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Effects of snowmelt timing, temperature, and soil moisture on flowering phenology and seed set of *Dryas octopetala*

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Master of science in Biology

Preface

This thesis finishes my master’s degree in biology at the Norwegian University of Life Sciences (NMBU). I have been interested in plants for a long time, and my fascination for vascular plants increased while studying biology. From the early beginning, I knew that my thesis should be on a flowering plant and including climate change in my topic sounded very interesting.

I want to thank my main supervisor, Kari Klanderud, who has always given me exceptional guidance and advice along my research journey. I would also thank my co-supervisor, Ruben E. Roos, for his encouragement and for always giving me invaluable tips, primarily through the statistical process. Both of you have been a constant source of support and have given me ideas to drive my research forward. I would also thank Erik Finne, who took me on a trip to Mt. Sanddalsnuten and inspired me to advance my research. Lastly, I want to extend my warmest thanks to my family and friends for their motivation and support throughout this journey.

Norwegian University of Life Sciences

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Abstract

Climate change advances the timing of life-cycle events (i.e., phenology) in plants, especially in cold biomes where the temperatures have increased twice as fast as in other biomes. In cold biomes, warmer temperatures will lead to earlier snowmelt and the risk of drought increases. These environmental conditions will differ on a small scale due to the topography and affect the timing of flowering. However, understanding which environmental factors influence phenology and how climate may impact those factors is important for predicting potential responses in alpine plant communities.

The main objective of this study is to examine how the flowering phenology and seed set of *Dryas octopetala* at Finse, Norway, are driven by snowmelt timing, ground surface temperature, and soil moisture. There were established 25 plots in three different elevations: low, middle, and high. Using time-lapse cameras and climatic loggers, I calculated the date of onset flowering, day of snowmelt, duration of the prefloration interval from snowmelt to the onset of open flowers (prefloration interval), average ground surface temperature, average soil moisture, and seed sets (%).

I found that plots with earlier snowmelt timing had an earlier flowering onset. The length of the prefloration interval was shorter at plots with warmer average temperatures and greater average soil moisture in the prefloration interval, as well as plots with delayed snowmelt. Plots at the middle elevation had an earlier snowmelt timing than the high elevation. The ground surface after snowmelt decreased with increasing elevation, and soil moisture was greater at the low elevation than at the middle elevation. There was no significant difference in seed sets among the three elevations, even though seed sets tended to decrease with elevation. These results suggest that earlier snowmelt will advance the date of onset flowering of *D. octopetala*. However, earlier snowmelt will only majorly impact the flowering phenology if the temperatures increase in the prefloration interval.

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1. Introduction

Shifts in the timing of life-cycle events (i.e., phenology) in plants are one of the most practical examples of climate change (Büntgen et al., 2022; Høye et al., 2007). Global air temperatures have increased by 1.09 °C from 1850 to 2022 and more rapidly over the last few decades (Pörtner et al., 2022). These temperature changes are expected to continue, but temperature increases will differ worldwide (IPCC, 2007). Under ongoing environmental change, average temperatures have increased across all regions and even twice as fast in cold biomes (Pörtner et al., 2022). Since plants in cold biomes are usually limited by low temperatures, many plants will change their flowering time (Anderson et al., 2012; Smith et al., 2012)(Dorji et al., 2020). Changes in the flowering time are observable today and are expected to continue in the future. This makes cold biomes an excellent place to examine how or to what extent future climatic changes will impact plant phenology.

Cold-adapted plant species manage to survive in harsh environmental conditions, such as long snow-covered winters, low temperatures, strong winds, and short summers (Bliss, 1962; Root et al., 2003). To cope with these environmental conditions, many alpine plants have evergreen leaves and produce flower primordia at the end of the previous growing season to have more time to complete their phenological development (Billings, 1974). Previous studies have found that the flowering phenology in cold biomes is driven by temperature (Prevéy et al., 2019), snowmelt timing (Bjorkman et al., 2015; Høye et al., 2007), and soil moisture (Inouye, 2020; Nord & Lynch, 2009; Zhu et al., 2016). These physical factors can vary within a few meters because the topography in alpine landscapes is often heterogeneous, creating small-scale variations in environmental conditions (Gehrmann, 2019; Høye & Forchhammer, 2008; Stanton et al., 1994). Small-scale variation in environmental conditions is predicted to equal or exceed the global climate change predictions, where air surface temperature decreases along an elevation gradient (McCain & Grytnes, 2010; Opedal et al., 2015).

Snow cover is important for the alpine plant communities throughout the season by projecting the alpine plants from harsh winter temperatures, blowing-snow particles, and frost during the winter (Happonen et al., 2019). The snow dynamic can vary along elevation gradient throughout the landscape, where the windward slopes have less snow buildup than the leeward slopes (Grünewald et al., 2014). Matiu et al. (2020) found that the snow depth in European Alps has decreased over the last few decades, whereas the maximum snow depth in West Norway has not changed over the last few decades (Roos et al., 2022). A decrease in snow layer and warmer temperatures has led to earlier snowmelt (Wipf et al., 2009), which in turn determines the length of the growing season (Ernakovich et al., 2014; Nybakken et al., 2011; Prevéy et al., 2019), as well as the onset of flowering (Høye et al., 2013; Livensperger et al., 2016).

Previous studies have found that cold-adapted plants have advanced (Dorji et al., 2020; Høye et al., 2013; Jabis et al., 2020), delayed (Hollister et al., 2005), or unchanged (Hoffmann et al., 2010) their flowering time in response to warmer temperatures. The initiation of preformed flower primordia responds very quickly after snowmelt when the average daily temperatures exceed 0 ºC (Bjorbækmo et al., 2010; Tieszen, 1978; Tieszen, 2012). Plant development is also predicted to accelerate due to warmer temperatures (Heide, 1992; Jonas et al., 2008). The frequency of frost damage on flower primordia and flowers increases by advancing their flowering time, which can have detrimental effects on flowering abundance and seed set. (Inouye, 2008; Wipf et al., 2009). From a long-term perspective, earlier flowering can disturb the interaction between plants and pollinated insects (Kudo & Ida, 2013). A disturbance between plants and pollinators can impact the seed set success of insect-pollinated flowers (Ohler et al., 2020).

Soil moisture is another abiotic factor that impacts the phenology of alpine plants (Hall et al., 2018). The availability of soil moisture during the growing season is greater in areas of delayed snowmelt than in areas of advanced snowmelt (Dorji et al., 2013), which impacts the relative growth rate and seed dispersal to plants (Bjorkman et al., 2018).

Dryas octopetala L. is one of ca 10000 flowering species adapted to cold environments (Körner, 2004). Previous studies have found that the flowering and the seed set of *D. octopetala* are sensitive to the snowmelt timing, temperature, and soil moisture after the date of the snowmelt (Høye et al., 2007; Welker et al., 1997). In mainland Norway, *D. octopetala* is classified as a near-threatened species, with an assumed reduction of 15% over the coming decades (Solstad H et al., 2021). Therefore, *D. octopetala* is used in numerous studies to understand how *D. octopetala* and the alpine plant communities respond to environmental change.

In this study, I will examine how the flowering phenology and seed set of *D. octopetala* are driven by snowmelt timing, ground surface temperature, and soil moisture at Mt. Sanddalsnuten near Finse, southern Norway. Here, I will use time-lapse imagery to quantify the flowering phenology and seed set success of *D. octopetala*. I aim to determine (1) how the onset of flowering is related to the timing of snowmelt, (2) how temperature and soil moisture after snowmelt impacts the phenological development stages of *D. octopetala* and (3) how the seed set differs along an elevation gradient. I predict snowmelt timing will occur earlier with increasing elevation because of less snow build-up. I also expect that increasing elevation will decrease ground surface temperature and soil moisture after snowmelt. I also predict that earlier snowmelt will advance the onset of flowering. However, the accumulated temperature sum before reaching the next phenological stage will be the same, independent of snowmelt timing.

2. Materials and methods

Study site

The study was conducted at Mt. Sanddalsnuten (60°36.9’ N, 7°31.023’ E), approximately 2 km north of Finse, southern Norway (Figure 1). Finse lies in the mid-alpine zone and is covered with snow for around 8-10 months, where the snow depth differs throughout the landscape (Filhol et al., 2019; Sjursen & Sømme, 2000). The average annual temperature at Finse has increased by 0.36 ° C per decade (Roos et al., 2022), with an average monthly temperature and rainfall of 7.5 ºC and 92 mm during June-August, respectively (MET, 2023).

The phenological observations of *D. octopetala* occurred near the summit on the southwestern slope of Sanddalsnuten (peak at 1554 m a.s.l). Sanddalsnuten is involved in the International Tundra Experiment (ITEX), where researchers study the effects of environmental change on cold-adapted plant species. The bedrock of Sanddalsnuten consists of dry, calcareous phyllite or shale gravel (Olsen & Klanderud, 2014). *Dryas octopetala* is a dominant species at Sanddalsnuten (Klanderud, 2005), which cover at least 80 % of the vegetation but gets more sparse as the elevation increase (Olsen & Klanderud, 2014). Sanddalsnuten is, therefore, a suitable location to study the effects of environmental change on the flowering phenology of *D. octopetala*.

