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an example of periodicity

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High Arctic plant phenology is determined by snowmelt patterns but duration of phenological periods is fixed: an example of periodicity

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Keywords: Spitsbergen, Svalbard, phenology, phenophase, phenoperiod, growing-season length, flowering

Supplementary material for this article is available online

Abstract

The duration of specific periods within a plant’s life cycle are critical for plant growth and performance. In the High Arctic, the start of many of these phenological periods is determined by snowmelt date, which may change in a changing climate. It has been suggested that the end of these periods during late-season are triggered by external cues, such as day length, light quality or temperature, leading to the hypothesis that earlier or later snowmelt dates will lengthen or shorten the duration of these periods, respectively, and thereby affect plant performance. We tested whether snowmelt date controls phenology and phenological period duration in High Arctic Svalbard using a melt timing gradient from natural and experimentally altered snow depths. We investigated the response of early- and late-season phenophases from both vegetative and reproductive phenological periods of eight common species. We found that all phenophases follow snowmelt patterns, irrespective of timing of occurrence, vegetative or reproductive nature. Three of four phenological period durations based on these phenophases were fixed for most species, defining the studied species as periodic. Periodicity can thus be considered an evolutionary trait leading to disadvantages compared with aperiodic species and we conclude that the mesic and heath vegetation types in Svalbard are at risk of being outcompeted by invading, aperiodic species from milder biomes.

Introduction

Phenological timing of key life-cycle events (phenophases) in relation to climatic constraints is crucial for individual plant growth and performance. Recent climate change has led to considerable temporal shifts of both the start and end of the growing-season and has been accompanied by phenological responses across tundra and other ecosystems (Parmesan and Yohe 2003, Menzel et al 2006, Oberbauer et al 2013). Climate change is especially pronounced in high-latitude areas (IPCC 2013), and its effects on phenology may have severe consequences for Arctic tundra ecosystems, because at the limits of terrestrial plant life, small changes in growing-season length constitute a large proportion of the extremely short season. Here, snowmelt determines growing-season start (Wipf and Rixen 2010, Cooper et al 2011), and observed shifts towards both earlier (Bulygina et al 2009, Brown et al 2010, Wang et al 2015, Boike et al 2016) and later snowmelt dates (Bhatt et al 2013, Bieniek et al 2015, Bjorkman et al 2015) represent key challenges for Arctic plant communities (Cooper 2014). In this study, we investigate the influence of snowmelt date on the phenology of eight common high-Arctic plant species.
Previous studies on the effects of snowmelt date have paid most attention to the timing of phenophase occurrence, often with a focus on early-season events (Arft et al 1999, Wipf 2010, Wipf and Rixen 2010, Bjorkman et al 2015, Livensperger et al 2016), while studies on durations of phenological periods (hereafter called ‘phenoperiods’) are rare and mainly focus on plant growth (Rumpf et al 2014, Livensperger et al 2016). However, the duration of specific phenoperiods are of particular importance for high-Arctic plant performance. For instance, the duration of the active growing period from green-up to senescence can determine the amount of flowers produced during the following season (Inouye et al 2002, Saavedra et al 2003, Høye et al 2007, Semenchuk et al 2013), and the seed maturation period from flower senescence to seed dispersal can determine propagule viability (Cooper et al 2011, Mallik et al 2011). In general, early-season phenophases, such as green-up or flower emergence, have been shown to closely follow snowmelt dates (Arft et al 1999, Wipf 2010, Wipf and Rixen 2010, Livensperger et al 2016), while late-season phases seem to be triggered by environmental thresholds of factors such as day length, light quality, temperature, and soil moisture (McGraw et al 1983, Arft et al 1999, Marchand et al 2004, Tsegay et al 2005, Fracheboud et al 2009). In Arctic ecosystems this means that the duration of many phenoperiods may be constrained by the timing of snowmelt, and shifts towards earlier or later snowmelt could elongate or shorten some of them.

