Phenological responses to small-scale spatial variation in snowmelt timing reveal compensatory and conservative strategies in subarctic-alpine plants

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Abstract

Background: In tundra ecosystems, the adjustment of phenological events, such as bud burst, to snowmelt timing is crucial to the climatic adaptation of plants. Natural small-scale variations in microclimate potentially enable plant populations to persist in a changing climate.

Aims: To assess how plant phenology responds to natural differences in snowmelt timing.

Methods: We observed the timing of eight vegetative and reproductive phenophases in seven dwarf-shrub species in relation to differences in snowmelt timing on a small spatial scale in an alpine environment in subarctic Finland.

Results: Some species and phenophases showed accelerated development with later snowmelt, thus providing full or partial compensation for the shorter snow-free period. Full compensation resulted in synchronous occurrence of phenophases across the snowmelt gradient. In other species, there was no acceleration of development. The timing of phenophases varied between two consecutive years and two opposing mountain slope aspects.

Conclusions: The results have shown three distinct patterns in the timing of phenophases in relation to snowmelt and suggest alternative strategies for adaptation to snowmelt timing. These strategies potentially apply to other species and tundra ecosystems and provide a framework, enabling one to compare and generalise phenological responses to snowmelt timing under different future climate scenarios.

Keywords: climate change; compensation; conservative strategy; natural snowmelt gradient; phenophases; plant phenology; subarctic; tundra
Introduction

In high latitude and high elevation ecosystems, snow cover can last for several months, profoundly affecting seasonal dynamics and plant life (Jonas et al. 2008; Estilow et al. 2015). Snow cover protects plants from harsh winter conditions such as low temperatures, ice blast, winter desiccation, frost damage and photoinhibition (Körner 2003; Zhang 2005; Bennie et al. 2010; Saarinen and Lundell 2010). During the growing season, the progression of snowmelt and the amount of snowpack also determine local soil moisture and nutrient conditions near the melting snowbeds (Björk and Molau 2007; Clement et al. 2012). The timing of snowmelt, along with a changing photoperiod and temperature, largely determines the onset of plant growth. Snowmelt directly increases the light and water available to the plant and coincides with higher temperatures and longer days (Billings and Mooney 1968; Jonas et al. 2008). Recently, it has further been suggested that the timing of spring snowmelt affects the timing of autumn senescence (Abbandonato 2014; Keenan and Richardson 2015). Thus year-round plant growth appears to be influenced by the duration of snow cover.

Climate change is predicted to affect the amount and duration of snow cover, especially at high latitudes (ACIA 2005; Callaghan et al. 2011; IPCC 2013). Higher temperatures, leading to earlier snowmelt in the spring have already been recorded in the western North American and the Northern European Arctic (e.g. Serreze et al. 2000; Stone et al. 2002). This can potentially alter the growing season length and can lead to shifts in the timing of seasonal events in plants (phenophases), flowering synchrony with the presence of pollinators, exposure to spring frost, and eventually to plant fitness (Inouye 2008; Wipf et al. 2009; Kudo and Ida 2013; Gillespie et al. 2016).

Snow manipulation experiments (addition or removal of snow) have been used in arctic, subarctic tundra and in alpine vegetation to study the short- and mid-term effects of simulated changes in winter climate on the timing of phenophases in plants (Henry and Molau 1997; Walker...
et al. 1999; Wipf and Rixen 2010; Cooper 2014; Wipf et al. 2015). In most studies, phenophases were affected by differences in snowmelt timing, for example they occurred on an earlier day of the year (DOY) when the snow melted earlier (Wipf et al. 2009; Wipf and Rixen 2010; Cooper et al. 2011; Livensperger et al. 2016); but in others, the DOY remained the same regardless of snowmelt timing (Dunne et al. 2003; Aerts et al. 2004). The photoperiod at a given location is always the same for a given DOY, so those phenophases found always to occur on the same DOY might be responding to photoperiod, i.e. they may be photoperiodic. Photoperiodism enables plants to delay phenophases until later in the season when temperature conditions are more stable if a longer day length is a signal for a later onset of development (Keller and Körner 2003). On the other hand, plants with less photoperiodism have the capacity to commence growth as a function of snowmelt, and this, in case of earlier melt-out, has the advantage of a longer growing season (Wipf et al. 2009). Phenological timing can also be assessed as the number of days required after snowmelt (days after snowmelt; DAS) until the beginning of growth or a new phenophase. The DAS may either remain the same (Borner et al. 2008) or vary (Petraglia et al. 2014; Bienau et al. 2015) for plants growing along snowmelt gradients. DAS can be used to characterise the rate of plant development after snowmelt, i.e. how fast a phenophase is attained (assuming that developmental processes begin on snowmelt). The rate of development is determined by genetic requirements and current environmental conditions, such as temperature, and can therefore give additional insights into the mechanisms that control the timing of phenology (Bliss 1962). How the timing of phenophases is affected by snowmelt timing depends on whether they are controlled by photoperiod alone or by other factors, such as temperature and soil moisture.

