Winter Climate Change in Tundra Ecosystems: The Importance of Snow Cover

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Chapter 1

General introduction

Dwarf shrub heath, or tundra, is one of the most widespread ecosystem types on the globe. It covers large regions at high latitudes and at high altitudes, accounting for 5 to 10 % of the world's land surface (Koerner, 1999; Post *et al.*, 1982). Studying the ecology of tundra ecosystems is of particular relevance in our world subject to rapid changes in climate: (1) the climate is changing fastest at high latitudes and altitudes, thus, these ecosystems are currently experiencing rapid changes in their natural environment (ACIA, 2004; IPCC, 2001). (2) Tundra soils store more than 90% of the carbon present in this ecosystem (IPCC, 2001), thus they have been a carbon sink for many centuries. Plant growth and litter decomposition are the two main processes driving carbon accumulation or release rates, and they both are highly sensitive to climate change. Changes in the balance between these two processes will decide upon whether tundras will be carbon sinks in the future, or develop into carbon sources, and thus, further enhance the greenhouse effect. Therefore, the response in plant growth and litter decomposition to changing climate conditions is a crucial component in predicting future climate warming.

Current climate warming, although often expressed as the rise in the global annual mean temperature, is not uniform in space and time. Warming rates have not only been greater at high latitudes and high altitudes than in other areas of the world, but temperatures in these regions have also increased more in winter than in summer (ACIA, 2004; IPCC, 2001). Climate scenarios over the next 100 years for the arctic predict that the future rise in temperatures will be approximately twice that of the global mean. Furthermore, the temperature increase is predicted to be much more pronounced in winter than the rest of the year (ACIA, 2004). Similar patterns of climate change have been found, and are predicted in the European Alps (Begert *et al.*, 2005; OcCC, 2004).

Warmer temperatures generally accelerate the hydrological cycle (driven by enhanced evaporation), and thus, an increase in precipitation is predicted on a global scale (IPCC, 2001). However, regional and seasonal predictions of future precipitation patterns are rather inaccurate compared to the relatively detailed predictions of the future warming patterns (Evans, 2006; IPCC, 2001). The consequences of increased summer temperatures on tundra ecosystem processes have been studied extensively in recent years (see Arft *et al.*, 1999; Dormann & Woodin, 2002; Walker *et al.*, 2006 for meta-analyses), but only few studies have looked at the effects of warmer winters, thinner snow covers, and decreased snow cover extents.

Climate change and the winter snow cover

Although the precipitation has risen at high latitudes (Evans, 2006) and in the European Alps over the last decades (Schmidli *et al.*, 2002, this thesis, chapter 5), the snow cover is decreasing in many regions of the world. The snow cover extent (i.e. snow covered surface * snow cover duration) has been decreasing rapidly on the Northern hemisphere, mainly due to an earlier snowmelt, not due to later snowfalls in autumn (Brown, 2000; Frei & Robinson, 1999; Rikiishi *et al.*, 2004). Snowmelt has advanced by several days per decade in most regions of the Arctic (see Fig. 1), but some continental areas show a delay in snowmelt, probably because winter precipitation has risen (Heino *et al.*, 2006). Generally, the advanced snowmelt is attributed to higher spring temperatures (Brown, 2000; Groisman *et al.*, 1994).

In mountain areas, snow depth as well as snow cover duration have decreased (Brown, 2000; Laternser & Schneebeli, 2003; Mote *et al.*, 2005). In the European Alps, the decreasing snow depths and earlier snowmelt dates at lower altitudes are caused by a combination of a decreasing snow:rain ratio over the year and warmer temperatures in spring (Beniston, 1997; Laternser & Schneebeli, 2003; Scherrer *et al.*, 2004).

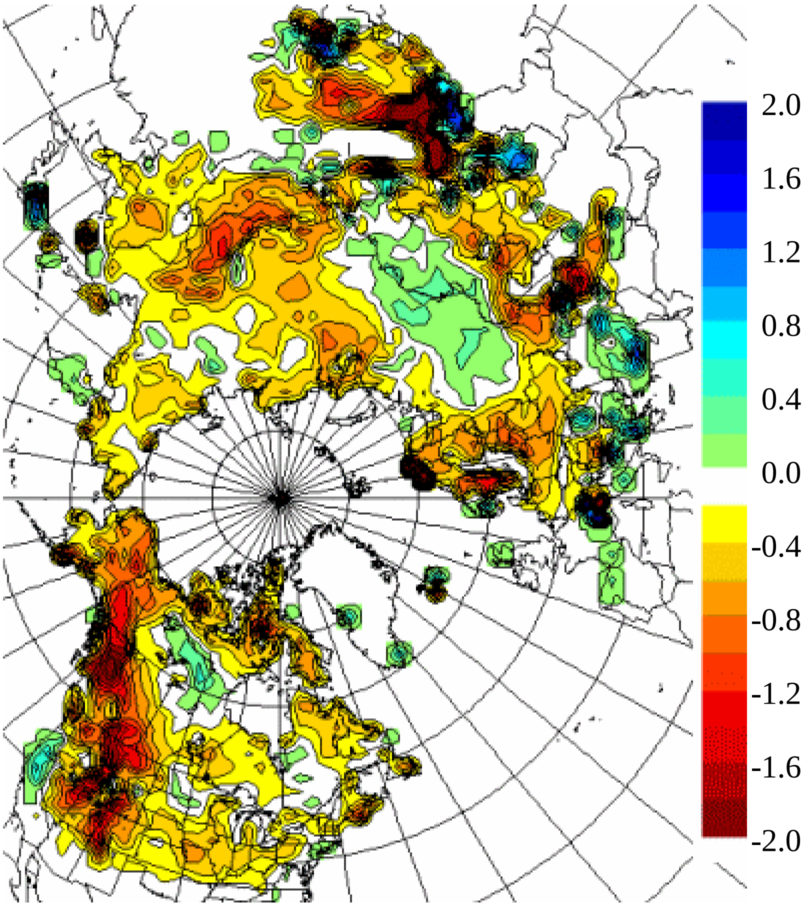


Figure 1. Average change in snow cover duration (in days per year) in the second half of the snow year (February-July) over the period 1972-2000. Derived from the NOAA weekly satellite snow cover dataset. Source: SOCC - State of the Canadian Cryosphere, http://www.socc.ca/snow/variability/index.cfm; 15.4.2006).

The role of snow in arctic and alpine ecosystems

Snow covers arctic and alpine landscapes for more than half of the year. By the ecologist, the snow covered period is often perceived as dormant, inactive, and thus irrelevant to biological research. However, many processes, especially biochemical ones, do not cease during winter, although slowing down considerably. Over the long duration of arctic and alpine snow seasons, however, these processes can add up to a significant amount of the annual ecosystem activity.

The snow cover characteristics influence the winter environment, and hence, the winter processes in terrestrial ecosystems of arctic and alpine regions in several important ways (Fig. 2, Table 1). Snow defines the plant and soil temperatures during winter due to its temperature insulation capacity (which mainly depends on snow depth and density (Rixen *et al.*, 2004; Sturm *et al.*, 1997; Taras *et al.*, 2002)). The depth of the snow cover, together with the spring temperatures, also defines how fast and when the snow cover disappears. The snowmelt date marks the start of the potential growing season, which is then ended by the formation of a continuous snow cover in autumn.

Besides these direct effects on winter temperatures and growing season length, the snow cover also indirectly influences the temperature conditions during the growing period. A very deep winter snow cover requires a high sum of above-freezing temperatures to melt, and therefore delays the start of the growing season to a point when daily temperatures are high and frost events are rare. The opposite could happen if thin snow covers melt during the first warm spring days, which are often followed by periods of cold weather again. Thus, under a climate with less snow and earlier snowmelt, tundra plants could face a trade-off between exploiting the prolonged growing season and experience more frosts and lower overall temperatures. Only little is known about how tundra plants plants deal with this trade-off, and how ecosystem processes and vegetation structure will be affected in the short and longer term.

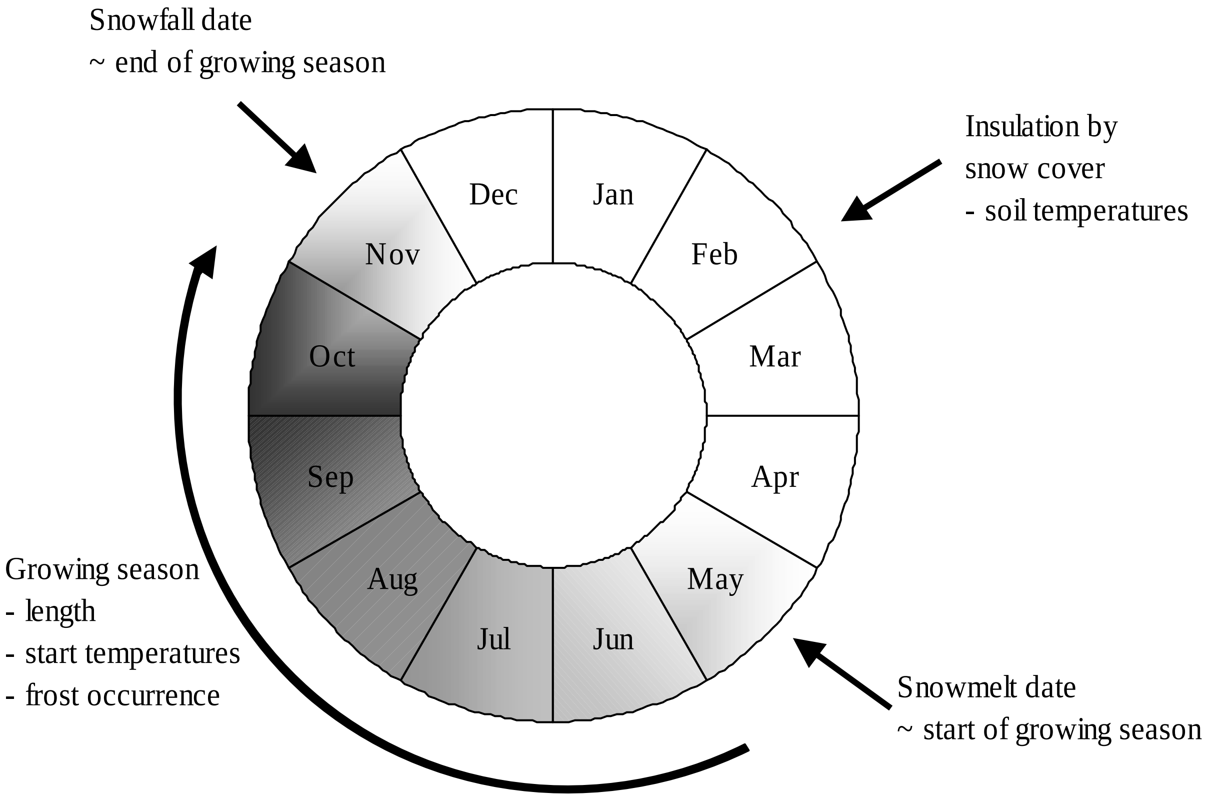


Figure 2. Main effects of the snow cover on soil and plant temperatures and growing season.

Table 1: Properties, ecological significance and impact of snow cover charateristics on soil and vegetation.

Snow property	Ecological significance	Impact on ecosystems
Physical properties		
Low temperature conductivity	Plant & soil temperature	→ Temperature insulation in winter → Decoupling of air and soil temperature (winter: $t_{air}>t_{soil}$, summer: $t_{air}<t_{soil}$) → Dampening of temperature fluctuations
Layer formation	Physical protection	→ Protection from trampling, grazing, scouring of ice crystals etc.
	Growing season length	→ Start of growing season is closely related to snowmelt (= increase in light, water, nutrient availability)
	Spring climate	→ Climate conditions just after snowmelt correlate to some degree with snowmelt date (the earlier, the lower are temperatures, and the more frequent frosts)
Specific weight (wet snow)	Mechanical damage	→ Heavy loads of wet snow can uproot or break plants
Viscosity	Mechanical damage	→ Snow setting, creeping, and gliding can uproot or damage plants
Mass movements	Mechanical damage	→ Bending, uprooting and breaking of plants through avalanches
	Snow redistribution	→ Redistribution of snow through avalanches and, thus, changes in snowmelt timing, nutrient & water input
Chemical properties		
Water content	Water supply	→ Water from snow cover is released as a pulse in a short time during snowmelt
Chemical composition	Nutrient supply, chemical compounds	→ Chemical compounds, nutrients, and litter particles accumulate in the snow pack and are released during snowmelt

Outline of this thesis

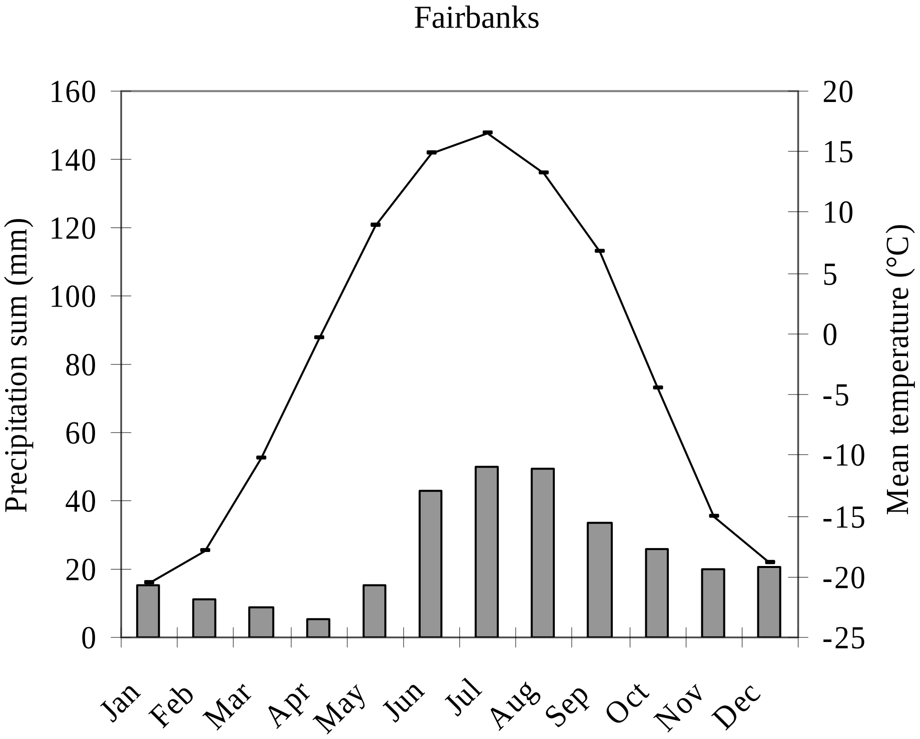
Study sites

The field studies for this thesis were conducted in subarctic tundra on Murphy Dome in Interior Alaska, USA (chapters 3 and 4) and in alpine dwarf shrub heath near on Stillberg, near Davos, Switzerland (subsequently called alpine tundra, chapters 5 and 6), as well as in several ski resorts in the Swiss Alps (chapter 7). The sites will be described in more detail in the individual chapters; here, I point out some common characteristics and differences between the subarctic and alpine site.

Both sites have similar annual mean temperatures, and both are continuously snow covered in winter over a similar proportion of the year. However, the temperature course over the year and the precipitation patterns, and thus, the snow cover are fundamentally different. Interior Alaska has a continental climate with very cold and dry winters and warm summers (Fig. 3). Precipitation amounts to approximately 300 mm per year, mostly falling in the warmest period (June to August), which is also the most important time for plant growth. The snow cover depth remains below 0.5 m in most winters, barely deep enough to cover the tundra dwarf shrubs. The insulation capacity of such a thin snow cover is not enough to decouple air and soil temperatures over winter (Haeberli, 1973), resulting in frozen soils and relatively high temperature fluctuations below the snow pack (Fig. 4).

In contrast, the winters at treeline in the central alpine valley of Davos are relatively mild and snow rich. Summers are cool and moist, with most of the annual precipitation falling as rain between June and September, but cold spells and snowfall can occur at any month (Fig. 3). Snow covers usually build up in October, and are deep enough to keep the soil temperatures decoupled from air temperatures, resulting in soil temperatures at around 0°C throughout much of the winter. However, the date of first snow cover formation is highly variable, and late snowfall in some years (e.g. in 2003, see Fig. 4), may cause the soils to freeze mildly at the start of the winter season.

At both sites, considerable changes in climate have been measured over the last decades. Temperature increases at both sites have been above global average, and greater in winter and spring than in summer (ACIA, 2004; Begert *et al.*, 2005; IPCC, 2001). The effects of rising winter temperatures on the snow cover, however, could be diametrically different at the two sites. In continental winters, such as in Interior Alaska, temperatures are often too cold for any precipitation to fall (Kitaev *et al.*, 2002). Thus, a warming in the winter could lead to a higher amount of winter precipitation. In contrast, higher temperatures could also decrease the rain:snow ratio in the “shoulder seasons”, i.e. during late fall when the snow cover forms, and during spring when it melts. Future climate change might therefore strongly influence early winter and spring conditions (Olsson *et al.*, 2003). In mountain regions, however, warmer temperatures during precipitation events will increase the snow line (i.e. the altitude above which precipitation falls as snow), resulting in a decreased snow:rain ratio and a decreased snow depth and snow cover extent over the year (Rebetez, 1996). At lower altitudes of the European Alps, this trend towards thinner snow covers and earlier snowmelt dates is significant (Beniston, 1997; Laternser & Schneebeli, 2003; Scherrer *et al.*, 2004), but higher altitudes might be affected in the near future (Hantel *et al.*, 2000; Wielke *et al.*, 2004).



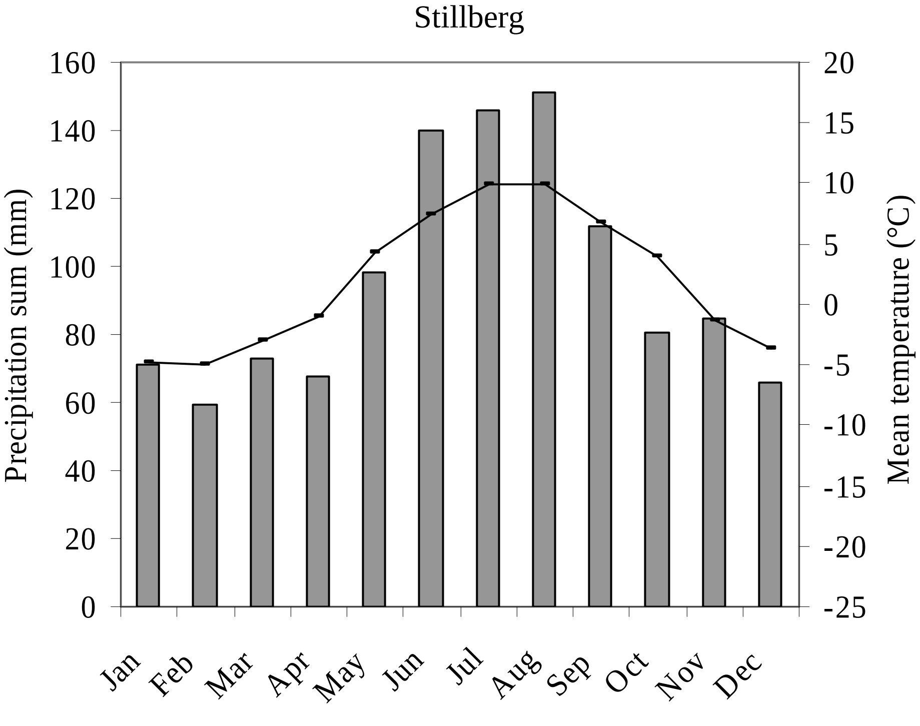


Figure 3: Climate diagrams for Fairbanks, Alaska (approx. 25 km from the Alaskan research site Murphy Dome) and Stillberg, Davos (approx. 300 m from my alpine research plots). Values are monthly means over 30 years (1971-2000 in Fairbanks, 1975-2004 on Stillberg). Bars: monthly precipitation, line: course of monthly mean temperatures.

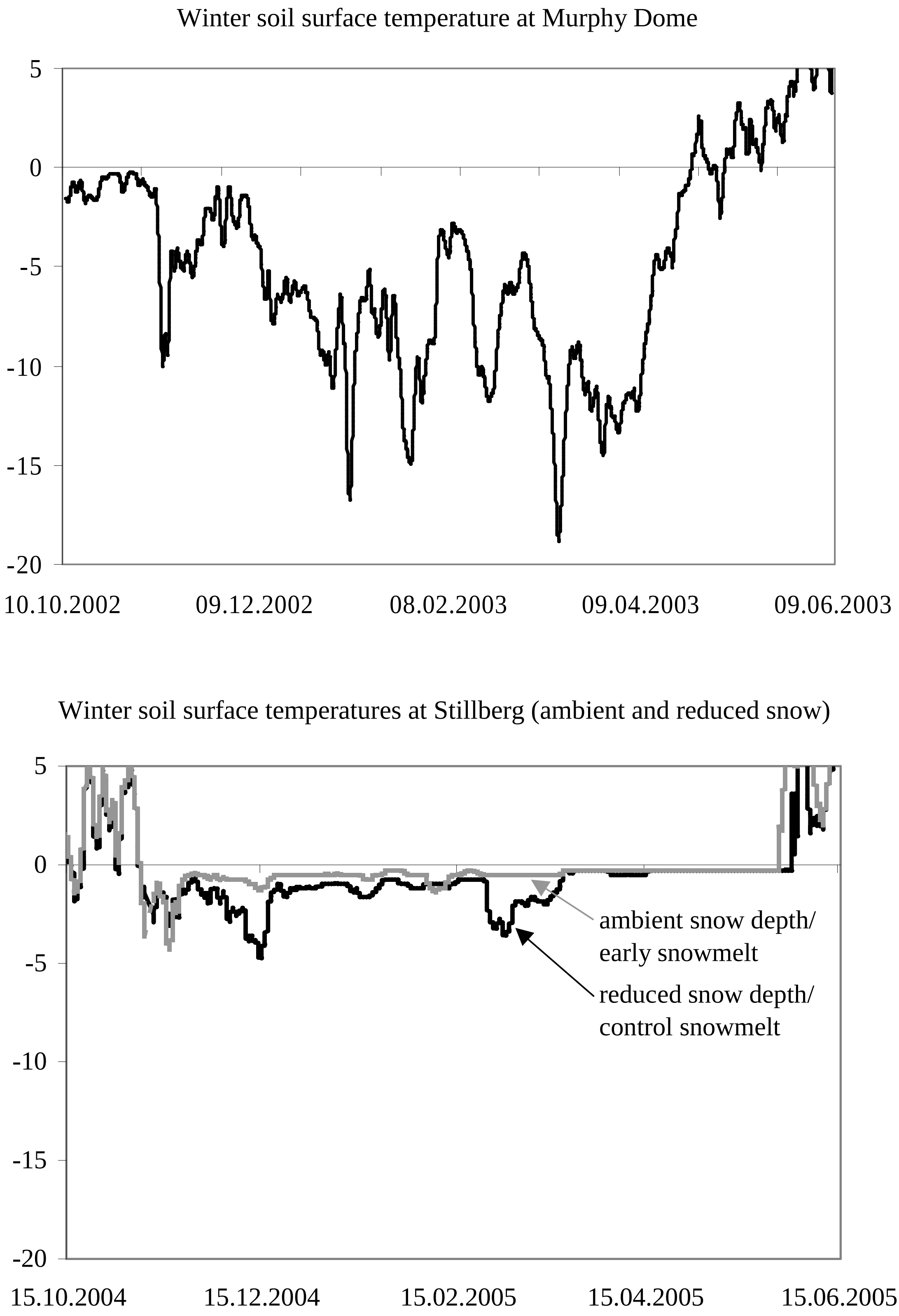


Figure 4: Winter temperatures at soil surface (daily means) in 3 representative study plots. Above, black line: plot with ambient snow depth (approx. 0.3 m) and ambient snowmelt at Murphy Dome, Fairbanks, Alaska in winter 2002/2003; below, grey line: plot with ambient snow depth (approx. 1.7 m) and advanced snowmelt; below, black line: plot with reduced snow depth (approx. 0.4 m) and ambient snowmelt. The two measurements below were taken at Stillberg, Davos, Switzerland in winter 2004/2005, at a distance of approx. 4 m.

Vegetation and study species

The tundra vegetation at both study sites is a relatively species poor dwarf shrub heath near treeline, dominated by ericoid species. The two sites, although lying on different continents, are relatively similar in vegetation structure and species composition (see Table 2). In our experiment, we included the species growing in at least 15 plots.

Table 2: List of the most abundant tundra species at the Alaskan and Swiss field sites, and their occurrence and frequency in the study plots prior to the start of the experiments. The mean abundance within plots where the species occurred was calculated as the mean percentage of squares occupied in a frame with 25 squares. The total number of plots was 27 in Alaska and 32 in Switzerland.

Murphy Dome, Fairbanks, Alaska USA (approx. 850 m asl)				
Scientific species name	Common name English	Growth form	Abundance in plots (%)	In % of plots
Ledum palustre L. ssp. *decumbens* (Ait.) Hultén	Labrador tea	Evergreen dwarf shrub	99	100
Vaccinium vitis-idaea L. ssp. *minus* (Lodd.) Hultén	Lingonberry	Evergreen dwarf shrub	92	100
Vaccinium uliginosum L.	Bog blueberry	Deciduous dwarf shrub	91	93
Carex bigelowii Torr. ex Schwein.	Bigelow's sedge	Graminoid	89	100
Empetrum nigrum L. ssp. *hermaphroditum* (Lange ex Hagerup) Böcher	Crowberry	Evergreen dwarf shrub	74	100
Cassiope tetragona (L.) D. Don	White mountain heather	Evergreen dwarf shrub	49	52
Betula nana L.	Dwarf birch	Deciduous dwarf shrub	48	100

Stillberg, Davos, Switzerland (2200 m asl)				
Scientific species name	Common name English German	Growth form	Abundance in plots (%)	In % of plots
Vaccinium myrtillus L.	Bilberry Heidelbeere	Deciduous dwarf shrub	92	100
Vaccinium uliginosum ssp. *gaultherioides* Bigelow	Alpine bog blueberry Rauschbeere	Deciduous dwarf shrub	82	97
Empetrum nigrum L. ssp. *hermaphroditum* (Lange ex Hagerup) Böcher	Crowberry Krähenbeere	Evergreen dwarf shrub	79	91
Loiseleuria procumbens (L.) Desv.	Alpine azalea Alpenazalee	Evergreen dwarf shrub	65	78
Vaccinium vitis-idaea L.	Lingonberry Preiselbeere	Evergreen dwarf shrub	61	41
Rhododendron ferrugineum L.	Rusty-leaved alprose Rostblättrige Alpenrose	Evergreen dwarf shrub	20	41
Recorded for changes in abundance: lichens, *Avenella flexuosa*, *Gentiana punctata*, *Helictotrichon versicolor*, *Homogyne alpina*, *Melampyrum sylvaticum*, *Nardus stricta*, *Solidago virgaurea*				

Experimental approaches

In this thesis, I explore the responses of arctic and alpine tundra plants to changes in winter climate, using snow manipulation treatments that are imitating relatively realistic scenarios of a future snow cover. Two different characteristics of the winter snow cover were manipulated in the field experiments described in this thesis: snowmelt timing and snow depth. The snowmelt timing, which is naturally influenced by the depth of the snow cover and the spring temperatures, was manipulated by adding or removing snow prior to snowmelt, when plants were still snow covered (to avoid mechanical damages). In the field experiments in subarctic tundra in Interior Alaska (chapters 3 and 4), the snowmelt was advanced and delayed by approximately one week compared to control plots to imitate the climate scenarios predicting an earlier snowmelt due to warmer springs, or a later snowmelt due to increased winter precipitation.

At the alpine treeline in Switzerland, moreover, the snow depth was reduced during winter by shovelling away the snow cover down to approximately 40 cm (approx. the natural snow depth at the subarctic site). The snow cover thus had a lower insulation capacity, causing the soil temperatures to drop and to become more variable (Fig. 4, blue line below). This snow reduction treatment was combined with that of an advanced spring snowmelt in a fully factorial experiment. Thus, the treatments imitate snow cover characteristics that could be occurring more often in the future as a consequence of a decreased rain:snow ratio, but also allow the quantification of the effects of the individual snow characteristics.

After the snow manipulation treatments, I recorded the differences in phenology, growth, reproduction and abundance of these species between different snow cover treatments (the latter only in the alpine site). Furthermore, we tested mechanisms that influence species growth, vegetation composition and carbon turnover by testing for hierarchical relationships between these different measurements, and by performing a study on species interaction and on litter decomposition processes. The duration of the studies was one year at the subarctic site and two years (and ongoing) at the alpine site.

Outline of the individual chapters

Chapter 2: Winter climate change in alpine and arctic ecosystems: a review of snow manipulation experiments (with Christian Rixen)

Snow manipulation experiments have been conducted in various ecosystems and have applied different types of snow treatments with different magnitudes of deviations from the natural state. Often, these experimental treatments do not match a specific scenario of future winter climate in that ecosystem. One reason for this might be that regional scenarios of future snow depth or future snowmelt dates are often not available. Another reason is that these scenarios, if available, are difficult to match in field experiments. The only manipulation, which can be obtained easily and without manpower, is that of a deeper snow cover: it can be created by drifts forming in the lee of snow fences. This may have contributed to the fact that more studies have increased snow depth and prolonged snow cover, although climate scenarios predict advanced snowmelt timings in most seasonally snow covered ecosystems.

In this chapter, we review 42 published papers on snow manipulation experiments in mainly arctic and alpine ecosystems, and classify them according to the climate scenario they are simulating with their treatments. These scenarios include (1) an increase in snow cover and/or delayed snowmelt, (2) an earlier snowmelt, and (3) an earlier snowmelt combined with a summer warming treatment. We summarize the ecosystem responses in below-ground processes, plant phenology, growth, reproduction, and species composition, and discuss the findings in the light of current changes in arctic and alpine ecosystems due to climate change.

Chapter 3: Snowmelt changes in subarctic tundra: short-term responses are strongest in early-developing plant species

The future winter climate and snow cover characteristics in the Arctic are difficult to assess. On one hand, temperatures in winter and spring have risen much more than those in summer and fall during the last decades, and snowmelt has generally gotten earlier (ACIA, 2004; Serreze *et al.*, 2000). These developments are predicted to proceed by various models (ACIA, 2004). On the other hand, deeper snow covers due to increased snowfall, as found in some parts of the Arctic (ACIA, 2004; Ye & Mather, 1997; Ye *et al.*, 1998) could require more time to melt, and thus delay snowmelt.

To explore the consequences of a changing snow cover for subarctic ecosystems, I conducted a snow manipulation experiment in a tundra community near Fairbanks, Alaska. By removing and adding snow in spring, I generated two snowmelt scenarios, one advancing, and one delaying snowmelt by approx. one week. I then compared plant survival, phenology, growth, and reproduction of the most frequent tundra species between plots with and without snowmelt manipulations. Furthermore, I calculated for each species the correlation between the timing of the phenological development and the timing of snowmelt, as a measure of “synchrony” of a species’ development with snowmelt, and I explored whether this synchrony with snowmelt depended on the temporal niche of a species (i.e. how soon after snowmelt its phenological development starts).

The results show that, although the phenological development differed between treatments, relatively few tundra species responded to snowmelt in their growth and reproduction. The synchrony between the start of phenological development and snowmelt timing was highest in early-developing species. This suggests that these species should be more sensitive to changes in snowmelt than late-developing ones. In fact, a qualitative overview partly agreed with this hypothesis: If responses in plant fitness or reproduction were found, they occurred in early-developing species. Opposite to previous expectations, however, they were often negatively related to early snowmelt. By starting their life cycle early after advanced snowmelt, plants might have suffered from low temperature events occurring after the natural snowmelt date, while plants from controls might not have started their development yet by then, and plots with delayed snowmelt were still covered by snow.

Chapter 4: Advanced snowmelt causes shift towards positive neighbour interactions in a subarctic tundra community (with Christian Rixen and Christa P.H. Mulder)

Within the same experimental set-up as in the previous chapter, we tested how plant neighbour interactions were affected by changes in snowmelt. The interaction of a plant with its neighbours can both be detrimental and beneficial. Neighbours compete for the same limited resources, but at the same time, they facilitate each others life by improving the microclimate and growing conditions (e.g. lower wind speeds, higher air and soil moisture, lower temperature fluctuations, cover from herbivores etc. (Koerner, 1999)). Whether positive or negative interactions prevail in a given community, is influenced by its productivity on one hand (the more productive, the more severe is competition), and by the environmental conditions on the other (the more stressful the environment, the more can neighbours ameliorate the growing conditions).

By comparing the performance (survival, phenology, growth and reproduction) of shoots of two species with and without neighbours, we quantified the net neighbour effect on these species, and tested whether the importance of neighbours was changed by manipulations in snowmelt date.

Under ambient conditions and after delayed snowmelt, positive and negative effects of neighbours were generally balanced. When snowmelt was advanced, we found a net facilitative effect of neighbours on survival, phenology, growth and reproduction of *Empetrum nigrum*, the earlier developing of the two target species. Earlier snowmelt correlated with harsher growing conditions (i.e. colder spring temperatures, higher number of frosts), thus, we conclude that neighbours played an important role in ameliorating the physical environment at the beginning of the phenological plant development, and that this facilitation in early spring had long-lasting effects throughout the growing season.

Chapter 5: Winter climate change: how do alpine tundra plants respond to reduced snow depth and advanced snowmelt? (with Peter Bebi and Veronika Stöckli)

In contrast to arctic tundra ecosystems, where soils are deep frozen during winter due to a relatively shallow snow cover, soil temperatures in alpine tundra ecosystems stay around 0°C during winter. If a lower proportion of the winter precipitation would fall as snow in future climates, thinner snow covers with a reduced temperature insulation capacity, and thus, colder soil temperatures in winter could develop. The thin snow covers would melt earlier in spring and lead to an advanced start of the growing season. A decreasing snow:rain ratio and an advancing snowmelt have already been found at the study area Stillberg in the Swiss Alps (near Davos, Switzerland).

We tested how these predicted winter and spring conditions could affect plant phenology, growth, reproduction and community composition in a two-year field experiment in an alpine dwarf shrub community above treeline. We reduced snow cover during winter and advanced snowmelt in spring in a fully factorial design, resulting in four treatments: ambient snow depth/ambient snowmelt; ambient snow depth/advanced snowmelt; reduced snow depth/ambient snowmelt; and reduced snow depth/advanced snowmelt. Reducing snow depth resulted in decreased winter soil temperatures (Fig. 4, below). Advancing snowmelt resulted in a longer growing season, but also in a higher number of low-temperature events in early spring. Most species showed negative responses in growth and reproduction to advanced snowmelt, while snow depth changes had only minor effects on plants.

Using path analyses, we explored the mechanisms leading to these changes in plant growth after snowmelt manipulations, by analysing the direct and indirect interactions between the climate factors snowmelt date, frost occurrence, temperatures, and the responses in plant phenology and growth. Only one species showed a direct reaction in growth on snowmelt timing. The start of shoot growth, the temperatures during growth, and the frequency of frost events played a major role and did indirectly link snowmelt date and growth.

Chapter 6: Changes in snow cover affect litter decomposability and decomposition rate in alpine tundra (with Frank Hagedorn)

Tundra ecosystems have been accumulating carbon over the past centuries because plant growth had been faster than the decomposition of the plant biomass produced over long time periods. One of the most important questions in global change research in arctic and alpine ecosystems is whether tundra ecosystems will turn into C sources in a warming climate due to rising decomposition rates, or stay C sinks due to increasing plant productivity.

A considerable fraction of the above-ground litter is getting decomposed during winter in alpine and arctic ecosystems, due to a relatively large microbial and fungal community being active near freezing temperatures. Thus, a high amount of carbon is lost during winter. However, the microbial activity, and hence, the decomposition rate and carbon efflux, is strongly controlled by temperature, and small changes in the soil temperature in winter, as caused by a changed snow cover, could have strong effects on these soil processes. Another strong control of decomposition is the chemical composition of the litter. The findings of the previous chapters suggest that snowmelt timing could affect the litter composition, and thus, indirectly influence the decomposition process.

We tested the effects of snow cover changes on the decomposition process in a two-year hierarchical experiment. The impact of snow cover changes on the litter quality was tested by manually manipulating snowmelt timing in alpine tundra (early and late snowmelt), and analysing the morphological and chemical characteristics of leaves of the two dominating deciduous dwarf shrubs. We then used their litter in a litter decomposition experiment in the following winter. Besides testing for differences in the decomposability of the two litter types, we also explored the effects of snow cover characteristics on the litter mass loss by manipulating snow depth over winter and snowmelt timing in spring.

Litter from leaves produced after early snowmelt in the first spring lost less mass than that from late-melting sites, although differences in the chemical composition were minor. The effect might have been caused by larger leaves, which are decomposed at a lower rate than small leaves. Reduced snow depth caused colder soil temperatures during the process of decomposition, which further decreased litter mass loss. Our experiment thus revealed two different ways how snow reduction could decrease litter decomposition, and thus slow down carbon and nutrient cycling in alpine tundra communities.

Chapter 7: Effects of ski piste preparation on alpine vegetation (with Christian Rixen, Markus Fischer, Bernhard Schmid and Veronika Stöckli)

To ensure a long enough skiing season in a changing winter climate with less snow, an increasing number of alpine ski resorts rely on the application of artificial snow. Artificial snow consists of small ice crystals, which form as water (often taken from rivers or lakes) is sprayed into the cold air. Artificial snow, which is applied additionally to the natural snow cover, roughly doubles the snow cover. Hence, the snow disappears much later on these pistes than on adjacent sites. On ski pistes with natural snow, on which the natural snow cover is compressed, however, soil temperatures are reduced and soil freezing induced, similar to our experiments in the previous two chapters. Thus, ski piste manipulations offer the opportunity to study the long-term effects of added snow and reduced soil temperatures on the alpine vegetation.

In 12 Swiss alpine ski resorts, we investigated the effects of ski piste preparation on the vegetation structure and composition using a pairwise design of 38 plots on ski pistes and 38 adjacent plots off-piste. Plots on ski pistes in general had lower species richness and productivity, and lower abundance and cover of woody plants and early flowering species than reference plots. The longer artificial snow had been used on ski pistes (2–15 years), the higher were the moisture and nutrient indicator values. Longer use also affected the vegetation composition by increasing the abundance of woody plants, snowbed species and late-flowering species, and decreasing the cover of wind-edge species.

All types of ski piste management caused deviations from the natural structure and composition of alpine vegetation, and led to lower plant species diversity. The reactions of species with different flowering timing, and from communities associated with extremely short (wind-edges) or long snow covers (snowbeds) were generally in line with the growth responses of such plant species in our previous experiments.

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Chapter 2

Winter climate change in arctic and alpine ecosystems: a review of snow manipulation experiments

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Abstract

Snow is an important climate factor in arctic and alpine ecosystems. It defines the soil temperatures during winter season, but also the start and the length of the growing season. The snow cover is strongly affected by climate change, as temperature and precipitation patterns are changing. Changes in snow depth and snowmelt timing can affect arctic and alpine ecosystems at different levels and modify vegetation, hydrology and nutrient and carbon cycling in the longer term. Interactions between snow and ecosystems have been studied with surveys and monitoring studies, and recently also by experimental studies manipulating the snow cover.

In this paper, we review 42 published papers on snow manipulation experiments in arctic and alpine ecosystems according to the climate scenario, which they are simulating with their experimental treatments. These scenarios include (1) an increase in snow cover and/or delayed snowmelt, (2) an earlier snowmelt, and (3) an earlier snowmelt combined with a summer warming treatment. We summarise the responses of soil processes, plant phenology, growth, reproduction, and species composition to these scenarios, and discuss them in the light of the current changes in climate in arctic and alpine regions.

Introduction

Snow is a crucial factor in arctic and alpine ecosystems. Its effects on ecosystems is not restricted to the winter season, during which it determines soil surface temperatures and frost depth, but it also affects the timing and amount of water and nutrient release in spring, and defines the start and length of the summer growing season. Global change is likely to affect high latitudes and altitudes most (ACIA, 2004; IPCC, 2001), and resulting changes in the timing, amount and duration of the winter snow cover in the Arctic (Brown, 2000; Frei *et al.*, 1999; Groisman *et al.*, 1994b; Serreze *et al.*, 2000) and in mountain ranges (Beniston, 1997; Laternser & Schneebeli, 2003; Mote *et al.*, 2005) are already evident. These changes in snow cover characteristics may affect ecosystems at different levels, and could alter e.g. species performance and species interactions in the short term, and vegetation patterns, biodiversity, ecosystem functioning, hydrology and biogeochemistry in the longer tem (Campbell *et al.*, 2005). Apparent vegetation and ecosystem changes attributed to changes in snow cover include the extension of shrub cover in Arctic tundra (Sturm *et al.*, 2001b; Tape *et al.*, 2006) or a trend to earlier greening in Arctic tundra (Shabanov *et al.*, 2002).

Potential consequences of changes in snow cover have been addressed in numerous experimental studies, but responses on multiple levels such as biogeochemistry, plant performance or vegetation composition have not yet been explored and combined in a comprehensive review. In contrast to experiments increasing CO2 or temperature, which often simulate well-defined scenarios (e.g. CO2 concentration expected in 2050), only few snow manipulation treatments match a specific winter climate scenario for the region or the community in question. The reason for this probably is that exact predictions for snow cover changes are often not available or difficult to match by manipulation treatments (a general problem in climate change experiments). Lastly, it has not been explored whether the response patterns found in snow manipulation studies are general enough to predict responses of different communities, or the reverse case (early / late snowmelt). These reasons emphasise the need for a comprehensive review that combines and discusses findings from a large number of different snow manipulation experiments.

In this review, we address the importance of snow as an ecological factor in the current climate change debate. We briefly resume the spatial and temporal aspects of snow cover variability and explore how snow defines the growing conditions for plants, and how snow modifies them under current climate change. We divide the published literature on snow manipulation experiments in alpine and arctic ecosystems into three categories of climate scenarios, which the studies have simulated with their snow treatments. We then review and generalise the responses in belowground processes, plant phenology, growth and reproduction, and species composition to these scenarios, and finally discuss these findings in the light of the current changes in climate and ecosystems.

Ecological significance of snow cover variations in space and time

Spatial aspects

Snow has long been known to determine many ecological processes. Due to the interaction between landscape relief and wind, avalanches and solar radiation, snow is deposited and ablated in irregular patterns, thereby creating large differences in snow depth and snow melt dates between sites (Table 1). The patterns of snow ablation are often very stable and recurrent year after year, while the absolute timing of snowmelt is highly variable between years. In arctic and alpine regions, the microtopography and the distribution of snow thus create a mosaic of sites with contrasting environmental conditions, which in turn can create clearly visible patterns in plant development, productivity, or communities (Choler, 2005; Schaefer & Messier, 1995; Walker *et al.*, 1993).

