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Perhaps in the future, man will go into the Arctic in the same way as in biblical times man journeyed into the desert in search of the truth.

Christiane Ritter, 1935

Svalbard, like other polar regions, has first and foremost been a man's world. Even today, the masculinity in some will greatly increase the moment they set their foot on the tundra, as if the polar air itself affects certain glands.

Svarhitt Birger Amundsen, 2001

Thank You

Danke liebe Gerda für deine lebenslange Unterstützung. Ohne deine Hilfe (und Strenge) und Toleranz wäre ich jetzt nicht hier.

I want to say thanks to Elisabeth for accepting me as a master student and for her patience with getting me into the system. I'm looking forward to a constructive teamwork in the future! Thanks to Stefan for his quick response on all my requests and questions and for his valuable advice. You both gave me the life changing opportunity to come up here. Thanks to UNIS for having me as a guest, providing me with the necessary logistics. A big thank you to Jarle and Leidulf from Klimalabben for their valuable advice and practical help.

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And finally I want to thank all Svalbardians for feeding me, tolerating my corrupted language, rescuing me after capsizing, teaching me how to enjoy Whisky and for all these enormous coffee breaks.

Table of Contents

Table of figures

Manuscript:

Phenological and reproductive responses of tundra plants to enhanced snow cover in high arctic Adventdalen, Spitsbergen

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Abstract

Climate change scenarios suggest, among others, an increase of solid winter precipitation in high latitude sites, leading to enhanced and more stable temperatures under a resulting deeper snowpack and later melt out dates of affected areas. Snow accumulations behind snow fences have been used to simulate an increase of snow cover in high arctic Svalbard and resulted in a delay of growing season of 11±4.48 days (mean±sd) in 2008. Phenology of five species was assessed visually throughout the season; flowers were counted for five species and germination rates of propagules of six species were investigated. Phenology behind fences was delayed for all species, whereas green-up of leaves was more delayed than (1) senescence of leaves for all but one species and (2) propagule dispersal for some species. Flowering rates were reduced due to delayed snow melt for all species. Germination rates were lower for two out of six species and to be very low for three stratified species compared to three non-stratified species from treatment and control areas. Different responses to enhanced snow cover have been found for different species. The evergreen shrub *Dryas octopetala* and the forb *Bistorta vivipara* experienced significant reduction of germination rates. The snow bed species *Cassiope tetragona* has shown a more flexible phenological development than other species making it more likely to dominate in an environment with later melt out dates. It has been suggested that species interactions will lead to positive feedbacks and increase the observed short-term responses in the long term leading to substantial community changes in the affected areas.

Keywords: phenology, high-arctic Svalbard, germination, snow manipulation

1 Introduction

The arctic is one of the world's regions most affected by the expected climate warming, and especially winter air temperatures are found to have changed during the last decades, which might lead to enduring alterations of hydrologic processes like precipitation amounts, states of aggregation, and snow distribution (e.g. Serreze et al., 2000; Dormann and Woodin, 2002; Acia, 2005; Lemke et al., 2007). Together with possible changes in spring and autumn temperatures, this could lead to a long term change of timing of snow melt. However, the lack of weather stations and large interannual and interdecadal variations of air temperature and precipitation values in arctic regions make it difficult to find a significant trend of changing values of rain and especially snow fall during recent decades (Groisman and Easterling, 1994; Acia, 2005). Measures of climate indices underlie temporally changing and national biases, depending on the time period considered, the data processing methods including correction factors and instruments used (Groisman and Easterling, 1994; Forland and Hanssen-Bauer, 2003), and the amount of sea-ice, cloud cover and other variables like climatic oscillations present in the considered time period, which are complex and up to now poorly understood (Serreze et al., 2000). Consequently, future snow cover scenarios are highly uncertain and involve deeper and prolonged snowpack as well as reduced snow heights and therefore extended growing season lengths.

Snow cover duration is an important driver of many plant ecophysiological processes like root respiration, biomass allocation, reproductive success, and phenology and hence ultimately controls the landscape-scale distribution of arctic and alpine plants. Species constrained to sites with particularly long-lasting snow cover as in high latitude ecosystems have to cope with short seasons (e.g. Schmidt et al., 2006), low nutrient turnover rates (Nadelhoffer et al., 1992) and strong intraseasonal moisture fluctuations (Scott and Rouse, 1995). Allocation of accumulated carbon into propagule production and energy storage for the next year is thought to be as dependent on season length as propagule recruitment and seedling survival.

Plant phenology has been identified as one key response variable to experimental climate change in tundra ecosystem studies by the International Tundra Experiment (ITEX; Molau and Edlund, 1996), and so far this method has mainly been used for experimental warming treatments (reviewed by Arft et al., 1999). Although some studies have been done to investigate long-term effects by assessing changes in species composition (e.g. Scott and Rouse, 1995; Wahren et al., 2005), studies using phenology as response variable to experimentally increased snow cover are scarce (Van der Wal et al., 2000; Wipf et al., 2006) and only two sites, namely the arctic site Toolik Field Station, Alaska and the alpine site Niwot Ridge, Colorado have used snow fences to achieve an increased snowpack throughout winter (Walker et al., 1999; Borner et al., 2008).

Reproductive success represents a crucial parameter for species survival and composition in a highly constrained ecosystem such as high arctic tundra (Hagen, 2002; Cooper et al., 2004) and has been found to be increased with raised temperatures (Arft et al., 1999) and increased nutrient availability (Wookey et al., 1994; 1995). Previous snow fence studies have shown that the phenological development is delayed and that the photosynthetic active period has been shortened through an enhanced snow cover, but also that flowering and therefore reproductive effort (compare Arft et al., 1999) has taken place despite the fact that the growing season was substantially shortened (Walker et al., 1999; Borner et al., 2008) it has not been tested whether seed viability is also influenced. It can be hypothesised that a short photoactive period leads to altered allocation of photosynthesis products in favour of below ground storage to ensure leaf set in the following spring rather than investing in reproduction, and therefore inhibits seed and bulbil ripening processes. A higher nutrient availability in spring after an earlier occurrence of snow cover in autumn and later melt out in spring initiated by snow fences in Toolik, Alaska, has been detected (Schimel et al., 2004). Together with the finding that increased nutrient availability increases seed viability (Wookey et al., 1994; 1995), this could counteract possible negative effects on reproductive success after a prolonged winter.

In this study we look at short-term responses of plants to enhanced snow cover in terms of phenology and reproductive success. Snow fences were used to increase snow depth in a controlled manner. In comparison to ambient conditions, a shorter growing season was expected to (1) delay phenological development, (2) decrease the amount of reproductive units (seeds and propagules) and (3) decrease the fraction of germinable seeds produced during one season.

2 Materials and methods

2.1 Study site

This study was carried out in Adventdalen (N78°10’, E16°06’), one of the biggest valleys on Spitsbergen, Svalbard archipelago. Normal monthly temperatures as measured at Svalbard airport from 1961 to 1990 range from -16.2°C to 5.9°C in February and July, respectively, with an annual mean of -6.7°C. However, daily extreme temperatures can reach over 2°C and 12°C in the coldest and warmest month, respectively, and warm spells during winter occur regularly. Normal monthly precipitation ranges from 6mm to 23mm in May and March/August, respectively, with an annual mean of 190mm, of which a large portion falls as snow producing an unknown amount of under catch (Forland & Hanssen-Bauer 2003).

Investigations were carried out in two habitat types, namely the *Cassiope tetragona* heath (heath) and the mesic meadow (meadow).

