well-mixed, homogeneous patch which is small relative to the surrounding area, so that herbivores do not rely on these specific plants for their survival, thus there is no feedback from the plant population dynamics to the herbivore population dynamics (as is the case for managed livestock, as well as some reindeer populations Lee *et al.* 2000). Both species consist of ramets with constant size and weight, so that any increase in the numbers of plants is equivalent to an increase in phytomass.

The model

Competition between ramets of defended (P_D) and undefended (P_U) plant species is modeled using a Lotka-Volterra approach (Begon *et al.* 1990) of coupled ordinary differential equations:

$$\frac{dP_U}{dt} = r_U \cdot P_U \cdot T_t \cdot \left(1 - \frac{P_U + P_D}{K}\right) - r_R \cdot T \cdot P_U - g_U \cdot P_U \qquad (1)$$

$$\frac{dP_D}{dt} = r_U \cdot (1-D) \cdot P_D \cdot T_t \cdot \left(1 - \frac{P_U + P_D}{K}\right) - r_R \cdot T \cdot P_U - g_U \cdot (1-D^b) \cdot P_D \qquad (2)$$

where $P_{U/D}$ = population size of undefended/defended plant type
r_U = relative growth rate of undefended plant species (0.3)
T = temperature function
K = carrying capacity (100)

r_R = respiration coefficient (0.1)

g_U = grazing function for grazing on undefended plant species

D = allocation to defence [0 - 1]

b = efficiency of defence (lower values = higher efficiency).

In words, plants exhibit a sigmoidal growth curve with a maximum value of K. The defended plant grows slower than the undefended one, as a proportion of its biomass is allocated to defence, not to growth. There is no *a priori* reason however to assume a lower carrying capacity for the defended plant species. The impact of grazing is proportional to the abundance of the species, but reduced for the defended plant (by the proportion allocated to defence to the power of its efficiency; b-values above 1 are never advantageous).

The grazing function g_U is modelled as a grazing pulse of random intensity (0 to 50 % of the population removed, average = 25%) and predetermined frequency ν (randomly sampled from the interval [0.5ν; 1.5ν]). Altering the quantity of grazing off-take produces qualitatively the same results (data not shown). Plants have no "safe size" where they are not eaten any more, i.e. they are shrubs, herbs or grasses, not trees.

The temperature function T(*temperature*) represents temperature-dependent growth, thus simulating winter as well as a warming climate. The actual function of *temperature* was derived by fitting two linked sinusoidal functions to temperature data from Longyearbyen, Svalbard (Audun Stien, unpublished data). This function has a parameter for the onset of spring, the onset of autumn, maximal summer temperature and minimal winter temperature. Furthermore, it assumes a temperature response of plant growth follows a Gaussian function $T = e^{-0.5\left(\frac{temp-20}{10}\right)^2}$. The relative growth rate r_U is set to be 0.3 at 20°C. Respiration is 10% per time step, also adjusted by the temperature function, with a minimal value of 0.05 to simulate a build-up of costs over the winter.

Grazing pressure is kept independent of species abundance, e.g. a grazing event would reduce P_U by $0.2 \cdot P_U$ and P_D by $0.2 \cdot (1 – D^b) \cdot P_D$. Herbivore grazing pressure is assumed to be unrelated to the abundance of either plant species, but rather governed by extrinsic factors (predation, winter survival, parasites, etc.).

To assess the intensity of competition, competition-free populations were modelled alongside, where the competition term $(1-((P_U-P_D)/K))$ was replaced by (1-

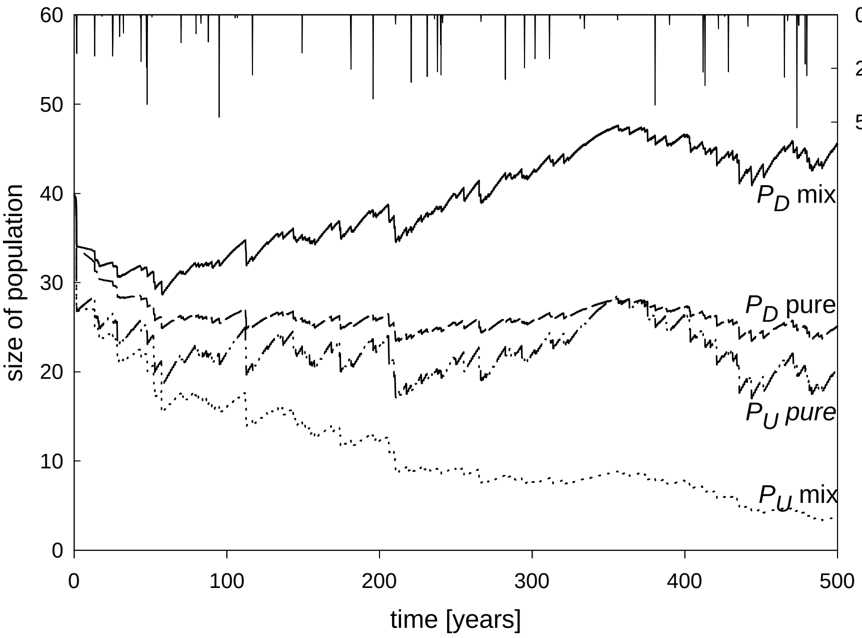

Fig. 1 Example of a model run, displaying the impact of competition in a grazed situation (difference between pure and mixed populations). Spikes at the top indicate moment and strength of grazing event. Settings: $b = 0.2$, $D^* = 0.761$, grazing frequency average = 1/10, initial value for P_D and P_U is 40.

($2P_{U/D}/K$)) (Fig. 1). For assessing competition without grazing, the grazing term was eliminated during the model runs. The model was run for 450 years after an initiation period of 50 years, with initial values for $P_D = P_U = 40$. Optimal defence allocation (D^*) was calculated iteratively by maximising population size of P_D after 500 years (mean of three runs).

The effect of warming was assessed by altering the temperature function (increasing the maximum summer temperature by 5°C and the minimum winter temperature by +10°C). A four week longer season (effectively a 25% increase) was simulated by taking the onset of spring forward by two weeks, and delaying the onset of autumn by two weeks. These alterations started in year 450 and the run was continued for another 50 years. Population sizes after 500 years (means of 10 runs) were then compared to those of unaltered conditions.

Competition and herbivory indices

To compare the impact of competition and herbivory on the population size of P_D and P_U, the model was run for plant types with and without competition, each with and without grazing, respectively. The following indices (Grace 1995; Markham & Chanway 1996) were then calculated for P_D and P_U: relative competition index (RCI) and relative herbivory index (RHI) (illustrated for P_U only).

$$RCI_{P_U} = \frac{P_U\,pure - P_U\,mix}{X} \quad \text{and} \quad RHI_{P_U} = \frac{P_U\,pure\ ungrazed - P_U\,pure\ grazed}{X},$$

where X is the bigger of the two values in the denominator (Markham & Chanway 1996). Index values range between –1 and +1, with positive values indicating negative net effects of competition (or herbivory) and negative values indicating positive net effects. These indices quantify the intensity of competition and herbivory at each point along the grazing frequency gradient.

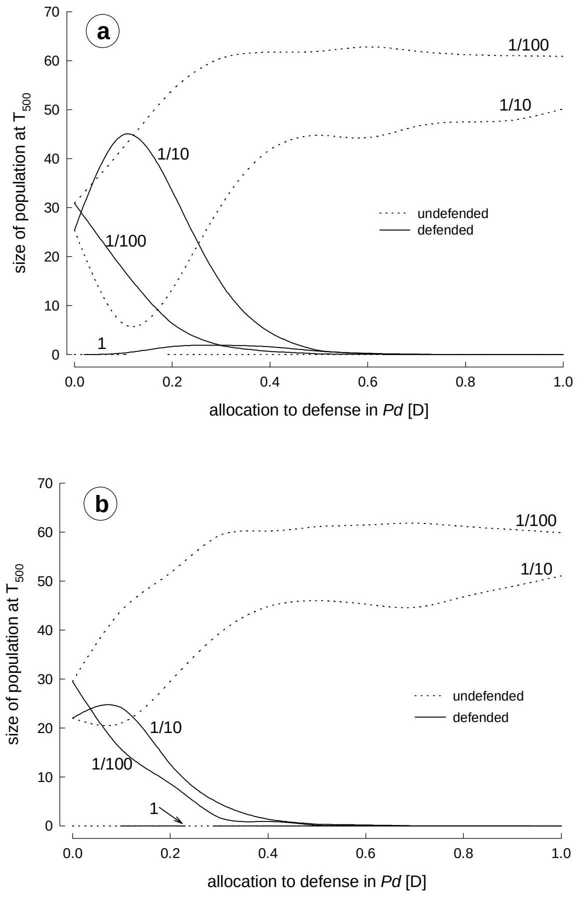

Fig. 2 Population size of undefended (dotted lines) and defended (solid) plant types for different allocation to defence (D) for the defended plant type at different grazing intensities (yearly: 1, every 10th year: 1/10; every 100th year: 1/100). **a)** $b = 0.2$. **b)** $b = 0.5$.

