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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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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.

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.

	Year						
Snow regime	2008	2009	2010	2011	2012	2015	Average
Shallow			132	149	150		144
Ambient	159	154	142	155	158	152	153
Medium			162	163	169	156	163
Deep	175	170	167	166	172	165	169
Average	167	162	151	158	162	158	

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.

(4) A shortened seed maturation period will lead to decreased seed viability.

(5) Species' responses will be species-specific, i.e. response patterns cannot be assigned to traits or growth forms.

(6) 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.

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 km^2 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 (*Alopecurus magellanicus, Bistorta vivipara, Cassiope tetragona, Dryas octopetala, Luzula arcuata, 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 *Seedripening* (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.

Table 2. Overview of phenophases and phenological periods (phenoperiods) used in this study. Phenoperiods are defined as periods between two distinct phenophases.

Periods	Phenophase	
	Snow melt	Start of exposure to direct daylight
Startup		
	Green-up	Start of photosynthetic period
Active		
	Senescence	End of photosynthetic period
	Flower emergence	First flower visible
Flowering		
	Flower senescence	First flower senesces
Seed-dispersal		
	Seed dispersal	Seeds disperse

To test viability of propagules, seeds and bulbils 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

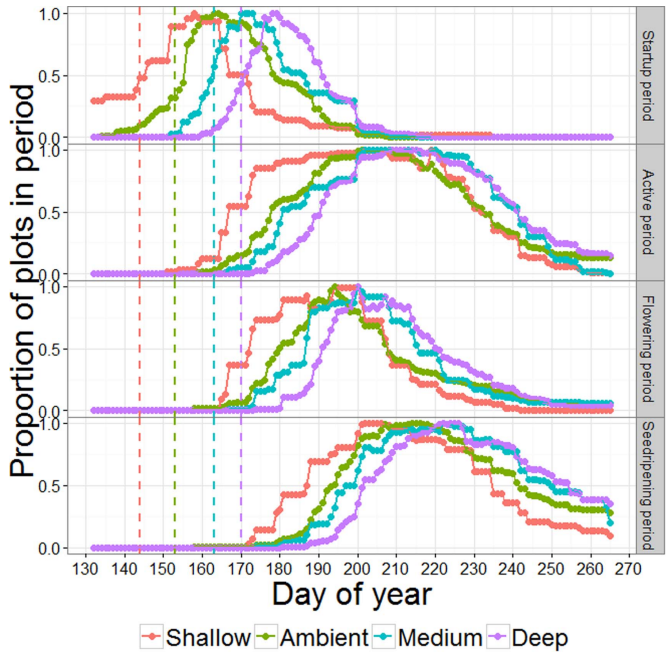

Figure 1. Proportions of sub-plots in each phenological period (phenoperiod) in each snow regime averaged over all species and years. Vertical lines denote average melt out dates of each snow regime.

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 ($p \leqslant 0.05$). 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*

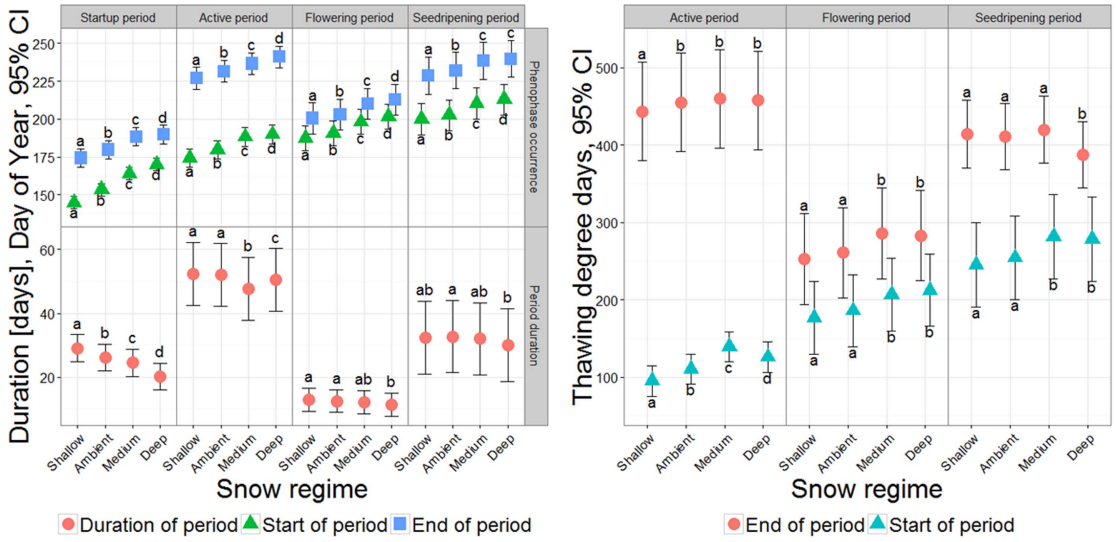

Figure 2. Estimates and 95% confidence intervals (CI) of duration, start and end of each phenological period (phenoperiod) in each snow regime averaged over all species and years in day of year (left) and thawing degree days (right) from linear mixed-effects models (see methods section for details). 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 *Startup* 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

