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A review of snow manipulation experiments in Arctic and alpine tundra ecosystems

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Abstract

Snow cover is one of the most important factors controlling microclimate and plant growing conditions for Arctic and alpine ecosystems. Climate change is altering snowfall regimes, which in turn influences snow cover and ultimately tundra plant communities. The interest in winter climate change and the number of experiments exploring the responses of alpine and Arctic ecosystems to changes in snow cover have been growing in recent years, but their outcomes are difficult to summarize because of the large variability in manipulation approaches, extents and measured response variables. In this review, we (1) compile the ecological publications on snow manipulation experiments, (2) classify the studies according to the climate scenarios they simulate and response variables they measure, (3) discuss the methods applied to manipulate snow cover, and (4) analyse and generalize the response in phenology, productivity and community composition by means of a meta-analysis. This meta-analysis shows that flowering phenology responded strongly to changes in the timing of snowmelt. The least responsive group of species were graminoids; however, they did show a decrease in productivity and abundance with experimentally increased snow covers. The species group with the greatest phenological response to snowmelt changes were the dwarf shrubs. Their abundance also increased in most long-term snow fence experiments, whereas species richness generally declined. We conclude that snow manipulation experiments can improve our understanding of recently observed ecosystem changes, and are an important component of climate change research.

Keywords

Meta-analysis; plant phenology; productivity; snow fence; snow removal; winter ecology.

Seasonal snow cover is a characteristic feature of most Arctic and alpine regions. Generally snow covers soil and plants for more than half of the year, and during this period determines important environmental variables such as soil temperatures and freezing depth, which in turn control various ecosystem processes. The melting of the snow cover defines the start and length of the summer growing season, and water and nutrients released from the snow pack influence soil moisture and nutrient status until later in the summer. Thus, the snow cover directly and indirectly impacts ecosystems in various ways, and its influence is not restricted to the winter season.

Arctic and alpine regions are among the most affected by climatic change (Symon et al. 2005; Solomon et al. 2007). Earlier snowmelt dates, decreased snow depths and an increasing proportion of winter precipitation falling as rain instead of snow have been recorded in the Arctic (Frei et al. 1999; Brown 2000; Serreze et al. 2000) and in mountain areas (Beniston 1997; Laternser & Schneebeli 2003; Mote et al. 2005; Marty 2008). Many Arctic and high-mountain areas have not (yet) experienced a significant change in the quantity of winter precipitation and in snow depth, but most regions are seeing an earlier melt-out resulting from warmer spring temperatures (Solomon et al. 2007). Climate change scenarios are rather vague about future snow conditions. In the future, the quantities of snow might increase in the Arctic and some continental mountain ranges because of rising levels of winter precipitation (Saha et al. 2006; Solomon et al. 2007). Lower altitudes and oceanic mountain ranges, however, might experience a decrease in the snow-to-rain ratio because of warmer winter temperatures. Regardless of the quantity of precipitation, such
regions could face a decline in snow cover and an advance in snowmelt timing (Lapp et al. 2005; Henry 2008).

With anthropogenic climate change, interactions between snow and Arctic and alpine plants have received increasing attention in the past two decades, and have been addressed in numerous studies; however, they have not yet been analysed in a comprehensive review. The purpose of this review is to compile publications on snowmelt manipulation experiments, and to generalize their findings about how snowmelt affects plant phenology and productivity. In particular, we will compile the publications on snow manipulation experiments with a focus on plant ecological responses, and will classify these studies according to the climate scenarios they actually simulate, then discuss the methods used for the snow manipulation, and finally analyse and generalize the response in phenology and productivity by means of a meta-analysis.

**Scenarios and methods used in snow manipulation experiments**

Table 1 lists existing publications on snowmelt experiments and their main characteristics, such as the start and duration of the experiment, the method used, the direction and extent of the snow manipulation, the characteristics of the natural snow cover, the climate scenarios applied and the response variables measured. We limited our list and review to studies with snow manipulation treatments that were performed in Arctic and alpine tundra, that investigated plant and vegetation responses, and in which the experimental treatments were not confounded with other climate change manipulations. Thus, studies from montane and boreal forest ecosystems (e.g., Boutin & Robitaille 1995; Groffman et al. 1999) and studies that focus on soil responses and experiments with all-summer warming treatments that start by melting the snow early (Harte et al. 1995) were not included.