RESULTS

Optimal defence allocation along grazing frequency gradient

Only at intermediate grazing frequencies (ν = 1/10years, Fig. 2) was allocation to defence the superior strategy ($P_D > P_U$). However, any slight deviation from optimal defence allocation (D^*) caused a marked decline in the population size of P_D and accordingly an increase in P_U (Fig. 2). At high values of D, P_D always outperformed P_U.

The absolute allocation to defence which proved optimal was strongly dependent on the grazing

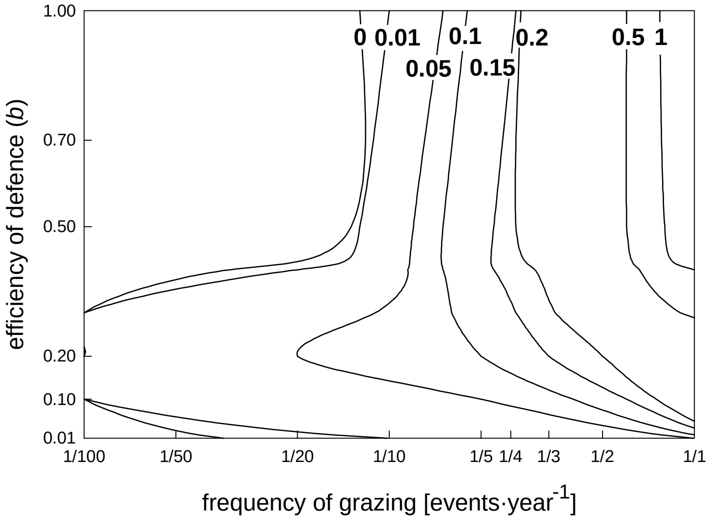

Fig. 3 Optimal allocation to defence (D^*), maximising P_D, for a range of grazing frequencies and defence efficiencies (b). Lines of same D^* are shown.

function. Figure 3 shows the dependency of D^* on b and grazing frequency. The absolute level of optimal defence was low for all grazing frequencies up to once per three years and all defence efficiencies ($D^* < 0.2$; Fig. 3). The relationship between D^* and grazing frequency was fairly constant for all defence efficiencies greater than 0.5. Highly efficient defence (e.g. $b = 0.01$) did not require high allocations to deter herbivores (Fig. 3).

At each b, D^* was linearly related to grazing frequency. The values from these regressions were used to calculate the D^* for the model runs.

Total population size ($P_D + P_U$) decreased with increasing grazing frequency. The proportion P_D of the total, however, increased steadily. For P_D to withstand yearly grazing events, b has to be < 0.2 (Fig. 4). With low defence efficiencies (e.g. $b = 0.5$), $D^* = 0$ until grazing frequency exceeds once in every 20 years; until then $P_D = P_U$ (Fig. 4b).

Intensity of competition and herbivory along a grazing frequency gradient

To separate effects of competition and herbivory, the model was run for species in pure and mixed stands, with and without grazing. The idea here is that this allows to determine the effect of competition in an ungrazed situation but with values for D

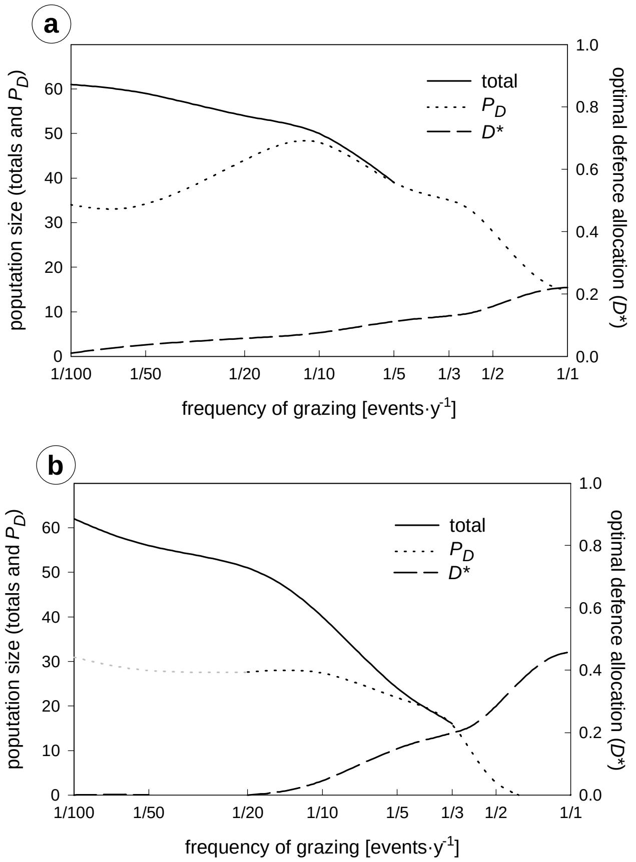

Fig. 4 Relative contribution of the defended plant type (P_D: dotted line) to the total plant population size (solid line), and optimal defence allocation (D*) along a gradient of grazing frequency. Note that at some grazing frequency the entire population is made up of the defended plant type. **a)** $b = 0.2$, **b)** $b = 0.5$. Note that $D* = 0$ for grazing frequencies less than 1/20 years (line of P_D in grey).

derived from the grazed scenario. The difference in RCI from grazed and ungrazed situations can then be attributed to the effect of grazing on competition.

Without grazing (grey lines in Fig. 5a), undefended plants grow better in mixture with the defended than in pure stands. This is because D* increases with grazing intensity, thus reducing the competitive ability of the defended plant under no-grazing conditions, leading to an increased dominance of the undefended plant species (compare grey lines in Fig. 5 a and b).

This picture is inverted under grazing (black lines in Fig. 5ab). The population size of undefended plants in pure stands decreases with increasing grazing frequency (Fig. 5a, solid black line), as does that of the defended plants (Fig. 5b, solid black line), although more slowly. When the two plant types grow in mixture (broken black line), the decrease is much more rapid for P_U, while P_D profits from the release from competition by P_U over intermediate grazing frequencies.

The competition and herbivory indices calculated for these four scenarios are presented in figure 5c and d. The black lines present the index calculated without the inclusion of herbivory (Fig. 5c) or competition (Fig. 5d), respectively. The undefended plant type dominates the defended one (negative values for P_U, positive

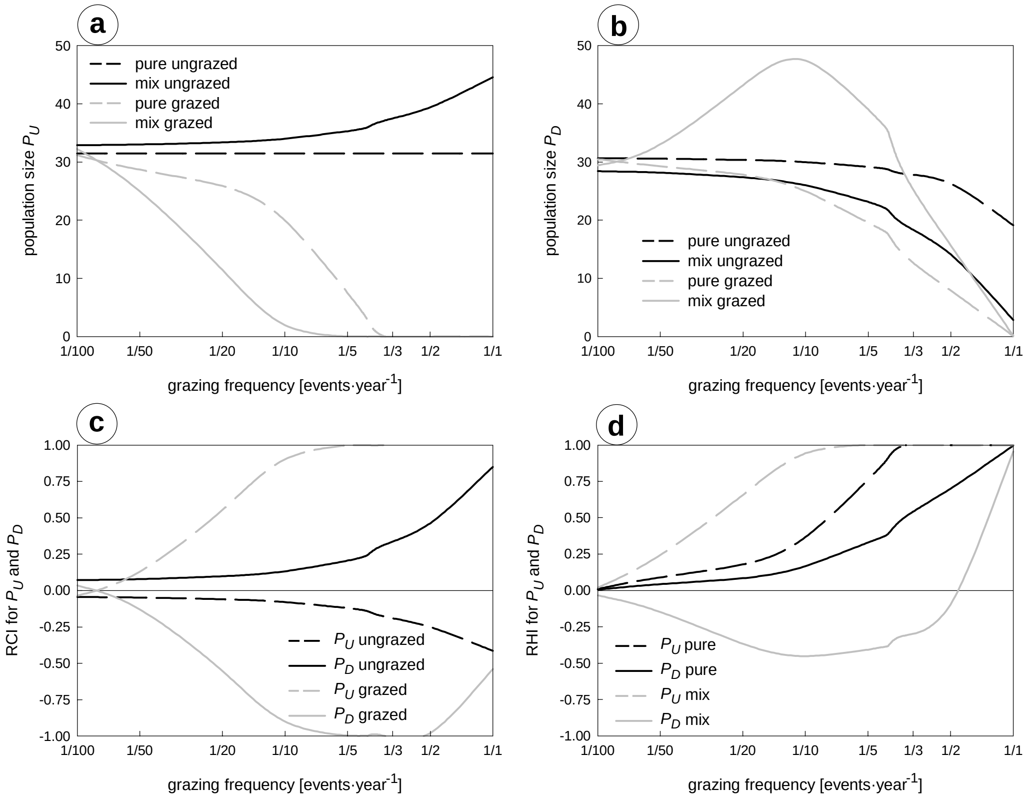

Fig. 5 Population size of **a)** undefended and **b)** defended plants along a grazing frequency gradient. Populations with (mix, solid lines) and without (pure, broken lines) competition, with (grey lines) and without grazing (black lines) are shown. **c)** Relative competition index (RCI) for undefended (P_U, broken lines) and defended (P_D; solid lines) plant types with (grey lines) and without grazing (black lines). **d)** Relative herbivory index (RHI) with (grey lines) and without competition (black lines).

ones for P_D) without grazing. With grazing (grey lines) this is altered and now the defended type profits from the mixed stands, as grazing leads to a reduction in competition from the undefended (and therefore heavily grazed) plant type (Fig. 5c). It is only when $P_U = 0$ (at grazing frequencies > 1/3) that the RCI for P_D starts to rise again.