Limited conclusions can be drawn from experimental simulations of snowmelt timing alone since they can only capture immediate and short-term acclimation responses of plants, but not their long-term adaptation to existing variations in local conditions (Wolkovich et al. 2012; Blume-Werry et al. 2016). In arctic and alpine ecosystems with uneven terrain, large variations in
snowmelt timing can occur naturally on a scale of a few metres, so that early-, mid- and late-melting areas are adjacent to each other (Körner 2003). A plant population occurring along such a gradient has adapted to the microclimatic variation, either genetically or through strong phenotypic plasticity, as seen in its successful establishment. This capacity to exist along gradients in snowmelt timing means that plant populations may be pre-adapted to the potential variations created by climate change in the future, i.e. plants with the capacity to adjust to future climatic changes may exist within a distance of just a few metres (Crawford and Abbott 1994). As short-term experiments may over-predict adverse effects of environmental changes due to the lack information about long-term adaptive responses, understanding natural variations of populations to snowpack duration is important (Blume-Werry et al. 2016). Reports from in situ observations of phenological events along natural snow duration gradients are relatively few (but see for example Kudo 1991; Kudo and Suzuki 1999; Dunne et al. 2003; Kudo and Hirao 2006; Sedlacek et al. 2015; Wheeler et al. 2015, 2016; Carbognani et al. 2016) compared to experimental studies. However, they are important for indicating the natural limitations of a species and whether a plant population is pre-adapted to diverse microclimates and therefore may be buffered against future climate change (Crawford 2008). Studying over the long term of natural small-scale environmental variations is therefore needed alongside experimental studies to assess the long-term success of a population.

This study aimed to evaluate how natural differences in the timing of spring snowmelt on a small spatial scale affected plant phenology. We studied how many days after snowmelt (DAS) and on which day of year (DOY) four vegetative and four reproductive phenophases began in three evergreen and four deciduous subarctic-alpine dwarf shrubs and examined how DAS and DOY were related to the timing of snowmelt. We also tested whether the relationship between the timing of phenophases and the timing of snowmelt varied between two years. Differences in snowmelt timing between the two years may be reflected in changes in DAS if this factor affects the rate of development. The study was conducted at two mountain slopes with different aspects (northeast- vs.
southwest-facing) to investigate whether the phenological responses are consistent across two
sampling locations. Different years and slope aspects involve differences in local surface
temperature, one of the possible drivers of phenology, so including these variables in a study can
give an insight into whether the effect of snowmelt timing is dependent on changes in temperature.

Specifically, we aimed to answer the following research questions addressing the
phenological timing of phenophases (Day of year, DOY) and their timing in relation to snowmelt
(Days after snowmelt, DAS):

(1) How do the DOY and DAS of different phenophases of seven subarctic alpine dwarf shrubs
respond to snowmelt timing?

(2) Is the response of DOY and DAS the same across two years and two slope aspects with
different snowmelt timing?

Materials and methods

Study site

The study was conducted on Saana mountain (69°02‘37" N, 20°51‘22" E), Scandes Range, north-
western Finland. At the Kilpisjärvi Biological Station (1.5 km away from the study site), the annual
mean temperature is -1.9 °C and January and July mean temperatures are -12.9 °C and 11.2 °C,
respectively (means from 1981-2010; Pirinen et al. 2012). The average annual precipitation is 487
mm and the average peak snow depth reaches 99 cm in March (Pirinen et al. 2012). The first snow-
free patches appear in April-May, but light snowfall can remain on the ground for up to 2 days
especially at higher altitudes until late June. The mountain birch (Betula pubescens ssp.
czerepanovii) treeline on Saana is formed at 600 m a.s.l. Above the treeline, the vegetation is a
subarctic alpine vegetation dominated by ericaceous dwarf shrubs such as Empetrum nigrum and
Vaccinium spp., and Betula nana and Salix spp. The humus layer is shallow (ca. 7-15 cm deep) and
the soil moisture is usually low (Eskelinen et al. 2009; Le Roux et al. 2013a). The bedrock consists
of siliceous and dolomitic rock resulting in nutrient-poor, acidic soils in some areas and calcium-rich, non-acidic soils in other areas. The study was restricted to acidic areas as these dominated the landscape.

We selected two areas (hereafter called ‘Site’) located at 700-770 m a.s.l. on the north-eastern (hereafter called ‘North’) and the south-western (hereafter called ‘South’) slopes of Saana (Supplementary Figure S1). The small differences in elevation did not appear to cause temperature differences (data not shown). These areas have previously been characterised by Le Roux et al. (2013b) and they are known to consist of representative heath vegetation. The progression of snowmelt was observed from early May 2014 and three groups of sequential timing of spring snowmelt (hereafter called ‘Snowmelt’) termed ‘Early’, ‘Mid’ and ‘Late’ were identified. In each group, three plots (two plots in South Mid) of 2 m × 2 m area each were marked in 2014. An additional plot (two additional plots in South Mid) was added at each Site-Snowmelt combination in spring 2015 (Figure S1). Plots within the same Site were between ca. 3 and 200 m apart.

Reindeer were sometimes observed in the area, but they did not appear to disturb the study plots.

