DEPARTMENT OF BIOLOGICAL AND ENVIRONMENTAL SCIENCES

FLOWERING TIME DEPENDENCE ON MICROCLIMATE ACROSS AN ELEVATIONAL GRADIENT IN ARCTIC PLANT COMMUNITIES

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Degree project for Bachelor of Science with a major in Biology

BIO602, Biology: thesis 15 hp

First cycle

Semester/year: Spring 2022

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Image on the front page: Geerte Fälthammar - de Jong, field season of 2020.

Contents

Abstract

The Arctic is the fastest-warming region on Earth. Arctic plant communities are highly sensitive to temperature change; temperature-dependent advancement of flowering dates has already been observed in the Arctic. Flowering time is critical for reproductive success. Flowering at the wrong time can reduce seed set through a decreased chance of getting pollinated, or frost damage of the flowers. Knowledge of the factors that influence phenological events gives insight to the response potential of both the community and individual species. This work aimed to investigate the relationship between flowering time and elevation. I attempted to answer the following question: "How does the flowering time relate to elevation?" I hypothesized that flowering would occur earlier at lower elevations because of the higher temperature and earlier snowmelt. To test my hypothesis, I compared the flowering time at five different elevations, spanning an elevational gradient between 700-1500 meters above sea level. I identified dates of flowering peaks using a series of timelapse images taken by field-deployed cameras in the summer of 2020 in Latnjajaure, Lapland. Additionally, I analyzed temperature data for the same locations. There was a strong correlation between elevation and temperature. However, the flowering time of the communities was not dependent on the elevation. Three species were found in more than one plot. Surprisingly, the flowering time of these species occurred almost 30 days later at the lower elevation. This extreme delay in flowering could be due to unusually late snowmelt in the plot, as the timing of snowmelt can vary on a very small scale. In conclusion, we see a high variation of flowering times at both community level and species level, likely as a result of large variation in environmental conditions other than temperature on a very small scale.

Keywords: the Arctic, flowering time, flowering phenology, elevation, elevational gradient, temperature, snowmelt, snow cover, microclimate.

Sammanfattning

Arktis är den plats på jorden som värms upp snabbast till följd av den globala uppvärmningen. Arktiska växtsamhällen är särskilt känsliga för temperaturhöjningar. Redan idag har tidigarelagd blomning och lövsprickning observerats. Blomningstiden är mycket viktig för växternas reproduktiva framgång. Blomning under fel tidsperiod kan orsaka utebliven pollinering eller att blommorna frostskadas. Förståelse för hur stor variation i blomningstid som finns på en lokal skala ger insikt i växtsamhällets och de individuella arternas förmåga att möta klimatförändringar. Syftet med detta arbete är att se hur blomningstiden skiljer sig mellan växtsamhällen på olika höjd. Jag ämnade att besvara följande fråga: Hur varierar blomningstiden med höjden? Min hypotes var att tidigare blomning skulle ske i växtsamhällen på lägre höjd, eftersom temperaturen generellt är högre där och snösmältningen sker tidigare. För att testa min hypotes, så jämförde jag blomningstiden på fem olika platser, höjden varierade från 700-1500 meter över havet. Jag bestämde datumet för maximal blomning utifrån serier av timelapse bilder tagna med kameror monterade i fält under sommaren 2020 i Latnjajaure, Lappland. Dessutom så analyserade jag temperaturdata för samma platser. Det fanns en stark korrelation mellan temperatur och höjd över havet. Men det fanns inget samband mellan blomningstid och höjd. Tre arter växte på fler än en höjd. Oväntat nog, blommade dessa tre arter nästan en månad tidigare på den lägre höjden. En möjlig förklaring till detta är den ojämna snösmältningen. Möjligtvis smälte snön ovanligt sent i det låg-höjds samhälle som jag analyserade, vilket därmed försenade blomningen i detta samhälle. Sammanfattningsvis, så finns det en stor variation i blomningstid i ett litet område både på samhällsnivå och artnivå, troligen på grund av stor variation i miljöfaktorer andra än temperatur.

Nyckelord: Arktis, blomningstid, fenologi, höjdgradient, temperatur, snösmältning, mikroklimat.