To date, many plant phenology studies in the Arctic have concentrated on a few or single species and have often either assumed or found that species sharing common traits, such as growth form or relative time of flower emergence, react similarly to snowmelt date (Starr et al 2000, Inouye et al 2002, Saavedra et al 2003, Høye et al 2007, Wipf 2010, Bjorkman et al 2015, Rosa et al 2015). However, this assumption is often based on limited data where, for example, growth forms are often represented by only two species. Further, meta-analyses have shown that this connection does not necessarily hold when taking a greater number of species into account (Menzel et al 2006, Oberbauer et al 2013, but see Wipf and Rixen 2010). This indicates that the phenology response to snowmelt date may be species-specific depending on the phenophase and species’ niche within a given ecosystem.

Here, we test how the duration of two vegetative and two reproductive phenoperiods of eight common plant species respond to a variety of snow regimes by recording six early and late-season phenophases in a long-term snow fence experiment in High Arctic Svalbard. We present the most complete multi-year and multi-species whole-growing-season cycle phenological data we are aware of, and test the following hypotheses:

1. Phenoperiod durations are shorter in late-melting than in early-melting snow regimes, because:
   a. Late-melting snow regimes delay the onset of early-season phenophases, such as green-up and flower emergence, and
   b. Late-season phenophases, such as senescence and seed dispersal, occur simultaneously independent of snow regime.

2. A shortened seed maturation period will lead to decreased seed viability.

3. Species’ responses will be species-specific, i.e. response patterns cannot be assigned to traits or growth forms.

4. Inter-annual differences in snowmelt timing elicit similar responses to our snow regimes (early melting years are equivalent to early melting snow regimes and vice versa).

Methods

Study site and experimental setup

Detailed site and experimental design descriptions can be found in Cooper et al (2011) and Morgner et al (2010). A short summary is given below.

To study the effects of snow regime on plant phenology and seed viability, we used a snow depth manipulation experiment with snow fences in a mesic meadow and dry heath low-land tundra in Adventdalen on the island of Spitsbergen, Svalbard. Situated in the maritime High Arctic, the average ambient growing-season lasts from early June to mid-September.

Table 1. Average snow melt timing in mean day of year across all snow regimes and years. Where missing, data were not collected for this study.

<table>
<thead>
<tr>
<th>Snow regime</th>
<th>2008</th>
<th>2009</th>
<th>2010</th>
<th>2011</th>
<th>2012</th>
<th>2015</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shallow</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>144</td>
</tr>
<tr>
<td>Ambient</td>
<td>159</td>
<td>154</td>
<td>142</td>
<td>155</td>
<td>158</td>
<td>152</td>
<td>153</td>
</tr>
<tr>
<td>Medium</td>
<td></td>
<td></td>
<td>162</td>
<td>163</td>
<td>169</td>
<td>156</td>
<td>163</td>
</tr>
<tr>
<td>Deep</td>
<td>175</td>
<td>170</td>
<td>167</td>
<td>166</td>
<td>172</td>
<td>165</td>
<td>169</td>
</tr>
<tr>
<td>Average</td>
<td>167</td>
<td>162</td>
<td>151</td>
<td>158</td>
<td>162</td>
<td>158</td>
<td></td>
</tr>
</tbody>
</table>
For this study, we used two natural and two manipulated snow regimes, together forming a snow depth and corresponding snowmelt timing gradient (see table 1) from Shallow (slightly elevated landscape features with snow depth of about 10 cm, melts out on average 24 May) through Ambient (most common snow depth over the study site, about 30 cm deep, melts out on average 2 June) and Medium (manipulated snow depth with snow fences, about 1 m deep, melts out on average 12 June) to Deep (snow fences, about 1.5 m deep, melts out on average 19 June). The increased snow depth in Medium and Deep was manipulated with 1.5 m high and 6 m long fences which collect snow drifts on their lee side. Deep is situated in the deepest point of the snow drift, while Medium is situated a few meters further away from the fences. Inter-annual snowmelt date variability is considerable, see Semenchuk et al (2013) for more details.