2.2 Snow fences

Twelve fences with an average height of 1.5m and an average length of 6.2m (Elke Morgner 2009) clustered in four blocks with three fences each were placed in two habitat types (heath and meadow) in autumn 2006. These fences were aligned perpendicular to the prevailing eastern winter winds and produced snow accumulations with a final height as high as the fences (about 1.5m) and of varying length on the lee side of each fence by reducing wind speed and forcing suspended snow to deposit. Each block of fences covers an area of not more than 200x200m and, in order to investigate spatial variances, distances between blocks are >500m. Two blocks are situated in heath, two in meadow vegetation. After snowmelt in 2007, six 75x75cm plots were established in the core zone behind each fence, i.e. the area with highest snow depth, and associated with six unaffected control plots of the same size which were located in immediate vicinity showing the same vegetation composition. Vegetation composition within a cluster of six connected plots was chosen to ensure that there were at least three plots enclosing *Dryas octopetala* and three plots containing *Cassiope tetragona*, representing the focus species in the study site. *Cassiope* could not be found in one fence area and therefore only three plots with *Dryas* were established behind this particular fence resulting in a total of 138 plots in the entire study area (69 fence and 69 control plots).

2.3 Phenology data

Timing of phenophases was assessed visually by defining a total of 13 phases taking the whole life cycle including vegetative and reproductive phases into account. Phenophases were defined in order to be easily recognized by morphological traits such as gain or loss of chlorophyll or appearance of flowers etc., with a focus on leaf senescence. Some phenophases were not applicable to all species, e.g. *Bistorta vivipara* could not be found with seeds because sexual reproduction could not be observed (see Molau and Edlund, 1996) and two special stages were assigned to *Salix polaris*. See Figure 1 for a more detailed description of the assigned phenophases.

The following 13 species were studied: *Dryas octopetala*, *Cassiope tetragona*, *Salix polaris*, *Saxifraga oppositifolia*, *Alopecurus magellanicus*, *Luzula arcuata* ssp. *confusa* , *Bistorta vivipara*, *Oxyria digyna*, *Papaver dahlianum*, *Stellaria crassipes*, *Pedicularis hirsuta*, *Cerastium arcticum* and *Cardamine bellidifolia*. All plots were observed on a weekly basis during the whole growing period from June until September in 2008. Duration of snow cover was assessed daily until all plots were snow free in 2008. Transitions between phenophases in each plot were registered when 50% or more individuals per species or, for large tuft forming species, 50% or more of the area covered by one species reached the next phenophase. Additionally, flowers of *Pedicularis hirsuta*, *Saxifraga oppositifolia*, *Stellaria crassipes*, *Cassiope tetragona* and *Dryas octopetala* were counted whenever visible.

2.4 Seed stratification and germination

If available, seeds of *Luzula arcuata* ssp. *confusa*, *Salix polaris*, *Cassiope tetragona*, *Alopecurus magellanicus*, *Dryas octopetala* and bulbils of *Bistorta vivipara* were collected upon visually assessed ripeness during the first two weeks of September 2008 and kept in paper bags at a sheltered, dry place outside until they were transported to Tromsø on September 15th 2008 where they were stored at 0.5°C in dry conditions. In order to keep the plots undisturbed for later investigations, seeds and bulbils were picked randomly around the plots within the treatment and related control areas with fences and control areas as replication units (not plots).

Germination and stratification were undertaken at Klimalabben Holt, Tromsø, Norway. Seeds and bulbils were sown out two to six weeks after collection.Hagen (2002) found that non-stratified seeds of *Luzula* and bulbils of *Bistorta* from Svalbard had germination rates over 80% when collected in middle of August 1998, which is one month before collection of propagules in this study, and seeds of *Salix polaris* are expected to be easily germinated without stratification (J. Nilsen, pers. comm. 2008) and seeds of other, alpine *Salix* species were found to have high germination rates when germinated unstratified (Bliss, 1958). Therefore, seeds of *Luzula* and *Salix* and bulbils of *Bistorta* were put to germination without stratification. Fresh *Dryas* seeds were found to have weak germination rates in other studies (e.g.Hagen, 2002) and seeds of *Cassiope* and *Alopecurus* are thought to have seed dormancy (ref; J. Nilsen pers. comm. 2008). Therefore, seeds of *Cassiope*, *Alopecurus* and *Dryas* were subjected to a stratification treatment with repeated freeze-thaw cycles over a period of 6 weeks prior to germination. Stratification was carried out in a programmable freezer subjecting the seeds to the following program: -2°C for 48h, +2°C for 48h, -2°C for 144h, +2°C for 96h and -4°C for three weeks. Germination for all propagules was carried out for twelve weeks at 18°C at continuous light to simulate the length of an optimum growing season (Cooper et al., 2004).

Non-stratified seeds and bulbils were sown out on filter paper connected to a water reservoir and covered with a plastic cup to ensure constant moisture. Stratified seeds were sown out on a wet mixture of 50% “Floralux” peat and 50% “Perlite” and covered with Petri dishes prior to stratification and kept in the same containers until the end of the germination period. All seeds and bulbils used for germination were randomly sown out in three subsets per fence and control area and each subset contained the same amount of seeds with a maximum number of 50 seeds/ subset.

Seeds or bulbils were observed visually every two to seven days during the whole germination period of twelve weeks and counted as germinated when they showed a radicle or cotyledon or both.

2.5 Statistical analyses

Each phenophase was analyzed separately. Timing of phenophases was measured as absolute timing, measured in Julian days showing the date of occurrence of each phenophase during the course of the year, and relative timing, measured in days after snowmelt indicating days needed for a particular phenophase to occur counted from the start of the growing season. The temporal distance of phenophase timing between control and fence treatments was determined by subtracting mean dates and days after snowmelt, respectively, as measured behind fences from values measured in controls (control minus fence values), with positive values indicating a later start (absolute timing) or a higher amount of days needed (relative timing) and negative values indicating an earlier start (absolute) or less days needed to reach a particular phenophase.

For germination studies, the total count of germinated seeds after twelve weeks averaged over all three subsets per fence and control area, respectively, was taken as the replicated response value.

Differences of phenophase timing and germination success between treatment (enhanced snow cover) and control areas were tested by linear mixed effects models (LME) to account for the blocked experimental setup. We used the function lme in the R-package *nlme* (Pinheiro et al., 2008) allowing for random effects (intercept and slope) of the four different blocks per treatment.

Flowers were not marked after being counted, so enduring flowers might have been counted several times during the season. In order to account for the number of flowers found and the duration of the flowering period, flower counts are analyzed as the sum, not as means of flowers, found during the whole growing season in fence and controls areas. However, Figure 3 provides an overview of the temporal characteristics of flower production.

Although the phenology of a total of 13 species has been observed, only species with sufficient abundance to produce statistically relevant phenology data (*Dryas octopetala*, *Salix polaris*, *Luzula arcuata* ssp. *confusa*, *Bistorta vivipara*, *Cassiope tetragona*) have been included in the statistical analysis.

3 Results

3.1 Phenology

Snow melted significantly later behind fences than in control areas (Julian date 174.87±3.8 and 163.91±2.08, respectively; mean±sd; T=-21; df=105.25; p<0.001; t-test). The prolonged snow cover resulted in a mean delay of the start of the growing period of approx. 11±4.48 days (mean±sd) behind fences.

Absolute timing of most species' vegetative and reproductive phenophases was delayed behind fences, i.e. they occurred significantly later in the year compared to controls ($p<0.05$, Figure 1). For some species, namely *Dryas octopetala*, *Bistorta vivipara* and *Cassiope tetragona*, flower senescence or ripening of seed heads, and therefore successful dispersal of reproductive units, occurred concurrently for both treatment and control groups, while all other phenophases including flower production for the same species were delayed behind fences. This leads to a significant difference ($p<0.05$) in days after snow melt for the same phenophase and species, with fewer days until entry of seed maturity or flower senescence behind fences (Figure 1). Additionally, only *Dryas* displayed a concurrent end of growing season for both treatment groups, implying a bond to external triggers accounting for total leaf senescence, although earlier leaf senescence phases were delayed behind fences.