Introduction

Arctic environmental conditions

Life in the Arctic environment is extraordinary. It is characterized by the long and snowy winters and late snowmelt. In the short snow-free window the vegetation must undergo the whole vegetative cycle, including budburst, flowering, seed set, bud formation, and nutrient accumulation for the next season (Bliss, 1962). During the two-month-long vegetative period, the air temperatures are usually between 5-8 °C (Bliss, 1962). The low summer temperatures limit plant growth since the reaction rates of the metabolic enzymes are highly sensitive to temperature. Arctic plants typically have shallow roots due to the permanently-frozen ground ("permafrost") that begins just a few centimeters below the soil surface (Bliss, 1962). Arctic light conditions are remarkable due to the great variation in day length throughout the year. During the winter there are days with no light, but during the summer day length in the Arctic is exceptionally long and in certain periods 24 hours (Bliss, 1962).

Plants growing in the Arctic have adapted to its conditions. A compact growth form, rarely higher than 10 cm, is common in the Arctic (Bliss, 1962). These low growth forms allow plants to take advantage of the warmer temperatures and less windy conditions close to the ground. Compact plants are also better adapted to withstand the heavy snow cover without breaking (Bliss, 1962). Earlier budburst and flowering extend the vegetative period; therefore, many Arctic plants form buds the year before. Perennial and evergreen growth is another adaptation to the short vegetative period (Bliss, 1962).

As a partial consequence of the harsh environmental conditions, the Arctic flora has few species of vascular plants compared to the temperate and tropical regions. With increasing latitude and altitude, bigger plants like trees disappear (Bliss, 1962).

Elevational gradient as an environmental condition

Elevation is a complex factor consisting of many environmental conditions that together form the environment that the vegetation is experiencing. Temperature is usually negatively related to elevation, with high elevation areas being colder and, as a result, having later snowmelt. High elevations also tend to be windier and more exposed (Mölders and Kramm, 2014), creating a less hospitable environment for plant growth.

Climate change in the Arctic

The Arctic is the fastest-warming place on Earth, warming three times as fast as the global average (IPCC, 2021). Because Arctic vegetation exists on the lower temperature threshold for growth, it is especially sensitive to even small changes in temperate (Bliss, 1962). Warming is changing the relative proportions of the species in the plant communities; the abundance of shrubs has increased during the last decades at many locations in the Arctic (Hallinger et al., 2010; Sturm et al., 2001; Tape et al., 2006). An increase in shrub abundance has also been observed in experimentally warmed plots (Bret-Harte et al., 2001; Dawes et al., 2011), and the treeline and shrubline are advancing to higher latitudes and higher elevations (Kullman, 2002; Myers-Smith and Hik, 2018). One of the most-studied consequences of climate warming in the Arctic is shifts in the timing of life events ("phenological shifts"; (Parmesan, 2007). Snowmelt and flowering dates have advanced in many places (Høye et al., 2007), with plants growing at colder sites found to be more sensitive to changes in temperature than those in warmer sites (Prevéy et al., 2017).

Changes in flowering phenology

Warming affects the time of flowering of individual plants, and hence also the flowering season at the community level. Flowering phenology is a very plastic trait that allows populations to respond to their local conditions (Elzinga et al., 2007), especially given interannual variation in temperature. Greater advancement of late flowering plants compared to early flowering plants can lead to a shorter flowering season overall as the climate warms (Høye et al., 2013; Prevéy et al., 2019). Arctic plants could be under selection for early flowering and growth, to extend the very short vegetative period (Prevéy et al., 2017).

Importance of timing of flowering

Flowering at the wrong time can be costly for a plant. If flowering occurs too early, and the plant has not yet accumulated enough nutrients, seed set could be reduced. On the other hand, there is a risk of not ending the reproductive cycle in time if the flowering is too late. Since the seed set of many plants is dependent on pollinators, the timing of flowering must also correspond with pollinator activity. Flowering at the wrong time can reduce the chance to be pollinated. The time of flowering is controlled by both genetic factors and environmental factors, such as temperature, light, and nutrient availability (Elzinga et al., 2007).

Knowledge of the factors that influence phenological events gives insight to the adaptation potential of both the community and individual species. The degree of reproductive isolation between the populations at different elevations plays its crucial role. On one hand, isolation allows for local adaptation. But on the other hand, small and isolated populations are at greater risk of extinction. Gene flow between the populations requires at least temporal overlap in flowering among populations at different elevations.