Temperature and snowmelt measurements

Air temperature at ca. 20 cm above the ground and soil surface temperature were logged at hourly intervals in duplicates at each plot with iButtons® (DS1922L-F5 thermochrons; Homechip Ltd., UK). The loggers measuring air temperature were protected from direct sunlight with a cylindrical radiation shield (height = 15 cm, diameter = 6 cm) made of white PVC. To calculate the air temperature for May 2014, before the loggers were placed, we correlated air temperatures from the Saana weather station (International identification number WMO 02701) with our temperature data from the summer 2014 and extrapolated temperatures backwards until snowmelt. The sum of average daily temperatures above 0 °C (accumulated thawing degree days, TDDs) was calculated for each Site and Snowmelt level from the date of snowmelt until 2 September in 2014 and 2015.
Accumulated TDDs measure the magnitude and duration of above-zero temperatures and are therefore an indication of the warmth and length of the growing season. In 2014, the day of snowmelt of early melting plots was estimated from two visits to the site. On the first visit on 8 May, the area was covered completely with snow and on the second visit on 26 May, it was snow-free, so snowmelt was estimated to have occurred in the middle of this period, i.e. 17 May or DOY 137. For the other plots, the day of snowmelt in 2014 was noted as the day when a plot was completely snow-free. This method was not possible in 2015 because some early-melting plots were already snow-free when the observations started on 20 May. Instead, the day at which the logged topsoil temperatures started fluctuating by about 5 °C was used as the day of snowmelt for those plots in 2015 (see Wipf 2010). Soil temperature fluctuations are a good indicator of snowmelt as the snow cover keeps the soil surface temperature at approximately 0 °C regardless of the air temperature (Havas 1966; Körner 2003). In 2014-2015, Early plots melted out between the beginning and middle of May, Mid plots between the end of May and the beginning of June and Late plots between mid-June and the beginning of July (Table 1). The plots therefore represented three phases in a natural gradient of snowmelt timing of five to seven weeks on the two opposing slopes.

Phenological observations

Phenological observations were made on the most commonly occurring species in the area. Four deciduous species Betula nana L., Salix herbacea L., Vaccinium myrtillus L., Vaccinium uliginosum L. and three evergreen species Empetrum nigrum ssp. hermaphroditum (Hagerup) Böcher, Phyllodoce caerulea (L.) Bab., and Vaccinium vitis-idaea L were observed in each plot. A plastic tie (width = 2.4 mm) was loosely attached to the base of 24 individual shoots of each of the examined species present in a plot. Due to species-specific affinities to snow, some species were not sufficiently abundant or were not present at all in some plots. V. vitis-idaea was present in all plots. S. herbacea and V. myrtillus only grew in late-melting plots, whereas B. nana did not grow in late-
melting plots and *E. nigrum* only grew in late-melting plots in the North. *P. caerulea* was not present in any early-melting plots and *V. uliginosum* was only present across the whole snowmelt gradient in the South Site.

Each marked shoot was observed every three to seven days and the DOY at which the first bud on the shoot reached a new phenophase was noted. Observations were made from 31 May to 2 September in 2014 and from 20 May to 4 September in 2015. Five vegetative and six reproductive phenophases were defined individually for each species (Figure S2):

### Vegetative phases

- Bud green (first evidence of green colour can be seen on the bud)
- Leaf unfolded (the bud has broken open and the first leaf has separated from the bud)
- Leaf expanded (the leaf is fully unfolded and the leaf angle is similar to mature leaves)
- Leaf senescence (first evidence of autumn colouration is visible on the adaxial leaf surface; the colour depends on the species)

### Reproductive phases

- Flower open (the petals have fully opened; stamens and styles are fully extended)
- Flower senescence (the petals are dry or have fallen off and stamens and styles have withered)
- Fruit set visible (first evidence that the ovary is swollen)
- Fruit ripe (the fruit is completely ripe).

For practical reasons, not every phenophase was recorded in all species, e.g. leaf senescence was not observed in evergreen species and bud greening was not observed in *P. caerulea* as its buds look green as soon as they become visible. In a small number of cases, some phenophases had already been reached before the beginning of the study period or had not been reached by the end of
it so they were excluded from the dataset as the exact timing of the phenophase was unknown in those cases. The final sample size for each species also varied due to the loss of tags and lack of flowers or leaf development on individual shoots.

**Statistical analyses**

The DOY at the onset of each phenophase was recorded individually for each shoot. The DAS was then calculated as the number of days from the day of snowmelt to the measured DOY. The effect of the factors Snowmelt (levels ‘Early’, ‘Mid’ and ‘Late’), Site (levels ‘North’ and ‘South’) and Year (levels ‘2014’ and ‘2015’) on DOY and DAS was evaluated separately for each species and phenophase with a linear mixed-effects model with Plot as a random effect. All factors and all possible interactions were included. In cases where there were no data for a species in all combinations of factor levels, separate models were fitted for subsets of the data which included the remaining possible interactions (see supplementary tables S1 and S2 for a list of all fitted models). The optimal model was determined using the maximum likelihood ratio test. Main effects and interactions of variables were tested for significance ($P<0.05$) with an analysis of variance (ANOVA). Normality, homogeneity and independence assumptions of ANOVA were evaluated by visual inspection of residual plots. In some cases, a constant variance function was applied to one or several variables to achieve homogeneity. Variation in the timing of phenophases with the timing of snowmelt, between the two years and slope aspects was evaluated based on the significance of Snowmelt, Year or Site as main effects. When a significant interaction was present, pairwise comparisons of least square means were carried out with t-tests within each year and site and the $P$-values were adjusted using the Holm’s method (Holm 1979) and a general trend was assumed to be present when most pair-wise interactions were significant. Where the ANOVA assumptions were not fulfilled, (see model results in Tables S1 and S2 marked as ‘Could not be tested’), the trend was estimated visually from the figures. All analyses were carried out in R (R Core Team 2016, version 3.3.1) using the packages nlme (Pinheiro et al. 2016), lsmeans (Lenth 2015) and stats (R Core Team...
Results

Temperature conditions

The accumulated thawing degree days indicated that the growing season was generally warmer in 2014 than in 2015 and on south-facing than on north-facing slopes in both years (Table 1). Accumulated thawing degree day at the end of the season was always highest in early melting plots and lowest in late melting plots (Table 1).