Four blocks were selected within 2 km² to represent the variation in soil moisture in the landscape. Each block contains three plots within a few 100 meters in a design where all four snow regimes are present in each plot. Sub-plots used for phenology observations (75 cm × 75 cm) consisted of Ambient and Deep plots (n = 6 per plot and snow regime), Medium plots (n = 3), and Shallow plots (n = 2), summing up to a total of 181 sub-plots.

Data
Phenology data used for this article were collected from 2007 to 2012 and in 2015 in Ambient and Deep, while Shallow and Medium were observed from 2010 to 2012 only. Additionally, Medium was also observed in 2015.

Phenology in each plot was surveyed every 7 days (once a week) for the 8 most common species of the study site representing important circum-Arctic species (Allopecurus magellanicus, Bistorta vivipara, Cassiope tetragona, Dryas octopetala, Luzula arctica, Pedicularis hirsuta, Salix polaris, Stellaria crassipes), except in 2015 when it was observed twice a week. A description of the 6 recorded phenophases can be found in table 2.

To answer our hypothesis on phenoperiod duration, two phenophases were always summarized to one period defined as the duration from the start to the end of two consecutive phases (in number of days), resulting in the four periods Startup (from snowmelt to green-up), Active (green-up to senescence), Flowering (flower emergence to flower senescence) and Seed-dripening (flower senescence to seed dispersal) (table 1).

To connect phenophase occurrence with temperature, thawing degree day (TDD) thresholds to reach each phenophase were calculated from air temperature data from Longyearbyen airport, about 12 km from the study site in the same valley (Norwegian meteorological institute, www.eklima.no). Thawing degree day was defined as the sum of average temperature of each day from snowmelt until occurrence of a phenophase and is a good measure to characterize a period’s temperature, because it incorporates the daily temperature fluctuations.

To test viability of propagules, seeds and bulbs were collected upon ripeness, i.e. as soon as they reached the seed dispersal phase, in 2008–2011 in close proximity to the phenology sub-plots. 150 propagules of all but two species (Stellaria crassipes and Pedicularis hirsuta which were not abundant enough to harvest enough seeds) were germinated in three batches with 50 seeds each on moist filter paper under a 24 h light regime at 18 °C for 12 weeks. For more details see Cooper et al (2011).

Statistical analyses
We used linear mixed-effects models (LMEs) for all phenology related data (i.e. day of year of occurrence, duration of periods, and TDD demands) and generalized LMEs with a binomial link for the germination data (i.e. proportions of germinated propagules), both from the lme4 package (Bates et al 2015) in R (R Core Team 2016). All models were fitted with random effects reflecting the spatial arrangement of sub-plots nested in plots nested in blocks.

To tackle the complexity of our data, we divided the statistical analyses into three separate parts where basically the combination of fixed and random effects in the models vary, with response variable being either phenophase timing (start and end of each phenoperiod), phenoperiod duration or propagule viability. The combination of fixed effects were (a) ‘snow regime’ alone, (b) ‘species’ by ‘snow regime’ interaction, and (c) ‘year’ by ‘snow regime’ interaction. In all cases, the omitted fixed effects terms were included in the random effects. To simplify the dataset, the ‘species’ by ‘snow regime’ interaction was analyzed on data from Ambient and Deep only. The ‘year’ by ‘snow

<p>| Table 2. Overview of phenophases and phenological periods (phenoperiods) used in this study. Phenoperiods are defined as periods between two distinct phenophases. |
|---------------------------------|-------------------------------------------------|--------------------------------------------------|</p>
<table>
<thead>
<tr>
<th>Periods</th>
<th>Phenophase</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Startup</td>
<td>Green-up</td>
<td>Start of photosynthetic period</td>
</tr>
<tr>
<td>Active</td>
<td>Senescence</td>
<td>End of photosynthetic period</td>
</tr>
<tr>
<td>Flowering</td>
<td>Flower emergence</td>
<td>First flower visible</td>
</tr>
<tr>
<td>Seed-dispersal</td>
<td>Seed dispersal</td>
<td>Seeds disperse</td>
</tr>
</tbody>
</table>

See table 1 for a description of the 6 recorded phenophases and phenological periods used in this study. Phenoperiods are defined as periods between two distinct phenophases.
regime’ interaction was repeated once with data from Ambient and Deep only, and once with all four snow regimes including years 2010–2012 only.