The two opposite sides of the gradient of snow deposition are ‘wind edges’, i.e. wind exposed ridges and edges with little or no snow deposited during winter, and therefore, unpersistent snow covers on one hand, and snowbeds, i.e. shady depressions or bowls, where snow accumulates and persists until late summer, on the other hand. Both extremes are habitats with strong constraints for plant growth: temperature extremes and fluctuations, freeze-thaw cycles, drought, wind and mechanical damages on wind edges and extremely short growing seasons, waterlogged, organic soils and slow nutrient turnover in snowbeds. Thus, the inhabiting plant species are highly specialized and form typical plant communities. Descriptions and classifications of the vegetation types in such extreme habitats might have been the very first studies of snow–plant interactions (Braun-Blanquet, 1973; Braun-Blanquet & Jenny, 1926; Harshberger, 1929; Heer, 1835) and are still made in recent times (Gibson & Kirkpatrick, 1985; Koroleva, 1999; Razzhivin, 1994; Tomaselli, 1991; Wahren *et al.*, 2001). As the first truly ecological approaches to understand the conditions of such extreme snow sites, the micro-climate and environmental characteristics were measured and environmental conditions for their specialized vegetation communities described (Bell & Bliss, 1979; Billings & Bliss, 1959; Canaday & Fonda, 1974). In the vicinity to wind edges and snowbeds, gradients of snow depth and season length are very steep, causing growing conditions, species occurrences, vegetation composition, and plant performance to change on a small spatial scale. These gradients and their effects on the vegetation composition, plant fitness and fecundity, and ecosystem processes have been the focus of many recent ecological studies (Evans *et al.*, 1989; Evans & Fonda, 1990; e.g. Holway & Ward, 1963; Kudo *et al.*, 1999; Ostler *et al.*, 1982; Stanton *et al.*, 1997).

Studies of environmental gradients are only of limited value to assess consequences of rapid changes in climate, though. As these gradients and the typical communities associated with them have developed over long time scales, short-term changes might result in considerably different communities than those existing along natural gradients. Therefore, additional experimental approaches are needed to assess short- and long-term environmental changes.

Table 1: Factors influencing snow depth and timing of snowmelt, and typical characteristics of sites at the two extreme ends of a snowline gradient, wind edges and snowbeds.

	“Wind edges”	Snowbeds
Wind	Ridges, edges, peaks	Bowls, lee sides of obstacles, such as rocks, shrubs etc.
Avalanches	Steep slopes and zones where snow is eroded	Avalanche runout zones
Solar radiation	Slopes exposed to south and west	Flats, slopes exposed to north and east
Resulting snow condition	Shallow, unpersistent snow cover, early melt	Deep snow cover, late melt
Examples of characteristic plant species in subarctic and European alpine communities	Lichens (*Cetraria* and *Cladonia* spp.), *Loiseleuria procumbens*, *Kobresia myosuroides*	*Cassiope tetragona*, Bryophytes (*Polytrichum sexangulare*), *Soldanella* spp.

Temporal aspects

There is a considerable natural variability of the snow cover, largely due to stochastic fluctuations in precipitation and temperature. Therefore, the ecologically significant traits related to snow cover, such as snow depth and the timing of snowmelt, are notoriously variable between years. Traditional knowledge about the ecological role of snow might have originated in the experience of snow variability and its consequences for single plant species (Brandegee, 1879) or the productivity of agricultural grasslands (Palmer, 1918). North-American farmers, as cited in Palmer (1918), were aware of beneficial effects of a deep snow cover on the productivity of their meadows, stating that “a snow year [is] a rich year” and terming snow as “poor man’s manure”. Increased insulation during winter, high water input in spring, or decreased spring frosts due to late snowmelt could all add to this overall positive effect of snow-rich winters. Studies of long time series have shown that responses in plant phenology, growth and reproduction to differing winter characteristics are often comparable to responses to summer conditions (Callaghan *et al.*, 1989; Inouye *et al.*, 2002; Selas, 2000; Walker *et al.*, 1995; Walker *et al.*, 1994).

Climate scenarios simulated in experimental studies

Effects of the snow cover on vegetation, communities and ecosystems have been described in numerous studies. Studies to evaluate the ecological effects of changes in snow cover in the context of future climate change include (1) research along natural snow gradients, (2) transplanting of plants or turfs between sites with a different snow regime, and (3) manipulations of snow conditions. In this review we focus on the studies on snow manipulation. Based on the actual snow treatments of the respective studies, we distinguish three different climate scenarios.

Climate scenario 1: Increased snowfall or snow accumulation, resulting in delayed snowmelt

Increases in winter precipitation are mainly expected in the arctic regions (IPCC, 2001). Moreover, increasing shrub cover, as currently establishing in the Arctic, and rises in treelines create sites of deep snow accumulations by trapping of snow between bushes and trees in regions with formerly low vegetation and shallow snow cover.

The main consequences of increased snowfall for the growth conditions of terrestrial ecosystems are (1) a deeper snow cover with a higher insulation capacity, leading to increased and less fluctuating winter ground temperatures in climates where the snow cover was previously not sufficient to uncouple air and soil temperatures, (2) an increased microbial activity (see Sturm et al. (2005) for a review), (3) a delayed snowmelt and thus a shortened growing season, and (4) an increase in soil moisture due to water released from the snow cover.

Climate change experiments have often simulated deeper snow cover by inducing snow accumulation in the lee of obstacles. Snow fences, as those originally constructed for winter road maintenance (Tabler, 1991), have most often been used to study snow-plant interactions in alpine (Bell & Bliss, 1979; Brooks *et al.*, 1997; Smith *et al.*, 1995; Stanley *et al.*, 1998; Walker *et al.*, 1993; Weaver & Collins, 1977; Webber *et al.*, 1976) and arctic ecosystems (Scott & Rouse, 1995; Wahren *et al.*, 2005; Walker *et al.*, 2001; Walker *et al.*, 1999; Walsh *et al.*, 1997). Open Top Chambers (OTCs), originally used to passively increase air temperatures during the growing season in ITEX experiments (Henry & Molau, 1997), also trap snow if left in place during winter (Marion *et al.*, 1997), and have recently been used to increase snow depth in an arctic site with shallow winter snow cover (Aerts *et al.*, 2004; Dorrepaal *et al.*, 2003). A few studies have combined increased winter snow cover with summer warming using the OTC passive warming method: the studies in Toolik Lake, (arctic tundra) and Niwot Ridge (alpine meadow) have used winter snow accumulation by fences in combination with warming by OTCs (Jones *et al.*, 1998; Walker *et al.*, 1999). Moreover, experiments with OTCs left in place over winter to accumulate snow, and used for passive warming in spring (thereby melting the snow earlier) and summer were conducted in a subarctic fen in Abisko (Aerts *et al.*, 2004; Dorrepaal *et al.*, 2003). In some approaches snow cover was manually increased in spring by shovelling snow on plots (Galen & Stanton, 1993; Knight *et al.*, 1979; Van der Wal *et al.*, 2000; Wipf *et al.*, 2006, this thesis, chapters 3 and 4), thereby delaying snowmelt, but not increasing insulation and soil temperatures in the coldest time of the winter.

Climate scenario 2: Decreased snowfall, resulting in advanced snowmelt and cold spring temperatures

Increases in temperature are predicted for many regions of the world, especially for high latitudes and high altitudes, and winter temperatures might be more affected than those in summer (IPCC, 2001). As a consequence, a higher proportion of the winter precipitation could fall as rain instead of snow and lead to shallower and less persistent snow cover in regions with previously deeper and longer snow covers. Signs for such processes are already apparent in different mountain areas (Mote *et al.*, 2005; Rikiishi *et al.*, 2004; Scherrer *et al.*, 2004).

The growth conditions for plants and soil organisms are affected in two ways: if snow depth falls below a threshold of approx. 30 to 50 cm, the insulation capacity of the snow cover is too low to decouple air and soil temperatures. As a consequence, a reduced snow cover due to warming can cause an increase in soil frosts and the frequency of freeze-thaw cycles, thus inducing “colder soils in a warmer world” (Groffman *et al.*, 2001a). The thinner the snow cover, the less energy is necessary for it to melt, and the more advanced will snowmelt be. On one hand, early snowmelt extends the growing season. On the other hand, however, a disproportionally early snowmelt can lead to an increased occurrence of cold temperatures and frost events, because the start of the growing season is shifted towards an earlier, usually cooler and often very variable time of the year. Thus, frost frequency at high altitudes could remain at a high level (Auer *et al.*, 2005) or could even increase.

As an example, correlations between climate parameters of a 30-year record (1975-2004) from the treeline research site of Stillberg, Davos (Switzerland) are shown (Table 2). Mean annual, winter, spring, and growing season temperatures have significantly and linearly increased since the start of the measurements. In line with the warmer temperatures, the proportion of snowfall at the total annual precipitation sum has decreased, and snowmelt has become significantly earlier. Regardless of the overall increase in temperature, the number of summer frosts (i.e. days with temperatures below freezing) has not decreased significantly over time. Rather, it was negatively correlated with snowmelt date, leading to a counter-intuitive situation: the earlier snow melted due to warming and the shift from snowfall to rain, the more numerous were frost events during the growing season.

To test for potential effects of an extended growing season with an earlier start and colder temperatures just after snowmelt, researchers have advanced snowmelt date and measured the impact on arctic and alpine ecosystems. Mostly, this was done by manually removing a large proportion of the snow cover in spring leading to an earlier snowmelt (Dunne *et al.*, 2003; Galen & Stanton, 1993; Oberbauer *et al.*, 1998; Saavedra, 2002; Starr *et al.*, 2000; Van der Wal *et al.*, 2000; Wipf *et al.*, 2006). More rarely, melting was accelerated by increasing the radiative energy input by spreading dark garment (Walsh *et al.*, 1997). Some experiments have looked into the effects of a reduced winter snow cover on tree roots by removing snow during winter (Boutin & Robitaille, 1995; Groffman *et al.*, 1999; Mellander *et al.*, 2004; Weih & Karlsson, 2002). Due to the labour involved, snow removal experiments were mostly applied on a smaller spatial scale, and over a shorter time than snow fence experiments. Some experiments are still in progress, e.g. in the Apennin Mountains (Italy, C. Siffi, personal communication), in the Swiss Alps (S. Wipf, chapters 5 and 6 of this thesis), and in the Southern Alps of New Zealand (T. Maegli, personal communication).

Climate scenario 3: Decreased snowfall and warming, resulting in advanced snowmelt combined with increase in spring temperatures

In very few experiments researchers have tested the climate scenario of an advanced snowmelt due to a switch from snow to rain or due to warmer spring temperatures, combined with a marked warming in summer. In a subalpine meadow, Harte and Co-workers (Harte & Shaw, 1995; Harte *et al.*, 1995) have established infrared heaters that accelerate and advance snowmelt by approximately one week, and increase summer temperatures after snowmelt to simulate future climate. The impact on the environmental conditions were threefold: in comparison to control plots, snowmelt was advanced, soil and air temperatures were enhanced, but soils were also considerably drier for most of the growing season due to the treatment. However, effects of snowmelt timing and summer drought cannot be separated easily in this experiment, hence we will not cover it in detail in this review of snow manipulation studies, although according to Dunne et al. (2004) phenological effects caused by the warming experiment were comparable to results from a pure snow manipulation experiment in the same area (Dunne *et al.*, 2003; Saavedra, 2002). In the Arctic, long-term studies with manually advanced snowmelt and soil heaters were carried out to simulate a warmer climate with earlier snowmelt (Oberbauer *et al.*, 1998; Starr *et al.*, 2000).

Table 2. Bivariate linear correlations between annual climate variables and their linear change over time (1975-2005), and correlations among variables at the Stillberg research site (2090 m asl) near the treeline of Davos, Switzerland. Mean air temperatures over the entire year (T_{air} year), winter (T_{air} winter, 1 Oct to 31 March), spring (T_{air} spring, 1 Apr to 30 June), and growing season (T_{air} grow. season, snowmelt to snowfall), snowfall (in % of the total precipitation), snowmelt date, and number of frosts during growing season (minimum daily air temperature below freezing, between snowmelt and 30 August). Pearson's correlation coefficients are shown. Bold = $P<0.05$, bold and in italics = $P<0.1$.

1975-2005	Year	T_{air} year	T_{air} winter	T_{air} spring	T_{air} grow. season	Snowfall	Snowmelt
T_{air} year	**0.63**						
T_{air} winter	**0.43**	**0.53**					
T_{air} spring	**0.61**	**0.61**	0.20				
T_{air} growing season	**0.38**	**0.56**	-0.11	0.26			
Snowfall (% of precipitation)	**-0.38**	***-0.32***	-0.26	**-0.36**	-0.12		
Snowmelt date	**-0.39**	**-0.36**	***-0.36***	**-0.75**	0.15	***0.32***	
Summer frosts	-0.28	**-0.36**	0.00	-0.03	**-0.49**	0.29	***-0.30***

Ecosystem responses to snow manipulation studies

Belowground processes

Even when frozen, soil microbes and fungi are active, because thin films of liquid water around soil particles are still available (Mikan *et al.*, 2002). Although biochemical winter processes are slow, they can add up to a significant share of the annual carbon and nitrogen budget over the long winters in the Arctic and Alpine (Oechel *et al.*, 1997; Zimov *et al.*, 1993).

In ecosystems with shallow snow cover and deep-frozen soils in winter (i.e. arctic tundra or windswept alpine ridges), snow addition caused a considerable rise in microbial activity due to warmer winter soil temperatures (Schimel *et al.*, 2004). Microbial biomass and thus N immobilization, N mineralization, and N_2O production were increased in winter (Brooks & Williams, 1999; Schimel *et al.*, 2004), and less nitrate was leached by melt water in spring (Brooks & Williams, 1999). Litter decomposition (Webber *et al.*, 1976; Williams *et al.*, 1998), ecosystem respiration (Chimner & Welker, 2005), and overall C efflux (Brooks *et al.*, 1997; Walker *et al.*, 1999; Williams *et al.*, 1998) in winter were stimulated by snow accumulation and increased microbial activity, but C loss was decreased in the following summer (Jones *et al.*, 1998; Welker *et al.*, 2000). After advanced snowmelt, both respiration and C uptake were stimulated by early snowmelt and soil warming, hence no net change in the carbon budget of arctic tundra resulted (Oberbauer *et al.*, 1998).

The effects of snow removal on soils that are normally covered by sufficient snow to decouple air and soil temperatures, has been tested in forest ecosystems. When soil freezing was induced by snow removal in N-American forests, large shifts in nutrient cycling were the consequence (Boutin & Robitaille, 1995; Fitzhugh *et al.*, 2001; Groffman *et al.*, 2001b; Groffman *et al.*, 1999; Pilon *et al.*, 1994): nitrate, total N and P values were increased in soils, which was probably caused by the dieback of fine roots due to mechanical processes (frost heaving) during soil freezing (Tierney *et al.*, 2001). N uptake of mountain birch seedlings was reduced after a winter with shallow snow cover, and more growth occurred below ground than above to replace the dead roots in the following summer (Weih & Karlsson, 2002).

After delayed snowmelt due to snow accumulation, leaf tissue from arctic tundra plants contained more N, and C/N ratios were decreased, indicating higher tissue quality (Van der Wal *et al.*, 2000; Walsh *et al.*, 1997; Welker *et al.*, 2005), while C/N ratios tended to be increased after advanced snowmelt (Van der Wal *et al.*, 2000, this thesis, chapter 5; Walsh *et al.*, 1997). Consequently, litter from plots with advanced snow had lower decomposability over winter (this thesis, chapter 6).

Phenology

The snowmelt is the most important threshold to plant growth in habitats with a persistent snow cover, although some species are known to be active under the snow cover, performing photosynthesis (Starr & Oberbauer, 2003), bud development (Sørensen, 1941), or even vegetative growth (Egerton & Wilson, 1993; Kimball & Salisbury, 1974) at a low level.

In most snowmelt experiments, the vegetation initially showed differences in the phenology between treatment and controls plots, but the differences often vanished in the course of the summer. This finding is attributed to a combination of two processes. First, the phenology of early-developing species is more sensitive to changes in snowmelt than that of late-developing ones (Dunne *et al.*, 2003, this thesis, chapter 3; Galen & Stanton, 1995), as visible from Fig. 1, where we compiled data on the sensitivity of the flowering phenology of various species to snowmelt timing from published studies (list of species available on request). Thus, effects of snowmelt manipulations on the phenological development may be obvious early in the year, but not visible anymore once later species dominate the aspect of the vegetation. Second, early stages in the development of individual species are often more sensitive to snowmelt timing than later ones. In other words, many species go through their phenological development more slowly after an earlier snowmelt, probably due to lower temperatures. Thus, the time span between snowmelt and a phenological stage is the longer, the earlier snow has melted (Rixen *et al.*, 2001; Starr *et al.*, 2000; Van der Wal *et al.*, 2000; Wipf *et al.*, 2006).

The timing of life cycle stages has important ecological consequences for a species' fitness by defining which growing conditions a plant encounters during each phenological stage. Changes in the phenology could therefore disrupt a species' interaction with its environment or its neighbours, competitors, herbivores, pathogens, and pollinators.

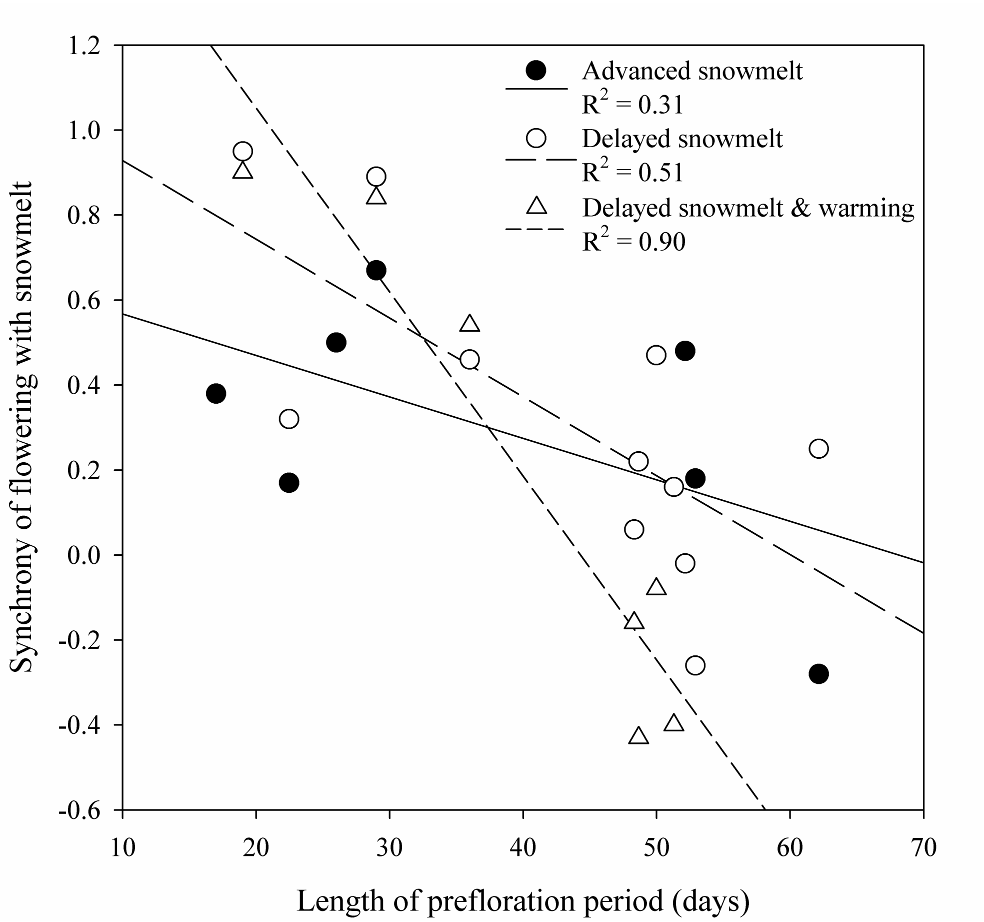

Figure 1. The synchrony between flowering and snowmelt (Y axis) in relation to the prefloration period (i.e. time between snowmelt and flowering) of the same species (X axis) in several snowmelt studies. The synchrony of a species' flowering with snowmelt was defined as: (flowering date in treatments – flowering date in controls) / (deviation in snowmelt caused by the snowmelt treatment (in days)). A ratio of 1 thus means that the duration between snowmelt and flowering was not influenced by the date of snowmelt (i.e. equal in treatment plots and controls). Thus, flowering date was parallel to the snowmelt date. At a ratio of 0, flowering took place at the same date in all treatments, independently of snowmelt date. With a negative ratio, flowering occurred earlier in plots with later snowmelt. Data from studies delaying snowmelt (Aerts *et al.*, 2004; Walker *et al.*, 1999; Wipf *et al.*, 2006), advancing snowmelt (Saavedra, 2002; Starr *et al.*, 2000; Wipf *et al.*, 2006), and combining delayed snowmelt with warming during summer (Aerts *et al.*, 2004; Walker *et al.*, 1999) were included.

Growth & productivity

Productivity and plant growth in natural communities are generally decreased near both extremes of the snow cover gradient, i.e. on wind swept ridges, and in snowbeds (Walker *et al.,* 1993), but in communities of intermediate snow cover, a relationship between plant growth and snow cover is not obvious (Choler, 2005). However, a review across several snow manipulation studies and locations revealed that changes in snow cover and a delay in snowmelt had strong effects on productivity, especially of communities with naturally early snowmelt (Fig. 2): communities with a natural snowmelt prior to June decreased productivity in response to a delay in snowmelt (Fig. 2, left of grey bar). The negative effects of snow addition was reversed, though, in most studies with a natural snowmelt later than mid-June (Fig. 2, right of grey bar), only in the study with the latest natural snowmelt and the greatest delay in snowmelt, the response was negative again. Unfortunately, no studies that measured the response of vegetation productivity to advanced snowmelt are published. However, advanced snowmelt generally increased growth or productivity of individual plant species, although often not significantly (*Bistorta* leaf area in Starr&Oberbauer 2001, *Luzula* and *Salix* leaf mass in van der Wal et al. 2000, *Delphinium* seedling leaf area in Saavedra 2002). An exception are our own studies from subarctic tundra with relatively early natural snowmelt timing, and from alpine tundra with medium snowmelt, where advancing snowmelt had mostly no or negative effects on individual plant growth (this thesis, chapter 3, 4 and 5, Wipf et al., 2006).

The response of vegetation productivity to snow manipulation may depend on the location of the community on the snow gradient: communities with naturally early snowmelt are probably adapted to a long growing season, which they require for optimal growth. A delay in the start of the growing season consequently has negative effects. Communities with a naturally late snowmelt, on the other hand, are adapted to a long and continuous snow cover. A delay in snowmelt causes no decrease in growth, rather the opposite: the long-lasting snow cover might have beneficial effects by protecting plants from the adverse climate, i.e. low temperatures and frost early in the year, and the remaining snowfree season is generally warmer after later snowmelt. If the reduction of the growing season is too extreme though, plants are probably not able to compensate for the delay in snwomelt any more.

Reproduction

Few snow manipulation studies have gone beyond measuring flowering phenology and have reported data on fecundity and reproduction. Most of those who did found delayed snowmelt to increase fecundity (Aerts *et al.*, 2004; Walker *et al.*, 1999; Wipf *et al.*, 2006, this thesis, chapters 3 and 4), most distinctly so when additional warming was applied (Aerts *et al.*, 2004; Walker *et al.*, 1999). Advancing snowmelt, however, often decreased fecundity (Saavedra, 2002 (in 3 of 4 sites); Wipf *et al.*, 2006, this thesis, chapter 5). As an exception, the study of Galen&Stanton (1993) from an alpine snowbed reported positive responses in reproduction (measured as seed mass) to advanced snowmelt in the latest-melting, and negatively to delayed snowmelt in the early-melting proportion of the snowbed site. Snowbed communities, however, are very extreme habitats in term of short duration of season length, and species at such habitats risk to lose their seeds before maturation regularly (Kudo, 1993; Molau, 1997), thus a longer growing season is likely to cause positive responses in their reproduction.

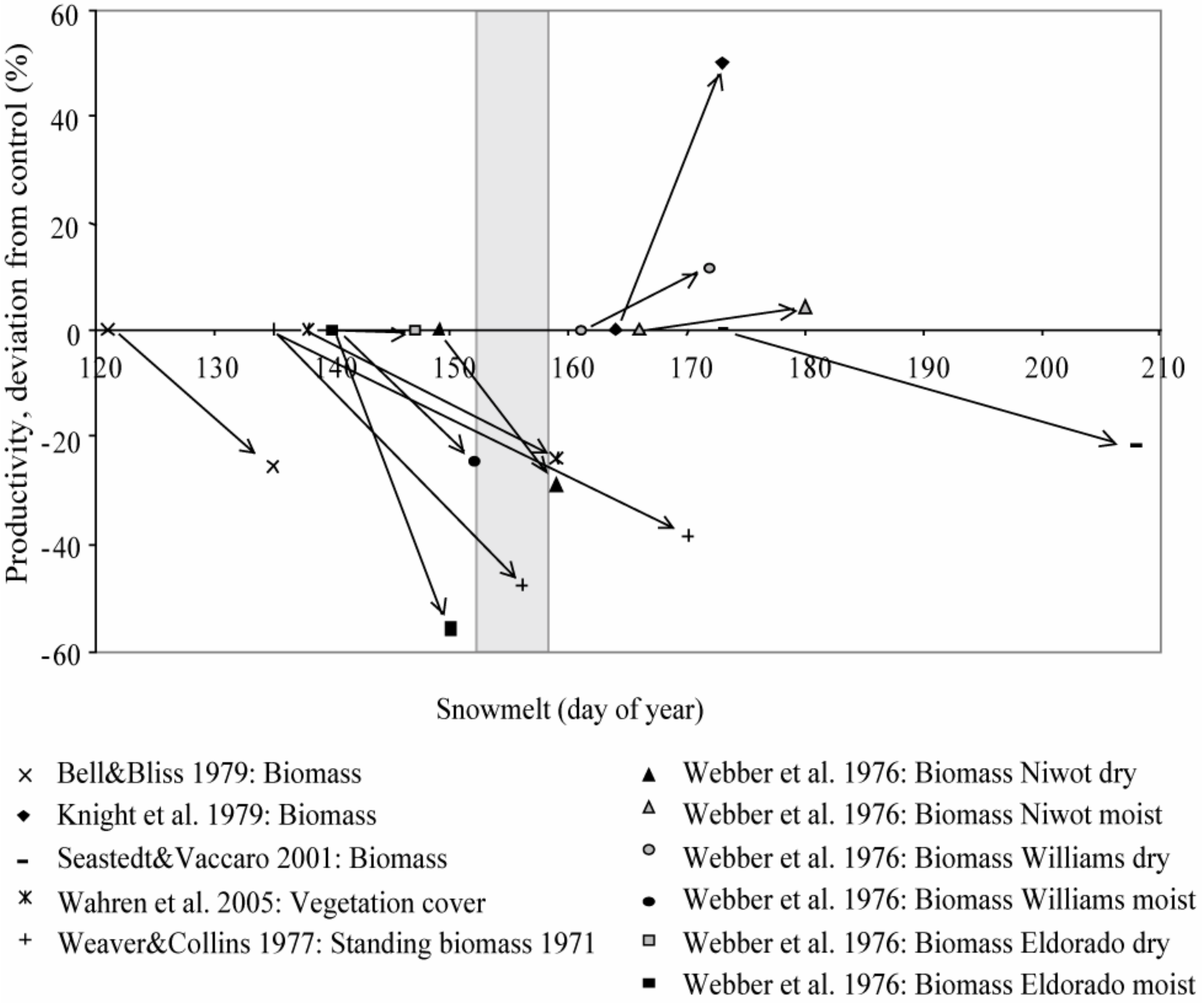

Figure 2. Productivity in relation to snowmelt dates published in snow manipulation studies from arctic (Wahren *et al.*, 2005) and alpine ecosystems (all other studies). To enable the comparison across studies, productivity in plots with snow manipulation is indicated as the percentage of that in unmanipulated controls. Arrows point from controls to manipulated plots. The grey area designates the threshold between two different response types. In communities with natural snowmelt prior to June (day 152 = 1 June) did the community productivity react negatively to a prolonged growing season. Afterwards, biomass responded positively to delayed snowmelt, except in the latest example. Productivity data of studies advancing snowmelt was not available.

Vegetation composition

The species composition of sites with naturally differing snow cover characteristics differ distinctly in their species composition (Ferrari & Rossi, 1995; Heegaard, 2002; Walker et al., 1993). In the experimental studies discussed above, some arctic and alpine species strongly reacted to changes in snowmelt timing in their growth or reproduction. We therefore expect changes in snow cover to cause the vegetation composition to change over time, which could lead to changes in ecosystem structure and functioning.

We summarize the response in species composition to delayed snowmelt (by shovelling or by snow accumulation behind a snow fences) from 12 experiments published in 8 papers on the level of functional groups (lichens, graminoids, forbs and woody species) in Table 3. Species diversity and vegetation composition was considerably affected by snow addition and delayed snowmelt. In 6 of 8 studies, the species number or diversity responded negatively to delayed snowmelt, but differences were not always significant in the individual studies. The cover or biomass proportion of lichens and graminoid species generally reacted negatively to added snow and late snowmelt, while the response of forbs and dwarf shrubs to late snowmelt was mostly neutral or positive. The results of our own study, which is the only one to assess the response of vegetation composition to advanced snowmelt, are partly in line with these findings (i.e. opposite to results from studies with delayed snowmelt): responses of forbs and deciduous shrubs to early snowmelt were negative, but no significant changes in lichen and grass species were found.

The reactions of lichens may be explained by their predominantly dry habitat. They often inhabit locations with thin snow cover and dry summer conditions. Addition of snow likely alters environmental conditions, shortening the growing season and adding additional water, to which lichens respond with a rapid decline. The decline in graminoid species after snow addition is in some studies the consequence of increasing competition of dwarf shrub species (Scott & Rouse, 1995; Wahren *et al.,* 2005), in other studies caused by the negative response of one dominant grass species, e.g. the wind-edge species *Kobresia myosuroides* in dry meadows at Niwot Ridge, which also resulted in a higher proportion of bare ground and an increase in litter (Bell & Bliss, 1977; Seastedt & Vaccaro, 2001).

Table 3. Qualitative responses of species diversity and vegetation composition (abundance of functional groups) to changes in snowmelt timing. The results summarized here were either reported as significant changes in the vegetation structure (marked with * in the column ‘parameter’), or listed in tables and figures describing the species composition. Empty cells either mean that a functional group was not present, or that no data was presented.

Study	Vegetation type	Parameter	Duration of experiment (y)	Natural snowmelt date	Deviation from nat. snowmelt	Diver-sity	Lichen	Woody species	Grami-noids	Forbs	Mosses
Knight *et al.*, 1979	Alpine dry meadow	Biomass	5	164	9	-			+	=	-
Knight *et al.*, 1979	Alpine mesic meadow	Biomass	5	154	8	-			+	-	
Scott & Rouse, 1995	Arctic tundra	Cover	13	NA	7	-	-	+	-		
Seastedt & Vaccaro, 2001	Alpine dry meadow	Cover	4	173	35	-	-	=	=	=	=
Seastedt & Vaccaro, 2001	Alpine mesic meadow	N species	4	173	35	-		+	-	+	
Smith *et al.*, 1995	Alpine wind edge	Cover*	32	NA	+NA	+	-				
Wahren *et al.*, 2005	Arctic dry tundra	Cover*	8	135	31	-	-	+			
Wahren *et al.*, 2005	Arctic moist tundra	Cover*	8	145	21	+	-	-	-		+
Weaver & Collins, 1977	Alpine meadow	Cover	6	135	9				-	+	
Weaver & Collins, 1977	Alpine meadow	Cover	6	135	20				-	+	
Welch *et al.*, 2005	Alpine moist tundra	Cover*	12	NA	6		-				
Wipf, thesis chapter 5	Alpine tundra	Cover*	2	150	-8		=	-	=	-	

Synthesis

Snow manipulation experiments have demonstrated that changes in snow cover characteristics can influence arctic and alpine ecosystems considerably. The ecosystem responses to changes in snow cover can be immediate and of a similar magnitude as other crucial climate factors such as temperature, summer precipitation, or CO2 concentration. Winter snow cover can modify the outcome of processes mainly attributed to summer warming: the insulation by the winter snowpack controls microbial activity and decomposition rates, and thus, nutrient availability to plants in the following summer. Furthermore, a changed winter snow cover may affect growing season soil moisture, which interacts with effects of summer temperatures, especially in regions with low summer precipitation (Chimner & Welker, 2005; Walker *et al.*, 1999). In fact, tundra plant productivity (measured as maximum NDVI in summer) was enhanced after winters with deep snow cover and late snowmelt in Siberia, regardless of summer climate (Grippa *et al.*, 2005).

The relevance of snow manipulation experiments is supported by observational studies, mainly in the Arctic. Thus, rising temperatures have led to decreasing snow cover extent (Brown, 2000; Dye & Tucker, 2003) and to significant changes in the vegetation and productivity of high latitudes (Dye & Tucker, 2003; Jia *et al.*, 2003), decreasing the albedo of the land surface, and consequently boosting the spring and summer warming (Chapin *et al.*, 2005; Groisman *et al.*, 1994a). Snow accumulation experiments can help explaining one of the salient ecosystem responses to climate change: the current increase in shrub cover in the Arctic (Sturm *et al.*, 2001b; Tape *et al.*, 2006). It is likely to be driven by a positive feedback between shrubs, deep snow drifts in their lee, and enhanced nutrient availability due to increased microbial activity in warmer soils under these drifts (Sturm *et al.*, 2001a; Sturm *et al.*, 2005). The rising temperatures, increased soil insulation by deeper snow cover, and consequent biogeochemical processes could lead to an overall increase in microbial activity and plant growth. Increased microbial activity, mainly during winter, could boost carbon release through decomposition of the organic matter stored in peat and tundra soils, while increased plant growth, mainly of shrubs, could bind more carbon in living biomass (Chapin *et al.*, 2000; Oechel *et al.*, 2000; Zamolodchikov *et al.*, 2000). Whether tundra ecosystems will be carbon sinks or sources under future climates, is subject to debates (Davidson & Janssens, 2006). Snow manipulation experiments, can help understanding how snow cover, soil processes and carbon release from arctic and alpine ecosystems interact.

The snow cover and respective ecosystems are influenced by climate change at different scales: (1) On a global scale, precipitation is predicted to increase due to a general increase of evaporation with rising temperatures (IPCC, 2001), thus precipitation especially at high latitudes and elevations could generally be enhanced. Overall, increased temperatures decrease the proportion of snow at the total precipitation. (2) On a continental scale, snowfall patterns are influenced by large scale weather patterns such as the winter Antarctic Oscillation (AO, Schaefer *et al.*, 2004), North Atlantic Oscillation (NAO, Clark *et al.*, 1999), North Pacific Oscillation (NPO, Clark *et al.*, 2001), El Niño/Southern Oscillation (ENSO, Clark *et al.*, 2001; Groisman *et al.*, 1994b), which may be changing with climate change. (3) On a local scale, changes in temperature and precipitation may differ considerably from larger scales. The temperatures at the time of a precipitation event define whether precipitation is falling in the form of snow or rain. This is especially apparent in mountain regions, where a rise of the mean snow line (i.e. the altitude above which snow is falling) can be observed.

Despite uncertainties about the future climate on a global, continental or local scale, observational and modelling studies allow an estimate of future snow cover characteristics, and snow manipulation studies provide an insight into the consequences of a changed snow cover for ecosystems. The most likely scenario in many snow-dominated regions of the world, especially in mid and high latitudes and mid-altitudes, is characterised by a rapid increase in temperatures, and a slightly increased or unchanged amount of snowfall during winter, resulting in an earlier snowmelt and longer growing season with warmer temperatures (approx. corresponding to

Scenario 3 in this review (Dye, 2002), see also Fig. 1 in this thesis, chapter 1). Although this scenario might affect the largest area of the three scenarios discussed in this review, it has been tested least in field experiments. Warming and snow manipulation experiments suggest that in an according scenario, conditions for plant growth and nutrient availability may be enhanced and plant growth and productivity increased. Several remote sensing (Silapaswan *et al.*, 2001; Tucker *et al.*, 2001) and monitoring studies (Stow *et al.*, 2004; Tape *et al.*, 2006) confirm that such processes are taking place.

Ecosystem reactions differ considerably from those in response to the previous scenario, if winter snow cover decreases without a significant increase in temperature (due to reduced winter precipitation, due to a rise in the snow line, or due to changes in large-scale precipitation patterns), as found in some mountain regions (corresponding to Scenario 2; see also red signatures in Fig. 1 in chapter 1 of this thesis for areas with rapidly advancing snowmelt). Early snowmelt due to decreased snow depth can reverse the effect of rising summer temperatures if combined with cold weather prevailing just after snowmelt. Frost damage of plants in spring could increase, if plant development starts just after early snowmelt, when temperatures are still low and variable (Inouye, 2000; Inouye *et al.*, 2002; Molgaard & Christensen, 1997). Frost damages mainly depend on the interaction of three factors (see Inouye (2000) for a review): the occurrence of a frost event with temperatures low enough to damage plant tissue (Jordan & Smith, 1995); the damage “potential”, (i.e. the plant parts exposed at the time of the event); and the temperature sensitivity of present plant parts at the time of a low-temperature event.

In Europe, the date of the last spring frost has advanced faster than the start of the phenological development of most species. This has decreased the risk of frost damage, but at the same time enhanced the damage potential in case a late frost should occur (Scheifinger *et al.*, 2003). The occurrence of low-temperature events is predicted to further decrease in the lower parts, but not in the high mountain regions of the European Alps (Auer *et al.*, 2005), where the start of plant development is strongly influenced by the timing of snowmelt (this thesis, chapter 5). In fact, frost damage in flowers or newly formed leaves was increased in field experiments with earlier onset of plant development due to warming (Molgaard & Christensen, 1997; Price & Waser, 1998) or advanced snowmelt (this thesis, chapter 5). Snow manipulation experiments also suggest that not all species might be equally affected by these processes, because the timing of the phenological development varies strongly between species (Dunne *et al.*, 2003, this thesis, chapter 3). Generally, the phenology of early developing species is more directed by snowmelt timing than that of later-developing ones (Fig. 1), suggesting that early-developing species would be most affected by early snowmelt followed by spring frosts. Results from monitoring studies are generally in line with these results from snow manipulation experiments. For instance was fecundity of several early-flowering alpine species reduced (Inouye & McGuire, 1991; Inouye *et al.*, 2002), and overall tundra plant productivity (max. NDVI in summer) inhibited (Stow *et al.*, 2004) by early snowmelt followed by cold weather. Similar patterns were also found in treering series from Siberia (Kirdyanov *et al.*, 2003).

In many regions however, annual precipitation, and also winter precipitation are likely to increase in a warmer climate. The total amount of snowfall might be unchanged or even increased, even if it accounts for a lower percentage of the total precipitation. This might explain why snow depth and winter season length remained largely unchanged at high elevations, but decreased at low elevations of Switzerland, although overall temperatures have risen (Laternser & Schneebeli, 2003). Higher snow depth during winter and a delay in snowmelt (approx. corresponding to Scenario 1) are expected in some continental arctic areas of Siberia and North America (see Fig. 1 in this thesis, chapter 1). In such a scenario, it is possible that the effects of increased snow depth outweigh effects of warmer summer temperatures, e.g. on productivity. Furthermore, ecosystem respiration may be enhanced due to the prolonged snow-covered season in combination with warmer winter soil temperatures and only a short growing season available for carbon acquisition of plants.

Future research

Several fields of winter ecology still require further investigations (for an overview see Campbell et al. 2005). The following points apply particularly to experimental approaches to snow ecological studies:

Many experiments have been set up to study basic patterns in the interactions between snow and ecosystems. Long-term studies focussing on climate change, and thus simulating realistic winter climate scenarios for the region or the ecosystem in question, are sparse. This especially applies to scenario 3 of this review (advanced snowmelt and increased spring and summer temperatures), which is predicted for many arctic and alpine areas.

Furthermore, the interdisciplinary approach to snow ecological studies should be strengthened in future research. Responses to snow cover changes on different levels of the ecosystem (such as biogeochemistry, plant performance, vegetation composition) and their interactions, should be studied and quantified in one experimental set-up to gain as much information and predictive power as possible. This is especially important as well designed, large-scale snow manipulation experiments are difficult to accomplish. A difficult but important challenge in snow ecology is to differentiate between episodic changes in winter/spring conditions and long-term changes in growing conditions. Some extreme events, such as an episodic dieback of flowers or shoots of a species due to frosts or drought, may have larger impacts on ecosystem processes and composition than slow and gradual changes in temperature or precipitation.

The snow cover is only one of several climate factors undergoing modifications in current climate change. Winter climate change should best be studied by taking changes in summer climate into account as well. Especially the growing conditions in spring, which for arctic and alpine plants starts with the melting of the snow cover, can have large effects on ecosystem processes. Therefore, winter, spring and summer climate scenarios should all be taken in to account and combined in future climate change experiments.

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Table 4: Summary of snow manipulation experiments reviewed in this article. If this information was available, we give an overview over the manipulation applied, the extent of the manipulation, and the characteristics of the natural snow cover. We divided the studies into 3 scenarios according to the winter climate they simulated and give a short indication of the response type studied. Scenarios: (1) delayed snowmelt, with or without increased winter snow cover; (2) advanced snowmelt; and (3) advanced snowmelt combined with a summer warming treatment. w=week, d=day, - = advanced or decreased, respectively; + = delayed or increased.