Timing of phenophases across species

The number of DAS until bud greening was lowest for *S. herbacea* and *V. myrtillus* which only grew in late-melting snowbeds, followed by the deciduous species *B. nana* and *V. uliginosum* and was greatest in the two evergreen species, *E. nigrum* and *V. vitis-idaea* (Figures 1 and 2). This ranking of species according to number of DAS was largely conserved across all vegetative phenophases. The ranking of species from earliest to latest was different for the DOY at which vegetative phenophases occurred: *V. uliginosum* < *B. nana* < *E. nigrum* < *S. herbacea* < *V. myrtillus* < *V. vitis-idaea* < *P. caerulea* (Figures 1 and 2).

*E. nigrum* required the smallest number of DAS for almost all reproductive phenophases among the studied species, followed by *V. myrtillus*, *P. caerulea*, *V. uliginosum* and *V. vitis-idaea* (Figures 3 and 4). The order of species according to the phenological timing in DAS remained almost the same throughout later reproductive phenophases except for fruit ripening in *V. myrtillus*, which occurred within the smallest number of DAS among all species (Figure 4). When arranging the species according to the DOY on which reproductive phenophases occurred, the order was similar except that *V. myrtillus* and *V. uliginosum* were in reverse order.
Ripe fruits were rarely observed, partially because some fruits did not reach this phase before the end of the fieldwork period, so data are only presented from a few cases.

*The effect of snowmelt on phenological timing*

The shifts in phenophases due to snowmelt timing could, in several cases, be described by generalised patterns indicated schematically by solid red lines in Figures 1 and 3. The conditions on which the schematic lines are based are described in the section “Statistical analysis” of the Materials and methods section. Most phenophases in the late-developing evergreen species *V. vitis-idaea* (except bud greening) and late phenophases in *P. caerulea*, such as fruit set and leaf expansion, responded similarly to snowmelt timing. They usually required more DAS to occur in early vs. late snowmelt (Figures 1b,e and 3b,d, Tables S1 and S2). These phenophases occurred synchronously on the same DOY. The reproductive phenophases and most vegetative phenophases of the deciduous species *V. uliginosum* (Figures 1c and 3c), which was among the early-flowering species, and the early phenophases of *P. caerulea* (flower opening and leaf unfolding; Figures 1b and 3b), also required more DAS to begin in early vs. late snowmelt (Tables S1 and S2). However, these phenophases occurred on a later DOY in late vs. early snowmelt (Tables S1 and S2). Conversely, most vegetative phenophases of *B. nana* and some in 2014 also of *V. uliginosum* and bud greening in *V. vitis-idaea* required a fixed number of DAS to occur, regardless of snowmelt timing (Figures 1a,c). These phenophases usually occurred on an earlier DOY in early vs. late snowmelt (Tables S1). These results fall into three patterns of 1) more DAS and the same DOY, 2) more DAS and later DOY and 3) the same DAS and later DOY in late vs. early snowmelt. In *E. nigrum*, snowmelt timing did not cause any clear response in the timing of phenophases (Figures 1d and 3a, Tables S1 and S2). Most vegetative phenophases occurred after more DAS in early vs. late snowmelt, but there were some exceptions (for example, leaf unfolding and leaf expansion in the South in 2014). Some phenophases occurred on the same DOY whilst others occurred later in late vs. early snowmelt (Figure 1d). The effect of snowmelt was also
inconsistent in reproductive phenophases of *E. nigrum* (Figure 3a). Depending on year and site, some of its phenophases required more DAS in early vs. late snowmelt and occurred on the same DOY, while others took a fixed number of DAS but occurred on an earlier DOY in early vs. late snowmelt. Only fruit set in the North in 2014 occurred within more DAS in early vs. late snowmelt, causing an earlier DOY of fruit set in those plots (Figure 3a).

**Variation in phenological timing between slope aspects**

In *V. vitis-idaea*, vegetative and reproductive phenophases began within fewer DAS at the North vs. the South site (Figures 1e and 3d, Table S1). Other species and phenophases usually required the same number of DAS to attain vegetative phenophases, regardless of the Site (Figures 1 and 2, Table S1) with the exceptions of leaf expansion in *E. nigrum*, which took significantly fewer DAS in the South vs. the North and senescence in *B. nana*, which required more DAS in the South vs. the North in 2015 (Figure 1a,d). *Vaccinium myrtillus* and *E. nigrum* began bud greening and leaf unfolding on an earlier DOY in the South vs. the North and the same effect was seen in leaf unfolding and leaf expansion in *B. nana* (Figures 1a,d and 2b).