The time span between snow melt and the appearance of individual phenophases (i.e. relative timing) showed varied patterns among species. In terms of days after snowmelt, some species used more, others less or equal numbers of days to reach a particular stage after an artificially delayed start of the season behind fences. Looking at the overall trends, the following response patterns could be found: (1) Compared to controls, it took *Dryas octopetala*, *Cassiope tetragona* and *Luzula arcuata* ssp. *confusa* more days in the first half and less days in the second half of the growing season to reach a particular stage. The transition (from a delayed to an accelerated phenological development) took place after flower production (Figure 1). Compared to ambient conditions, these species needed more days to reach leaf maturity and produce flowers. Hence, the effect of shortening the season (by later snow melt) was reinforced by slower early development further decreasing the number of days available to reach seed ripening (and leaf senescence). Some variations of the described pattern in *Cassiope* and *Luzula* can be found when it comes to flower senescence which sets in after the same number of days in treatment and control groups (Figure 1). (2) Both treatment groups of *Bistorta vivipara* showed an equal use of days for all phenophases until flowering whereas fewer days were needed to reach later phenophases behind fences. However, the total end of season for this species did not show differences in relative timing (Figure 1). (3) As in the species of the first group, it took *Salix polaris* longer until flower production, but the consecutive development was not accelerated in this species, thus producing a general delay of all phenophases in terms of absolute timing (Figure 1).

3.2 Flower counts

Table 1 shows the total number of flowers found during the whole growing season in plots behind fences and in controls. Areas with enhanced snow cover had a clearly reduced flower production compared to areas with ambient snow cover. Figure 3 shows time series of mean flower numbers per plot and week and illustrates the reduced rate and delayed start, end and peak of flowering behind fences. However, flowering seems to be synchronized when analyzed in relative terms, i.e. in weeks after snowmelt. This effect can also be clearly observed in the field when areas behind snow fences are the only areas without flowers while full flowering occurs in control areas.

3.3 Germination

The fraction of germinable propagules varied with species and treatment and a significant treatment difference could only be found in *Bistorta vivipara* and *Dryas octopetala* (Figure 2). *B. vivipara* bulbils and *Dryas octopetala* seeds from control areas had a sprouting/germination success of

85±4.1% and 8.6±5.26% whereas only 66.8±9.6% and 0.5±0.87% of propagules from fence areas sprouted showing a significant difference between the two treatments, respectively (mean±sd; df=67 and 52, respectively; p<0.005), indicating a quality loss of dispersal units through shortening of growing season.

Luzula arcuata ssp. *confusa* showed a non-significant decreased fraction of germinable seeds in fence compared to control areas (26.8±9.2 and 36.3±16, respectively; mean±sd; df=58; p=0.119) indicating a possible loss of reproductive success that could be explained by enhanced snow cover and a resulting shortened growing season.

The difference of germination success of *Salix polaris, Alopecurus magellanicus* and *Cassiope tetragona* seeds from control compared to fence treatment was not significant (Figure 2) indicating that a shortened growing season does not have an effect on the quality of these species' seeds. However, for the latter two species this comparison had very low statistical power due to overall low germination rates.

Out of the 72 interconnected plot pairs, dispersing seeds of *Salix polaris* and *Dryas octopetala* were found in 54 and 39 control but only in 36 and 4 fence plots, respectively, indicating that the fence treatment and resulting shorter growing season reduced the quantitative reproductive success. No other species showed the effect of an unbalanced number of plots going through seed ripening, although the total number of flowers per plot was lower behind fences.

4 Discussion

4.1 Vegetative response

Fences installed in Adventdalen clearly delayed start of and therefore shortened growing season by later snow melt in spring but did not change summer and autumn conditions. This resulted in a delay of most phenophases of all investigated species as was observed in previous snow fence studies in the Alaskan arctic (Walker et al., 1999; Borner et al., 2008). However, the delay of senescence for most species behind fences compared to controls is smaller than the delay of start of season, i.e. the period between start of season and senescence is shorter behind fences than in controls. As a consequence, phenological development is condensed to fit into the shorter growing period, i.e. the whole life cycle is completed within a shorter period.

The two evergreen shrubs *Cassiope tetragona* and *Dryas octopetala* and the forb *Bistorta vivipara* show this shorter time used to reach a phenophase in a very extreme way when it comes to dispersal of seeds, which happened simultaneously behind fences and in controls. This indicates that timing of late phenological phases and especially of seed dispersal is independent of spring snow melt events in these species but rather controlled by external cues like temperature or light wavelength (Marchand et al., 2004; Aerts et al., 2006). In contrast, the other observed species, namely the graminoid *Luzula arcuata* ssp. *confusa* and the deciduous shrub *Salix polaris*, do show later seed dispersal with later snowmelt indicating a less flexible reproductive development under varied season lengths. This lower temporal plasticity seems to be a generic feature of the early phenophases, as early season green-up and flowering were mostly delayed for all studied species behind snow fences.

Borner et al. (2008) and Walker et al. (1999) have found similar late-season responses, i.e. an externally triggered leaf senescence, for *Betula nana*, *Salix pulchra*, *Eriophorum vaginatum*, *Vaccinium vitis-idaea* and *Dryas octopetala* in the Alaskan arctic but the triggers of these late season processes have not been clearly identified yet. Generally, day length cannot be a driving factor for induction of any kind since the study area is far enough inside the polar circle that midnight sun is given throughout most of the growing period. However, the spectral composition of daylight in high latitudes with a continuous light regime changes during the transition from midnight sun to polar night to a higher content of far-red light (and vice-versa), which can be sensed by photoreceptor proteins, mainly phytochromes, in vascular plants and therefore act as cues for growth cessation inducing leaf senescence and seed ripening (Olsen and Junttila, 2002; Tsegay et al., 2005). Accounting for temperature sums would eventually allow for more unambiguous conclusions about the ecophysiology of induction of each phenophase for each species. This analysis could not be carried out in this study since complete data sets of temperature in the study sites are missing. However, the observed shortening of growing season might have important implications on plant growth, if reduced season length is not compensated by faster growth due to accelerated decomposition and mineralization rates introduced by a possible increase of microbial activity through higher and more stable soil temperatures under the deeper soil pack providing an increased amount of plant available nutrients (Schimel et al., 2004).

4.2 Reproductive response

Reproductive success is clearly reduced through an increased snowpack. Although viability of propagules of all species except *Bistorta vivipara* and *Dryas octopetala* is not affected by a shortened growing season and therefore less time to ripen, the number of flowers and, consequently, dispersing seed heads is strongly reduced during a shorter growing period. The reduced number of flowers can be a response to a previous shortened season with less time for photosynthetic activity and resource allocation, since flower buds for many arctic species are established in previous years. Additionally, start of flowering and the peak of flower production are delayed through later melt out dates, which in the case of insect pollinated species can have influences (1) on survival of pollinators foraging for flowers and (2) on pollination of the flowering plants themselves if the synchronicity of flower and pollinator phenology and therefore the pollination network is disturbed (Olesen et al., 2008). The reduced number of dispersing seed heads of *Dryas octopetala* behind fences might be due to a lack of pollinators present when this species was in full bloom.

The very low germination rates for the three stratified species *Cassiope tetragona*, *Alopecurus magellanicus* and *Dryas octopetala* might be due to two reasons. First, the year 2008 was an exceptionally cold year and first ripe seed heads were found much later than for example in the year when seeds were collected by Hagen (2002). It's possible that not all species were able to produce fully ripe seeds until the time of seed collection and maybe ripe seeds of many species were very scarce that year. Second, the stratification methods might have been destructive for the three species' seeds, causing the low germination rates, and further studies will have to be conducted in order to find the right treatments and highest germination yields for those and many other arctic species' propagules.

4.3 Ecosystem responses

Suddenly increasing snow cover by means of fences can be considered as transforming the affected area into a natural snow bed (compare Bell and Bliss, 1979). If this happens to a whole community in the long term, i.e. for several seasons in a row, this can have consequences on community structures by pushing particular species to their physiological limit of growth, inhibiting generative reproduction, and by altering species interactions and therefore survival and fitness of individual species with varied adaptations to natural variations of snow depth and snow melt timing as has been found by Scott and Rouse (1995) in upland tundra. A more flexible adaptation to growing season start as shown by the snow bed species *Cassiope tetragona* will be advantageous in the case of increased snow cover and no losses in carbon uptake and energy storage can be expected for this species, whereas other, less flexible species might have substantially reduced growth rates through a shortened season. This might explain the dominance of *Cassiope tetragona* in snow-bed communities whereas *Dryas octopetala*, which has a more conservative photoactive period, is constrained to windswept ridge communities with a very low snow cover. However, sexual reproduction in the context of numbers of flowers is reduced behind fences for all studied species.