In the 39 publications, 22 experiments from alpine and sub-alpine and 19 from Arctic and sub-Arctic ecosystems were described. Although most (22) publications report on experiments that had been running for 1–2 years, Smith et al. (1995) described vegetation changes caused by a snow fence over 32 years. Established in 1959, this experiment in alpine New Zealand probably holds the record for the oldest continuously running snow ecology experiment. Of the experiments reviewed, 23 delayed snowmelt, eight advanced it and eight did both. In addition to the snowmelt treatment (and not confounded with it), a warming treatment was applied in 14 experiments, mainly in Arctic ecosystems.

The snow manipulation experiments listed in Table 1 can roughly be categorized into three types, differing in the climate scenarios they actually simulate: increased snow and/or delayed snowmelt; earlier snowmelt; and earlier snowmelt combined with a summer warming treatment. Each of these three scenarios are discussed below.

**Increased snow and/or delayed snowmelt**

Increased winter precipitation in the form of snow is expected in most Arctic regions (Solomon et al. 2007), and also in some high-alpine regions (OC^CC Consortium 2007), in future decades. With the concurrent warming trend, however, the deeper snowpack is likely to melt faster, and therefore snowmelt may not be considerably delayed. Most snow manipulation experiments that simulated increased quantities of snow have done so by accumulating wind-drifted snow, e.g., behind snow fences or within open-top chambers (OTCs). Once installed, these experiments do not require the presence of researchers over winter, which may partly explain the fact that more than half of the experiments reviewed for this paper applied this method. However, as the accumulated snow will take longer to melt, it must be carefully considered whether a postponed snowmelt date is an appropriate climate scenario for a given region. Alternatively, a spring warming treatment may be applied to speed up snowmelt (e.g., by using OTCs, as in Abisko, see below). In addition, a methodological flaw of snow fences is that they can trap wind-drifted litter in their lee (Fahnestock et al. 2000), thus increasing the nutrient influx.

**Earlier snowmelt**

An increased occurrence of midwinter thawing events and less winter precipitation in the form of snow (because of above-zero winter temperatures) have already become apparent in some oceanic and continental mountain regions (Rikiishi et al. 2004; Scherrer et al. 2004; Mote et al. 2005). The effects on environmental conditions that ecosystems experience are two-fold. If snow depth remains below a certain threshold (Sturm et al. 1997), soil frosts and the frequency of freeze–thaw cycles could increase and induce “colder soils in a warmer world” (Groffman et al. 2001). Moreover, a thinner snow cover will cause snow to melt more quickly, shifting the growing season towards an earlier, usually colder time of the year, unless this is compensated by a strong warming trend. In experiments, the scenario of less snow is most frequently created by either manipulating snow depths manually (i.e., shovelling away snow) or by increasing...
Table 1 Summary of the snow manipulation experiments reviewed in this article. If available, we give information about the manipulation applied, the extent of the manipulation and the characteristics of the natural snow cover. We divided the studies into three scenarios according to the winter climate they simulated, and give a short indication of the response variables 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.