The effect of Site on the number of DAS required by reproductive phenophases was only consistent in the species which took a relatively high number of DAS until flowering (Figures 3 and 4, Table S2). In *V. uliginosum*, flowers from early-melting plots in 2015 took more DAS to open and to senesce in the South vs. the North site and the effect was the same in all phenophases of *V. vitis-idaea* (Figure 3c,d). A significant effect of Site remained in the DOY of flower opening in *V. vitis-idaea* but the site at which the phenophases occurred later varied with snowmelt timing (Table S2). Reproductive phenophases of *V. uliginosum* and *V. myrtillus* did not differ strongly between sites, but flower phenophases of *E. nigrum* and *P. caerulea* (in 2015) and fruit ripening in *E. nigrum* (in 2014) usually occurred on an earlier DOY in the South vs. the North (Figures 3a,b,c and 4).
Variation in phenological timing between years

Reproductive phenology responded more strongly to variation between the years compared to vegetative phenology. Reproductive phenophases always required more numbers of DAS in 2015 vs. 2014, approximately the same value, regardless of snowmelt timing (Figures 3 and 4). This was significant in almost all possible pair-wise comparisons of the two years and apparent in all species and phenophases, apart from *E. nigrum* (Table S2). This difference between the years persisted in the DOY at which flowering phases occurred.

Inter-annual differences in the DAS needed to reach vegetative phenophases increased in the late phenophases compared to earlier phenophases of evergreen species (Figures 1 and 2). Leaf expansion always took significantly more DAS for these species and occurred on a later DOY in 2015 vs. 2014 (Table S1). The vegetative phenology of deciduous species was affected less by inter-annual variations than that of evergreen species. The only significant delay in 2015 vs. 2014 was in the leaf senescence of *V. myrtillus* and *V. uliginosum* (Table S1, Figures 1c and 2b). Some inter-annual differences could be seen in the DOY at which vegetative phenophases were reached, but the year during which phenophases occurred later varied by phenophase and site. Differences between the years in the DOY of attaining vegetative phenophases were irregular and often varied by phenophases and site, except in the case of a significantly later occurrence of senescence in *V. uliginosum* in 2014 (Figure 1c).

Discussion

Patterns in the phenological response to snowmelt

Our results for plant phenology along a natural snowmelt gradient are consistent with results from experimental systems in comparable arctic and alpine environments (delayed DOY: Wipf et al. 2009; Wipf 2010; Cooper 2014; or unaltered DOY: Bienau et al. 2015). We additionally examined the number of DAS required to begin a phenophase and found similar responses to those reported
by, for example, Petraglia et al. (2014) (increased DAS) and Cooper et al. (2011) (unaltered DAS) for various arctic and alpine dwarf shrubs in similar ecosystems.

Some studies found that responses of phenological timing to earlier snowmelt cluster according to life form with graminoid phenology advancing the most, followed by deciduous and then evergreen dwarf shrubs (Khorsand Rosa et al. 2015; Livensperger et al. 2016). In other cases, the relative timing of phenology among species (for example, early-flowering versus late-flowering species) determined how a species responded to differences in snowmelt timing (Wipf 2010; Petraglia et al. 2014). However, the detailed results we present from four deciduous and three evergreen dwarf-shrub species and eight phenophases cannot confirm that growth form or temporal niche correspond to a particular response to snowmelt timing (Figure 5).

The discrepancy between our findings and results from earlier research may be due to the fact that previous studies either included only a few species or few phenophases, or focused only on one response variable for phenological timing, limiting the possibility to identify more general response patterns. In contrast, we compared how the timing of several phenophases of several species corresponded to snowmelt timing in terms of both DAS and DOY. This indicated a novel clustering of phenophases into three distinct patterns according to their responses to snowmelt timing:

(1) **Compensation:** The number of DAS required to reach a certain phenophase decreases with later snowmelt timing. This reduction translates into acceleration of growth and compensates for the delay caused by the late snowmelt, leading to synchronous occurrence of phenophases in plots with different snowmelt timing (Figure 5a). This response was mostly seen in *V. vitis-idaea* and in the late phenophases of *P. caerulea*.

(2) **Under-compensation:** The number of DAS required to reach a certain phenophase decreases with later snowmelt timing, but this acceleration is not sufficient to compensate for the delayed start of the growing season caused by late snowmelt. Therefore, phenophases are
reached at a later DOY in late-melting plots compared to early-melting plots, but this
difference is smaller than the corresponding difference in the snowmelt timing (Figure 5b).
This response was seen in most phenophases of *V. uliginosum* and the early phenophases of
*P. caerulea*.

(3) *Conservativeness (no compensation):* The number of DAS required to reach a certain
phenophase is the same along the snowmelt gradient. Late snowmelt poses a natural delay to
development so that phenophases occur at a later DOY in late- compared to early-melting
plots and this difference is equal to the corresponding difference in the snowmelt timing
(Figure 5c). This response was mostly seen in the vegetative phenophases of *B. nana* and in
2015 in some phenophases of *V. uliginosum*.