A potential increase of *Cassiope tetragona* and a possible increase or decrease of other species could have positive and negative effects on neighboring vegetation and therefore increase the effects of a deepened snowpack through positive feedbacks. Wipf et al. (2006) have found facilitative neighbor interactions for two dwarf shrubs in sub-arctic Alaska which is probably attributable to the change of microclimate in immediate vicinity of a dense canopy by decreasing wind speed, water loss and other physical properties. *Cassiope tetragona* is one of the highest growing and most abundant species in the study site and therefore constitutes an important part of the canopy. Its increase of abundance could lead to a change of canopy structure and trigger positive feedbacks for its own and other, associated species' growth and survival which are dependent on a stable microclimate during the growing season and on an early onset of a protective snow cover in autumn through the snow trapping properties of a higher canopy (Sturm et al., 2005). Competitive neighbor interactions could be that this relatively high growing shrub outcompetes species with a narrower time-of-snowmelt range, as has been suggested by Heegaard and Vandvik (2004) for alpine snow cover gradients. It has been proposed that snow bed species are restricted to habitats with a relatively late melt out date due to their low competitiveness, not due to their physiological inability to grow in early melting habitats (Heegaard and Vandvik, 2004; Björk and Molau, 2007). A changed, deeper snowpack with a consequent later melt out date than before as used in the present study can therefore be hypothesized to favor snow bed species over ridge and intermediate snow depth species and in the long term contribute to a change in species composition in affected areas.

A later start of season and a consequently later production of live biomass will have severe consequences for the Svalbard reindeer and ptarmigan, the only herbivores overwintering on the Svalbard archipelago, which are surviving on limited reserves during winter and mainly depend on energy reserves collected during the short summer (Unander and Steen, 1985; Van der Wal et al., 2000). Therefore, a delay of two weeks before forage becomes available can have effects on the whole population, especially following a cold or short summer the previous year.

5 Conclusion

The present study shows the possible effects of one suggested climate change scenario which projects an increase of snow cover in arctic regions (e.g. Acia, 2005). In accordance with other studies (Walker et al., 1999; Borner et al., 2008), the use of snow fences to simulate such a delayed snow melt has clearly demonstrated short-term changes of plant performance and fitness by altering phenology and reproductive success of the investigated species. Phenology was delayed and the photoactive period was shortened for all studied species but one. The onset of seed dispersal and leaf senescence are shown to be externally triggered processes for some species, and the nature of these processes will have to be identified. Germination rates were not influenced by a delay of snow melt for all investigated species but two, which implies different degrees of reproductive plasticity among the investigated species. In the context of long-term increases of snow cover, physiological constrains and facilitative as well as competitive species interactions can be expected to lead to substantial changes in species composition.

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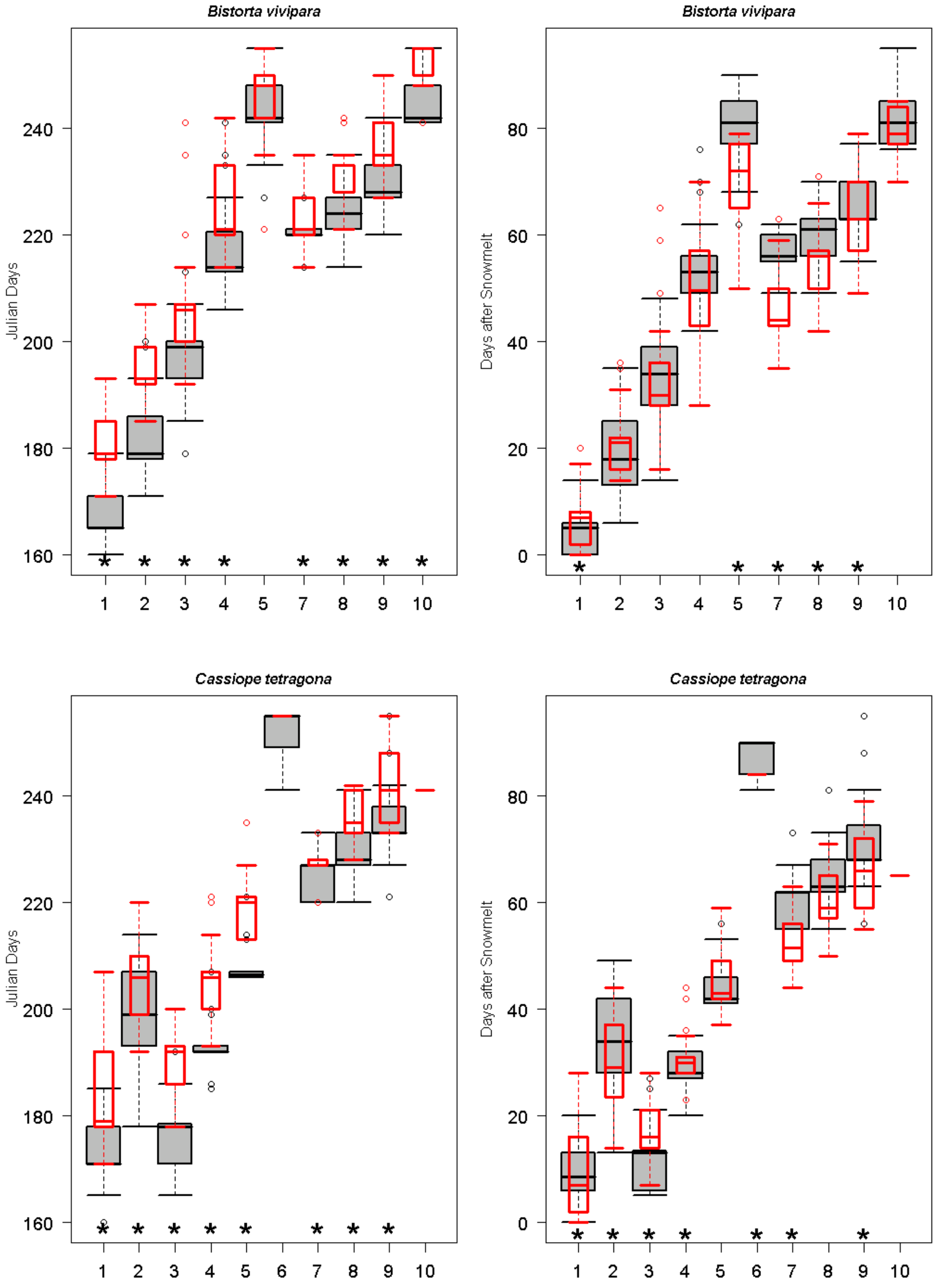
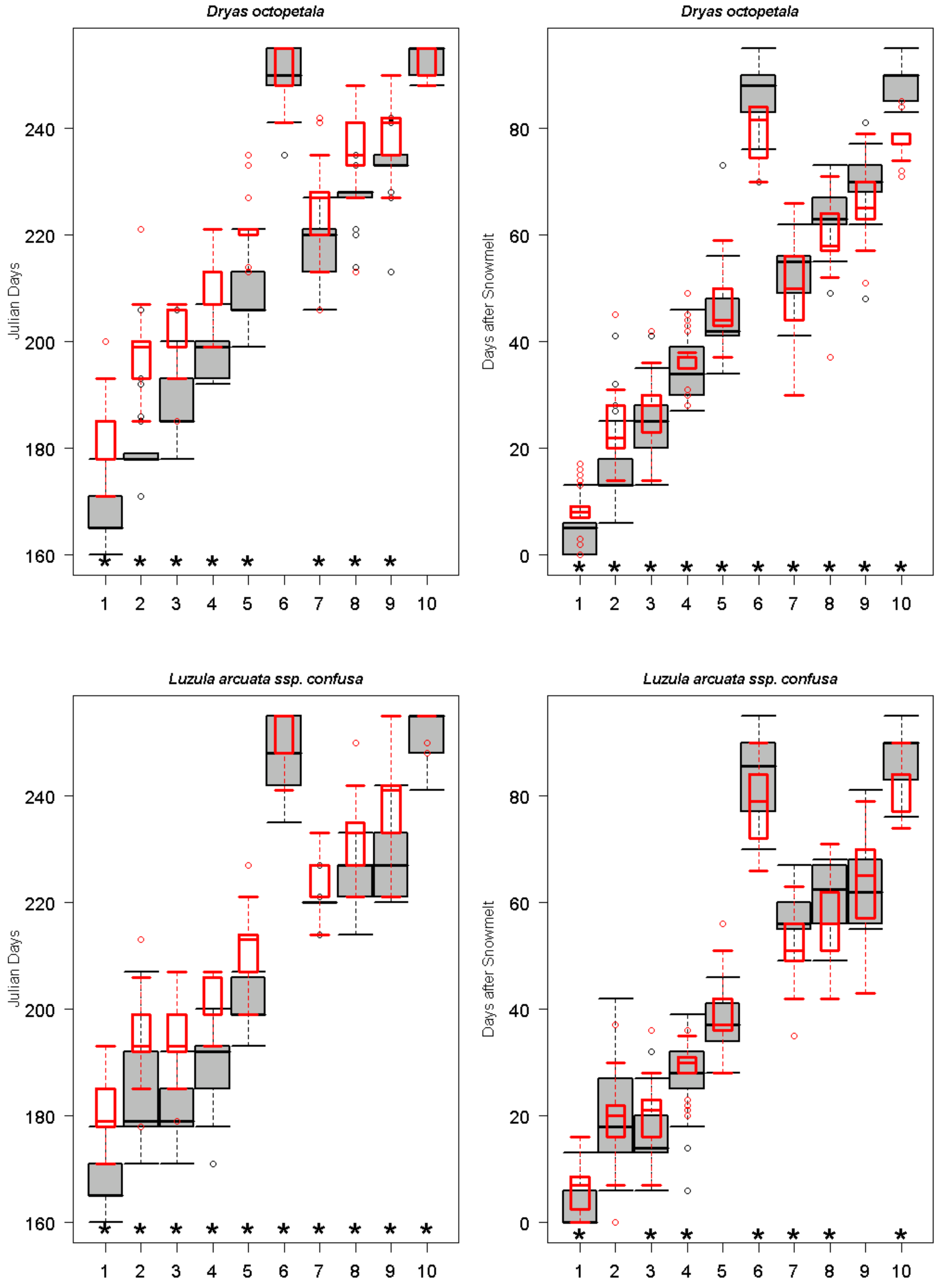
7 Tables and Figures