After fitting, the distribution of each model’s residuals in each model parameter was observed visually and no deviation from normality was detected. None of the generalized LMEs were over-dispersed (using RVAideMemoire package (Hervé 2016)).

95% Confidence intervals (CIs) of each models’ fixed effects factors and p-values for pairwise comparisons of all contrast combinations adjusted with the Tukey method were calculated with the multcomp (Hothorn et al 2008) and lsmeans (Lenth 2016) packages and presented in graphs as letters denoting significant differences (p ≤ 0.05). For a better overview of the phenology models with the ‘species’ by ‘snow regime’ interaction in the fixed effects, effect sizes and 95% CIs of each contrast were calculated and each species’ snow regime contrast presented in figures, to be interpreted as the difference between Ambient and Deep snow regimes, and a lack of overlap with zero considered as statistically significant.

Results

Overall snow regime effects
Across all species and years, both the start and end of each phenoperiod were affected by snow regime, with deeper snow regimes leading to significantly later occurrences of all phenophases (figures 1 and 2). Phenophase occurrences in Deep were delayed between 11 and 25 days compared to Shallow regardless of the start or the end of any phase. Such a marked delay is well captured by the temporal resolution of our field observations of 7 days.

Period durations followed the snow regime pattern closely for the Startup period only (shorter duration with deeper snow), while durations of the other periods showed only minor effects (figure 2). The difference between Shallow and Deep duration was 5 days in one comparison (Active period) but otherwise never larger than 2 days, except for the Startup duration where it was 9 days.

Thawing degree days to reach the start of each period were generally higher in deeper snow regimes, especially for the Active period (figure 2), although the maximum difference between Shallow and Deep was never more than 36 TDDs. To reach the end of the Active and Seedripening periods (i.e. late-season phenophases), TDDs did not differ across snow regimes, except for a small effect of less than 16 TDDs in Shallow during the Active period, and less than 33 TDDs in Deep during the Seedripening period. Deeper snow regimes needed 30 more TDDs to reach the end of Flowering.

Propagule viability followed snow regime patterns, with significantly lower viability in deeper snow regimes. Since data of all species were averaged, the effect, however, was small and not significant across all snow regimes (see supporting material figure S3).

Snow regime effects on individual species
The effects of the Deep compared to the Ambient snow regime on the start and end of most phenoperiods were in the same direction across species (earlier in Ambient), the only exception being the end of the Seedripening period where Stellaria and Cassiope

Figure 1. Proportions of sub-plots in each phenological period (phenoperiod) in each snow regime averaged over all species and years. Vertical lines denote average melt out dates of each snow regime.
Flowering and regime across species, with many species not reacting to snow each year period, the overall snow regime effect remained intact. Even though there was significant differences across each set of duration, start or end, with the same letter meaning that the group contrasts are not significant (Tukey contrasts, p-value threshold 0.05). Please note that duration, start and end were modeled independently for each period.

Figure 2. Estimates and 95% confidence intervals (CI) of duration, start and end of each phenological period (phenoperiod) in each snow regime averaged over all species and years in day of year (left) and thawing degree days (right) from linear mixed-effects models (see methods section for details). Letters denote statistically significant differences across each set of duration, start or end, with the same letter meaning that the group contrasts are not significant (Tukey contrasts, p-value threshold 0.05). Please note that duration, start and end were modeled independently for each period.

showed no significant difference between snow regimes. The Start-up period was shortened by deeper snow for the majority of species. The effect on Active, Flowering and Seedripening durations, however, varied across species, with many species not reacting to snow regime (figure 3). Shorter durations were found in Active for Alopecurus and Stellaria, in Flowering for Stellaria and in Seedripening for Cassiope and Luzula.