Study details and characteristics					Climate change manipulations				Snow cover/snowmelt characteristics				Scenario applied			Response type studied
Author, year	Biome	Elevation (m asl)	Start snow manip. experiment	Duration of study (y)	Snowmelt	Snow depth manip.	Warming	Manipulation technique	Natural snow depth	Manipulated snow depth	Natural snowmelt	Snowmelt deviation from control	1	2	3	
Fahnestock *et al.*, 2000	Arctic	700	1996	3	+	+	+	fence&OTC	shallow	2.8 m	mid to late May	+3 to +4 w	X			Plant phenology, C and N dynamics
Jones *et al.*, 1998	Alpine	3500	1994	2	+	+	+	fence&OTC	deep	2.8 m	mid to late May	+3 to +4 w	X			C dynamics
Seastedt & Vaccaro, 2001	Alpine	3500	1994	4	+	+	+	fence&OTC	deep	2.8 m	early to mid June	+5 to +6 w	X			Species composition, productivity
Wahren *et al.*, 2005	Arctic	700	1994	8	+	+	+	fence&OTC	shallow	2.8 m	mid to late May	+3 to +4 w	X			Species composition
Walker *et al.*, 2001	Alpine	3500	1994	1	+	+	+	fence&OTC	deep	2.8 m	early to mid June	+5 to +6 w	X			Overview
Walker *et al.*, 1999	Arctic, Alpine	700	1994	1	+	+	+	fence&OTC	shallow	2.8 m	mid to late May	+3 to +4 w	X			Plant phenology, growth, C and N dynamics
Welker *et al.*, 2000	Arctic	700	1994	1	+	+	+	fence&OTC	shallow	2.8 m	mid to late May	+3 to +4 w	X			C dynamics
Welker *et al.*, 2005	Arctic	700	1994	1	+	+	+	fence&OTC	shallow	2.8 m	mid to late May	+3 to +4 w	X			Plant C and N contents
Bell & Bliss, 1979	Alpine	3600	1971	1	+	+	none	fence	shallow	1.2 m	late April	+14 d	X			Plant survival, growth
Brooks *et al.*, 1997	Alpine	3500	1994	1	+	+	none	fence	deep	2.8 m	early to mid June	+5 to +6 w	X			Soil C and N dynamics
Brooks & Williams, 1999	Alpine	3500	1994	1	+	+	none	fence	deep	2.8 m	early to mid June	+5 to +6 w	X			Soil C and N dynamics
Chimner & Welker, 2005	Subalpine	1930	2002	1	+	+	none	fence	NA	deep	NA	NA	X			C dynamics
Bean & Henry, 2002	Arctic	NA	1982	ongoing	+	+	none	fence	NA	4 to 6 m	NA	NA, many w	X			Plant survival, vegetation composition
Schimel *et al.*, 2004	Arctic	700	1994	1	+	+	none	fence	shallow	2.8 m	mid to late May	+3 to +4 w	X			Soil C and N dynamics
Scott & Rouse, 1995	Arctic	0	1979	13	+	+	none	fence	0.25 m	1.2 m	mid to late May	+1 w	X			Species composition
Smith *et al.*, 1995	Alpine	1600	1959	32	+	+	none	fence	0.1 m	2 m	NA	NA	X			Vegetation composition, productivity, structure
Stanley *et al.*, 1998	Alpine	1600	1995	2	+	+	none	fence	NA	0.8 m	NA	NA	X			Plant population dynamics
Sturges, 1989	Subalpine	2400	1983	5	+	+	none	fence	1.5 m	4.6 m	NA	NA	X			Plant survival
Weaver & Collins, 1977	Subalpine	2380	1969	6	+	+	none	fence	0.3-0.6 m	1.2 m	early to mid May	+3 to +4 w	X			Species composition, productivity

Webber *et al.*, 1976	Alpine	3500	1974	1	+	+	none	fence	deep	1.2 m	mid May	+10 d	X			Plant survival, growth
Welch *et al.*, 2005	Alpine	1000	1986	17	+	+	none	fence	NA	deep	late april	+1 to +2 w	X			Species composition
Williams *et al.*, 1998	Alpine	3500	1994	1	+	+	none	fence	deep	2.8 m	early to mid June	+5 to +6 w	X			Soil C and N dynamics
Knight *et al.*, 1979	Subalpine	3100	1973	5	+	none	none	shovelling	NA	no manip.	mid to late June	+7 to +9 d	X			Species composition, productivity
Walsh *et al.*, 1997	Arctic	NA	1993	2	-/+	+	none	fence, dark garment	0.2 m	deep	late May	NA	X	X		Plant C and N contents
Galen & Stanton, 1993	Alpine	3750	1991	1	-/+	none	none	shovelling	deep	no manip.	early to late July	+15 to +20 / -15 to -17 d	X	X		Plant phenology, abundance, reproduction
Galen & Stanton, 1995	Alpine	3750	1991	3	-/+	none	none	shovelling	deep	no manip.	early to late July	+15 to +20 /	X	X		Plant phenology, abundance
Galen & Stanton, 1999	Alpine	3750	1991	4	-/+	none	none	shovelling	deep	no manip.	early to late July	+15 to +20 /	X	X		Plant reproduction
Van der Wal *et al.*, 2000	Arctic	NA	1998	1	-/+	none	none	shovelling	NA	no manip.	mid June	-5 / +9 d	X	X		Plant phenology, growth, C and N contents
Wipf, thesis chapter 3	Subarctic	900	2003	1	-/+	none	none	shovelling	shallow	no manip.	late April	-8 / +9 d	X	X		Plant phenology, growth, reproduction
Wipf *et al.*, 2006, thesis chapter 4	Subarctic	900	2003	1	-/+	none	none	shovelling	shallow	no manip.	late April	-8 / +9 d	X	X		Plant interactions
Aerts *et al.*, 2004	Subarctic	NA	2000	2	-	+	+	OTC winter & summer	0.1-0.2 m	0.3-0.4 m	mid to late April	+5 to +7 d	X		X	Plant phenology, reproduction
Dorrepaal *et al.*, 2003	Subarctic	NA	2000	2	-	+	+	OTC winter & summer	0.1-0.2 m	0.3-0.4 m	mid to late April	+5 to +7 d	X		X	Moss growth
Groffman *et al.*, 1999	Montane		1996	1	-	-	none	shovelling	0.6 m	shallow	mid April	-1 to -2 w		X		N fluxes
Groffman *et al.*, 2001a	Montane	470-650	1997	2	-	-	none	shovelling	0.6 m	shallow	mid April	-1 to -2 w		X		Methods
Groffman *et al.*, 2001b	Montane	470-650	1997	2	-	-	none	shovelling	0.6 m	shallow	mid April	-1 to -2 w		X		C and N dynamics
Hardy *et al.*, 2001	Montane	470-650	1997	2	-	-	none	shovelling	0.6 m	shallow	mid April	-1 to -2 w		X		Soil temperatures, moisture
Tierney *et al.*, 2001	Montane	470-650	1997	2	-	-	none	shovelling	0.6 m	shallow	mid April	-1 to -2 w		X		Plant root growth
Dunne *et al.*, 2003	Alpine	~3000	1996	3	-	none	none	shovelling	deep	no manip.	late Apr to mid May	-1 w		X		Plant phenology
Saavedra, 2002	Alpine	~3000	1996	2	-	none	none	shovelling	deep	no manip.	early to mid May	-1 w		X		Plant phenology, reproduction
Dunne *et al.*, 2004	Alpine	~3000	1996	3	-	none	+	shovelling	deep	no manip.	late Apr to mid May	-1 w		X	X	Plant phenology
Oberbauer *et al.*, 1998	Arctic	760	1995	2	-	none	+	shovelling& warming	shallow	no manip.	early to mid May	-8 to -24 d		X	X	C dynamics
Starr *et al.*, 2000	Arctic	760	1995	2	-	none	+	shovelling& warming	shallow	no manip.	early to mid May	-8 to -24 d		X	X	Plant phenology, growth, physiology

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Chapter 3

Snowmelt changes in subarctic tundra: short-term responses are strongest in early-developing plant species

Abstract

The duration of snow cover is an important factor for the structure and composition of arctic and alpine tundra communities. Over the last few decades, snowmelt has gradually become earlier, causing the start of the growing season to advance. Little is known about the direct effects of advanced snowmelt on plant performance. In a field experiment in subarctic tundra in Interior Alaska, I manipulated the timing of snowmelt and measured the response in mortality, phenology, growth and reproduction of eight dominant plant species. Moreover, I explored whether there were links between the temporal niche of a species (i.e. the timing of its phenological development), and its response in phenology, fitness and reproduction. Differences in the phenology between treatments were only found for the first phenological stages, and mostly in early-developing species. The earlier the temporal niche of a species, i.e. the sooner after snowmelt it usually develops, the more its phenology was dependent on snowmelt, and thus, the more it responded to snowmelt manipulations. Reactions in the reproductive fitness were predominantly found in early-developing species, but contrary to my expectations, reactions were positive to delayed snowmelt. Growth was not directly affected by snowmelt manipulations, in spite of the recorded changes in vegetative phenology. In conclusion, early-developing species were most susceptible to changes in snowmelt timing, especially in their phenology. Changes in phenology, however, seemed not to influence plant fitness and fecundity after snowmelt experiments. In no species did an earlier snowmelt and a longer snow-free season lead to enhanced plant fitness.

Introduction

Under current climate change, the arctic region is experiencing among the greatest warming rates on earth (IPCC, 2001). The most pronounced changes have happened in winter and spring (Serreze *et al.*, 2000). Along with it, decreased snow cover extents (Robinson & Frei, 2000), earlier snowmelt (Dye, 2002; Rikiishi *et al.*, 2004), and earlier onset of the growing season (Shabanov *et al.*, 2002) have been recorded. In ecosystems dominated by a persistent winter snow cover, snowmelt is the first threshold to plant development. The timing of snowmelt defines the start and length of the growing season, but due to the sinus-shaped temperature course over the summer, it also impacts the temperatures that plants experience once released from the snow. With these effects on the plant environment, snow cover is among the most important drivers of arctic and alpine plant community composition, as seen from the close correlation between snowmelt and vegetation patterns (Friedel, 1961; Harshberger, 1929). However, the long-term processes leading to these patterns, and the responses to rapid changes in snow cover due to climate change are poorly understood.

Experimental studies aim at explaining plant-vegetation interactions and predicting the effects of changes in snow cover on arctic and alpine plant communities, either by using fences that accumulate snowdrifts in their lee, and thus, extend snow cover duration (i.e. Knight *et al.*, 1979; Scott & Rouse, 1995; Wahren *et al.*, 2005; Walker *et al.*, 1999; Walsh *et al.*, 1997), or by removing snow in spring, and thus, by advancing snowmelt (Dunne *et al.*, 2003; Galen & Stanton, 1993; Starr *et al.*, 2000; Van der Wal *et al.*, 2000; Wipf *et al.*, 2006). The plant responses to such snow manipulations were manyfold, complex and often species specific. Responses to increased snow cover reached from minor reactions in phenology, physiology and growth (Walker *et al.*, 1999; Walsh *et al.*, 1997) to the total die-back of certain species and major changes in vegetation composition (Scott & Rouse, 1995; Wahren *et al.*, 2005; Walker *et al.*, 1999), while responses to advanced snowmelt were often minor or non-significant (Saavedra, 2002; Starr *et al.*, 2000; Van der Wal *et al.*, 2000). However, only short-term effects to advanced snowmelt have been studied yet.

Plant phenology has recently gained attention as an indicator of climate change (Fitter & Fitter, 2002). The phenological development of alpine and arctic plants has often been reported to respond to snow manipulations (Aerts *et al.*, 2004; Dunne *et al.*, 2003; Rixen *et al.*, 2001). The strongest response in phenology to changes in snowmelt has often been found in early-developing species (Dunne *et al.*, 2003; Galen & Stanton, 1995; Rixen *et al.*, 2001; Wipf *et al.*, 2006). For the fitness of early-developing species, it could be advantageous to have their phenology synchronized with snowmelt in order to exploit the whole growing season (Stinson, 2004), while for that of later-developing species, a phenology sensitive to temperature or day length could be advantageous in order to benefit from stable, relatively warm summer temperatures or peak pollinator densities (Molau, 1997). However, whether there is a link between the temporal niche of a species (i.e. the timing of its phenological development), and the sensitivity to changes in snowmelt of its phenology, vegetative or reproductive fitness, has not been tested yet.

In this study, I explored how mortality, phenology, growth and reproduction of the eight dominating plant species in a sub-arctic tundra community were affected by manipulations of snowmelt timing. I wanted to test the hypotheses that (1) the phenological development reacts to snowmelt timing, and that within each species, the earliest stages react most, that (2) vegetative and reproductive fitness react positively to a prolonged growing season, especially if the phenological development is advanced after advanced snowmelt, and that (3) the phenological development of early-developing species is most synchronised with snowmelt timing, and therefore, their fitness should respond most to snowmelt manipulations.

Material and methods

Study site and species

I conducted this study from August 2002 to August 2003 in a sub-arctic ecosystem at timberline on Murphy Dome (64°57’N, 148°22’W, 850 m asl) near Fairbanks, Interior Alaska, in the same location and setup as described in (Wipf *et al.*, 2006). The climate is dry and continental; precipitation was 530 mm over the year of the study at a nearby NOAA weather station, mean snow depth on site was 22 cm, and mean temperatures were –20°C in January (coldest month, measured in Fairbanks), and +12°C in July (warmest month, measured on site). The winter 2002/2003 was relatively mild, with mean temperatures of 5 degrees above and snow depths 50% below normal (measured in Fairbanks AK, NOAA, Sept 2002 - Aug 2003). The vegetation is a species-poor tundra dominated by deciduous and evergreen ericaceous dwarf shrubs. I studied the 8 most frequent plant species, namely *Vaccinium uliginosum*, *Vaccinium vitis-idaea*, *Ledum palustre*, *Empetrum nigrum*, and *Cassiope tetragona* (dominating dwarf shrubs), *Betula nana* (deciduous shrub, responsive to climate change (Bret-Harte *et al.*, 2002)), *Carex bigelowii* and *Calamagrostis* sp. (most frequent graminoids).

Experimental design and treatments

In August 2002, I established a total of 27 plots of 1m^2, grouped in 9 blocks of 3 plots at 3 sites in homogeneous terrain (3 sites x 3 blocks per site x 3 plots per block). Distance between sites was 300 to 400 m, between blocks 15 to 30 m, and between plots 3 to 4 m. I tagged a random shoot or individual per species (if present) in the corners and the centre of each plot (subsequently called ‘shoots’), amounting to two to five shoots per species and plot, and to a total of 989 shoots. Snow depth within plots was measured twice monthly from January to March 2003 to check for natural between-plot variability of the snow cover. On 18 April 2003, I randomly assigned one of three snowmelt treatments to each of the three plots per block: 1) advanced snowmelt, by reducing the snow cover to approx. 10 cm and letting it melt naturally; 2) delayed snowmelt, by adding approx. 50 cm of snow and letting it melt naturally; and 3) unmanipulated control. A temperature logger per plot measured soil surface temperatures to the nearest 0.5°C in 3-hour intervals from January to summer. Along with regular visits, this allowed me to detect melt-out as the first day when temperatures reached either +5°C at day or +1°C at night, and the daily amplitude exceeded 5°. I measured soil moisture two weeks after snowmelt to check for effects of snow removal or addition, using a Delta-T HH2 and ML2 sensor (Delta-T Devices, Cambridge UK). Plots were snowfree on average on 28 April in controls, 20 April in plots with advanced, and 5 May in plots with postponed snowmelt. Mean snow depth, winter soil temperatures, and soil moisture were not significantly affected by the snowmelt manipulations (results not shown).

Plant responses

After snowmelt, I visited the plots every 3 to 5 days to record the number of living shoots, their phenological state, and the number of flower buds, flowers, and fruits. I recorded the phenological development as the date when a shoot entered a new phenological stage, and calculated the length of every stage as the difference between two starting dates. I defined the following vegetative stages: 1) onset of greening, i.e. first leaf entirely green in evergreens (reduction of anthocyanins), or first leaf part visible in deciduous species, 2) total green, i.e. all leaves green and unfolded, and 3) start of vegetative growth. On a larger spatial scale, the first two stages are important indicators of greening in remote sensing studies (e.g. Reed *et al.*, 1994). Reproductive stages were defined as: 1) flower buds swelling, 2) flower open, 3) flower senescent, 4) fruit developing, and 5) fruit ripe. In mid-August 2003, I harvested the shoots of *E. nigrum, V. vitis-idaea, V. uliginosum, C. tetragona* and *L. palustre* (harvesting the other, larger species would have been a major destructive intervention) and dried them to constant weight at room temperature. I measured shoot increments and mass of ripe fruits. Only variable-by-species combinations present in at least 15 plots were included in the analysis.

Statistical analysis

The data of the marked shoots per species and plot were pooled (i.e. means for continuous variables, proportions for binary variables). I analysed whether mortality, timing and duration of phenological stages, growth, fecundity, and berry mass differed between snowmelt treatments with mixed model ANOVAs (type I sums of squares). Residuals were checked for normality, and transformations were applied where necessary (indicated in the results). First, I analysed whether the group of all species reacted to snowmelt treatments and whether their response differed between species, by performing an ANOVA with treatment and species as fixed and block as random factors. Second, I tested whether individual species responded to snowmelt treatment with the same ANOVA without the factor ‘species’ and interactions thereof. Third, I tested whether the synchrony of a species’ phenology with snowmelt depended on its temporal niche, i.e. the time of year when a species’ phenological development occurs. As a measure of synchrony I calculated for each species the correlation between the date of each phenological stage and the date of snowmelt and recorded its standardized correlation coefficient. Then, I tested with linear regression whether this synchrony depended on the normal date of each phenological stage (i.e. mean of unmanipulated control plots). Analyses were conducted using SPSS 11.0 (SPSS Inc., 2001).

Table 1: Effects of snowmelt manipulation on a) mortality and onset of greening, b) vegetative growth, and c) reproductive phenology and fitness of the dominating species in subarctic tundra. The positive and negative direction of significant (P<0.05) and marginally significant (in brackets, P<0.1) relationships to the timing of snowmelt are indicated. Species names appear in ascending order of the date (control plots) of the start of a) leaf greening, b) vegetative growth, and c) budswell. For description of the statistical analysis and test statistics, see text. All species=set of all species tested together, B=Betula nana, C=Cassiope tetragona, Cala=Calamagrostis sp., Cx=Carex bigelowii, E=Empetrum nigrum, L=Ledum palustre, V=Vaccinium vitis-idaea, Vu=Vaccinium uliginosum, grey=not measured.

a)

Greening & Mortality	all species	C	V	E	B	L	Vu	Cala	Cx
Dormancy (time lag to onset of greening)	–		–		–	–	–	–	–
Leaves start greening	+	+	+	+	+				
All leaves green							–		
Mortality	–		(–)						

b)

Vegetative growth	all species	E	Vu	V	L
Start of vegetative growth		–	(–)		
Shoot increment					

c)

Reproduction	all species	E	Cx	Vu	L
Dormancy (time lag to budswell)	–	–		–	–
Start of budswell	+	+			
Start of flowering		(+)			
Fecundity	+	(+)		(+)	
Berry mass			▨		▨

Results

Mortality

A total of 96% of 989 shoots survived the experiment. The mortality (arcsin-transformed) differed significantly between species ($F_{7,47}$=3.4, P=0.006) and snowmelt treatments ($F_{2,16}$=3.7, P=0.047, Table 1a). It ranged from 0% in *Carex bigelowii* and *Calamagrostis* to 10.3% in *Vaccinium vitis-idaea.* Although low in total, mortality was by far highest in early-melting plots (64% of all dead shoots) and lowest in late-melting plots (7% of dead shoots). This difference was marginally significant on the species level for *V. vitis-idaea* ($F_{2,16}$=3.5, P=0.054).

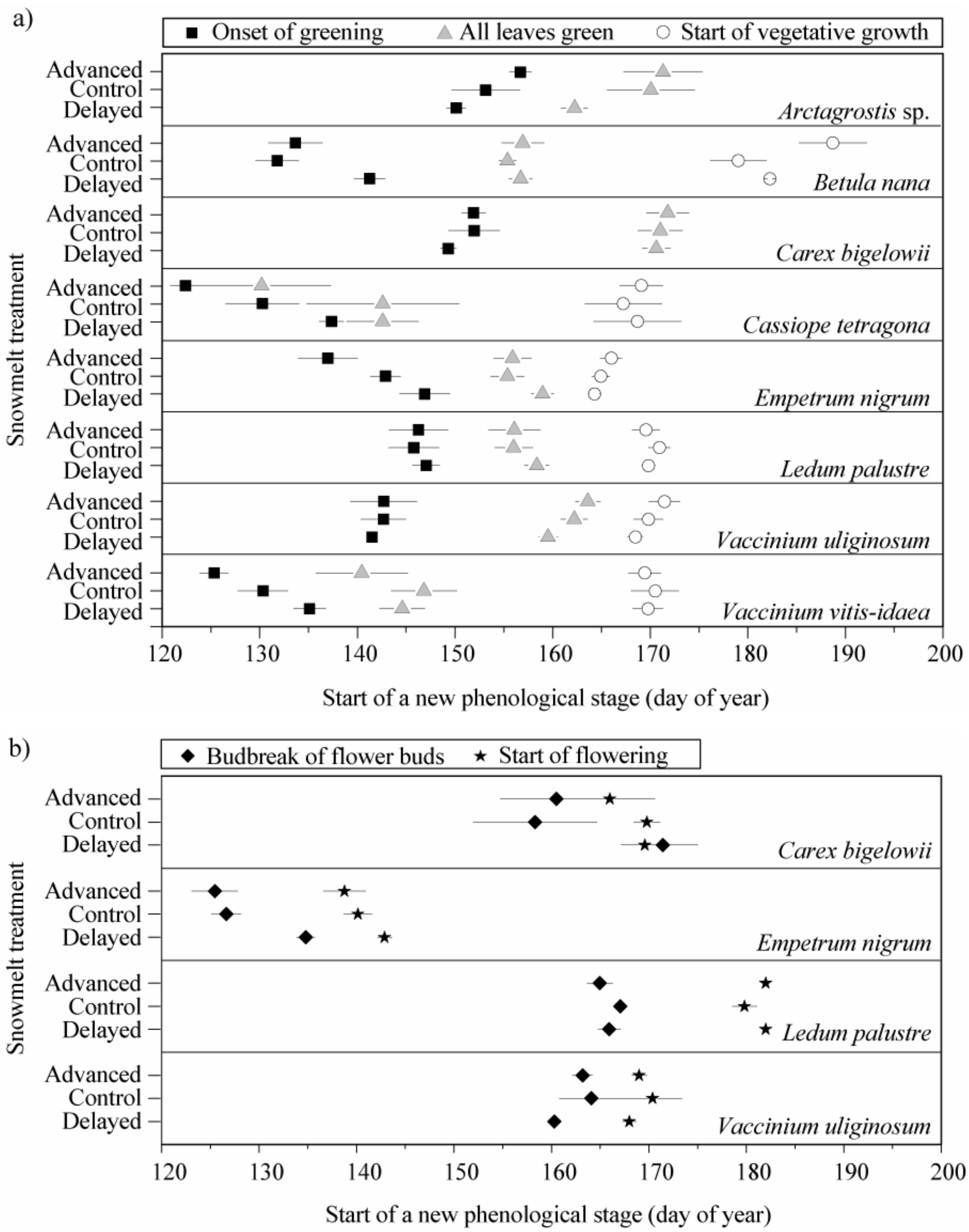

Figure 1. The phenology of frequent tundra species after manipulations of snowmelt timing: a) vegetative development, and b) reproductive development. Symbols mark the mean date when a phenological stage was reached; error bars=1SE.

Phenology

The phenology of all species responded to the snowmelt manipulation treatments, but only the vegetative development and the first stages of reproductive development were affected (Table 1a-c, Fig. 1a, b). The earlier snow melted, the longer shoots remained in dormancy (i.e. snowmelt date to onset of greening; $F_{2,16}$=33.1, P<0.001), but the effect differed between species and blocks (interactions species*treatment and block*treatment; $F_{14,87}$=2.8 and 2.0, P=0.002 and 0.021). Tested individually, the treatment effect was significant for all species except *Cassiope tetragona* and *Empetrum nigrum*. Over all species, there was a significant effect of snowmelt manipulation on the first phenological stage, onset of greening ($F_{2,16}$=11.8, P<0.001), but the extent differed between species (species*treatment interaction, $F_{14,87}$=2.8, P=0.002). On the species level, snowmelt treatment significantly affected onset of greening of *C. tetragona* ($F_{1,6}$=13.1, P<0.01), *V. vitis-idaea* ($F_{1,16}$=9.9, P<0.01), *E. nigrum* ($F_{1,16}$=4.6, P<0.05) and *Betula nana* ($F_{1,15}$=4.2, P<0.05), onset of greening being later after delayed snowmelt (Fig. 1a). Plants from late-melting plots lost their anthocyanins and unfolded their leaves faster, respectively (snowmelt treatment $F_{2,16}$=4.1, P=0.037; not significant in any species alone). Once all leaves were green, the difference in phenology between snowmelt treatments had therefore mostly vanished. Over all species, there was no uniform treatment effect on the total green state ($F_{2,16}$=0.79), but some species tended to react to snowmelt date (interaction species*snowmelt date $F_{7,46}$=2.1, P=0.059). Tested individually, total greening of *Vaccinium uliginosum* was significantly affected by snowmelt treatment ($F_{2,14}$=5.8, P=0.015), with shoots from early-melting plots having their leaves exposed 4 days later than shoots from late-melting plots. The timing when shoot elongation started (log-transformed) was affected by snowmelt treatment in some species only (species*treatment interaction, $F_{8,52}$=2.4, P=0.026), vegetative growth starting earliest after late snowmelt. The negative relationship between snowmelt and start of vegetative growth was significant for *E. nigrum* and marginally significant for *V. uliginosum* ($F_{1,8}$=6.4 and $F_{1,7}$=3.6, P=0.035 and P=0.099, Fig. 1a).

Effects of snowmelt on the reproductive development were weaker than those on the vegetative development, and the earliest-flowering species *E. nigrum* showed the strongest response. After snowmelt, the time span to bud swell was shortest in late-melting and longest in early-melting plots ($F_{2,16}$=26.0, P<0.001), but the response differed between species (species*treatment interaction, $F_{6,19}$=2.1, P=0.012, Table 1b). On the species level, the treatment effect was significant in *E. nigrum* ($F_{2,14}$=5.8, P=0.015), *Ledum palustre* ($F_{2,6}$=8.8, P=0.016) and *V. uliginosum* ($F_{2,10}$=24.8, P<0.001). When flowerbuds started swelling, plants from late-melting plots were still delayed (snowmelt treatment $F_{2,16}$=8.4, P=0.003), but the extent differed between species (species*treatment interaction $F_{6,19}$=3.8, P=0.012, Fig. 1b). On the species level, budswell of *E. nigrum* only responded to snowmelt treatment ($F_{2,14}$=13.4, P<0.001). When plants started flowering, the differences in phenology had mostly vanished, only *E. nigrum* tended to flower later in late-melting plots ($F_{2,13}$=2.9, P=0.092). Later reproductive stages did not differ between treatments in any species (data not shown).

The sooner after snowmelt the temporal niche of species, the more sensitive to snowmelt timing was its phenological development, measured as the synchrony with snowmelt (Fig. 2a, b). The relationship between the degree of synchrony with snowmelt and the temporal niche of the development was significantly negative for the first stages of the vegetative development (onset of greening: linear regression $F_{1,6}$=15.0, P=0.008, Fig. 2a, total greening: $F_{1,6}$=6.2, P=0.047, Fig. 2b). There was no relationship between sensitivity to snowmelt and temporal niche for later vegetative and reproductive stages, however, these were only analysed for 4 species (table 1b, c). In general, early-developing species responded more often to snowmelt treatments or date than those developing later in the summer (Table 1a-c).

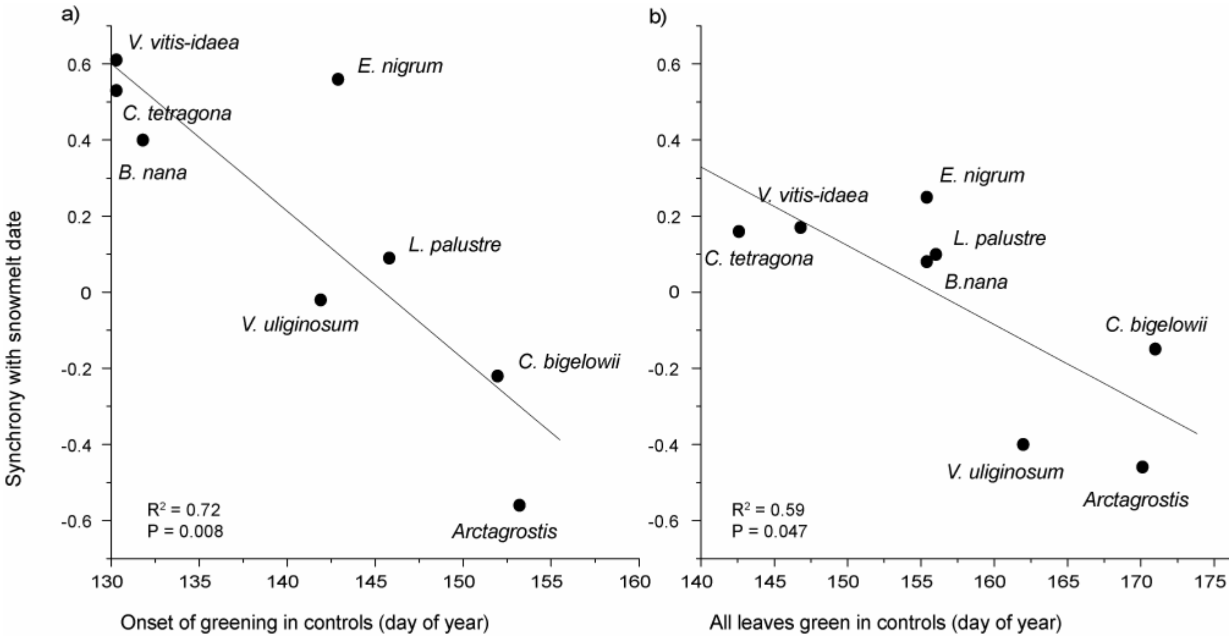

Figure 2. The synchrony of a species' phenology with snowmelt in relation to the temporal niche of species (i.e. date of the respective phenological stage in control plots, on X-axis). Synchrony with snowmelt was expressed as the standardized correlation coefficients between snowmelt date and the phenological stages a) start of greening of leaves, and b) all leaves green with snowmelt. For species abbreviations, see Table 1.

Growth and reproduction

Neither the proportion of shoots showing vegetative growth, nor the length of shoot increments (log10-transformed) differed between snowmelt treatments ($F_{2,16}$=0.1 and 0.6). Fecundity (proportion of shoots with ripe berries) was highest in *E. nigrum* (Fig. 3). Over all species, late snowmelt tended to enhance fecundity ($F_{2,16}$=2.7, P=0.098). On the species level, this increase was marginally significant in *E. nigrum* and *V. uliginosum* ($F_{2,16}$=2.6 and $F_{2,14}$=2.8, P=0.10 and 0.095, Fig. 3). Number and dry mass of *E. nigrum* and *V. uliginosum* berries were not affected by treatment.

Discussion

This snow manipulation experiment revealed that relatively small and short-time changes of snowmelt timing can affect the mortality, phenology, and reproduction of the most frequent plant species in a sub-arctic tundra community. Strong responses in phenology were found immediately after snowmelt, but as hypothesised, differences between treatments vanished towards later phenological stages. Overall effects on mortality and reproduction were found, but contrary to my expectations, they were negatively related to snowmelt timing, while growth did not respond to snowmelt manipulations at all. The timing of the first phenological stages was the more synchronised with snowmelt the earlier in the year a species developed. Most significant responses to snowmelt treatments were found in early-developing species, which suggests that they are most sensitive to snowmelt.

Snowmelt as a main factor controlling the phenology of early-developing species was found in earlier studies, too (Canaday & Fonda, 1974; Dunne *et al.*, 2003; Galen & Stanton, 1995; Thorhallsdottir, 1998; Walker *et al.*, 1995; Wipf *et al.*, 2006). Other studies, however, concluded that growing degree days are the main driver of phenology in alpine and arctic plants, i.e. that a plant has to accumulate a certain amount of growing temperatures before reaching a phenological stage (Kudo & Suzuki, 1999; Molau *et al.*, 2005). In early-developing species, the growing temperature accumulation to the first phenological stage is very low or even zero (S. Wipf, unpublished data); therefore, their temperature dependency is questionable. More probably, the phenology of early-developing species is controlled by snowmelt directly, or by factors strongly related to it (e.g. the presence of liquid water released from the snow cover). The weak or lacking response of the vegetative phenology of late-developing species to snowmelt manipulations suggests that the phenology of later-developing species may have been controlled by temperature (as proposed by Molau et al. (2005) in a long-term study of a similar community). Due to the lack of on-site temperature measurements, however, I am not able to test this hypothesis directly.

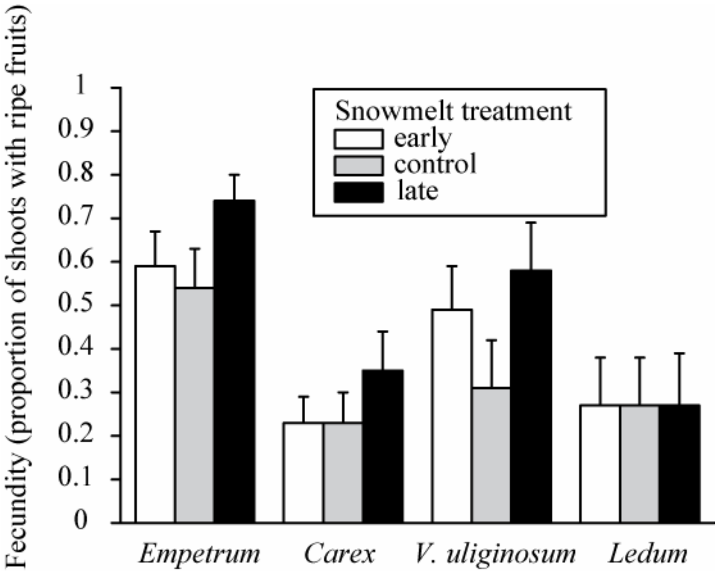

Figure 3. Fecundity (i.e. proportion of shoots with ripe fruits per plot) in response to snowmelt manipulations. Error bars=1SE. Order of species according to the timing of flowering in controls (earliest to latest). For full species names and significances, see text and table 1.

The temporal niche of flowering of a species is important for its reproductive success, which is, between arctic species, the higher the later flowering occurs (Molau, 1993), although in some years, early onset of winter might destroy the seeds of late-flowering species (Kudo, 1993; Molau, 1997). Between species, this was not the case in our study. Within species, however, the phenology of *Empetrum nigrum*, the earliest-flowering species, showed such a pattern: budswell and flowering were delayed, but fecundity was increased after late snowmelt and delayed phenology. Delayed snowmelt in snow manipulation experiments, or due to natural interannual variation, often increases the mean temperature of the remaining growing season by pushing its start to a later, thus usually warmer period of the summer, while the opposite, decreased temperatures and higher frost occurrence, often occur after advanced snowmelt (Wipf *et al.*, 2006). Reproductive fitness of late-flowering species was often enhanced under experimentally increased temperatures (Arft *et al.*, 1999; Hollister *et al.*, 2005; Sandvik & Totland, 2000), regardless of whether flowering phenology was advanced (e.g. in Arft *et al.*, 1999; Hollister *et al.*, 2005), or controlled by other factors than temperature (Hollister *et al.*, 2005). Reproductive fitness of early-flowering species, on the other hand, was often decreased after advanced snowmelt, due to plants being in full bloom when the latest spring frosts occurred ((Inouye, 2000; Molau, 1997; Price & Waser, 1998). Delayed snowmelt may therefore enhance plant reproductive fitness by ameliorating climate conditions over the snowfree period, but only if seeds are ripe before winter onset. Therefore, we would expect the relationship between snowmelt timing, flowering phenology and reproduction to be highly weather dependent, and thus, variable between years and sites. The differential outcome of snow manipulation experiments in various studies agrees with this hypothesis (Aerts *et al.*, 2004; Galen & Stanton, 1993; Saavedra, 2000; Stinson, 2004).

Reproduction is predominantly clonal in many tundra dwarf shrubs (Bliss, 1971), thus in the short term, climate change effects on survival rates and vegetative growth are more important indicators of vegetation turnover than effects on reproductive fitness. In this study, mortality was low in total, but highest in early-melting plots, indicating that growing conditions were harshest after advanced snowmelt (see also Wipf *et al.*, 2006). Shoot growth did not significantly respond to snowmelt, not even after changes in vegetative phenology, which is in line with results of some other studies (Starr *et al.*, 2000; Van der Wal *et al.*, 2000; Walsh *et al.*, 1997; Wipf *et al.*, 2006).

In this experiment, the reaction in the phenological development alone would not have made a meaningful response variable to study the effects of snowmelt manipulations. First, phenology as such is not a direct measure of fitness, although it may have indirect effects due to its interactions with climate or frost (Inouye, 2000), or with other species (e.g. herbivores (Van der Wal *et al.*, 2000), or pollinators (Kudo, 1993; Molau, 1997)). Second however, there was seldom a response in vegetative or reproductive fitness after responses in phenology to snowmelt timing were found in this study. Third, if there was a response in fecundity, it was in the opposite direction of what I had hypothesised previously. Thus, conclusions about longer-term effects drawn from changes in phenology remain speculative.

Still, this short-term study shows that changes in snowmelt timing can affect various frequent species from sub-arctic tundra, as well as interactions between species (Wipf *et al.*, 2006). The phenology early-developing species depended most on snowmelt, and reactions in mortality and fecundity were mostly found in those species, hence, we expect them to show the greatest response in the longer term. To assess whether, how and over which time period the structure, function and composition of tundra ecosystems could change under climate change, we need to incorporate changes in snowmelt into the climate scenarios, quantify the sensitivity of single species or species groups to it, and test effects of snowmelt changes, in interaction with other climate components, over the long-term.

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Chapter 4

Advanced snowmelt causes shift towards positive neighbour interactions in a subarctic tundra community

(with Christian Rixen [1] and Christa P.H. Mulder [2])

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Advanced snowmelt causes shift towards positive neighbour interactions in a subarctic tundra community

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Abstract

Positive and negative species interactions are important factors in structuring vegetation communities. Studies in many ecosystems have focussed on competition; however, facilitation has often been found to outweigh competition under harsh environmental conditions. The balance between positive and negative species interactions is known to shift along spatial, temporal and environmental gradients and thus is likely to be affected by climate change.

Winter temperature and precipitation patterns in Interior Alaska are rapidly changing and could lead to warmer winters with a shallow, early melting snow cover in the near future. We conducted snow manipulation and neighbour removal experiments to test whether the relative importance of positive and negative species interactions differs between three winter climate scenarios in a subarctic tundra community. In plots with ambient, manually advanced or delayed snowmelt, we assessed the relative importance of neighbours for survival, phenology, growth and reproduction of two dwarf shrub species. Under ambient conditions and after delayed snowmelt, positive and negative neighbour effects were generally balanced, but when snowmelt was advanced we found overall facilitative neighbour effects on survival, phenology, growth and reproduction of *Empetrum nigrum*, the earlier developing of the two target species. As earlier snowmelt was correlated with colder spring temperatures and a higher number of frosts, we conclude that plants experienced harsher environmental conditions after early snowmelt and that neighbours could have played an important role in ameliorating the physical environment at the beginning of the growing season.

Keywords: dwarf shrub heath, *Empetrum nigrum*, facilitation, growth, neighbour removal experiment, phenology, reproduction, *Vaccinium vitis-idaea*, winter climate change

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Introduction

Negative species interactions like competition are a main force in structuring species assemblages and communities (Grime, 1974, 1977). However, depending on environmental conditions, the disadvantage of having neighbours competing for the same resources may be outweighed by the advantages, such as amelioration of the physical environment (Bertness, 1991; Greenlee & Callaway, 1996; Tielbörger & Kadmon, 2000). Thus, either competitive or facilitative effects may dominate species interactions in a given community. Models predict that the net positive effect of neighbour interactions should be greater under harsh growing conditions (Bertness & Callaway, 1994; Callaway & Walker, 1997; Brooker & Callaghan, 1998). Indeed, facilitation has been found to outweigh competition in ecosystems of various harsh environments, such as deserts (Muller, 1953; Wilby & Shachak, 2004), sand dunes (Franks & Peterson, 2003), salt marshes (Bertness, 1991; Mulder & Ruess, 1998), alpine (Choler *et al.*, 2001; Callaway *et al.*, 2002) and arctic communities (Carlsson & Callaghan, 1991; Dormann & Brooker, 2002; Olofsson, 2004).

The balance between positive and negative species interactions is not stable but can shift along spatial and environmental gradients (Choler *et al.*, 2001; Callaway

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et al., 2002), or as a reaction to temporal fluctuations in climate (Tielbörger & Kadmon, 2000). Therefore, the balance between competition and facilitation can be expected to shift under climate change, which could eventually result in the dominance of some species and the competitive exclusion of others. Thus, understanding the balance between positive and negative species interactions could help to assess the potential of climate change effects on vegetation dynamics.

In tundra plant communities, neighbour removal experiments have induced positive (Sammul *et al.*, 2000; Gerdol *et al.*, 2002), negative (Shevtsova *et al.*, 1997; Aksenova *et al.*, 1998) and neutral responses (i.e. no interactions, or positive and negative interactions equally strong) (Bret-Harte *et al.*, 2004; Totland *et al.*, 2004). Thus, competition and facilitation are both of importance in tundra communities and whether one or the other factor dominated can vary in space, time or between species studied. Such balanced systems are probably sensitive to even minor environmental changes and may therefore be especially suitable to test for vegetation responses under climate change.

Climate change is predominantly affecting high latitudes (Serreze *et al.*, 2000). Especially Alaska is experiencing a great warming; since the 1960s the annual mean temperature has risen by 3 °C and the winter mean temperature by 4.5 °C (Alaska Regional Assessment Group, 1999). The growing season in Interior Alaska has lengthened by 2.6 days per decade, while leaf onset has advanced by 1.1 days per decade (Keyser *et al.*, 2000). Future rises in air temperatures, too, are projected to be greater in winter rather than summer: by 2050, December–February temperatures are predicted to increase by up to 6 °C, June–August temperatures by up to 3 °C (projections by the Canadian Centre for Climate Modelling and Analysis, Boer *et al.*, 2000).

A likely impact of rising temperatures and changing precipitation patterns is an earlier snowmelt, which recently has been detected in high latitudes of the Northern hemisphere (Serreze *et al.*, 2000; Dye, 2002). For the vegetation, an earlier snowmelt potentially results in a longer growing season and higher growing-degree days. However, an increase in frost damages due to a higher number of frost events (i.e. subzero temperatures), or due to earlier dehardening and thus higher frost sensitivity of plants are a possible consequence of earlier snowmelt (Kimmins & Lavender, 1992; Cumming & Burton, 1996; Inouye, 2000; Gorsuch & Oberbauer, 2002).

In this short-term experiment, we study how neighbour removal and advanced and postponed melt-out affect the survival, phenology, growth and reproduction of two common subarctic dwarf shrub species, *Empetrum nigrum* and *Vaccinium vitis-idaea*. We test whether and how the balance between positive and negative species interactions is affected by modifications of snowmelt, which is a likely consequence of a changed spring climate in subarctic tundra ecosystems. We expect the positive effect of neighbours to increase as the harshness of growth conditions increases. Our results will thus help to clarify whether advanced or postponed snowmelt will improve or impair growth conditions for tundra species in the short term.

Methods

Study site and species

We conducted our study above treeline at Murphy Dome, near Fairbanks, AK, USA (64°57′N, 148°22′W, 850 m a.s.l.) from August 2002 to August 2003. Mean air temperatures ± SD and minimum temperatures (in parentheses) for the summer months (measured to the nearest 0.1 °C every 15 min by a shaded HOBO temperature logger (Onset Computer Corporation, Pocasset, MA, USA)), were 5.1 ± 7.1 °C (−11.1) in May, 11.7 ± 6.7 °C (−2.9) in June, 11.9 ± 5.7 °C (−1.5) in July and 9.8 ± 5.0 °C (−2.4) from 1 to 18 August 2003 (end of experiment). The vegetation community is a subarctic, species-poor tundra and corresponds to the low-shrub subshrub tundra of the low-arctic zone (Bliss, 1981). Evergreen and deciduous dwarf shrubs, many of the Ericaceae family, dominate this tundra type. Frequent species in this community include *Vaccinium uliginosum*, *E. nigrum*, *V. vitis-idaea*, *Ledum decumbens*, *Carex bigelowii*, *Betula nana* and various *Salix* species (Viereck & Little, 1986, order according to abundance in our plots). In our study, we focused on *E. nigrum* ssp. *hermaphroditum* (Hagerup) Böcher (crowberry, Empetraceae) and *V. vitis-idaea* ssp. *minor* (Lodd.) Hultén (lowbush cranberry, Ericaceae) (see Ritchie, 1955; resp. Bell & Tallis, 1973 for descriptions). The phenological development of *E. nigrum*, one of the earliest-flowering tundra species, is probably synchronized with snowmelt (S. Wipf, unpublished data); thus its performance is likely to be more sensitive to changes in snowmelt timing than that of *V. vitis-idaea*, which flowers later in summer.

