The influence of snow cover and cold-season temperatures on growing-season processes

Ecosystem respiration, nutrients, plant growth and phenology in the high Arctic

Philipp R. Semenchuk

A dissertation for the degree of Philosophiae Doctor

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Cover picture: To simulate a climate change scenario with deeper snow cover, we erected snow fences which collected snow drifts on their lee side. This picture was taken shortly before all ambient snow melted away. We can see that the snow behind the fence is substantially deeper and will melt away significantly later than its surroundings. Photograph by Philipp Semenchuk.
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ABSTRACT

Arctic terrestrial ecosystems are dominated by a long cold-season, during which snow cover protects the canopy and soil from cold air temperatures. Hence, temperatures plants and soil experience are higher and more stable than the surrounding atmosphere. The ecosystem is adapted accordingly, and many processes are governed by this relationship. Increasing air temperatures and associated increases of precipitation during the cold-season are observed and projected following climate change. Deeper snow, and thereby higher soil temperature and delayed snow melt could be the result. Both the low productivity and carbon (C) uptake by plants and C loss by ecosystem respiration might be increased following increases of snow depth, with impacts on Earth’s atmosphere’s CO₂ concentration.

To estimate the ecosystems response to the changing snowpack, we increased snow depth with fences and measured plant phenology, growth and chemistry, flower abundance, and soil C mineralization and nitrogen (N) concentration. Delayed melt out caused by deeper snow could influence phenology such that the growing-season and time for C assimilation is shortened, and net C uptake of the ecosystem is decreased. Simultaneously, warmer soil during the cold-season could increase plant available nutrients and N and chlorophyll concentrations and growth, thereby counteracting the shortened growing-season by increased C uptake. Warmer soils also mean higher C loss during the cold-season, which could lead to whole year C losses if not balanced by C uptake during the growing-season.

The snow fences increased soil temperatures during the cold-season, and delayed melt out. Leaf green-up was delayed accordingly, while senescence was synchronous with ambient areas. This points out that the growing-season as experienced by the plants was indeed shortened by increased snow, and that C uptake was therefore reduced. However, actual plant growth was only reduced for some species, while other species even increased growth. Because of warmer temperatures and therefore higher microbial activity during the cold-season, areas under deep snow had higher plant available nutrients, and leaves higher N and chlorophyll content. This could balance the C losses caused by a shortened growing-season. Warmer soils also emitted more CO₂ during the cold-season, which potentially used up and altered substrates for microbial activity and reduced CO₂ emissions during the growing-season. This complicates the connection between snow depth and C balance of Arctic terrestrial ecosystems.

Our results demonstrate how cold-season conditions can carry over to growing season processes and influence C balance in a variety of ways. Most processes are interacting with each other, and the multi-disciplinary approach we chose helped to discover that. The short and long-term changes we observed are important to investigate further in order to understand how a changing snowpack influences C balance of Arctic tundra.
INTRODUCTION

THE ARCTIC IS COLD

Indeed, it is cold. Using Spitsbergen, Norway (78°13′N, 15°33′E), the focus island of this thesis, as an example, the annual mean air temperature from 1961-1990 was -6.7 °C, and the mean of the coldest month February -16.2 °C (Norwegian meteorological institute, www.eklima.met.no). This is cold compared to, for example, Tromsø (annual mean 2.5°C, coldest month -4.4°C), around 8° latitude further south on the Norwegian mainland, or the more continental Fairbanks, Alaska, around 14° lat. further south (annual -2.8°C, but coldest month -23°C). Although there are also colder places on Earth (e.g. central Siberia or high Alpine), these figures can be misleading in what terrestrial ecosystems actually experience during the cold season. The snow cover modulates soil and canopy temperatures by its insulating properties and protects soil and plants from temperature extremes and chilling winds during the cold-season (see for instance Olsson et al. 2003; Sturm et al. 2005).

Temperature is not the only challenge Arctic ecosystems have to face. With snow cover lasting around 9 months per year, the Arctic growing-season is particularly short and the non-growing or cold-season particularly long. This balance between thawed and frozen season is the real specialty of the Arctic and also one of the topics of this thesis.