Many species did not alter their TDD demand to reach certain phases (figure 3). Bistorta, Cassiope and Pedicularis did not alter their TDD demands in any of the periods’ phases and no species’ TDD demand was altered to reach the end of the Seedripening period. Lower TDDs were recorded for both start and end of Active period for Salix, and for Flowering period in Luzula and Salix. For absolute values on each species’ timing and TDD demands, see figure S1.

Three out of six species had a significantly lower germination proportion (and as such lower viability) of propagules in Deep than in Ambient, even though the effect for Bistorta was ecologically negligible given its high germination rate of over 87% (figure 4). The shrubs, Cassiope and Dryas, had particularly reduced germination at deep snow regimes.

Modulation of snow regime effects by years

Even though there was significant across-year variation of duration, timing and TDD demand for each period, the overall snow regime effect remained intact each year (figure 5). Similarly, the intra-annual variation of each variable was retained across all snow regimes.

The seasonal pattern of phenophase occurrence and most period durations were generally retained throughout all phenophases and snow regimes (i.e. some years were always earlier or later than others throughout all phenophases), even though the pattern became less clear with later phases (figure 5 and S2). For instance, 2008 and 2012 were rather late years, while 2010 and 2011 were often the earlier years. This was often also the case with TDD demands, although in individual years the pattern was reversed in later phases (i.e. years which needed more TDDs in early phases needed fewer TDDs in late phases). For instance in 2012, TDD demands were among the highest to reach many phenophases, while they were lowest to reach the end of the Seedripening period.

The timing and TDD demand patterns did not fit together very well, i.e. a late year did not necessarily have a higher or lower TDD demand and vice versa. For instance, while 2008 was in many cases among the late years, it was not among the years with the highest TDD demand to reach a particular phenophase. For further details on this and exceptions from the general patterns, we refer the reader to figures 5 and S2.

Seed viability was generally lower in deeper snow regimes, however, inter-annual variability was larger than the snow regime effect (figure 6).

Discussion

Species-specific responses

We present the responses to snow melt timing combined and for each species. Comparisons between figure 2 and 3, and also between figure 4 and S3 clearly show improved understanding comes from exploring the individual species responses, rather than only averaging of the response of all eight species. A later snow melt resulted in shorter period durations for two
Figure 3. Effect sizes of contrasts of Deep in relation to Ambient snow regime and 95% confidence intervals (CI) of duration, start and end of each phenological period (phenoperiod) for each species averaged over all years (Species’ Snow regime interaction) in days (left) and thawing degree days (right) from linear mixed-effects models (see methods section for details). Positive values indicate longer duration or later occurrence or higher TDD thresholds in the Deep snow regime. If CIs overlap zero (dotted line), the effect size is considered statistically non-significant. Effect sizes were estimated for each Species by Snow regime combination and CIs adjusted for multiple hypothesis testing for a total of 120 contrasts. For overview, we here only present the within-species contrasts. Please note that duration, start and end were modeled independently for each period. Also note that the start of the Startup period is basically representing the contrast of snow melt date between Deep and Ambient and is, hence, the same for each species.
species in *Active* (*Alopecurus* and *Stellaria*), one in *Flowering* (*Stellaria*) and one in *Seedripening* (*Luzula*), but none throughout all periods. Likewise only half of the study species (*Cassiope*, *Dryas* and *Bistorta*) showed reduced propagule germination with later snow melt.