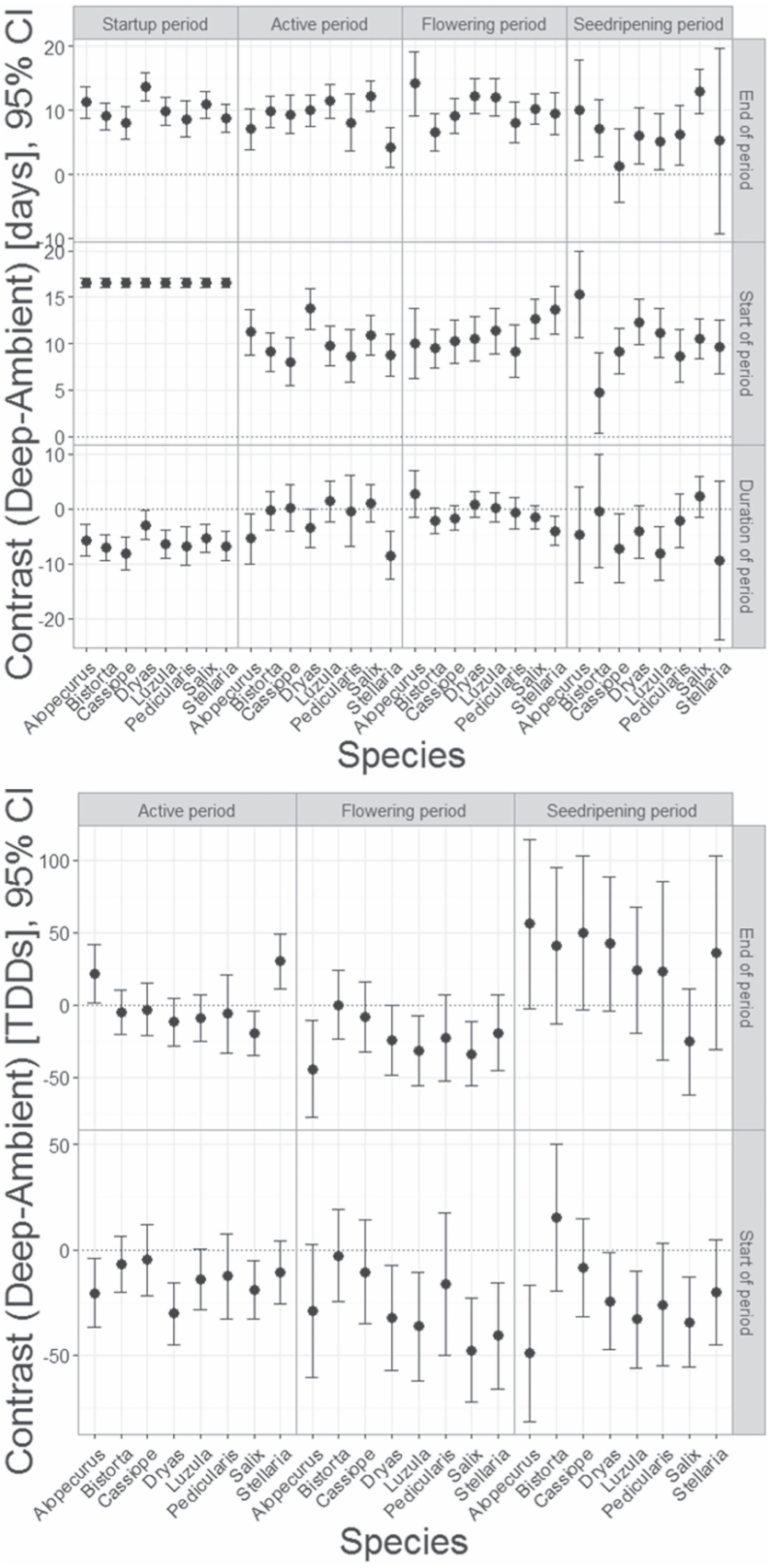

Figure 3. Effect sizes of contrasts of Deep in relation to Ambient snow regime and 95% confidence intervals (CI) of duration, start and end of each phenological period (phenoperiod) for each species averaged over all years (Species*Snow regime interaction) in days (left) and thawing degree days (right) 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.