<table>
<thead>
<tr>
<th>Study details and characteristics</th>
<th>Climate manipulations</th>
<th>Snow cover/snowmelt characteristics</th>
<th>Scenario</th>
<th>Response variables recorded</th>
</tr>
</thead>
<tbody>
<tr>
<td>Study author &amp; year</td>
<td>Biome</td>
<td>Elevation (m a.s.l.)</td>
<td>Start of experiment</td>
<td>Duration of study (years)</td>
</tr>
<tr>
<td>Abisko OTC</td>
<td></td>
<td>Ni&lt;sup&gt;c&lt;/sup&gt;</td>
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<td>2</td>
</tr>
<tr>
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<td>Ni</td>
<td>2000</td>
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<td>Ni</td>
<td>2000</td>
<td>2</td>
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<td>sub-Arctic</td>
<td>Ni</td>
<td>2000</td>
<td>2</td>
</tr>
<tr>
<td>Abisko snow fence</td>
<td></td>
<td>Ni</td>
<td>2000</td>
<td>2</td>
</tr>
<tr>
<td>Seastedt &amp; Vaccaro (2001)</td>
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<td>3500</td>
<td>1994</td>
<td>4</td>
</tr>
<tr>
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<td>3500/700</td>
<td>1994</td>
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<tr>
<td>Pennsylvania Mountain</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Galen &amp; Stanton (1993)</td>
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<td>3750</td>
<td>1991</td>
<td>1</td>
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<tr>
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<td>3750</td>
<td>1991</td>
<td>3</td>
</tr>
<tr>
<td>Galen &amp; Stanton (1999)</td>
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<td>3750</td>
<td>1991</td>
<td>4</td>
</tr>
<tr>
<td>Rocky Mountain meadow experiment</td>
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<td>ca. 3000</td>
<td>1996</td>
<td>3</td>
</tr>
<tr>
<td>Dunne et al. (2004)</td>
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<td>ca. 3000</td>
<td>1996</td>
<td>3</td>
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<tr>
<td>Saavedra (2002)</td>
<td>alpine</td>
<td>ca. 3000</td>
<td>1996</td>
<td>2</td>
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<tr>
<td>Stinson (2004)</td>
<td>alpine</td>
<td>ca. 3000</td>
<td>1996</td>
<td>2</td>
</tr>
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<td>Study details and characteristics</td>
<td>Climate manipulations</td>
<td>Snow cover/snowmelt characteristics</td>
<td>Scenario</td>
<td>Response variables</td>
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<tr>
<td>Study author &amp; year</td>
<td>Biome</td>
<td>Elevation (m a.s.l.)</td>
<td>Start of experiment</td>
<td>Duration of study (years)</td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Stinson (2005)</td>
<td>alpine</td>
<td>2700/3700</td>
<td>1996</td>
<td>2</td>
</tr>
<tr>
<td>Toolik snow fence</td>
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<td></td>
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</tr>
<tr>
<td>Borner et al. (2008)</td>
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<td>700</td>
<td>1994</td>
<td>1</td>
</tr>
<tr>
<td>Fahnestock et al. (2000)</td>
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<td>700</td>
<td>1994</td>
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</tr>
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<td>Wahren et al. (2005)</td>
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<td>700</td>
<td>1994</td>
<td>8</td>
</tr>
<tr>
<td>Walker et al. (1999)</td>
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<td>700</td>
<td>1994</td>
<td>1</td>
</tr>
<tr>
<td>Welker et al. (2005)</td>
<td>Arctic</td>
<td>700</td>
<td>1994</td>
<td>1</td>
</tr>
<tr>
<td>Toolik snow fence</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>La Puma et al. (2007)</td>
<td>Arctic</td>
<td>760</td>
<td>1995</td>
<td>1</td>
</tr>
<tr>
<td>Starr et al. (2000)</td>
<td>Arctic</td>
<td>760</td>
<td>1995</td>
<td>2</td>
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<tr>
<td>Starr et al. (2008)</td>
<td>Arctic</td>
<td>760</td>
<td>1995</td>
<td>3</td>
</tr>
<tr>
<td>Glas Maol snow fence</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Scott et al. (2007)</td>
<td>Alpine</td>
<td>1000</td>
<td>1986</td>
<td>17</td>
</tr>
<tr>
<td>Welch et al. (2005)</td>
<td>Alpine</td>
<td>1000</td>
<td>1986</td>
<td>17</td>
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<tr>
<td>Stillberg snow manipulation</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wipf (2006)</td>
<td>sub-Alpine/alpine</td>
<td>900</td>
<td>2003</td>
<td>1</td>
</tr>
<tr>
<td>Wipf et al. (2009)</td>
<td>alpine</td>
<td>2200</td>
<td>2004</td>
<td>2</td>
</tr>
<tr>
<td>Other experiments</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bell &amp; Bliss (1979)</td>
<td>alpine</td>
<td>3600</td>
<td>1971</td>
<td>1</td>
</tr>
</tbody>
</table>
The superscript numbers after the response variables indicate that data were used in the meta-analysis of: 1 phenology, 2 total vegetation biomass or 3 species productivity.