Experimental design and treatments

To quantify the relative importance of competition vs. facilitation, we compared the performance of shoots with and without plant neighbours. Because of the clonal growth of both species, we used shoots as the basic unit of this study. We chose shoots for our experimental treatments that were not directly surrounded by other shoots of the same species to minimize impacts of clonally integrated neighbours outside of the treatment area. In each of a total of 12 plots of approximately 1 m^2 at two sites (six per site) we wired and flagged six shoots of each species that were randomly chosen within these criteria. The distance was approximately 400 m between sites, 3–15 m between plots at each site and 0.4–1 m between shoots within plots. A neighbour removal treatment was randomly assigned to three marked shoots per species in each plot in the end of August 2002. Within a circle with a radius of 0.1 m around a shoot, we carefully clipped and removed all biomass to approximately 2 cm below the surface of the bryophyte cover. A 3-day cold spell 10 days after the treatment (from 9 September 2002 onwards) probably ended the 2002 growing season and thus prevented clipped plants from resprouting. Freeze-up was uniform in the three sites equipped with miniature temperature loggers during the whole experiment: soil surface temperatures reached freezing on 1 October and constantly remained below 0 °C until snowmelt.

To test whether the relative importance of competition vs. facilitation may be altered by winter climate change, we randomly assigned one of three different snowmelt treatments to each plot on 18 April 2003: (1) advanced snowmelt, by manually reducing the snow cover by half to approximately 10 cm and then letting it melt naturally; (2) delayed snowmelt, by adding approximately 50 cm snow on an otherwise continuous snow cover; and (3) unmanipulated control plots.

Miniature temperature loggers in each plot measured the subnivean temperatures at soil surface to the nearest 0.5 °C in 3 h intervals between January and snowmelt. These measurements, along with regular inspections (twice per week), allowed us to estimate the day of melt-out as the first day when temperatures at soil surface reached either + 5 °C at day or + 1 °C at night and when the daily temperature amplitude exceeded 5 °C (i.e. temperature characteristics that could not have developed under snow). Snow depth within plots and at the location of the logger was measured twice per month between January and March 2003 to check for natural variability of the snow cover.

To compare the number of potential frost events and growing-degree days that shoots experience after different snowmelt treatments, we used data from the nearest weather station (Keystone Ridge, approximately 5 km from our study site on 500 m a.s.l.). Potential frost days were recorded as the number of days with a minimum temperatures of below 0 °C between snowmelt and the end of the experiment. Growing-degree days were calculated as the sum of all daily mean temperatures above 5 °C between snowmelt and the end of the experiment (mid-August 2003).

Plant response

After snowmelt, we visited the plots every 3–5 days to record the number of living shoots, the phenological state and the presence and number of flower buds, flowers, fruits and preformed generative buds for 2004 for each shoot. We recorded the phenology as the date when a shoot entered a new vegetative or reproductive stage. We defined the following vegetative stages: (1) first leaf entirely green (reduction of anthocyanins, see Oberbauer & Starr, 2002), (2) all leaves entirely green and (3) apical growth of shoot. Reproductive stages were defined as (1) flower buds swelling, (2) first flower open, (3) first flower senescent, (4) first fruit developing and (5) first fruit ripe. In mid-August 2003, we harvested the shoots and dried them to constant weight at room temperature. We then measured shoot length, growth increments, length of the longest new leaf and number and mass of berries of all surviving shoots. The relative neighbour effect (RNE) was calculated according to Markham & Chanway (1996) as

$$\mathrm{RNE} = (P_{-N} - P_{+N})/x,$$

where P is the performance of a plant without ($_{-N}$) and with ($_{+N}$) neighbours and x is either P_{-N} or P_{+N}, whichever is greater. As for example Callaway *et al.* (2002), we present our results in reverse, with positive values indicating facilitation (i.e. positive greater than negative species interactions) and vice versa.

Statistical analysis

We used R 2.1.0 (R Development Core Team, 2004) for Generalized Linear Models (GLMs) and SPSS 11.0.0 (SPSS Inc., 2001) for all other analyses. Because of their clonal nature and, thus, possible genetic similarity between close neighbours, we used the means of the three shoots per species, plot and removal treatment in all analyses and checked for differences between the two sites, which were nonsignificant. Binomial variables (survival, occurrence of vegetative growth, reproduction in 2003 and formation of flower buds for 2004) were analysed using GLMs with a logistic regression model for proportions with a logit link and a binomial error function (for reproduction 2003 and buds 2004 we employed a quasibinomial error function because deviances were overdispersed). Deviances were tested for significance with a χ^2 test. We analysed whether the odds that a shoot in a plot was alive, growing vegetatively, producing berries in 2003 or preforming generative buds for 2004 responded to neighbour removal and melt-out treatments and whether the effects of neighbour removal depended on the melt-out treatment (interaction between neighbour removal and snowmelt treatment). Continuous variables were analysed with ANOVA with type I sequential sums of squares and the same explanatory variables. Standardized residual deviances and sums of squares, respectively, were visually checked for normality and homogeneity and log-transformation was applied to shoot growth increments to meet the assumptions of ANOVA. Whether the RNE per species and treatment differed from 0 was tested with one-sample *t*-tests.

Results

Effects of snowmelt treatments on snow depth and temperature

Snow depths and winter soil surface temperatures did not differ between the three snowmelt treatments before snow manipulation ($F_{2,9} = 0.57$ and 0.50, respectively). Timing of and temperatures during natural melt-out (on 28 April in control plots) were close to the long-term mean, although winter mean temperatures had been approximately 5 °C above and snow cover depth 50% below long-term mean (as measured in Fairbanks, AK, USA, NOAA, 2002–2003). Snow manipulations caused melt-out to occur on 20 April in advanced plots and 7 May in postponed plots, changing the length of the growing season (snow-free to first frost below −5 °C) by + 6% and −7%, respectively. Correspondingly, the temperature sum accumulated (i.e. growing-degree days above 5 °C) was increased by 6% and decreased by 5% in the advanced and postponed melt-out treatments, respectively ($F_{2,9} = 22.5$, $P < 0.001$, Fig. 1). The number of potential frosts (air temperatures below 0 °C) during the growing season, however, was the higher the earlier snow had melted ($N = 12$, $R^2 = 0.94$, $P < 0.001$, Fig. 1) and was increased by 21% and decreased by 45% by the advanced and postponed melt-out, respectively ($F_{2,9} = 19.6$, $P < 0.001$). The mean summer temperature was decreased by 0.3 °C in early melting and increased by 0.6 °C in late melting plots ($F_{2,9} = 12.4$, $P = 0.003$, Fig. 1).

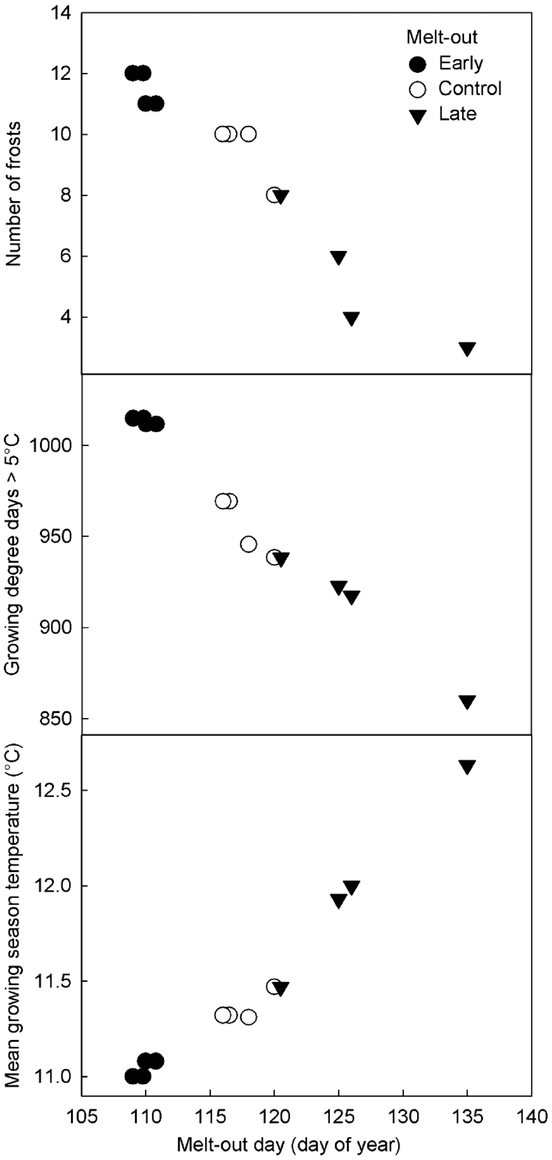

Fig. 1 The number of frost events (days with subzero temperatures), growing-degree days (sum of daily mean temperatures >5 °C) and mean growing season temperatures in relation to the corresponding day of melt-out and melt-out treatment.

Survival

Overall, 86% of a total of 72 *E. nigrum* shoots had survived at the end of our experiment. There was a significant interaction between effects of snow treatment and neighbour removal on the survival of *E. nigrum* shoots ($\chi^2_2 = 7.8$, $P = 0.02$, Fig. 2). More than 80% of the shoots growing with neighbours, or growing in controls and late melting plots survived, but only 50% of shoots with advanced melt-out survived when neighbours had been removed. The RNE on survival of *E. nigrum* shoots indicated a facilitative effect of neighbours in early melting sites (one-sample *t*-test, $N = 4$, $t = 3.0$, $P = 0.058$, Fig. 4). Forty per cent of *V. vitis-idaea* shoots died during our experiment. The survival was lower in plots with advanced melt-out and controls than in plots with delayed melt-out ($\chi^2_2 = 12.9$, $P = 0.002$, Fig. 2), but was not affected by neighbour removal ($P > 0.1$). Therefore, no RNE on survival of *V. vitis-idaea* was detected.

$P = 0.007$), this effect being largest in plots with advanced melt-out (interaction snowmelt × neighbour removal treatment, $F_{2,18} = 4.9$, $P = 0.021$). The time between melt-out and swelling of flower buds was shortest in late melting plots ($F_{2,18} = 15.1$, $P < 0.001$, Fig. 3b), furthermore, neighbour removal tended to decrease this time span in plots with advanced melt-out and increase it in control plots (interaction snowmelt × neighbour removal treatment, $F_{2,18} = 3.1$, $P = 0.084$). The timing of all other reproductive stages was unaffected by snowmelt and neighbour removal treatments (Fig. 3b).

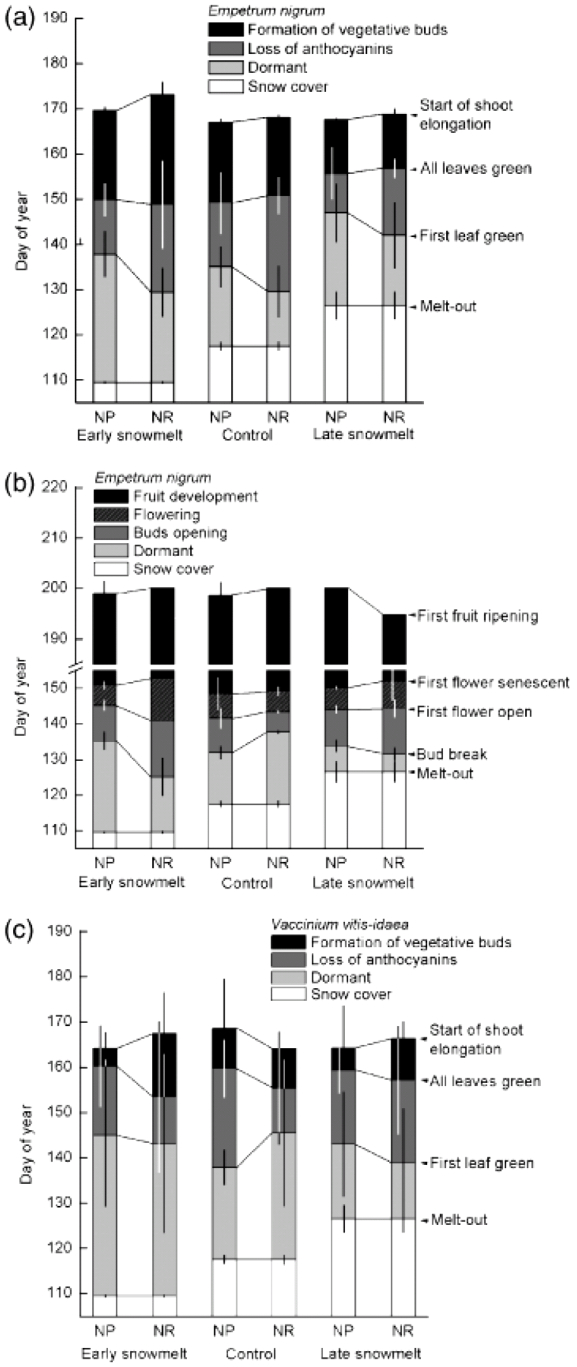

Fig. 3 Effects of melt-out and neighbour removal treatments on the phenological development of *Empetrum nigrum* and *Vaccinium vitis-idaea* shoots (means ± standard error of dates and duration of phenological traits). (a) Vegetative and (b) reproductive stages of *E. nigrum*, (c) vegetative stages of *V. vitis-idaea*. Reproduction of *V. vitis-idaea* only occurred in three plots and was therefore ommited. NP, neighbours present; NR, neighbours removed.

The RNE indicated facilitation in the first phenological stages and in early melting plots only. In plots with early melt-out, the presence of neighbours advanced the date of first greening (RNE = 0.1; one-sample *t*-test $N = 4$, $t = 4.2$, $P = 0.025$) and shortened the time between melting and the beginning of greening (RNE = 0.52; $t = 8.3$, $P = 0.014$) and between melting and swelling of flower buds (RNE = 0.53; $t = 4.3$, $P = 0.024$).

In the phenology of *V. vitis-idaea*, there was no difference between snowmelt treatments except for the time lag between snowmelt and start of greening, which was inversely related to the timing of melt-out, i.e. longest in early and shortest in late melting plots ($F_{2,18} = 4.0$, $P = 0.038$, Fig. 3c). Neighbour removal did not affect the timing of the phenological development and thus, RNE did not differ from 0 in any treatment at any stage.

Growth

Vegetative growth in *E. nigrum* was generally negatively affected by neighbour removal and advanced melt-out. The proportion of surviving *E. nigrum* shoots that showed vegetative growth in 2003 was reduced after neighbour removal ($\chi^2_1 = 8.7$, $P = 0.003$), but unaffected by snow treatments ($\chi^2_2 = 1.5$; Fig. 2). The growth increments of shoots were reduced by advanced melt-out ($F_{2,18} = 3.8$, $P = 0.043$) and neighbour removal ($F_{1,18} = 7.4$, $P = 0.014$), however, the negative effect of neighbour removal tended to diminish from advanced to postponed melt-out (interaction snowmelt × neighbour removal treatment, $F_{2,18} = 3.0$, $P = 0.073$, Fig. 2). The length of the longest leaf produced in 2003 differed between snowmelt treatments ($F_{2,16} = 3.6$, $P = 0.05$), being smallest in early and greatest in late melting plots (Fig. 2). Within shoots without neighbours, growth increments were negatively correlated to the amount of standing biomass that had been removed by the neighbour removal treatment in 2002 ($N = 12$, $R^2 = 0.52$, $P = 0.008$). Furthermore, the RNE on growth was positively correlated with standing biomass removed ($N = 12$, $R^2 = 0.49$, $P = 0.011$). This suggests that the facilitative effect of the neighbouring vegetation on growth was related to the amount of its standing biomass. The RNE was moreover positively correlated

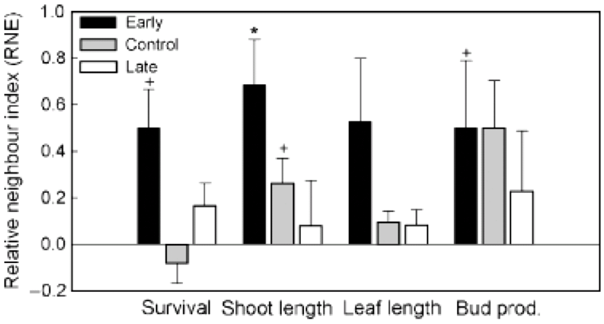

Fig. 4 The relative neighbour effect (RNE) on survival rate, shoot length, leaf length and the proportion of shoots with preformed generative buds for 2004 of *Empetrum nigrum* in each melt-out treatment (mean and standard error). Significant and marginally significant differences from 0 (one-sample *t*-test) are indicated by $^{*}P<0.05$ and $^{+}P<0.1$.

with snowmelt date ($N=12$, $R^2=0.56$, $P=0.005$) and facilitation was strong and significant in plots with advanced melt-out (one-sample *t*-test, $N=4$, $t=3.51$, $P=0.039$) and weak and only marginally significant in control plots ($t=2.48$, $P=0.089$, Fig. 4). The proportion of live *V. vitis-idaea* shoots that showed vegetative growth did not respond to snowmelt manipulation or neighbour removal. However, shoot growth increments tended to be reduced after advanced melt-out compared with controls and plots with delayed melt-out ($F_{1,17}=3.5$, $P=0.053$, Fig. 2). Other growth parameters and RNE were not significantly affected by the experimental treatments.

Reproduction

All parameters of reproduction of *E. nigrum* in the 2003 season were unaffected by snowmelt treatments and neighbour removal: the proportion of shoots bearing berries, the proportion of generative buds (performed in the previous year) that had developed into ripe berries and the number and dry mass of berries did not respond to our treatments (Fig. 5). However, advanced melt-out and neighbour removal tended to reduce the proportion of shoots with generative buds preformed for the following year ($\chi^2_2=5.3$, $P=0.069$ and $\chi^2_1=2.7$, $P=0.099$, Fig. 5), indicating that a negative effect of advanced melt-out and neighbour removal on reproduction might have been found in the following year. The RNE on future reproduction (i.e. the proportion of shoots bearing preformed generative buds) tended to be positively related to snowmelt date ($N=12$, $R^2=0.28$, $P=0.078$) and facilitation was marginally significant in early melting plots (one-sample *t*-test, $N=4$, $t=3.0$, $P=0.058$, Fig. 4). *V. vitis-idaea* reproduced in three of 12 plots only, thus, we omitted all analyses of reproductive parameters.

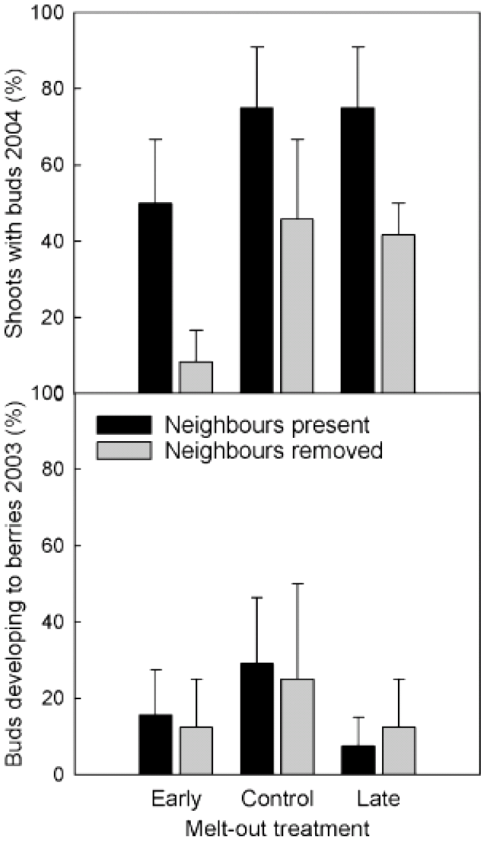

Fig. 5 Effects of melt-out and neighbour removal treatments on the proportion of shoots with preformed generative buds for 2004 and on the proportion of buds that developed into ripe berries in 2003 of *Empetrum nigrum* (mean and standard error).

Discussion

Snowmelt date and plant performance

Our results demonstrate that changes in winter climate and snow cover characteristics can affect the performance of dominant subarctic plants in the short term. This is in line with other studies from arctic and alpine communities, which found that snow cover characteristics and the timing of snowmelt affect plant phenology (Rixen *et al.*, 2001; Dunne *et al.*, 2003), shoot growth (Walker *et al.*, 1995; Kudo *et al.*, 1999; Dorrepaal *et al.*, 2003), reproduction (Galen & Stanton, 1991; Inouye *et al.*, 2002; Saavedra *et al.*, 2003) and species abundance (Bell & Bliss, 1979; Galen & Stanton, 1993) in the short term and species composition (Scott & Rouse, 1995; Wahren *et al.*, 2005; Wipf *et al.*, 2005) in the long term. Thus, there is a growing body of evidence indicating that changes in snow quantity and winter temperatures and resulting changes in snowmelt timing are key factors that have to be considered in climate change ecology in addition to changes in summer temperatures, nutrients and solar radiation. The melt-out treatments changed the pace of phenological development such that shoots from plots with advanced melt-out went through their first phenological stages more slowly than those from later melting plots. As a consequence, differences in phenology vanished throughout the summer in both target species. However, the initial differences between snowmelt treatments were greater and lasted longer in the early-flowering *E. nigrum* than in the later-flowering *V. vitis-idaea*. Both findings correspond to those of other snowmelt experiments with arctic and alpine species (Van der Wal *et al.*, 2000; Rixen *et al.*, 2001; Dunne *et al.*, 2003; Aerts *et al.*, 2004). The generally great synchrony between the phenology of early-developing species and the date of snowmelt (Galen & Stanton, 1995; Inouye *et al.*, 2000; Dunne *et al.*, 2003) might explain the fact that only *E. nigrum*, but not *V. vitis-idaea* strongly reacted to snowmelt treatments.

The phenological development is thought to be driven to a large extent by temperature (e.g. Sørensen, 1941; Thorhallsdottir, 1998 for tundra plants). The accumulated temperature (expressed as growing-degree days summed up from snowmelt to the date of a phenological trait) is often inversely related to the date of a phenological trait (Lindsey & Newman, 1956; Dunne *et al.*, 2003). However, as the phenological stages after differing melt-out timings aligned to each other, growing-degree days are unsuitable predictors of phenological development in snow manipulation experiments, but also in warming experiments in arctic tundra (Starr *et al.*, 2000; Hollister *et al.*, 2005). Thus, other factors related to snowmelt date (Galen & Stanton, 1995; Price & Waser, 1998) or to the occurrence, timing or intensity of frost (Schlussel *et al.*, 2000) seem to dominate or mediate the effects of temperature on phenology (Hollister *et al.*, 2005).

Although the timing of later phenological traits after advanced snowmelt did not differ from controls, vegetative growth and the preformation of next year's flower buds responded negatively to advanced snowmelt in *E. nigrum*. The growth response of *V. vitis-idaea*, however, was nonsignificant. Negative and neutral responses to advanced melt-out are in accordance with numerous studies conducted in communities with relatively early natural snowmelt (Bell & Bliss, 1979; Starr *et al.*, 2000; Van der Wal *et al.*, 2000; Stinson, 2004). Our findings differ, however, from several snow manipulation studies where plant growth or fitness responded positively to advanced melt-out, a result that was often found in communities with late natural melt-out (Galen & Stanton, 1993, 1995; Saavedra *et al.*, 2003) or with additional warming treatments (Price & Waser, 1998; Walker *et al.*, 1999; Starr *et al.*, 2000; de Valpine & Harte, 2001; but see Saavedra *et al.*, 2003). Delayed snowmelt, on the other hand, had no effect on growth and reproduction of both target species in our study, which corresponds to previous examples where a moderate delay in melt-out, although shortening the growing season, did not affect plant growth (Bell & Bliss, 1979; Scott & Rouse, 1995; Smith *et al.*, 1995; Walsh *et al.*, 1997; Walker *et al.*, 1999).

The varying responses to snow manipulations suggest that the effects of melt-out manipulations strongly depend on the conditions into which plants are released, but that the response is species specific. In our study, negative effects associated with early snowmelt (such as low temperatures at the start of the growing season, reduced mean summer temperatures, enhanced number of postmelt frosts or increased frost susceptibility of plants with early development), seemed to have outweighed the positive effects, such as increased growing season length and greater overall temperature accumulation (growing-degree days). However, longer term studies are needed to confirm our short-term results and to analyse the interactions between snow cover, timing of snowmelt, spring temperatures and frosts. Future studies might find positive effects of a prolonged growing season on plant fitness in years or sites with a mild spring climate, in communities with naturally late snowmelt or in experiments with additional warming treatments. Nevertheless, even a short-term experiment like ours points to the important role of changes in snow cover for the performance of subarctic plants.

Snowmelt date and neighbour effects

Positive species interactions were more pronounced after advanced melt-out in our study. Furthermore, reactions to neighbour removal were more pronounced in *E. nigrum*, which was also more responsive to snowmelt manipulation than *V. vitis-idaea*. As advanced melt-out generally resulted in unfavourable growing conditions, as shown by the mostly negative plant response to advanced snowmelt, our results confirm that positive species interactions are stronger under harsher conditions. This is consistent with numerous models (Grime, 1974, 1977; Brooker & Callaghan, 1998; Brooker *et al.*, 2005) and field studies (Choler *et al.*, 2001; Callaway *et al.*, 2002; Olofsson, 2004). A widely accepted explanation for this is that neighbours ameliorate the growing conditions within a plant community by forming a closed canopy and thereby lessening e.g. wind exposure, water loss and radiative and wind cooling (see Koerner, 1999 for a summary). Thus, plywood shelters could have similar positive effects on arctic plants as neighbours (Carlsson & Callaghan, 1991). Our finding that the net positive effect of neighbours was higher in plots with more standing biomass indicates that physical protection among neighbours might in fact have been a key factor in this study.

During the period between fall frosts and the formation of a persistent snow cover, protection by neighbouring plants could be just as crucial as during spring and growing season. For practical reasons, we conducted the neighbour removal treatments before freeze-up; therefore, we cannot assess whether the physical protection by neighbours was more important during freeze-up or during melt-up and the growing season. However, as freeze-up occurred at the same time in all sites and treatments were randomly assigned, we do not expect the timing of the neighbour clipping treatment to have any influence on snowmelt by neighbour interactions.

Our results suggest that positive and negative species interactions are close to being in balance in this subarctic tundra community, but that this balance can be tipped through relatively moderate modifications in climate: the RNE on most variables and both species was neutral in controls, but shifted to facilitation after advanced melt-out. Similarly, shifts between net competition and net facilitation in the same community resulting from small changes in conditions have been found for different microsites (Choler *et al.*, 2001; Olofsson, 2004), different years (Shevtsova *et al.*, 1995) or different species (Choler *et al.*, 2001). Therefore, it is likely that the balance between positive and negative species interactions will be affected by climate change.

Conclusions

Advanced snowmelt, although lengthening the growing season, resulted in harsher growing conditions for subarctic dwarf shrubs, mainly affecting the early flowering *E. nigrum*. Thus, its shoots performed poorly after early snowmelt (as measured by survival, growth, leaf length and future reproduction), while shoots from late melting plots were able to compensate for the shortened growing season by accelerating their phenological development. Positive and negative species interactions were in balance in control plots, but facilitation was found in plots with advanced melt-out, which supports the concept that positive species interactions became more important under a harsher climate. We conclude that the balance between positive and negative species interaction in this tundra community is fragile and that a shift in this balance was induced through a moderate and realistic change in climate (i.e. advancing snowmelt by 1 week). However, our results display short-term reactions of single species and species interactions only. We recommend that future research be conducted to determine whether and over which time periods such changes in the balance of neighbour interactions will lead to changes in the composition of subarctic tundra vegetation.

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Chapter 5

Winter climate change: how do alpine tundra plants respond to reduced snow depth and advanced snowmelt?

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Abstract

Snow is an important component of the climate system in alpine ecosystems. With current climate warming, the snow:rain ratio is decreasing, and the snow cover vanishes earlier in the year. In a two-year field experiment near the treeline in the Swiss Alps, we are investigating how a substantial decrease in snow depth and an earlier snowmelt affect plant phenology, fitness, reproduction, and species composition of the native tundra community. In a fully factorial experiment we 1) reduced the snow depth during winter, leading to colder soil temperatures due to a lower insulation capacity, and 2) removed snow in spring to advance snowmelt. Besides prolonging the growing season, an advanced snowmelt also increased the frost frequency and the sum of growing season temperatures. In addition to the experiment, we used path analyses to explore the mechanisms leading to changes in plant growth after snowmelt manipulations.

Changes in snowmelt date had more pronounced effects on plant performance than changes in snow depth. After advanced snowmelt, responses in fitness and growth of the most frequent tundra dwarf shrub were mostly negative. The reproductive phenology was advanced throughout much of the season after earlier snowmelt, reproductive traits, however, were negatively affected. Shallow snow depth did in some species increase these effects of snowmelt manipulations. Path analysis showed for one species only a direct impact of snowmelt date on growth. The timing when shoot growth started, the temperatures during growth, and frost events played a major role and did indirectly link snowmelt date and growth. Increased frost damages after advanced snowmelt were also visible as increased leaf damages and mortality of flower buds. First changes in species abundance in response to snow manipulation treatments were already apparent after two years, and in part correlate with the negative effects on the fitness of these species.

We conclude that changes in snow cover can have a wide range of effects on alpine tundra on the scale of individual plants, community composition, and ecosystem processes. Thus, snow cover changes should be taken into consideration when exploring and predicting the effects of climate change on alpine ecosystems.

Introduction

Climate warming in the last decades has been strongest at high altitudes (Diaz & Bradley, 1997) and latitudes (ACIA, 2004; IPCC, 2001), and future warming rates are predicted to be above average for these areas (ACIA, 2004; IPCC, 2001). Moreover, warming has been, and will be stronger in winter and spring than in summer (ACIA, 2004; Giorgi *et al.*, 1997). Thus, future changes in alpine and arctic climate may be more pronounced in winter than in summer.

Under current climate change, the winter snow cover is already one of the fastest-changing climate factors in alpine areas. The warmer winter temperatures change the precipitation patterns by decreasing the proportion of the precipitation falling as snow (Rebetez, 1996). Together with the increased spring temperatures, this fosters an earlier and faster spring snowmelt. Correspondingly, the snow cover extent and duration in arctic and in alpine areas worldwide have decreased over the last decades (Brown, 2000; Mote *et al.*, 2005; Robinson & Frei, 2000; Serreze *et al.*, 2000). In mountain areas, these changes are especially evident by an upward shift of the snow line, and a decrease in the snow cover duration at lower altitudes (Diaz *et al.*, 2003; Lopez-Moreno, 2005; Mote *et al.*, 2005). In the European Alps, decreases in snow depth and duration have been greatest below 1300 m asl (Beniston, 1997; Laternser & Schneebeli, 2003; Scherrer *et al.*, 2004). However, the altitude affected by significant changes in snow cover will rise further (Hantel *et al.*, 2000; Scherrer *et al.*, 2004).

The snow cover is an important component of alpine ecosystems (this thesis, chapter 1). It covers alpine plants during the cold season, and defines the soil temperatures due to its insulation capacity, which decouples air and soil temperatures when snow depths of 50 to 80 cm are reached (Haeberli, 1973; Rixen *et al.*, 2004). Low subnivean temperatures due to a shallow snow cover can significantly influence belowground processes (root survival, microbial activity, nutrient cycling; see this thesis, chapter 6), but do probably not damage aboveground plant parts, as plant tissue in winter can withstand lower temperatures than the ones reached under snow. The disappearance of the snow cover in spring marks the start and thus, defines the length of the potential vegetation period. Thus, changes in winter climate are very likely to affect vegetation and ecosystem processes in seasonally snow covered regions.

In recent decades, different vegetation responses related to snow cover changes have been recorded. An earlier spring greening-up of arctic (Myneni *et al.*, 1997; Shabanov *et al.*, 2002) and alpine vegetation (Defila & Clot, 2005; Studer *et al.*, 2005) is documented in time series of leaf budburst of individual species (Fitter & Fitter, 2002; Menzel & Fabian, 1999; Studer *et al.*, 2005), and on satellite images recording the Normalized Differential Vegetation Index (NDVI) (Dye & Tucker, 2003; Reed *et al.*, 1994). Although closely linked to a warmer climate, it is not clear whether the earlier greening of arctic and alpine communities is mainly driven by temperature or snowmelt (Myneni *et al.*, 1997). In snow manipulation experiments, the greening of leaves strongly responded to snowmelt date, especially in early-developing species, while later phenological stages and later-developing species were less sensitive to snowmelt timing (Dunne *et al.*, 2003, this thesis, chapter 3; Galen & Stanton, 1995). Another strong indication for the important role of snow cover changes for tundra ecosystems is the increased productivity of tundra vegetation in response to deeper snow covers in the Arctic (Grippa *et al.*, 2005; Sturm *et al.*, 2001). Increased over-winter soil temperatures due to better insulation (especially in the lee of tall vegetation) and less cold air temperatures increase microbial activity and litter decomposition, increasing the nutrient availability for tundra plants (Sturm *et al.*, 2005).

In a two-year experiment at timberline, we factorially reduced snow depth and advanced snowmelt. Thus, we simulated a potential future winter climate with a lower snow:rain ratio, and thus, a shallower, earlier-melting winter snow cover (see chapter 1, Fig. 3). The reductions in snow depth induced lower soil temperatures below the remaining snow cover. The advanced snowmelt led to a prolonged vegetation season and increased the temperature sum over the whole summer, but temperatures just after snowmelt were lower (especially in early spring), and the number of low-temperature events increased. We measured and tested the response in phenology, fitness and fecundity of the most abundant tundra plant species, as well as changes in species abundances after two years with manipulations of winter climate. We used path analysis to explore the mechanisms leading to changes in plant growth after snowmelt manipulations for different plant species and to disentangle the direct and indirect relationships between the climate factors snowmelt date, frost occurrence, and temperature, and the plant responses in phenology and growth.

We hypothesise that snowmelt manipulation will have larger short term effects on plant performance than snow depth manipulations, because the winter temperatures under the reduced snow cover would still not be low enough to have any direct negative effects on plant tissues. Moreover, we expecte snowmelt manipulation to advance the timing of the phenological development, and thus increase the plant fitness and growth due to the longer period available for growth and resource allocation. However, harsher growing conditions in the first phase after advanced snowmelt could reverse this growth response. Moreover, the reactions to changes in snow cover and time of snowmelt could differ between species.

Our experiment quantifies in detail the changes in the environment and the reactions in plant performance after mimicking a specific and relatively realistic snow cover scenario. The experimental approach chosen thus allows us to explore the vegetation reactions and to disentangle their causes in detail. The results of our study will therefore give us more insight into the complex and so far barely considered responses of alpine ecosystem to changes in snow cover characteristics that could be expected in a warmer climate.

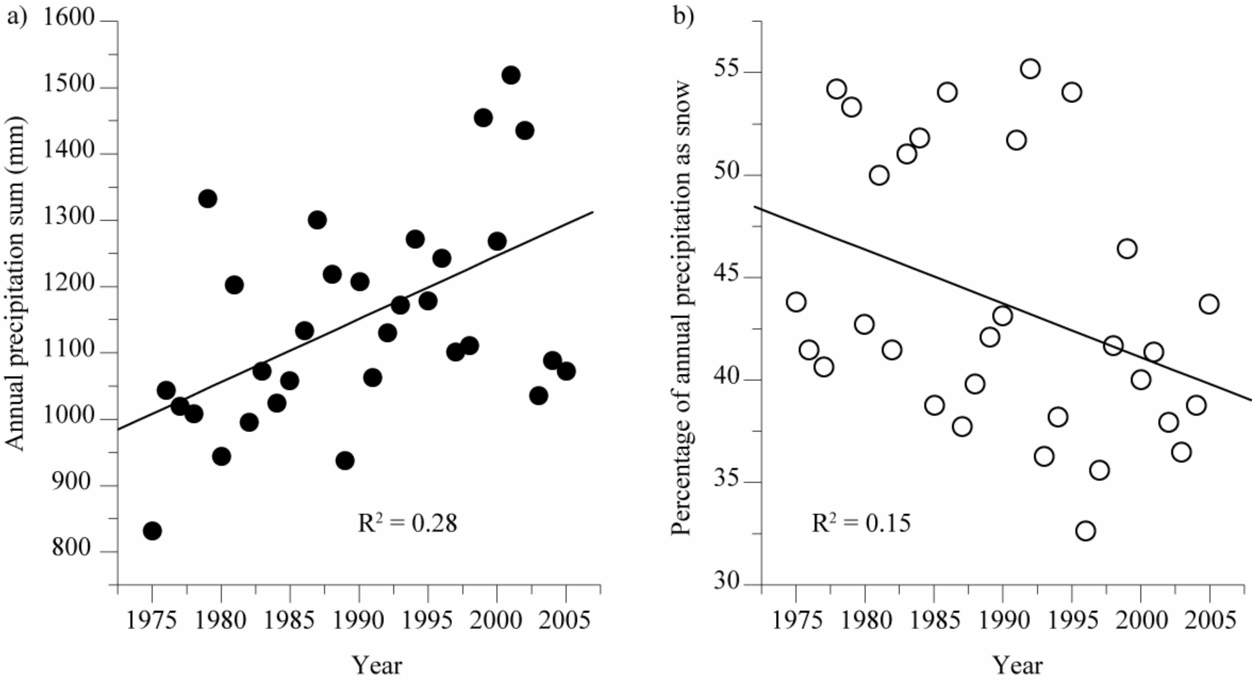

Figure 1. a) Annual precipitation sums, and b) percentage of snow at the total annual precipitation from 1975 to 2004 at the research site Stillberg, Davos, Switzerland, 2090 m asl. Precipitation as snow was defined as the sum of precipitation falling at or below 0°C (derived from 1 h mean values). Both correlations are significant at the *P* = 0.05 level.

Methods

Study site

The site of our study is within the research site of Stillberg, Davos (Central Alps, Switzerland, 47°28'N 7°30'E), situated on a NE exposed slope close to the treeline at 2200 m asl. Climate data were continuously measured by a nearby weather station at 2090 m asl since 1975, and the data presented here are means from 1975 to 2004 (see chapter 1 of this thesis for a climate diagram). Total annual precipitation amounted to 1150 mm per year (SD = +/- 164 mm), 48% of which fell during the vegetation period between June and September. The mean air temperatures were 2.0°C (+/- 0.7°C) over the year and 8.5°C (+/- 1°C) over the vegetation period (June to September), February being the coldest month (on average -4.9°C +/- 2.3°C), and July and August the warmest (both 9.9°C +/- 1.5°C). Snow cover at the weather station lasted on average from 18 October (+/- 16 days) to 26 May (+/- 10 days), and the annual maximum snow depth averaged 143 cm (+/- 31 cm). From 1975 to 2004, the proportion of the annual precipitation falling as snow (i.e. the amount of precipitation falling at temperatures below or equal to 0°C, measured in 1h-intervals) significantly decreased by 3% per decade (linear regression, $F_{1,28}$=4.8, P = 0.04; Fig. 1), and the snowmelt date became significantly earlier by 4 days per decade (linear regression, $F_{1,28}$=5.2, P = 0.03).

The vegetation on our plots, growing on a 5 to 20 cm deep organic topsoil layer on siliceous gneiss (Bednorz *et al.*, 2000), consists of a relatively species-poor tundra type dominated by the deciduous dwarf shrub species *Vaccinium myrtillus* (bilberry) and *Vaccinium uliginosum* ssp. *gaultherioides* (alpine bog blueberry, subsequently called *V. uliginosum*), and the evergreen *Empetrum nigrum* ssp. *hermaphroditum* (crowberry, subsequently called *E. nigrum*). See chapter 1, Table 2 for a list of the most frequent plant species and their abundances.

Experimental design and treatments

In autumn 2003 and spring 2004, we established 8 blocks at sites with visually homogeneous vegetation, each block consisting of 4 plots of 1 m^2 at a distance of approximately 3 to 4 m. Our climate change treatments consisted of a snow reduction treatment, simulating a climate with warmer temperatures or less winter precipitation and thus, less snowfall, and an advanced snowmelt treatment, simulating an early snowmelt due to decreased snow depths in winter or increased spring temperatures. These two types of manipulations were combined within a fully factorial design, resulting in the following four treatments, which were randomly assigned to one plot each within a block: ambient snowmelt and ambient snow cover depth (i.e. controls), ambient snowmelt/shallow snow depth, advanced snowmelt/ambient snow depth, and advanced snowmelt/shallow snow depth. Miniature temperature loggers in each plot recorded the temperatures at the soil-snow interface in 3-hour intervals from autumn to snowmelt to the nearest 0.5°C. These measurements allowed us to quantify the effects of the snow reduction treatment on the soil temperatures, and, along with regular visits, to detect melt-out as the first day when temperatures reached either +5°C at day or +1°C at night, and when the daily temperature amplitude exceeded 5°C.

For the snow reduction treatment, we kept the snow depth at approximately 40 cm during winter by shovelling away most of the snow after each snowfall period, carefully avoiding compression of the remaining snow. The snow cover thus still covered the vegetation, but its reduced insulation capacity led to a decrease in subnivean temperatures (see chapter 1, Fig. 3 for an example of the temperature course over winter). The snow removal treatment decreased the minimum temperatures under the snow in general, but especially in the first year (from –2.9 to –4.8° C in 2004, and from –4.5 to –5.1°C in 2005; effect of snow depth treatment: $F_{1,7}$=4.7, P=0.07, effect of year*snow depth treatment: $F_{1,2}$=67.9, P=0.01). The mean temperatures under a persistent snow cover (measured at the soil surface from 10 October 2003 to 16 May 2004 and from 11 November 2004 to 20 May 2005) differed only in 2005, reaching –1.0°C below decreased snow covers and –0.5°C in control plots (vs. –0.2°C in both treatments in 2004; year*snow depth treatment: $F_{1,2}$=10.9, *P*=0.08). The snow reduction treatment was stopped towards spring, and due to new snowfalls and wind redistribution, the snow depths on treatment and control plots were approximately level when the spring snowmelt started.

The natural variation in snowmelt (i.e. snowmelt dates in unmanipulated plots) ranged from 1 to 17 June in 2004, but only from 30 May to 3 June in 2005 due to an unusual warm spell. This warm period made it difficult to define the snowmelt timing. To reach a significant difference in snowmelt dates between plots with early snowmelt and controls, we delayed the melting process on control plots by adding an additional 30 to 50 cm of snow (added when the ground was still snow covered). For better comprehensibility, we nevertheless call this treatment "ambient snowmelt" throughout the manuscript. Moreover, the 2005 data of an entire block and 2 plots were excluded from analysis because they were snowfree before the start of the snowmelt manipulations.

When the first patches in the region were snowfree, we simulated earlier snowmelt by carefully removing most of the remaining snow (60 to 80 cm), without damaging the vegetation, and letting the last 10 to 20 cm of snow melt naturally. In total, snowmelt manipulations advanced snowmelt by 11.3 days in 2004 and by 6.2 days in 2005 (effect of melt date: $F_{1,7}$=52.6, *P*<0.001, effect of year*melt date: $F_{1,6}$=11.7, *P*=0.01). Assuming the same advance in snowmelt as during the previous 30 years, this treatment corresponds to a realistic snowmelt scenario for 15 to 30 years from now. The snowmelt treatment prolonged the potential vegetation period (i.e. the time period between melt out and the first heavy frosts in fall) by 11% in 2004 and by 6% in 2005. Moreover, due to the advanced snowmelt the number of frost events during the growing season (i.e. days with a minimum temperature below 0°C) were increased by 4 (+45%) in 2004 and by one (+16%) in 2005 (effect of melt date: $F_{1,7}$=15.9, *P*<0.01, effect of year*melt date: $F_{1,6}$=17.3, *P*<0.01).

From the daily mean temperatures of the nearby weather station we calculated two types of growing degree days (Gdd) for each plot: the sum of all daily mean temperatures above 5°C from snowmelt to end of the vegetation period (Gdd season), and from the start of the vegetative growth of each study species to the end of the vegetation period (Gdd growth, calculated for the 6 species listed below).