**Periodicity**

It has been shown at other high-latitude sites that the timing of early-season phenophases is triggered by snow-melt date (Bjorkman *et al.* 2015, Livensperger *et al.* 2016), and this study confirms these findings. However, we also show that late-season phases occur after a given amount of time after snow melt, irrespective of time of year. Thus, the species at our study site are so-called periodic, a term rarely used in the literature (Sørensen and Gleerup 1941, Starr *et al.* 2000, Wookey *et al.* 2009). Periodicity is a concept suggesting that the time to reach late-season phenophases (i.e. the duration of phenoperiods) is genetically fixed rather than cued by environmental factors such as day length, temperature or soil moisture thresholds signaling that environmental conditions become unfavorable (Sørensen and Gleerup 1941, Starr *et al.* 2000, Wookey *et al.* 2009). We speculate that a potential mechanism driving periodicity could be an internal clock or program, the pace of which depends on a variety of climate and weather factors such as temperature (here represented by thawing degree days, TDDs) or moisture (Oberbauer *et al.* 2013), rather than an external cue (see below). This implies that in a future warmer growing-season climate, the phenology of periodic species might be advanced and period durations accelerated rather than stretched, independent of snowmelt date, because physiological processes such as cell division and growth might proceed faster. This is similar to the suggestion made by Bjorkman *et al.* (2015), who found that background warming could offset later snowmelt date, perhaps by accelerating the seed maturation and other periods. Few studies directly or indirectly report periodicity of high-latitude species (Starr *et al.* 2000, Oberbauer *et al.* 2013) and here we show that all studied species show periodicity in either vegetative and reproductive periods or both.

Periodicity might represent internal constraints limiting the studied species’ responses to snow regimes and growing-season durations, where the age of a certain organ (e.g. flowers or leaves) determines its senescence (Oberbauer *et al.* 1998, Starr *et al.* 2000). This is contradictory to other studies where the occurrence of late-season phenophases was found to be controlled by thresholds of external environmental cues such as day length, light quality, temperature, or soil moisture (McGraw *et al.* 1983, Arft *et al.* 1999, Marchand *et al.* 2004, Tsegay *et al.* 2005, Fracheboud *et al.* 2009). This indicates that periodicity might be an adaptation to our study site’s generally short and cold growing-seasons or to other factors connected to its high latitude (e.g. lack of day length cues during late-season or highly variable inter annual conditions but comparatively predictable long-term conditions) compared to many other study areas. This is supported by a meta-analysis showing differential phenological responses of tundra plants from colder climates.
Figure 5. Estimates and 95% confidence intervals (CI) of duration, start and end of each phenological period in each snow regime and year averaged over all species (Year × Snow regime interaction) in days (left) and thawing degree days (right) from linear mixed-effects models (see Methods section for details). Letters denote statistically significant differences across each set of duration, start or end, with the same letter meaning that the group contrasts are not significant (Tukey contrasts, p-value threshold 0.05). Please note that duration, start and end were modeled independently for each period.
many species, the emergence of Arctic pollinators is season-length dependent on the response of the key insect species and other weather variables. As with the flowers of many species, the emergence of Arctic pollinators is closely linked to the timing of snowmelt (Hoey and Forchhammer 2008), and a delayed emergence with late snowmelt may maintain the synchrony between flower and insect emergence (Gillespie et al. 2016). However, it is not clear how the flight period length of Arctic insects will respond when the growing-season is effectively shortened by late snowmelt because the cues for the end of adult activity are not well known for many Arctic species (Iler et al. 2013). Wind-pollinated plants may be unaffected by snowmelt delays, although shorter seasons in a warmer climate may limit opportunities for fertilization.

**Impacts of period durations**

If *Active* period duration was the only predictor of plant productivity (Myneni et al. 1997, Wang et al. 2004), our results suggest that two of the studied species (*Alopecurus* and *Stellaria*) are likely to react to deeper snow regimes with reduced growth. However, this is not the case (see Rumpf et al. 2014 for a study on growth), which strongly suggests that other factors such as soil moisture and/or nutrient availability, both of which are increased in *Deep* (Semenchuk et al. 2015), are likely to play a more important role in plant growth and productivity than *Active* period duration alone. The lack of dependence of plant size on growing-season length is also in line with other studies (Jonas et al. 2008, Livensperger et al. 2016), but has yet to be incorporated in models based on remotely sensed data (Park et al. 2016).

The duration of the *Flowering* period, representing flower longevity, was also unaffected by snow regime for all but one species. This is similar to findings from other studies (Wipf 2010, Rosa et al. 2015, Gillespie et al. 2016), and Hoey et al. (2013) demonstrated that flowering duration is more closely linked to temperature, with shorter flowering-seasons occurring with increasing temperatures. The implications of our findings for the reproduction of insect pollinated plants will depend on the response of the key insect species and other weather variables. As with the flowers of many species, the emergence of Arctic pollinators is closely linked to the timing of snowmelt (Hoey and Forchhammer 2008), and a delayed emergence with late snowmelt may maintain the synchrony between flower and insect emergence (Gillespie et al. 2016). However, it is not clear how the flight period length of Arctic insects will respond when the growing-season is effectively shortened by late snowmelt because the cues for the end of adult activity are not well known for many Arctic species (Iler et al. 2013). Wind-pollinated plants may be unaffected by snowmelt delays, although shorter seasons in a warmer climate may limit opportunities for fertilization.

Propagule viability could not be explained by the duration of the *Seedripening* period for two out of four species (*Dryas* had lower viability in spite of a periodic *Seedripening* period, while *Luzula* showed no effect to an aperiodic, shortened *Seedripening* period). Neither could the duration of the *Active* or *Flowering* periods explain viability, so the species appear to have different sensitivities to phenophase duration. The effects of reduced growing-season length on germination has only previous been studied for a few High Arctic species, but *Dryas*, *Cassiope* and *Bistorta* all responded with lower viability (Cooper et al. 2011, Mallik et al. 2011). In fact, average germination (i.e. mean of all species combined, shown in figure 6), correlated with the TDD needed to reach the end of the *Active* period (of the year studied, see figure S2) with an $\hat{r}^2 = 0.5$ (data not shown), and was most likely driven by the response of the thermally most sensitive species, *Dryas* and *Cassiope*. *Dryas* experienced generally low TDDs in *Active* and *Flowering* periods in the late melting treatment, and is likely to be particularly sensitive to a reduced growing season temperature. Other Arctic studies have shown that warming increases the viability of 

**Figure 6.** Estimates and 95% confidence intervals (CI) of propagule germination in each snow regime and year averaged over all species (Year*Snow regime interaction) from linear mixed-effects models (see methods section for details). Left plot includes all snow regimes (Shallow and Medium were only observed in two years), right plot includes all years. Letters denote statistically significant differences across year and snow regime with the same letter meaning that the group contrasts are not significant (Tukey contrasts, $p$-value threshold 0.05).
Arctic tundra species, especially Dryas and Bistorta (Wookey et al 1995, Arft et al 1999, Müller et al 2011). Our other study species, Alopecurus, Luzula and Salix seem to have well developed mechanisms to cope with varying growing-season starts by keeping seed viability constant or even high despite a late start.

**Intra-annual variability and methodological limitations**

Our snow regime gradient shows that in a climate with shifting snowmelt timing, an earlier or later start of phenoperiods caused by changes in snow melt date could lead to a corresponding earlier or later ending, respectively. This is represented within our intra-annual comparison, where earlier melting years show earlier occurrences of most phenophases. However, if TDD thresholds triggered phenophase occurrence (as it seems to do across snow regimes), then this threshold should be the same each year independent of snowmelt date or absolute temperature. This is not the case here, and we suggest three potential explanations of both mechanistic and methodological nature.

First, the lack of coherence between year and TDD threshold suggests that phenophase occurrence is a combination of both temperature and season length. If in one year the TDD demand is low even though the timing is late, this suggests that more time to reach that phenophase can offset colder periods. Conversely, if in another year TDD demand is high while timing is early, this suggests that development can be accelerated during warmer periods. Therefore, the suggested periodicity may not be rigid enough to lead to exact phenophased durations or TDD demands each year, given the other constraints of this study as outlined below.