- Advanced or decreased;
- Delayed or increased.

a Open-top chamber.
b NI, no information available.
c Personal communication.
d NA, not applicable.
snowmelt rates (i.e., using dark cloth covers to accelerate snowmelt) in spring. In general, these two methods are the most flexible in terms of the snowmelt scenarios that can be simulated, and can also be used to delay snowmelt (by increasing snow depth or using reflective cloth covers). However, there is a risk of unwanted side effects, such as snow compaction or changes in the level of light penetrating the snowpack. Moreover, these techniques are generally labour intensive, and require the labour to be performed near natural snowmelt, which varies from year to year and cannot be predicted far in advance. Another type of experiment transplants plants and soil between sites with different snow cover characteristics. Scenarios are limited to currently existing snow regimes, which are often persistent between years (Buus-Hinkler et al. 2006; Edmonds et al. 2006). Plot sizes are usually small (below 1 m²), and the transplanting poses a significant disturbance to the ecosystem. Extensive replication and the use of true controls, i.e., comparing plots transplanted between sites with those transplanted within sites, can account for these disadvantages.

Earlier snowmelt combined with a summer warming treatment

The most realistic scenario for probably most Arctic and alpine regions is the combination of experimentally advanced snowmelt and spring and summer warming. In experiments, this scenario is simulated by applying a warming treatment that starts before the snow has melted, and therefore accelerates and advances snowmelt. To date, this scenario has only been addressed in a relatively small number of studies, mostly using OTCs (Table 1). With the use of overhead infrared heaters or heating cables, such experiments are now on the increase. However, the responses to earlier snowmelt and to the subsequent warming are not quantified separately in most of these warming experiments. As we focus on snow manipulation treatments in this review, of the studies using scenario 3 we therefore only consider “true” snowmelt experiments, in which snow manipulations were conducted in addition to the warming treatment, and not confounded with it (Table 1).

Meta-analysis

To generalize the response patterns found in snow manipulation experiments, we analysed the response of target species (phenology, growth and productivity) or species groups (total productivity and vegetation composition) to snowmelt manipulation in a meta-analysis using results from subsets of the studies listed in Table 1. From data reported in texts, tables or figures, we calculated the treatment effects (i.e., our response variable) as the percentage deviation from controls (Dormann & Woodin 2002). A classical meta-analysis approach, which expresses effect size as multiples of standard deviations, was not possible because too few experiments published the information necessary for these calculations. Furthermore, the number of studies did not allow testing for effects of regions, community types or duration of the experiment. However, the studies are distributed widely across regions and communities, and therefore allow generalizations. We collected a data set of 66 species and year combinations of flowering phenology and 38 of species productivity (Table 2). In addition, we analysed 18 cases where the response in above-ground productivity of the whole plant community was reported. For the meta-analysis of the phenology data, both results from experiments with advanced and delayed snowmelt could be used. Most experiments that reported above-ground vegetation productivity or productivity of target species had applied a snow fence approach, and thus delayed snowmelt. For the analysis of this productivity data, we therefore excluded the very few studies with advanced snowmelt to obtain a balanced design.

The flowering phenology was indicated as the average preflowering period in a plot, i.e., the time span between snowmelt and flowering. Flowering was reported as the date of peak flowering in most studies, but in some cases was reported as the date flower buds opened or the date of the appearance of the first flower. Productivity was based on measures of biomass production, but in the cases of some dwarf shrubs it was given as stem elongation or as the dry mass of leaves produced in a year.

We tested with general linear models (glms) whether the response variables were affected by species characteristics (e.g., functional group, sensu Chapin et al. [1994], or flowering timing), and by characteristics of the snow cover and the snow treatment (i.e., natural snowmelt timing or deviation in snowmelt caused by the manipulations). For the analysis of species phenology, we additionally tested for differences in species response to experiments with advanced and delayed snowmelt (see Table 3). For the analysis of vegetation and species productivity, only data from experiments delaying snowmelt were analysed because of a lack of data. The main factors and two-way interactions were initially included in the model, but interactions with $F$ values < 2 were subsequently pooled with the error term (Green & Tukey 1960).