Plant responses

In each plot, we marked 4 (if present) shoots of each of the seven most abundant species: *Empetrum nigrum*, *Vaccinium uliginosum*, *V. myrtillus*, *V. vitis-idaea*, *Rhododendron ferrugineum* (in 2005 only), and *Loiseleuria procumbens*. After snowmelt, we visited the plots every 3 to 5 days in both years to record the number of living shoots, their phenological state, and the presence and number of flower buds, flowers, and ripe fruits. We recorded the phenological development as the dates when a shoot entered a new vegetative or reproductive stage, and calculated the length of every stage as the difference between two starting dates. The following vegetative stages were recorded: 1) greening up, i.e. all leaves entirely green in evergreens (reduction of anthocyanins, see Oberbauer & Starr, 2002), or first leave entirely visible and unfolded in deciduous species, 2) start of vegetative shoot growth, and 3) first leaves with fall coloration. Reproductive stages were defined as: 1) flower buds swelling, 2) flower open, and 3) flower senescent.

In summer 2004 and 2005, we measured the chlorophyll content of a random sample of 4 leaves per plot of the two deciduous dwarf shrub species, *V. myrtillus* and *V. uliginosum* using a Minolta Spad-502 chlorophyll meter. We then took random samples of a minimum of 7 leaves per plot and species to record their area, length, and the loss of leaf area due to herbivory. We scanned the leaves with a flatbed scanner and marked the parts that were missing due to herbivory by hand on the digital pictures. From the pictures, we measured the mean area of the present and missing leaf parts, and the mean leaf length (i.e. longest diameter) of leaves unaffected by herbivory, using ImageJ (Rasband, 1997-2006), and calculated the total leaf area as the sum of present and missing leaf parts. We weighed the dry leaves and calculated the LMA (leaf mass per unit area, in g*m^{-2}) of undamaged leaves. In 2004, we assessed the total carbon and nitrogen content, and calculated the C:N ratio of *V. myrtillus* and *V. uliginosum* leaves harvested at the end of the season.

In autumn 2004 and 2005, we harvested the ripe berries of *E. nigrum* and the three *Vaccinium* species from the marked plants and an additional sample of a minimum of 5 random berries per species and plot, dried them at 60° C and recorded their dry weight. In October 2005, after the second growing season, we harvested all marked shoots. We determined plant fitness by measuring the shoot growth increments of the last 2 years in all dwarf shrub species, and the length of the shoot part with living leaves in all evergreen shrub species using calipers.

In mid-June 2005, two consecutive cold nights (air temperatures below -7°C) with clear sky caused damages in newly formed leaves and flower buds of *V. myrtillus* and *V. uliginosum*. Frost damages on leaves and apical buds were visible as blackened and aborted tissue and could therefore easily be determined. We counted the proportion of marked shoots per plot of these two species that had frost damages on an apical bud or three or more leaves. Frost most probably also caused abortion of flower buds which had just started to develop at the time of the frost event, but frost damages of flower buds were not clearly distinct from other damages. We therefore calculated the survival rate of buds (i.e. the proportion of buds that developed into flowers) for each plot and species as an estimate of frost damage, although bud mortality might also have been influenced by other factors.

We recorded the abundance of a total of 14 species as the number of squares occupied in a 0.5 x 0.5 m frame divided into 25 squares in mid-August 2003 and September 2005, and calculated the relative change in abundance during the two years of the experiment. The 14 species are listed in chapter 1, Table 2 of this thesis.

Statistical analysis

The data of the maximum 4 shoots per species and plot were pooled, i.e. means for continuous values, and proportions for binary variables were calculated and used as response variables in our analysis. To test for the effects of the snow manipulation treatments, we used ANOVAs with type I sums of squares. We analysed whether the response variables (timing of phenological stages, growth and leaf parameters, fecundity and berry production, herbivory and frost damages) differed between years, snowmelt treatments, and snow depth treatments, and whether there were interactions betweens these factors. Due to the blockwise structure of our experiment, we defined snowmelt treatment, snow depth treatment and year as fixed, and block as random factors. Residuals were visually checked for normality and homogeneity, and transformations were applied if necessary (indicated in the results sections).

To explain how the timing of snowmelt could directly and indirectly affect shoot growth of the six dwarf shrub species *E. nigrum*, *L. procumens*, *R. ferrugineum*, *V. myrtillus*, *V. uliginosum*, and *V. vitis-idaea*, we explored possible causal relationships with path analyses (Mitchell, 2001), using the variables snowmelt date, number of frost occurrence, phenology (start of vegetative growth) and temperature (growing degree days >5°C during snowfree season, and during actual shoot growth) over both years of our study as explanatory variables. We hypothesised that snowmelt date could influence shoot growth via 4 mechanisms (see Fig. 4, hypothesis): 1) directly, due its effect on the length of the season available for plant activity and photosynthesis; 2) via growing degree temperatures accumulated during the snowfree season, 3) via the impact of snowmelt timing on phenology, which could either affect growth directly, or define the accumulation of growing degree temperatures during the actual period of shoot growth; and 4) via the control of snowmelt timing on the number of growing season frosts, which could decrease shoot growth by damaging the plants directly, or inhibit the phenological development. All analyses were conducted in SPSS 11.0 (SPSS Inc., 2001).

Results

Phenology

The vegetative phenology of all species except *V. vitis-idaea* was affected by snow manipulation (Fig. 2a, c, Table 1a). Earlier snowmelt generally advanced the first phenological stage, i.e. the timing when all leaves were entirely green (in evergreens) and unfolded (in deciduous species). In the two deciduous species, also snow depth manipulations affected the phenology: reducing snow cover during winter advanced leaf greening in *V. uliginosum*, and decreased the difference in phenological state between plots with early snowmelt and controls in *V. myrtillus*. The start of leaf senescence (i.e. start of fall coloration) in these two species tended to be advanced by early snowmelt in the first year of our study. Leaf senescence in the only evergreen species with distinct fall coloration, *L. procumbens,* was not affected by the snow treatments.

The time span between snowmelt and vegetative growth was longer after advanced snowmelt in *E. nigrum*, *L. procumbens, V. uliginosum*, and *V. myrtillus* (more in 2004 than 2005 in *E. nigrum* and *V. uliginosum),* and tended to be longer after a winter with reduced snow cover in *L. procumbens, V. myrtillus* (only in 2005), and *V. uliginosum*. Still, vegetative growth started earlier after advanced snowmelt in *E. nigrum* (marginally significant), *L. procumbens*, and *V. uliginosum* (in 2004 only). In *V. myrtillus,* advanced snowmelt tended to delay the start of vegetative growth, especially in 2005 and after a winter with reduced snow cover.

The reproductive phenology was affected by snow manipulations in all species (Fig. 2b, d, Table 1b). Swelling flower buds were recorded earlier in plots with advanced snowmelt than in controls in *E. nigrum* and *V. uliginosum*. Flowering dates in these two species were also advanced after early snowmelt (*V. uliginosum* in 2004 only), moreover did reduced snow cover over winter tend to advance flowering in *E. nigrum* and *V. uliginosum*. Flowers tended to be senescent earlier in advanced plots in *E. nigrum, V. myrtillus* and *V. uliginosum*. In the latter species, flower senescence was also advanced after a reduced winter snow cover in 2004.

Shoot growth

Mortality was low in total (3% in 2004 and 6% in 2005), and did not differ between treatments. Growth reactions to snowmelt and snow depth manipulations were variable between years and species (Fig. 3a, b). Advanced snowmelt tended to decrease growth increments (log-transformed) in *E. nigrum,* most in plots with reduced snow cover, and in *V. uliginosum*. *L. procumbens* differed from these species by reacting positively to earlier snowmelt: its shoots tended to grow more after early snowmelt in the first year of our study. Reducing snow cover tended to increase growth in *R. ferrugineum* in 2004. At the end of the experiment, the shoot section with living evergreen leaves (log-transformed) was shorter in plots with earlier snowmelt in *E. nigrum* and *R. ferrugineum*, but only in plots with reduced snow cover.

With the path diagrams (Fig. 4), we can further explain how the timing of snowmelt, frost occurrence, phenology and temperature directly and indirectly affected shoot growth. Shoot growth of *R. ferrugineum* and *V. vitis-idaea* were not significantly explained by any of the explanatory paths explored in the path analysis (results not shown). Earlier snowmelt date decreased both the growing degree days (Gdd) of the snowfree season (i.e. the accumulated daily mean temperatures greater than 5°C over the snowfree season), and the number of frosts (i.e. number of days after snowmelt with minimum temperatures below freezing). A direct link between snowmelt date and shoot growth was only found in *L. procumbens*: this species tended to benefit from an increased growing season length after early snowmelt. Greater Gdd over the snowfree season had a positive impact on the shoot growth of *V. uliginosum* (marginally significant), but not on other species. In all species, variables related to phenology and frost occurrence had important effects on shoot growth. Shoot growth started earlier after early snowmelt in all species but *V. myrtillus.* In most species, there was a link between the date of the start of shoot growth (i.e. the time available for shoot growth) and the length of the shoot

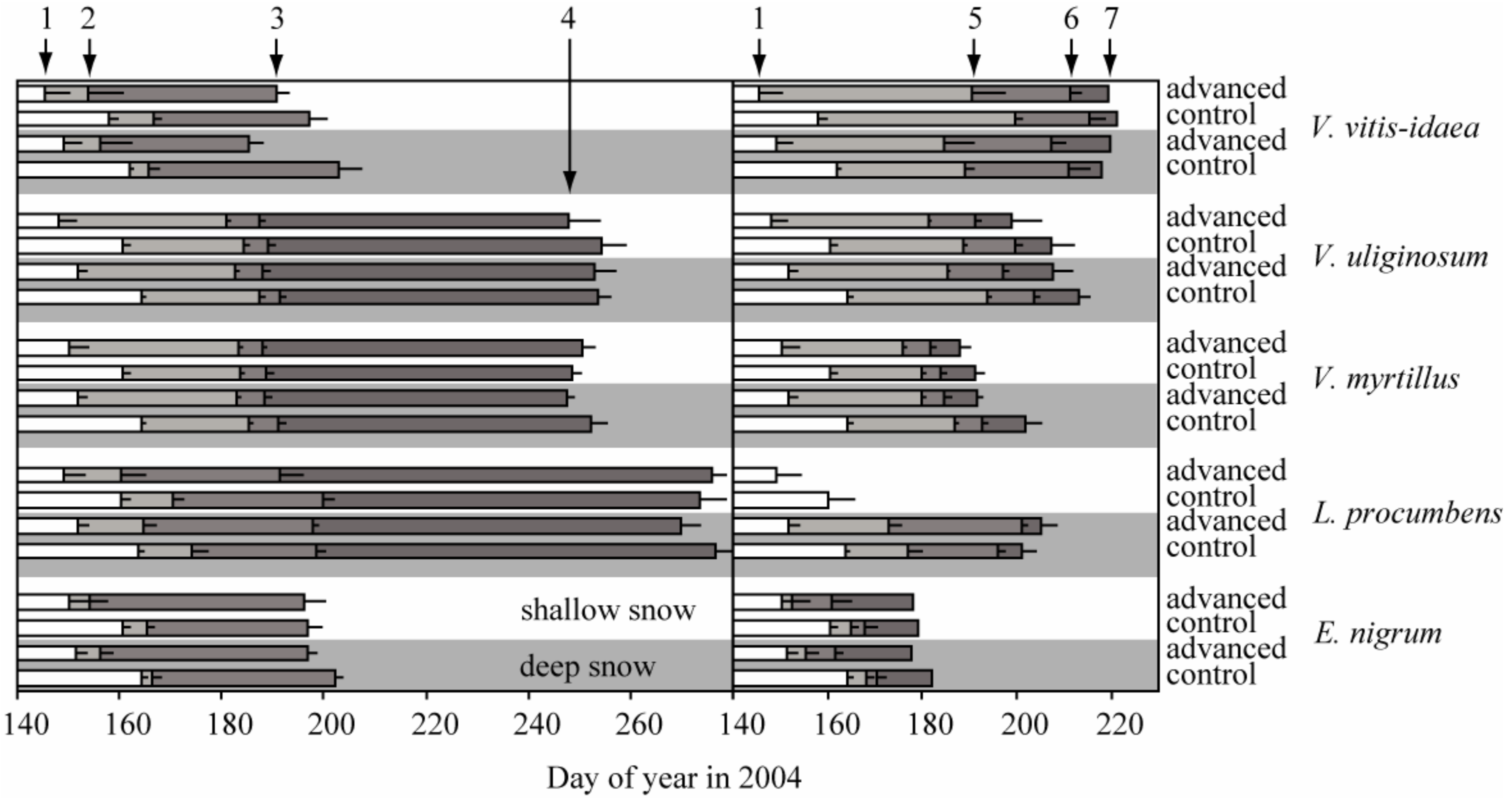

Figure 2. Phenology of the vegetative and reproductive development of our study species in 2004. The phenological stages recorded after snowmelt (1) were: (2) Leaves expanded and green, (3) start of vegetative shoot growth, (4) leaf senescence or fall coloration, (5) swelling of flower buds, (6) first flower open, and (7) first flower senescent.

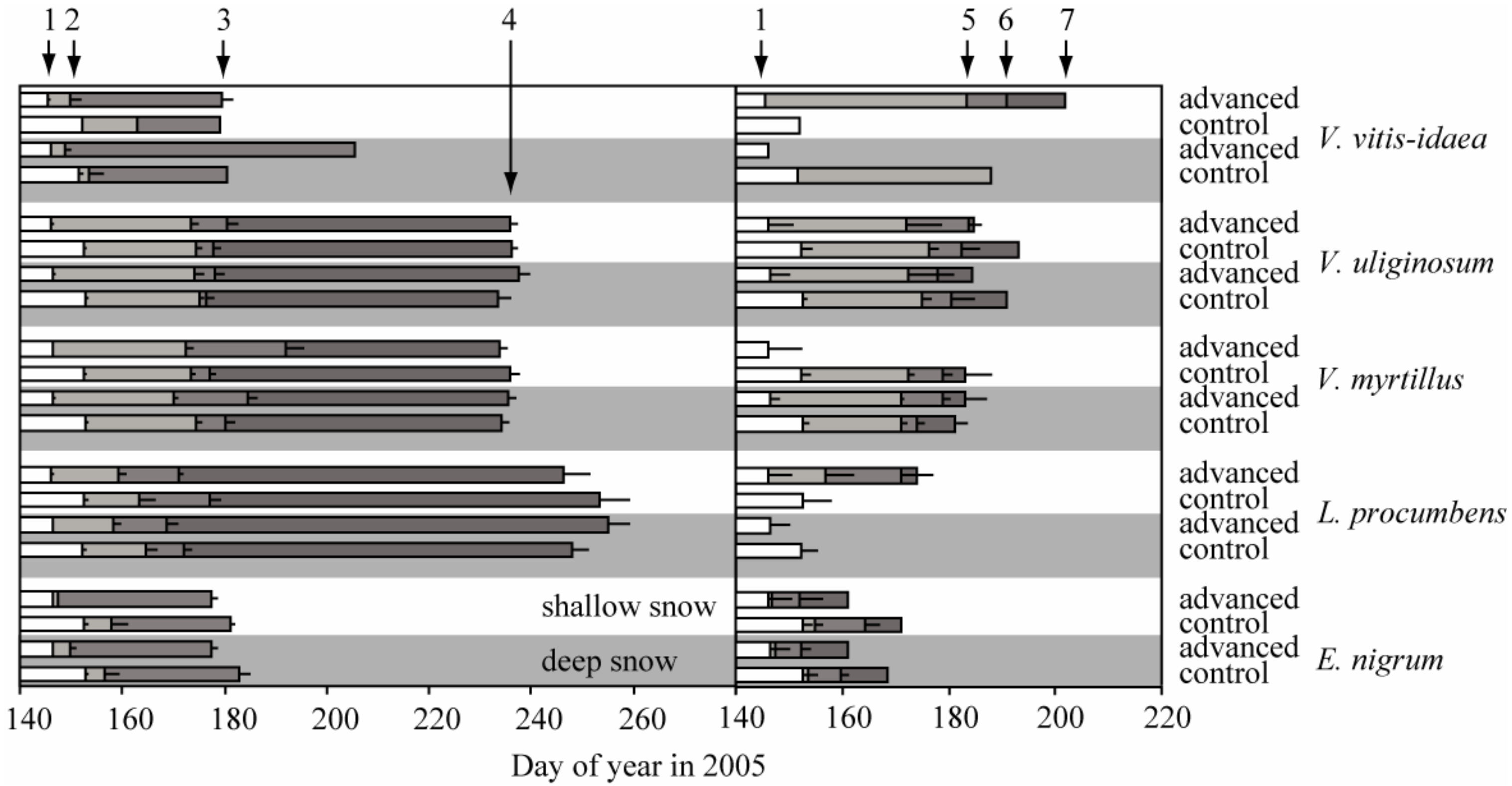

Figure 2, cont. Phenology of the vegetative and reproductive development of our study species in 2005. For codes of the phenological stages, see above.

increment produced (marginally significant in *E. nigrum*). Opposite to our hypothesis, the direct impact of phenology on shoot growth was positive, i.e. shoots grew more when growth started late. The indirect pathway via temperature, however, revealed a negative component of late phenology: higher Gdd during the period of vegetative growth had a positive effect on shoot growth of all species, but was reduced by the late start of vegetative growth. The net effect of phenology on growth thus depended on the balance of these two opposing processes. A higher number of frost days tended to negatively affect the shoot growth increments of *V. uliginosum.* In all other species, a higher number of frosts merely delayed the start of shoot growth. When indirect and direct effects of snowmelt date on shoot growth were summed up, we found that earlier snowmelt date had a negative impact on the length of the shoot increments produced by *E. nigrum*, *V. uliginosum* and *V. myrtillus*, and a positive one on *L. procumbens*, confirming the results of the ANOVA analysis.

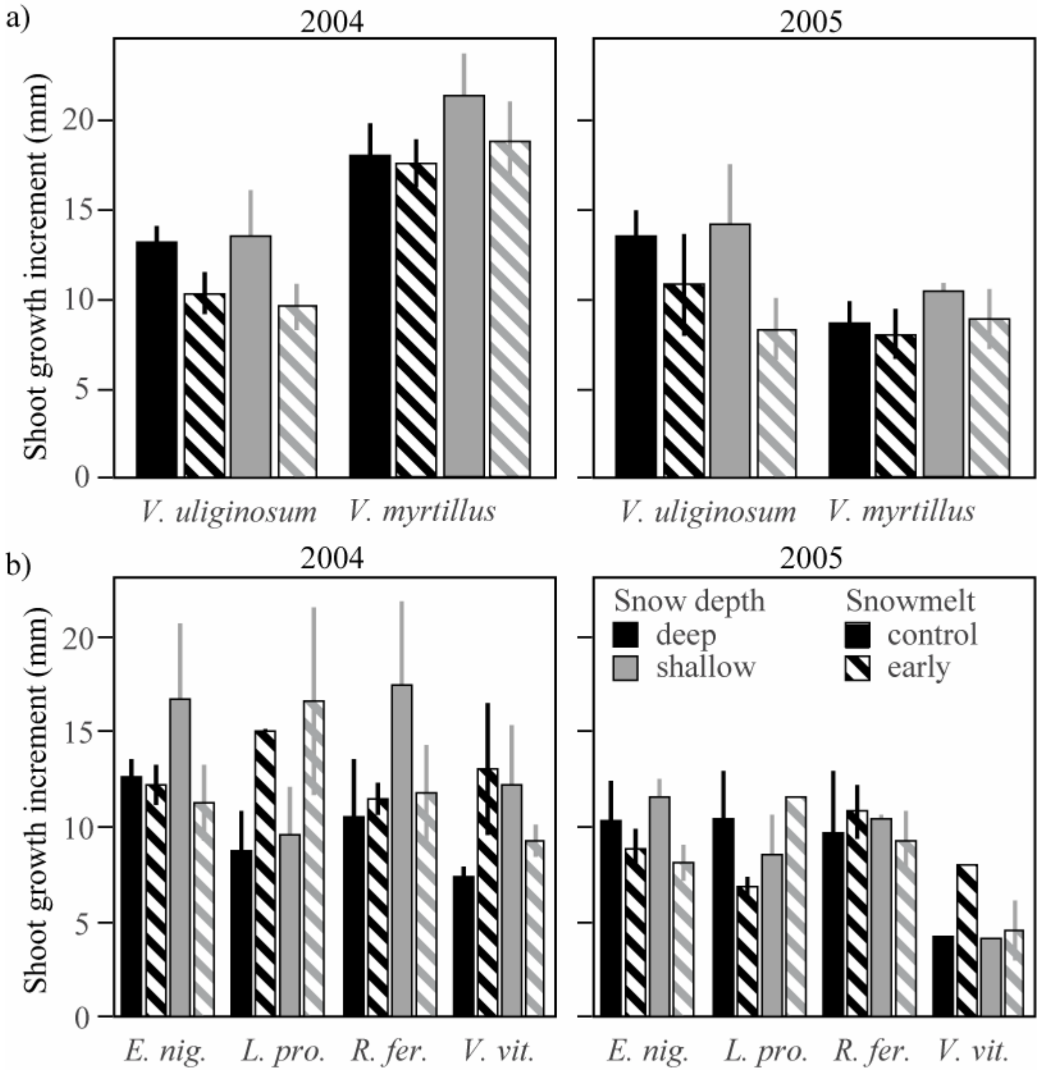

Figure 3. The effects of snow cover manipulations on the vegetative growth of a) the deciduous dwarf shrubs species *Vaccinium myrtillus* and *V. uliginosum*, and b) the evergreen *Empetrum nigrum (E. nig.), Loiseleurea procumbens (L. pro.), Rhododendron ferrugineum (R. fer.),* and *Vaccinium vitis-idaea (V. vit.),* measured as the length of their shoot increments in 2004 and 2005. Black bars: ambient snow depth over winter, grey bars: reduced snow depth over winter; solid: control snowmelt, hatched: early snowmelt. Error bars = +/- 1SE.

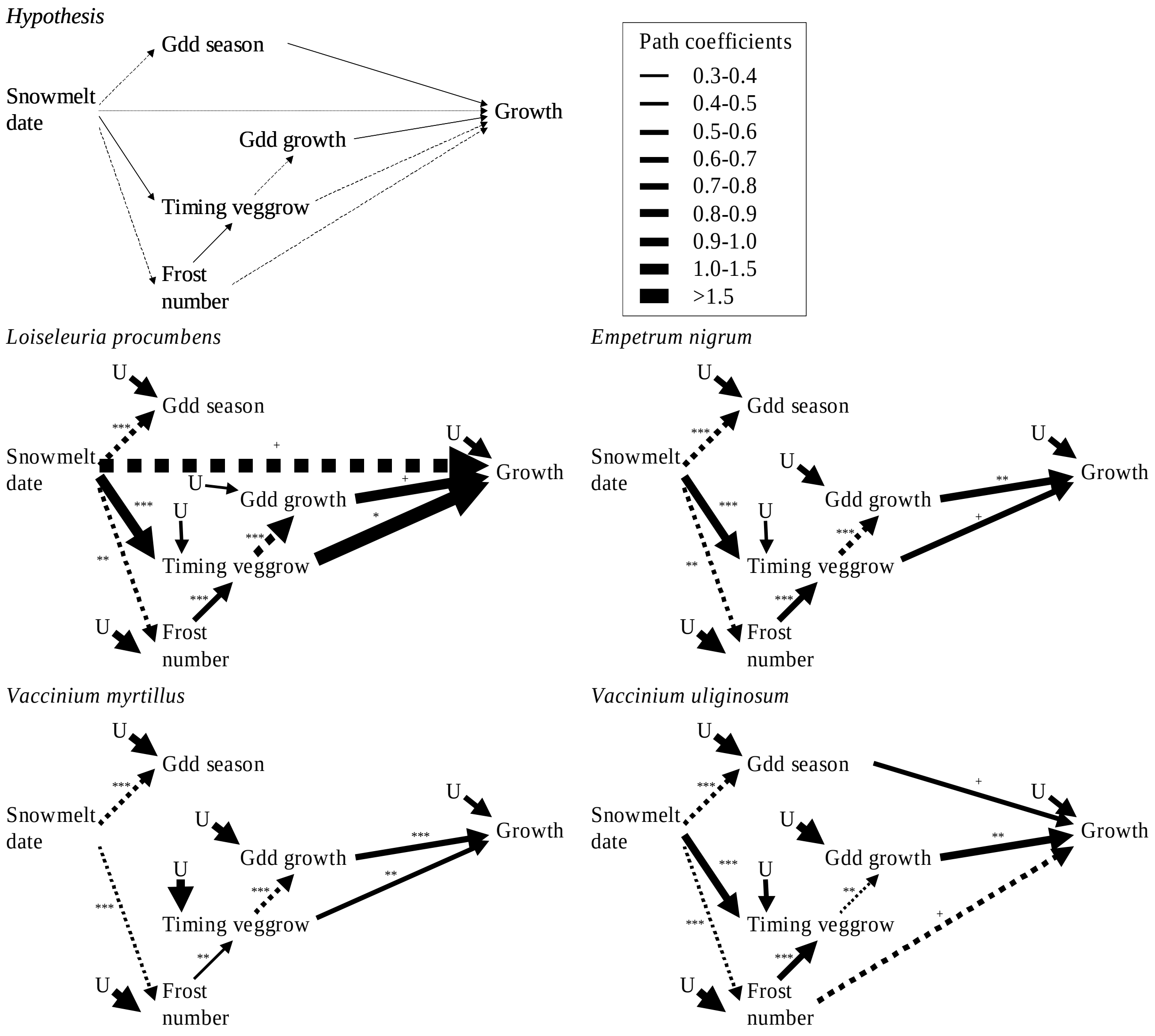

Figure 4. Path diagrams of the direct and indirect controls of snowmelt timing on shoot growth over two years in 4 alpine tundra dwarf shrub species. Relationships with a significance level (P) below 0.1 are indicated as arrows. Solid lines: positive relationship, dashed lines: negative relationship. Line widths indicate the magnitude of the path coefficients and thus, the strength of the relationship. Significance levels: *** = $P<0.001$, ** = $P<0.01$, * = $P<0.05$, + = $P<0.1$. Growth: length of the annual shoot increment; frost number: number of days with minimum temperatures <0°C; timing veggrowth: date when vegetative growth (i.e. shoot elongation) started; Gdd season: Growing degree days >5°C over the growing season; Gdd growth: Growing degree days >5°C over the period of vegetative growth; U: unexplained variance.

Leaf size, leaf chemical composition and herbivory

Leaf length (Fig. 5a) and leaf mass of *V. uliginosum* and *V. myrtillus* were reduced after advanced snowmelt in both species and over both years of our study, the effect of the treatment being greater in 2005 than in 2004. LMA (leaf mass per unit area) of *V. myrtillus* was increased in plots with advanced snowmelt, but only after a winter with reduced snow depth (Table 1). Chlorophyll content of *V. myrtillus* leaves was positively affected by advanced snowmelt in 2005. Leaf carbon content of *V. myrtillus* leaves in 2004 was decreased in plots with advanced snowmelt by a small but significant margin ($F_{1,7}$=20.0, *P*=0.003), but nitrogen content and C:N ratio did not differ between treatments. When the start of vegetative growth, and thus, the timing of leaf formation was used as an explanatory variable, there was a significant negative impact of an early start of vegetative growth on leaf N content ($F_{1,7}$=16.2, *P*=0.005), and a significant positive one on C:N ratio ($F_{1,7}$=16.1, *P*=0.005). The quality of *V. myrtillus* leaves thus decreased with an earlier start of leaf formation. The percentage of *V. myrtillus* and *V. uliginosum* leaf area eaten by herbivores was decreased by advanced snowmelt, but the difference between snowmelt treatments was only significant in *V. uliginosum* and differed strongly between years (Fig. 5b).

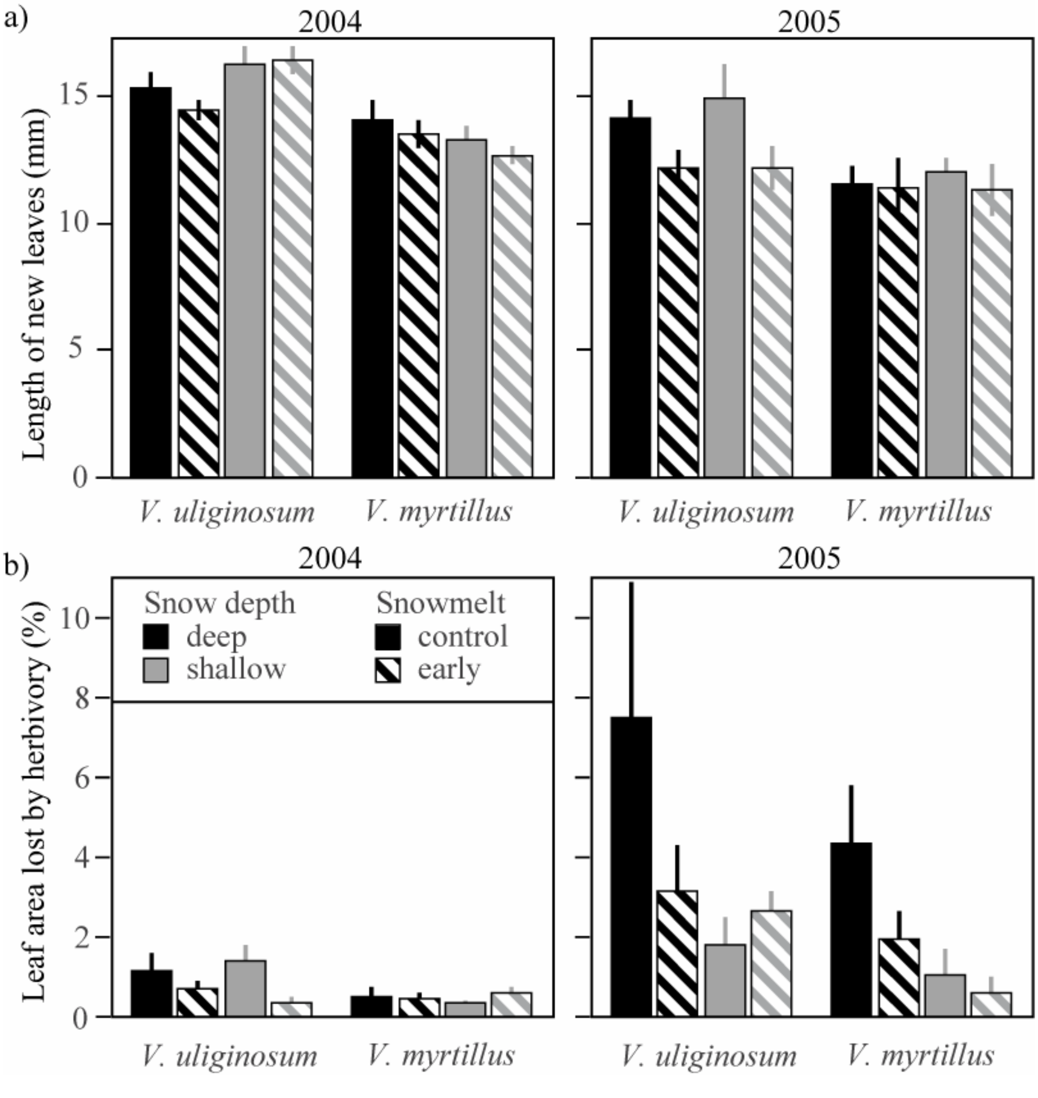

Figure 5. The effects of snow cover manipulations on a) leaf length and b) leaf herbivory (i.e. the proportion of leaf area eaten by herbivores) of the deciduous shrubs *Vaccinium myrtillus* and *V. uliginosum* in 2004 and 2005. Black bars: ambient snow depth over winter, grey bars: reduced snow depth over winter; solid: control snowmelt, hatched: early snowmelt. Error bars = +/- 1SE.

Frost damages in 2005

The proportion of *V. myrtillus* and *V. uliginosum* shoots with visible frost damages (arcsin-transformed) was significantly increased in plots with advanced snowmelt. Within these, frost damages were most abundant in plots with reduced snow cover over winter; in plots with ambient snowmelt, however, did reduced snow cover decrease the abundance of damaged leaves (interaction snowmelt*snow depth treatment significant in *V. myrtillus*; Fig. 6). The proportion of flower buds aborted before flowering, probably as a consequence of frost damage, was increased by advanced snowmelt in *R. ferrugineum, V. myrtillus* and *V. uliginosum,* but only significantly so in the latter two (tested with block as a random instead of fixed factor, due to the small sample size; Fig. 6). In *V. myrtillus,* all buds were aborted before flowering. *E. nigrum* showed no reaction in flower bud survival due to snow manipulation treatments.

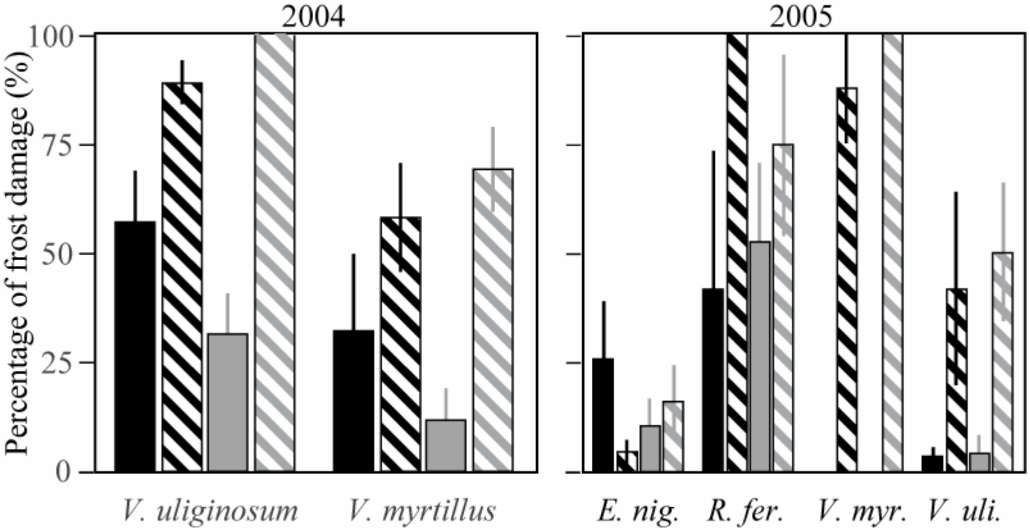

Figure 6. The effects of snow cover manipulations on the occurrence of frost damage in the leaves and shoots of the two deciduous dwarf shrub species *Vaccinium myrtillus* and *V. uliginosum* (left, recorded as the proportion of marked shoots with damaged leaf tissue just after a frost event in mid-June 2005), and on the rate of flower buds aborted before flowering in *Empetrum nigrum (E. nig.), Rhododendron ferrugineum (R. fer.), Vaccinium myrtillus (V. myr.)* and *V. uliginosum (V. uli.).* Black bars: ambient snow depth, grey bars: reduced snow depth over winter; solid: control snowmelt, hatched: early snowmelt. Error bars = +/- 1SE.

Reproduction

Fecundity, i.e. the proportion of marked shoots with ripe fruits was decreased by reduced snow cover in the previous winter in *L. procumbens* (especially in 2004), and in *E. nigrum,* but only in plots with ambient snowmelt in 2005. The proportion of shoots bearing reproductive buds was higher in 2004 than 2005 in *E. nigrum*, *V. uliginosum* (both marginally significant) and *V. vitis-idaea*. Over all berry producing species, 23% of the buds developed into ripe berries (29% in 2004, 15% in 2005). No treatment effects were detected, but in *V. myrtillus*, differences between years were high and significant (56% in 2004 and no berries in 2005). Berries of *E. nigrum* (dry mass) were heavier in 2004 than 2005, and heavier with deep than with reduced snow cover in 2005. Berries of *V. vitis-idaea* were only produced in 2004, and their mass tended to be lower after earlier snowmelt ($F_{1,2}$=11.1, *P*=0.08).

Species abundance

After two years manipulating winter snow depth and snowmelt date, some effects on the vegetation composition and species abundance of our plots were already detectable. On the species level, the most abundant species in the community, *Vaccinium myrtillus*, proofed to be very sensitive to manipulations of snowmelt timing. Its cover decreased by 10.3% in plots with advanced snowmelt, corresponding to the disappearance from 2.3 squares in our 25 square frame (vs. +3.3% in plots with ambient snowmelt; $F_{1,6}$=16.8, *P*<0.01). *V. myrtillus* abundance in 2005, after two years of snowmelt manipulations, was decreased in early-melting plots (occurrence in 23.4 squares, vs. in 19.8 in plots with ambient snowmelt), but this difference was not significant (F1,6=3.3, *P*=0.12). *Homogyne alpina*, the most abundant forb species, decreased by 8.4% (-1.2 squares) in plots with early snowmelt, and increased by 16.0% in plots with ambient snowmelt ($F_{1,6}$=11.6, *P*=0.01), but no differences in net abundance between treatments in 2005 was found. *Avenella flexuosa*, the most abundant grass species, tended to decrease after early snowmelt in plots with reduced snow depth (-3.9%/-0.8 squares), but increased in all other treatments (+71.2% with ambient snowmelt/reduced snow depth, and +30.4% with early snowmelt/ambient snow depth, vs. +1% in control plots (ambient snowmelt and snow depth; interaction snow depth x snowmelt treatment: $F_{1,2}$=11.8, *P*=0.07). These changes resulted in a significantly decreased *A. flexuosa* abundance in plots with early snowmelt in 2005 (occurrence in 6.9 squares in plots with advanced snowmelt, vs. in 12.1 in plots with ambient snowmelt; $F_{1,6}$=5.8, *P*=0.05). *Nardus stricta* generally decreased over the study period, but more so in plots with reduced snow depth than in plots with ambient snow depth over winter (-15.6%/-0.3 squares vs. –10.2%/-0.25 squares; $F_{1,1}$=117.5, *P*=0.06). Correspondingly, its abundance in 2005 tended to be lower in plots with reduced snow depth (occurrence in 3.3 squares) than in plots with ambient snow depth (in 5.4 squares; F1,1=61.5, *P*=0.08).

Discussion

Plant responses to advanced snowmelt

Our field experiment revealed that manipulating snow cover characteristics can affect the life cycle and performance of alpine plants in the following growing season in various ways. As expected was snowmelt timing the more important driver of plant phenology, fitness and reproduction than snow depth. There were differences in the magnitudes of the effects between the two years, but patterns were largely the same. Vegetative and reproductive phenology was advanced by earlier snowmelt, which is generally interpreted as a positive response in terms of plant fitness, because plants have more time available for growth and resource allocation. In fact, most other snowmelt experiments found plant growth to be negatively affected by delayed, but positively, or not at all by advanced snowmelt (see this thesis, chapter 2 for a review of snow manipulation studies). In contrast, however, did plant performance (shoot growth, length of green shoot parts, or leaf size) in our experiment respond negatively to advanced snowmelt in most species, namely in *Empetrum nigrum*, *Rhododendron ferrugineum*, *Vaccinium myrtillus*, and *V. uliginosum*. Exceptions were *V. vitis-idaea* (no response) and *Loiseleuria procumbens* (positive response).

In our experiment, *L. procumbens*, a typical inhabitant of windswept ridges with low and discontinuous winter snow covers (Grabherr, 1980), was the only species that showed a positive response to advanced snowmelt. In sites close to the lower extreme along a snow cover gradient, i.e. windswept sites where virtually no snow is accumulated in winter, mostly negative growth reactions to delayed snowmelt were found in snow fence studies (see chapter 2, Fig. 2). In other words, the closer to this extreme the growing conditions at a site are, the more limiting is the factor snow cover (Choler, 2005), and the more should the plants of a community be adapted to the extremely harsh conditions related to shallow snow covers. We therefore would expect typical species from such sites to respond differently to snowmelt manipulations than species typically occurring in habitats with abundant snow cover. The lack of response in *V. vitis-idaea* is in line with a similar experiment in a subarctic tundra community, where this species also proofed to be little responsive to changes in snowmelt timing (Wipf *et al.*, 2006, this thesis, chapters 3 and 4).

Combined effects of reduced snow depth and advanced snowmelt

The plant responses to reduced winter snow depth was much less pronounced than to advanced snowmelt timing in spring. The timing of the first phenological stages advanced in some cases by reduced snow depth, maybe as a reaction to light penetrating the snow cover. Only a small fraction of light penetrates a snow cover with a depth of approx. 40 cm (as created by our experimental treatment), but this might be sufficient to induce plant responses e.g. in leaf physiology (Kimball *et al.*, 1973), growth or seed germination (Richardson & Salisbury, 1977).

The reduced snow cover interacted with advanced snowmelt by further increasing the already negative impact of early snowmelt on shoot growth of several dwarf shrubs. Our snow reduction treatment did not expose plants, thus, these negative effects were probably not due to low temperatures, mechanical damage or winter desiccation directly. Rather than effects on aboveground plant parts, we expect belowground processes to modify plant responses. Other experiments reducing snow depth and inducing soil freezing found a dieback of fine roots (Tierney *et al.*, 2001; Weih & Karlsson, 2002, S. Wipf, unpublished data) and of microbes (Schimel & Clein, 1996), and consequently, an increase in nitrogen (NH_{4+} and NO_{3-}) and phosphorus in the soil in spring (Fitzhugh *et al.*, 2001; Groffman *et al.*, 2001, M. Bauer, unpublished data). These nutrients can readily be used by plants and microbes in spring (Bilbrough *et al.*, 2000; Bowman & Bilbrough, 2001). Hence, how reduced snow depth affect plant growth may depend on the balance between its negative (root damages) and positive effects (increased nutrient availability).

To our knowledge, our field experiment is the first, which allows quantifying the effects of snow cover reduction and advancing snowmelt date independently. Experiments that factorially increased snow depth and summer temperatures have relatively often been conducted previously, but in all of them did the increase in snow depth also lead to a delay in snowmelt, which is not in line with current climate change scenarios (see thesis, chapter 2 for a review).

Herbivory

Leaf area eaten by herbivores (mainly by grasshoppers (Asshoff & Hattenschwiler, 2005), more seldom moth larvae, S. Wipf, personal observation) in the two deciduous species *V. myrtillus* and *V. uliginosum* was relatively low compared to other studies from mountain ecosystems (Blumer & Diemer, 1996; Roy *et al.*, 2004), and was further decreased by advanced snowmelt. In contrast to our results, greater herbivore loads, diversity and damages were found in early-melting plots in an experiment where snowmelt was advanced due to year-round warming (Roy *et al.*, 2004). The researchers proposed that the large snowfree patches could have attracted insect herbivores when the landscape around them was still covered in snow. In our experiments, the small size of the snowfree patches (approx. 2-3 m^2), and the presence of other snowfree patches at the time of advanced snowmelt probably avoided such an early spring “plot choice” effect

Many invertebrate herbivores can select for high quality forage, especially for plant tissue with high N contents (Schadler *et al.*, 2003). In high altitude ecosystems with generally short growing seasons and low temperatures, high food quality might be of special importance for fast growth and completion of the life cycle (Asshoff & Hattenschwiler, 2005). Several snow manipulation experiments found leaf quality to be lower after earlier snowmelt (Van der Wal *et al.*, 2000; Walsh *et al.*, 1997). In line with this, leaf quality (i.e. low carbon:nitrogen (C:N) ratio, high N content) in our experiment was negatively affected by an early start of plant development, which could explain why herbivory was decreased after advanced snowmelt in our study. Besides reduced leaf quality, smaller leaf areas, and increased tissue density (i.e. LMA) were found in *V. myrtillus* leaves after early development in our experiment. These leaf characteristics reacted in the same way along natural snowmelt gradients in alpine and arctic ecosystems (Choler, 2005; Kudo *et al.*, 2001; Kudo *et al.*, 1999), and could also affect herbivory.