For the impact of herbivory, this picture is less complex (Fig. 5d). In pure stands (black lines), grazing obviously affects undefended plants more than defended ones. When plants co-occur (grey lines), herbivory has a positive effect on defended plants as it takes its toll on the population of the undefended plant type, thereby reducing competition.

In other words this means that competition is the more important factor for the defended plant, while herbivory rules the undefended one. Most importantly,

Table 1 Absolute and relative (% in parentheses) changes of the population size relative to unaltered climate of undefended and defended plants simulating warming (summer +5°C, winter +10°C), longer seasons (+25%, i.e. earlier spring and later autumn), and their interaction for 50 years. Grazing frequency refers to a grazing event with average frequency of once every 100, 50, 20, 10, 5, 4, 3, 2 or 1 year. -- indicates that calculations were not performed as the population size was < 1.

grazing frequency		**1/100**	**1/50**	**1/20**	**1/10**	**1/5**	**1/4**	**1/3**	**1/2**	**1**
warming	PU	0.74	1.25	1.36	0.42	0.02	0.00	0.00	0.00	0.00
		(2.29)	(5.00)	(11.85)	(21.31)	--	--	--	--	--
	PD	0.79	2.74	3.20	5.05	6.46	6.23	6.44	3.99	0.05
		(2.67)	(8.28)	(7.41)	(10.64)	(16.54)	(17.72)	(23.15)	(25.51)	--
longer season	PU	-0.94	-0.04	0.27	-0.68	0.00	0.00	0.00	0.00	0.00
		(-2.91)	(-0.15)	(2.38)	(-34.6)	(-8.06)	(1.48)	--	--	--
	PD	0.35	0.37	-0.14	-1.03	0.75	-0.99	0.15	0.94	0.03
		(1.19)	(1.11)	(-0.33)	(-2.18)	(1.92)	(-2.82)	(0.52)	(6.02)	--
both	PU	-0.41	1.99	1.43	0.05	-0.02	0.00	0.00	0.00	0.00
		(-1.27)	(7.95)	(12.43)	(2.54)	--	--	--	--	--
	PD	1.15	2.71	3.78	2.96	3.83	-0.78	4.92	3.37	0.05
		(3.92)	(8.21)	(8.74)	(6.24)	(9.80)	(-2.23)	(17.66)	(21.55)	--

however, is the way that herbivory puts the undefended plant at a selective disadvantage, thereby inverting its competitive dominance into becoming highly susceptible to competition by the defended plant.

Effect of altered environment

When modelling plant response to altered environment, plant allocation to defence was kept constant, i.e. at the same value obtained for D^* in the unaltered conditions. This is because allocation pattern probably evolved over longer time scales than the modelled 50 years of environmental change. Hence quick re-adaptation to the new environmental conditions is unlikely.

Warming by 5°C in the summer and 10°C in winter over 50 years caused slight to pronounced absolute increases in P_D, while it had no effect on the absolute population size of P_U (Table 1). P_D profited most from elevated temperatures at lower grazing intensities, although the absolute changes were small. Longer seasons led to no important absolute difference for either plant type (Table 1). Interaction of warming and longer season caused slight counteracting effects for P_D at intermediate grazing frequencies.

Changes in environmental conditions had no effect on important effect on competition and herbivory indices, as the defended plant type could profit more than the undefended, and for both types changes were relatively small (data not shown).

Increased nutrient availability will lead to a higher value of K, which has no qualitative consequences for species abundances or interactions using this type of model. Moreover, it is not known how a, say, 15% increase in nutrient availability would translate in terms of K, thus no such calculations were performed.

DISCUSSION

The optimal investment into anti-herbivore defence in face of competition depends obviously on grazing pressure (frequency and intensity) and defence efficiency. For low defence efficiencies and grazing pressure, no defence is the best strategy (Fig. 4b), but with higher grazing pressure, optimal defence allocation (D^*) increases as well. Plant populations are then dominated by the defended type, and will eventually only contain this plant type. At high defence efficiency, D^* exceeds 0 even at very low grazing frequencies. By definition, allocation to defence is the superior strategy as soon as $D^* > 0$. It is striking, however, that this is the case for all investigated grazing frequencies (at $b = 0.2$), i.e. that simple re-growth after grazing is never an optimal strategy.

Herbivory plays a major role in shaping the outcome of competition between the defended and undefended plant type (P_D and P_U, respectively). Without grazing, P_U obviously always outcompetes P_D. When grazed, this situation is inverted. Surprising is the strength of competition acting on P_D in the grazed situation (Fig. 5c), which arises from the fact that P_D greatly profits from the presence of undefended plants, being released from competition.

The inversion of competitive outcome by grazing is intrinsic in the model structure, as well as having been shown repeatedly in the field (e.g. Reader 1992; see Crawley 1997 for overview). It has been argued however, that in harsh environments plant-plant competition would not act and therefore not be important for structuring the community (Grime 1979). This was rejected by the model-based work of Chesson & Huntly (1997), who found that in extreme environments the balance between surviving and dying is more fragile, thus competition would not have to be strong to drive one species to extinction. Explicitly modelling the determinant of severity, i.e. in this case temperature, the data presented here supports their findings. Despite total plant population size being far from carrying capacity (usually at less than 60% of *K*), competition is a major determinant of population size. Evolutionary pressure on the realisation of *D**, reducing competition along the way, is thus high, even at grazing frequencies of only once every 20 years.

Climate changes – but without

The simulated potential effects of global climate change on this herbivory-competition-complex are relatively small. Increased growth of plant populations is particularly noticeable in the defended plant type, while the undefended hardly responds. No change in competitive balance could be observed. It thus seems, that changes in herbivore density (and thus grazing pressure) are much more likely to cause changes in plant community composition then direct effects of climate changes. How reindeer density on Svalbard will change with increasing temperature can only be speculated, as correlations between reindeer population growth and North-Atlantic Oscillation anomalies are based one twenty year study of an introduced population (Aanes *et al.* 2000).

Several parameters have not been changed, e.g. relative growth rate, carrying capacity, respiration constant, shape of competitive interaction and random function of grazing intensity and frequency. Their alterations have no qualitative effect on the outcome of the model, i.e. lead only to different scales of the axes. The model assumes no trade-off between anti-herbivore defence and re-growth after grazing other than a proportional reduction in realised growth. It has been argued that this trade-off exists, but supportive data are limited to one study (Van der Meijden *et al.* 1988). De Jong (1995) also argued in favour of this concept, but his model, depending on the assumption of this trade-off, yielded optimal defence allocation only for realised growth rates higher than those in this model. He finds a high investment into defence in slow growing species, which rapidly drops off as growth rate increases.

The model presented here is an extremely simplified version of the real world. Although on Svalbard only two vascular plant species, *Luzula confusa* and *Salix polaris* are present in the vegetation type under investigation by the author (see

General Introduction), there are mosses, absorbing atmospherically deposited nutrients, ground water percolation that leads to the import of nutrients and alters soil temperature and many other factors, which have an impact on the performance of a given species. Furthermore, model assumptions might not hold, e.g. grazing might be less selective (i.e. defence less efficient), trampling effects more prevalent, interannual variation in growing conditions more important and the shape of the logistic competition function unrepresentative. Unfortunately, data are not available for any of these factors. However, choosing a simple model produces very specific predictions which can be tested by field experiments: 1. Undefended plant types (e.g. grasses) should increase inside herbivore exclosures. 2. Competition between plants plays a major role in determining vegetation structure. 3. Along a gradient of reindeer grazing pressure, total plant population size should decrease, while the proportion of defended plants should increase. 4. This pattern should be detectable independent of variations in season length and air temperature differences between sites.

Some preliminary results and observations support these predictions: On Svalbard, a four year reindeer exclosure lead to an increase in the abundance of grasses and forbs, but also in the dominant (and defended) woody species (personal observation). Higher reindeer densities were accompanied by higher cover of grasses and a decrease in (highly palatable) lichens (Van der Wal & Brooker 2001; Van der Wal *et al.* 2001a). A field experiment detected strong competitive interactions between two plant species, incidentally a defended and an undefended (CHAPTER 5). Although these data are insufficient to validate the model, they underline the importance of herbivory in the High Arctic and the congruence with the model hints at a role for competition in the structuring forces of arctic vegetation.