Phenology

Snowmelt is an important threshold to plant activity in habitats with a persistent snow cover. Although some
plants are known to be active under the snow (e.g.,
performing photosynthesis, Starr & Oberbauer 2003;
developing buds, Sørensen 1941; or growing vegetatively,
Kimball & Salisbury 1974), most species only start to
show signs of phenological development after snowmelt.
After manipulations of snowmelt timing, important
stages in the life cycle of plants, such as flowering, were
often reached at a different time of year than usual.
Generally, the length of the prefloration period, i.e., the time
span between snowmelt and flowering, changed as a result
of snow manipulations, showing a certain plasticity
of the phenological development in response to snow-
melt. Typically, the prefloration period became longer
after an advanced and shorter after a delayed snowmelt
(Figs. 1, 2). The slope of the regression over all species
suggests that the prefloration period was shortened or
prolonged by an average of 7.9% per each week that
snowmelt was delayed or advanced, respectively (Fig. 1).
The phenological response to snowmelt variations was
not only influenced by the growth form, but also by the
specific flowering timing of a plant species. In experi-
ments with delayed snowmelt, the later in the season a
plant usually flowered (i.e., the longer the prefloration
period in control plots), the more it was able to accelerate
its life cycle by shortening the prefloration period (Fig. 2).
This pattern was especially pronounced when snowmelt
was delayed very strongly (i.e., by three or more weeks;
Fig. 2). In experiments with advanced snowmelt,
however, the prefloration period was prolonged by about
the same time span in all experiments, regardless of the
timing of a species' flowering (see the regression line
parallel with the 1:1 line in Fig. 2).
Changes in phenology can have considerable conse-
quences for plant fitness. Advanced plant development
after early snowmelt increases the risk of frost damage
(Inouye 2000; Wipf et al. 2009), which can decrease plant
populations directly as a result of die-off (Molau 1997), or
indirectly as a result of negative effects on plant reproduc-
tion or establishment (Inouye 2008). Snowmelt-induced
changes in the phenology can also affect the synchrony of
species with species-specific pollinators or pests (Roy et al.
2004; Inouye 2008). Unfortunately, however, the direct
or indirect links between snowmelt timing, plant phenol-

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**Table 2** Characterization of meta-data sets used for the analysis of species phenology, above-
ground productivity of the total vegetation and of target species in response to manipulations in
snowmelt. Columns indicate the number of species, sites and years that were recorded in a snowmelt
experiment. Data sets with more than one manipulation type or treatment level are specified under
"additional treatments".

<table>
<thead>
<tr>
<th>Phenology</th>
<th>n species</th>
<th>n sites</th>
<th>n years</th>
<th>Additional treatments</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aerts et al. (2004), Aerts et al. (2006)</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Borner et al. (2008)</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>Two snow depth levels</td>
</tr>
<tr>
<td>Dunne et al. (2004)</td>
<td>1</td>
<td>3</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Saavedra (2002)</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Walker et al. (1999)</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Weaver &amp; Collins (1977)</td>
<td>9</td>
<td>1</td>
<td>1–2</td>
<td>Two snow depth levels</td>
</tr>
<tr>
<td>Wipf (2010)</td>
<td>8</td>
<td>1</td>
<td>1</td>
<td>Advanced and delayed</td>
</tr>
<tr>
<td>Wipf et al. (2009)</td>
<td>6</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>

**Above-ground productivity**

| Knight et al. (1979) | 2 | 1 | |
| Seastedt & Vaccaro (2001) | 1 | 1 | |
| Wahren et al. (2005) | 1 | 1 | |
| Weaver & Collins (1977) | 1 | 3 | Two snow depth levels |
| Webber et al. (1976) | 8 | 1 | |

**Productivity of target species**

| Bell & Bliss (1979) | 1 | 2 | 1 |
| Dorrepaal et al. (2006) | 4 | 1 | 2 |
| Knight et al. (1979) | 6 | 1–2 | 1 |
| van der Wal et al. (2000) | 2 | 1 | 1 |
| Weaver & Collins (1977) | 3 | 1 | 2 | Two snow depth levels |
| Wipf et al. (2006) | 2 | 1 | 1 | |
Functional group 3 11.2
Phenology
analysis.
analysed for productivity responses derived from experiments with
included in the analysis of the phenological response, as all the data
ment indicated either advanced or delayed snowmelt, and was only
manipulated and unmanipulated plots (number of days). Snowmelt treat-
melt was calculated as the difference in snowmelt date between
when snow melted in unmanipulated control plots. The deviation in snow-
grasses. Natural snowmelt dates were expressed as the days of the year
when snow melted in unmanipulated control plots. The deviation in snow-
melt was calculated as the difference in snowmelt date between
manipulated and unmanipulated plots (number of days). Snowmelt treat-
ment indicated either advanced or delayed snowmelt, and was only
included in the analysis of the phenological response, as all the data
analysed for productivity responses derived from experiments with
delayed snowmelt. All response variables were log-transformed prior to
analysis.