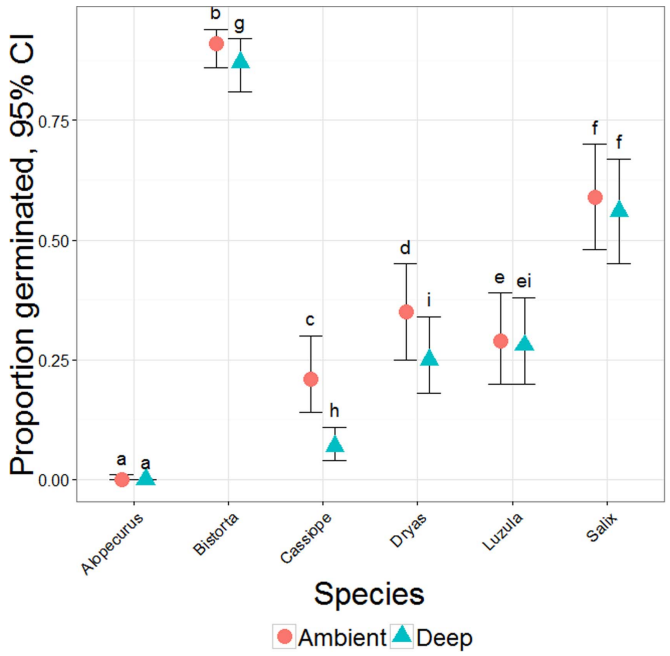

Figure 4. Estimates and 95% confidence intervals (CI) of propagule germination for each species averaged over all years (Species*Snow regime interaction) from linear mixed-effects models (see methods section for details). Letters denote statistically significant differences across snow regimes and species with the same letter meaning that the group contrasts are not significant (Tukey contrasts, *p*-value threshold 0.05).