ACKNOWLEDGEMENTS

This chapter profited from the discussions I had on various occasions with Colin Birch and Dominic Standing. I am grateful to Audun Stien for his valuable technical aid and that he allowed me to use his temperature function for Longyearbyen. Steve Albon and Sarah Woodin are acknowleged for their comments on an earlier draft.

CHAPTER 10

SYNTHESIS

The descriptive ecology of the terrestrial High Arctic (Summerhayes & Elton 1928; Warren Wilson 1966; Dierßen 1996; Rønning 1996) has laid the basis for using it as a model ecosystem. Vegetation composition is simple, diversity low, abiotic factors are of seemingly overriding importance for the growth and survival of all its inhabitants, and trophic ladders are very short indeed. Venturing into the details and minutia of arctic plant ecology revealed a surprising complexity of adaptations to both obvious (coldness, length of winter) and less obvious (anoxia, radiation) environmental conditions (e.g., Crawford 1989; Lee 1999). All these may or may not affect the way plants respond to environmental changes, such as elevated temperature, increased nutrient availability or increased grazing intensity.

The High Arctic is predicted to be exposed to major climate change (IPCC 1998), and is likely to be very sensitive to the changes. However, biotic interactions within arctic ecosystems are not well enough understood to enable us to make good predictions of responses. The mutual impetus for these studies was to address the potential knock-on effects of changing climate onto plants, and through plants onto herbivores. Therefore one needs to understand the principal interactions of the natural, unperturbed system. In consequence, this synthesis first pulls together how climate, plants and herbivores are interconnected in the High Arctic, before, in a second step, aims at predicting possible effects of alterations of this situation.

SPECIES INTERACTION

Only little is know about plant-plant interactions in the High Arctic. Summerhayes & Elton (1928) already described a successional pattern of vegetation development from barren rocks with lichens, over mosses, cushion plants towards a denser turf of dwarf shrubs and herbs, but the mechanisms behind this change were, to my knowledge, never explored. Weathering of rocks, accretion of silt and clay and the build-up of organic matter continuously changes the substrate of plant growth, giving advantage from opportunistic lichens and mosses to vascular plants. We can only presume that mosses outcompete lichens and then get themselves overgrown by higher plants, but there seems to be no experimental evidence.

Only recently have plant ecologists performed removal experiments to investigate plant-plant interactions in the Arctic (see discussion in CHAPTER 5). Moreover, only one experiment (Hobbie *et al.* 1999) included mosses in the species pool. The result (*Sphagnum* removal resulted in a positive response of birch) indicates that indeed cryptogame-phanerogame interactions are present, although in this case *Sphagnum* controls growing conditions of *Betula*, rather than exerting direct competitive influence. For higher plant-plant interactions, the shelter that plants provide for themselves and their neighbours is a factor of great importance in the Arctic (CHAPTER 4, Carlsson & Callaghan 1991). The removal of facilitation causes more stress than the release from competition can make up for, hence removal experiments more often find positive than negative plant-plant interactions (Hobbie *et al.* 1999; Shevtsova *et al.* 1997). Using a different experimental approach, this problem can be solved, as demonstrated in CHAPTERS 4 and 5: even in the High Arctic plants do compete with one another, making competition an important factor in structuring plant communities. One important consequence of this finding is that we need to quantify the importance of competition and facilitation compared with abiotic checks on plant performance. This will require more sophisticated field experiments, which manipulate competition without manipulating facilitation, which look at the effect of plant density (of both neighbours and target species) on growth and, of course, an investigation into the mechanisms of facilitation and competition. In small pilot experiments, I could find no immediate temperature benefit for *Salix polaris* in stands of *Luzula confusa* or for it finding an associational refuge (Hay 1986) from grazing.

In comparison with plant-plant competition, herbivory in the High Arctic has been much more intensively investigated. However, due to the lack of long-term herbivore exclosures (but see Bazely & Jefferies 1986; Jefferies *et al.* 1994; Virtanen *et al.* 1997) we are still only beginning to understand the consequences of grazing in this ecosystem. Moreover, even for the most important food plants data are scarce. The best investigated example surely is the case of grazing by snow geese in La Perouse Bay, Canada, where due to a dramatic increase in bird numbers the system changed from a grazed to a “ploughed” salt marsh, with virtually no vegetation remaining (Bazely & Jefferies 1986; Hik *et al.* 1992; Jefferies *et al.* 1994; Cargill & Jefferies 1984).

On Svalbard, vegetation development is influenced by reindeer (Van der Wal & Brooker, in prep.). Grasses in particular profit from the trampling and grazing of mosses, which otherwise hinder soil warming, thereby impeding the growth of vascular plants (Van der Wal *et al.* 2001b). In the data set from their survey, however, no correlation of *Salix polaris* abundance and grazing intensity could be detected (René van der Wal, pers. comm.), suggesting no lasting effect of reindeer grazing on that particular species. In CHAPTER 7, I suggest that this is must not be the case. The experimental exclusion of reindeer was a drastic measure, leading to a shift in the female-male-ratio, increased growth rates and increased allocation to secondary compounds. These may have long-term consequences, from pollination bottlenecks, through altered vegetation composition to reduced nutrient cycling due to less degradable leaf litter (Hobbie 1992). On the other hand, nutrient turnover by decomposition is extremely slow in the Arctic, taking decades to centuries (Dowding *et al.* 1981; Chapin *et al.* 1988). Hence, this is the time scale we would expect indirect effects of altered nutrient cycling to be detectable in the vegetation.

Furthermore, herbivores may influence the quality of their forage. Work especially from Scandinavia on Mountain Birch (*Betula tortuosa*) has shown the importance of (delayed) induced resistance for further usage of the same tree by the moth *Epirrita autumnata* (Haukioja & Neuvonen 1985; 1985a; 1985b). Our data from a simulated browsing experiment indicate a very fast increase in phenolics (within 15 minutes), but no resistance over a longer term (CHAPTER 7). On the contrary, phenolic levels were actually *reduced* in grazed plots compared to those where grazing was excluded for three years (CHAPTER 6). This ties in with the data of Chapin *et al.* (1985), who also reported a lack of inducible resistance for three Alaskan woody species. Thus, in our system, continuous grazing seems to maintain higher food quality (as reflected in the selection of clipped plots over controls: CHAPTER 7), hinting at maintenance of forage grounds by ungulate herbivores (“cyclic grazing”, as reviewed in Drent & Van Der Wal 1999).

IMPACT OF GLOBAL CLIMATE CHANGE ON TERRESTRIAL HIGH ARCTIC ECOSYSTEMS

In which way will environmental changes influence the functioning of arctic ecosystems, especially a) the growth of plants and the interactions between b) plants and plants and c) plants and herbivores? CHAPTER 2 reviews the results of field experiments carried out in the Arctic, investigating the effects of elevated temperature, increased UV-B, etc. The general result is that, as nutrient limitation is limiting to plant growth in most circumstances, all treatments that alleviated this limitation had a significant impact on plant growth (such as fertilisation, elevated temperature and shading). Plant responses to manipulations were highly individualistic (species specific), but grasses and shrubs seem to be the plant types gaining most from the climate of the future. This was indeed observed in an experiment manipulating air temperature (CHAPTER 5), where the deciduous shrub *Salix polaris* increased biomass in warmed plots, while the wood rush *Luzula confusa* did not (the interaction between these two species are discussed below).

However, some factors, such as season length, winter conditions, have been neglected in experimental approaches, although there is first evidence that they are indeed important (Van der Wal *et al.* 2000c; Walsh *et al.* 1997; Galen & Stanton 1999). Season length was also a significant determinant of the abundance of *Polygonum viviparum* plants along a snowmelt gradient (CHAPTER 3), although it had no effect on the actual biomass of the plants. But, as biomass was negatively correlated with soil water content, and soil water content decreased with earlier snowmelt, season length may have indirect effects on the performance of *Polygonum viviparum*. These data serve also as test of the idea that the high within-species, ecotypic diversity provides a buffer against environmental change: the two tested genotypes of *Polygonum viviparum* did not differ in temperature-dependence of their germination, nor did soil water content affect them differently (CHAPTER 3). This by no means rejects the principle idea of intraspecific variability buffering species against environmental change. However, the first reliable data supporting this notion are still to be produced. Predictions of the resilience of species and communities to global change are of great interest to science and society, and work of this type (i.e. linking a species' variability to its resilience) should be encouraged.