Table 3 Effects of plant, site and snow manipulation characteristics on
phenology and productivity of tundra vegetation. The responses of the
tree target variables were expressed as percentage change compared
with control plots, and were analysed with general linear models. Details
of the publications where the data was extracted from are indicated in
Tables 1 and 2. Phenology was measured as the prefloration period i.e.,
the duration between snowmelt and flowering). Species were divided into
four functional groups: deciduous and evergreen dwarf shrubs, forbs and
grasses. Natural snowmelt dates were expressed as the days of the year

<table>
<thead>
<tr>
<th>Effect</th>
<th>df</th>
<th>F</th>
<th>P</th>
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<tr>
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<td>ns</td>
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<tr>
<td>Deviation in snowmelt</td>
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<tr>
<td>Prefloration period in control x natural</td>
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<td>2.0</td>
<td>ns</td>
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<td>snowmelt date</td>
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<tr>
<td><strong>Productivity of total vegetation</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Natural snowmelt date</td>
<td>1</td>
<td>1.0</td>
<td>ns</td>
</tr>
<tr>
<td>Deviation in snowmelt</td>
<td>1</td>
<td>0.05</td>
<td>ns</td>
</tr>
<tr>
<td>Error</td>
<td>15</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><strong>Productivity of target species</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Functional group</td>
<td>3</td>
<td>3.4</td>
<td>0.018</td>
</tr>
<tr>
<td>Natural snowmelt date</td>
<td>1</td>
<td>0.02</td>
<td>ns</td>
</tr>
<tr>
<td>Deviation in snowmelt</td>
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<td>0.08</td>
<td>ns</td>
</tr>
<tr>
<td>Natural snowmelt date x deviation in snowmelt</td>
<td>1</td>
<td>4.9</td>
<td>0.033</td>
</tr>
<tr>
<td>Error</td>
<td>33</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

ns, not significant.

gogy and plant fitness are only rarely studied in the context of snow manipulation experiments, and too often phenol-
ology was studied as the sole response variable.

Our meta-analysis, as well as several other studies
(Rixen et al. 2001; Dunne et al. 2003; Rixen et al. 2008)
show that after an experimental delay of snowmelt, treat-
ment and control plots initially show differences in the
phenology, but that these differences diminish over the
course of summer. This means that, depending on
the timing of their life cycle, different species may be
differentially affected by the snowmelt manipulations.
After delayed snowmelt, the date of flowering, and thus,
the time span for fruit maturation, will be changed more
severely in early-flowering species than in late-flowering
ones (Wipf et al. 2006). Moreover, if the snow-free period
is shortened, the overlap of species’ flowering periods
within a community may increase (Molau 1997; Morales
et al. 2005). The consequence—more species flowering
at the same time—seems especially unfavourable for
early-flowering species, as the number and activity of
pollinators is low in early summer (Molau 1997; Wipf
unpubl. data). Whether this could have negative effects
for populations of early-flowering species has, to our
knowledge, not been studied in detail.

Growth and productivity

The response of above-ground productivity of the whole
community was analysed with 18 data sets from snow
manipulation experiments with delayed snowmelt (there
were not enough data from experiments with advanced
snowmelt). Over all the studies, a delayed snowmelt
decreased productivity by 13.1% (one-sample Student’s
t-test, t = −2.4, df = 17, P = 0.03). There was no clear
pattern with regard to natural snowmelt date or to the
level of snow manipulation (Fig. 3, Table 3). The growth
responses of target species to delayed snowmelt differed
between plant growth forms: grasses generally responded
negatively and forbs positively (decrease in productivity by
27% and increase by 30%, respectively; Fig. 4, Table 3),
whereas deciduous and evergreen dwarf shrubs showed
no clear response pattern (Fig. 4). The significant interac-
tion between natural snowmelt and the experimentally
induced delay of snowmelt (Fig. 4, Table 3) suggests that
the growth response of target species was most negative
with later natural snowmelt and longer delays (Fig. 4). In
experiments with a moderate delay in snowmelt,
however, there was no relationship between growth
response and natural snowmelt timing (Fig. 4). The overall negative effect of a delay in snowmelt on
community productivity may be caused by the high
specialization of plant communities growing on either
extreme of a snow cover gradient. The dominating species
from windswept habitats with very early snowmelt, for
instance, are often negatively affected by a long snow lie,
such as certain lichen (Benedict 1990; Welch et al. 2005),
moss (Scott et al. 2007) and sedge species (Bell & Bliss
1979; Wahren et al. 2005). Such species probably suffer
from high respiration losses when winter temperatures are
increased because of deeper snow cover (Bell & Bliss
1979; Walker et al. 1999). In habitats with naturally late
snowmelt, on the other hand, plant growth may be strongly
limited by the short growing season. If the snow-free
season is additionally shortened, productivity is likely to be
further decreased. In the short term, such processes will
merely lead to a reduction in the productivity of single
species, but in the longer term it may lead to a turnover
in species composition (Bell & Bliss 1979; Knight et al.
The few examples of a delayed snowmelt enhancing above-ground productivity were measured at sites with an intermediate snowmelt date (after 6 June in Fig. 3), where the positive effects of the additional snowpack (increased moisture and nutrients, and protection from spring frost events) might outweigh the potentially negative effects of a shortened growing season. Similarly, the productivity of target species was most negatively affected where late snowmelt and a strong experimental delay in snowmelt (>2 weeks; Fig. 4) concurred. It remains unclear whether the same patterns would also hold true when snowmelt was advanced instead of delayed, as productivity data from snow removal experiments are too scarce to be included in the meta-analysis.

Vegetation composition

The abundance of functional groups (lichens, graminoids, forbs and shrub species), and thus the vegetation composition, was considerably affected by snow addition and delayed snowmelt (see Table 4 for the response in species composition of 12 experiments with delayed snowmelt). Lichens and graminoid species (measured as proportion cover or biomass) generally decreased in abundance in response to added snow and late snowmelt, whereas forbs and dwarf shrubs remained neutral or increased in abundance (Table 4). In most studies (six out of eight), species diversity also declined as a result of delayed snowmelt, although not always significantly.
The responses in vegetation composition are generally in line with the growth responses of the functional groups presented above. One explanation for the decline in graminoid species after snow addition may be the increasing competition by woody species in some studies (Scott & Rouse 1995; Wahren et al. 2005). Graminoids also showed the least flexible phenology in response to snowmelt changes in our meta-analysis. Their inability to develop more rapidly after late snowmelt could account for why they were negatively affected in their productivity and, eventually, in their abundance. In several studies of the dry alpine meadows in the Rocky Mountains, one dominant graminoid species, the wind-edge species *Kobresia myosuroides*, showed a very negative response to increased snow (Bell & Bliss 1977; Seastedt & Vaccaro 2001), and thus strongly contributed to the finding that graminoid species declined. The negative reaction of lichens to delayed snowmelt could be expected given that their main habitats are locations with thin snow cover and dry summer conditions (Flock 1978). Whether it is the shortened growing season or the additional water and nutrient input that causes lichens to decline rapidly in snow-addition experiments remains unclear (Benedict 1990). Forbs, which primarily showed a positive growth response to delayed melt-out, also increased in abundance over the longer term. Many species specialized in habitats with long snow cover duration are forbs (Galen & Stanton 1995; Björk & Molau 2007), and these so-called snowbed species were found to benefit from prolonged snow duration in other studies as well (Wipf et al. 2005).

**Conclusions and wider context of snow cover changes**

The meta-analysis of snow manipulation studies can be summarized as follows.
Changes in the prefloration period caused by altered snowmelt timing were most pronounced in early-flowering species. The more that experimental and natural snowmelt differed, the stronger was the change in the prefloration period.

Overall community productivity was decreased by experimentally delayed snowmelt, but plant functional groups differed in their response: forbs were enhanced in growth by later snowmelt, but grasses declined.

Delayed snowmelt caused an overall decline in diversity that was mostly caused by a decline in abundance of lichens and graminoids.