In the Arctic, two more-or-less unique characteristics are of importance for various processes which influence and form the ecosystem as we see it today. (1) First, the availability of water and light are very restricted due to the short duration of the growing-season. Sub-zero temperatures and snow cover deprive this ecosystem’s flora of these two vital prerequisites for growth and reproduction, and forces plants into a dormant stage for two thirds or more of the year. (2) Second, being frozen for the better part of the year, decomposition and mineralization – both temperature dependent processes – are slow and undecomposed plant litter and soil organic matter (SOM) accumulate and store nitrogen (N) in a form unavailable to plants. Therefore, Arctic peat is low in plant available nutrients, which restricts primary production in addition to the short season.

The growth conditions described above (and likely other features of the Arctic environment, which are not covered by this thesis) are reflected in the visual appearance of a classic Svalbard lowland tundra: we can see a dominance of low-growing dwarf shrubs, together with short graminoids and herbaceous species forming a thin layer of vegetation not higher than around 30 cm. The short growing season and low nutrient availability restricts growth of larger species and individuals (bird cliffs with external nutrient inputs are different, but not part of this thesis). Ecosystem components not visible to the eye are also controlled by these prerequisites: decomposition of old plant material is slow and leads to carbon (C) stocks so large that they are significant even in comparison to Earth’s atmospheric CO₂ pool (Tarnocai et al., 2009). Changing
some components of the governing growth characteristics might change this ecosystems structure and function.

THE ARCTIC IS GETTING WARMER

In particular, changes during the cold-season have been observed and are anticipated to continue to change in the future (Solomon et al., 2007; Førland et al., 2011). Cold-season air temperature increases lead to higher water holding capacity of the ambient atmosphere and stronger snow fall all over the European Arctic (Callaghan et al., 2011a). A deeper snowpack can lead to warmer soils due to its insulative properties and at the same time delay snowmelt and thereby shorten the growing season even more. This relaxes one of the two above mentioned conditions affecting Arctic ecosystems by increasing plant available nutrients, but impairs the other even more by shortening the growing-season.

On the one hand, warmer soils during the long cold-season could accelerate biochemical reactions involved in decomposition and mineralization (Schimel et al., 2004). Although soils are frozen during winter, these reactions are not halted (Oechel et al., 1997). Indeed, N and C mineralization increase strongly with only small increases of temperature, even at sub-zero temperatures (Nadelhoffer et al., 1991; Grogan & Jonasson, 2006; Nobrega & Grogan, 2007; Morgner et al., 2010). Even though these reactions are still relatively slow compared to during thawed conditions, a small increase will have a large impact given the long duration of the cold-season. This could relax nutrient limitation and increase plant growth and thereby the ecosystems C uptake.

On the other hand, a delayed start of the growing season would put further pressure on the already very limited access to light and water. Plant growth would start later in the year, while the end of the growing season – probably triggered by temperature drops and decreasing light intensities during autumn – will not be delayed (Wipf & Rixen, 2010; Callaghan et al., 2011a). This would lead to less C assimilation per year if the increase of nutrient availability caused by warmed winter temperature is not having a strong enough impact.

Further effects of climate change could be an increase of extreme climatic events in the form of warm spells and rain-on-snow events during winter (Callaghan et al., 2011a; Smith, 2011; Bokhorst et al., 2011; Hansen et al., 2012), which again alter the quality and depth of the snowpack, thereby changing insulating and melt-out properties (Olsson et al., 2003). These carryover effects from cold-season conditions to growing-season processes and their changes is what this thesis focuses on (see Fig. 1 for an overview).

OVERALL OBJECTIVES

We tried to investigate some of the aspects of anticipated cold-season climate change on a few ecosystem processes in high Arctic Svalbard. Given the cold-season’s dominance and expected changes of its characteristics, we conducted an experimental study which would give us the opportunity to simultaneously
alter soil temperature and spring snow melt timing. Snow fences were used to increase soil temperature and thereby delay melt out dates (see cover picture). We used these environmental perturbations to observe potential changes on the following processes as treated in the attached papers. The fences were erected in autumn 2006, and data included in this thesis was collected from 2008 to 2012. As suggested by Wipf & Rixen (2010), we applied an interdisciplinary approach including biogeochemistry and ecophysiology. Such, we investigated different aspects of the ecosystem and discussed their interactions. See Fig. 1 for an overview of growth conditions and processes treated in this thesis.