Aim and hypothesis

The rapid warming in the Arctic highlights the importance of understanding the environmental drivers, especially temperature, of phenological variation at the local scale.

This study aims to understand what environmental factors influence flowering phenology in Arctic plants. Temperature dependent flowering phenology is a key factor which affects the species composition balance of the community. In turn, the temperature is expected to vary throughout the elevation gradient. Consequently, studying phenology on an elevational gradient provides a good opportunity to examine temperature effect on flowering time in a limited geographical area.

In this work I attempt to answer the following question: How does the timing of flowering relate to elevation? I hypothesize that flowering occurs earlier at lower elevations because temperature is higher, and snowmelt generally happens earlier there.

Methods

Study site

Flowering phenology was recorded near Latnjajaure field station, in northernmost Swedish Lapland (68.35°N, 18.49°E). Latnjajaure field station is located on the east side of lake Latnjajaure. The elevation of the valley spans between 700-1500 m above sea level (Scharn et al., 2021).

Species

The studied species were common tundra plants, they were all perennials with a compact growth form, and many of them were evergreen. Many of the species studied were representatives of the heather family, *Ericaceae*, including the evergreen dwarf shrubs *Empetrum nigrum*, *Loiseleuria procumbens*, *Cassiope tetragona,* and *Phyllodoce caerulea,* and the deciduous dwarf shrubs *Harrimanella hypnoides*, *Vaccinium myrtillus,* and *Vaccinium uliginosum*. The *Diapensiaceae* family was represented by the evergreen shrub *Diapensia lapponica*. Further, two semi-parasitic herbs in the *Orobanchaceae* family were observed: *Pedicularis hirsuta* and *Pedicularis lapponica*, as well as the herb *Bistorta vivipara*, in the *Polygonaceae* family, which forms a thick rhizome, and commonly reproduces through the formation of bulbils (Mossberg and Stenberg, 2018).

Setup of the plots

In the summer of 2020, members of EDGE-lab set up 64 plots at Latnjajaure. The methodology followed a protocol developed for vegetation surveys on Disko Island, Greenland in 2019 (unpublished). The choice of location for the plots was done to ensure the plots cover as wide a variety of microclimates as possible. Therefore, the area was classified into five elevation bands (Figure 1a). Each elevation band was then divided into three vegetation greenness classes, using satellite data. Vegetation greenness can be used as a proxy for the productivity of the area (Myers-Smith et al., 2011). The area was further divided into two moisture classes using satellite data (Figure 1b). In total, there were (5 elevations) × (3 greenness) × (2 moisture) = 30 categories of plots. The location of the plots was chosen randomly. However, some plots were found impossible to access (e.g., too steep slopes or located in a river). Therefore, each such inaccessible plot was replaced with another randomly selected plot of the same category.

The plots were circular with a radius of 2 meters. The center of each plot was marked with a tent peg. Air temperature was measured 10 cm above the soil surface in all plots, using a TOMST TMS-4 logger. The TOMST loggers were placed close to the center of the plot and programmed to take measurements once every 10 minutes. At each plot, vegetation inventories were performed. The vegetation conditions over time were recorded with cameras (Wingscapes Timelapse Pro). Each plot was equipped with a camera on a tripod, placed outside of the plot, and facing towards the plot. The cameras took one picture every 6 hours from late June to late August.