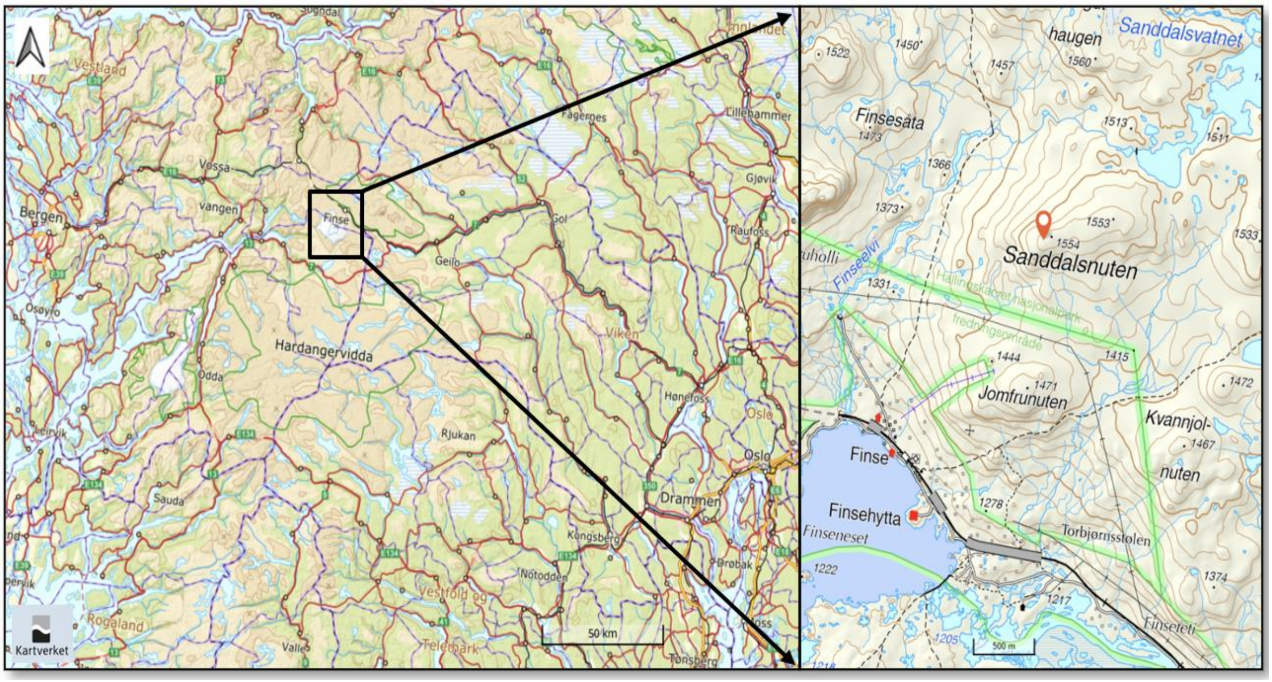

Figure 1: Map of the study site of Mt. Sanddalsnuten, Finse, southern Norway. Source: (Kartverket, 2023)

Study species

Dryas octopetala is an alpine-arctic dwarf shrub with a circumpolar distribution (Figure 2). The flowering shrub has 8-10 white petals, approximately 2 cm in diameter, and grows as a dense mat (Figure 2) (Walker, 2015). The flowers of *D. octopetala* are either hermaphrodites or males (Wada et al., 1999) and are insect-pollinated, mainly pollinated by flies. *Dryas octopetala* is a long-lived shrub with a lifespan of over 100 years and starts to produce seeds at three years old (Walker, 2015). The flowering phenology of *D. octopetala* is completed when the fruits are feathery and ready to be spread by the wind.

To handle short summer, *D. octopetala* has a set of traits for completing their phenology before the growing season ends. For instance, *D. octopetala* has evergreen leaves and can start photosynthesis when the ground surface temperature rises above 0 °C (Bucher & Römermann, 2020; Tieszen, 1978). In addition, *D. octopetala* produces flower primordia during the previous season and has petals that follow the sun's movements to maximize the level of energy from photosynthesis to survive and reproduce (Kjellberg et al., 1982; Lamprecht et al., 2006).

Figure 2: Photo of *D. octopetala* at Mt. Sanddalsnuten, Finse, southern Norway. June 2021. Photo: Stian Andresen (2022).

Experimental setup

The fieldwork of this study was carried out by Roos et al. (2023, unpublished manuscript) from January 1st to October 22nd, 2021. They established 25 plots at three different elevations along the slope of Sanddalsnuten, named low elevation, middle elevation, and high elevation (Figure 3), where the difference in altitude was 50 m between each elevation respectively. There were deployed 5 plots at the low elevation, 15 in the middle elevation, and 5 at the high elevation. Each plot had a size of 50 x 50 cm and was placed a few meters apart. The location of the plots was chosen after the following criteria: 1) *D. octopetala* was the dominant plant in the plot, and 2) *D. octopetala* would probably produce flowers in the upcoming season (based on the remaining flower stems from the 2020 season). The plots were selected at different elevations to maximize the range of microclimatic conditions in the phenological development of *D. octopetala*.

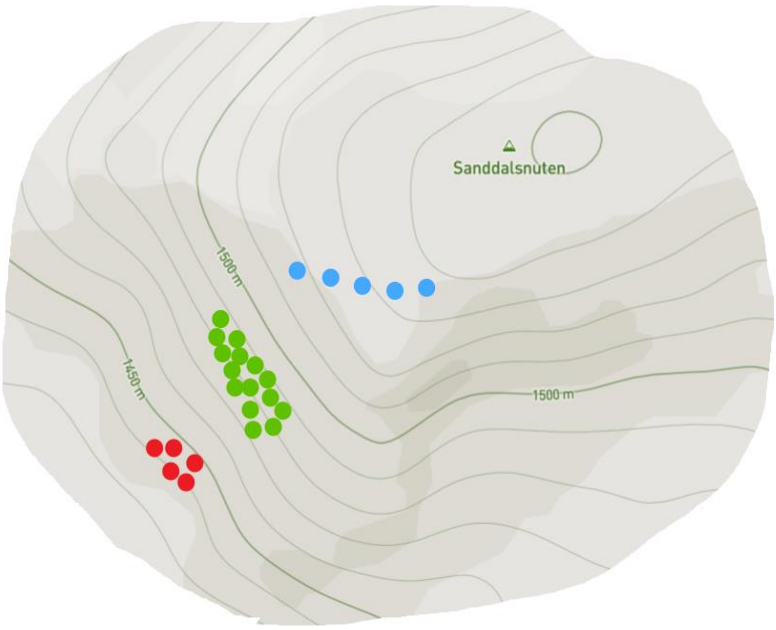

Figure 3: The location of the 25 plots three elevations at Mt. Sanddalsnuten, Finse, southern Norway. Low elevation with red dots (1444 m.a.s.l), middle elevation with green dots (1471 m.a.s.l), and high elevation with blue dots (1512 m.a.s.l). Each plot at Sanddalsnuten was marked with a unique ID number from 0 to 24. Source from (Mapbox, 2023)

At each plot, a Moultrie Wingscapes Timelapse Cam Pro® (Mettler Toledo, Greifensee, Switzerland) was installed to capture snowmelt timing and flowering phenology of *D. octopetala*. The cameras were mounted around 60 cm from the ground level on a frame of metal tubes and faced downward, capturing 30 x 20 cm of the flowering vegetation (Figure 4). The cameras were set to take images from May 11th to October 22nd, where image-sampling frequency increased in the flowering season to maximize the number of successful images of the flowering phenology.

Each plot also had a TMS-4® (TOMST s.r.o, Czech Republic) loggers that measured the soil moisture (5 cm below the ground) and the temperature at three different depths of -6 cm, +2 cm, and +15 cm above the ground surface. The TMS-4 loggers were placed near the outside of the camera angle and took measurements once every quarter from January 1st to October 22nd.