PHENOLOGY AND REPRODUCTION

Plant phenology is an important aspect of Arctic plant life in the face of short growing-seasons. Early snowmelt and therefore start of the growing-season could result in a more productive year solely by an increase of time available for C assimilation (Wipf & Rixen, 2010). Primary production, i.e. growth of above
and belowground vegetative organs, could be enhanced and thereby increase the C uptake of the studied ecosystem. Besides that, also reproductive activities might increase. For instance, longer growing-seasons might enable plants to assimilate more energy for production of overwintering flower buds and thereby increase flower numbers (Bliss, 1971). Later snowmelt would result in the opposite, i.e. less time for growth and reproduction. In the long run, both scenarios might change species composition even when the other effects of changed snow depth are ignored (Callaghan et al., 2011b).

In the context of this thesis, we observed five growing-seasons (2008-2012) of plant phenological phases such as leaf emergence/ green-up, flower emergence, and leaf senescence of a total of 13 species (Paper 1: Cooper et al. 2011). We wanted to know if plants could compensate for a later snow melt by accelerating their early season phenophases or by delaying senescence or both, which could have implications for primary production.

We also counted flower abundances over five seasons (2008-2012), with the hypothesis that a shortened growing-season would result in fewer pre-formed flower primordia and thereby fewer flowers the following growing season (Paper 2: Semenchuk et al. 2013). During the five years of monitoring, we observed two years with heavy rain events during the cold season, which removed a significant part of the snow cover and revealed an additional function of the snowpack, namely the protection of overwintering flower primordia.

**PLANT GROWTH**

The hypothesized responses of plant phenology to a delayed start of the growing season would ultimately result in changes of primary production. This would impact the C sink capacity of the investigated tundra ecosystem in Svalbard. A shortened season would result in less growth and smaller plants, i.e. reduced C assimilation and input into the ecosystem. On the other hand, our method of shortening the growing season is confounded with a simultaneous increase of winter temperatures; the consequent increase of plant available nutrients (see below) might counteract that effect and increase plant growth in spite of a shorter season.

We measured in situ plant growth of five species during one whole season (2011) to get an overview over size at peak season and growth timing and thereby the average size during the whole growing-season (Paper 3). The following year (2012) we measured plant size of three species only at peak season based on data from Paper 3 to compare our results with nutrient availability (Paper 4). We expected two different outcomes, namely that plant growth would either be reduced by shortened growing-seasons, or enhanced by higher nutrient availability.

**N MINERALIZATION AND RESPIRATION**

Through the warming effects of increased snow depth, higher microbial activities are likely to occur during the long cold-season (Olsson et al., 2003; Schimel et al., 2004; Sturm et al., 2005; Elberling, 2007; Nobrega & Grogan,
These activities include the breakdown of plant material and SOM, thereby releasing stored N into the soil as plant available nutrients which might be accessible to plants during the following growing season (Schimel et al., 2004; DeMarco et al., 2011). This could lead to higher plant N and chlorophyll content and subsequently to faster C assimilation (Walsh et al., 1997; Welker et al., 2005; Torp et al., 2009; Leffler & Welker, 2013). As with most aerobic processes, the energy needed for N mineralization is mainly derived from breaking down C rich compounds, with release of CO₂ into the atmosphere as an end product. Warmer cold-season soils could therefore increase mineral N content in the soil, but also increase CO₂ emissions from, and potentially use up, C stocks in the soil (Davidson & Janssens, 2006).

We collected soil samples during one growing season (peak season to autumn) six years after erection of the snow fences (2012) and analyzed it for plant available nutrients, such as ammonium (NH₄⁺) and nitrate (NO₃⁻). Simultaneously, we collected leaves of the deciduous dwarf shrub Salix polaris and analyzed their C, N, and δ¹⁵N content (Paper 4). We knew from an earlier study in the same field site that the increase of temperature under deepened snow is sufficient to significantly increase CO₂ emissions during winter (Morgner et al., 2010) and hypothesized that this would lead to higher plant-available nutrients in the soil during the growing-season, leading to higher N content in the leaves.

Morgner et al. (2010) measured whole year ecosystem respiration (ER) in our field site two years after erection of the snow fences (2007/8) and found increased ER under deeper snow with higher soil temperatures, while ER during the growing season was unchanged. Based on that study, we repeated ER measurements at a higher temporal and spatial resolution to gain more insights into species-specific responses after five years of enhanced snow depth during 2010/11 (Paper 5). Since a slight increase of temperature during nine months per year could result in proportionally large CO₂ production, losses of microbial substrates from the soil are conceivable (Davidson & Janssens, 2006). We therefore hypothesized an overall decrease of ER after five years of increased cold season ER.