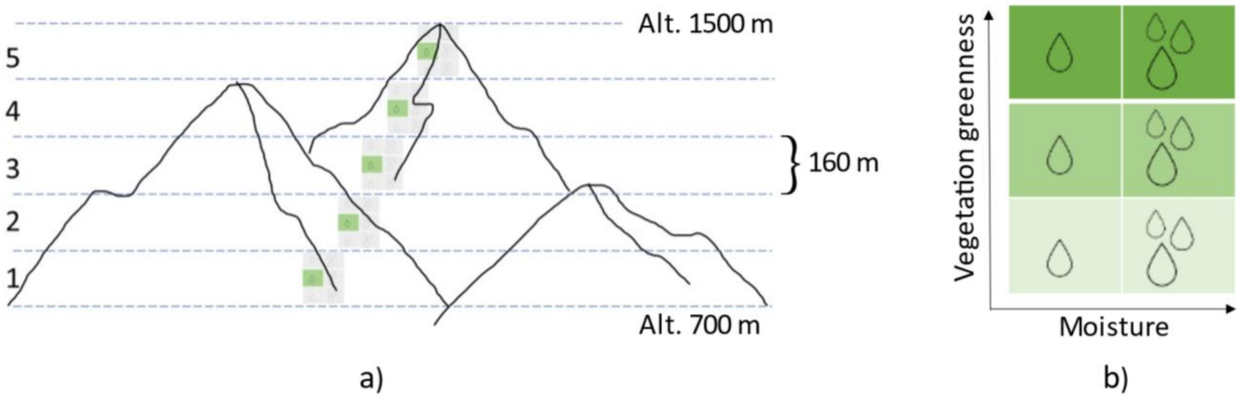

Figure 1: Experimental setup. (a) The area was divided into 5 elevation bands starting from the bottom, at 700 meters. And then adding 160 meters for each elevation band. (b) There were three vegetation greenness classes: low, medium, and high. And two moisture classes: dry and wet. Combined six vegetation greenness and moisture classes. For this project, I analyzed the medium greenness – dry class across all five elevation bands.

Choice of plots for the project

For the project, we chose one plot at each of the five elevation bands. To reduce variation in environmental conditions, we chose plots of the same vegetation greenness and moisture class at each elevation. We chose the class of medium vegetation greenness and low moisture. This choice was done to maximize the number of overlapping species between the five plots. If vegetation greenness was low, then there was a problem to find overlapping species with the high elevation plots. If the vegetation greenness was high or wet, it was hard to see anything but dwarf birch, *Betula nana,* in the low elevation plots.

Data extraction and analysis

I analyzed the images recorded at Latnjajaure as described above. First, I separated the usable images from the non-usable ones. The primary criterion for using a photo was that the vegetation was in focus and visible. There were many reasons why an image could not be used: too dark, fog, shaking due to wind, or water on the camera lens. Then I went through the images and identified the flowering species using the vegetation inventory lists of the plots. This way, the number of potential species were limited to a small number of possible species.

Then, per each plot and day, I annotated one photograph, by marking every flower with a rectangle referring to the species, using VGG image annotator software (Dutta, 2018). The annotation data was then downloaded as a comma-separated file, .CSV, where each line represented one rectangle, containing information of the species name and the name of the image to which that rectangle belong to. The image name contained date and location. This .CSV file was then imported and further processed in R software platform, version 4.1.2 (R Core Team, 2021). The date was transformed into the day-of-year format using *lubridate* package (Grolemund and Wickham, 2011). I added elevation data into an additional column which corresponded to the five locations. I calculated the number of flowers present of each species at each location during each day using *dplyr* package (Wickman et al., 2022) in R. Further, I identified the peak flowering date for each species in each location, defined as the day with the maximum number of flowers.

The processed data proceeded then into the analyses. First, I determined the relationship between peak flowering and elevation using a linear regression. Significance was determined according to a reference level alpha of 0.05. Next, I compared flowering times of species that existed in multiple plots. For this, I plotted day of peak flowering of each species against elevation. Different species were expected to flower for different intervals of time, therefore the flowering intensities over time between the different elevations and species were compared. Flowering intensity was calculated as a ratio between current and maximum number of flowers. Mean seasonal air temperature was calculated from the temperature data obtained from the TOMST loggers. A linear regression was used to describe the relation between average seasonal temperature and elevation (alpha = 0.05). All graphs were made using *ggplot2* package (Wickham, 2016).

Results

Temperature was strongly negatively correlated with elevation across the five study plots ($p = 0.0003$). Each 100-meter gain in elevation corresponded to a temperature decrease by 0.68 °C by. Across the entire elevational gradient temperature varied by 4 °C (Figure 2).