The snow manipulation experiments analysed in this review have demonstrated that changes in snow cover can be immediate and of a similar magnitude as the responses to other crucial climate factors, such as temperature, summer precipitation and CO₂ concentration. Changes in winter snow cover can show impacts that are still visible during the following growing season, thus influencing processes mainly attributed to summer. For instance, the insulation by the winter snowpack can control microbial activity and decomposition rates, and thus the nutrient availability to plants the following summer (Williams et al. 1998; Schimel et al. 2004; Rixen et al. 2008). Furthermore, altered winter snow cover can affect growing season soil moisture, which interacts with the effects of summer temperatures, especially in regions with low summer precipitation (Walker et al. 1999; Chinner & Welker 2005). In fact, tundra biomass productivity (measured as maximum normalized difference vegetation index in summer) was enhanced after winters with deep snow cover and late snowmelt in Siberia, regardless of the summer climate, which is attributed to higher nutrient and water availability (Grippa et al. 2005). Early snowmelt followed by cold spring temperatures, on the other hand, reduced tundra productivity (Stow et al. 2004) and boreal tree growth (Kirdyanov et al. 2003). In ecosystems where the growing season length is extremely short, such as in snowbeds, early snowmelt usually fosters biomass production (Walker et al. 1994; Björk & Molau 2007).

### Future research

Campbell et al. (2005) raised a number of ideas on how winter ecological processes should best be investigated. In particular, they emphasize the need for standardized protocols for winter measurements, and integrative approaches over different levels of the ecosystems and different spatial scales. In addition to these suggestions, we would like to raise the following points that apply particularly to snow ecology experiments.

Long-term studies simulating realistic snow cover scenarios for the region or the ecosystem in question are sparse. This especially applies to the advancement of snowmelt, which is a realistic scenario for many Arctic and alpine ecosystems. The ecosystem responses to changes in snow cover can be immediate and of a similar magnitude as the responses to other crucial climate factors, such as temperature, summer precipitation and CO₂ concentration. Changes in winter snow cover can show impacts that are still visible during the following growing season, thus influencing processes mainly attributed to summer. For instance, the insulation by the winter snowpack can control microbial activity and decomposition rates, and thus the nutrient availability to plants the following summer (Williams et al. 1998; Schimel et al. 2004; Rixen et al. 2008). Furthermore, altered winter snow cover can affect growing season soil moisture, which interacts with the effects of summer temperatures, especially in regions with low summer precipitation (Walker et al. 1999; Chinner & Welker 2005). In fact, tundra biomass productivity (measured as maximum normalized difference vegetation index in summer) was enhanced after winters with deep snow cover and late snowmelt in Siberia, regardless of the summer climate, which is attributed to higher nutrient and water availability (Grippa et al. 2005). Early snowmelt followed by cold spring temperatures, on the other hand, reduced tundra productivity (Stow et al. 2004) and boreal tree growth (Kirdyanov et al. 2003). In ecosystems where the growing season length is extremely short, such as in snowbeds, early snowmelt usually fosters biomass production (Walker et al. 1994; Björk & Molau 2007).
well-designed, large-scale snow manipulation experiments are very difficult and laborious to accomplish.

Only a few studies simulate episodic extreme events in winter and spring, such as midwinter thawing or spring frosts, although such events may have even larger impacts on ecosystems than slow and gradual changes in the winter climate. Specific experimental approaches, as well as long-term data series combining ecosystem and winter climate parameters, are needed to study ecosystem responses to gradual changes as well as to extreme events. Long-term studies require reliable measurements of winter climate data such as winter precipitation, snow depth, snowmelt timing and temperatures.

Apart from winter conditions, the growing conditions in spring, which for Arctic and alpine plants starts with the melting of the snow cover, can also have considerable effects on plant fitness and ecosystem processes (Jonas et al. 2008). Therefore, winter and spring climate scenarios should be taken into account and combined in future climate change experiments.

There is ample evidence that winter climate change has a great potential to modify ecosystem processes in Arctic and alpine ecosystems. Experimental studies of snow cover changes can improve our understanding of ecosystem changes that have been observed in recent years, such as the increase in shrub cover in the Arctic (Sturm et al. 2005; Tape et al. 2006). Compared with summer processes, however, there are still many open questions requiring further investigation in the field of Arctic and alpine winter ecology.

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