RESULTS AND DISCUSSION

Our snow depth manipulation via snow fences created snow drifts with a maximum depth of around 1.5 m, while the most common ambient snow depth was between 20 and 30 cm. During five years of snow fence influence, the snow drifts melted away in average 17 days later than ambient snow (Table 1 in Paper 2). Soils under the snow drifts were up to around 14 °C warmer and temperatures much more stable than in unmanipulated areas (Fig. 1 in Paper 2). The soil under the snow drifts never cooled down sufficiently before establishment of an insulating snow cover to absorb the insulating effect of the increased snow (Groffman et al., 2001), although in some years snow cover established after onset of sub-zero temperatures. This could be because the
fences trap wind transported snow and therefore establish a sufficiently deep snowpack earlier than ambient areas.

**PHENOLOGY**

*Paper 1* presents data from the 2008 growing-season, i.e. 2 seasons after erection of the snow fences. In that year, plants under the snow drifts melted out about 2 weeks later than surrounding plants, with an average delay of early season phenophases (leaf green up and flowering) across all species of almost 22 weeks, as well (see Fig. 2). However, that effect was stronger in early developing species, whereas late developing species were able to buffer the delayed snow melt by accelerating early season development leading to a shorter delay. This seems to be a common observation after experimentally delayed snow melt (Wipf & Rixen, 2010).

In our study, air temperatures right after melt out were not as warm after normal melt out as after delayed melt out, so that plants which melted out later experienced a warmer start of the season. Therefore, we hypothesize that (1) early phenophases of early developing species (such as *Dryas* which delayed green-up for the same duration as snowmelt was delayed) are dependent on the duration of available daylight (i.e. days after snowmelt) while (2) late developing species (such as *Stellaria* for which green-up delay was shorter than melt out delay) might be more dependent on accumulated temperature sums, which are higher after delayed snowmelt. A preliminary analysis including data

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Fig. 2 The deep snow drift produced by the snow fences delayed melt out and thereby flower emergence of *Cassiope tetragona* and other species. This picture is showing how *Cassiope* is flowering extensively outside of the fence area (white dots in foreground), while the area behind the fence, which melted out around two weeks later, is not in flower yet (area in white line). Around two to three weeks later, this relationship was reversed, with flowers only in the fence area, while flowers in ambient areas were already withered. Photograph by Philipp Semenchuk.
from four more years shows that the matter is more complicated (Fig. 3): if we isolate the 2008 growing season, hypothesis 1 seems to be supported, while hypothesis 2 seems falsified; *Dryas* (an early developing species) used the same amount of days until green-up but different temperature sums in both snow regimes, while *Stellaria* (a late developing species) used both more days and more temperature in the unmanipulated snow regime. However, when considering all seasons, we see that these effects are not consistent across seasons, and further data analyses are needed to pin-point the mechanism behind green-up timing of these species.

Late season phenophases such as leaf senescence were not delayed as severely by the delayed melt out, such that plants growing in the fence sites would have fewer days after snowmelt and green-up until senescence, leading to a shortening of time for C assimilation. Preliminary analyses show that this trend is largely consistent across years and species (*Dryas* and *Stellaria*, data not shown). Senescence in many species is probably triggered by the red:far-red ratio of the ambient light, which changes when the sun angle becomes lower (Tsegay et al., 2005), and could explain the relative synchrony of senescence across snow regimes.

Fig. 3 Estimated temperature sums (Thawing degree days TDD of soil) and number of days after snowmelt (DAS) until leaf green-up for (a, b) *Dryas octopetala* and (c, d) *Stellaria crassipes*. Normal = unmanipulated snow depth, Deep = increased snow depth and delayed melt out date. Error bars are 95% confidence intervals from a linear mixed effects model.
REPRODUCTION

Data on flower abundances are presented in Paper 2 (and partly Paper 1). Of the six observed species, only Cassiope tetragona and Stellaria crassipes responded with a significant decrease of flower abundance following delayed melt out. For both species, we attribute this response to shortened growing seasons the year prior to the observed losses of flower abundance. However, different mechanisms are responsible in the two species.