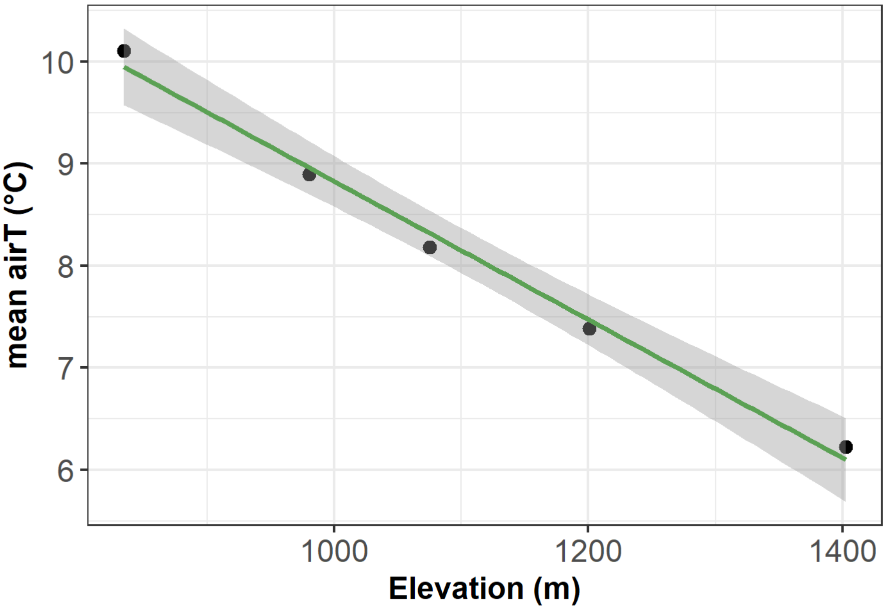

Figure 2: Mean seasonal air temperature as a function of elevation in meters. The linear regression was significant $p=0.0003<0.05$. The function of the regression was $y = -0.0068x + 16$

There was no relationship between community flowering time and elevation (Figure 3; $p=0.6$). Flowering time in the community at 980 m was approximately 30 days later than in the rest of the communities. Among the other four communities, the variation in average flowering time was about 5 days. In the community at the elevation of 1200 m, one outlier species (*Bistorta vivipara*) flowered much later (approximately 20 days) than the rest of that community. There is large variation in the number of flowering species between the communities, from one to seven species.

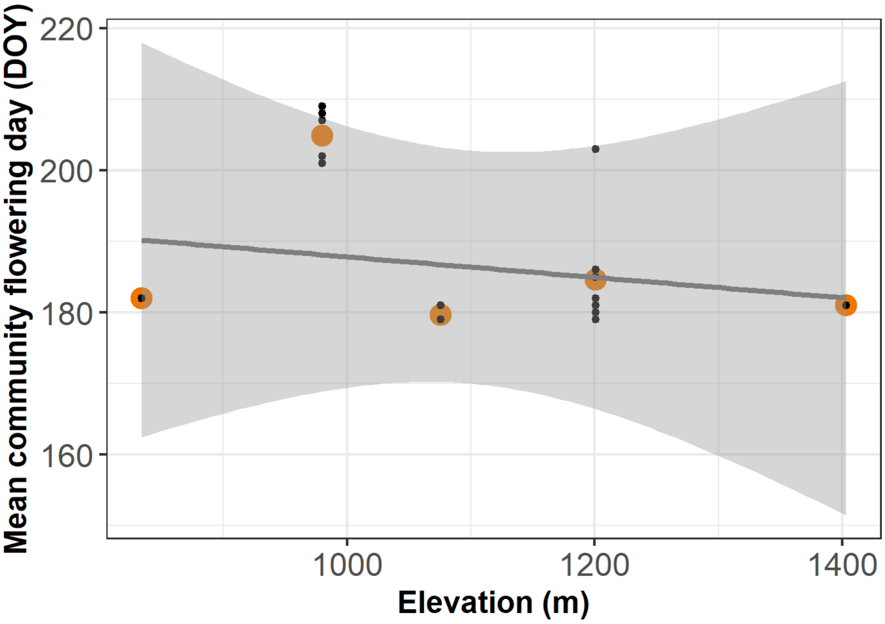

Figure 3: Mean community flowering day (measured in DOY = day of year) as a function of elevation (meters). In orange are the mean flowering peaks of the communities. The linear regression is fitted to these orange dots. The regression was not significant, $p=0.6>>0.05$. The smaller black dots are the flowering peaks of the individual species growing in that community.

Three species were found in more than one plot. The flowering peak of these elevations occurred almost 30 days earlier in elevations 3 and 5 compared to elevation band 2 (Figure 4). The flowering peak of these three species was very close in time at elevations 3 and 5. In elevation band 2, the variation of the flowering peak for the same species was in the same order (4 days). This indicates that the flowering time of the whole community at elevation band 2 was substantially later.