Table 1 Total numbers of flowers found behind snow fences which accumulate snow and under ambient conditions as counted during the whole season of five species growing in high-arctic tundra in Svalbard.

Species	**Controls**	**Fences**
Stellaria crassipes	641	279
Saxifraga oppositifolia	236	55
Pedicularis hirsuta	492	257
Dryas octopetala	848	280
Cassiope tetragona	25578	17035


Bistorta vivipara
Julian Days
240
220
200
180
160
1
2
3
4
5
7
8
9
10
Bistorta vivipara
Days after Snowmelt
80
60
40
20
0
1
2
3
4
5
7
8
9
10
Cassiope tetragona
Julian Days
240
220
200
180
160
1
2
3
4
5
6
7
8
9
10
Cassiope tetragona
Days after Snowmelt
80
60
40
20
0
1
2
3
4
5
6
7
8
9
10


Dryas octopetala
Julian Days
160
180
200
220
240
Dryas octopetala
Days after Snowmelt
0
20
40
60
80
Luzula arcuata ssp. confusa
Julian Days
160
180
200
220
240
Luzula arcuata ssp. confusa
Days after Snowmelt
0
20
40
60
80
1
2
3
4
5
6
7
8
9
10
*

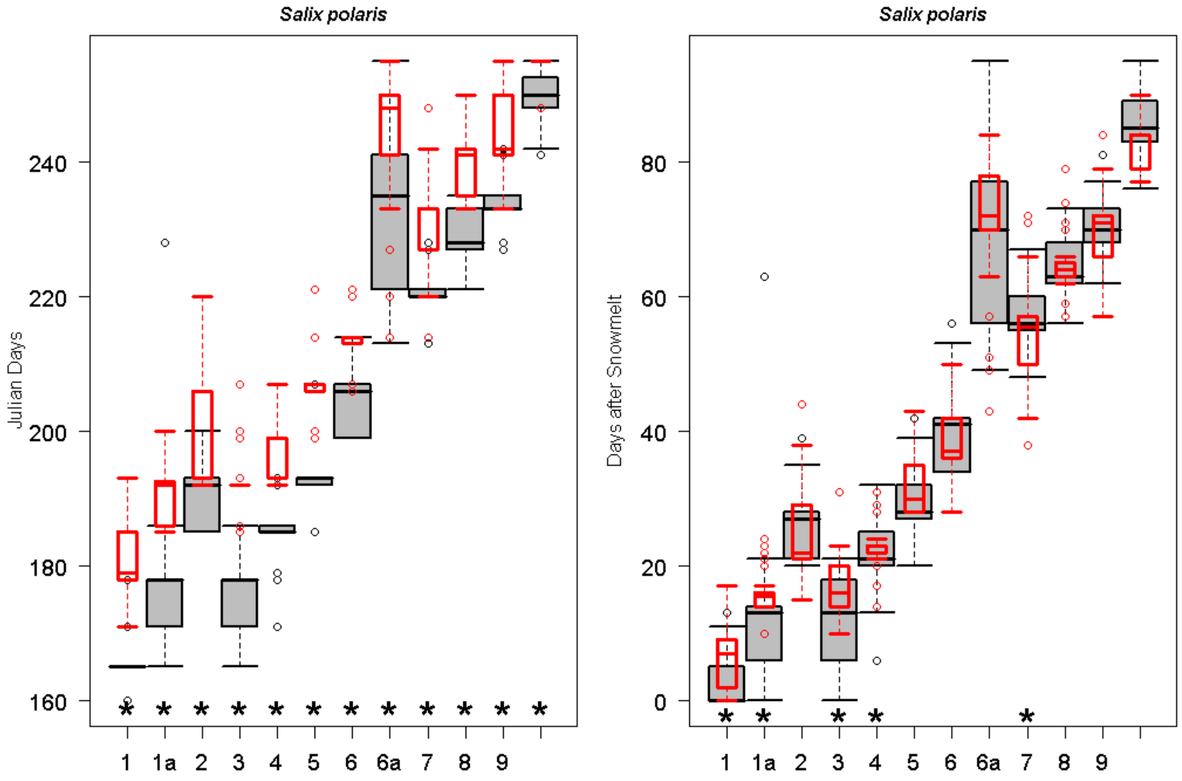


Figure 1 Results of visual assessment of timing of phenophases of five high-arctic tundra species in Svalbard growing either behind snow fences which enhanced snow cover (red boxes) or under ambient conditions (black boxes). Absolute timing given in Julian date, relative timing given in days after snowmelt. Phenophases: 1=First response after snow melt, i.e. leaves starting to become green or starting to develop, buds of *Salix polaris* swollen. 1a=Bud burst of *Salix polaris,* furled leaves visible. 2=Leaves fully open or green. 3=Flower buds visible. 4=Flowers open. 5=Flowers senesced. 6=Seed heads ripe or swollen ovaries of *Salix polaris*. 6a=Ovaries of *Salix polaris* burst open, i.e. dispersal of seeds. 7=25% of leaves of individuals/area per species senesced. 8=50% of leaves of individuals/area per species senesced. 9=75% of leaves of individuals/area per species senesced. 10=All leaves per species senesced, i.e. end of growing season. Note that not all species have every stage. Values significantly different at p<0.05 between fences and controls indicated with *.