*Cassiope* produces overwintering flower buds in leaf axillae during seasons preceding flowering (Bliss, 1971). *Paper 3* and other studies show that that species produces shorter annual shoot increments in situations with shortened or colder growing-seasons (Rozema *et al.* 2009; Mallik *et al.* 2011; Weijers *et al.* 2012) and therefore fewer leaves and leaf axillae, which are the location of flower bud formation. Thus, we conclude that delayed snow melt decreased flower bud production through shortening of the growing-season and thereby a decrease of time and/or energy available for flower bud production.

*Stellaria*, on the other hand, produces its flowers in the same season when flowering occurs. The observed reduction of flower abundance after delayed snow melt might be caused by a shortened time from melt out to induction of flowering, the so-called pre-floration period. This assumption, however, is not supported by the 2008 phenology data from *Paper 1*, when *Stellaria* did not show a shortened pre-floration period after late melt out. Also, the effect of reduced flower abundance only started after the fourth year of delayed melt out and was not apparent during earlier seasons. We conclude therefore that long-term rather than seasonal processes are responsible for our observation and suggest that delayed costs of reproduction (direct fecundity costs) could be responsible for loss of reproductive activity of *Stellaria* after four years of shortened growing-seasons: energy reserves used up by previous years’ reproduction could not be replenished during a shortened duration of C assimilation (Obeso, 2002).

Depending on which definition we want to follow, ‘climate extremes’ (Smith, 2011) or ‘warm’ and ‘extremely warm’ (Hansen *et al.*, 2012) periods in the form of rain-on-snow events occurred in two of the five years we monitored flower abundances (2010 and 2012). These events are commonly removing large parts of the snow cover and its insulating effect, and expose plants to cold air. That can be detrimental to crucial overwintering plant tissues such as meristems or, in our case, flower buds (Gates, 1912; Raatikainen & Väminen, 1988; Taulavuori *et al.*, 1997; Inouye, 2008; Bokhorst *et al.*, 2008; Mallik *et al.*, 2011). Again, it was *Cassiope* which reacted most strongly to these warm spells evidenced through reduced flower abundances in areas with ambient snow cover, while individuals under deepened snow stayed protected because the rain event was not severe enough to remove the snow drift. Of all the observed species, *Cassiope* carries its flower buds furthest away from the soil, thereby exposing them to the air, which might explain why this species is most affected (see Fig. 4).
Data on plant growth are presented in Paper 3 (and partly Paper 4). We described the overall finding as ‘idiosyncratic’ because the responses of leaf growth of eight species on shortened growing-seasons were in all directions, i.e. from decreased to increased growth, and no relationships between growth form or habitat associations could be identified.

Reduction of leaf sizes following delayed snow melt is easily explained by the loss of growing-season length, as demonstrated in Paper 1. The corresponding loss of light and accumulated temperature led to slower or less growth of Salix polaris, Cassiope tetragona, Pedicularis hirsuta, and Stellaria crassipes. However, the positive effect of shortened growing seasons on leaf growth of Alopecurus magellanicus, Dryas octopetala and Bistorta vivipara can be attributed to the simultaneous increase of nutrient availability under the snow drifts as shown in Paper 4 and elsewhere (Schimel et al., 2004). Fast growth rates during the beginning of the growing period and therefore higher photosynthetic area during the whole season, together with higher chlorophyll concentrations (at least in Salix, which did not grow bigger, Paper 4) suggest that deepened snow could lead to an increase of C uptake, although at the

**PLANT GROWTH**

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ecosystem scale, that could be buffered by reduced growth of the other species keeping ecosystem C assimilation constant (Shaver & Chapin III, 1986).

Obviously, the first mentioned set of species were not able to benefit from increased nutrient availability, at least when it comes to above ground growth. This might be due to a less dynamic root system or a later start of nutrient assimilation, which makes these species poor competitors despite a potential peak of nutrient availability early after snowmelt (Schimel et al., 2004). Also, a co-limitation of temperature is suggested, in which case simultaneous temperature increases are needed to facilitate utilization of extra nutrients (Havström et al., 1993). However, we cannot exclude growth responses other than leaf sizes of these species, such as below ground or woody growth (Parsons et al., 1994; Wookey et al., 1994), and minirhizotrons are already installed to investigate that possibility in future research.

**N MINERALIZATION**

As already mentioned, *Paper 4* explores the relationship between snow depth and nutrient availability. Soil samples of the upper 5 cm soil horizon, collected weekly from mid-season until senescence in 2012, confirm that soils under deeper snow have higher plant available nutrient concentrations over the whole growing-season. We attribute this to increased cold-season temperatures and associated higher mineralization rates under the snow drifts (Schimel et al., 2004).