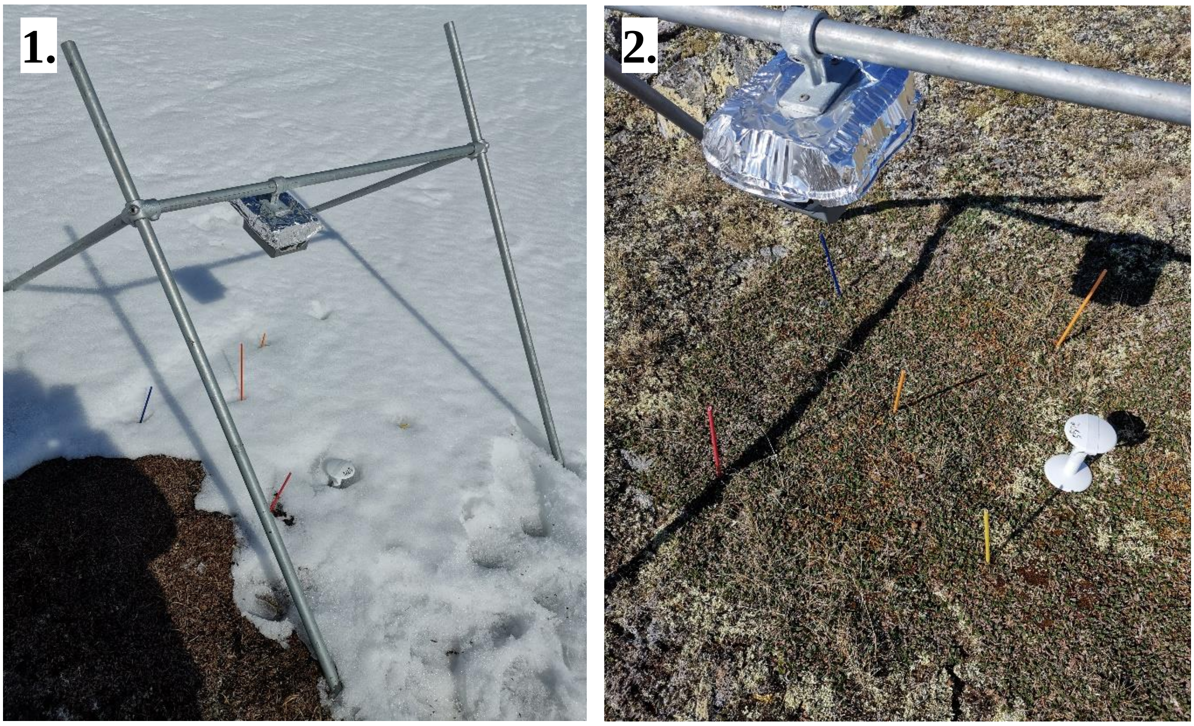

Figure 4: Illustration of the metal frame construction with camera and TMS-4 logger at Mt. Sanddalsnuten, Finse, southern Norway. Images were taken on 1) 14 May 2021 and 2) 10 June 2021. Colored stick in the vegetation shows the plot size to observe the snowmelt and the phenological development of *D. octopetala*. Photo: Ruben E. Roos (2021).

Image handling

In an earlier study, Roos et al. (unpublished manuscript) observed the flowering phenology using eight images daily, which worked very well. Therefore, I decided to subset the frequency of images to four images daily, resulting in a total of 13306 taken images from 25 cameras. The images I kept had a six-hour interval between each other, one at 00:00 AM, 06:00 AM, 12:00 PM, and 6:00 PM. A few cameras had gaps in the time-lapse imagery with different duration and frequencies (Appendix 1). These gaps did not skip any phenological development stages of *D. octopetala*.

To quantify *D. octopetala* phenology and snow cover, the images were uploaded to a software called VGG image annotator (VIA) (Dutta & Zisserman, 2019). Then, each image was annotated by manually drawing bounding boxes around *D. octopetala* individuals and the snow cover. Finally, drawn boxes were given a class that defined how much snow there was in the images and which phenological stage a plant was in (Tables 1 and 2).

Table 1: Classification of the snow cover (Roos et al., unpublished manuscript)

Group	Visual criteria
Snow-covered	The surface is completely covered with snow.
Partially snow-covered	The surface contains patches of snow.
Snow-free	No snow on the surface.
New snow	New snowfall.

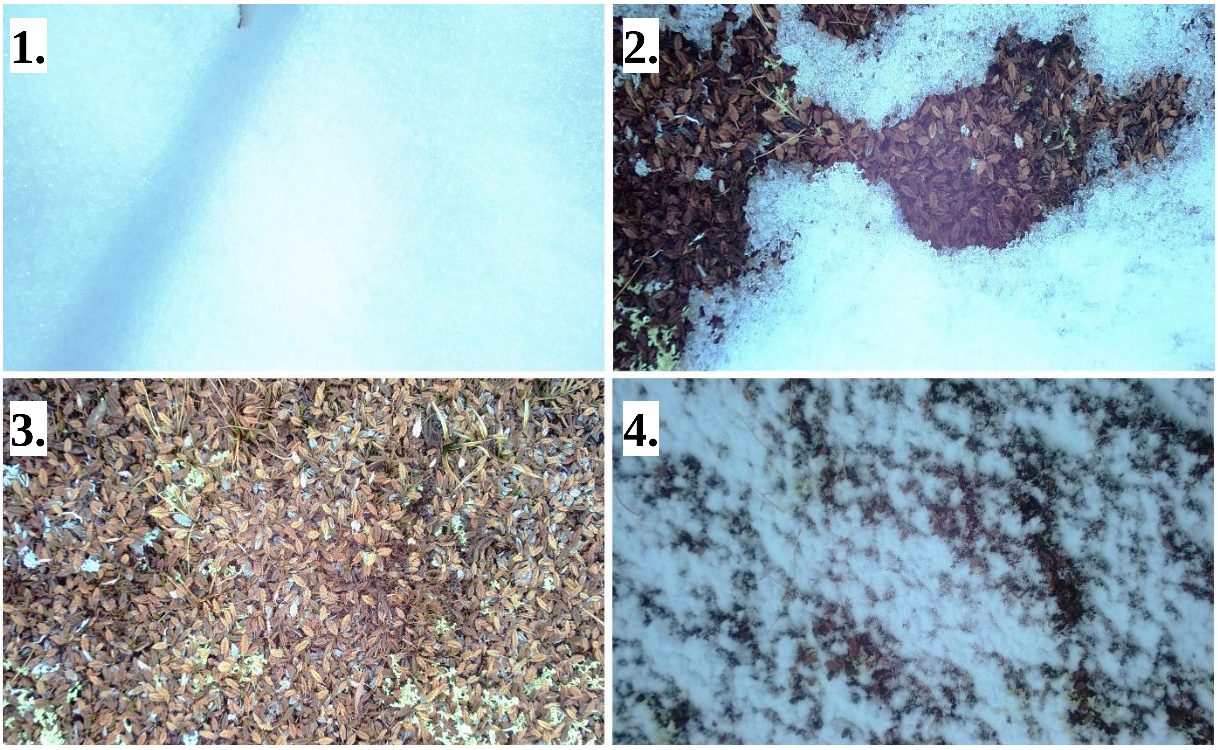

Figure 6: Example of annotation of the snow cover 1) 100% snow-covered, 2) Partially snow-covered, 3) Snow-free, 4) New snowfall.

Table 2: The phenological classes of *D. octopetala* (Roos et al., unpublished manuscript)

Stage	**Visual criteria**
Bud	Floral primordia start to grow.
Opening bud	White flower petals, not fully extended.
Open flower	White flower petals fully extended.
Withered flower	Brown or fallen petals.
Seed development	Swelling of the ovary.
Open seed head	Seed matured and included pappus.