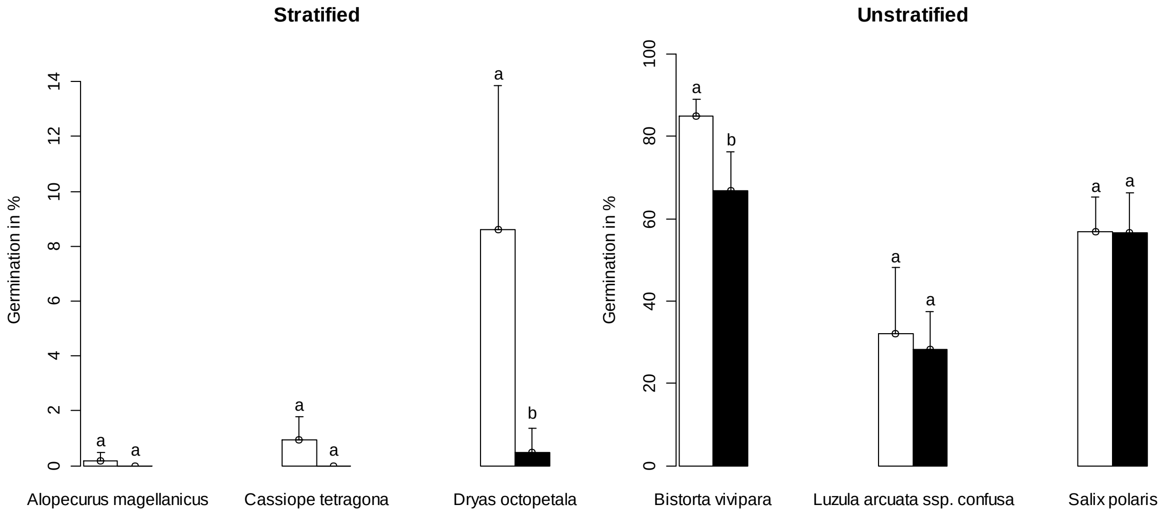
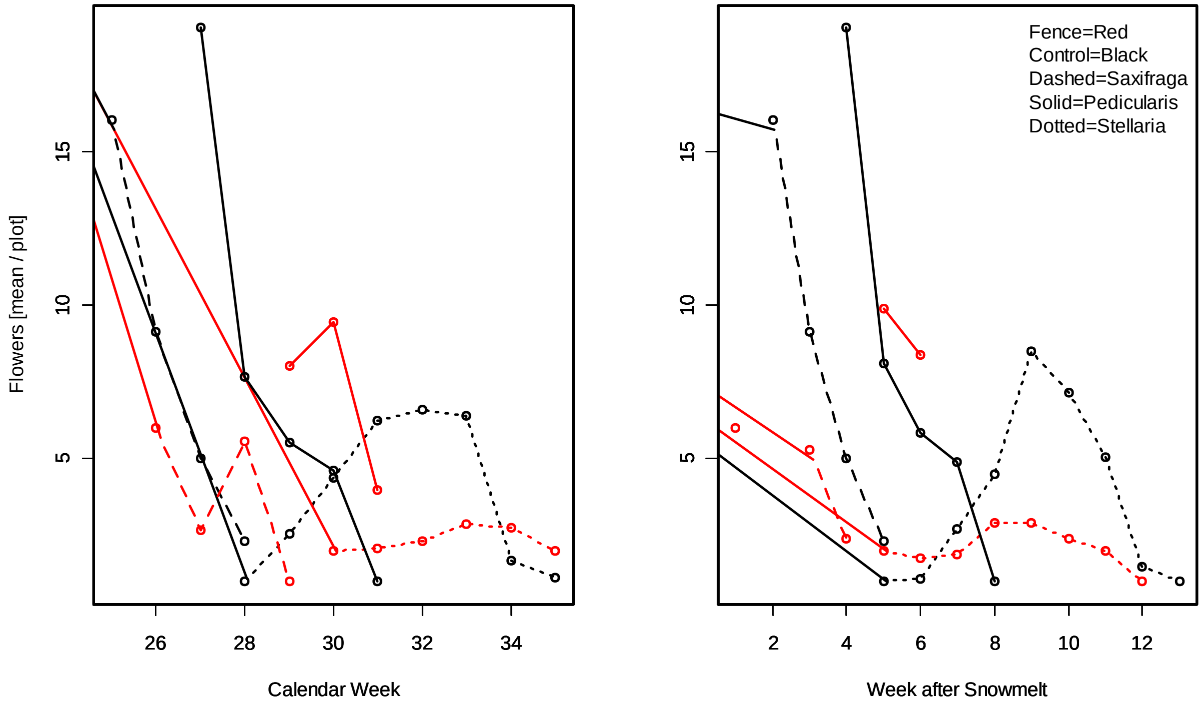
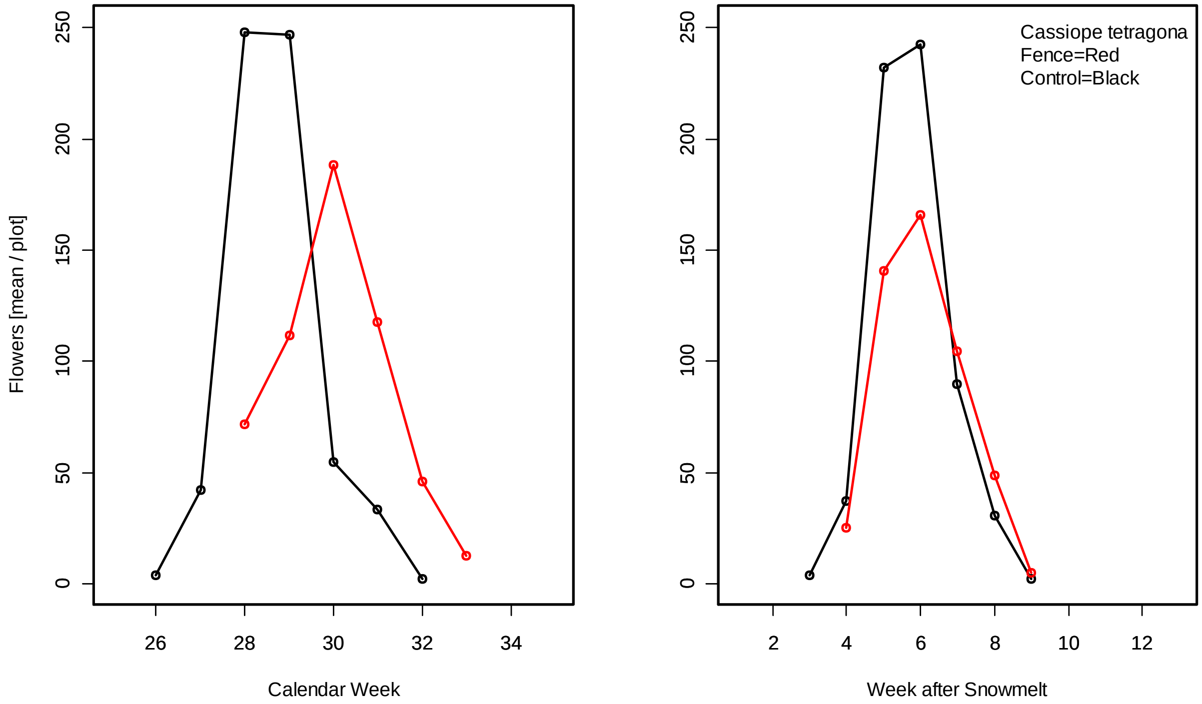


Figure 2 Germination success of propagules of six high-arctic tundra species in Svalbard collected either behind fences which enhance snow cover resulting in a delayed melt out and a shortened growing season (black) or under ambient conditions (white). Values are percentages of seeds sown, Error bars represent SD. Different letters indicate significantly different germination rate ($p<0.05$). Note the different scales of the y-axes. See materials and methods section for stratification methods.