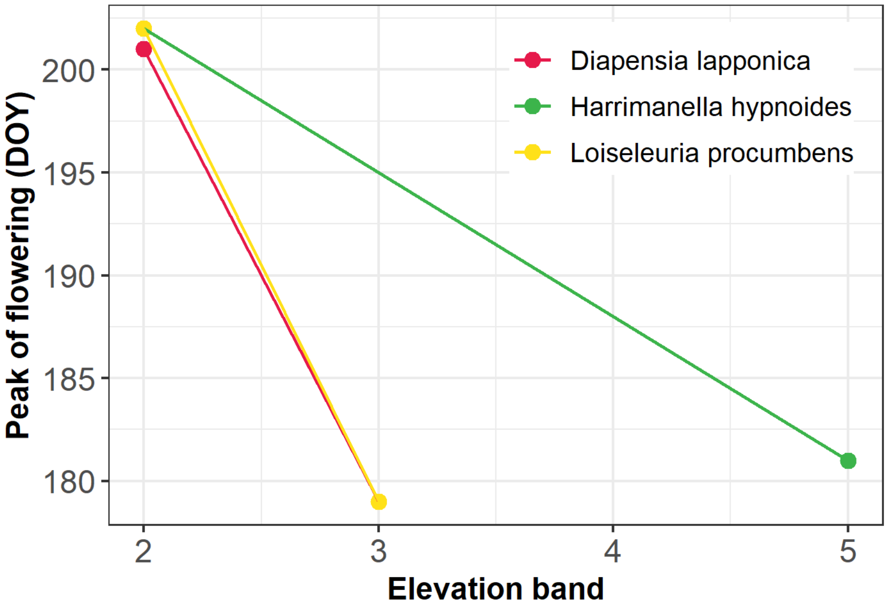

Figure 4: For species that occur in more than one plot we compare the dates of flowering peaks. Time for flowering peak (measured in DOY = Day of Year) plotted against elevation. We observe an earlier flowering in the higher elevations compared to plot 2.

The duration and peak of flowering varies by both species and location (Figure 5). In all plant communities except the community at elevation 2, however, we only observed the decrease in flowering intensity, but not the start of flowering. Most likely the flowering peak of these communities was missed. Probably, the flowering of the early flowering species was also missed. At elevation 2, on the other hand, we see the start, peak, and end of all species we observe. Another exception is *Bistorta vivipara* at elevation 4. In contrast to the other species at this elevation band, the start, peak, and end of this species were observed.