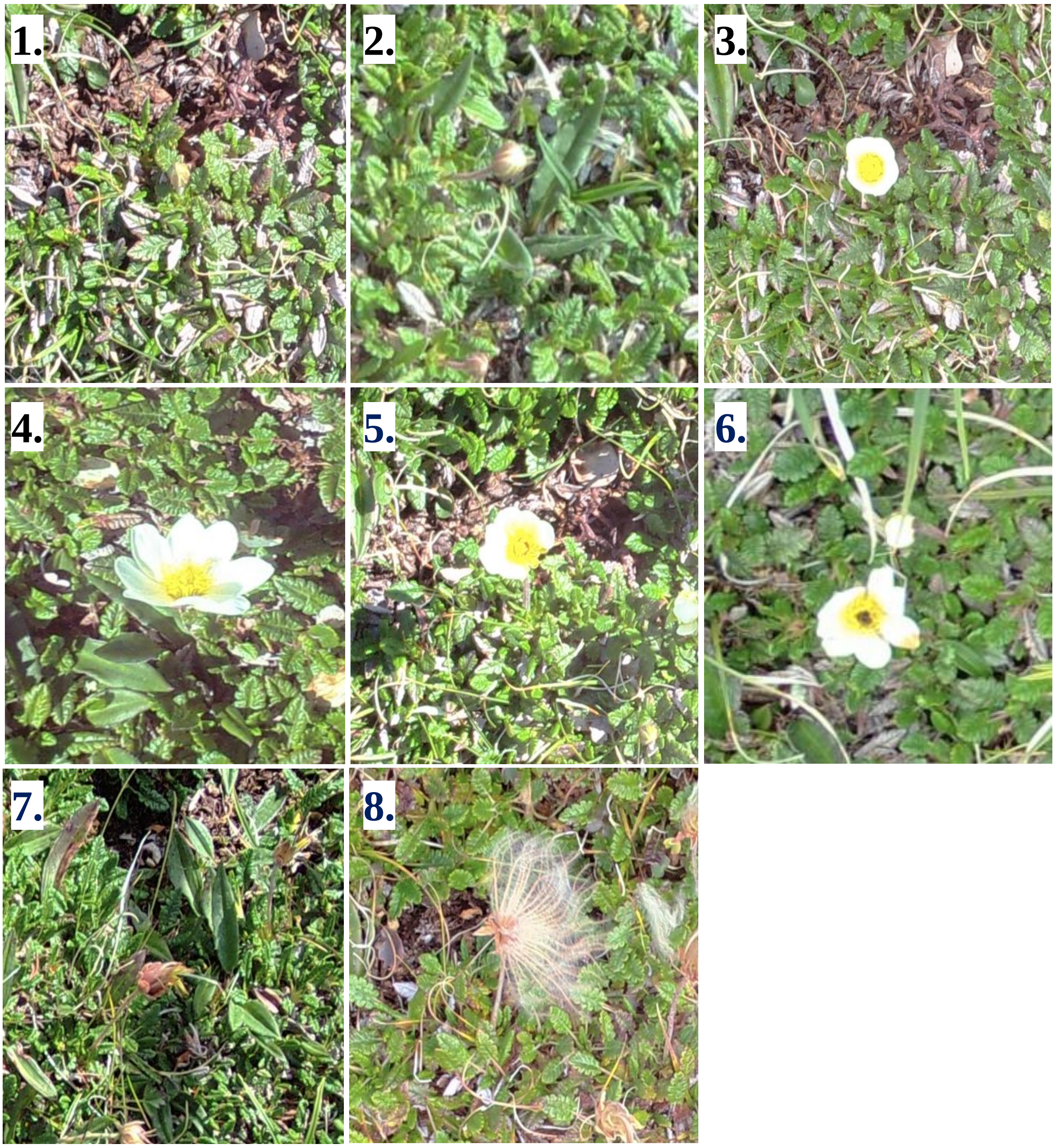

Figure 7: The phenological stages *of D. octopetala*: 1) Bud, 2-3) Opening bud, 4) Open flower, 5-6) Withered flower, 7) Seed development, 8) Open seed heads with pappus.

Data analyses

I used the temperature and soil moisture measurements from TMS-4 loggers and imagery annotations to examine how the flowering phenology of *D. octopetala* is related to snowmelt timing, temperature, and soil moisture. I used +2 temperature measurements (hereafter ground surface temperature) as it will be most relevant to the snowmelt timing and phenology.

To calculate the day of snowmelt, I used the snow cover annotations and the daily average ground surface temperature. First, I find the snowmelt from the loggers by calculating the daily minimum and maximum ground surface temperature. I then defined the calculated snowmelt timing as the day when the difference between the daily maximum and minimum ground surface temperature exceeded 10 °C. Then, I defined the observed thy of snowmelt as the day an image was annotated as snow-free for the first time after the permanent snow cover. The observed day of snowmelt was when an image was annotated as snow-free after the permanent snow cover for the first time. Finally, to check for any difference in the snowmelt between the two methods, I compared the observed snowmelt dates with the calculated snowmelt.

To quantify the environmental conditions before and after snowmelt, I calculated the daily average ground surface temperature and soil moisture. I then converted the soil moisture to %vol using the loamy sand calibration curve recommended in the TMS-4 user manual (TOMST, 2023).

To examine how the flowering of *D. octopetala* responds to snowmelt timing and ground surface temperature, I used annotated flowering images to find the onset dates of each phenological stage. I then calculated the duration of the prefloration interval before the onset of open flower in each plot by calculating the number of days from the snowmelt timing to the onset of each phenological stage. I also calculated the average ground surface temperature and soil moisture during the prefloration interval of open flowers by calculating the average daily ground surface temperature and soil moisture from snow melt to the onset of each phenological stage.

To test if the phenological development of *D. octopetala* is controlled by the ground surface temperature, I calculated the accumulated thawing degree (TDD) before the onset of flowering stages by using the following formula:

$$\sum_{i=1}^{n} \frac{(Tmax\text{-}Tmin)}{2} - Tb = 0\ °C)$$

, where T_{max} and T_{min} are the maximum and minimum daily average temperature at ground level, and T_b is the threshold temperature. Growing degree days is a good indicator to say how often cold events occurs during the growing season.

Lastly, I calculated the percentage of buds that developed open seed heads to examine the difference in seed sets among the elevations.

Statistical analysis

To test whether the ground surface temperature and soil moisture before and after snowmelt, as well as the day of snowmelt, the onset of each phenological stage, accumulated thawing degree days, and seed sets (%), differed among the three elevations, I performed a Kruskal-Wallis test, followed by Dunn’s test to identify which elevations are significantly different. A Kruskal-Wallis test is used because the variables were non-normally distributed.

To examine if there was a relationship between the onset of open flowers and snowmelt timing at each plot, I used Spearman’s correlation because the snowmelt timing variable was not normally distributed. To test if there was a relationship between snowmelt timing and ground surface temperature in the prefloration interval or snowmelt timing and soil moisture in the prefloration interval, I used Pearson correlation because the variables were normally distributed.

To quantify the accuracy between the observed and calculated snowmelt timing in each plot, I used the Pearson correlation. A strong correlation existed between observed and calculated snowmelt timing ($R^2 = 0.624$, $p = 2.9e^{-06}$) (Figure 8A). Moreover, one plot had a huge difference between observed and predicted snowmelt, and by removing this plot, the correlation got even stronger ($R^2 = 0.884$, $p = 7.5e^{-10}$)(Figure 8B). From the camera’s perspective, there was a little trend to overestimate the snow melt-out dates, while later, snow melt-out underestimated the snowmelt timing compared to the calculated snowmelt timing.

All statistical analyses and plotting are performed in RStudio (version 4.2.2) (Appendix 2-3).

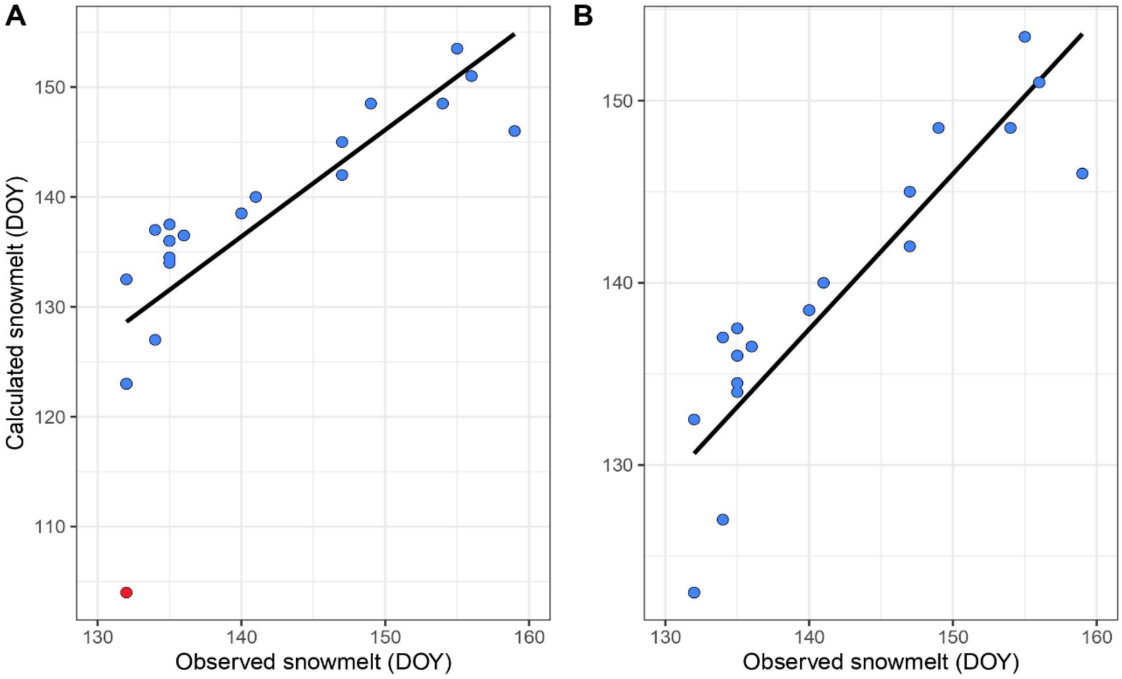

Figure 8: Correlation between observed snowmelt timing dates and calculated snowmelt timing A) when all 25 plots are included and B) when one plot is removed (red dot).

3. Results

Differences in the day of snowmelt

The average ground surface temperature differed more through the first six months than the last six months (Figure 9). There was a significant difference in snowmelt timing with 11 days earlier snowmelt at the middle than at the high elevation (Dunn's, p = 0.049) (Figure 10). There was no significant difference in the day of snowmelt timing between the low and middle elevation (Dunn's, p = 0.194) or between the low and high elevation (Dunn's, p = 1).