Flowers [mean / plot]
5
10
15
26
28
30
32
34
Calendar Week
5
10
15
2
4
6
8
10
12
Week after Snowmelt
Fence=Red
Control=Black
Dashed=Saxifraga
Solid=Pedicularis
Dotted=Stellaria


Flowers [mean / plot]
0
50
100
150
200
250
26
28
30
32
34
Calendar Week
0
50
100
150
200
250
2
4
6
8
10
12
Week after Snowmelt
Cassiope tetragona
Fence=Red
Control=Black

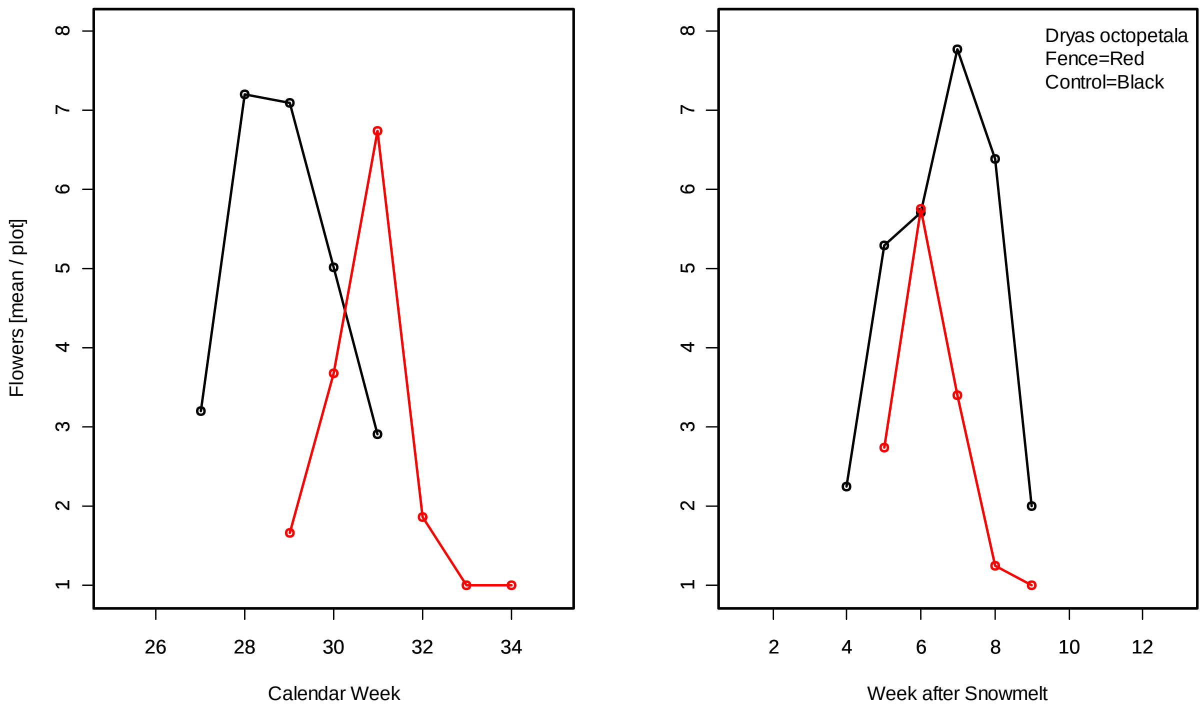


Figure 3 Mean number of flowers per plot and week of *Saxifraga oppositifolia*, *Pedicularis hirsuta*, *Stellaria crassipes, Cassiope tetragona* and *Dryas octopetala* in absolute (Calendar Week; left) and relative (Week after Snowmelt; right) timing. Fence plots in red, control plots in black.

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Appendix I: Zusammenfassung/ Überblick

Arktische Regionen gehören zu den Gegenden der Erde welche vom Klimawandel am meisten betroffen sind. Insbesondere Wintertemperaturen haben sich in den letzten Jahrzehnten verändert und es werden längerfristige Veränderungen hydrologischer Prozesse wie z.B. Niederschlagsmengen und -formen (flüssig, fest) und Verteilung von Schneemassen diskutiert (z.B. Serreze et al., 2000; Dormann and Woodin, 2002; Acia, 2005; Lemke et al., 2007). Messfehler, inkonsequente Mess-Methoden, lückenhafte Messreihen, natürliche Witterungsschwankungen und nicht ausreichend bekannte makroklimatische Prozesse führen zu unsicheren Trendberechnungen und Klimawandelszenarios (Groisman and Easterling, 1994; Serreze et al., 2000; Forland and Hanssen-Bauer, 2003; Acia, 2005). Dementsprechend ungenau sind Modelle zur Berechnung der Schneedecke und die Vorhersagen für die nächsten Jahrzehnte reichen von höheren Schneetiefen mit entsprechend verzögertem Abschmelzen und dadurch verkürzten Vegetationsperioden bis zu reduzierten Schneetiefen mit verfrühtem Abschmelzen.

Hocharktische Regionen sind aufgrund niedriger mittlerer Jahrestemperaturen ausgezeichnet durch späte Schneeschmelze und daher durch kurze Wachstumsperioden (Schmidt et al., 2006), geringe Nährstoffumsätze (Nadelhoffer et al., 1992) und ausgeprägte intra-saisonale Feuchtigkeitsschwankungen (Scott and Rouse, 1995). Die Dauer der Schneedecke steuert viele ökophysiologische Prozesse und damit letztlich Fitness und Reproduktionserfolg, welche die Artenzusammensetzung auf Landschaftsniveau entscheidend mitbestimmen. Es wurde gezeigt, dass der Reproduktionserfolg hocharktischer Arten mit steigenden Temperaturen (Arft et al., 1999) und Nährstoffverfügbarkeit (Wookey et al., 1994; 1995) zunimmt. Walker (1999) und Borner (2008) haben festgestellt, dass Diasporenproduktion stattfand, obwohl die Phänologie verzögert und die photoaktive Periode durch experimentell erhöhte Schneedecke verkürzt war. Es wurde allerdings nicht getestet, ob die Reproduktionseinheiten fruchtbar waren oder nicht. Wir vermuten, dass eine verkürzte Wachstumsperiode zu einem Mangel an Photosyntheseprodukten führt und Fruchtreifungsprozesse hemmt und dadurch Reproduktionserfolg verringert.

In dieser Arbeit wurde die Schneehöhe mittels Zäunen erhöht und der Einfluss dieser Veränderung auf Phänologie und Reproduktionserfolg im Vergleich zu nicht manipulierten Umgebungsbedingungen getestet. Unsere Arbeitshypothesen waren, dass erhöhte Schneetiefe und damit einhergehender verzögerter Start der Wachstumsperiode (1) die phänologische Entwicklung verzögert, (2) die Anzahl an Diasporen verringert und (3) die Keimfähigkeit von Reproduktionseinheiten (Samen und Brutknollen) verringert. Die Studie wurde in Adventdalen, Spitzbergen (N78°10’, E16°06’) durchgeführt. Die lokalen klimatischen Eckdaten sind Jahresmitteltemperaturen von -6.7°C und jährliche mittlere Niederschlagsmengen von 190mm. Schneezäune wurden senkrecht zur vorherrschenden Windrichtung aufgestellt, um ca. 1.5m hohe Schneeansammlungen auf der Leeseite der Zäune zu produzieren.

Die Phänologie von insgesamt 13 Arten wurde wöchentlich aufgenommen, wovon fünf in der vorliegenden Arbeit präsentiert werden (*Bistorta vivipara, Cassiope tetragona, Dryas octopetala, Luzula arcuata* ssp. *confusa, Salix polaris*) (Figure 1). Gleichzeitig wurden Blüten von fünf Arten gezählt (*Stellaria crassipes, Saxifraga oppositifolia, Pedicularis hirsuta, Dryas octopetala, Cassiope tetragona*) (Figure 3). Samen von sechs Arten wurden gesammelt, sobald sie reif erschienen, und drei Arten wurden direkt (*Bistorta vivipara, Luzula arcuata* ssp. *confusa, Salix polaris*), drei Arten nach Stratifizierung (*Alopecurus magellanicus, Cassiope tetragona, Dryas octopetala*) zum Keimen gebracht. Alle zwei bis sieben Tage über einen Zeitraum von 12 Wochen wurde die Anzahl der gekeimten Samen überprüft, und gekeimte Samen/Brutknollen entfernt (Figure 2).