Simultaneously, *Salix polaris* leaves had higher N, chlorophyll, and δ¹⁵N concentrations in snow drift areas, confirming that the soil N concentrations were elevated enough to have an impact on plant uptake, even though plant sizes were not always enhanced. Fertilizer addition experiments in the Arctic have shown that plants can react with enhanced growth of organs other than leaves, such as woody structures or below ground organs (Shaver & Chapin III, 1986; Parsons et al., 1994; Wookey et al., 1994). This means that species which seemed to be unaffected or negatively affected by later snow melt caused by the snow drifts (*Paper 3*) might have responded by increasing carbon allocations to organs other than leaves and thereby counteracted the loss of growing-season length. However, it is unlikely that for instance *Cassiope tetragona*, which hardly increased its length (*Paper 3*) and experienced clear losses of flower abundances (*Paper 2*) following later melt out, grew elsewhere. *Cassiope* is probably the species which suffered most under the snow depth increase, although it is a species which is commonly found in areas with intermediately deep snow; it seems to be successful in a delicate balance between the protective influence of snow on flower buds and leaves and available time for growth.

**ECOSYSTEM RESPIRATION**

*Paper 5* shows that cold-season ER was still increased after five years of continuous snow depth and soil temperature increase (2010/11). At the same time, growing-season ER was decreased in our and a low Arctic site at Daring Lake, Canada, operated by colleagues who shared their data with us (Casper T.
Christiansen and Paul Grogan), although summer soil temperatures were not influenced by the snow drifts.

We explained the decrease of ER during the growing-season by a potential decrease of labile substrates during elevated cold season ER, which are easily accessible by soil microbes as opposed to recalcitrant substrates which are less accessible and result in lower ER (Davidson & Janssens, 2006; Conant et al., 2011). We assume that this is a similar mechanism as discovered after long term growing-season warming (Rustad et al., 2001; Hartley et al., 2008, 2009), however, in our case we can show that the effect is carried over to another season. Further, an increase of N containing small compounds could form humic acids with middle-aged and old substrates and thereby make them inaccessible to microbes (Berg, 2000). Paper 4 showed an increase of such compounds throughout the growing season, and we believe that this might be the second pathway by which changes in cold-season conditions can influence growing season ER.

Surprisingly, cold season ER was not reduced after five years of warming. Since microbial activity during winter can be limited by labile carbon availability (Buckertidge & Grogan, 2008), one reason for this might be a replenishment of labile C during the preceding growing-season by, for instance, root exudates. This possibility is likely, especially given the potential of ecosystem wide increases of C assimilation demonstrated in Paper 3 and Paper 4. Alternatively, or in addition, ER during the cold-season has recently been shown to be partly fuelled by old, recalcitrant C, just as during the growing season (Hartley et al., 2013). Unfortunately, our study does not permit a satisfactory analysis of long-term ER changes during the cold-season, since we cannot control for the ER increasing effects of temperature under the snow drifts which might confound a potential substrate change effect.

CONCLUSIONS

I believe this thesis demonstrates that an interdisciplinary approach is possible also in a small team of researchers. The study includes a wide range of observations and measurements in one common experimental setup and showed that changes of physical conditions during the cold-season can affect processes during the growing-season in a variety of pathways (Fig. 1).

First, a deepened snow pack shortened growing-season length (Paper 1), thereby reducing plant growth of some species (Paper 3). However, it also increased nutrient availability (Paper 4) and thereby growth of other species which compensated for the loss of growing time. In fact, these species-specific response patterns make it difficult to estimate or predict responses at the ecosystem level and highlight the importance of multi-species studies. For instance, total net ecosystem C assimilation might not have changed, while the relative contribution of different species might have. Changes in plant-plant competition might be the result and, together with altered reproductive activities (Paper 2), lead to changes in species composition in the long run. Further,
species-specific litter qualities might have a stronger impact on variation of
decomposition and ER rates than temperature alone (Hobbie, 1996; Cornellissen
et al., 2007; Aerts et al., 2012), and plant mediated changes of ER in our snow
manipulation site might occur even before species composition changes take
place.