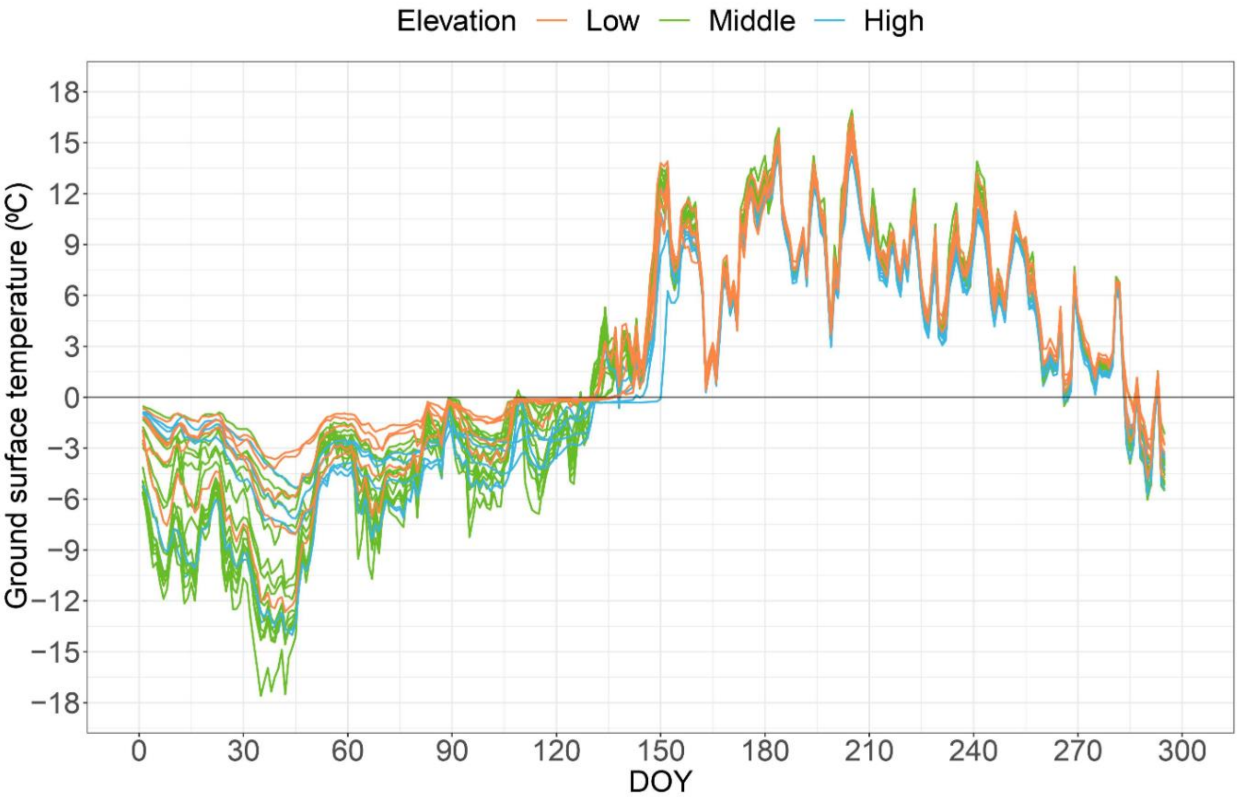

Figure 9: Daily average ground surface temperature during the 2021 season (1st January – 22nd October) at Sanddalsnuten, Finse. Each line indicates the ground surface temperature for each plot grouped into the low elevation (orange lines), middle elevation (green lines), and high elevation (blue lines).

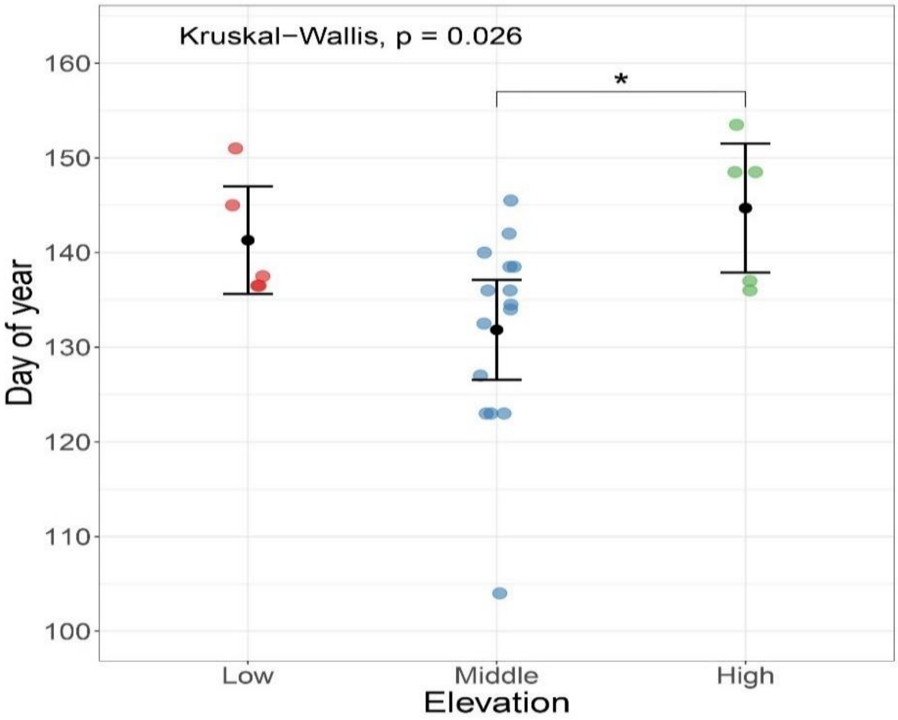

Figure 10: The snowmelt timing at three elevations at Sanddalsnuten, Finse, with 95% confidence intervals.

There were no significant differences in ground surface temperature before snowmelt among the three elevations. However, the ground surface temperature at the low elevation was 1.7 ºC warmer than the high elevation and 2,15 ºC warmer than the middle elevation (Figure 11A). There was no significant difference in soil moisture among the elevations (Figure 11B).

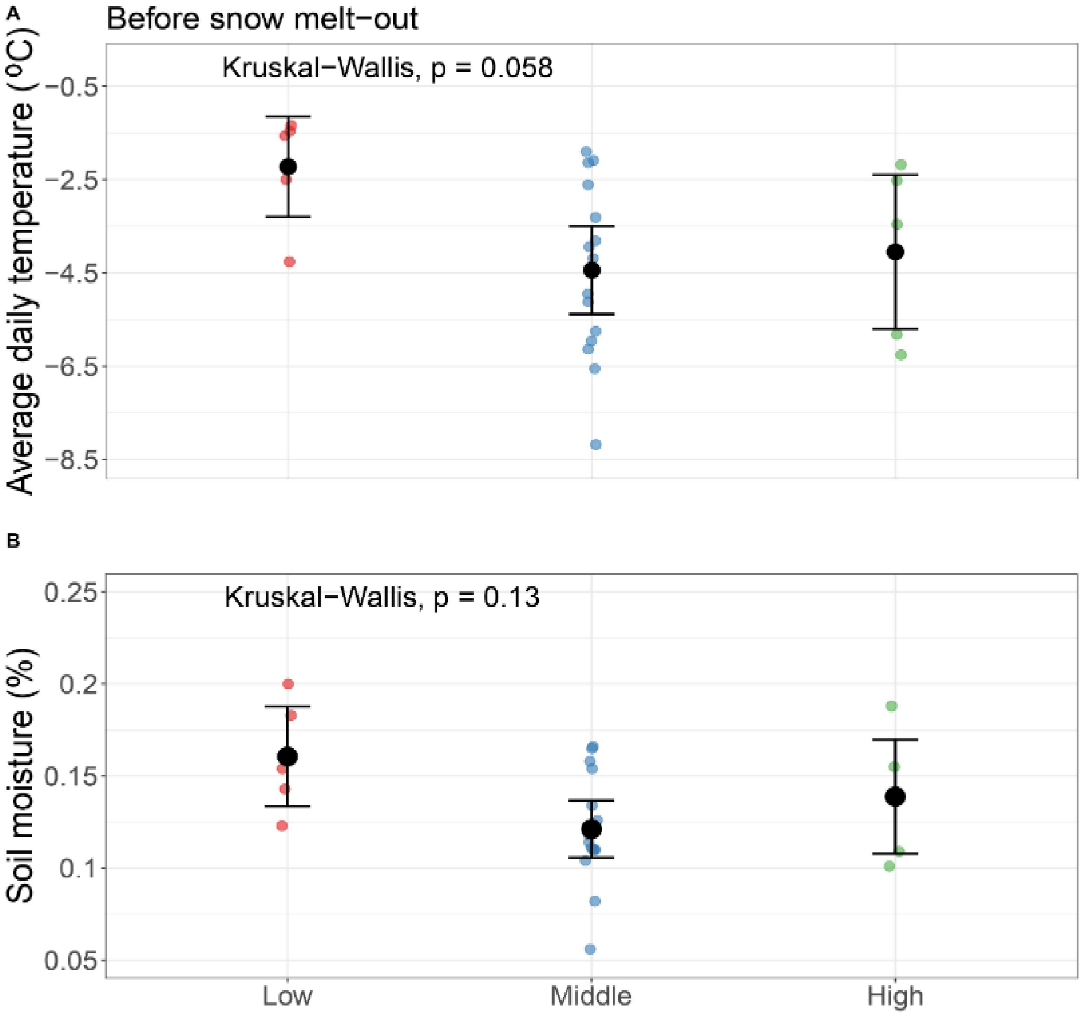

Figure 11: Daily average A) ground surface temperature and B) average soil moisture before snowmelt at three elevations with 95% confidence intervals.

Differences in ground surface temperature and soil moisture after snowmelt

The ground surface temperature at the low elevation was significantly 0.84 ºC warmer than the high elevation (Dunn’s, p = 0.013) (Figure 12A). There was no difference in ground surface temperature between the middle and the highest elevation (Dunn’s, p = 0.108) or between the middle and low elevation (Dunn’s, p = 0.062).