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

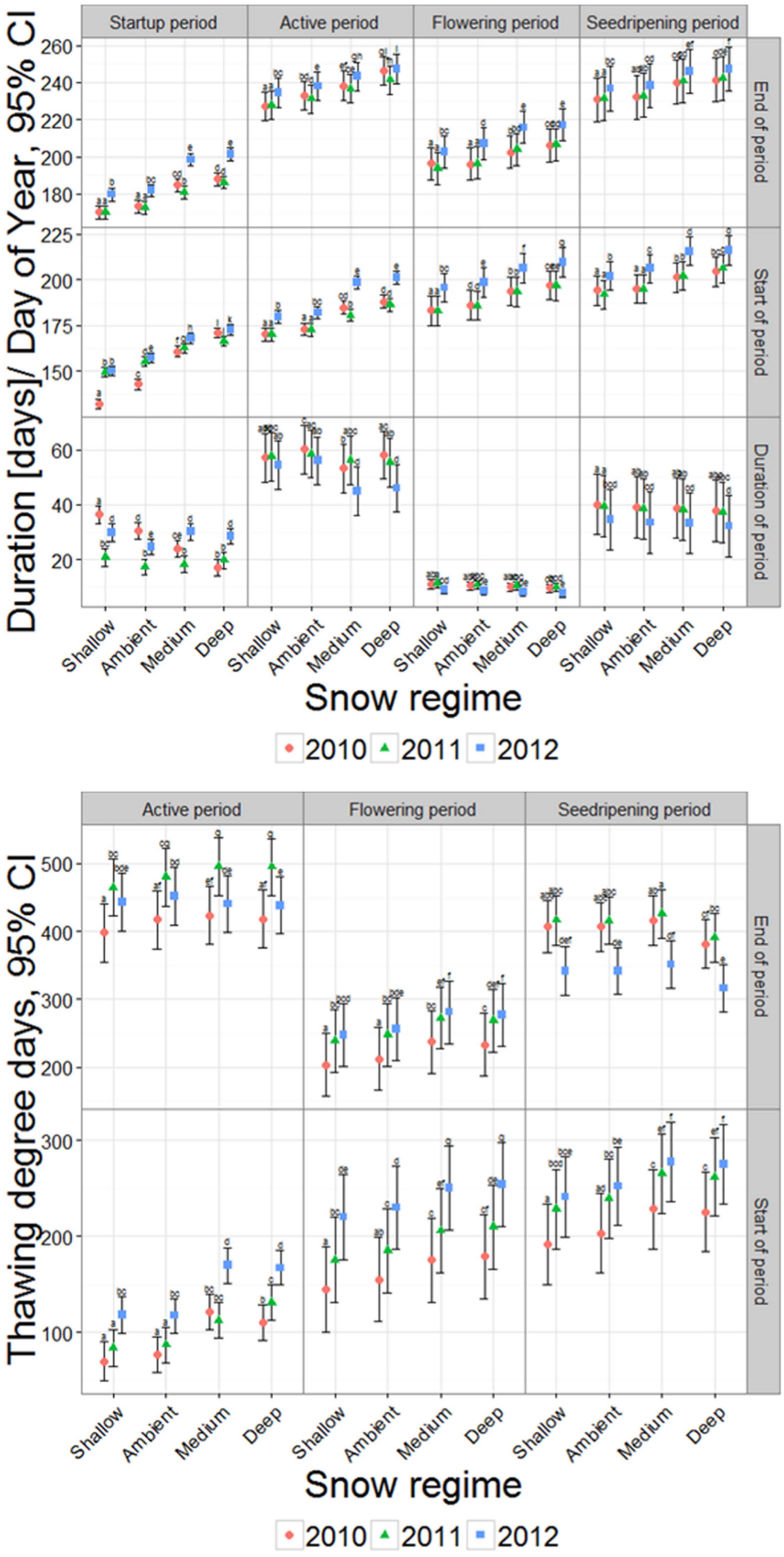

Figure 5. Estimates and 95% confidence intervals (CI) of duration, start and end of each phenological period in each snow regime and year averaged over all species (Year*Snow regime interaction) in days (left) and thawing degree days (right) from linear mixed-effects models (see Methods section for details). 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.

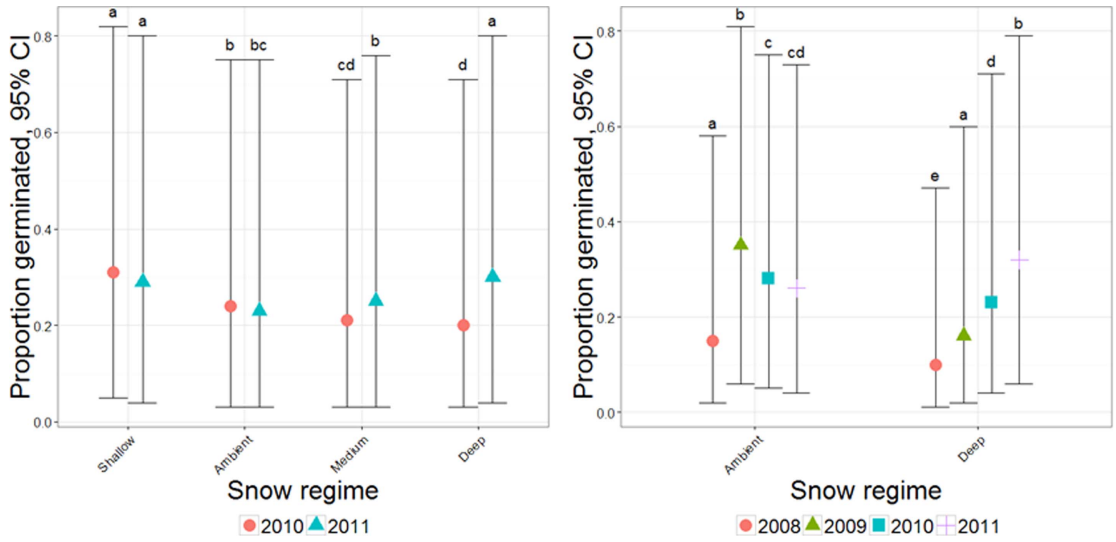

Figure 6. Estimates and 95% confidence intervals (CI) of propagule germination in each snow regime and year averaged over all species (Year*Snow regime interaction) from linear mixed-effects models (see methods section for details). Left plot includes all snow regimes (Shallow and Medium were only observed 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).

compared to warmer sites (Prevéy *et al* submitted), suggesting that regional adaptations to growing-season temperatures or other long term conditions could control phenology.

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 Høye *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 (Høye 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 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 $r^2 = 0.5$ (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

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 phenoperiod 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 ocurred 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* (Roalsø *et al* 2012). If such species demonstrate aperiodic characteristics, they can fully exploit changing or variable snow regime patterns (Wookey *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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