Plant-plant interactions

Only a handful of arctic studies tried to assess the impact of altered environments on interactions between plant species: Jonasson (1992) factored fertilisation with neighbour removal and found no interaction between these factors, indicating that facilitative effects are equally strong in fertilised and control plots. This is in line with the conclusions of Hobbie *et al.* (1999), who "… found no significant interactions between warming and species removal, suggesting that increased temperature per se will not alter the intensity of species interactions." (p.417). In contrast Shevtsova *et al.* (1997) found various cases where neighbour removal altered the response of plant species to warming or watering, but not always increased growth: *Empetrum nigrum* grew *worse* in warmed plots when its dominant neighbour *Vaccinium vitis-idaea* was removed. A similar result was obtained in the study of Hobbie & Chapin (1998a), where *Populus tremuloides* showed a reduced biomass in warmed plots with neighbours removed, while it responded positively to warming when the surrounding vegetation was left intact.

The results of the experiment presented in CHAPTER 5 support the latter conclusions: in mixed stands under elevated temperatures, *Salix polaris* outperformed *Luzula confusa* when compared to ambient temperatures. This change in competitive balance might have repercussions on the reindeer, which prefer *Salix* over *Luzula*, as well as on the nutrient cycling in the tundra, as *Salix* leaves decompose faster than those of *Luzula*, which remain attached to the plant for two or more years. However, this is the first study to show a change in *competition* rather than a change in *facilitation*. Hence the interplay of facilitation and competition in tundra ecosystems has to be incorporated into experiments and predictive models of vegetation change in the Arctic (see also CHAPTER 4).

Plant-herbivore interactions

Herbivores alter plant-plant interactions, as well as plant competition alters the effects of herbivory (CHAPTER 9). This simple statement hides the complexity of the connections and interrelationships that competition and herbivory have. In most studies of one factor the other is neglected, although presumably all plants experience both factors at some point in their life. Often enough, field experiments on competition delivered spurious results, because herbivory was not considered (Reader 1992). It is well documented that herbivory can cause shifts in competitive dominance (CHAPTER 9, Crawley 1983), alter vegetation composition and ecosystem properties (Milchunas & Lauenroth 1993). Similarly, competition is regularly invoked as the ultimate cause of plant species replacement during succession (Glenn-Lewin & van der Maarel 1992). The simultaneous and synergistic action of competition and herbivory however deserves more consideration, especially by field experiments (see, e.g., Bonser & Reader 1995; Dormann *et al.* 2000; Van der Wal *et al.* 2000a). The simple modelling approach performed in CHAPTER 9 illustrates how complex the results of interacting biotic agents can be (e.g. leading to amplifications or damping of another factor, depending on the intensity of both), and how complex the environment is that plants are evolving into. Including facets of the abiotic environment in the model can be a first step to estimate the effect of changes in this environment. Not all changes, say in temperature, will effect plant-plant or plant-herbivore interactions, while others might tip the balance between dominance and extinction.

As mentioned in the introduction, so far only two field studies have tried to address the consequences of climate change on Arctic ungulate herbivores. Both (Walsh *et al.* 1997; Van der Wal *et al.* 2000c) manipulated the timing of snowmelt, simulating different season lengths, and their results are complementary, finding reindeer/caribou utilising early snowmelt patches more than late snowmelt patches, as biomass is higher there, independent of higher C/N-ratios. Plant defence (measured as phenolics in Van der Wal *et al.* 2000c) were similarly high throughout the experiment and hence could not serve as selection clue.

If one accepts that plant-herbivore interactions in boreal and arctic systems are at least partly determined by secondary compounds (Bryant & Kuropat 1980; 1981; 1991b; 1991a), then changes in secondary chemistry are among the most likely effects of altered climate to affect herbivore population dynamics. The carbon-nutrient balance hypothesis (Bryant *et al.* 1983) predicts decreases in plant defence compounds with increases in the relative availability of limiting nutrients (e.g. nitrogen). This was indeed the result of a two year shading × fertilisation experiment (CHAPTER 8). Independent of the mechanism of alteration of the C/N-balance (i.e. either by increasing the N uptake and keeping C-assimilation constant, or by decreasing C-assimilation and keeping N uptake the same), *Salix* secondary compounds decreased linearly with increasing N-content of leaves. However, the fertilisation and shading levels required to produce a significant change in leaf-N are dramatic, and beyond the most extreme predictions for arctic climate change. Elevated temperature, on the other hand, although increasing plant growth, did not alter the C/N-ratio of the leaves and accordingly had no detectable effect on plant defence chemistry (CHAPTER 8). Thus, judging from this short-term (two years) experiment, global climate change is unlikely to cause major bottom-up benefits or restrictions to the reindeer population.

FUTURE CHALLENGES

Although some features, such as plant growth, of arctic ecosystems have received much attention, quite some are still only insufficiently known. The recent rise in publications investigating **soil processes in the context of global climate change** (Nadelhoffer *et al.* 1991; 1997; Jonasson *et al.* 1993; 1999; Schmidt *et al.* 1999) is a promising step towards understanding the "hidden two-thirds" of terrestrial arctic ecosystems. However, all ecosystem processes are extremely slow in the Arctic, thus requiring long-term (>10 years) research, sensitive methods (e.g. isotope analysis, Robinson 2001) and the support of modelling approaches. The latter are especially rare for tundra ecosystems (Reynolds & Leadley 1992), and some vegetation change models still treat the soil as a black box (e.g. Epstein *et al.* 2000). On the other hand, as CHAPTERS 5 and 9 indicate, biotic interactions are at least partly driven by resource availability. In how far alterations of nutrient cycling will affect plant competition or plant-herbivore interactions is at present beyond our understanding. In a first step, determination of *in situ* decomposition rates for litter of different plant species may give us some idea as to which plants will have the biggest influence on nutrient cycling. Such experiments are underway in the Low Arctic (Hans Cornelissen, University of Amsterdam, personal communication), but need to be extended to the much harsher conditions of the High Arctic. In a next step, fertilisation experiments with *low* levels of nitrogen and phosphorus addition can be used to estimate the impact of altered nutrient availability on plant species composition. At present, fertilisation experimentsemploy much too high doses to mimic nutrient cycling processes (see CHAPTER 2).

The gaps in our knowledge of ecosystem processes are not restricted to soil processes. We only begin to unravel the **impact of grazing** on plant growth, nutrient cycling, vegetation composition, vascular-non-vascular plant interactions and so forth (Zimov *et al.* 1995; Milchunas & Lauenroth 1993; Manseau *et al.* 1996; De

Mazancourt *et al.* 1999; Olofsson *et al.* 2001; Van der Wal & Brooker 2001). Moreover, herbivory often interacts with plant-plant-competition in other ecosystems (Reader 1992; Dormann *et al.* 2000), making it a factor acting on multiple levels of the system. In the low arctic salt marsh at La Perouse Bay, where 80 to 100% of the net primary productivity is consumed by geese, nutrient cycling through faeces allows plant to overcompensate for grazing off-take (Belsky 1987; Hik & Jefferies 1990). In the case of mammalian grazing, off-take is usually much lower, and faeces deposition less homogenous. Clearly, the impact of reindeer grazing on productivity and species composition in tundra ecosystems needs further investigation. At the same time, both direct and indirect grazing effects might alter plant-plant interactions with long-term consequences for plant population dynamics (Mulder & Ruess 2001).

If we want to use the **tundra as a model ecosystem**, we have to understand what it has in common, and in which respects it differs from other ecosystems. For example, Are the factors limiting plant growth comparable?, Are seasonal effects of importance for ecosystem functions?, Does grazing affect the tundra more or less than temperate or tropic systems?, What are the roles of competition and facilitation between plants in shaping the vegetation and hence the primary productivity? Field experiments are a crucial part in the answering of these questions, they provide the parameters for ecosystem models, and they open our eyes for further hypotheses and ideas. One important step taken was the foundation of the International Tundra EXperiment (ITEX), which tries to integrate research across the Arctic, with similar experimental protocols and objectives. Similar networks e.g. for mountainous areas in Europe (GLORIA, etc.) are providing first steps towards a comparison across latitudinal gradient. To allow a synthesis of these experiments, simple common approaches, such as the competition experiments of CHAPTER 4, herbivore exclosures (CHAPTER 7) and nutrient availability measurements (CHAPTER 5), need to be employed.

Finally, **long-term monitoring**, e.g. by aerial photography or satellite imagery plus permanent plots in the field, can provide useful data on two processes that are usually beyond the time scale of experimentation: soil formation/erosion and catastrophic events. Arctic soils display constant mixing due to frost heave (cryoturbation). This is more pronounced in wet than in dry tundra, and it acts over decades (Kuntze *et al.* 1994). As a consequence, soil is constantly destroyed, eroded and reborn, and plant life has to adapt to an unstable ground, as arctic plants can life decades to centuries (Crawford 1989). Equally important might be catastrophic events like heavy erosion, snow-free winters or grazing destruction. The implications of these rare catastrophes are utterly unknown.