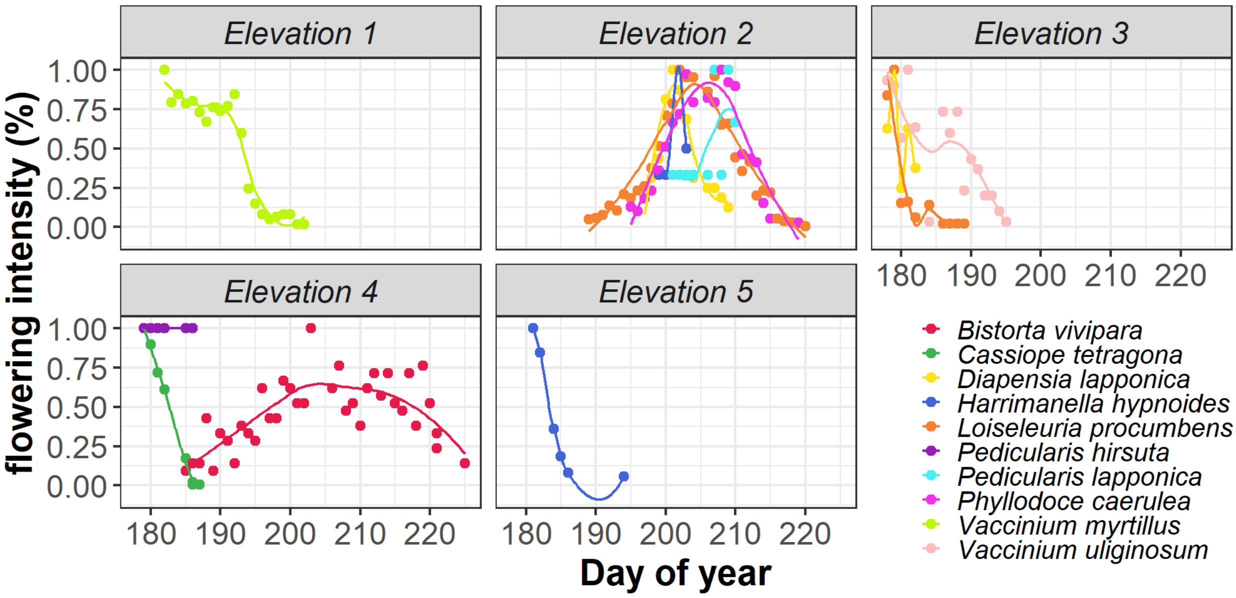

Figure 5: Flowering intensities of different species (measured as a percentage of the peak of flowering) over time (measured in day of year). Separated by the elevation bands. Different colors represent different species

Discussion

Despite the strong correlation between elevation and temperature, no relationship between elevation and flowering time was found. This suggests that temperature is not the main driver of flowering phenology along this elevational gradient. This is surprising, since many other studies observed clear effect of temperature on earlier flowering (Høye et al., 2013, 2007; Prevéy et al., 2019). Experimental warming also triggered earlier flowering, suggesting that temperature is a key driver for timing of flowering (Dunne et al., 2003). In contrast, this study found no relation between flowering time and elevation, hence temperature. Other environmental factors, such as snow depth and duration, could explain the timing of flowering.

Snowmelt effect on vegetation and flowering

The timing of snowmelt could explain variation in the onset of flowering. It has been well established by previous studies that relatively late snowmelt will lead to late flowering in a community. According to a study conducted by Cooper et al. (2011) on Svalbard, it took on average three weeks from snowmelt to green-up and five weeks to flowering start. In a test with manipulated snow cover, where the snow melted about two weeks later compared to the controls, they saw a delayed start of the growing season and hence also delayed flowering. They found that the early phenological phases like budburst and flowering were more affected by the timing of snowmelt than the late phenological phases like leaf senescence and seed dispersal (Cooper et al., 2011). Furthermore, a review of multiple snow manipulation experiments revealed that the phenology of early flowering species is highly delayed by late snowmelt (Wipf and Rixen, 2010).

Irregular snow cover and snowmelt

Topographically varied areas create a greater heterogeneity of microclimates (Opedal et al., 2015). Snow cover is strongly affected by the topography (Molotch et al., 2005); therefore, mountains that have a complex topography usually have a large variability of snow depth across a very small area (López-Moreno and Stähli, 2008).

Snow from open places is blown away by the wind. Dense snowbeds are formed in the folds of landscape and behind boulders, at the leeside (Föhn, 1980; Vestergren, 1902). Big snowflakes fragmentize into smaller and rounder grains when they crash into each other accelerated by the heavy wind. These small and compact grains pack denser than big snowflakes (Vestergren, 1902). The wind speed usually increases with the altitude (Bañuelos-Ruedas et al., 2010). The thin snow on the ridges melts earlier than the thick snowbeds (Billings and Bliss, 1959).

The irregular snow cover itself can cause irregular snowmelt. But the microclimate also affects the rate of snowmelt. High temperature, south-facing slopes (Cazorzi and Dalla Fontana, 1996), and high rainfall (Marks et al., 2001) are factors that help the snow cover to melt.

Outlier flowering time at elevation 2

Spatial variation in snowmelt could explain the observed outlier timing of flowering at elevation band 2, which flowered almost 30 days later on both the community level (Figure 3) and species level (Figure 4). Small-scale variations in snowmelt have been observed in Latnjajaure (Figure 6). Elevational band 2 at Latnjajaure field station is at the valley floor (Scharn et al., 2021) and could therefore be topographically different from the other elevational bands. Flowering time particularly in the analyzed plot at elevation 2, could be determined by this topography-driven variation in the timing of snowmelt. The following year (2021) the snowmelt in the same plot at elevation 2 was average, but this can vary from year to year based on the amount of snowfall and the direction of the wind.

Variation in flowering time among communities can often be explained by differences in community composition, since typical flowering times vary between species. However, flowering times of species overlapping between communities indicate that the microclimatic conditions, not species composition, drive the variation. These microclimatic conditions are likely driven at least in part by variation in snowmelt, but variations in soil depth, level of wind exposure, or winter temperatures have also been found to influence flowering phenology.