Frost effects

Several studies of climate change effects on plants pointed out that frosts might play an important role in defining the survival, growth, and reproduction of alpine plants in future climates (see Inouye, 2000 for a review). Under certain scenarios, the number of low-temperature events during the snow free season could increase with a warmer climate and earlier snowmelt, especially if the amount of snow, which usually covers plants during the cold season, decreases considerably and melts much earlier (Inouye *et al.*, 2002). Earlier onset of plant development after early snowmelt, moreover, could lead to more frequent and more serious frost damages (Inouye *et al.*, 2002; Molau, 1997; Price & Waser, 1998).

The occurrence of frost damages depends on two factors: the occurrence of temperatures low enough to damage plant tissue, and the presence of plant parts sensitive to these low temperatures at the time of this event. The frost sensitivity of plant tissue varies between species, but also within a species over the year, and between different plant parts (Koerner, 1999; Ulmer, 1937). For instance, overwintering leaves of alpine evergreen shrubs can endure temperatures far below freezing in winter, but new leaves are damaged at –2°C to –6 °C in summer (Taschler & Neuner, 2004; Ulmer, 1937). Meristems or flowers are more sensitive to low temperatures than shoots or leaves. Due to the combination of these factors, low temperature events occurring late in the growing season generally cause severe damages in plants (Inouye, 2000; Ulmer, 1937).

The quantification of frost damage, and thus the estimate of its consequences in a changing climate, is difficult. Especially if damages are non-lethal, they might lead to relatively unspecific symptoms (e.g. slow phenological development, changes in growth rate or form), which might not be detected, or not attributed to low temperature events. The number of days with minimum temperatures below 0°C, which we used to describe the effects of low-temperature events, is unlikely to have a direct, or even cumulative negative effect on plants. It is rather a relatively unspecific proxy variable representing the number of low temperature events that might have caused damages in plants. A more accurate variable would need the efforts to quantify the phenological stage of each species, and its specific sensitivity to low temperature events (Bannister *et al.*, 2005; Taschler & Neuner, 2004). Although our measure of frost occurrence is by no means a direct measurement of frost damage, it correlated well with the proportion of frost-damaged shoots of *V. myrtillus* and *V. uliginosum* we counted in 2005 (S. Wipf, unpublished data).

Species abundance

We observed negative effects of advanced snowmelt on the performance of several dwarf shrub species. However, none of the effects were lethal for any of these species, and no differences in mortality of marked shoots between treatments were found. Even the enhanced frost damages in flower buds due to the snowmelt treatment should not immediately affect reproduction and species composition, as all species in our study are clonal and perennial. We therefore would not expect to see any changes in species composition to happen in only two years. Nevertheless, the abundance of several species, among which the most frequent dwarf shrub and grass species, significantly changed in response to snow manipulation. These changes in abundance were only partly in line with the growth responses of individual plant species. *V. myrtillus*, which showed the greatest negative response to advanced snowmelt (in terms of absolute cover), did not show the greatest negative response in its growth; however, it was the species most negatively affected by frost damages in 2005 (Fig. 6). Although these frost damages were generally not lethal (S. Wipf, personal observation), it could have affected the growth form and thus the cover of this shrub species by damaging its vegetative buds.

Conclusions

In conclusion, we found various species of alpine tundra to significantly respond to changes in snow cover and snowmelt timing. Growth and fitness responses of alpine and arctic tundra plants to climate warming and earlier snowmelt have often been assumed as a relatively simple positive relationship with temperature and growing season length (Fosaa *et al.*, 2004; Hinzman *et al.*, 2005; Kudo *et al.*, 1999). Our study, however, suggests that these responses and the related processes are more complex. Reactions to snow cover changes differed between species and micro-sites, and they may include non-linear relationships and feedback mechanisms, which should be taken into consideration when exploring the effects of climate change on alpine ecosystems. The ongoing snow manipulations will show whether these initial changes in fitness and species composition will gradually proceed and result in significantly changed community composition and structure in the longer term.

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Table1. F statistics of the ANOVA analysing the responses in a) vegetative phenology, b) reproductive phenology, and c) growth of alpine dwarf shrubs to manipulations of snowmelt timing (advanced, ambient) and winter snow depth (reduced, ambient) over two winters (2003/04 and 2004/05). For details of the analysis, see statistics section in the method chapter. df = degrees of freedom of the numerator and denominator; bold = significant at the level of $P < 0.05$; italics = marginally significant at the level of $P < 0.1$; ns = not significant.

a)

		Block			Year			Snowmelt treatment			Snow depth treatment			Year * Snowmelt			Year * Snow depth			Snowmelt * S.depth			Year * S.melt * S.depth		
Species	N	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P
Leaves entirely green																									
Empetrum nigrum	54	7, 2	2.3	ns	1, 6	35.9	**<0.001**	1, 7	24.1	**0.002**	1, 7	0.7	ns	1, 6	3.3	ns	1, 6	0.0	ns	1, 5	1.6	ns	1, 2	0.5	ns
Loiseleuria procumbens	47	6, 1	0.9	ns	1, 5	11.8	**0.02**	1, 6	13.2	**0.01**	1, 6	1.0	ns	1, 5	2.9	ns	1, 5	0.8	ns	1, 5	0.3	ns	1, 1	0.2	ns
Rhododendron ferrugineum		No distinct winter leaf coloration																							
Vaccinium myrtillus	58	7, 4	15.5	**0.01**	1, 6	541	**<0.001**	1, 7	25.8	**0.001**	1, 7	0.0	ns	1, 6	1.5	ns	1, 6	1.1	ns	1, 7	10.7	**0.01**	1, 4	0.2	ns
Vaccinium uliginosum	56	7, 3	1.7	ns	1, 6	134	**<0.001**	1, 7	12.1	**0.01**	1, 7	9.4	**0.02**	1, 6	1.6	ns	1, 6	0.7	ns	1, 6	0.3	ns	1, 3	0.8	ns
Vaccinium vitis-idaea	24	3, 0			1, 2	61.0	**0.02**	1, 3	3.0	ns	1, 3	0.1	ns	1, 1	1.5	ns	1, 2	5.6	ns	1, 2	3.4	ns	1, 0		
Start of vegetative shoot growth																									
Empetrum nigrum	54	7, 2	3.6	ns	1, 6	209.0	**<0.001**	1, 7	4.1	***0.08***	1, 7	0.8	ns	1, 6	1.0	ns	1, 6	0.1	ns	1, 5	0.5	ns	1, 2	0.0	ns
Loiseleuria procumbens	47	6, 1	8.2	ns	1, 5	247.4	**<0.001**	1, 6	23.7	**0.003**	1, 6	0.0	ns	1, 5	0.0	ns	1, 5	4.2	***0.10***	1, 5	1.3	ns	1, 1	3.9	ns
Rhododendron ferrugineum	10	Not enough samples																							
Vaccinium myrtillus	58	7, 4	1.7	ns	1, 6	14.6	**0.01**	1, 7	4.8	***0.07***	1, 7	2.1	ns	1, 6	30.6	**0.001**	1, 6	4.1	***0.09***	1, 7	8.1	**0.02**	1, 4	4.4	ns
Vaccinium uliginosum	56	7, 3	2.9	ns	1, 6	180.4	**<0.001**	1, 7	0.6	ns	1, 7	0.0	ns	1, 6	5.2	***0.06***	1, 6	2.8	ns	1, 6	0.1	ns	1, 3	0.4	ns
Vaccinium vitis-idaea	15	Not enough samples																							
Start of leaf senescence																									
Empetrum nigrum		Leaf colouration after observation period																							
Loiseleuria procumbens	42	6, 1	10.6	ns	1, 5	34.4	**0.002**	1, 6	0.8	ns	1, 6	0.1	ns	1, 3	0.7	ns	1, 4	1.0	ns	1, 3	0.0	ns	1, 1	26.1	ns
Rhododendron ferrugineum		No distinct winter leaf coloration																							
Vaccinium myrtillus	58	7, 4	1.7	ns	1, 6	14.6	**0.01**	1, 7	4.8	***0.07***	1, 7	2.1	ns	1, 6	30.6	**0.001**	1, 6	4.1	*0.09*	1, 7	8.1	**0.02**	1, 4	4.4	ns
Vaccinium uliginosum	56	7, 3	2.9	ns	1, 6	180	**<0.001**	1, 7	0.6	ns	1, 7	0.0	ns	1, 6	5.2	***0.06***	1, 6	2.8	ns	1, 6	0.1	ns	1, 3	0.4	ns
Vaccinium vitis-idaea		Leaf colouration after observation period																							

b)

		Block			Year			Snowmelt treatment			Snow depth treatment			Year * Snowmelt			Year * Snow depth			Snowmelt * S. depth			Year * S.melt * S.depth		
Species	N	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P
Budburst of flower buds																									
Empetrum nigrum	47	7, 2	3.6	ns	1, 5	343	**<0.001**	1, 7	22.4	**0.002**	1, 6	0.0	ns	1, 4	9.4	**0.04**	1, 5	0.0	ns	1, 3	0.0	ns	1, 2	0.3	ns
Loiseleuria procumbens	3	Not enough samples																							
Rhododendron ferrugineum	9	Not enough samples																							
Vaccinium myrtillus	21	7, 1	0.0	ns	1, 2	80.0	**0.01**	1, 2	1.6	ns	1, 2	3.7	ns	1, 0			1, 0			1, 0			0, 1		
Vaccinium uliginosum	46	7, 1	0.7	ns	1, 6	93.2	**<0.001**	1, 7	8.3	**0.02**	1, 7	1.3	ns	1, 4	2.7	ns	1, 3	2.6	ns	1, 3	0.1	ns	1, 1	0.0	ns
Vaccinium vitis-idaea	13	Not enough samples																							
Start of flowering																									
Empetrum nigrum	50	7, 2	3.5	ns	1, 5	123	**<0.001**	1, 7	50.2	**<0.001**	1, 7	0.0	ns	1, 5	0.4	ns	1, 5	5.2	***0.07***	1, 4	0.1	ns	1, 2	2.1	ns
Loiseleuria procumbens	3	Not enough samples																							
Rhododendron ferrugineum	9	Not enough samples																							
Vaccinium myrtillus	23	7, 1	1.2	ns	1, 2	112	**0.01**	1, 3	1.3	ns	1, 3	5.3	ns	1, 0			1, 0			1, 0			1, 1	0.0	ns
Vaccinium uliginosum	45	7, 1	63.5	***0.10***	1, 6	190	**<0.001**	1, 7	2.6	ns	1, 7	2.8	ns	1, 4	6.5	***0.06***	1, 3	11.3	**0.04**	1, 2	0.2	ns	1, 1	26.8	ns
Vaccinium vitis-idaea	11	Not enough samples																							
Start of flower senescence																									
Empetrum nigrum	48	7, 1	11.5	ns	1, 5	454	**<0.001**	1, 7	22.1	**0.002**	1, 7	0.4	ns	1, 5	10.4	**0.02**	1, 4	0.3	ns	1, 4	0.3	ns	1, 1	8.7	ns
Loiseleuria procumbens	3	Not enough samples																							
Rhododendron ferrugineum	9	Not enough samples																							
Vaccinium myrtillus	22	7, 1	0.7	ns	1, 2	6.4	ns	1, 3	7.7	***0.07***	1, 2	2.3	ns	1, 0			1, 0			1, 0			0, 1		
Vaccinium uliginosum	33	7, 0			1, 5	457	**<0.001**	1, 5	4.9	***0.08***	1, 6	4.5	***0.08***	1, 1	0.9	ns	1, 1	445	**0.03**	1, 0			1, 0		
Vaccinium vitis-idaea	11	Not enough samples																							

c)

		Block			Year			Snowmelt treatment			Snow depth treatment			Year * Snowmelt			Year * Snow depth			S. melt * S. depth			Year * S.melt * S.depth		
Species	N	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P
Length of shoot increment																									
Empetrum nigrum	53	7, 4	35.2	**0.03**	1, 6	22.0	**0.003**	1, 7	3.7	***0.09***	1, 7	0.0	ns	1, 6	0.0	ns	1, 6	1.0	ns	1, 7	7.4	**0.05**	1, 4	0.9	ns
Loiseleuria procumbens	21	4, 0			1, 3	2.2	ns	1, 2	5.9	ns	1, 2	0.0	ns	1, 1	41.7	***0.10***	1, 1	1.8	ns	1, 0			1, 0		
Rhododendron ferrugineum	33	5, 1	34.9	ns	1, 4	2.4	ns	1, 5	0.3	ns	1, 4	0.2	ns	1, 3	0.3	ns	1, 2	27.0	**0.04**	1, 1	8.5	ns	1, 1	0.9	ns
Vaccinium myrtillus	58	7, 4	4.3	***0.09***	1, 6	895	**<0.001**	1, 7	1.2	ns	1, 7	1.5	ns	1, 6	0.6	ns	1, 6	0.2	ns	1, 7	1.4	ns	1, 4	0.0	ns
Vaccinium uliginosum	56	7, 3	10.7	**0.04**	1, 6	4.2	***0.09***	1, 7	6.1	**0.04**	1, 7	1.6	ns	1, 6	0.7	ns	1, 6	1.3	ns	1, 6	0.0	ns	1, 3	0.1	ns
Vaccinium vitis-idaea	22	3, 0			1, 2	4.4	ns	1, 3	0.4	ns	1, 3	0.0	ns	1, 0			1, 0			1, 2	1.4	ns	1, 0		
Leaf length																									
Vaccinium myrtillus	58	7, 4	5.5	***0.06***	1, 6	94.5	**<0.001**	1, 7	0.5	ns	1, 7	1.6	ns	1, 6	0.1	ns	1, 6	1.6	ns	1, 7	0.0	ns	1, 4	0.0	ns
Vaccinium uliginosum	58	7, 4	1.3	ns	1, 6	28.0	**0.002**	1, 7	9.0	**0.02**	1, 7	1.8	ns	1, 6	5.3	***0.06***	1, 6	3.3	ns	1, 7	0.1	ns	1, 4	0.1	ns
Leaf mass																									
Vaccinium myrtillus	58	7, 4	25.7	**0.004**	1, 6	7.5	**0.03**	1, 7	3.0	ns	1, 7	0.2	ns	1, 6	25.7	**0.002**	1, 6	0.6	ns	1, 7	0.1	ns	1, 4	1.2	ns
Vaccinium uliginosum	58	7, 4	4.3	***0.09***	1, 6	33.0	**0.001**	1, 7	4.8	***0.06***	1, 7	0.2	ns	1, 6	11.3	**0.02**	1, 6	0.1	ns	1, 7	0.4	ns	1, 4	0.0	ns
LMA (leaf mass/area)																									
Vaccinium myrtillus	58	7, 4	5.0	***0.07***	1, 6	103	**<0.001**	1, 7	1.0	ns	1, 7	0.0	ns	1, 6	0.1	ns	1, 6	1.9	ns	1, 7	5.6	**0.05**	1, 4	2.8	ns
Vaccinium uliginosum	58	7, 4	2.0	ns	1, 6	304	**<0.001**	1, 7	0.0	ns	1, 7	1.0	ns	1, 6	0.1	ns	1, 6	1.0	ns	1, 7	0.5	ns	1, 4	0.5	ns
Chlorophyll content (SPAD units)																									
Vaccinium myrtillus	58	7, 4	2.3	ns	1, 6	18.6	**0.01**	1, 7	0.6	ns	1, 7	2.0	ns	1, 6	7.5	**0.03**	1, 6	2.3	ns	1, 7	0.4	ns	1, 4	0.0	ns
Vaccinium uliginosum	58	7, 4	7.0	**0.04**	1, 6	0.0	ns	1, 7	0.4	ns	1, 7	0.1	ns	1, 6	0.1	ns	1, 6	0.7	ns	1, 7	0.0	ns	1, 4	0.3	ns
Herbivory																									
Vaccinium myrtillus	58	7, 4	0.8	ns	1, 6	15.4	**<0.001**	1, 7	2.1	ns	1, 7	8.5	ns	1, 6	2.3	ns	1, 6	18.3	ns	1, 7	3.9	ns	1, 4	1.1	ns
Vaccinium uliginosum	58	7, 4	0.7	ns	1, 6	11.6	**0.01**	1, 7	7.0	**0.03**	1, 7	1.4	ns	1, 6	0.4	ns	1, 6	2.7	ns	1, 7	0.1	ns	1, 4	0.4	ns

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Chapter 6

Changes in snow cover affect litter decomposability and decomposition rate in alpine tundra

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Abstract

Whether tundra ecosystems will turn into carbon sources in a warming climate due to accelerated decomposition, or become C sinks through increasing plant productivity is controversial. Our study aimed at investigating the role of snow cover on decomposition in an alpine tundra community. We tested how the length of the snow season affects litter quality and thus the decomposability, and how snow cover controls decomposition during winter through its influence on soil temperature in a hierarchical two-year experiment.

We advanced and delayed snowmelt timing manually, and tested for effects on plant growth, leaf size and leaf chemical composition (total C and N, extractable phenolics, C and N) of *Vaccinium myrtillus* and *V. uliginosum,* the two dominating deciduous dwarf shrub species contributing most litter. We used their litter for a litterbag experiment in the following winter, in which we tested the decomposability of the two litter proveniences, and the controls of the snow cover on the litter mass loss by factorially manipulating snow depth and snowmelt timing.

Litter from leaves produced after earlier snowmelt lost less mass during the next winter, although leaf chemistry had not been affected by the snow manipulation. However, larger leaves were produced after earlier snowmelt. The reduced snow depth during the litter decomposition experiment in the following winter lowered soil temperatures and suppressed litter decomposition. Regressing decomposition with soil temperature suggested that winter mass loss slowed down by 10% through a cooling from -0.5° to -1°C. The subsequent change in snowmelt timing did not affect litter mass loss. In summary, our experiment revealed two different ways, how a decrease in snow cover could negatively affect litter decomposition and thus, slow down carbon and nutrient cycling in alpine tundra communities.

Introduction

Decomposition is a key process regulating between the release of nutrients from litter and the accumulation of organic matter in soils. In alpine and tundra ecosystems decomposition is slow and thus, tundras usually have a lower nutrient availability but relative greater fractions of their C stocks in soils than temperate ecosystems (Hobbie *et al.*, 2000). More than 90% of the tundra ecosystem's carbon is stored in soils (IPCC, 2001) - a small change in the balance between carbon inputs and decomposition will alter the ecosystem C storage. Decomposition responds sensitive to a changing climate: either directly due to the response of microbial activity to increasing temperatures, or indirectly due to the effects on plants diversity and productivity and hence, litter quality and quantity (Aerts, 2006).

The temperature sensitivity of decomposition is thought to increase with decreasing temperature (Kirschbaum, 1995). In contrast to unfrozen soils, microbial activity in frozen soils is no longer controlled by a direct kinetic effect, but by the distribution of unfrozen and frozen water limiting the extracellular diffusion and desiccation of soil microbes (Mikan *et al.*, 2002). As a consequence, soil respiration increases abruptly with thawing of soils, and a relatively small rise in temperature of soils close to thawing has large effects on decomposition.

Soil temperatures in winter are directed by the depth, duration and structure of the snow cover (Rixen *et al.*, 2004; Sturm *et al.*, 1997). Snow thus is an important factor controlling decomposition rates, and changes in the snow cover, as predicted by climate change scenarios (IPCC, 2001), are likely to directly impact nutrient cycling and decomposition processes (Monson *et al.*, 2006). Snow cover also influences decomposition indirectly by changing plant productivity (see this thesis, chapter 1 and 5), diversity (Scott & Rouse, 1995; Seastedt & Vaccaro, 2001), and tissue quality, with increasing C/N ratios after earlier snowmelt timing (Van der Wal *et al.*, 2000; Walsh *et al.*, 1997; Welker *et al.*, 2005, this thesis, chapter 5) .

Temperatures and snowfall are predicted to further increase in the arctic, and could put into motion a positive feedback loop enhancing shrub cover in the tundra (Sturm *et al.*, 2005), a phenomenon that can already be observed (Sturm *et al.*, 2001; Tape *et al.*, 2006). In mountain regions, a rise in the snow line (i.e. the altitude, above which precipitation falls as snow) and a decrease in the snow:rain ratio due to increased temperatures could however lead to decreased snow depth, inducing 'colder soils in warmer world' (see Groffman *et al.*, 2001), and increasing the number of freeze-thaw cycles. Decreased snow depths and snow cover duration, mainly since the 1980ies, have already been detected at lower altitudes (below approx. 1500 m asl), and a decreased snow:rain ratio in the European Alps (Beniston, 1997; Laternser & Schneebeli, 2003, this thesis, chapter 5).

Snow augmentation experiments in ecosystems with seasonally frozen soils in winter (arctic tundra, high-alpine meadows) have shown that snow depth is crucial for microbial activity and for net N mineralization (Brooks & Williams, 1999; Schimel *et al.*, 2004; Williams *et al.*, 1998). With increasing snow depth and thus warmer soils, the availability of N is increasing, which may stimulate plant growth in the subsequent season and increase leaf N status (Welker *et al.*, 2005). So far, the effects of snow cover on belowground processes have mainly been studied in the arctic tundra. In alpine environments, snow cover effects might be more important as in the arctic tundra, since the winter climate is warmer and thus, snow can protect soils from freezing, which would otherwise decrease microbial activity abruptly (e.g. Mikan *et al.*, 2002). In contrast to arctic regions, where winter precipitation might rise, less snow, and as a consequence, colder soils may be a more realistic future climate scenario in alpine regions (see this thesis, chapter 2). However, its effects on ecosystem processes is largely unknown.

To quantify the direct and indirect impact of winter climate change on ecosystem processes in alpine tundra, we explored the effects of a decreased snow depth and advanced snowmelt timing on litter decomposition in a hierarchical, two-year experiment. First, we manipulated snowmelt timing in alpine tundra in spring and analysed its effects on the litter producing plants, and on the characteristics of the litter produced in the following summer.

Second, we conducted a litter decomposition experiment in the following winter and spring using plant litter from the first snowmelt experiment, and tested whether litter mass loss depended on 1) snowmelt timing in the plots of origin, 2) snow depth, and 3) snowmelt timing during the incubation of the litter.

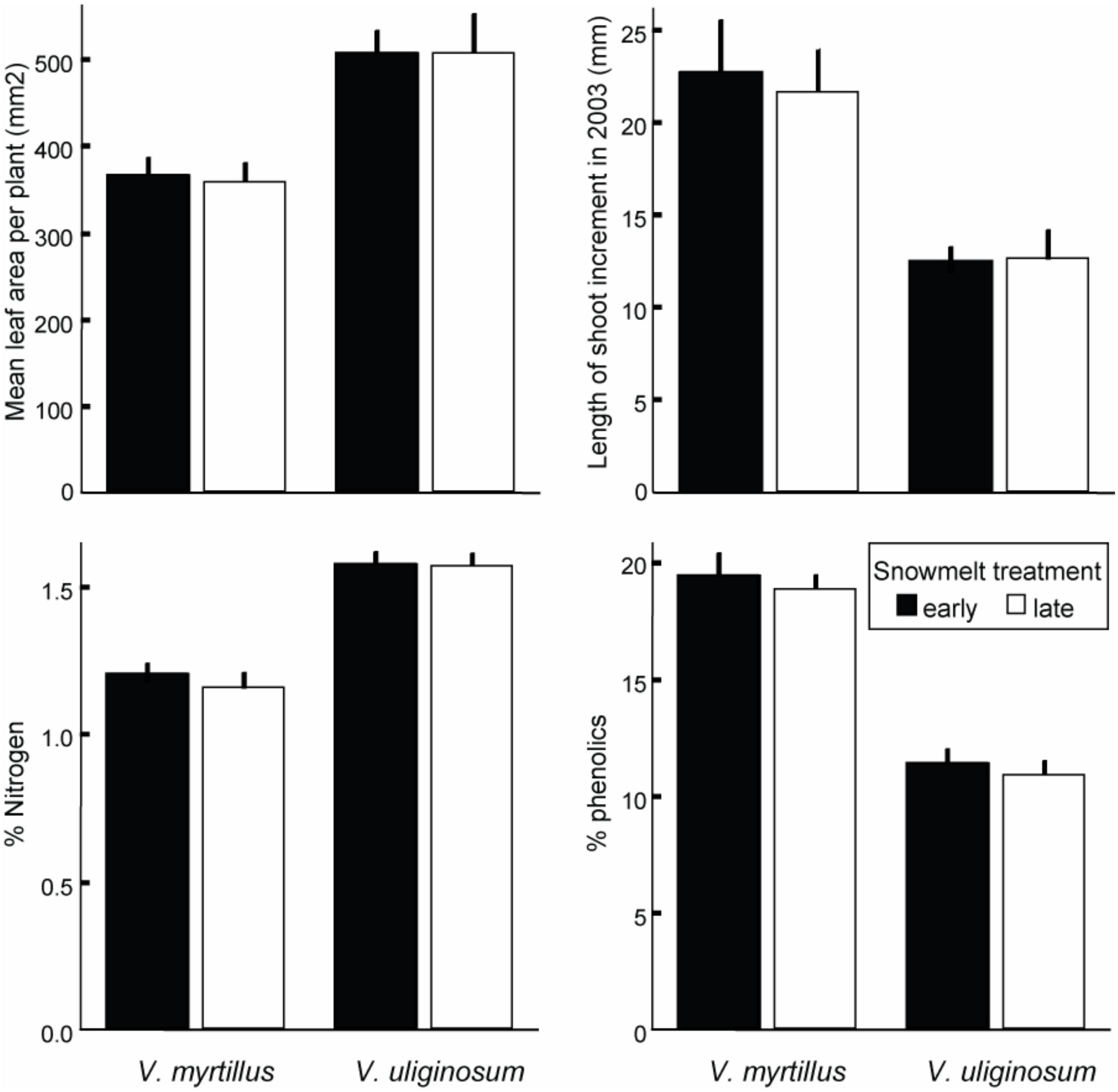

Figure 1. The leaf area per shoot (mean leaf area*number of leaves), shoot growth increments, and the chemical composition of leaves produced by *Vaccinium myrtillus* and *V. uliginosum* after manipulation of snowmelt date in an alpine tundra near treeline, 2200m a.s.l. (means + 1SE).

Methods

Study site

We conducted the first part of our study at the research site of Stillberg, Davos (Central Alps, Switzerland, 47°28'N 7°30'E). The plots of our experiment were situated on a NE exposed slope close to treeline at 2200 m asl. Climate data were continuously measured by a weather station at 2090 m asl since 1975, and the data presented here are means from 1975 to 2004 (see chapter 1 of this thesis for a detailed climate diagram with monthly means). In short, total annual precipitation amounts to 1150 mm per year (SD=+/- 164 mm), 48% of which falls during the vegetation period, between June and September. Mean air temperature is 2.0°C (+/- 0.7°C) over the year, and 8.5°C (+/- 1°) over the vegetation period (June to September), February being the coldest month (on average -4.9° +/- 2.3° C), July and August the warmest (both 9.9° +/- 1.5° C). Snow cover lasts on average from 18 October (+/- 16 days) to 26 May (+/- 10 d), and mean maximum snow depth in winter is 143 cm (+/- 31 cm). From 1975 to 2004, the proportion of the yearly precipitation that fell as snow (i.e. sum of precipitation falling at temperatures below or equal to 0°C, measured in 1h increments) significantly decreased by 3% per decade, and the snowmelt date became significantly earlier by 4 days per decade (see this thesis, chapters 2 and 5). The vegetation at this sites, growing on a 5 – 20 cm deep organic topsoil layer on siliceous gneis (Bednorz *et al.*, 2000), consists of a relatively species-poor tundra type dominated by the deciduous dwarf shrub species *Vaccinium myrtillus* (bilberry) and *Vaccinium uliginosum* ssp. *gaultherioides* (alpine blueberry, subsequently called *V. uliginosum*), and the evergreen *Empetrum nigrum* ssp. *hermaphroditum* (crowberry). A list of the most frequent plant species and their abundances is included in chapter 1 of this thesis.

Experimental set-up and measurements

We established a total of 18 plots of 1 m^2 at three sites with homogeneous alpine tundra vegetation (subsequently called tundra plots), the distance between plots within a site being approx. 2 m, between sites approx. 100 m. In spring 2003, when first patches of tundra were snowfree, we randomly assigned the plots to one of two snowmelt treatments: advanced snowmelt, by manually removing snow, and delayed snowmelt, by adding a layer of snow. The treatments resulted in a mean difference in snowmelt date of 9 days between the early- and late-melting plots. As we did not remove or add a standard amount of snow, the plots became snowfree over a range of three weeks (9 May to 1 June), causing an artificial snowmelt gradient in our study plots.

In early September 2003, we estimated the cover of *Vaccinium uliginosum* and *V. myrtillus*, the two dominant deciduous species that contribute most to the yearly litter mass in our plots (S. Wipf, personal observation), collected 3 shoots per plot of both species, and measured the length of the 2003 growth increment with calipers and counted the number of leaves produced. Furthermore, we sampled approx. 20 leaves per plot and species, and scanned them on a flatbed scanner. We determined their length and area using the program ImageJ (Rasband, 1997-2006). Moreover, we determined the area eaten by herbivores as the lacking leaf area (drawn with the freehand tool of the program), and calculating its percentage on the original leaf area (i.e. the sum of present and lacking leaf area). As a measure of litter produced by a plant, we multiplied the mean leaf area by the number of leaves. Leaf litter of the two species was collected in autumn 2003 and air dried at room temperature. Before laboratory analyses, the litter material was further dried at 40°C for 24 h. The litter was analyzed for its C and N content by a CN-analyzer (NA2500, Carlo Erba). Water extractables were measured by extracting 0.5 g of milled samples three times with 25 ml of hot water (85°C) and once with cold water (15 minutes each). Water-extractable C and N was measured with Shimadzdu TOC-V; water-extractable phenolics by the Folin-Denis colorimetric method (Swain & Hillis, 1959).

To measure litter decomposition over winter in response to snowmelt manipulation in spring 2003 (affecting the litter production in the tundra plots and thus, its decomposability) and to snow cover and snowmelt manipulations in the subsequent winter/spring 2003/2004 (affecting the litter decomposition rate directly), we collected current year litter, mainly containing *V. uliginosum* and *V. myrtillus* leaves, in late September and dried it to constant weight at room temperature. We then prepared two litterbags per tundra plot (8 x 8 cm nylon bags with 0.5 mm mesh size) with a previously weighed dry litter sample (mean litter mass 1.1 g).

On 28 November 2003, we established a litter decomposition experiment on a readily accessible meadow in Davos (1550 m asl) to test for effects of different snow cover characteristics on litter loss: we marked 18 plots of 0.5 x 0.5 m arranged in a approx. rectangular grid (subsequently called decomposition plots). In each plot, we pinned two randomly chosen litterbags (but not from the same plot) to the ground with chopsticks and wire, and placed a temperature logger at the soil surface to measure subnivean temperatures (i.e. below snow) as an estimate of litter temperatures during winter. After the first snowfall two days later and after each subsequent snowfall event, we reduced the snow cover of 9 randomly chosen decomposition plots to approx. 0.3 m to reduce the snow isolation capacity, and measured snow depth regularly. The markers of two plots originally receiving the reduced snow treatment collapsed in an early winter storm, and their exact location could not be re-established. We left these plots under ambient snow cover for the remaining winter and denoted them as controls in the analysis. Differences in the temperature due to the snow reduction prior to the storm were accounted for by using soil temperature variables in the statistical analysis.

In spring, we randomly applied one of three snowmelt scenarios (very early, early, and control) to each decomposition plot by shovelling away most of the snow cover to a depth of approx. 10 cm at 4 April and 14 April, and letting controls melt naturally, respectively. Litterbags were free of snow within 1 to 2 days after snow removal, and controls on 21 April on average. On 30 April, we collected the litterbags, dried the remaining content at room temperature, weighed it and calculated litter decomposition as the percentage of initial litter mass lost over the period of the experiment.

In summary, our two-winter experiment manipulated winter conditions for both plant growth (spring 2002/2003) and for decomposition of the litter (winter and spring 2003/2004), and combined all of the following treatments: (1) litter: grown after differing snowmelt dates; (2) snow depth during decomposition: reduced and ambient snow depth; (3) snow melt during decomposition: very early, early, and ambient snowmelt. This resulted in 12 treatments with 3 replicates each.

Statistical analysis

We analysed the effects of snowmelt timing in 2003 on growth and leaf characteristics (length, total N, C/N ratio, and phenolics) of *Vaccinium myrtillus* and *V. uliginosum* with general linear models (glm) with Type 1 Sums of Squares for each species separately. We first performed an analysis to test for effects of location (3 sites) and snow manipulation treatment (early/late). Then we tested for the effects of the snow treatment and site after accounting for the date of snowmelt, i.e. the variable, which we suspected would be the most important factor explaining plant and leaf characteristics. The measured shoot increments and leaf lengths per plot and species were pooled and log-transformed for statistical analysis. *V. myrtillus* growth and leaf characteristics were not affected by site or snowmelt variables, therefore we only show the analysis of *V. uliginosum* in the results section of this paper.

We analysed the effects of snowmelt in spring 2003 (on tundra plots), snow depth during winter 2003/2004, and snowmelt in spring 2004 (on decomposition plots) on litter mass loss (log10 transformed) in a similar way as described above, however, we included two covariables: (1) The variation in litter mass obtained from the tundra plots, and hence, the variation in initial litter mass in the litter bags was very high. We therefore accounted for the initial difference in litter mass by including it as covariable. (2) We also had to account for the spatial characteristics of the meadow, where the decomposition experiment was conducted, due to a snow depth and shading gradient across the field caused by nearby buildings and trees. We did this by numbering the rows of plots of the rectangular field in X and Y direction, and coding the position of each decomposition plot along the X and Y axis of the experimental field. We included these two "coordinates" and their interaction as covariables in our analysis.

Analogous to the glm used with the tundra plot data, we first tested for effects of the location of the tundra plots, and for the three different manipulation treatments (early/late snowmelt in spring 2003, deep/shallow snow cover in winter 2003/04, and very early/early/ambient snowmelt in spring 2004). Then, we added the variables that described the changes in environmental conditions due to the snowmelt manipulations best: The snowmelt date in 2003, the mean soil surface temperature and its variability (standard deviation) during the winter 2003/2004, and the snowmelt date in 2004. By accounting for these variables before those indicating the manipulation treatments in the glm, we could test for effects of the manipulation treatments on litter loss that were not explained by the environmental variables alone. For all figures and for the path analyses (see below), we used values of litter mass loss that where corrected for the effect of the covariables (i.e. we calculated the residuals of a glm with the four covariables, and added them to the grand mean over all litter bags).

To assess the causal relationships between snowmelt date in 2003, characteristics of leaves grown after various snowmelt dates, and their controls on litter decomposition, we conducted a path analysis (Mitchell, 2001; Wright, 1934) to test an a priori hypothesis (Fig. 4, above) of these relationships. Path diagrams are models to describe the relationships between variables, and to decompose their correlations into causal and non-causal relationships. Causality is merely assumed, though, as additional unmeasured variables might be the true cause of correlations. The path coefficients are calculated as the standardized regression coefficients of multiple regressions, and indicate the strength of the direct effect of an independent on a dependent variable. The unexplained variance is calculated as $(1-R^2)^{1/2}$ (R^2 being the total variation of a dependent variable explained by the regression).

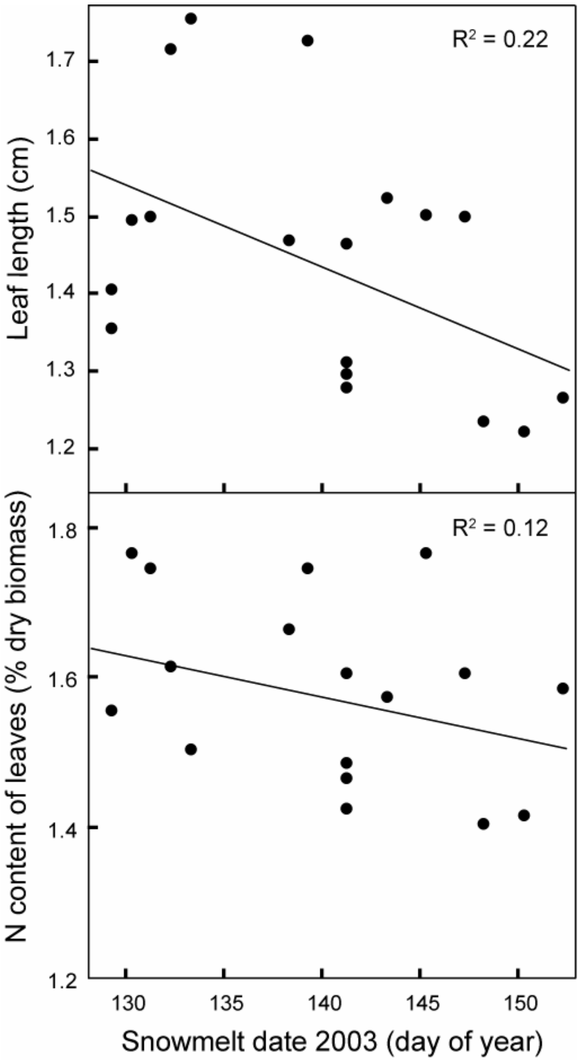

Figure 2. The relationship between snowmelt date in 2003 (gradient caused by manipulation of snowmelt) and mean length (above) and nitrogen content (below) of *Vaccinium uliginosum* leaves produced in the summer following the snowmelt manipulation experiment. Each sample is the mean of approx. 20 randomly collected leaves per plot.

Results

The snowmelt treatment in spring 2003 did significantly advance snowmelt by 9 days ($F_{1,14}$=7.1, P=0.02), but treatment alone did not affect any of the leaf characteristics of *Vaccinium uliginosum* and *V. myrtillus* (Fig. 1). The snowmelt date, however, significantly affected leaf characteristics of *V. uliginosum*: leaves were longer after earlier snowmelt ($F_{1,13}$=7.9, P=0.02; Fig. 2), and tended to contain more nitrogen ($F_{1,12}$=3.8, P=0.08; Fig 2). These leaf characteristics also differed between sites ($F_{2,11}$=6.7 and 6.0, P=0.01 and 0.02), but snowmelt manipulation treatment did not explain any significant additional variation after snowmelt date was accounted for. No significant effects of snowmelt treatment or date on shoot growth ($F_{1,12}$=0.01), number of leaves ($F_{1,12}$=0.4), herbivory ($F_{1,12}$=2.7), other chemical characteristics (leaf C/N ratio ($F_{1,12}$=0.0), content of water-extractable C, N and phenolics, $F_{1,12}$=0.6, 2.2, and 0.3), and leaf characteristics of *V. myrtillus* were found.

The litter mass loss was greater from smaller litter samples, plus there was a spatial gradient of litter decomposition across the site where the decomposition experiment was established, expressed as a significant effect of the covariables (i.e. initial litter mass, and interaction between X and Y axis of the decomposition plots (Table 1)). When these covariables were accounted for, none of the main factors and interactions (location and snowmelt treatment in tundra plots; snow reduction and snowmelt treatments in decomposition plots) had significant effects on litter mass loss in the winter 2003/2004 (Table 1a). However, the snowmelt date prior to leaf growth, as well as the temperature mean and variability in the winter, during which decomposition took place, all influenced litter mass loss (Table 1b). Early snowmelt in the spring before leaf production reduced litter decomposability (Fig. 3). Snow depth reduction during decomposition, which caused a cooling and greater fluctuations of soil temperature, suppressed litter mass loss (Table 1, Fig. 3). The slope of regression suggests that the litter mass loss decreased by 20% per 1 K. In contrast to the snow depth, the snowmelt date of decomposition plots in spring 2004 did not affect decomposition.

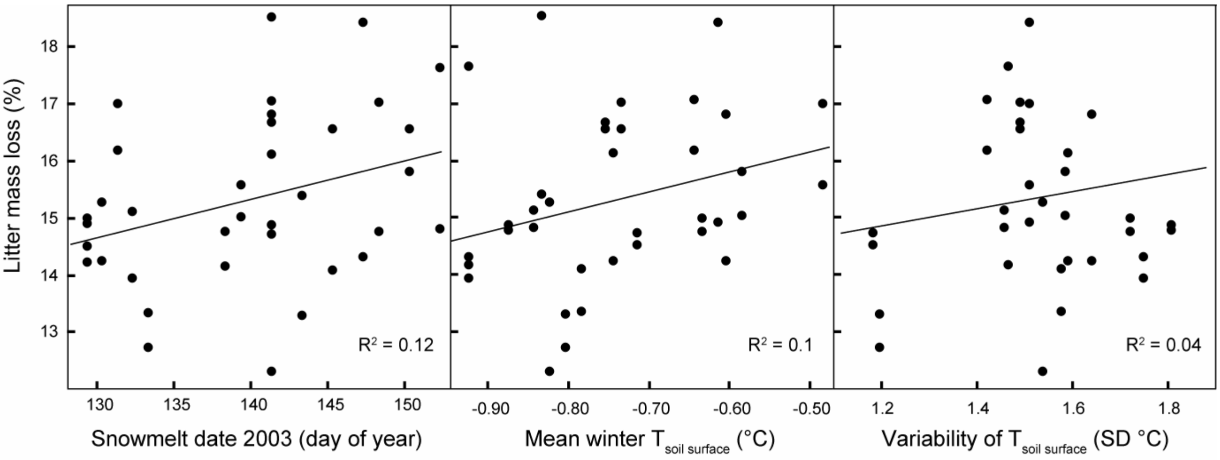

Figure 3. The relationship between litter mass loss during the winter 2003/2004 and snowmelt date in spring 2003 (prior to the growth of leaves that were used in the litter decomposition experiment, left), the mean soil temperature (center), and the temperature variability during the winter of decomposition (right).

In the path analysis, the causal relationships between snow cover manipulations, leaf properties of *V. uliginosum* (size, content of nitrogen and phenolics), temperatures and decomposition were explored (Fig. 4). The path diagram revealed that decomposition was strongly controlled by the composition of the litter, and negatively affected by higher *V. uliginosum* frequency in plots where litter was collected. Snowmelt date in 2003 and decomposition of the subsequently produced leaves were linked directly (or indirectly through unmeasured variables), but decomposability was not directly influenced by morphological leaf characteristics (leaf size). Larger leaves, as produced after early snowmelt, contained more nitrogen, which favored decomposition. Regardless of this negative indirect impact, the net effect of early snowmelt was a lower decomposition rate.