Second, a deepened snow pack increased cold-season soil temperature, thereby
increasing C mineralization rates (Paper 5) and likely also N mineralization
(Schimel et al., 2004), leading to the increased nutrient levels (Paper 4) and
diverse growth responses (Paper 3) described above. Simultaneously, growing-
season ER decreased not until after more than two years of deepened snow,
probably because the substrate pools were large enough to delay the effect
caused by a likely decrease of substrates. This reduction of growing-season ER
might compensate for the increased cold season C losses, although the back-of-
the-envelope calculation at the end of Paper 5 shows otherwise. In any case,
increased cold-season soil temperatures changed the balance between growing-
and cold-season C losses towards the cold-season, emphasizing its importance
due to its disproportionate duration during the year.

**FUTURE WORK**

As with many other studies, this thesis is not without flaws, and a number of
novelties could be incorporated to improve further research. The most obvious
shortcoming of this study is the more-or-less unrealistic ‘side-effect’ of the
delayed melt out of the deepened snowpack. Although we used it to investigate
species-specific growth and reproductive responses, later melt out is an unlikely
scenario in future climate change predictions for Arctic regions where an
opposite trend has been observed during the last decades (Solomon et al., 2007;
Wipf & Rixen, 2010; Callaghan et al., 2011a). Additionally, although we can
reason against it, delayed melt out might be a confounding factor in some of our
findings in that it controls plant growth to some extent. We suggest that future
studies try to achieve a simultaneous melt out of deepened and ambient snow as

When it comes to measuring plant growth and associated C assimilation and
input to the soil system, we suggest a full above- and below-ground harvesting
approach or a similar whole plant measure for future studies. Measuring leaf
size might be sufficient for a general approximation of the direction of response,
but allocation of C and energy to different organs than leaves following
perturbations is likely (Shaver & Chapin III, 1986; Parsons et al., 1994; Wookey
et al., 1994; Sullivan & Welker, 2005) and we missed identifying these
parameters. For future studies, a smart harvesting scheme would provide whole-
plant metrics and would allow the researchers to quantify the whole-ecosystem
response and estimate if an overall trend of changing C assimilation is
happening.

A lot of the presented research attempts to draw conclusions about if, and how,
increased snow depth alters the ecosystems net C exchange with the atmosphere
(NEE), which is the balance between ER and C uptake. We do have detailed whole year ER measurements, however, no quantifiable C uptake data, although we did derive trends of increases or decreases of C assimilation from growth and N content data. The difference between ER and ecosystem (or even species specific) C assimilation could be measured with a transparent chamber or a dark chamber with a PAR (photosynthetic active radiation) emitting light source. The second approach might be better since it allows control over the light intensity. An attempt to measure net ecosystem C uptake in our study site with a transparent chamber failed because the equipment proved unsatisfactory. These data in addition to ER data would allow a quantification of NEE and direct estimates of changes in C balance after snow increase.

Our interpretation of loss of growing-season ER is based on changed chemical properties of soil organic matter caused by increased ER rates and N mineralization during the cold season. However, with the exception of mineral N concentrations, we did not investigate any of the hypothesized reasons for altered ER. I strongly advise any research group with enough capacity for such work to contact the PIs of the snow fence project in Adventdalen and kindly ask for soil samples to investigate if our assumptions hold – if they have not done so themselves by then.

There might have been other shortcomings of the study I did not mention here, knowingly (e.g. nutrient and litter deposition caused by the fences, Fahnestock et al. (2000)) or unknowingly. As already hinted at the beginning of the conclusions section, we were a small team, and some of the mentioned weaknesses were simply unavoidable due to the lack of (wo)manpower and other logistical constraints (e.g. snow removal). Others were unavoidable because of instrument failure (e.g. photosynthesis measurements), and yet others because of lacking resources (e.g. detailed SOM studies). Nevertheless, I do believe we added to the existing knowledge about the winter ecology of Arctic tundra systems and could raise a couple of new questions. Research on winter ecology and influences of snow cover on the ecosystem are continuing in Adventdalen and other sites by our and other research groups, and the questions raised by this thesis will hopefully be answered in the near future.

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**ERRATUM**

In *Paper 2* (Semenchuk *et al.*, 2013) Figure 2 the legend is labeled wrongly: accumulative precipitation is the dashed line, while absolute precipitation is the solid line. The description in the figure caption is correct.

*Paper 1:*
Paper 2:

Paper 3:

Paper 4:

Paper 5:
