

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

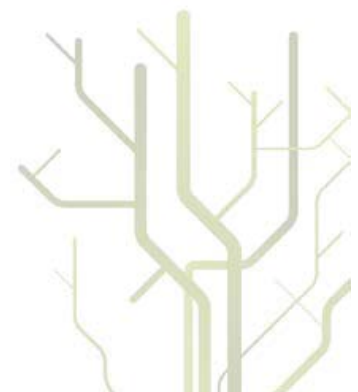
Ecosystem respiration, nutrients, plant growth and phenology in the high Arctic



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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A dissertation for the degree of Philosophiae Doctor (PhD)

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LIST OF PAPERS

Paper 1:

Cooper EJ, Dullinger S, Semenchuk PR (2011) Late snowmelt delays plant development and results in lower reproductive success in the High Arctic. *Plant science : an international journal of experimental plant biology*, **180**, 157–67.

Paper 2:

Semenchuk PR, Elberling B, Cooper EJ (2013) Snow cover and extreme winter warming events control flower abundance of some, but not all species in high arctic Svalbard. *Ecology and Evolution*, doi: 10.1002/ece3.648.

Paper 3:

Rumpf SB, Semenchuk PR, Dullinger S, Cooper EJ (201X) Idiosyncratic Responses of High Arctic Plants to Changing Snow Regimes. *PloS one*, submitted.

Paper 4:

Semenchuk PR, Elberling B, Amtorp C, Winkler J, Rumpf S, Michelsen A, Cooper EJ (201X) Deeper snow alters soil nutrient availability, leaf nutrient status and plant growth in high Arctic tundra. *Manuscript*.

Paper 5:

Semenchuk PR, Christiansen CT, Morgner E, Grogan P, Elberling B, Cooper EJ (201X) Long-term experimentally deepened snow decreases summertime CO₂ release rates in distinct High and Low Arctic tundra ecosystems. *Global Change Biology*, submitted.

1 **ABSTRACT**

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

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

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

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

43 INTRODUCTION

44 THE ARCTIC IS COLD

45 Indeed, it is cold. Using Spitsbergen, Norway (78°13'N, 15°33'E), the focus
46 island of this thesis, as an example, the annual mean air temperature from 1961-
47 1990 was -6.7 °C, and the mean of the coldest month February -16.2 °C
48 (Norwegian meteorological institute, www.eklima.met.no). This is cold
49 compared to, for example, Tromsø (annual mean 2.5°C, coldest month -4.4°C),
50 around 8° latitude further south on the Norwegian mainland, or the more
51 continental Fairbanks, Alaska, around 14° lat. further south (annual -2.8°C, but
52 coldest month -23°C). Although there are also colder places on Earth (e.g.
53 central Siberia or high Alpine), these figures can be misleading in what
54 terrestrial ecosystems actually experience during the cold season. The snow
55 cover modulates soil and canopy temperatures by its insulating properties and
56 protects soil and plants from temperature extremes and chilling winds during the
57 cold-season (see for instance Olsson *et al.* 2003; Sturm *et al.* 2005).

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

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

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

86 some components of the governing growth characteristics might change this
87 ecosystems structure and function.

88 THE ARCTIC IS GETTING WARMER

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

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

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

115 Further effects of climate change could be an increase of extreme climatic
116 events in the form of warm spells and rain-on-snow events during winter
117 (Callaghan *et al.*, 2011a; Smith, 2011; Bokhorst *et al.*, 2011; Hansen *et al.*,
118 2012), which again alter the quality and depth of the snowpack, thereby
119 changing insulating and melt-out properties (Olsson *et al.*, 2003). These carry-
120 over effects from cold-season conditions to growing-season processes and their
121 changes is what this thesis focuses on (see Fig. 1 for an overview).

122

123 OVERALL OBJECTIVES

124 We tried to investigate some of the aspects of anticipated cold-season climate
125 change on a few ecosystem processes in high Arctic Svalbard. Given the cold-
126 season's dominance and expected changes of its characteristics, we conducted
127 an experimental study which would give us the opportunity to simultaneously

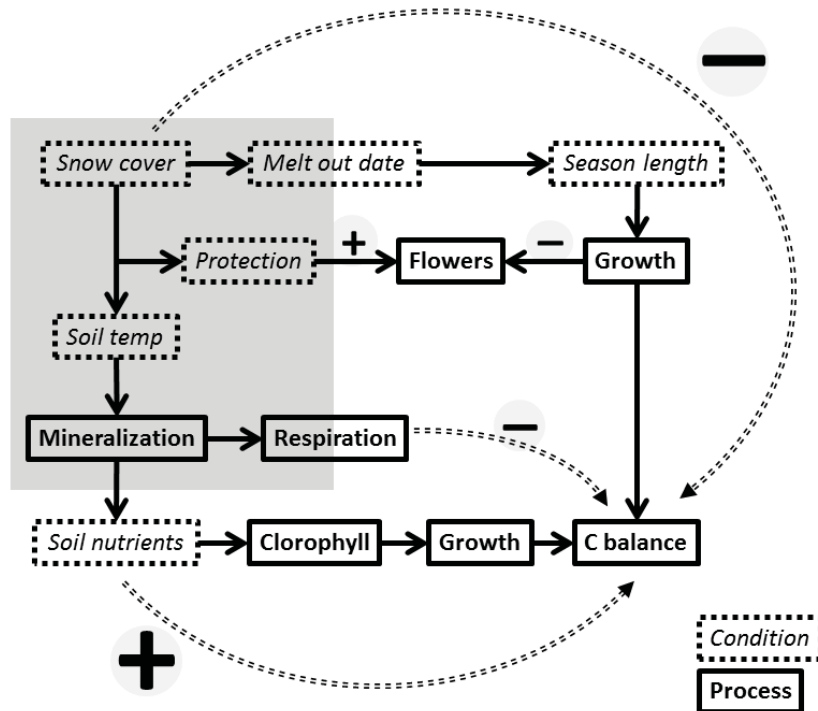


Fig. 1 Overview schematic of how deepened snow can influence cold- and growing-season conditions and processes (cold-season symbolized by grey square). *Top-right arc*: Increased snow depth leads to delayed melt out date, thereby shortens the growing-season and decreases growth. C assimilation is decreased, which influences the ecosystems C balance negatively. Simultaneously, decreased growth decreases flower production and flower abundances. *Bottom-left arc*: Increased snow depth leads to warmer soils and thereby higher microbial activity during the cold-season, such as N mineralization. Resulting increased nutrient availability during the growing-season increases N concentrations and chlorophyll production in leaves and leads to increased C assimilation, which influences the ecosystems C balance positively. However, increased mineralization rates also increase ecosystem respiration during the cold-season – C loss through this process influences the C balance negatively. Deepened snow also protects overwintering flower buds from cold air and thereby increases flower abundance the following year.

128 alter soil temperature and spring snow melt timing. Snow fences were used to
 129 increase snow depth and thereby soil temperature, and to delay melt out dates
 130 (see cover picture). We used these environmental perturbations to observe
 131 potential changes on the following processes as treated in the attached papers.
 132 The fences were erected in autumn 2006, and data included in this thesis was
 133 collected from 2008 to 2012. As suggested by Wipf & Rixen (2010), we applied
 134 an interdisciplinary approach including biogeochemistry and ecophysiology.
 135 Such, we investigated different aspects of the ecosystem and discussed their
 136 interactions. See Fig. 1 for an overview of growth conditions and processes
 137 treated in this thesis.

138 PHENOLOGY AND REPRODUCTION

139 Plant phenology is an important aspect of Arctic plant life in the face of short
 140 growing-seasons. Early snowmelt and therefore start of the growing-season
 141 could result in a more productive year solely by an increase of time available for
 142 C assimilation (Wipf & Rixen, 2010). Primary production, i.e. growth of above

143 and belowground vegetative organs, could be enhanced and thereby increase the
144 C uptake of the studied ecosystem. Besides that, also reproductive activities
145 might increase. For instance, longer growing-seasons might enable plants to
146 assimilate more energy for production of overwintering flower buds and thereby
147 increase flower numbers (Bliss, 1971). Later snowmelt would result in the
148 opposite, i.e. less time for growth and reproduction. In the long run, both
149 scenarios might change species composition even when the other effects of
150 changed snow depth are ignored (Callaghan *et al.*, 2011b).

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

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

164 PLANT GROWTH

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

174 We measured *in situ* plant growth of five species during one whole season
175 (2011) to get an overview over size at peak season and growth timing and
176 thereby the average size during the whole growing-season (*Paper 3*). The
177 following year (2012) we measured plant size of three species only at peak
178 season based on data from *Paper 3* to compare our results with nutrient
179 availability (*Paper 4*). We expected two different outcomes, namely that plant
180 growth would either be reduced by shortened growing-seasons, or enhanced by
181 higher nutrient availability.

182 N MINERALIZATION AND RESPIRATION

183 Through the warming effects of increased snow depth, higher microbial
184 activities are likely to occur during the long cold-season (Olsson *et al.*, 2003;
185 Schimel *et al.*, 2004; Sturm *et al.*, 2005; Elberling, 2007; Nobrega & Grogan,

186 2007; Natali *et al.*, 2011). These activities include the breakdown of plant
187 material and SOM, thereby releasing stored N into the soil as plant available
188 nutrients which might be accessible to plants during the following growing
189 season (Schimel *et al.*, 2004; DeMarco *et al.*, 2011). This could lead to higher
190 plant N and chlorophyll content and subsequently to faster C assimilation
191 (Walsh *et al.*, 1997; Welker *et al.*, 2005; Torp *et al.*, 2009; Leffler & Welker,
192 2013). As with most aerobic processes, the energy needed for N mineralization
193 is mainly derived from breaking down C rich compounds, with release of CO₂
194 into the atmosphere as an end product. Warmer cold-season soils could therefore
195 increase mineral N content in the soil, but also increase CO₂ emissions from,
196 and potentially use up, C stocks in the soil (Davidson & Janssens, 2006).

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

207 Morgner *et al.* (2010) measured whole year ecosystem respiration (ER) in our
208 field site two years after erection of the snow fences (2007/8) and found
209 increased ER under deeper snow with higher soil temperatures, while ER during
210 the growing season was unchanged. Based on that study, we repeated ER
211 measurements at a higher temporal and spatial resolution to gain more insights
212 into species-specific responses after five years of enhanced snow depth during
213 2010/11 (*Paper 5*). Since a slight increase of temperature during nine months
214 per year could result in proportionally large CO₂ production, losses of microbial
215 substrates from the soil are conceivable (Davidson & Janssens, 2006). We
216 therefore hypothesized an overall decrease of ER after five years of increased
217 cold season ER.

218

219 RESULTS AND DISCUSSION

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



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.

230 fences trap wind transported snow and therefore establish a sufficiently deep
 231 snowpack earlier than ambient areas.

232 PHENOLOGY

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

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

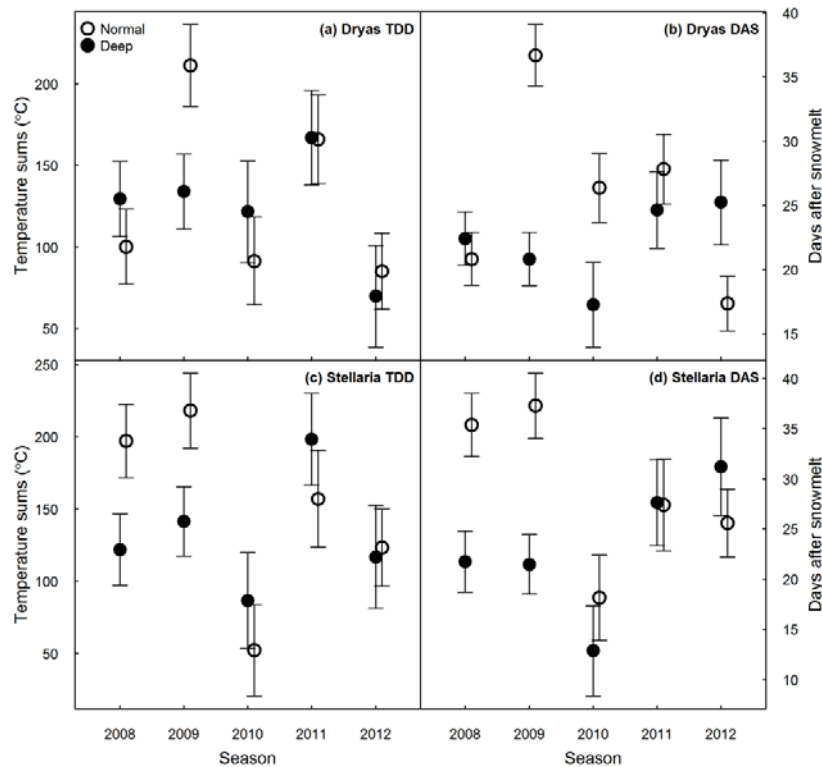


Fig. 3 Estimated temperature sums (Thawing degree days TDD of soil) and number of days after snowmelt (DAS) until leaf green-up for (a, b) *Dryas octopetala* and (c, d) *Stellaria crassipes*. *Normal* = unmanipulated snow depth, *Deep* = increased snow depth and delayed melt out date. Error bars are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

251 from four more years shows that the matter is more complicated (Fig. 3): if we
 252 isolate the 2008 growing season, hypothesis 1 seems to be supported, while
 253 hypothesis 2 seems falsified; *Dryas* (an early developing species) used the same
 254 amount of days until green-up but different temperature sums in both snow
 255 regimes, while *Stellaria* (a late developing species) used both more days and
 256 more temperature in the unmanipulated snow regime. However, when
 257 considering all seasons, we see that these effects are not consistent across
 258 seasons, and further data analyses are needed to pin-point the mechanism behind
 259 green-up timing of these species.

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

269 REPRODUCTION

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

276 *Cassiope* produces overwintering flower buds in leaf axillae during seasons
277 preceding flowering (Bliss, 1971). *Paper 3* and other studies show that that
278 species produces shorter annual shoot increments in situations with shortened or
279 colder growing-seasons (Rozema *et al.* 2009; Mallik *et al.* 2011; Weijers *et al.*
280 2012) and therefore fewer leaves and leaf axillae, which are the location of
281 flower bud formation. Thus, we conclude that delayed snow melt decreased
282 flower bud production through shortening of the growing-season and thereby a
283 decrease of time and/or energy available for flower bud production.

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

298 Depending on which definition we want to follow, 'climate extremes' (Smith,
299 2011) or 'warm' and 'extremely warm' (Hansen *et al.*, 2012) periods in the form
300 of rain-on-snow events occurred in two of the five years we monitored flower
301 abundances (2010 and 2012). These events are commonly removing large parts
302 of the snow cover and its insulating effect, and expose plants to cold air. That
303 can be detrimental to crucial overwintering plant tissues such as meristems or, in
304 our case, flower buds (Gates, 1912; Raatikainen & Vänninen, 1988; Taulavuori
305 *et al.*, 1997; Inouye, 2008; Bokhorst *et al.*, 2008; Mallik *et al.*, 2011). Again, it
306 was *Cassiope* which reacted most strongly to these warm spells evidenced
307 through reduced flower abundances in areas with ambient snow cover, while
308 individuals under deepened snow stayed protected because the rain event was
309 not severe enough to remove the snow drift. Of all the observed species,
310 *Cassiope* carries its flower buds furthest away from the soil, thereby exposing
311 them to the air, which might explain why this species is most affected (see Fig.
312 4).

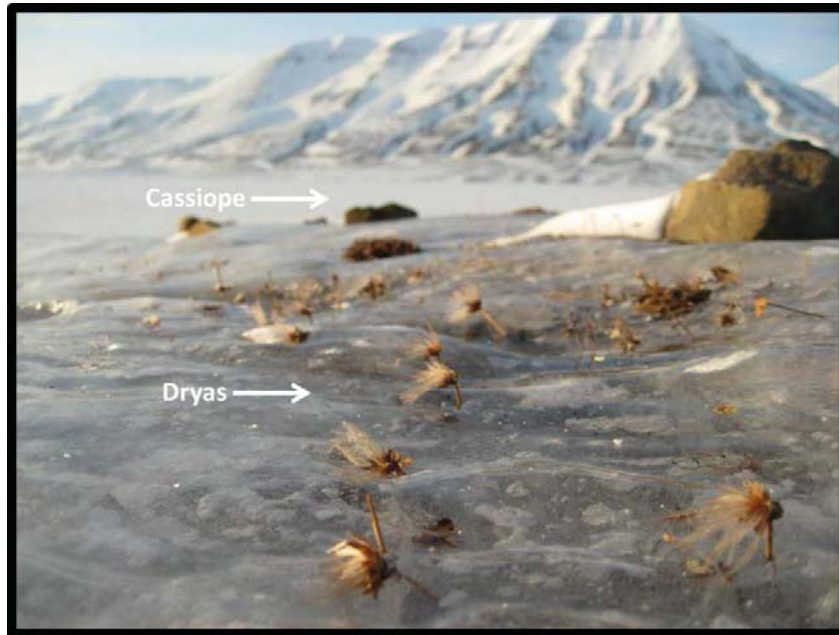


Fig. 4 Winter warming events, often occurring together with rain, can substantially remove snow cover and thereby expose plants to cold winter air. Depending on morphology, different parts of the plant can be directly exposed. On this picture, we see *Dryas octopetala* seed heads (foreground) from the previous growing season protrude through the remaining ice layer after a warming event in early 2010. The rest of the plant, including meristems and flower primordia, are still somewhat protected by the ice. In the background we can see a patch of *Cassiope tetragona* protruding through the ice; in this case, the whole plant including flower primordia is exposed, which might be one reason why this species experienced a loss of flowers the following season. The snow drifts behind the snow fences were still intact during that year, and both species were well protected. Photograph by Philipp Semenchuk.

313 PLANT GROWTH

314 Data on plant growth are presented in *Paper 3* (and partly *Paper 4*). We
 315 described the overall finding as ‘idiosyncratic’ because the responses of leaf
 316 growth of eight species on shortened growing-seasons were in all directions, i.e.
 317 from decreased to increased growth, and no relationships between growth form
 318 or habitat associations could be identified.

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

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

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

344 N MINERALIZATION

345 As already mentioned, *Paper 4* explores the relationship between snow depth
346 and nutrient availability. Soil samples of the upper 5 cm soil horizon, collected
347 weekly from mid-season until senescence in 2012, confirm that soils under
348 deeper snow have higher plant available nutrient concentrations over the whole
349 growing-season. We attribute this to increased cold-season temperatures and
350 associated higher mineralization rates under the snow drifts (Schimel *et al.*,
351 2004).

352 Simultaneously, *Salix polaris* leaves had higher N, chlorophyll, and $\delta^{15}\text{N}$
353 concentrations in snow drift areas, confirming that the soil N concentrations
354 were elevated enough to have an impact on plant uptake, even though plant sizes
355 were not always enhanced. Fertilizer addition experiments in the Arctic have
356 shown that plants can react with enhanced growth of organs other than leaves,
357 such as woody structures or below ground organs (Shaver & Chapin III, 1986;
358 Parsons *et al.*, 1994; Wookey *et al.*, 1994). This means that species which
359 seemed to be unaffected or negatively affected by later snow melt caused by the
360 snow drifts (*Paper 3*) might have responded by increasing carbon allocations to
361 organs other than leaves and thereby counteracted the loss of growing-season
362 length. However, it is unlikely that for instance *Cassiope tetragona*, which
363 hardly increased its length (*Paper 3*) and experienced clear losses of flower
364 abundances (*Paper 2*) following later melt out, grew elsewhere. *Cassiope* is
365 probably the species which suffered most under the snow depth increase,
366 although it is a species which is commonly found in areas with intermediately
367 deep snow; it seems to be successful in a delicate balance between the protective
368 influence of snow on flower buds and leaves and available time for growth.

369 ECOSYSTEM RESPIRATION

370 *Paper 5* shows that cold-season ER was still increased after five years of
371 continuous snow depth and soil temperature increase (2010/11). At the same
372 time, growing-season ER was decreased in our and a low Arctic site at Daring
373 Lake, Canada, operated by colleagues who shared their data with us (Casper T.