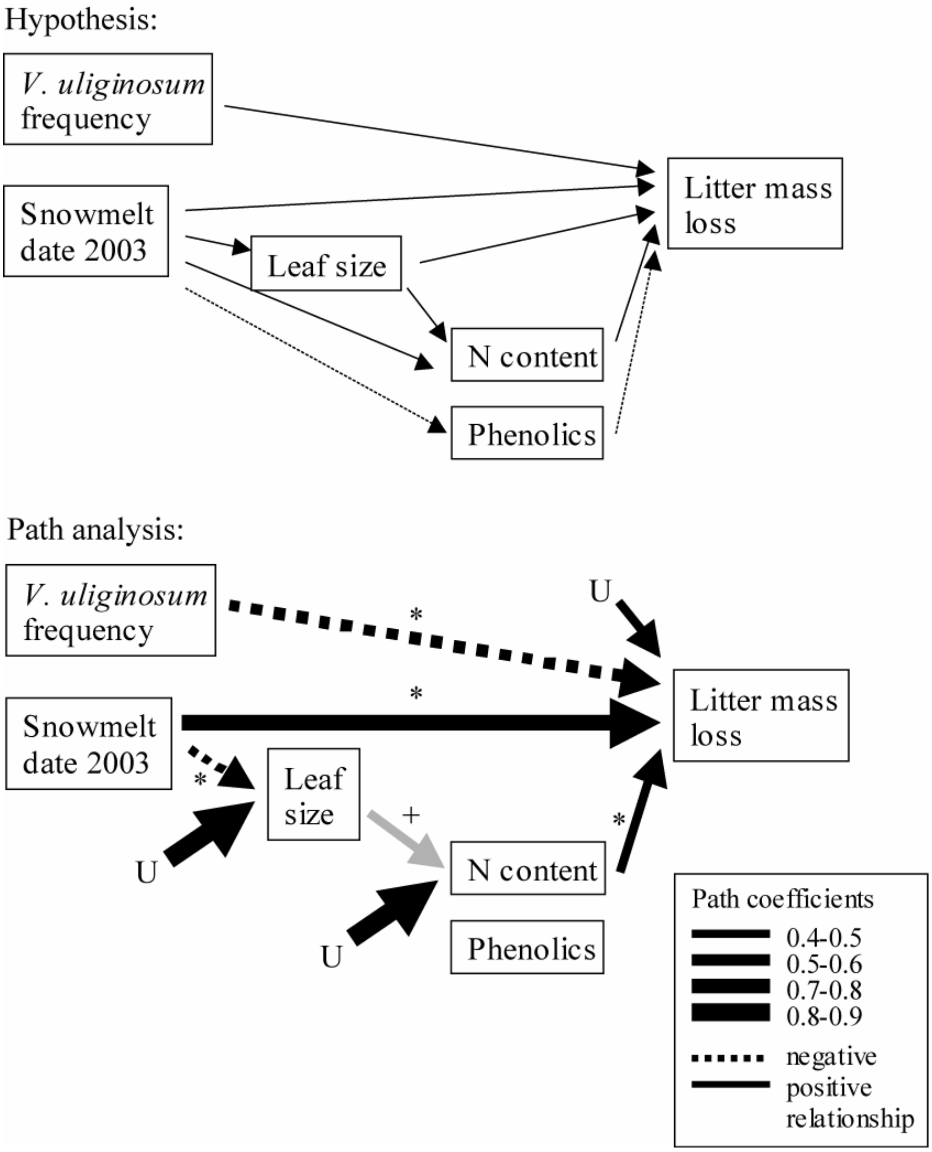

Figure 4. Path diagrams of the hypothesis (above) and path analysis of the effects of snowmelt date in 2003 on size and chemical composition of *Vaccinium uliginosum* leaves (produced in the following summer), and the effects of these leaf characteristics on litter mass loss (in %) in a litter bag experiment over the following winter. *V. uliginosum* frequency was expressed as the percentage cover at the total cover of deciduous dwarf shrubs (leaves of which litter mainly contained). Leaf length and the content of nitrogen and phenolics were measured from a random sample of approx. 20 leaves per plot. Solid arrows = positive effects, dashed arrows = negative effects. U = unexplained variation. The line width is proportional to the strength of the relationship. Significance levels: * = $P<0.05$; + = $P<0.7$ (grey). The total number of plots was 18, and we used the data of one (out of two) randomly chosen litterbag with litter from each plot in the analysis.

Discussion

In arctic and alpine ecosystems, microbial processes in winter play a key role for the ecosystem functioning. In spite of the low temperatures that occur below arctic and high-alpine snow packs, soil microbes are still active (Clein & Schimel, 1995; Hobbie *et al.*, 2000; Lipson *et al.*, 1999), and mass loss of fresh litter is higher during the first winter than in the following summer (Hobbie & Chapin, 1996; Steltzer & Bowman, 2005). During the long winters, there is a net mineralization of N that is thought to determine the N supply of plants during the next growing season (Bilbrough et al. 2000; Schimel et al., 2004; Welker et al., 2005). Our results indicate that the thickness and length of the snow cover affect decomposition rates and litter decomposability. As a consequence, deep snow covers do not only protect plants from direct negative impacts (see this thesis, chapter 1), but also foster the release of nutrients from decomposing litter and thus, nutrient availability for plants.

Our hierarchical two-winter snow manipulation experiment shows that winter conditions affect decomposition in two ways. The length of snow cover duration can influence the size and quality of the leaves of the dominating species, thereby defining the decomposability of plant material grown after varying snowmelt dates. During the subsequent winter, the depth and duration of the snow cover defines the soil temperatures, which control the decomposition rate, and thus, litter mass loss.

Snow characteristics and soil temperatures as drivers of decomposition

Soil temperature during winter is one of the main drivers for microbial activity (Brooks *et al.*, 1998; Monson *et al.*, 2006; Schimel *et al.*, 2004), and thus, for litter decomposition (Kirschbaum, 1995; Robinson, 2002) and nutrient cycling rates (Schimel *et al.*, 2004). The temperature conditions below the snow pack depend on the air temperature on one hand, and on snow characteristics of the snow cover (timing, depth and density) on the other hand (Rixen *et al.*, 2004; Sturm *et al.*, 1997). The changes in winter climate, as predicted for many alpine and arctic areas by climate change scenarios, are likely affecting the snow cover characteristics and winter soil temperatures, and hence, impact litter decomposition and the cycling of carbon and nutrients. Besides directly affecting the composition and activity of the microbial community, temperatures could indirectly enhance decomposition processes when freezing-thawing cycles foster mechanical disruption of the soil and litter structures (Grogan *et al.*, 2004; Hobbie & Chapin, 1996; Tierney *et al.*, 2001), which could explain why a higher temperature variability, additionally to decreased soil temperatures, tended to enhance litter mass loss in our study.

Most studies experimentally altering the snow cover and studying the impact on belowground processes of tundra have been conducted in arctic or high-alpine ecosystems. There, soils are frozen over winter (Olsson *et al.*, 2003; Walker *et al.*, 1999), and although increased snow covers considerably increased the soil temperatures under snow, they were still well below freezing (Brooks & Williams, 1999; Jones *et al.*, 1998). In the case of alpine tundra like ours, soils remain unfrozen at around 0°C during most winters (Rixen *et al.*, 2004), and small changes in the snow cover and soil temperatures could have large effects on biochemical processes, if this temperature deviation defines whether the soil freezes or not. Soil respiration for instance, showed a nearly exponential decrease with a temperature drop from 0 to –1°C, but was much less sensitive to changes of 1 K further below freezing (Monson *et al.*, 2006).

In our experiment, the litter mass loss during winter decreased by 14% in response to a slight cooling of 0.5 K induced by snow removal. This difference in soil temperature is equal to the natural variance of the subnivean soil temperatures measured at the Stillberg site (mean +/- SD over 30 years = -0.06+/-0.25). Thus, we presume that the litter decomposition can easily vary by this factor from year to year. However, we would expect the variability of soil temperatures and thus, of litter mass loss rates to be even greater between sites with different snow covers due to snow redistribution than between years.

Litter quality as a driver of decomposition

Besides soil temperature, litter quality is an important driver of decomposition in tundra ecosystems (Grogan & Jonasson, 2005). Generally, decomposition increases with decreasing C/N ratios and contents of lignin and phenolics (Heim & Frey, 2004; Swift *et al.*, 1979). In our experiment, an advanced snowmelt prior to the formation of leaves of the two deciduous study species significantly reduced their decomposability, although leaf chemistry (measured as C/N ratios, water-extractable C, N, and phenolics) was largely unaffected, except for a small but marginally significant increase of leaf N with earlier snowmelt. This contrasts with other studies, where an advanced snowmelt decreased leaf nitrogen contents, and increased C/N ratios of deciduous dwarf shrubs (Van der Wal *et al.*, 2000; Walsh *et al.*, 1997). We therefore speculate that the reduced decomposability of leaves after early snowmelt was not caused by lower litter quality, but rather by larger leaf sizes. Larger leaves have a smaller surface area per mass, which makes the litter less accessible for decomposers and less vulnerable to leaching (Swift *et al.*, 1979). Alternatively, leaves produced after early snowmelt and hence, under cooler temperatures, and probably higher light stress, might contain some protecting agents that are difficult to decompose during the following winter (Rieley *et al.*, 1995; Semerdjieva *et al.*, 2003). Our analysis of phenolics as potential such compounds might have been too unspecific to support this hypothesis.

The decreasing litter decomposability with earlier snowmelt is supported by a herbivory experiment at the same site (see this thesis, chapter 5), showing that dwarf shrub leaves from early-melting plots had been eaten less. Herbivory is driven by the digestibility of leaf tissues and thus, by their quality (Schadler *et al.*, 2003; Wardle *et al.*, 2002). Chemical compounds repelling herbivores are also hard to decompose (Cornelissen *et al.*, 1999; Cornelissen *et al.*, 2004; Grime *et al.*, 1996). Since an earlier snowmelt reduced both herbivory and decomposability of leaves, these two effects are adding up.

Conclusions

Feedbacks between carbon availability, microbial activity and winter climate are important drivers of carbon balance and nutrient cycling of alpine tundra (Brooks *et al.*, 2005; Monson *et al.*, 2006). So far, these links were mostly studied in the arctic, where more snow and rising winter temperatures are predicted, and could lead to warmer soils. A positive feedback loop how winter climate change and increasing snow depths interact with shrubs and foster further increases in shrub abundance is proposed by (Sturm *et al.*, 2005) for the Arctic. Our results propose that the opposite might hold true for winter climate change in alpine ecosystems. Earlier snowmelt can suppress litter decomposability, and decreasing snow depths can cool soils and reduce decomposition. Consequently, the response of decomposition may not be a positive one to rising air temperatures, but might rather be controlled by the timing and amount of snowfall.

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Table 1a, b. Results of general linear models (glm) analysing the environmental controls over litter mass loss during the winter 2003/2004. After accounting for the covariables (see methods for details), we tested for a) effects of the snowmelt treatment in the spring 2003 (prior to litter production), the snow reduction treatment during the time of decomposition in winter 2003/04, the spring snowmelt in spring 2004, and interactions between those treatments. In a second analysis (b), we tested for effects of the environmental variables, which were mainly changed by the treatments, before testing for additional effects of the treatments that were not accounted for by the environmental variable. These variables were snowmelt date in spring 2003 and 2004, changed by the respective snowmelt treatments, and winter soil temperature mean and variability (standard deviation), which were changed by the snow reduction treatment.

a)

Source of variance	Type I SS	df	F	P
Covariables				
Original litter mass	19.4	1	9.2	**0.010**
X Axis on experimental field 03/04	50.0	1	0.0	ns
Y Axis on experimental field 03/04	1.4	1	0.6	ns
X Axis * Y Axis	17.8	1	8.5	**0.013**
Snow manipulation treatments				
Spring snowmelt treatment 2003	1.0	1	0.5	ns
Site 2003	11.4	2	2.7	ns
Snow depth treatment 2003/2004	2.5	1	1.2	ns
Spring snowmelt treatment 2004	11.5	2	2.7	ns
Snowmelt 03 * Site 03	2.1	2	0.5	ns
Snowmelt 03 * Snow depth 03/04	0.8	1	0.4	ns
Snowmelt 03 * Snowmelt 04	6.3	2	1.5	ns
Snow depth 03/04 * Snowmelt 04	0.1	2	0.0	ns
Site 03 * Snow depth 03/04	9.7	2	2.3	ns
Site 03 * Snowmelt 04	6.7	4	0.8	ns
Error	25.2	12		
Total	115.8	35		

b)

Source of variation	Type I SS	df	F	P
Covariables				
Original litter mass	19.4	1	10.0	**0.005**
X Axis on experimental field 03/04	0.0	1	0.0	ns
Y Axis on experimental field 03/04	1.4	1	0.7	ns
X Axis * Y Axis	17.8	1	9.1	**0.006**
Environmental variables and snow treatments				
Snowmelt date spring 2003	9.4	1	4.8	**0.039**
Site 2003	5.2	2	1.3	ns
Snow depth treatment 2003/2004	0.3	1	0.1	ns
Mean winter soil temperature 2003/04	11.2	1	5.7	**0.026**
Variability of winter soil temp. 2003/04 (SD)	6.5	1	3.4	**0.081**
Snow depth treatment 2003/2004	0.4	1	0.3	ns
Snowmelt date spring 2004	1.6	1	0.8	ns
Spring snowmelt treatment 2004	1.7	2	0.4	ns
Error	40.9	21		
Total	115.8	35		

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Chapter 7

Effects of ski piste preparation on alpine vegetation

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Effects of ski piste preparation on alpine vegetation

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Summary

1. Ski resorts increasingly affect alpine ecosystems through enlargement of ski pistes, machine-grading of ski piste areas and increasing use of artificial snow.
2. In 12 Swiss alpine ski resorts, we investigated the effects of ski piste management on vegetation structure and composition using a pairwise design of 38 plots on ski pistes and 38 adjacent plots off-piste.
3. Plots on ski pistes had lower species richness and productivity, and lower abundance and cover of woody plants and early flowering species, than reference plots. Plots on machine-graded pistes had higher indicator values for nutrients and light, and lower vegetation cover, productivity, species diversity and abundance of early flowering and woody plants. Time since machine-grading did not mitigate the impacts of machine-grading, even for those plots where revegetation had been attempted by sowing.
4. The longer artificial snow had been used on ski pistes (2–15 years), the higher the moisture and nutrient indicator values. Longer use also affected species composition by increasing the abundance of woody plants, snowbed species and late-flowering species, and decreasing wind-edge species.
5. *Synthesis and applications.* All types of ski piste management cause deviations from the natural structure and composition of alpine vegetation, and lead to lower plant species diversity. Machine-grading causes particularly severe and lasting impacts on alpine vegetation, which are mitigated neither by time nor by revegetation measures. The impacts of artificial snow increase with the period of time since it was first applied to ski piste vegetation. Extensive machine-grading and snow production should be avoided, especially in areas where nutrient and water input are a concern. Ski pistes should not be established in areas where the alpine vegetation has a high conservation value.

Key-words: artificial snow, biodiversity, functional groups, machine-grading, snow ecology, Switzerland

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Introduction

The structure of alpine vegetation is affected by altitude, aspect and inclination. Some alpine habitats are extraordinarily rich in species, while communities in the highest and most extreme regions consist of only a few specialists (Ellenberg 1988). Furthermore, most communities are characterized by specific proportions of functional groups, such as dwarf shrubs, grasses and herbs. The communities can consist of species from special ecological groups, for example snowbed species, indicating depressions with a long-lasting snow cover and a very short vegetation period, or wind-edge species, indicating a long vegetation period and extreme winter temperatures (Körner 1999).

Alpine ecosystems are sensitive and susceptible to changes in land use and climate (Chapin & Körner 1995; Fischer & Wipf 2002; Laiolo *et al.* 2004). Perturbations of the alpine habitats and changes in snow cover characteristics, for example through skiing, are likely to have impacts on species composition, diversity and productivity of alpine vegetation, which in turn may have negative effects on ecosystem functioning and stability (Tilman 1996; Mulder, Uliassi & Doak 2001). As ski tourism is

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one of the most important economical factors in European alpine regions (Abegg *et al.* 1997; Elsasser & Messerli 2001), the area affected by ski pistes or by constructions related to tourism is still increasing.

Skiing and ski piste preparation by snow-grooming vehicles are likely to cause mechanical damage to the vegetation and the soil (Cernusca *et al.* 1990; Rixen *et al.* 2004). Furthermore, the winter preparation of ski pistes leads to a thin and compressed snow cover with decreased temperature insulation capacity. Soils and vegetation under these ski pistes may experience temperatures lower than −10 °C (Rixen, Haeberli & Stoeckli 2004), while under undisturbed snow-packs, temperatures rarely fall below 0 °C (Rixen 2002; Rixen, Stoeckli & Ammann 2003). As a result, plant species with insufficient cold hardiness and plants sensitive to mechanical stress may be damaged, resulting in shifts among functional groups and a higher proportion of unvegetated ground. In summer, piste construction measures, such as machine-grading, are carried out to remove obstacles like trees and rocks or to level rough or bumpy soil surfaces. In the process of machine-grading, the upper soil layers and the vegetation are removed or heavily damaged (Pröbstl 1990; Haeberli 1992; Bayfield 1996; Titus & Tsuyuzaki 1999; Ruth-Balaganskaya & Myllynen-Malinen 2000). Seed mixtures are often applied to accelerate revegetation, but the success of revegetation measures declines with height above sea level (a.s.l.) (Urbanska 1997).

In response to ongoing climatic changes, artificial snow production is increasingly used in most ski resorts of the world. Climate-change scenarios predict changes in seasonal snowfall patterns, with the snow season beginning later and ending earlier, and a rise in the snow line (IPCC 1996, 1998, 2001). As a consequence, the minimum altitude termed snow-secure for winter sports in the European Alps would rise from 1200 m today to 1500 m a.s.l. within the next 30 years (Abegg 1996). Winters with little snow have already been a major concern of winter sport resorts since the mid-1980s (Seilbahnen Schweiz 2001). As a strategy to minimize the dependence on natural snowfall, ski areas invest in systems for artificial snowing.

Effects of ski piste manipulation in single resorts and single effects of artificial snowing or machine-grading have been investigated in earlier studies (Urbanska 1997; Kammer 2002). In our comprehensive study, sites covered a wide range of locations, altitudes and aspects in 12 Swiss ski resorts. We investigated plots on ski pistes and adjacent control plots beside pistes. With a total of 76 vegetation records arranged in a factorial design, we addressed the following specific questions. (i) Do productivity, species richness and composition of the vegetation on ski pistes differ from the vegetation off pistes? (ii) What are the impacts of machine-grading on productivity, species richness and composition of ski piste vegetation? (iii) How does the use of artificial snow modify environmental conditions on ski pistes and how do productivity, species richness and composition of the vegetation respond? (iv) Do the effects of artificial snow differ between graded and ungraded ski pistes?

Materials and methods

STUDY SITES AND DESIGN

We studied the vegetation of plots on and next to ski pistes in 12 ski resorts in the Swiss Alps (see Appendix 1), ranging in altitude between 1750 and 2550 m a.s.l. and representing a wide range of vegetation types (mostly alpine grasslands on acidic or calcareous bedrock and dwarf shrub heath), time since grading and years of application of artificial snow. The study sites were chosen on machine-graded or ungraded ski pistes with either natural or artificial snow, resulting in four different ski piste types: natural snow/ungraded (ns), artificial snow/ungraded (as), natural snow/graded (nsg) and artificial snow/graded (asg). Sites were selected in consultation with the local ski piste managers to ensure that the pistes had received the same management continuously in previous years.

At each study site, we randomly chose a plot on a ski piste and an undisturbed control plot in the nearest off-piste area to allow for pairwise comparisons. The distance between piste and control plot was 15–50 m and the pair of plots did not differ significantly in altitude, inclination, aspect and management. All ski pistes were prepared by snow-grooming vehicles and were used annually by skiers from approximately mid-November/early December to Easter (mid-April). Artificial snow had been produced in all ski resorts for 2–15 years (n = 21 pistes, mean 7·1 years). On 17 pistes in nine resorts, machine-grading (i.e. construction of ski pistes during which vegetation and topsoil are removed) had been carried out 4–30 years ago (n = 17 pistes, mean 18·7 years). On 10 machine-graded plots, revegetation had been encouraged by sowing seed, but details of seed mixtures and sowing techniques were not available.

VEGETATION DATA

From 1 July to 24 August 2000, we visited each site to collect vegetation records. In 4 × 4-m plots, we noted the presence of each vascular plant species and estimated its cover in seven classes according to Braun-Blanquet (Müller-Dombois & Ellenberg 1974). We assigned a cover value to each class for further calculations (0·01% to '*r*', 0·1% to '+', midpoint to other classes). To compare site conditions between plots, we calculated weighted indicator values for moisture (F), soil reaction (R), nutrients (N) and light (L) per plot according to Landolt (1977). For each plot, we also estimated the percentage area not covered by vascular plants.

To assess productivity, we randomly selected three patches of 0·2 × 0·2 m plot^{-1}, harvested the biomass 3 cm above ground and pooled the samples. In cases where plots had been grazed, we randomly sampled ungrazed areas with similar vegetation within 5 m distance from the plot. Three grazed plots with no undisturbed vegetation nearby were omitted from biomass sampling. We measured annual productivity as the total biomass excluding litter, dead biomass and woody shoots older than 1 year. The biomass was dried at 70 °C and weighed to the nearest 0·01 g.

For each plot we calculated species number and Shannon's index of diversity as $H = -\Sigma P_i \ln P_i$, where P_i is the abundance class of species i. We calculated the abundance of four functional groups: graminoids (Poaceae, Cyperaceae, Juncaceae), woody plants, legumes and remaining forbs (including Pteridophyta), to obtain taxonomical and plant functional characteristics of the plots. According to their habitat preference in relation to snow cover and length of growing season (Ellenberg 1988; Wilmanns 1998; Delarze, Gonseth & Galland 1999), we classified 26 of 322 species as inhabiting snowbeds and 30 as inhabiting wind-edges (Wipf *et al.* 2002). Depending on their phenology, we also classified 67 species as early flowering and 94 as late-flowering, according to the flowering period indicated in Lauber & Wagner (2001). For the four functional, two ecological and two phenological groups, we calculated the proportions relative to total species number and total vegetation cover. See Appendix 2 for a list of species and their classification.

STATISTICAL ANALYSIS

We analysed our data with hierarchical analysis of variance (ANOVA) models. Differences in the type of bedrock, aspect, slope and hours of sunshine between pairs were taken into account by the pairwise design of piste and off-piste plots. Moreover, we considered altitude as a covariate in all analyses. To mirror the study design with pairs of plots on and next to pistes, we fitted the type of plot pairs, i.e. the type of piste treatment of the piste plot in the pair. Next we fitted the factor piste, which indicated differences between plots on and next to pistes within the pairs, across all types of piste treatment. Then, we fitted the interactions of type of pair (machine-grading or years of artificial snow) and piste, which indicated whether the difference between plots on and next to the piste depended on the type of piste treatment. We considered machine-grading, which is applied only once, as a binary factor, and artificial snowing as a continuous variable (time since start of application of artificial snow) because of its potentially cumulative impacts. Three-way interactions between resort, type of plot pair and piste indicated whether effects of machine-grading and artificial snow differed between resorts. To analyse the effect of succession and revegetation measures on the vegetation of machine-graded ski pistes, we performed the same analysis on a reduced data set (pairs of graded piste and control plots) and included years since machine-grading as a continuous variable and sown as a binary factor. If necessary, dependent variables were transformed prior to analysis to reach normality. Residuals were checked visually for normal distribution. Analyses were carried out with SPSS 10·0·5 (SPSS 1999).

Results

IMPACTS OF SKI PISTES VS. NO PISTE

The indicator values of the vegetation composition showed an increased supply in moisture and nutrients available for plants (indicator value F, $P = 0{\cdot}098$; N, $P = 0{\cdot}003$; Tables 1 and 2 and Fig. 1) and a tendency for higher base content of the soil (R, $P = 0{\cdot}059$; Tables 1 and 2) on ski pistes. Despite the favourable environmental conditions for growth, plant productivity on ski pistes was lower than beside the pistes (Tables 1 and 3 and Fig. 2). The mean number of species per plot was 11% lower on piste plots than on off-piste plots ($P = 0{\cdot}047$; Tables 1 and 3 and Fig. 2). The pistes thus had a negative effect on the species richness in alpine grassland and dwarf shrub vegetation.

Woody plants covered 24·3% of unmanipulated control plots, but were significantly less frequent on ski pistes (10·5% cover, $P = 0{\cdot}003$; Tables 1 and 4 and Fig. 3), mainly because of their low abundance on machine-graded pistes (1·7% cover, see next section). The same pattern was found in the proportion of woody species (Tables 1 and 5 and Fig. 3). Legume species were more abundant and had higher cover on piste plots than on control plots. Both cover and species number of early flowering species were lower on piste than on control plots ($P = 0{\cdot}005$; Tables 1 and 6 and Fig. 4). Thus, the snow compaction changed the plot composition of functional and ecological groups.

MACHINE-GRADING OF SKI PISTES

The proportion of ground not covered by vegetation was almost five times higher on graded than on ungraded piste plots ($P = 0{\cdot}008$; Tables 1 and 3 and Fig. 2) but was unaffected by revegetation measures (sowing) or time since machine-grading. Corresponding with the high proportion of ground not covered by vegetation, the light input for the plants (expressed as indicator value L) was higher on graded piste plots than on ungraded ones ($P = 0{\cdot}002$; Tables 1 and 2 and Fig. 1). Nutrient availability to the vegetation (expressed as indicator value N), which was generally increased on ski pistes, reached even higher values on graded pistes than on ungraded ones ($P = 0{\cdot}07$; Tables 1 and 2 and Fig. 1). Whereas the productivity on ungraded piste plots was similar to that of off-piste plots, it was reduced 4·6 times on graded piste plots ($P = 0{\cdot}011$; Tables 1 and 3 and Fig. 2). Machine-graded pistes that had been revegetated by sowing supported fewer species ($P = 0{\cdot}098$). The Shannon index was lower for all graded piste plots ($P = 0{\cdot}03$; Tables 1 and 3 and Fig. 2).

Machine-grading also affected the vegetation composition: woody plants, which were generally less common

Table 1. The effects of ski piste treatments on the parameters describing the vegetation in 12 Swiss ski resorts: Predicted means and slopes of the correlation with years of artificial snow. The n in parentheses refer to the biomass measurements (n lower because of missing values)

	Total $n = 76$ (73) Mean	Off-piste $n = 38$ (36) Mean	Piste $n = 38$ (37) Mean	Piste graded $n = 17$ (16) Mean	Piste ungraded $n = 21$ Mean	Correlation with years of artificial snow Slope
Indicator values						
F*	2·85	2·83	2·87	2·88	2·87	0·000
R†	2·55	2·50	2·59	2·61	2·58	0·007
N‡	2·46	2·38	2·54	2·56	2·53	0·003
L§	3·80	3·76	3·85	4·03	3·71	0·01
Diversity and productivity						
Species number	36·4	38·5	34·3	31·7	36·5	0·30
Shannon index	3·6	3·8	3·4	2·8	3·8	−0·02
Annual productivity (g m^{-2})	158·0	173·1	143·3	46·9	216·7	−0·25
Proportion of cover (%)						
Grasses	41·4	38·8	44·0	38·7	48·4	−0·93
Forbs	24·2	26·5	22·0	20·5	23·1	0·13
Woody plants	17·4	24·3	10·5	1·6	17·7	0·38
Legumes	5·1	2·9	7·4	10·6	4·8	0·15
Snowbed species	8·4	7·3	9·6	14·0	6·0	1·36
Wind-edge species	7·5	7·7	7·4	8·0	6·9	−0·27
Early flowering species	35·6	40.8	30·5	22·9	36·6	−1·26
Late-flowering species	30·5	28·0	32·9	34·1	32·0	0·03
Bare ground	11·8	7·0	16·1	28·6	6·0	0·26
Proportion of species (%)						
Grasses	27·9	27·9	27·8	27·2	28·2	−0·13
Forbs	60·2	59·8	60·6	63·2	58. 5	0·09
Woody plants	11·9	13·0	10·8	6·9	14·0	−0·23
Legumes	7·8	6·6	9·1	10·9	7·6	0·21
Early flowering species	33·4	35·7	31·1	25·5	35·7	−0·71
Late-flowering species	31·0	29·9	32·2	32·5	31·9	0·25

*F = 2, medium dryness; 3, medium humidity.
†R = 2, acid soils; 3, neutral or weakly alkaline soils.
‡N = 2, nutrient-poor soils; 3, medium- to nutrient-poor soils.
§L = 3, half-shaded conditions; 4, full-light conditions.

Table 2. ANOVA table for the indicator values of the vegetation for moisture (F), soil acidity (R), nutrient (N) and light availability (L) measured on 38 ski piste plots and 38 corresponding off-piste plots in 12 Swiss ski resorts. The type of piste treatment (machine-grading and years of artificial snowing) was fitted for pairs of piste/off-piste plots. The factor ski piste indicates the difference between piste and off-piste plots. The dependent variables were ($\ln(x + 1)$)-transformed prior to analysis. Three plots were excluded from biomass sampling. The sample size for productivity is therefore 73, and the degrees of freedom are indicated in parentheses. MS, mean squares; F, variance ratio; subscripts refer to source of variation (*)$P < 0·1$, *$P < 0·05$, **$P < 0·01$, ***$P < 0·001$

	Skeleton analysis						
				Variance ratio			
Source of variation	MS	F	d.f.	F-value	R-value	N-value	L-value
Altitude	MS_E	MS_E/MS_{Rest}	1	3·14	5·87(*)	70·23**	37·19**
Resort	MS_R	MS_R/MS_{Rest}	11	3·34	4·87(*)	4·43(*)	1·83
Type of plot pair	MS_T	MS_T/MS_{RT}	3	0·16	0·50	0·25	0·75
Piste	MS_P	MS_P/MS_{RP}	1	3·27(*)	4·42(*)	14·64**	9·46*
Grading × piste	MS_{LP}	MS_{LP}/MS_{RLP}	1	0·32	2·68	4·51(*)	24·36**
Duration of snowing × piste	MS_{AP}	MS_{AP}/MS_{RAP}	1	3·68(*)	4·80(*)	3·26(*)	0·13
Grading × duration of snowing × piste	MS_{LAP}	MS_{LAP}/MS_{Rest}	1	1·02	0·03	0·03	0·06
Resort × type of plot pair	MS_{RT}	MS_{RT}/MS_{Rest}	23	1·42	1·52	3·97(*)	0·87
Resort × piste	MS_{RP}	MS_{RP}/MS_{Rest}	11	0·51	0·45	0·93	0·24
Resort × grading × piste	MS_{RLP}	MS_{RLP}/MS_{Rest}	7	0·37	0·44	1·31	0·18
Resort × duration of snowing × piste	MS_{RAP}	MS_{RAP}/MS_{Rest}	11	0·34	0·51	0·44	0·15
Rest	MS_{Rest}		4				
Total			76				

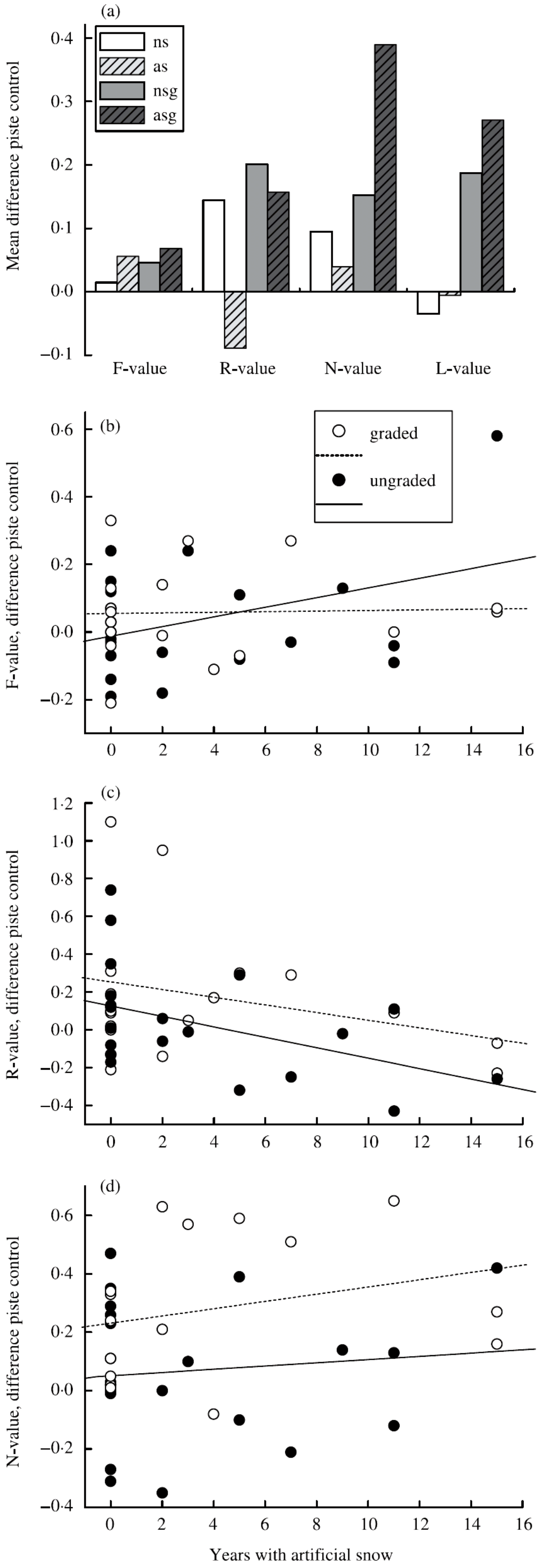

Fig. 1. Differences in indicator values between ski piste plots and corresponding control plots. (a) Mean differences in indicator values for the four ski piste treatments (ns, ungraded pistes with natural snow; as, ungraded pistes with artificial snow; nsg, graded pistes with natural snow; asg, graded pistes with artificial snow; F, moisture indicator value; R, reaction (soil acidity) indicator value; N, nutrient indicator value; L, light indicator value). (b–d) The relationship between the differences in (b) F (moisture), (c) R (soil acidity) and (d) N (nutrient) indicator values and the time since conversion to artificial snow.

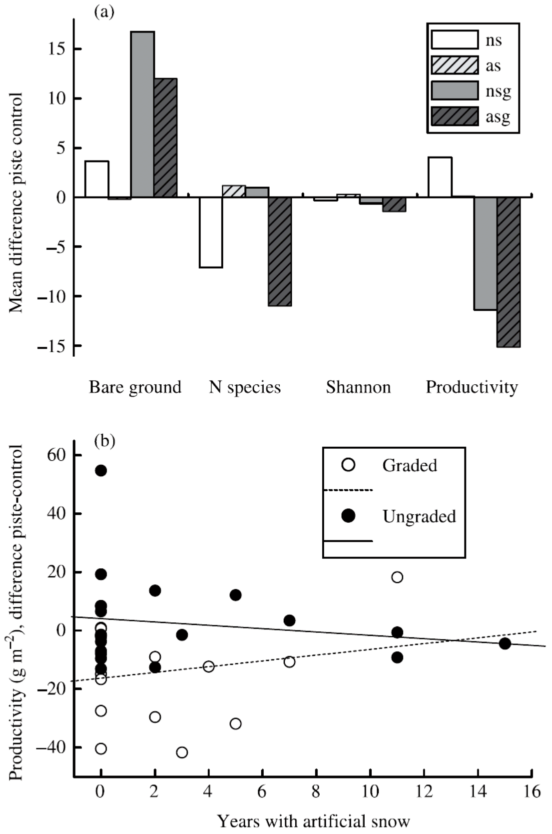

Fig. 2. Differences in productivity and diversity between ski piste plots and corresponding control plots. (a) Mean differences in productivity, species number, Shannon index and the proportion of open ground for the four ski piste treatments (ns, ungraded pistes with natural snow; as, ungraded pistes with artificial snow; nsg, graded pistes with natural snow; asg, graded pistes with artificial snow). (b) The relationship between the differences in annual productivity and the time since conversion to artificial snow.

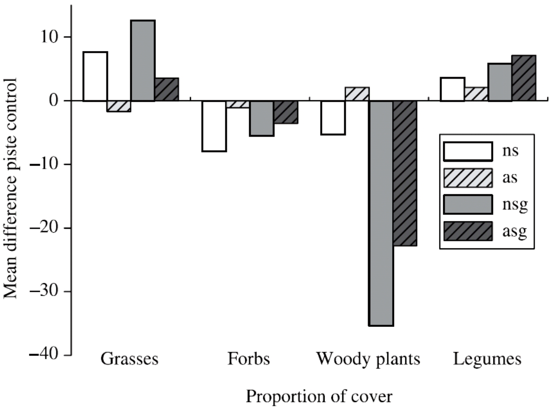

Fig. 3. Differences in species composition between ski piste plots and corresponding control plots. Mean differences in the percentage cover of the four functional groups for the four ski piste treatments (ns, ungraded pistes with natural snow; as, ungraded pistes with artificial snow; nsg, graded pistes with natural snow; asg, graded pistes with artificial snow).

on piste plots, were reduced by 91% on graded piste plots in comparison with ungraded ones ($P = 0{\cdot}03$; Tables 1 and 4 and Fig. 3). Whereas only 6·9% of the species on graded piste plots were woody species, they accounted

Table 3. ANOVA table for the proportion of bare ground, annual productivity, species number and Shannon index measured on 38 ski piste plots and 38 corresponding off-piste plots in 12 Swiss ski resorts. The type of piste treatment (machine-grading and years of artificial snowing) was fitted for pairs of piste/off-piste plots. The factor ski piste indicates the difference between piste and off-piste plots. Three plots were excluded from biomass sampling. The sample size for productivity therefore is 73, and the degrees of freedom are indicated in parentheses. (*)$P < 0·1$, *$P < 0·05$, **$P < 0·01$, ***$P < 0·001$

	Skeleton analysis						
				Variance ratio			
Source of variation	MS	*F*	d.f.	Bare ground (%)	Productivity	Species	Shannon number
Altitude	MS_E	MS_E/MS_{Rest}	1	254·41***	79·96**	5·59(*)	0·58
Resort	MS_R	MS_R/MS_{Rest}	11	9·53*	2·13	5·06(*)	8·00*
Type of plot pair	MS_T	MS_T/MS_{RT}	3	3·18	4·32(*)	1·33	1·62
Piste	MS_P	MS_P/MS_{RP}	1	8·81*	9·78**	5·02*	4·21(*)
Grading × piste	MS_{LP}	MS_{LP}/MS_{RLP}	1	13·64**	10·71*	0·35	7·27*
Duration of snowing × piste	MS_{AP}	MS_{AP}/MS_{RAP}	1	0·02	0·01	0·23	0·26
Grading × duration of snowing × piste	MS_{LAP}	MS_{LAP}/MS_{Rest}	1	2·02	1·83	9·81*	9·99*
Resort × type of plot pair	MS_{RT}	MS_{RT}/MS_{Rest}	23	7·74*	1·01	1·90	2·21
Resort × piste	MS_{RP}	MS_{RP}/MS_{Rest}	11	8·18*	0·90	1·09	2·68
Resort × grading × piste	MS_{RLP}	MS_{RLP}/MS_{Rest}	7	6·05(*)	0·93	1·16	1·85
Resort × duration of snowing × piste	MS_{RAP}	MS_{RAP}/MS_{Rest}	11 (9)	2·74	1·60	0·85	2·27
Rest	MS_{Rest}		4 (3)				
Total			76 (73)				

Table 4. ANOVA table for the proportion of the four functional groups, grasses, woody plants, forbs and legumes, at the plot area measured on 38 ski piste plots and 38 corresponding off-piste plots in 12 Swiss ski resorts. The type of piste treatment (machine-grading and years of artificial snowing) was fitted for pairs of piste/off-piste plots. The factor ski piste indicates the difference between piste and off-piste plots. Three plots were excluded from biomass sampling. The sample size for productivity therefore is 73, and the degrees of freedom are indicated in parentheses. (*)$P < 0·1$, *$P < 0·05$, **$P < 0·01$, ***$P < 0·001$

	Skeleton analysis						
				Variance ratio			
Source of variation	MS	*F*	d.f.	Cover grass (%)	Cover woody plants (%)	Cover forbs (%)	Cover legumes (%)
Altitude	MS_E	MS_E/MS_{Rest}	1	40·49**	0·30	3·28	0·44
Resort	MS_R	MS_R/MS_{Rest}	11	6·37*	3·76	6·70*	9·95*
Type of plot pair	MS_T	MS_T/MS_{RT}	3	1·02	1·58	0·61	2·38
Piste	MS_P	MS_P/MS_{RP}	1	1·76	13·87**	2·47	5·39*
Grading × piste	MS_{LP}	MS_{LP}/MS_{RLP}	1	0·72	7·67*	0·00	1·54
Duration of snowing × piste	MS_{AP}	MS_{AP}/MS_{RAP}	1	29·86***	9·20*	0·69	0·20
Grading × duration of snowing × piste	MS_{LAP}	MS_{LAP}/MS_{Rest}	1	0·00	0·12	0·99	0·81
Resort × type of plot pair	MS_{RT}	MS_{RT}/MS_{Rest}	23	5·21(*)	1·01	2·69	4·66(*)
Resort × piste	MS_{RP}	MS_{RP}/MS_{Rest}	11	3·23	0·70	1·77	5·30(*)
Resort × grading × piste	MS_{RLP}	MS_{RLP}/MS_{Rest}	7	1·53	1·19	1·02	2·83
Resort × duration of snowing × piste	MS_{RAP}	MS_{RAP}/MS_{Rest}	11	0·26	0·40	0·54	4·14(*)
Rest	MS_{Rest}		4				
Total			76				

for 14% of the species on ungraded piste plots ($P = 0·02$; Tables 1 and 5). The reactions of forb and grass species were not uniform: in six resorts the proportion of forb species was higher on graded compared with ungraded pistes (resort × grading × piste, $P = 0·02$). The proportion of grass species depended on the time since machine-grading: compared with ungraded control plots, the proportion was higher in recently graded pistes, and lower the older the graded pistes were ($P = 0·016$). Species that flower early in the year were reduced in abundance by 28% ($P = 0·018$; Tables 1 and 6) and covered 37% less ground on graded piste plots than on ungraded ones ($P = 0·004$; Tables 1 and 6).

ARTIFICIAL SNOW

The longer artificial snow had been applied on ski pistes, the higher the moisture and nutrient availability, and the lower the soil base content (indicator values F, N and R: $P = 0·081$, 0·099 and 0·051, respectively; Tables 1 and 2 and Fig. 1). However, we could not detect any effects of artificial snow on plant productivity (Fig. 2).