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APPENDIX

Table A 1 Response variables and there grouping for analysis.

group	Response parameter measured	
Biomass-group	1 total biomass (g)	7 apical abovegr. growth (g·m^{2})
	2 aboveground biomass (living tissue) (g)	8 shoot growth (g)
	3 below-ground biomass (g)	9 stem growth (g)
	4 total above-gr. biomass (dead + live) (g)	10 relative stem growth (g·y^{-1})
	5 individ. leaf or shoot biomass (g)	11 leaf growth (g·y^{-1})
	6 total leaf mass (g)	
Chemistry-group	1 N-pool aboveground (g·m^{-2})	14 Mn-content of leaves (mg·g^{-1})
	2 P-pool aboveground (g·m^{-2})	15 B-content of leaves (mg·g^{-1})
	3 K-pool aboveground (g·m^{-2})	16 sugar content of leaves (mg·g^{-1})
	4 Ca-pool aboveground (g·m^{-2})	17 polysaccharide content of leaves (mg·g^{-1})
	5 Mg-pool aboveground (g·m^{-2})	18 protein N content of leaves (mg·g^{-1})
	6 N-content of leaves (mg·g^{-1})	19 amino acid N content of leaves (mg·g^{-1})
	7 P-content of leaves (mg·g^{-1})	20 soluble organic P content of leaves (mg·g^{-1})
	8 K-content of leaves (mg·g^{-1})	21 sol. phenolic content of leaves (mg·g^{-1})
	9 Ca -content of leaves (mg·g^{-1})	22 condensed-tannin content of leaves (mg·g^{-1})
	10 Mg-content of leaves (mg·g^{-1})	23 total chlorophyll content of leaves (µmol·g^{-1})
	11 Zn-content of leaves (mg·g^{-1})	24 carotinoids content (g·m^{-2})
	12 Cu-content of leaves (mg·g^{-1})	25 UV-B compounds (mg·g^{-1})
	13 Fe-content of leaves (mg·g^{-1})	26 leaf total non-structural carbon (mg·g^{-1})
leaf-group	1 leaf area (mm^{2}·tiller^{-1})	4 leaf area (cm^{2}·leaf^{-1})
	2 shoot or leaf length (mm)	5 relative leaf growth rate (cm·y^{-1})
	3 leaf width or thickness (mm)	6 specific leaf area (m^{2}·g^{-1})
reproduction-group	1 length of prefloration period (d)	8 fruit or bulbil dry weight/flower or spike (mg)
	2 inflorescence densitiy (nr.·m^{-2})	9 fruit fresh weight (mg)
	3 seed setting flowers (m^{-2})	10 fruit density (nr.·m^{-2} or plant^{-1})
	4 flowering (%)	11 fruits (flower^{-1})
	5 nr. of seeds or bulbils (per flower or spike)	12 spike or pedicel length (cm)
	6 capsule volume (mm^{3})	13 allocation to seeds (%)
	7 fruit or bulbil dry weight (mg)	14 germination rate (%)
physiology-group	1 leaf δ^{13}C (‰)	11 carboxylation efficiency (%)
	2 meristems active (%)	12 N-uptake (g·m^{-2}·y^{-1})
	3 CO$_2$-uptake rate (µmol·m^{-2}·s^{-1})	13 P-uptake (g·m^{-2}·y^{-1})
	4 transpiration rate (mg·m^{-2}·s^{-1})	14 nitrate reductase activity (µmol·gFW^{-1}·h^{-1})
	5 area net photosynthesis (µm·m^{-2}·s^{-1})	15 ascorbate peroxidase act. (nkat·mg rotein^{-1})
	6 weight net photosynthesis (µm·g^{-1}·s^{-1})	16 glutathione reductase act. (nkat·mg protein^{-1})
	7 N net photosynthesis (µmol·gN^{-1}·s^{-1})	17 phosphatase activity (µmol·g^{-1}·h^{-1})
	8 P net photosynthesis (µmol·gP^{-1}·s^{-1})	18 exocellulase activity (µmol·g^{-1}·h^{-1})
	9 light saturation rate (Amax: µmolCO$_2$·m^{-2}·s^{-1})	19 endocellulase activity (µmol·g^{-1}·h^{-1})
	10 apparent quantum yield (molCO$_2$·mol photon^{-1})	

Table A 2 Studies incorporated in the database, showing which data were used (response variables: for coding see Table A1). "Year" refers to the duration of the experiment when measurements were taken. "Factors" are: acid = simulation of acid rain, CO_2 = elevated CO_2, F = fertilisation, L = shading, N = nitrogen addition, P = phosphorus addition, removal = selective species removal treatment, UV-B = increased UV-B radiation, T = elevated temperature, W = watering; + and × indicate treatments combined additively or factorially, respectively.

location	references	experiment	factors	year	species	response variable
Ellesmere Island, Canada	Henry *et al.* 1986	1	F, W	2	*Carex membranacea*	biomass-2,4
78,9°N					*Eriophorum angustifolium*	biomass-2,4
30 m a.s.l. (?)					*Cassiope tetragona*	biomass-2,4; reproduction-2
					Dryas integrifolia	biomass-2,4; reproduction-2
					Eriophorum angustifolium	biomass-2,4; reproduction-2
					Juncus biglumis	biomass-2,4; reproduction-2
					Luzula arctica	biomass-2,4; reproduction-2
					Papaver lapponicum	biomass-2,4
					Polygonum viviparum	biomass-2,4; reproduction-2
					Salix arctica	biomass-2,4; reproduction-2
500 m a.s.l.	Stenström *et al.* 1997	2	T	1	*Saxifraga oppositifolia*	reproduction-2,11,12
				2	*Saxifraga oppositifolia*	reproduction-2,11,12
				3	*Saxifraga oppositifolia*	reproduction-2,11,12
30 m a.s.l.	Jones *et al.* 1997	3	T	1	*Salix arctica*	biomass-5; leaf-2; reproduction-1,10,11
Barrow, Alaska	Jones *et al.* 1997	4	T	1	*Salix rotundifolia*	biomass-5; leaf-2, reproduction-1,10,11
71,3°N						
5 m a.s.l.						
Eagle Creek, Alaska	Shaver & Chapin 1986	5	F	3	*Eriophorum vaginatum*	biomass-1
65°26'N 145°30'W					*Carex bigelowii*	biomass-1
730 m a.s.l.					*Vaccinium uliginosum*	biomass-1
					Betula nana	biomass-1
					Rubus chamaemorus	biomass-1
					Vaccinium vitis-idaea	biomass-1
					Empetrum nigrum	biomass-1
					Andromeda polifolia	biomass-1
					total	biomass-1

Kurapuk Ridge, Alaska	Shaver & Chapin 1986	6	F	3	*Petasitis frigidus*	biomass-1
68°37'N 149°18'W					*Polygonum bistorta*	biomass-1
917 m a.s.l.					*Pyrola secunda*	biomass-1
					Saxifraga punctata	biomass-1
					Calamagrostis spec.	biomass-1
					Eriophorum vaginatum	biomass-1
					Carex bigelowii	biomass-1
					Vaccinium uliginosum	biomass-1
					Betula nana	biomass-1
					Salix pulchra	biomass-1
					Rubus chamaemorus	biomass-1
					Vaccinium vitis-idaea	biomass-1
					Ledum palustre	biomass-1
					Cassiope tetragona	biomass-1
					Empetrum nigrum	biomass-1
					total	biomass-1
				5	*Petasitis frigidus*	biomass-1
					Calamagrostis spec.	biomass-1
					Poa arctica	biomass-1
					Eriophorum vaginatum	biomass-1
					Carex bigelowii	biomass-1
					Betula nana	biomass-1
					Salix pulchra	biomass-1
					Salix reticulata	biomass-1
					Vaccinium vitis-idaea	biomass-1
					Ledum palustre	biomass-1
					Cassiope tetragona	biomass-1
					Empetrum nigrum	biomass-1
					total	biomass-1
Sagwon, Alaska	Shaver & Chapin 1986	7	F	5	*Polygonum bistorta*	biomass-1
69°37'N 148°40'W					*Calamagrostis spec.*	biomass-1
388 m a.s.l.					*Eriophorum vaginatum*	biomass-1
					Carex bigelowii	biomass-1