Figure 6: Variations in snowmelt on the small scale in Latnjajaure. Image by Anne Bjorkman, 2020

Outlier flowering Bistorta vivipara does not experience late-flowering limitation

In most cases, the flowering time of species within a plot are more similar to each other than across plots. However, *Bistorta vivipara* is a clear outlier in this regard, flowering at least 20 days after the other species in the plot (Figure 3). This is surprising given the likely strong disadvantage of late flowering for the successful development and maturation of seeds before the onset of autumn (Totland, 1997).

In contrast to most of the other species I observed, *B. vivipara* often reproduces vegetatively: either from bulbils that bud off from the inflorescence and grow into new plants (Bauert, 1993; Molau and Edlund, 1996) or rhizomes – underground stems from which new shoots sprout out (Diggle et al., 1998). *B. vivipara* is, therefore, not so dependent on flowering for reproductive success (Diggle et al., 1998). This could explain how it can flower at unusual times.

Clonal reproduction leads to genetically similar offspring (Diggle et al., 1998). Low genetic diversity has less potential for adaptation, and hence, poses a higher risk for extinction under changing conditions (Frankham, 2005). However, *B. vivipara* is widely abundant in most northern regions and grows well in a variety of microclimates (Marr et al., 2013; Mossberg and Stenberg, 2018). This suggests that *B. vivipara*'s success is not hampered by low genetic diversity in the species as a whole; possibly because the small percentage of sexual reproduction that occurs is sufficient for maintaining high genetic diversity.

Limitations and future work

Although my project conclusively demonstrates the importance of factors other than temperature in influencing flowering phenology at Latnjajaure, several limitations of this study preclude more general conclusions. First, early flowering was missed due to late camera setup, thus leading to a late-bias in the estimate of peak flowering in all plots except elevation 2. Furthermore, the small number of analyzed plots limited the statistical power of the observed tendencies. Nevertheless, there was no relationship between flowering time and temperature, despite a relatively large elevation and temperature gradient among these five plots, which indicates that other microclimatic parameters not analyzed influenced flowering phenology.

This work can further be developed by analyzing more plots, and possibly training an AI algorithm to recognize and quantify the different flowering species. Earlier plot setup would allow to observe the early flowering species as well as the early phenological phases of these. Collecting data for snow depth and dates for snowmelt would allow to evaluate their contribution to the variation in flowering. Another direction for further work could be to study the consequences of variation in phenology for an individual's reproductive success, for example by measuring seed set of the outlier communities. The following research questions could be addressed: Does the number of seeds relate to flowering time? Does their quality (weight or nutrient composition) vary with the flowering time? And, does their germination rate depend on flowering time (can be tested with cultivation experiments)?

Conclusions

No relationship between flowering time and temperature or elevation was found. Timing of flowering across this elevational gradient is better explained by other environmental factors, than temperature, possibly the timing of snowmelt or level of wind exposure. This highlights that even if temperature is a parameter that is certainly changing due to climate change, on the local scale there are other factors just as important if not more important that will influence plant communities' response to climate change.

Studying flowering phenology across an elevational gradient provides a rough estimate of how reproductively isolated the populations are, and thus how independent their responses to warming would be. However, no conclusions about gene flow across the elevational gradient could be made That is because (1) many of the compared species in the communities were unique to only one community; and (2) three species that overlapped between several plots, overlapped with the outlier community. Therefore, this comparison could not be conclusive.

Although a larger sample size would strengthen our understanding of the relation between phenology and elevation, the results of my study suggest that temperature alone is insufficient to explain variation in flowering time across a large spatial gradient in the Arctic tundra. This suggests that future climate warming may be less important than other environmental changes (e.g. changes in the total snowfall or duration of snow cover) in determining future phenological shifts.

Acknowledgments

Thanks to my supervisor Anne Bjorkman, for showing interest in my work and thoughts, for constructive feedback throughout the entire process from R to writing, and for creating an open and including working environment in the group. Thanks to my wonderful co-supervisor Geerte Fälthammar - de Jong, for instructions, patience, support, and great advice. Thanks to Konsta Happonen and Erik Ljungstrand for valuable discussions. And thanks to rest of the EDGE-group for support and an opportunity to activate my English :).

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