The soil moisture at the low elevation was 9% greater than at the middle elevation (Dunn's, p = 0.016). There was no significant difference in soil moisture between the low and high elevation (Dunn's, p = 0.876) or between the middle and high elevation (Dunn's, p = 0.414) (Figure 12B).

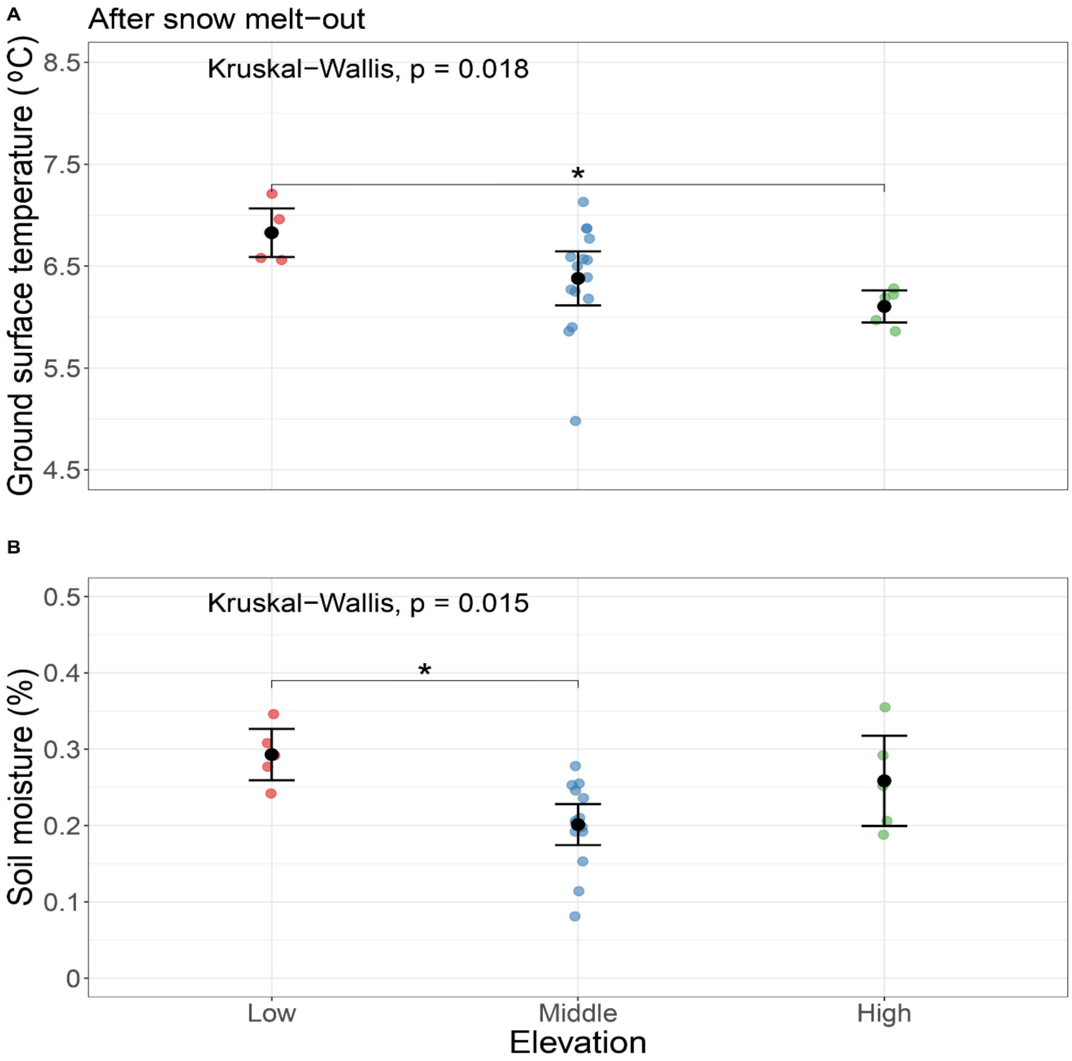

Figure 12: Daily average A) ground surface temperature and B) soil moisture at three elevations after snowmelt with 95% confidence intervals.

Flowering phenology and seed set

There was no significant difference in the date onset buds and opening buds among the elevations (Figure 13A-B). The date of onset open flowers in the low elevation was almost significantly earlier than in the high elevation (Figure 13C). The date of onset withered flowers in the low elevation was 10 days earlier than in the high elevation (Dunn's, p = 0.047)

(Figure 13D). There were no differences in the date of onset withered flowers between the middle and highest elevation (Dunn’s, p = 0.186) or the lowest and middle elevation (Dunn’s, p = 0.943). The date of onset seed development and open seed heads were not significantly different among the elevations (Figure 13E-F).

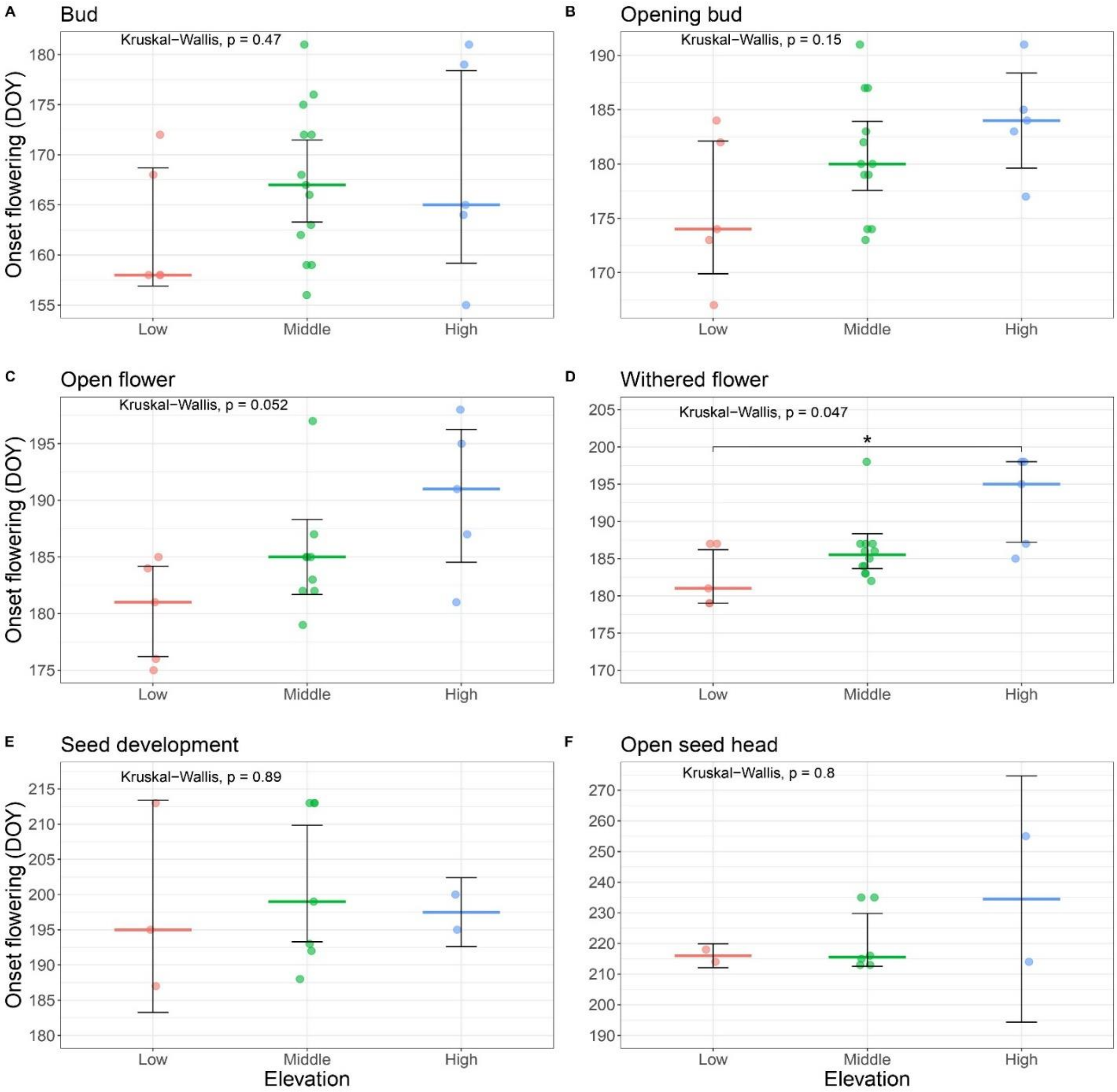

Figure 13**:** The onset dates of A) buds, B) opening buds, C) open flowers, D) withered flowers, E) seed development, and f) open seed heads among the elevations with 95% confidence intervals.

The middle elevation was almost significantly higher accumulated thawing degree days (TDD) before the onset of buds and opening buds than the low elevation (p = 0.51)(p = 0.51)(Figure 14A-B). Accumulated thawing degree days before the onset of open flowers and withered in the middle elevation were, on average, 70 °C and 75 °C higher than the low elevation (Dunn’s, p = 0.261) (Dunn’s, p = 0.023). There was no significant difference in accumulated thawing degree days between the low and high elevation (Dunn’s, p = 0.261) (Dunn’s, p = 0.102) or between the middle and high elevation (Dunn’s, p = 1) (Dunn’s, p = 1). Accumulated thawing degree days before the onset of seed development and open seed heads were not significantly different among the elevations (Figure 14E-F).