The only species which did not tend to follow any of these patterns was *E. nigrum*. Its
patterns of phenological timing along the snowmelt gradient varied greatly with site and year within
the same phenophase. *E. nigrum* grows ubiquitously in the study area and it can be found on wind-
blown ridges and in places with thick snow cover (authors’ pers. observation; Bell and Tallis 1973).
This suggests that it can cope with a large range of variation in snow depth and snowmelt timing. *E.
nigrum* always developed earliest after snowmelt among the studied species and its flower bud
break had often already begun prior to snowmelt (authors’ pers. observation), showing a strong
adjustment to snowmelt timing. Large trait variation along natural snow depth gradients has also
been found in *Empetrum* by Bienau et al. (2014) as well as in a snow removal experiment in alpine
*Empetrum*, which showed plasticity in developmental timing of bud greening and flowering after
one or two years (Wipf et al. 2009; Wipf 2010). This suggests at least partial plasticity in the
response of *E. nigrum* to snowmelt which we observed. It is likely that its divergent responses to
snowmelt timing seen in different years, sites or phenophases are modulated by, for example,
prevailing temperatures.
While these patterns show that the timing of snowmelt affects the timing of phenophases, the variation in the responses within and between species indicate a more complex control on phenology than snowmelt alone can explain. This is likely, at least partially, due to the confounding effects of snowmelt with other environmental variables which affect phenology, such as soil moisture variation during snowmelt and higher temperatures in late-melting plots at the time of snowmelt. Snowmelt as a predictor of phenology is also partially limited by the preferences of species for certain snow depth niches, so that some of our species studied did not grow along the whole gradient and hence were not exposed to all snowmelt timings. A finer snowmelt gradient and additional species with a broad habitat range could be used in future studies to avoid the limitations we encountered. Mating systems can also influence the timing of phenophases beyond the influence of snowmelt timing, as strictly outcrossing species must flower synchronously for successful reproduction. In our study, only *E. nigrum* can commonly self-fertilise due to its bisexual flowers in northern populations (Bell and Tallis 1973) which may explain the great variability in the timing of its phenophases, but does not explain why there is great variation among the other species with obligatory or preferentially outcrossing mating systems.

*Modulation of phenological timing by environmental variations between years and slope aspects*

In those cases where the phenological timing varied between the years, phenophases usually developed on a later DOY or required more DAS in the relatively colder year of 2015, suggesting that low temperatures limit phenological development in these subarctic-alpine plant species. This accelerating effect of warm years has also been found in the dwarf shrub *Cassiope tetragona* in a similar subarctic-alpine ecosystem (Molau 1997) and in several other arctic plant species, which had a shorter pre-floration period in years with higher spring temperatures (Bjorkman et al. 2015). Semenchuk et al. (2016) also report that the timing of phenophases varied between years, but this could not be explained by temperature sums because the cumulative TDDs until the occurrence of
each phenophase was not constant between the years. This indicates that other factors, for example variation in soil moisture, modulate the responses in different years, as has been suggested by Oberbauer et al. (2013). In our comparison between years, we found the strongest responses in the reproductive phenology and stronger effects on late- vs. early-developing species, suggesting a higher flexibility in responding to short-term environmental fluctuations, in particular phenophases of certain species. Hence, reproductive phenophases and late-developing species have a greater advantage as they can respond to favourable conditions, for example they can extend the available time for reproductive processes by developing earlier in a warmer year. This could also hold future advantages when acclimatising to changing conditions.

The response of phenology to the aspect of the mountain slope was inconsistent within almost all species and phenophases, apart from \textit{V. vitis-idaea}. Overall, Site mainly appeared to modulate developmental timing in the colder year of 2015. The slope aspect has rarely been included in previous studies of phenological timing and Iversen et al. (2009) found only a small effect of slope aspect on the timing of phenology when comparing north-, south- and east-facing slopes. In their study, phenological development was slower in the South compared to the North but slope aspect was overall a poor predictor of phenology. In addition to our own results, the findings of Iversen et al. (2009) suggest that environmental or genetic differences between the two sites not accounted for in our study are likely to have caused the variation that we observed.

**Limitations and adaptations of phenology**

Plants which follow the compensatory pattern (Figure 5a) respond flexibly to snowmelt timing. This indicates an adjustment to the environmental differences at the time of snowmelt, such as higher temperatures later in the season when late-melting plots become snow free, compared to the lower temperatures in spring when early-melting plots melt out. Indeed, Livensperger et al. (2016) found that the timing of leaf appearance in \textit{V. vitis-idaea} and other shrubs was advanced both by warming and by early snowmelt, but warming usually had no additional effect on the timing of leaf
expansion later in the season. In the same study, early snowmelt slowed down rates of leaf
development in many species, suggesting that early-season development may be slowed down by
the colder temperatures and a slower accumulation of temperature sums. Later phenophases, on the
other hand, may be regulated by other physiological requirements, as temperatures are already high
when they occur and are unlikely to be restricting. Specific temperature accumulation requirements
to phenophases are not uncommon in subarctic and alpine species, as evident in the studies by
Wheeler et al. (2016) and Huelber et al. (2006) in which the growing degree days above 5 °C until
the onset of reproductive phenophases in several alpine plant species were identical along an
elevational and snowmelt gradient. However, variations in the degree-day sensitivity are also
common with respect to habitat, growth form or latitude (Kudo and Suzuki 1999; Molau et al. 2005;
Prevéy et al. 2017). The photoperiod reaches 24 h on DOY 142 at our study site, so the occurrence
of phenophases on the same DOY as seen in this pattern is unlikely to be caused by day length.

The under-compensating pattern (Figure 5b) follows a similar concept of flexibility as the
compensatory pattern. However, in this case there is more limitation on how strongly phenology
responds to snowmelt, as the number of DAS does not vary as strongly along the snowmelt gradient
compared to the first pattern.