Second, other factors than those considered in this study, such as soil moisture or nutrient status, or other weather related parameters which may vary across years, such as amounts of photosynthetically active radiation (PAR), may control the timing of phenophases, leading to the observed intra-annual variability of TDD thresholds. For example, if the studied species react to soil moisture thresholds (Jonas et al 2008), a generally drier year might lead to advanced phenology. This is complicated by the fact that rain events could modulate soil moisture (and PAR by cloud formation) during different parts of the year and affect different phenophases. In this study, the deeper snow regimes are slightly moister (Semenchuk et al 2015) and the potential soil moisture threshold to trigger late-season phenophases might be reached later in the season. Further, if soil moisture is a co-factor for late-season phenophase timing, then other factors might control phenology in sites wetter than our mesic and heath tundra (Marchand et al 2004). Winter warming events followed by icing can expose and freeze preformed buds and reduce flowering (Semenchuk et al 2013). Deeper snow protects sensitive buds and plant parts from damage. This may also affect flower formation and subsequent seed viability. Further research on these potential mechanisms is recommended.

Finally, the between-year variability observed could be a methodological artefact in the form of systematic observer error (Gottfried et al 2012, Morrison 2016). Each year, data has been acquired by different field personnel (usually two to three people) with a different field leader every other year. While a calibration at the beginning of each field day was a central part of data acquisition, it has been shown that cover estimates by eye in particular can be biased and individually different (Morrison 2016). This could lead to a bias between years where, for example, the team or individual team members of one year systematically over-estimate cover and hence note the occurrence of a phenophase (50% cover per plot) earlier than teams of other years would have.

Snow regime effects are consistent in all years and most species, making our conclusions on phenophase timing and period durations robust and valid. However, our absolute phenophase timing estimates may be late-biased because we assumed the phenophase occurred the day it was recorded, while in reality it occurred at an unknown point in time between the last observation date and the date of recording (Bjorkman et al 2015). Since this constraint is consistently applied throughout the study, it does not interfere with our results on snow regime effects, but warrants caution when interpreting phenophase occurrences and comparing them with other studies.

The results derived from the methodology used in this study complement findings from landscape scale remote sensing studies and highlight the need for scaling plot level responses to landscape scale responses (Karlsen et al 2014, Anderson et al 2016, Boike et al 2016). This has already been shown to have a potential value as the onset of the growing season based on field observations has been successfully quantified based on NDVI threshold methods (Karlsen et al 2014, Anderson et al 2016). In fact, large-scale remote sensing studies from other biomes are also starting to report that the timing of autumn senescence is affected by the timing of spring phenology (Keenen and Richardson 2015), and our study verifies these findings on plot-scale level.

**Conclusions**

The presence of periodicity in our study species might render the plant community vulnerable to future changes in snowmelt patterns. First, period durations of periodic species might not be able to adapt to changing growing-season durations, while those of aperiodic species are more likely to. Second, while changing snowmelt patterns might change phenology
timing, its effects may be modulated by increasing growing-season temperatures accelerating and, hence, shortening some periods (Bjorkman et al 2015). This may apply specifically for periodic species and give them a further disadvantage compared to aperiodic species. A recent study suggests that late-season warming trends are stronger than those of early-season (Boike et al 2016). This could lead to a proportionally higher post-senescence respiratory loss of periodic species compared to aperiodic ones.

We conclude that periodic species are likely to be limited in their ability to adapt to changing snowmelt dates and may be disadvantaged compared to some of the invading species on Svalbard such as Rumex longifolius, Ranunculus acris, Ranunculus repens, Epilobium montanum, and the grass species Deschampsia cespitosa and Poa pratensis (Roos et al 2012). If such species demonstrate aperiodic characteristics, they can fully exploit changing or variable snow regime patterns (Wooley et al 2009). We suggest that besides factors such as temperature or nutrient limitations, periodicity might be a key plant trait predicting competitiveness of a species in response to climate change in tundra ecosystems.

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