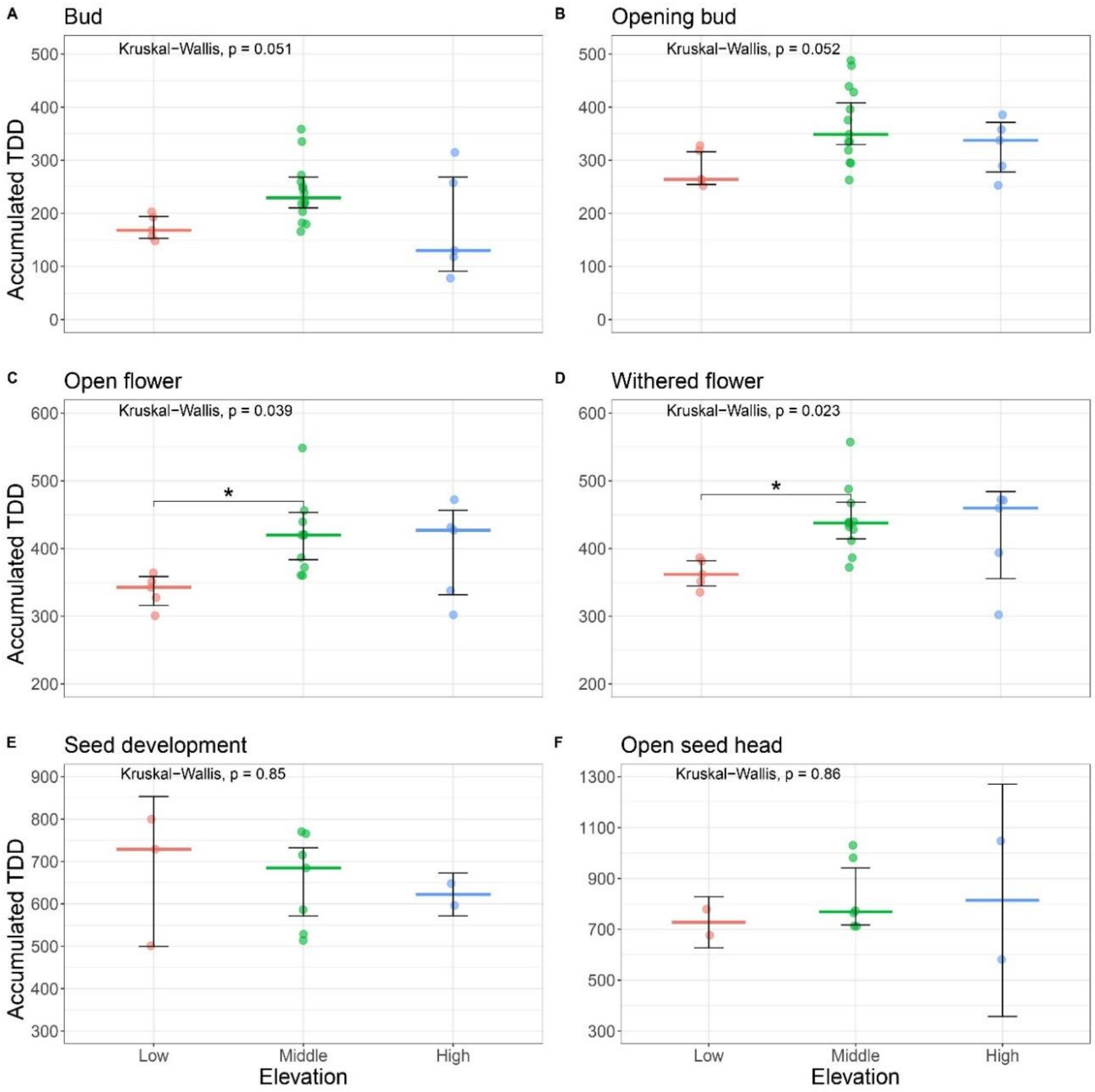

Figure 14: Accumulated thawing degree days (TDD) before the onset of A) bud, B) opening bud, C) open flower, D) withered flower, E) seed development, and F) open seed heads among the elevations with 95% confidence intervals.

There was a significant positive relationship between the onset of open flowers and snowmelt timing (Spearman, R2 = 0.260, p = 0.025) (Figure 15A) (Appendix 4 for other phenological stages). Duration of the prefloration decreased with delayed snowmelt ($R^2 = 0.423$, p = 0.025) (Figure 15B).

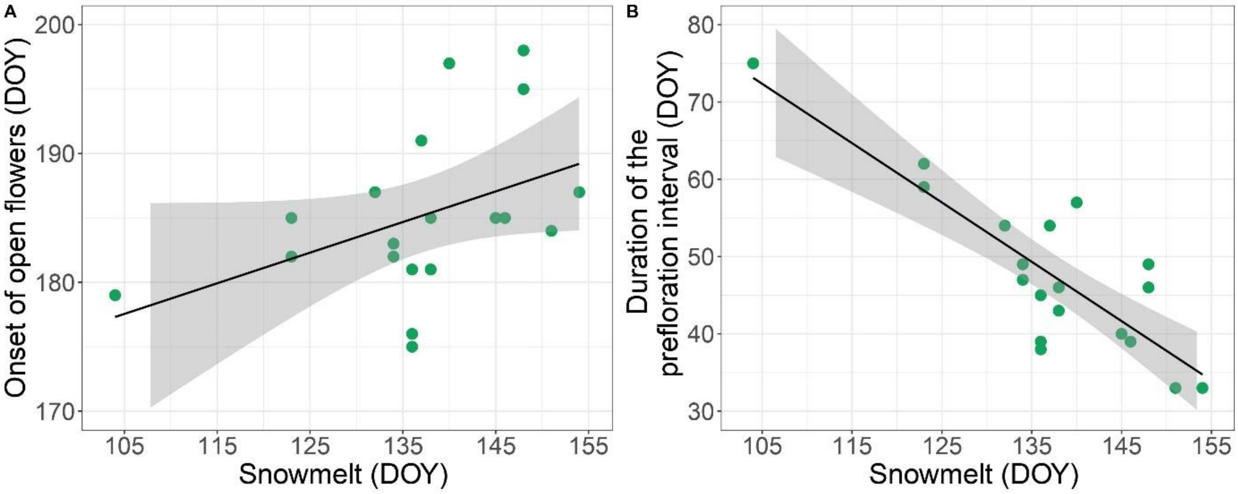

Figure 15: Correlation between snowmelt date and A) onset of open flowers and B) duration of the prefloration interval before the onset of open flowers.

Duration of the prefloration interval decreased with average warmer ground surface temperature during the prefloration interval ($R^2 = 0.401$, p = 0.004) (Figure 16A). Average greater soil moisture during the prefloration interval decreased the duration of the prefloration interval (R2 = 0.336, p = 0.008) (Figure 16B).

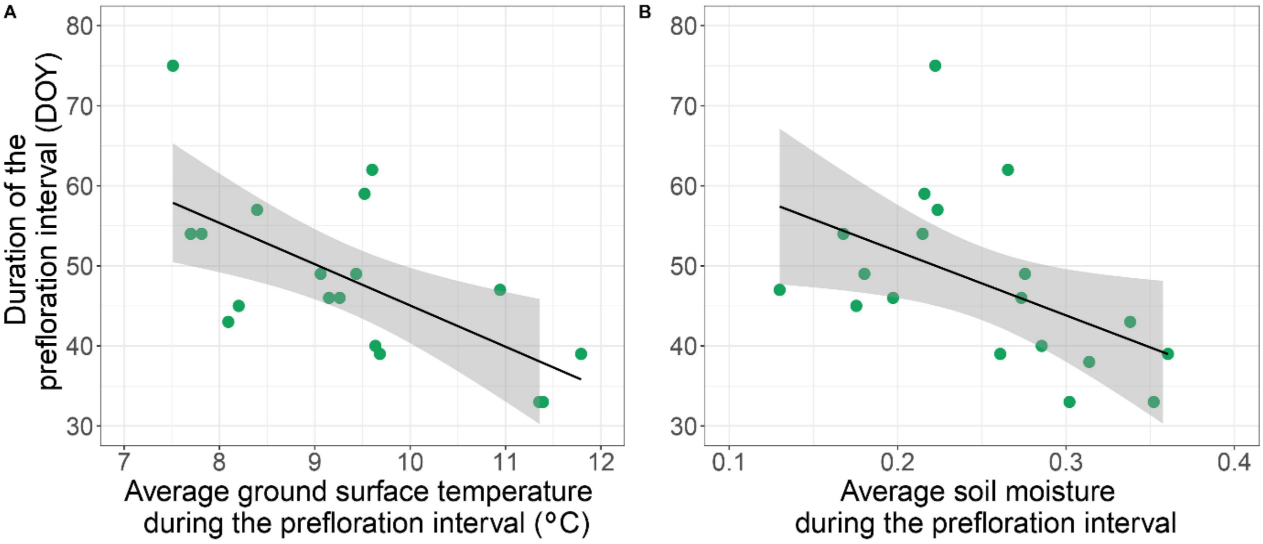

Figure 16: Correlation between the duration of the prefloration interval before the onset of open flowers and A) the average ground surface temperature during the prefloration interval and B) the average soil moisture during the prefloration interval

The high elevation had almost twice as many buds as the low elevation, with 128 and 70 buds, and the middle elevation had 114 buds. At the low elevation, there were two plots that, in total, formed 31 open seed heads, six plots with a total of 31 open seed heads at the middle elevation, and two plots with a total of 18 open seed heads at the high elevation.