In conservative, group (Figure 5c), the number of DAS required to reach a phenophases is
the same along the snowmelt gradient. This implies that despite the environmental differences, such
as temperature differences upon snowmelt, these phenophases do not respond flexibly to snowmelt
timing, likely due to an internal physiological requirement or a genetic regulation which is
independent of the environmental differences between plots with different snowmelt timing. This
was also suggested by Borner et al. (2008), who likewise found no differences in the rates of
phenological development in B. nana or in other arctic plant species along an experimental
snowmelt gradient.
The role of small-scale spatial differentiation and developmental strategy in a changing climate

Climate simulations for northern Finland predict a decrease in the amount of snowfall and the duration of snow cover for the period 2070-2099 (Jylhä et al. 2009; Räisänen and Eklund 2012). However, small-scale variability in snow cover may retain diverse environments in the future, likely including suitable habitats for plants under changed conditions (Friedel 1961). The potential of microhabitat variability to prevent habitat loss in the future and provide buffers against climate change has been recognised previously especially with respect to thermal differentiation by Scherrer and Körner (2010, 2011) and Scherrer et al. (2011). In our study, the microclimatic conditions at our current mid-melting plots would correspond to those of the current early-melting plots if climate change causes an overall advance in snowmelt. Similarly, current late-melting plots will correspond to mid-melting plots. Although we cannot say whether the strategies we have identified are genotypic or phenotypic in nature, the plants overall show differential responses to snowmelt timing within the same population.

In some of our studied species, the timing of phenology varied significantly between the two years. In addition, tundra and alpine species in general are known to mainly reproduce vegetatively. These characteristics make it likely that the responses of these species are at least partially due to phenotypic plasticity. Sedlacek et al. (2015) confirmed that phenotypic acclimation rather than genotypic adaptation to snowmelt timing was present in the leaf phenology of *S. herbacea* in an alpine ecosystem. Patterns which can describe the phenotypic plasticity of phenology in response to snowmelt timing, such as those we present here, can indicate the capacity of plants to respond to these differences in general, and therefore give us an idea of how climate change-induced advances in snowmelt might affect them specifically. We cannot conclude how plants in the early-melting plots might respond to even earlier snowmelt, as these plots constituted the earliest area of our snowmelt gradient and were also one of the earliest areas to melt out in the region. However, plants
in currently late- or mid-melting habitats will experience a forward shift in snowmelt timing and therefore can be expected to respond similarly to those in currently mid- or early-melting habitats, respectively, if phenotypic plasticity is present. Phenophases following the first pattern (Figure 5a) will likely still occur on the same DOY, whilst phenophases following the second or third pattern (Figure 5b, c) will probably occur on an earlier DOY. In reproductive phenophases, this possible shift in phenology may cause a mismatch of peak flowering time with the peak abundance of pollinators if the pollinators do not shift to the same extent with consequences for reproductive success (Kudo and Ida 2013; Gillespie et al. 2016). A study from the Arctic showed that late flowering individuals advance faster than early flowering individuals in the case of an advance in snowmelt timing, causing a contraction in the flowering period and an associated decline in resource availability for pollinators (Høye et al. 2007, 2013). However, Cortés et al. (2014) found that gene flow in *S. herbacea* continues between microhabitats with different snowmelt due to seed dispersal so that sub-populations are not genetically separated.

Conclusions

Our results suggest that the extent to which a plant population shows variable phenological timing in response to the timing of snowmelt can be inferred from the length of the period after snowmelt individual subpopulations require to attain phenophases under current natural conditions. Comparing this requirement of DAS to the response of phenology measured as the DOY allowed us to define three patterns of species’ responses which correspond to distinct developmental strategies reflecting species’ means of adaptation to variations in the timing of snowmelt. Contrary to previous classifications of phenological responses, the patterns we found are not dependent on any particular functional classification (such as growth form), number of species studied, or a particular type of ecosystem. This framework facilitates the comparison of phenological responses among various studies and would even potentially allow previous results to be classified according to these patterns. Achieving a greater uniformity in reporting research results would improve our
understanding of how plant phenology responds to the environment. Furthermore, these strategies raise ideas about the underlying physiological processes and environmental factors which control plant phenology and are not fully understood yet.

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Disclosure statement

The authors declare no conflicts of interest.
References


manipulation effects do not scale up to long-term legacies: effects of an absent snow cover on boreal forest plants. Journal of Ecology 104:1638–1648.


Le Roux PC, Lenoir J, Pellissier L, Wisz MS, Luoto M. 2013b. Horizontal, but not vertical, biotic
interactions affect fine-scale plant distribution patterns in a low energy system. Ecology 94:671–682.


R Core Team. 2016. R: A language and environment for statistical computing.


Wipf S. 2010. Phenology, growth, and fecundity of eight subarctic tundra species in response to


**Supplemental data**

Supplemental data for this article can be accessed here.
Table 1. Average date and day of year (DOY; with standard errors) of snowmelt timing and average accumulated thawing degree days (TDD) after snowmelt at two Sites (North and South) and three levels of snowmelt timing (Early, Mid and Late) in 2014 and 2015. Accumulated TDDs were calculated as the sum of average daily temperatures above 0 °C from the date of snowmelt until 27 September. Each average was calculated from one or two temperature loggers per plot from three plots (two in South Mid) in 2014 and from four plots in 2015. See main text for how snowmelt timing was estimated.

<table>
<thead>
<tr>
<th></th>
<th>Snowmelt date (DOY±SE)</th>
<th>TDD±SE</th>
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<tbody>
<tr>
<td>2014</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>North</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Early</td>
<td>17/5 (137±0)</td>
<td>1041±16</td>
</tr>
<tr>
<td>Mid</td>
<td>05/6 (156±0)</td>
<td>963±23</td>
</tr>
<tr>
<td>Late</td>
<td>26/6 (177±1.7)</td>
<td>803±22</td>
</tr>
<tr>
<td><strong>South</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Early</td>
<td>17/5 (137±0)</td>
<td>1071±19</td>
</tr>
<tr>
<td>Mid</td>
<td>05/6 (156±0)</td>
<td>1004±2</td>
</tr>
<tr>
<td>Late</td>
<td>30/6 (181±0)</td>
<td>805±10</td>
</tr>
<tr>
<td>2015</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>North</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Early</td>
<td>22/5 (142±1.4)</td>
<td>927±15</td>
</tr>
<tr>
<td>Mid</td>
<td>03/6 (154±1.2)</td>
<td>850±12</td>
</tr>
<tr>
<td>Late</td>
<td>28/6 (179±0.8)</td>
<td>700±23</td>
</tr>
<tr>
<td><strong>South</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Early</td>
<td>01/5 (121±5.3)</td>
<td>1007±32</td>
</tr>
<tr>
<td>Mid</td>
<td>28/5 (148±0.8)</td>
<td>954±19</td>
</tr>
<tr>
<td>Late</td>
<td>18/6 (169±3.4)</td>
<td>813±24</td>
</tr>
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Figure 1. Number of days after snowmelt and day of year on which four vegetative phenophases (Bud green, leaf unfolded, leaf expanded, leaf senescence) in five subarctic dwarf shrubs (a–e) occurred for the first time along a natural gradient of snowmelt timing (Early, Mid and Late). The phenophases were observed at two mountain slope aspects (North and South). Closed symbols denote observations from 2014 and open symbols observations from 2015. The solid schematic lines (in red) indicate the generalised trend in the phenophase shifts along the snowmelt gradient. A flat line corresponds to no shift along the snowmelt gradient in all or most pairwise comparisons. No red line indicates that no clear pattern was identified. For full species’ names and description of the snowmelt gradient see “Methods”. Note that overlapping points have been dodged sideways.

Figure 2. Number of days after snowmelt and day of year on which four vegetative phenophases (Bud green, leaf unfolded, leaf expanded, leaf senescence) in two subarctic dwarf shrubs (a–b) occurred for the first time. The phenophases were observed at two mountain slope aspects (North and South) in a late-melting snowbed. Closed symbols denote observations from 2014 and open symbols observations from 2015. For full species’ names and description of the snowmelt gradient see “Methods”. Note that overlapping points have been dodged sideways.

Figure 3. Number of days after snowmelt and day of year on which four reproductive phenophases (Flower open, flower senescence, fruit set visible, fruit ripe) in four subarctic dwarf shrubs (a–d) occurred for the first time along a natural gradient of snowmelt timing (Early, Mid and Late). The phenophases were observed at two mountain slope aspects (North and South). Closed symbols denote observations from 2014 and open symbols observations from 2015. The solid schematic lines (in red) indicate the generalised trend in the phenophase shifts along the snowmelt gradient. A flat line corresponds to no shift along the snowmelt gradient in all or most pairwise comparisons. No red line indicates that no clear pattern was identified. For full species’ names and description of the snowmelt gradient see “Methods”. Note that overlapping points have been dodged sideways.

Figure 4. Number of days after snowmelt and day of year on which four reproductive phenophases (Flower open, flower senescence, fruit set visible, fruit ripe) in *V. myrtillus* occurred for the first time. The phenophases were observed at two mountain slope aspects (North and South) in a late-melting snowbed. Closed symbols denote observations from 2014 and open symbols observations from 2015. For full species’ names and description of the snowmelt gradient see “Methods”. Note that overlapping points have been dodged sideways.
Figure 5. Schematic representation of patterns in plant phenology with regards to snowmelt timing. Phenological timing is represented as days after snowmelt (DAS) until the onset of a phenophase (continuous line) and as the day of year (DOY) of the onset of a phenophase (dashed line). The occurrence of phenophases in response to snowmelt timing clustered in the present study into three patterns:

(a) *Compensation:* The number of DAS required to reach a certain phenophase decreases with later snowmelt timing. This reduction translates into acceleration of growth and compensates for the delay caused by the late snowmelt, leading to synchronous occurrence of the observed phenophases in plots with different snowmelt timing.

(b) *Under-compensation:* The number of DAS required to reach a certain phenophase decreases with later snowmelt timing but this acceleration is not sufficient to compensate for the delayed start of the growing season caused by late snowmelt. Therefore, phenophases are reached at a later DOY in late-melting plots compared to early-melting plots, but this difference is smaller than the corresponding difference in the snowmelt timing.

(c) *Conservativeness (no compensation):* The number of DAS required to reach a certain phenophase is the same along the snowmelt gradient. Late snowmelt poses a natural delay to development so that phenophases occur at a later DOY in late- compared to early-melting plots and this difference is equal to the corresponding difference in the snowmelt timing.

Note the different slopes in the solid lines in (a) and (b) and the dashed lines in (b) and (c).