					Betula nana	biomass-1
					Salix pulchra	biomass-1
					Vaccinium vitis-idaea	biomass-1
					Ledum palustre	biomass-1
					total	biomass-1
Toolik Lake	Shaver & Chapin 1986	8	F	5	*Polygonum bistorta*	biomass-1
68°38'N 149°34'W					*Calamagrostis spec.*	biomass-1
760 m a.s.l.					*Eriophorum vaginatum*	biomass-1
					Carex bigelowii	biomass-1
					Vaccinium uliginosum	biomass-1
					Betula nana	biomass-1
					Salix pulchra	biomass-1
					Rubus chamaemorus	biomass-1
					Vaccinium vitis-idaea	biomass-1
					Ledum palustre	biomass-1
					Cassiope tetragona	biomass-1
					Empetrum nigrum	biomass-1
					total	biomass-1
LTER, Toolik Lake, Alaska	Chapin & Shaver 1985 [1]	9	L, T, F	1	*Eriophorum vaginatum*	biomass-1,3,5,8; chemistry-1,2,6,7; chemistry-16-22 [3]
68°38'N, 149°39'W	Shaver, Chapin & Gartner 1986 [2]			2	*Aulacomnium turgidum*	biomass-5 [1]
760 m a.s.l.	Chapin, Shaver & Kedrowski 1986 [3]				*Betula nana*	biomass-5 [1]
					Carex aquatilis	biomass-5 [1]
					Carex bigelowii	biomass-5 [1]
					Empetrum nigrum	biomass-5 [1]
					Eriophorum angustifolium	biomass-5 [1]
					Eriophorum vaginatum	biomass-5 [1]; biomass-1,3,8; chemistry-1,2,6,7]; chemistry-16-22 [3]
					Ledum palustre	biomass-5 [1]
					Polygonum bistorta	biomass-5 [1]
					Rubus chamaemorus	biomass-5 [1]
					Salix pulchra	biomass-5 [1]
					Vaccinium vitis-idaea	biomass-5 [1]
	Chapin *et al.* 1995 [1]	10	L, T, F	3	*Aulacomnium* spec.	biomass-2,7 [1]

Chapin & Shaver 1996 [2]				*Betula nana*	biomass-2,7 [1]; biomass-5; chemistry-6,7; physiology-6 [2]
				Carex bigelowii	biomass-2,7 [1]
				Eriophorum vaginatum	biomass-2,7 [1]; biomass-5; chemistry-6,7;11,12; physiology-6 [2]
				Hylocomium splendens	biomass-2,7 [1]
				Ledum palustre	biomass-2,7 [1]; biomass-5; chemistry-6,7; physiology-2,6 [2]
				Rubus chamaemorus	biomass-2,7 [1]
				Sphagnum spec.	biomass-2,7 [1]
				Vaccinium vitis-idaea	biomass-2,7 [1]; biomass-5; chemistry-6,7; physiology-2 [2]
				total	biomass-2,7; chemistry-1-5; physiology-12,13 [1]
			9	*Aulacomnium* spec.	biomass-2,7 [1]
				Betula nana	biomass-2,7 [1]
				Carex bigelowii	biomass-2,7 [1]
				Eriophorum vaginatum	biomass-2,7 [1]
				Hylocomium splendens	biomass-2,7 [1]
				Ledum palustre	biomass-2,7 [1]
				Rubus chamaemorus	biomass-2,7 [1]
				Sphagnum spec.	biomass-2,7 [1]
				Vaccinium vitis-idaea	biomass-2,7 [1]
				total	biomass-2,7; chemistry-1-5; physiology-12,13 [1]
Shaver *et al.* 1998	11	L, F×T	6	*Carex cordorrhiza*	biomass-1; chemisty-6,7
				Carex rotundata	chemisty-6,7
				Eriophorum vaginatum	chemisty-6,7
				Trichophorum caespitosum	biomass-1
				moss	biomass-1; chemisty-6,7
				graminoids	biomass-1; leaf-4
				total	biomass-1-3; chemisty-1,2; ecosystem-1-3
Tissue & Oechel 1987	12	CO2, CO2+T	1	*Eriophorum vaginatum*	chemistry-26; leaf-1,5; physiology-3,4
Moorhead & Linkins 1997	13	CO2, water Table		*Eriophorum vaginatum*	physiology-14,19
				Betula nana	physiology-14,17-19
Molau & Shaver 1997	14	T, F	9	*Eriophorum vaginatum*	reproduction-3,9
Hobbie & Chapin 1998	15	T	1	*Alnus crispa*	reproduction-14
				Betula papyrifera	reproduction-14
				Picea glauca	reproduction-14

				Populus balsamifera	reproduction-14
				Populus tremuloides	reproduction-14
			2	*Alnus crispa*	biomass-8
				Betula papyrifera	biomass-8
				Picea glauca	biomass-8
				Populus balsamifera	biomass-8
				Populus tremuloides	biomass-8
Hobbie *et al.* 1999 [1]	16	T × removal	1	*Carex bigelowii*	leaf-2 [1]
Hobbie & Chapin 1998A [2]				*Eriophorum vaginatum*	leaf-2 [1]
				Betula nana	leaf-2 [1]
				Ledum palustre	leaf-2 [1]
				Vaccinium vitis-idaea	leaf-2 [1]
				Hylocomium splendens	leaf-2 [1]
				Sphagnum spp.	leaf-2 [1]
			2	*Carex bigelowii*	leaf-2 [1]
				Eriophorum vaginatum	leaf-2 [1]
				Betula nana	leaf-2 [1]
				Ledum palustre	leaf-2 [1]
				Vaccinium vitis-idaea	leaf-2 [1]
				Hylocomium splendens	leaf-2 [1]
				Sphagnum spp.	leaf-2 [1]
			3	*Rubus chamaemorus*	biomass-4 [1]
				Vaccinium uliginosum	biomass-4 [1]
				Betula nana	biomass-4 [1]
				Andromeda polifolia	biomass-4 [1]
				Cassiope tetragona	biomass-4 [1]
				Empetrum nigrum	biomass-4 [1]
				Ledum palustre	biomass-4, reproduction-5,8 [1]
				Vaccinium vitis-idaea	biomass-4, reproduction-5,8 [1]
				Carex bigelowii	biomass-4, reproduction-5,8 [1]
				Eriophorum vaginatum	biomass-4 [1]
				Pedicularis spp.	biomass-4 [1]
				Polygonum bistorta	biomass-4 [1]

					Aulacomnium turgidum	biomass-1 [1]
					Dicranum spp.	biomass-1 [1]
					Hylocomium splendens	biomass-1 [1]
					Sphagnum spp.	biomass-1 [1]
					lichens	biomass-1 [1]
					total	biomass-4 [1]
		17	T	4	*Eriophorum vaginatum*	biomass-2,3; chemistry-1; physiology-13 [2]
					Carex bigelowii	biomass-2,3; chemistry-1; physiology-13 [2]
					Betula nana	biomass-2,3; chemistry-1; physiology-13 [2]
					Rubus chamaemorus	biomass-2,3; chemistry-1 [2]
					Vaccinium uliginosum	biomass-2,3; chemistry-1 [2]
					Vaccinium vitis-idaea	biomass-2,3; chemistry-1; physiology-13 [2]
					Ledum palustre	biomass-2,3; chemistry-1; physiology-13 [2]
					Cassiope tetragona	biomass-2,3; chemistry-1 [2]
					Empetrum nigrum	biomass-2,3; chemistry-1 [2]
					Andromeda polifolia	biomass-2,3; chemistry-1 [2]
					Pedicularis spp.	biomass-2,3; chemistry-1 [2]
					Polygonum bistorta	biomass-2,3; chemistry-1 [2]
					Sphagnum spp.	biomass-5; chemistry-1; physiology-13 [2]
					Aulacomnium turgidum	biomass-5; chemistry-1; physiology-13 [2]
					Dicranum spp.	biomass-5; chemistry-1; physiology-13 [2]
					Pleurozium schreberi	biomass-5; chemistry-1 [2]
					Polytrichum spp.	biomass-5; chemistry-1 [2]
					Tomenthypnum nitens	biomass-5; chemistry-1 [2]
					Ptilium crista-castrensis	biomass-5; chemistry-1 [2]
					lichens	biomass-5; chemistry-1; physiology-13 [2]
					total	biomass-2,3 [2]
Eagle Summit, Alaska 65°26'N 145°30'W 1050 m a.s.l.	McGraw 1985	18	N, P, L, W	3	*Dryas octopetala*	biomass-2
					forbs	biomass-2
					graminoids	biomass-2
					shrubs	biomass-2
					total	biomass-2
Disko Island, Greenland	Mølgaard & Christensen 1997	19	T	1	*Papaver radicatum*	biomass-2, reproduction-5