374 Christiansen and Paul Grogan), although summer soil temperatures were not
375 influenced by the snow drifts.

376 We explained the decrease of ER during the growing-season by a potential
377 decrease of labile substrates during elevated cold season ER, which are easily
378 accessible by soil microbes as opposed to recalcitrant substrates which are less
379 accessible and result in lower ER (Davidson & Janssens, 2006; Conant *et al.*,
380 2011). We assume that this is a similar mechanism as discovered after long term
381 growing-season warming (Rustad *et al.*, 2001; Hartley *et al.*, 2008, 2009),
382 however, in our case we can show that the effect is carried over to another
383 season. Further, an increase of N containing small compounds could form humic
384 acids with middle-aged and old substrates and thereby make them inaccessible
385 to microbes (Berg, 2000). *Paper 4* showed an increase of such compounds
386 throughout the growing season, and we believe that this might be the second
387 pathway by which changes in cold-season conditions can influence growing
388 season ER.

389 Surprisingly, cold season ER was not reduced after five years of warming. Since
390 microbial activity during winter can be limited by labile carbon availability
391 (Buckeridge & Grogan, 2008), one reason for this might be a replenishment of
392 labile C during the preceding growing-season by, for instance, root exudates.
393 This possibility is likely, especially given the potential of ecosystem wide
394 increases of C assimilation demonstrated in *Paper 3* and *Paper 4*. Alternatively,
395 or in addition, ER during the cold-season has recently been shown to be partly
396 fuelled by old, recalcitrant C, just as during the growing season (Hartley *et al.*,
397 2013). Unfortunately, our study does not permit a satisfactory analysis of long-
398 term ER changes during the cold-season, since we cannot control for the ER
399 increasing effects of temperature under the snow drifts which might confound a
400 potential substrate change effect.

401

402 CONCLUSIONS

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

408 First, a deepened snow pack shortened growing-season length (*Paper 1*), thereby
409 reducing plant growth of some species (*Paper 3*). However, it also increased
410 nutrient availability (*Paper 4*) and thereby growth of other species which
411 compensated for the loss of growing time. In fact, these species-specific
412 response patterns make it difficult to estimate or predict responses at the
413 ecosystem level and highlight the importance of multi-species studies. For
414 instance, total net ecosystem C assimilation might not have changed, while the
415 relative contribution of different species might have. Changes in plant-plant
416 competition might be the result and, together with altered reproductive activities
417 (*Paper 2*), lead to changes in species composition in the long run. Further,

418 species-specific litter qualities might have a stronger impact on variation of
419 decomposition and ER rates than temperature alone (Hobbie, 1996; Cornelissen
420 *et al.*, 2007; Aerts *et al.*, 2012), and plant mediated changes of ER in our snow
421 manipulation site might occur even before species composition changes take
422 place.

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

435

436 FUTURE WORK

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

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

460 A lot of the presented research attempts to draw conclusions about if, and how,
461 increased snow depth alters the ecosystems net C exchange with the atmosphere

462 (NEE), which is the balance between ER and C uptake. We do have detailed
463 whole year ER measurements, however, no quantifiable C uptake data, although
464 we did derive trends of increases or decreases of C assimilation from growth and
465 N content data. The difference between ER and ecosystem (or even species
466 specific) C assimilation could be measured with a transparent chamber or a dark
467 chamber with a PAR (photosynthetic active radiation) emitting light source. The
468 second approach might be better since it allows control over the light intensity.
469 An attempt to measure net ecosystem C uptake in our study site with a
470 transparent chamber failed because the equipment proved unsatisfactory. These
471 data in addition to ER data would allow a quantification of NEE and direct
472 estimates of changes in C balance after snow increase.

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

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

494

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520

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674

675 **ERRATUM**

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

679

Paper 1:

Cooper EJ, Dullinger S, Semenchuk PR (2011) Late snowmelt delays plant development and results in lower reproductive success in the High Arctic. *Plant science : an international journal of experimental plant biology*, **180**, 157–67.

Paper 2:

Semenchuk PR, Elberling B, Cooper EJ (2013) Snow cover and extreme winter warming events control flower abundance of some, but not all species in high arctic Svalbard. *Ecology and Evolution*, doi: 10.1002/ece3.648.

Paper 3:

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Paper 4:

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