Flächen hinter den Zäunen wurden 11±4.48 Tage später schneefrei als unbeeinflusste Kontrollflächen, was dazu führte, dass die meisten Phenophasen hinter den Zäunen verzögert zu den Kontrollflächen begannen (Figure 1). Samenreife bzw. Blütenseneszenz einiger Arten trat jedoch gleichzeitig hinter den Zäunen und in Kontrollflächen ein, was einen Verlust an Reifungszeit impliziert: Es wurde hinter den Zäunen weniger Zeit nach Schneeschmelze, also nach Beginn der Wachstumsperiode, zum Reifen der Diasporen benötigt als in Kontrollflächen. Das Erscheinen individueller Phenophasen in Tagen nach der Schneeschmelze zeigte unterschiedliche Reaktionsformen für verschiedene Arten: (1) Individuen von *Dryas*, *Cassiope* und *Luzula* hinter den Zäunen brauchten in der ersten Hälfte der Wachstumsperiode (von Schneeschmelze bis Blütenbildung) mehr Zeit, um bestimmte Phenophasen zu erreichen als in der zweiten Hälfte. Produktion von photosynthetisch aktiven Blättern und Blüten nahm mehr Zeit in Anspruch als in Kontrollflächen und verstärkte somit den Effekt der Verkürzung der Wachstumsperiode und gab Samenreifungsprozessen noch weniger Zeit. (2) Die gleiche Anzahl an Tagen für Phenophasen vor Blütenproduktion hinter Zäunen und in Kontrollen wurde von *Bistorta* benötigt, für die Seneszenzphasen und Reifung der Brutkörper wurden allerdings weniger Tage benötigt. (3) Salix brauchte länger für Phenophasen vor Blütenproduktion, spätere Phenophasen waren allerdings nicht beschleunigt.

Die Bluetenanzahl hinter den Zäunen war stark reduziert und der Anfang, Höhepunkt und Schluss der Blühperiode war verzögert, benötigte aber die gleiche Anzahl an Tagen nach Schneeschmelze (Figure 3).

Bistorta Brutknospen und *Dryas* Samen von Versuchsflächen mit erhöhter Schneedecke hatten geringere Keimungsraten als Brutknospen/Samen von Kontrollflächen. *Luzula* zeigte insignifikante geringere Keimungsraten hinter Zäunen und *Salix*, *Alopecurus* und *Cassiope* zeigten keine reduzierte Keimungsfähigkeit (Figure 2).

Die vorliegende Studie zeigt ähnliche Ergebnisse wie frühere Studien (Walker et al., 1999; Borner et al., 2008), und zwar dass eine erhöhte Schneedecke und der daraus resultierende verspätete Start der Wachstumsperiode zur Verkürzung der photoaktiven Periode führt: Frühe Phenophasen benötigen die gleiche Zeit bzw. teilweise länger, während späte Phenophasen der meisten Arten nach kürzerer Zeit einsetzen. Das weist darauf hin, dass frühe Phenophasen wie Produktion photosynthetisch aktiver Blätter und Blüten unabhängig von externen Einflüssen ist, also womöglich genetisch determiniert sind, während spätere Phenophasen wie Fruchtreife und Seneszenz von äußeren Signalen wie Temperatur und spektraler Zusammensetzung des Lichts beeinflusst werden (Marchand et al., 2004; Aerts et al., 2006).

Der Reproduktionserfolg wurde durch eine erhöhte Schneedecke stark reduziert. Zwar wurde die Keimfähigkeit von Samen bzw. Brutknospen von nur zwei der sechs getesteten Arten beeinträchtigt, aber die Anzahl der Blüten, und damit der Samen, aller Arten war hinter Zäunen weit geringer als in

Kontrollflächen. Das könnte eine Reaktion auf eine verkürzte Wachstumsperiode der vorigen Saison sein, da einige arktische und alpine Arten Blütenknospen für das nächste Jahr bereits im Vorjahr ansetzen. Die Blühphenologie war desweiteren zeitlich versetzt, und das könnte langfristige Folgen für die Symbiose mit bestäubenden Insekten haben, insbesondere wenn die Blütenentwicklung nicht mit der Bestäuberentwicklung synchronisiert ist (Olesen et al., 2008).

Langfristig gesehen könnte eine durch erhöhte Schneedecke herbeigeführte Verkürzung der Wachstumsperiode die Artenzusammensetzung der betroffenen Gebiete verändern. Arten, welche auf geringe Schneetiefen angewiesen sind (z.B. *Dryas*) könnten an die Grenze ihrer physiologischen Wachstumsfähigkeit geraten und von anderen Arten, welche flexiblere Wachstumsschemata haben und an hohe Schneetiefen angepasst sind (z.B. *Cassiope*) abgelöst werden. Positive und negative Interaktionen zwischen benachbarten Individuen der gleichen und anderer Arten könnten diesen Prozess verstärken (Heegaard and Vandvik, 2004; Wipf et al., 2006).

Appendix II: CV

Contact Information

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Citizenship

Germany

Born

29. August 1980

Education

March 2003 to present

University of Vienna, Austria

Diploma program in Ecology sciences

- Thesis Topic: The influence of enhanced snow cover on high arctic tundra plants (working title; Advisors: Prof. Elisabeth Cooper (UiT) and Prof. Stefan Dullinger (univie)

January 2008 to June 2008

University of Bergen (UiB), Norway;

- ERASMUS exchange semester

Work Experience in academic Institutions

July 2009 to July 2013

PhD candidate, University of Tromsø and UNIS, Norway

- Experimental arctic ecosystem research supervised by Elisabeth Cooper (UiT, Tromsø) and Bo Elberling (UiT and UNIS) with the following topics:
- Effect of different lengths of season on biomass production, plant phenology and reproductive success
- Frost tolerance and performance of seedlings of high arctic plant species under different environmental conditions
- Effects of different temperature regimes on carbon fluxes of high arctic soils during all seasons in the field and under simulated conditions
- Change of microbial communities and nutrient cycles in high arctic ecosystems during the year and through change of season length

June 2008 to present

Master Project, University of Vienna and Tromsø

- Fieldwork and sample collection on Spitsbergen
- Includes collaboration with Dr. Sarah Elmendorf (collection and processing of soil cores) and assistance of Elke Morgner (CO2 flux measurements).

November and December 2008

Internship Molecular Biology

- Lab assistant for Post.Doc. Ullrich Hermann on the project “Regulatory networks in plant cells: The role of dually targeted transcription factors for the development of cells and organisms” of Prof. Kirsten Krause at UiT Tromsø, Norway.
- Includes training in techniques like PCR, gel electrophoresis, cell preparation and transformation and treatment of plants.

February 2007 to September 2007

Technical assistant, University of Vienna, Austria

- Animal keeping and environmental enrichment for birds (Kea) at the Austrian Science Fund Project “Social Learning and physical Cognition on the Kea, Nestor notabilis” at the Konrad Lorenz

Institute of comparative behavioural studies (KLIVV), Vienna, Austria under the supervision of PostDoc. Gyula Gajdon.

Work Experience with non-academic institutions

September 2007

Deadwood monitoring

- Monitoring and mapping of potentially drift-off endangered trees and logs along the Thaya riverbank, Thayatal nationalpark, Austria, under supervision of Helmut Habersack and the park authorities.

April 2006 to June 2006

Monitoring of Mosquito larvae

- Repeated inspections and management of mosquito populations in floodplains and riparian forests after floodings along Fischa and Danube rivers, Austria, for municipalities along the rivers under supervision of Dr. Bernhard Seidl.

August and September 2004

Mapping of hamster dens

- Inspections and mapping of Common Hamster (Cricretus cricretus) dens on arable fields in the area Mannheim / Heidelberg, Germany, for the Institute of Faunistik, Heidelberg, under supervision of Dr. Ulrich Weinhold.

Publications in preparation

Semenchuk, P.R., S. Dullinger and E.J. Cooper 2009. Phenological and reproductive responses of high arctic tundra plants on enhanced snow cover in Adventdalen, Spitsbergen (working title). Manuscript to be submitted.

Elmendorf, S., **P.R. Semenchuk**, et al. Influence of different climate treatments on arctic soil nutrient content using chemical analysis and ion exchange membranes. Manuscript in prep.