69°17'N 53°45'W				2	*Papaver radicatum*	biomass-2, reproduction-5
				3	*Papaver radicatum*	biomass-2, reproduction-5
				4	*Papaver radicatum*	biomass-2, reproduction-5
Abisko, Sweden	Johanson *et al.* 1995 [1]	20	UV-B (15%)	1	*Empetrum hermaphroditum*	biomass-9,10 [1]
68°21'N 18°49'E	Taulavuori *et al.* 1998 [2]				*Vaccinium myrtillus*	biomass-9,10 [1]
360 m a.s.l.	Gehrke 1999 [3]				*Vaccinium uliginosum*	biomass-9,10 [1]
					Vaccinium vitis-idaea	biomass-9,10 [1]
					Hylocomium splendens	biomass-8, leaf-2, chemistry-25[3]
					Polytrichum commune	biomass-8, leaf-2, chemistry-25[3]
				2	*Empetrum hermaphroditum*	biomass-9,10; leaf-3,4 [1]
					Vaccinium myrtillus	biomass-9,10; leaf-3,4 [1]
					Vaccinium uliginosum	biomass-9,10; leaf-3,4 [1]
					Vaccinium vitis-idaea	biomass-9,10 [1]
					Hylocomium splendens	biomass-8, leaf-2 [3]
					Polytrichum commune	biomass-8, leaf-2 [3]
				3	*Empetrum hermaphroditum*	biomass-5 [1]
					Vaccinium myrtillus	biomass-5, leaf-3,4 [1]
					Vaccinium uliginosum	biomass-5, leaf-3,4 [1]
					Vaccinium vitis-idaea	biomass-5, leaf-3,4 [1]
					Hylocomium splendens	biomass-5,8, leaf-2,3, chemistry-23-25[3]
					Polytrichum commune	biomass-5,8, leaf-2,3, chemistry-23-25[3]
				7	*Vaccinium myrtillus*	chemistry-25; physiology-15,16 [2]
360 m a.s.l.	Gwynn-Jones *et al.* 1997	21	CO2 × UV-B	1	*Empetrum hermaphroditum*	leaf-2
					Vaccinium myrtillus	leaf-2; reproduction-10
				2	*Empetrum hermaphroditum*	leaf-2
					Vaccinium myrtillus	leaf-2; reproduction-10
				3	*Empetrum hermaphroditum*	leaf-2
					Vaccinium myrtillus	leaf-2,3; reproduction-10
					Vaccinium vitis-idaea	leaf-3
380 m a.s.l.	Karlsson 1985	22	W, F+W	1	*Vaccinium uliginosum*	biomass-7; chemistry-6-8, leaf-4
					Vaccinium vitis-idaea	biomass-7; chemistry-6-8, leaf-4
				2	*Vaccinium uliginosum*	biomass-7; chemistry-6-8, leaf-4
					Vaccinium vitis-idaea	biomass-7; chemistry-6-8, leaf-4

	Wookey *et al.* 1995 [1]	23	T × W × F	1	*Empetrum hermaphroditum*	biomass-2,8,9,11 [2]; reproduction-7,10 [1]
	Parsons *et al.* 1994 [2]				*Vaccinium vitis-idaea*	biomass-2,8,9,11 [2]
	Parsons *et al.* 1995 [3]				*Vaccinium uliginosum*	biomass-2,8,9,11 [2]
	Potter *et al.* 1995 [4]				*Vaccinium myrtillus*	biomass-2 [2]
	Press *et al.* 1998 [5]			2	*Calamagrostis lapponica*	biomass-2; leaf-2; reproduction-4 [3]
					Empetrum hermaphroditum	biomass-2,6,7,9 [2]
					Vaccinium vitis-idaea	biomass-2,6,7,9 [2]
					Vaccinium uliginosum	biomass-2,6,7,9 [2]
					Vaccinium myrtillus	biomass-2,6,7,9 [2]
				3	*Calamagrostis lapponica*	biomass-2; leaf-2; reproduction-4 [3]
					Hylocomium splendens	biomass-2; leaf-2 [4]
					Polytrichum commune	biomass-2; leaf-1 [4]
				5	shrubs	biomass-2 [5]
					herbs	biomass-2 [5]
					grasses	biomass-2 [5]
					ferns	biomass-2 [5]
					bryophytes	biomass-2 [5]
					lichens	biomass-2 [5]
450 m a.s.l.	Havström *et al.* 1993 [1]	24	L × F, F × T (2 levels)	3	*Cassiope tetragona*	biomass-5; leaf-2 [1]
	Michelsen *et al.* 1996 [2]			5	*Cassiope tetragona*	biomass-2; chemistry-6,23; physiology-1 [2]
	Graglia *et al.* 1997 [3]				*Empetrum hermaphroditum*	biomass-4; chemistry-6,23; physiology-1 [2]
	Jonasson *et al.* 1999 [4]				deciduous shrubs	biomass-4, chemistry-1,2,6,7 [4]
					evergreen shrubs	biomass-4, chemistry-1,2,6,7 [4]
					herbs (grasses & forbs)	biomass-4, chemistry-1,2,6,7 [4]
					mosses	biomass-4, chemistry-1,2,6,7 [4]
				6	*Arctostaphylos alpina*	biomass-5; leaf-1 [3]
					Betula nana	biomass-5; leaf-1 [3]
					Rhododendrom lapponicum	biomass-5; leaf-1 [3]
					Vaccinium uliginosum	biomass-5; leaf-1 [3]
					Empetrum hermaphroditum	biomass-5; leaf-1 [3]
					Vaccinium vitis-idaea	biomass-5; leaf-1 [3]
					Salix polaris x herbacaea	biomass-5; leaf-1 [3]
981 m a.s.l.	Stenström *et al.* 1997	25	T	2	*Saxifraga oppositifolia*	reproduction-1,5,10,11

				3	*Saxifraga oppositifolia*	reproduction-1,5,10,11
1150 m a.s.l.	Havström *et al.* 1993 [1]	26	L x F, F x T	3	*Cassiope tetragona*	biomass-5; leaf-2 [1]
	Michelsen *et al.* 1996 [2]			5	*Cassiope tetragona*	biomass-2; chemistry-6,23; physiology-1 [2]
	Graglia *et al.* 1997 [3]				deciduous shrubs	biomass-4, chemistry-1,2,6,7 [4]
	Jonasson *et al.* 1999 [4]				evergreen shrubs	biomass-4, chemistry-1,2,6,7 [4]
					herbs (grasses & forbs)	biomass-4, chemistry-1,2,6,7 [4]
					mosses	biomass-4, chemistry-1,2,6,7 [4]
				6	*Arctostaphylos alpina*	biomass-5; leaf-1 [3]
					Betula nana	biomass-5; leaf-1 [3]
					Rhododendrom lapponicum	biomass-5; leaf-1 [3]
					Vaccinium uliginosum	biomass-5; leaf-1 [3]
					Empetrum hermaphroditum	biomass-5; leaf-1 [3]
					Vaccinium vitis-idaea	biomass-5; leaf-1 [3]
					Salix polaris x herbacaea	biomass-5; leaf-1 [3]
Latnjajaure, Abisko, Sweden	Jones *et al.* 1997	27	T	1	*Salix herbacea*	reproduction-1,10,11
68°21'N 18°30'E	Welker *et al.* 1997	28	T	1	*Dryas octopetala*	reproduction-9,12
981 m a.s.l.	Alatalo & Totland 1997	29	T	2	*Silene acaulis*	reproduction-1,9-11
	Molau & Shaver 1997	30	T	1	*Eriophorum vaginatum*	reproduction-1,9
				2	*Eriophorum vaginatum*	reproduction-1,9
				3	*Eriophorum vaginatum*	reproduction-1,9
	Stenström & Jónsdóttir 1997	31	T	1	*Carex bigelowii*	leaf-2,3; reproduction-1,4,5,12
				2	*Carex bigelowii*	leaf-2,3; reproduction-1,4,5,12
	Molau 1997	32	T	1	*Cassiope tetragona*	leaf-2; reproduction-1,11
				1	*Ranunculus nivalis*	leaf-2,3; reproduction-1,5,9,11
				2	*Cassiope tetragona*	leaf-2; reproduction-1,11
				2	*Ranunculus nivalis*	leaf-2,3; reproduction-1,5,9,11
				3	*Cassiope tetragona*	leaf-2; reproduction-1,11
				3	*Ranunculus nivalis*	leaf-2,3; reproduction-1,5,9,11
	Shevtsova *et al.* 1997	33	T x W x acid x removal	2	*Empetrum nigrum*	leaf-5
				2	*Vaccinium vitis-idaea*	leaf-5
				3	*Empetrum nigrum*	biomass-5,7-10; leaf-2,5

				3	*Vaccinium vitis-idaea*	biomass-5,7-10; leaf-2,5,6
Ny-Alesund, Svalbard, Norway	Havström *et al.* 1993	34	F x T x L	2	*Cassiope tetragona*	biomass-5; leaf-2
78°56'N 11°50'E	Wookey *et al.* 1993 [1]	35	F x T x L	1	*Dryas octopetala*	reproduction-2,3 [1]; biomass-5,6; chemistry-6; physiology-1 [2]
22 m a.s.l.	Welker *et al.* 1993 [2]			2	*Polygonum viviparum*	biomass-1; leaf-2,3,4,6,; reproduction-5,7,8,12-14 [3]
	Wookey *et al.* 1994 [3]			3	*Dryas octopetala*	biomass-2; chemistry-6-8; leaf-6; reproduction-2,5,8,12-14; physiology-5-8 [4]
	Wookey *et al.* 1995 [4]					
	Baddeley *et al.* 1994	36	N x P	1	*Cassiope tetragona*	biomass-2; chemistry-6,7; physiology-7-11
				1	*Dryas octopetala*	biomass-2; chemistry-6,7; physiology-7-11
				1	*Salix polaris*	biomass-2; chemistry-6,7; physiology-7-11