Table 5. ANOVA table for the proportion of the four functional groups, grasses, woody plants, forbs and legumes, of the total species number per plot measured on 38 ski piste plots and 38 corresponding off-piste plots in 12 Swiss ski resorts. The type of piste treatment (machine-grading and years of artificial snowing) was fitted for pairs of piste/off-piste plots. The factor ski piste indicates the difference between piste and off-piste plots. The dependent variables of were $(\ln(x + 1))$-transformed prior to analysis. Three plots were excluded from biomass sampling. The sample size for productivity therefore is 73, and the degrees of freedom are indicated in parentheses. (*)$P < 0·1$, *$P < 0·05$, **$P < 0·01$, ***$P < 0·001$

	Skeleton analysis						
				Variance ratio			
Source of variation	MS	MS	d.f.	Grass species (%)	Woody species (%)	Forb species (%)	Legume species (%)
Altitude	MS_E	MS_E/MS_{Rest}	1	2·72	0·08	22·07**	8·59*
Resort	MS_R	MS_R/MS_{Rest}	11	11·33*	2·01	18·79**	2·44
Type of plot pair	MS_T	MS_T/MS_{RT}	3	0·29	0·45	0·26	1·99
Piste	MS_P	MS_P/MS_{RP}	1	0·30	5·72 *	0·24	7·31*
Grading × piste	MS_{LP}	MS_{LP}/MS_{RLP}	1	1·28	10·18 *	0·31	3·19
Duration of snowing × piste	MS_{AP}	MS_{AP}/MS_{RAP}	1	0·02	0·01	0·04	0·08
Grading × duration of snowing × piste	MS_{LAP}	MS_{LAP}/MS_{Rest}	1	0·04	0·09	3·22	0·01
Resort × type of plot pair	MS_{RT}	MS_{RT}/MS_{Rest}	23	3·03	2·36	11·63*	1·11
Resort × piste	MS_{RP}	MS_{RP}/MS_{Rest}	11	6·93*	0·90	6·21	0·36
Resort × grading × piste	MS_{RLP}	MS_{RLP}/MS_{Rest}	7	4·19(*)	0·58	17·73**	1·13
Resort × duration of snowing × piste	MS_{RAP}	MS_{RAP}/MS_{Rest}	11	3·44	0·79	11·84*	0·53
Rest	MS_{Rest}	MS_E/MS_{Rest}	4				
Total			76				

Table 6. ANOVA table for the proportion of snowbed and wind-edge, as well as early flowering and late-flowering species, of the total vegetation cover in a plot (%) measured on 38 ski piste plots and 38 corresponding off-piste plots in 12 Swiss ski resorts. The type of piste treatment (machine-grading and years of artificial snowing) was fitted for pairs of piste/off-piste plots. The factor ski piste indicates the difference between piste and off-piste plots. Three plots were excluded from biomass sampling. The sample size for productivity therefore is 73, and the degrees of freedom are indicated in parentheses. (*)$P < 0·1$, *$P < 0·05$, **$P < 0·01$, ***$P < 0·001$

	Skeleton analysis						
				Variance ratio			
Source of variation	MS	MS	d.f.	Snowbed species (%)	Wind-edge species (%)	Early flowering (%)	Late-flowering (%)
Altitude	MS_E	MS_E/MS_{Rest}	1	85·42***	34·45**	51·38**	5·29(*)
Resort	MS_R	MS_R/MS_{Rest}	11	3·45	3·79	2·45	1·93
Type of plot pair	MS_T	MS_T/MS_{RT}	3	2·18	1·04	1·24	0·61
Piste	MS_P	MS_P/MS_{RP}	1	3·14	0·07	13·90**	3·92(*)
Grading × piste	MS_{LP}	MS_{LP}/MS_{RLP}	1	0·29	0·01	17·93**	2·12
Duration of snowing × piste	MS_{AP}	MS_{AP}/MS_{RAP}	1	13·19**	6·68*	5·68*	0·09
Grading × duration of snowing × piste	MS_{LAP}	MS_{LAP}/MS_{Rest}	1	0·43	0·84	7·35(*)	1·21
Resort × type of plot pair	MS_{RT}	MS_{RT}/MS_{Rest}	23	4·09(*)	0·83	2·87	2·13
Resort × piste	MS_{RP}	MS_{RP}/MS_{Rest}	11	0·79	0·22	1·68	0·74
Resort × grading × piste	MS_{RLP}	MS_{RLP}/MS_{Rest}	7	2·77	2·28	0·86	0·72
Resort × duration of snowing × piste	MS_{RAP}	MS_{RAP}/MS_{Rest}	11	1·56	0·55	1·20	1·74
Rest	MS_{Rest}	MS_E/MS_{Rest}	4				
Total			76				

The impact of artificial snow on diversity was ambiguous. While the use of artificial snow had negative effects on species number and Shannon index on graded pistes, the opposite was found for ungraded pistes (three-way interaction between piste, grading and duration of snowing, $P = 0·034$; Tables 1 and 3).

The application of artificial snow affected the relative proportion of plant functional groups. The longer artificial snow had been used, the more it had reduced the negative effect of the ski piste treatment on the cover of woody plants per plot ($P = 0·011$; Tables 1 and 4). However, the proportion of a plot covered by grass species declined the longer a ski piste had been treated with artificial snow ($P < 0·001$; Tables 1 and 4). The effect of artificial snow on the species proportion of forbs and the cover of legumes was not uniform but differed between ski resorts (three-way interaction resort × artificial snow × ski piste, $P = 0·014$ and $P < 0·083$, respectively; Tables 5 and 6). The longer artificial snow had been applied to a ski piste, the higher the cover of

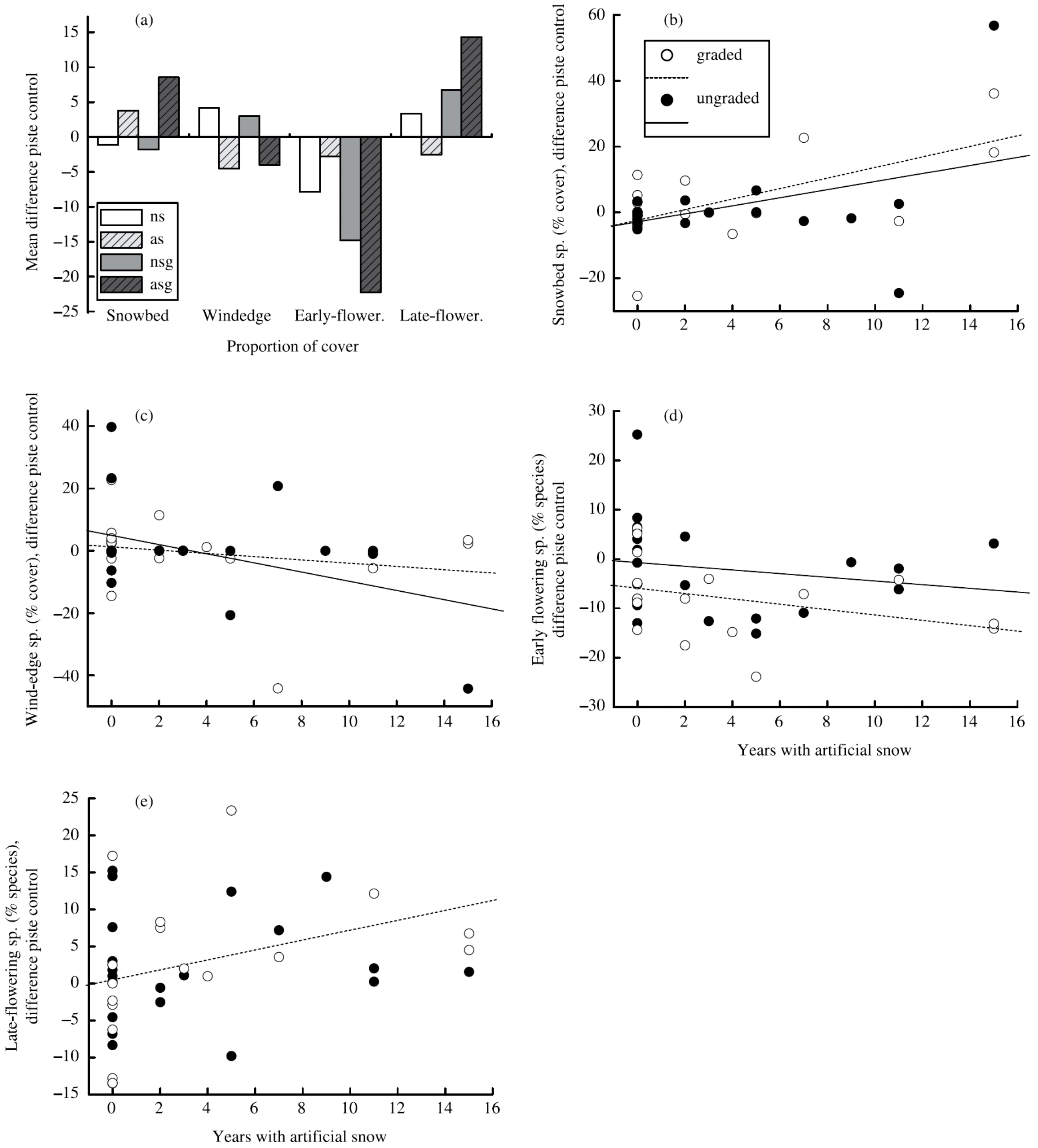

Fig. 4. Differences in ecological groups between ski piste plots and corresponding control plots. (a) Mean differences in the proportion of plot covered by ecological groups for the four ski piste treatments (ns, ungraded pistes with natural snow; as, ungraded pistes with artificial snow; nsg, graded pistes with natural snow; asg, graded pistes with artificial snow). (b–e) The relationship between the differences in (b) percentage cover of snowbed species, (c) percentage cover of wind-edge species, (d) proportion of early flowering species and (e) proportion of late-flowering species and the time since conversion to artificial snow.

snowbed species ($P = 0{\cdot}004$; Tables 1 and 6 and Fig. 4). Wind-edge species showed the opposite reaction. They covered less ground the longer a ski piste had been treated with artificial snow ($P = 0{\cdot}024$; Tables 1 and 6 and Fig. 4). The longer artificial snow had been applied, the lower the cover of early flowering plants on piste plots ($P = 0{\cdot}036$; Tables 1 and 6 and Fig. 4). On the other hand, the relative number of late-flowering species tended to increase the longer artificial snow had been used ($P < 0{\cdot}096$; Tables 1 and 6 and Fig. 4). Overall, the potentially snow-sensitive groups were affected most by the production of artificial snow.

Discussion

IMPACTS OF SKI PISTES VS. NO PISTE

The changes in indicator values for soil nutrients, moisture and reaction (base content) under ski pistes may be considered beneficial for plant growth (in terms of enhancing growth). However, other non-beneficial factors, including disturbance, seem to prevail because overall productivity and species richness on ski pistes are decreased. The negative effects may be the direct result of disturbance of the vegetation via snow compaction under skiing and via mechanical abrasion. Although some types of disturbance can increase biodiversity by suppressing dominant species in productive environments (Connell 1979; Vujnovic, Wein & Dale 2002), abiotic stress reduces productivity and dominance in alpine habitats and therefore reverses any positive effects of disturbance on plant diversity (Kammer & Möhl 2002).

The changes in the cover of woody plants on the ski pistes may also be explained by mechanical disturbance. Woody plants (mainly dwarf shrubs of the *Ericaceae*) are particularly sensitive to mechanical injuries because of their size, longevity and vulnerability of their hibernation buds (Körner 1999).

In contrast to woody plants, legumes were more abundant on pistes than next to pistes, perhaps because of decreased competition from shrubs. Legumes may have been responsible for the increased nutrient indicator values on piste plots as a consequence of their ability to fix nitrogen. The reduced abundance of early flowering species on pistes in our study was most probably the result of a narrowed temporal niche for those species. In field surveys, the flowering time of early seasonal species was postponed after soil frosts on pistes with natural snow (Baiderin 1981; Köck *et al.* 1989). A delay in flowering often decreases fecundity and, consequently, can negatively affect the abundance of early flowering species (Kudo 1993; Stanton & Galen 1997).

IMPACTS OF MACHINE-GRADING

Vegetation responses were highly pronounced on graded pistes, most probably because machine-grading of ski pistes is a drastic measure where soil and plants are removed in summer during active plant growth. There was a strong compositional shift from woody plants to grasses or forbs, the extent of which depended partly on the resort and partly on the successional stage of the ski piste. The increased indicator values for nutrients and light may be the result of the disturbance itself (through mobilized nutrients and opened vegetation cover), or of characteristics of the following pioneer species, which often grow with high light and nutrient levels (Grime & Jarvis 1975; Grime 1977). Graded ski pistes with high proportions of bare ground are particularly prone to increased surface runoff and erosion during heavy rain (Löhmannsröben & Cernusca 1987). Revegetation processes at high altitudes are slow, even if revegetation measures such as sowing and planting are applied (Bayfield, Urquart & Rothery 1984; Urbanska 1995; Titus & Tsuyuzaki 1999; Fattorini 2001). In our study, the proportion of vegetation cover on graded pistes was negatively correlated with altitude, but positively affected by neither sowing nor time since machine-grading. This indicates how difficult it is to achieve revegetation at high altitudes. Machine-grading therefore is a particularly damaging management activity, the consequences of which are more severe and long lasting at higher altitudes.

IMPACTS OF ARTIFICIAL SNOW

Application of artificial snow increased the moisture indicator values of the vegetation on piste plots. Artificially snowed pistes contained twice as much snow mass as normal pistes at our study sites in the winter of 1999–2000 (Stoeckli & Rixen 2000). Because water for artificial snow making is taken from lakes, rivers or ground water, it usually contains minerals and other chemical compounds (Kammer & Hegg 1990; Kammer 2002), and thus provides a nutrient input during spring melting for about 4 weeks in late spring. Accordingly, the vegetation on piste plots with artificial snow had an increased nutrient indicator value. Adding artificial snow to the ski pistes appeared to mitigate the mechanical disturbance of skiing because woody species became more abundant the longer artificial snow had been applied. Artificial snow is usually produced at the beginning of the winter and lasts beyond the end of the skiing season in spring.

The increase in snowbed and late-flowering species, and the decrease in wind-edge and early flowering species, on pistes with artificial snow probably reflect the shortened growth period resulting from a delay in snowmelt of 2–3 weeks (Newesely 1997; Stoeckli & Rixen 2000). Similar to the effects on normal pistes with their compacted natural snow, the narrowed temporal niche in spring presumably conferred a competitive advantage to the snowbed and late-flowering species over wind-edge and early flowering species (Cernusca *et al.* 1990; Newesely 1997; Rixen *et al.* 2001).

Plant diversity reacted differently to artificial snow on the graded and ungraded pistes. The increase in diversity on the ungraded pistes might be because of the decreased mechanical disturbance. The decrease in diversity on the graded pistes, on the other hand, might be a consequence of a decelerated revegetation process because of the shortened growing period. These effects can be enhanced if ice layers in the artificial snow cover decrease gas permeability (Newesely, Cernusca & Bodner 1994).

Whether the impact of artificial snow on alpine vegetation is considered positive or negative depends on the current state of the vegetation and the environmental objectives of a specific ski resort. If mechanical disturbance through snow-grooming vehicles or ski edges is a major problem, the increased protection afforded by artificial snow can be considered beneficial. However, in the case of endangered habitats poor in nutrients, like oligotrophic fens or nutrient-poor grasslands, the additional nutrients input by the melt water of artificial snow is clearly a negative impact.

We have shown that ski pistes in general, and machine-grading and artificial snow production in particular, cause deviations from natural plant species composition and decrease plant species richness. Machine-grading constitutes the most drastic vegetation disturbance on ski pistes. It should be avoided wherever possible, as it causes lasting damage that cannot be overcome even by revegetation measures, particularly at higher altitudes. Impacts of ski pistes in general, and of artificial snowing in particular, appear comparatively moderate, but are by no means negligible. With the ongoing intensification of ski resorts, the use of artificial snow will become more prevalent and the vegetation will change over an increasing area. Moreover, impacts of artificial snowing are cumulative and will become even more pronounced in the long term. In summary, mountain regions with a high proportion of areas with extensive outdoor recreation activities, like the European Alps, are facing continuous change of their traditional unique environment and vegetation. Therefore, we recommend that environmental goals in ski resort management should be established and respected. In particular, we recommend carefully recording the vegetation in a specific area before any intensification of use as ski piste, and complete avoidance of areas with vegetation of particularly high conservation value. Moreover, we recommend that large-scale machine-grading should be avoided, and that long-term snow production should be banned in areas where any increase in the supply of nutrients and water is a concern. Overall, the establishment of ski pistes should not be allowed in areas where any changes in vegetation composition or any decrease in plant species richness cannot be tolerated.

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Supplementary material

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/JPE/JPE1011/JPE1011sm.htm.

Appendix 1. List of study sites

Appendix 2. List of species

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Chapter 8

Summary and conclusions

Recent changes in climate have been more pronounced in winter than in summer, and high latitudes and altitudes were among the most affected regions in the world. Plant growth and ecosystem processes in the Arctic and Alpine are strongly constrained by the harsh climate and the short growing seasons, thus, any changes in the growing conditions is expected to affect plant growth and the composition and functioning of arctic and alpine ecosystems. While various studies on the effects of a warmer summer climate on these plant communities and ecosystems have been performed, the effects of a an earlier snowmelt and of a thinner alpine snow cover are still poorly understood.

This thesis aims at exploring and understanding the short-term responses of subarctic and alpine tundra ecosystems to changes in the winter climate by simulating a winter snow cover that might be realistic in one to two decades. Responses were recorded at the level of the dominant and most frequent tundra species (mortality, phenology, growth, and reproduction), at the level of species interactions (plant neighbour interactions, herbivory), at the level of ecosystem processes (decomposition), and at the level of plant species composition.

Responses in phenology, growth and reproduction at the species level

Differences in the phenology after manipulations of snowmelt date are the most obvious, and probably also most often measured short-term response to snow cover manipulations (see review in chapter 2). Initial differences in phenology in response to snow cover manipulations vanished over the course of the summer (chapter 3 and 5), mainly due to two reasons: (1) the response in phenology was strongest in early-developing species. As shown in chapter 3, the first phenological stages were closely correlated with snowmelt date, while those of later-developing ones were probably controlled by other factors, such as temperature or day-length. (2) The response in phenology was, if present at all, most pronounced in early life-cycle stages of all species, and vanished towards later stages. Thus, individual species went through their life cycle slower after earlier snowmelt. In early-developing species, the difference in phenology was still visible in later stages than in later-developing ones.

An advanced snowmelt followed by an earlier phenological development is often interpreted as positive for individual plant growth and fitness, because of the longer summer season available for growth and resource allocation. However, a positive response in shoot growth was only found in one out of 11 species (see paragraph “community composition” below). At the subarctic study site, changes in snowmelt timing did not affect shoot growth of tundra species at all, even if differences in the phenological development had been seen previously. At the alpine study site, the shoot growth 4 out of 6 species was negatively affected by advanced snowmelt timing. The causal relationships between snowmelt timing, phenology, frosts, and temperature during growth, and their direct and indirect effects on shoot growth were analysed in more detail using path analysis (chapter 5). The interplay between these variables is relatively complex. The results show that the timing when shoot growth started and the temperatures during the period of growth had a great impact on the length of the shoots produced. Frost events directly affected the phenology of all species, but direct negative effects on shoot growth were only found in one species, although we had recorded substantial frost damages at leaves and flowers in the second year of our study. Thus, species are able to compensate for these damages later in the growing season. These species-specific responses in growth suggest that the study species differ in their sensitivity to climate factors influenced by our manipulations of winter climate.

All species studied in this thesis are clonal, and vegetative growth seems to be the predominant way of reproduction (Alsos *et al.*, 2002; Bell & Tallis, 1973; Wolf *et al.*, 2004), although some species are producing plenty of fruits and seeds (Hill & Van der Kloet, 2005). Hence, changes in fecundity induced by winter climate change are not expected to be as relevant in the short term as changes in mortality and growth (see previous paragraph). In the longer term, however, sexual reproduction is of crucial importance in a changing climate, as it allows for dispersal to reach new, suitable habitats, and for genetic adaptation to the "new" growing conditions. The fecundity of most species was not significantly affected by the snow cover manipulations. If responses were found, they were either negative to early snowmelt (in two alpine species), or positive to late snowmelt (in two subarctic species). One possible reason for a decreased fecundity after advanced snowmelt is an increased abortion of flowers due to cold temperatures in spring (chapter 5).

Responses in species interactions

Three types of species interactions might be of special relevance for ecosystems subjected to winter climate change: (1) Positive interactions between plant neighbours could become more relevant under future climates, as shown by the shift in the effect of neighbours after advancing snowmelt (chapter 4). Some possible consequences are discussed in the paragraph "community composition" below. (2) The changes in leaf chemical composition found in the two deciduous species at the alpine site (chapters 5 and 6) could affect the plant-herbivore interaction, which we already found as a decrease in insect herbivory after earlier snowmelt (insect herbivory, chapter 6). Insect-plant interactions could also be of relevance if a shift in the timing of flowering is induced by changes in winter snow cover, which could impact the pollination rates and fecundity of plant species on one hand, and the fitness of pollinators on the other. (3) The fruits of several species studied in this thesis (especially the three *Vaccinium* species and *Empetrum nigrum*) are an essential source of food for numerous vertebrate species, such as grouse, bears and humans. Therefore, any effect of changes in snowmelt timing on reproduction might have further consequences for their population dynamics. Hence, changes in species interactions due to winter climate change could have significant effects on the species composition and food webs of tundra ecosystem.

Responses in carbon and nutrient cycle

Whether tundras will stay carbon sinks or develop into carbon sources under future climate is one of the most important questions in current climate change biology. Our study on the effects of winter climate change on decomposition processes contributes to that discussion by adding a new insight (chapter 6). Our results show that snow cover characteristics can influence decomposition processes in two ways: (1) Snow cover characteristics directly affect the winter soil temperatures, which in turn control the microbial activity and thus, the amount of litter consumed and decomposed by the microbial community over winter. The strong positive relationship between snow cover and decomposition, and thus, carbon efflux into the atmosphere has previously been described in studies from various ecosystems (see chapter 2). (2) However, we furthermore demonstrated (to our knowledge for the first time) a positive relationship between the snowmelt timing prior to the summer when the litter was produced and litter mass loss in the following winter. Reduced litter decomposability after early snowmelt, and reduced decomposition rates during winters with reduced snow depths, could interact and significantly slow down the carbon cycling and carbon efflux in alpine tundras under a future winter climate.

Leaf size and nitrogen contents seemed to contribute to this effect, but we suppose that other unmeasured chemical compounds could play a major role in changing the decomposability of leaves under winter climate change. Future investigations with increased sample size, more detailed analyses of the litter composition, and more accurate measurements of litter input would help to clarify the relationships between snowmelt timing, litter decomposition, and carbon and nutrient cycling.

Responses in community composition

The results of this thesis give indications about possible changes in tundra vegetation composition in response to winter climate change. Evidence for such a response is the change in the performance of single species (chapters 3 and 5), their interactions with neighbours (chapter 4), and short-term changes in abundance (chapter 6) in response to manipulations of the snow cover. Furthermore, changes in the vegetation composition after long-term modifications of the snow cover on ski pistes have been found in alpine ski areas (chapter 7). Overall, the findings give some indications, which species could possibly be affected in abundance, and why.

Changes in mortality, growth and fitness can in the longer term lead to a shift in species abundance, and eventually, species occurrence. Mortality was low in total, as our manipulations were probably subtle enough to not damage plants lethally. Only one species at the subarctic site showed a significantly increased mortality after early snowmelt (chapter 3).

In alpine tundra, first changes in species abundance were already detected within two years of the start of experimental modifications of the snow cover (chapter 5). The temporal niche of a species, i.e. the timing of its phenological development in relation to the snowmelt timing, is a characteristic that could define a species' sensitivity to winter climate changes, and thus, influence its fate in a changing climate. In the snowmelt experiments at the subarctic site (chapter 3), the phenology of early-developing species was more controlled by snowmelt date than that of later-flowering ones. The high synchrony with snowmelt timing could be an advantage in a future climate with earlier snowmelt, if early-developing species can use the prolonged growing season for growth and resource allocation. If an earlier snowmelt is accompanied by a higher frost occurrence, however, the early development might be a disadvantage due to increased frost damages, as shown in chapter 5. Under a climate scenario with a delayed snowmelt, which is the opposite of that predicted for many arctic and alpine regions, such mechanisms seem to play a role, too. On ski pistes with several years of delayed snowmelt due to artificial snow (chapter 7), the abundance of early-flowering species was reduced, while later-flowering species had increased.

The ecological niche of a species along the natural snow cover gradient could be an indicator of how the species will behave under a changed winter climate and snow cover regime. Out of the 11 species at two sites investigated in this thesis, only one responded positively to advanced snowmelt (see chapter 5). This species, *Loiseleuria procumbens*, is a dominant species of "wind-edges", which in alpine tundras represent the "low" extreme along a snow cover gradient (in terms of shallow or no snow cover in winter). More evidence for this hypothesis was found in the review of productivity in arctic and alpine communities in response to delayed snowmelt (chapter 2). Communities with natural snowmelt timing early in the year responded negatively to added snow and delayed snowmelt. In contrast, the communities towards the centre of the natural snowmelt gradient, i.e. with later natural snowmelt timing, increased their productivity. Similarly, our ski piste survey (chapter 7) revealed that character species from "wind-edges" decreased due to the application of artificial snow. Species and communities at the low extreme of the snow gradient hence might cope well with the harsh conditions and high environmental stress of a habitat characterized by little winter snow cover, but they seem to be negatively affected by deep snow covers and/or late snowmelt. Species from the opposite end of the snowmelt gradient, i.e. from snowbeds, were not among the species studied in our snow manipulation experiment. On ski pistes, however, they increased in cover in response to added artificial snow.

The results of the neighbour removal experiments (chapter 4) showed that negative and positive neighbour interactions were both of similar importance in subarctic tundra ecosystems. Under the harsher conditions of an earlier snowmelt followed by relatively cold weather, the net neighbour effect shifted from neutral to positive, i.e. the positive effects of having neighbours that ameliorate the growing conditions through a closed canopy was more important than the negative effect of competition for resources. A higher importance of positive neighbour interactions with increasing climatic stress in higher altitudes or wind exposed sites, had also been found in a series of experiments in arctic and alpine ecosystems (Callaway *et al.*, 2002; Choler *et al.*, 2001; Olofsson, 2004). Our study is the first, however, to show that changes in the snow cover can shift the balance between positive and negative neighbour interactions. Species interactions are important drivers of ecosystem composition, and higher facilitation correlates with higher species richness and a non-random, clumped distribution of individual species in a community (Kikvidze *et al.*, 2001). If the climatic stress and the changed balance between competition and facilitation persist under climate change, we would expect the species composition to change in the long-term, especially through the establishment of species that are poor competitors and an increase in species numbers.

Outlook: future research needs

Climatology

Predictions of future rises in temperature, and in some regions also of precipitation, are relatively accurate and spatially explicit. In contrast, predictions of future snow cover and winter climates are vague. However, regional climate scenarios that include specific predictions of the amount of winter precipitation, snow cover depths, or snowmelt timing are necessary to imitate future climates and explore the ecosystem reactions to winter climate change. Such predictions would greatly help climate change ecologists to choose the most relevant climate scenarios for their field experiments (see chapter 2).

Besides an increased regional resolution of climate predictions and an augmented focus on snow cover processes, the implementation of “ecosystem-relevant” climate variables is of great need. Climate variables are mostly given in a monthly, seasonal or annual resolution, which is indispensable for the detection of climate changes over time, or for comparisons between regions. Although also often used by ecologists, these variables are not particularly useful to understand the interactions between climate and ecosystem processes in arctic and alpine regions characterized by a seasonal snow cover. To describe the climatic conditions that a tundra community experiences, and to compare them over time and between sites, the period between snowmelt and snow cover formation is of highest relevance. An “ecosystem-relevant” temporal resolution of climate variables should therefore at least include information about the start, length, and temperature conditions of the snow-free season. An example how temperature indices can vary between calendar dates and “ecosystem-relevant” time periods is given in Table 1. Mean temperatures over the snow-free period, within which most vegetation processes occur, have been warming at only half the rate compared to summer mean temperatures over a fixed 3-month summer period at our Swiss study site. The reason probably is that the snowmelt timing had also advanced within the same period, gradually extending the period of measurement, and shifting the start of the snow-free season to an earlier, usually cooler time of the year.

Table 1: Increasing mean summer and growing season temperatures from 1975 to 2005 at the Stillberg research site (2090m asl, Davos, Switzerland). Means over the climatic summer quarter (1 June to 31 August) and the snow-free period (on average from end of May to mid-October) were calculated from a 30-year record of daily mean temperature and snow depth. For further climate indices and correlations of the same station, see chapters 2 and 5.

Period of temperature mean	Rate of change 1975-2005	P (linear regression)
Climatic summer period	0.75°C / decade	>0.001
Snow-free period	0.39°C / decade	0.036

Ecology

Various ecosystem processes have been shown to respond to changes in winter climate (chapter 2). These findings have been obtained from a growing number of experiments in different regions and ecosystems, but still, many research questions are unexplored. Ecological processes that could significantly change under a changed winter climate are the interactions and feedbacks between above- and belowground processes, the interactions of plants with their specific pollinators, herbivores, pathogens, or plant neighbours, or the nutrient and carbon cycling between soil microbes, plants and litter. As in all ecological experiments, the results obtained from short-term experiments should possibly be verified by comparing them with results from long-term manipulations, from natural snow cover gradients, or by carrying on the experiments for a longer duration. Future experiments simulating winter climate change should take care to mimic an explicitly stated snow cover scenario, which is relevant (in its direction and magnitude) for the biome and region where it is set up. Especially studies that deal with reduced snow covers and advanced snowmelt are still rare, although this scenario is realistic for many regions. As not only winter, but also year-round climate is subject to change, experiments that factorially manipulate both summer and winter conditions, and their interactions, would be of great value. Such well-designed experiments might require winter fieldwork and knowledge in snow science, and they are relatively laborious and difficult to carry out, thus, an interdisciplinary approach, bringing together researchers from various fields of ecological science, climatology and hydrology, would be extremely valuable.

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Zusammenfassung und Schlussfolgerungen

Im Zuge des globalen Klimawandels haben sich in den letzten Jahrzehnten die Temperatur- und Niederschlagsmuster vieler Regionen stark verändert. Die Veränderungen, vor allem der Temperaturanstieg, war stärker im Winter als im Sommer, und Gebiete hoher Breiten und Höhen waren überdurchschnittlich stark betroffen. Pflanzenwachstum und Ökosystemprozesse in solch arktischen und alpinen Gebieten sind stark durch das rauhe Klima bestimmt und begrenzt. Bei verrändertem Klima erwartet man entsprechend eine rasche Reaktion des Pflanzenwachstums, der Zusammensetzung sowie der Prozesse in arktischen und alpinen Ökosystemen. Viele Studien haben Auswirkungen von wärmeren Sommertemperaturen auf diese Ökosysteme untersucht; über die Auswirkungen eines veränderten Winterklimas ist allerdings erst wenig bekannt.

Diese Dissertation hat zum Ziel, die kurzfristigen Auswirkungen von winterlichen Klimaveränderungen auf subarktische und alpine Zwergstrauchheiden (im Folgenden „Tundra“ genannt) zu erforschen und zu verstehen. Zu diesem Zweck wurden Schneehöhen und Ausaperungsdaten (d.h. Datum, wann die Schneedecke geschmolzen ist) experimentell verändert. Auswirkungen dieser Manipulationen wurden auf der Stufe „Art“ (Überleben, Phänologie, Wachstum und Reproduktion der häufigsten Arten), der Stufe „Interaktionen“ (zwischen benachbarten Pflanzen, zwischen Pflanzen und Herbivoren), der Stufe „Ökosystem-Prozesse“ (Biomasse-Abbau, Kohlenstoff- und Nährstoffumsatz), und der Stufe „Artenzusammensetzung der Vegetation“ erfasst.

Auswirkungen auf einzelne Arten

Unterschiede in der Phänologie (d.h. dem zeitlichen Ablauf der jährlichen Entwicklung) nach veränderter Ausaperung waren die offensichtlichsten Reaktionen der Tundrapflanzen. Anfängliche phänologische Unterschiede zwischen verschiedenen Ausaperungsbehandlungen verschwanden allerdings im Lauf der Vegetationsperiode, einerseits, weil früh im Jahr entwickelnde Arten stärker reagierten, andererseits, weil in jeder Art die frühesten Entwicklungsstadien am meisten reagierten.

In vielen bisherigen Studien wurde ein früherer Beginn der phänologischen Entwicklung als positiv für die Pflanzenfitness gewertet, da dann eine längere Zeit für Wachstum und Nährstoffspeicherung zur Verfügung steht. In unseren Experimenten reagierte allerdings nur eine von insgesamt 11 untersuchten Arten positiv auf verfrühte Ausaperung (gemessen als Triebwachstum). Während am subarktischen Standort keine Wachstumsreaktionen gefunden wurden, reagierten am alpinen Standort 4 von 6 Arten negativ auf frühere Ausaperung. Eine detaillierte Analyse der kausalen Beziehungen zwischen Ausaperungsdatum, Phänologie, Frösten und Temperaturbedingungen und Pflanzenwachstum ergab, dass das Zusammenspiel dieser Variablen relativ komplex ist und je nach Art variiert. Der Zeitpunkt des Wachstumsbeginns sowie die Temperaturen während des Wachstums hatten grossen Einfluss auf die resultierende Trieblänge. Fröste beeinflussten den Zeitpunkt des Wachstumsbeginns, aber direkte negative Einflüsse auf die Trieblänge wurden nur bei einer Art gefunden, obwohl in einem der beiden Studienjahren grosse Frostschäden an Blättern und Blüten festgestellt wurden - anscheinend hatten diese aber keine negativen Konsequenzen für das Wachstum.

Da sich die meisten der untersuchten Arten vornehmlich vegetativ fortpflanzen, sind die Auswirkungen von Klimaänderungen auf das Wachstum als kurzfristig wichtiger einzustufen als diejenigen auf die sexuelle Reproduktion. Langfristig ist sexuelle Reproduktion in einem sich ändernden Klima jedoch äusserst wichtig, da die Samenproduktion einerseits zur Ausbreitung einer Art und zum Erreichen neuer Habitate beiträgt, und andererseits eine genetische Anpassung an neue Lebensbedingungen erlaubt. Die Fekundität war bei den meisten Arten nicht von den experimentellen Schneedeckenänderungen beeinflusst. Wurde eine Reaktion gefunden, war sie entweder negativ nach verfrühter Schneeschmelze (zwei alpine Arten) oder positiv nach verspäteter Schneeschmelze (zwei subarktische Arten).

Auswirkungen auf Interaktionen zwischen Organismen

Positive Interaktionen zwischen benachbarten Pflanzen (Facilitation) wurden in der subarktischen Tundra ausgeprägter nach verfrühter Schneeschmelze, während sich in den Kontrollplots positive und negative Interaktionen die Waage hielten. Negative und positive Interaktionen zwischen Pflanzennachbarn haben Auswirkungen auf die Zusammensetzung einer Pflanzengesellschaft (siehe Paragraph „Artenzusammensetzung“).

Die chemischen Inhaltsstoffe und der Nährstoffgehalt von untersuchten Blättern waren durch die veränderte Ausaperung beeinflusst. Dies kann die Interaktionen zwischen Pflanzen und Herbivoren beeinflussen, was in dieser Studie als verminderte Frassschäden (von Insekten) an den nährstoffärmeren Blättern aus verfrüht schneefreien Plots zutage trat.

Weitere wichtige Interaktionen zwischen Pflanzen und Tieren betrifft das Zusammenspiel von Blüten und Bestäubern, welches durch die sich verschiebende Ausaperungs- und Blühzeitpunkte verändert werden könnte. Darüber hinaus bilden die Früchte einiger untersuchter Arten (Heidelbeeren, Preiselbeeren etc.) eine wichtige Nahrungsgrundlage für Tiere und Menschen. Zusammengefasst sind Interaktionen zwischen Pflanzen oder zwischen Pflanzen und Tieren wichtige Bestandteile von Tundra-Ökosystemen, und ihre Veränderung durch ein sich änderndes Klima könnte Auswirkungen auf die Zusammensetzung und die Nahrungsketten dieser Lebensgemeinschaften haben.

Auswirkungen auf Kohlenstoffkreisläufe

Eine wichtige Frage betreffend Klimawandel und arktisch-alpinen Ökosystemen ist, ob Tundren unter zukünftigem Klima Kohlenstoff-Senken bleiben (d.h. mehr Kohlenstoff aufnehmen als abgeben), oder ob sie sich in Kohlenstoff-Quellen entwickeln und dadurch den Treibhauseffekt weiter verstärken. In dieser Studie wurde der Einfluss einer veränderten Schneedecke auf den Biomasseabbau, einem wichtigen Prozess im Kohlenstoffkreislauf, experimentell untersucht.

Die Schneedecke beeinflusste den Abbau von Blattstreu auf zwei Arten: Erstens war die Abbaurate der Streu stark durch die Bodentemperaturen unter der Schneedecke gesteuert (je kälter desto langsamer). Die Temperaturen wiederum waren stark abhängig von der Mächtigkeit der Schneedecke, d.h. weniger Schnee bewirkte kältere Bodentemperaturen und weniger Streuabbau. Zweitens war die Abbaubarkeit der Blätter abhängig vom Ausaperungszeitpunkt im Frühling (bevor diese Blätter produziert wurden). Dass Blätter nach verfrühter Ausaperung schlechter abbaubar waren als solche nach später, könnte mit der Blattgrösse und dem Stickstoffgehalt zusammenhängen. Eine schlechtere Biomasse-Abbaubarkeit nach früher Schneeschmelze und ein langsamerer Abbauprozess unter dünnen Schneedecken könnten zusammen den Kohlenstoffzyklus von Tundra-Ökosystemen bremsen und den Ausstoss von CO_2 verringern, würden andererseits aber auch den Nährstoffkreislauf verlangsamen.

Auswirkungen auf die Artenzusammensetzung

Die vorliegende Studie gibt verschiedene Hinweise dazu, wie sich die Artenzusammensetzung der Tundravegetation unter veränderten Winterbedingungen verändert. Hinweise darauf kommen von den untersuchten Reaktionen einzelner Arten, der Interaktionen zwischen Arten und der Abundanz von Arten auf veränderte Schneedeckeneigenschaften. Darüber hinaus geben Vegetationsveränderungen auf Schipisten Informationen darüber, wie die Vegetation auf Schneeveränderungen über längere Zeitperioden reagiert. Diese verschiedenen Resultate erlauben erste Schlüsse, welche Arten wohl am ehesten zu- oder abnehmen würden. Vegetationsveränderungen könnten relativ rasch eintreten, so waren nach zweijähriger Schneemanipulation in der alpinen Tundra schon erste Veränderungen in der Abundanz einzelner Arten zu verzeichnen.

Die zeitliche Nische einer Art (d.h. der Zeitpunkt ihrer Entwicklung), könnte eine der Charakteristiken sein, welche die Sensibilität gegenüber Schneedeckenveränderungen bestimmt. Die Phänologie von sich früh entwickelnden Arten war stärker durch das Schneeschmelzdatum beeinflusst als diejenige von sich später entwickelnden. Dies könnte in einem zukünftigen Klima dann ein Vorteil sein, wenn diese Arten die längere Vegetationszeit effizienter nutzen können. Wenn sich allerdings nach früherer Schneeschmelze häufiger Frühfröste einstellen, könnte eine frühe phänologische Entwicklung eher nachteilig sein und zu vermehrten Frostschäden führen. Im Falle von Langzeitveränderungen der Schneedecke auf Schipisten, wo durch hinzufügen von Kunstschnee die Ausaperung verzögert wurde, spielte die zeitliche Nische eine Rolle: frühblühende Arten nahmen ab und spätblühende zu.

Die ökologische Nische einer Art, vor allem bezogen auf ihr natürliches Vorkommen im Bezug auf besondere Schneedeckencharakteristika, könnte weitere wertvolle Hinweise zu ihrer Sensitivität auf Klimaveränderungen sein. Nur eine Art von 11 untersuchten reagierte positiv auf verfrühte Ausaperung, und diese Art, *Loiseleuria procumbens* (Alpenazalee) ist eine typische Bewohnerin von Windheiden, d.h. windgefegte Standorte, an denen sich oft keine mächtige, dauerhafte Schneedecke ausbildet. Arten, die an solche Standorte angepasst sind und gut mit deren rauhem Klima zurechtkommen, scheinen auf eine sehr lange Vegetationszeit angewiesen zu sein: in einer Übersicht über experimentelle Schneemanipulationen in anderen arktischen oder alpinen Gegenden der Welt war ersichtlich, dass gerade solche natürlicherweise früh ausapernden Standorte mit verminderter Produktivität auf künstlich verlängerte Schneebedeckung reagierten, während Standorte mit mittlerer Schneebedeckung positiv darauf reagierten. In die gleiche Richtung gehen die Vegetationsveränderungen auf Schipisten: typische Arten von extrem schneereichen und spät ausapernden Standorten (Schneetälchen genannt) nahmen bei Anwendung von Kunstschnee (welche die Ausaperung verzögert) zu, aber Windheidearten ab.

Negative und positive Interaktionen zwischen Pflanzennachbarn waren in subarktischer Tundra ähnlich wichtig, hielten sich also die Waage. Nach verfrühter Ausaperung war jedoch die positive Wirkung von benachbarten Pflanzen (die wahrscheinlich aus einem verbesserten Mikroklima in einer geschlossenen Vegetationsdecke bestand) grösser als die negative (v.a. Konkurrenz). Negative und positive Interaktionen zwischen Pflanzenarten sind wichtig Einflussgrössen auf die Vegetationszusammensetzung. Nach einer Änderung von neutralen zu positiven Nachbarschaftseffekten könnte man mit der Zeit eine Veränderung der Artenzusammensetzung erwarten, beispielsweise durch die Etablierung oder Zunahme konkurrenzschwacher Arten.

Weiterer Forschungsbedarf

Bedeutende Lücken bei der Erforschung der Interaktionen zwischen Klimawandel, Schnee und Ökosystemen bestehen auf Seiten der Klimatologie und der experimentellen Ökologie. Die Voraussagen über zukünftige Winterklima, Schneemengen und Ausaperungsdaten sind momentan noch zu wenig genau und hoch aufgelöst, um realistische Szenarien für einzelne Regionen und Höhenstufen abzulesen. Ein weiteres Problem besteht darin, dass ökologisch relevante Variablen oft nicht verfügbar sind. Klimavariablen sind oft als monatliche, vierteljährliche oder jährliche Werte angegeben, um den Vergleich zwischen Jahren und Regionen zu ermöglichen. Um die Wachstumsbedingungen von arktischen und alpinen Pflanzen zu beschreiben und zu vergleichen, müssten auch Informationen über den Beginn, das Ende und die Temperaturen während der schneefreien Zeit bekannt sein.

Trotz der steigenden Zahl von Studien zur Interaktion zwischen Schneedecke und Pflanzen in verschiedenen Ökosystemen sind viele Forschungsfragen offen. Speziell sind Ökosystemprozesse, welche sich über mehrere ökologische Disziplinen erstrecken, im Zusammenhang mit dem sich ändernden Winterklima schlecht oder nicht erforscht. Beispielsweise können die Interaktionen zwischen ober- und unterirdischen Wachstumsprozessen, zwischen Pflanzen und Bestäubern, Herbivoren oder Pathogenen, oder die Nährstoff- und Kohlenstoffkreisläufe und –aufteilung zwischen Pflanzen und Bodenmikroorganismen stark durch die veränderte Schneedecke beeinflusst sein. Eine weitere

Lücke besteht bei den Langzeitversuchen. Die meisten bisherigen Experimente erstreckten sich über ein oder wenige Jahre, und deshalb nur in beschränktem Mass Schlüsse über langfristige Veränderungen bei Klimaveränderung zulassen. Solche Resultate könnten durch Vergleiche mit Messungen in Langzeitversuchen oder entlang natürlicher Klimagradienten jedoch unterstützt und verifiziert werden.

Die wenigen bekannten Langzeitexperimente simulieren eine wesentlich mächtigere Schneedecke und verspätete Ausaperung. Experimente, in denen die Schneedecke reduziert wurde und/oder früher wegschmolz, dauerten bisher nie länger als zwei Jahre, obwohl dieses Szenario in vielen Regionen realistischer wäre. Natürlich ist nicht nur das Winterklima in Veränderung begriffen. Experimente, die faktoriell sowohl sommerliche wie auch winterliche Klimaveränderungen simulieren, wären deshalb sehr wertvoll. Solche Experimente wären allerdings sehr aufwändig und würden am besten in interdisziplinären Projekten durchgeführt, welche neben verschiedenen ökologischen Fachrichtungen auch WissenschafterInnen aus der Klimatologie, Hydrologie und Schneeforschung miteinbeziehen.

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