There was a non-significant decrease in seed sets with increasing elevation (Figure 17). The seed sets at the low elevation were 7,3 % and 24,4 % higher than the middle and the high elevation.

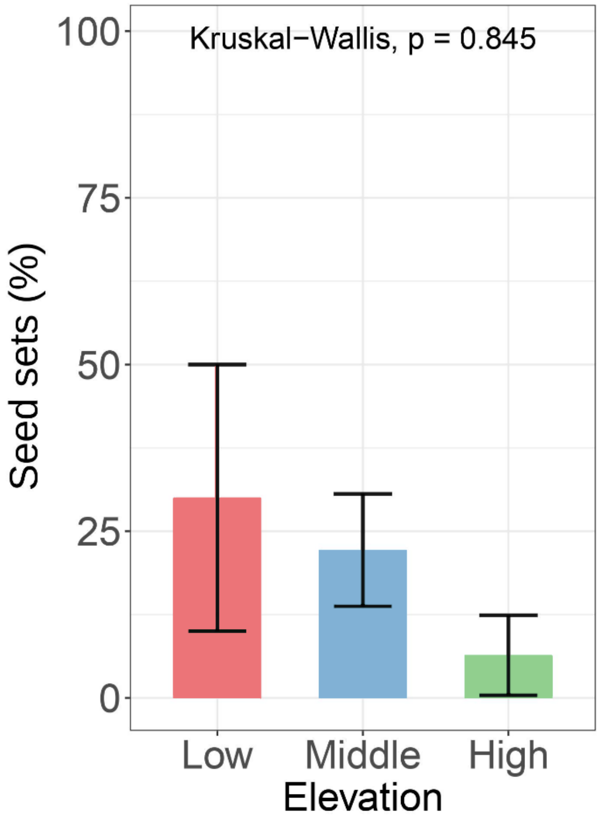

Figure 17: The seed sets (%) of *D. octopetala* at the low, middle, and high at Sanddalsnuten, Finse, with standard error intervals.

4. Discussion

Small-scale variations in environmental conditions are complex and influence the flowering phenology of alpine plant communities. In this study, I examine the short-term effects of snowmelt timing, ground surface temperature, and soil moisture on the flowering phenology and seed set of *D. octopetala* along an elevation gradient at Finse, southern Norway. I found that snowmelt timing, ground surface temperature, and soil moisture influence the onset of flowering and the seed set of *D. octopetala*. However, the snowmelt timing may majorly impact the flowering phenology if the ground surface temperatures increase in the prefloration interval. Finally, I found that seed set success was statistically the same between the three elevations.

The effects of snowmelt on phenology

The middle elevation had an earlier snowmelt timing than the high elevation. Therefore, my prediction that the day of snowmelt would occur earlier with increasing elevation was not met. This suggests that topography at Finse is rough, and snowmelt timing can vary at small scales. Moriana-Armendariz et al. (2022) found that increasing winter soil temperatures associated with deeper snow depth at Svalbard. They also noted that plots with thinner layers of snow had earlier snowmelt timing. In this study, the ground surface temperature before snowmelt did not differ among the elevation, even though the temperature was, on average higher than the low elevation. This may indicate that snow depth was deepest at the low elevation.

Interestingly, the prefloration interval was longer in plots with earlier snowmelt. On the other hand, plots with earlier snowmelt had an earlier onset of flowering than plots with delayed snowmelt. This may indicate that changes in snowmelt timing could shift the flowering phenology of *D. octopetala*. This supported my prediction that earlier snowmelt led to earlier flowering onset, but I did not expect the prefloration interval to extend when the snow melts earlier. This is in accordance with Høye et al. (2007), who also found that earlier snowmelt extended the prefloration and advanced the flowering date of *D. octopetala* in Greenland. These findings also align with other alpine flowering species, such as *Papaver radicatum* in Canada (Frei & Henry, 2021), *Luzula arctica*, and *Saxifraga oppositifolia* at Svalbard (Gillespie et al., 2016).

There was a trend of earlier onset of open flowers with increasing elevation, with significant differences between low and middle elevation in the onset of withered flowers. This is unexpected, considering that the middle elevation had an earlier snowmelt timing than the high elevation, and the onset of flowering should therefore be earlier at the middle elevation. That may indicate that other abiotic drivers may influence the phenology of alpine plants, such as ground surface temperature and soil moisture.

The effects of ground surface temperature

As predicted, the ground surface temperature after snowmelt decreased with increasing elevation. I also found that plots with shorter prefloration interval were associated with warmer ground surface temperatures in the prefloration interval. This is also in line with Høye et al. (2007), who found that the prefloration interval of *D. octopetala* shortened with higher temperatures in prefloration interval. This is also in line with other flowering species, such as *Saxifraga stellaris* L. at Finse (Sandvik & Totland, 2000) and *Saxifraga oppositifolia* in the Tyrolean Alps (Wagner et al., 2012). The length of the prefloration interval of alpine plants can also be associated with daily temperature fluctuations (Huelber et al., 2006). Semenchuk et al. (2016) found that *D. octopetala* had to reach a threshold value of 150 TDD and 250 TDD before developing open flowers and open seed heads could start. My findings revealed that *D. octopetala* had to reach twice as high accumulated TDD before the onset of open flowers and seed heads. An explanation for this difference could be that we used different methods to collect temperature measurements. Semenchuk and co-authors used air temperature measurements from Longyearbyen Airport while I measured the ground surface temperature at the study site.

Semenchuk et al. (2016) also found that accumulated TDD before flowering differs between years, likely due to low temperatures that increase the prefloration interval. This is like my results, which show that accumulated TDD before the onset of flowering was significantly higher at the middle elevation than at the low elevation. My prediction that there was a threshold value of thawing degree temperatures before reaching the next phenological stage, regardless of snowmelt timing, was not met. This may indicate that earlier snowmelt timing may only have a major impact on flowering if the temperatures increase during the prefloration interval.

The effects of soil moisture

Soil moisture decreased with elevation up to the middle elevation, followed by an increase at the high elevation. This increase in soil moisture could be explained by the snowmelt timing being earlier at the middle elevation than at the high elevation. This suggests that areas of delayed snowmelt have greater soil moisture during the growing season.

I found that greater soil moisture during the prefloration interval led to a shorter prefloration interval. This is algin with Hall et al. (2018), who found that greater soil moisture shortened the prefloration of *Silene acaulis* at Niwot Ridge. Zhu et al. (2016) found that lower soil moisture during the flowering season delayed the flowering phenology of plants in alpine meadows, whereas Vorkauf et al. (2021) found that soil moisture has a minor effect on *Trifolium alpinum* due to a short growing season. These results indicate that soil moisture seems to have a major impact on flowering phenology if it is associated with higher temperatures in the growing season.

Seed set of *D. octopetala*

There were no significant differences in seed set among the three elevations at Sanddalsnuten. Interestingly, seed set success tended to decrease with increasing elevation. A similar trend was observed by Hovde (2021), who found that number of seeds produced by *S. acaulis* between two elevations was significantly higher at the lowest elevation at Sanddalsnuten. Climatic and biotic factors may explain the seed sets success of *D. octopetala*. Straka & Starzomski (2015) found that low temperatures and frost damage may harm the seed set success of flowering plants in Canada because the growing season was too short for seed maturing. While higher elevation seems to be limited by temperature, Totland (2001) found that *Ranunculus acris* at the lower elevation at Finse may be more susceptible to pollen limitation than at higher elevation because of selective pressure on flower size. However, higher elevation could also be pollen limited since the abundance of pollinators declines with elevation (Adedoja et al., 2020), and the flying behavior is lower in areas with more wind and colder temperatures (Møller, 2019). I did not measure the wind speed, but Lundemo & Totland (2007) found that higher wind speed increase with elevation at Sanddalsnuten, indicating that the insect activity may be lowest at the high elevation.

Use of time-lapse camera in flowering phenology studies

Instead of physically observing the flowering phenology in the field, I used time-lapse imagery to capture the snow cover and the flowering phenology. Image-based monitoring gives more detailed information about the phenological development throughout the growing season than physical observation. The cameras only require changing batteries, which was done once during this study. Cameras make it possible to collect data from different plots at different locations. In this study, I had images of the flowering phenology during 295 days at 25 plots. Limitations of using cameras was that few cameras had some technical issue, leading to recoding gaps with different duration and frequency of images throughout the season. In addition, the image-based methodology is more expensive than other methods and requires more image handling after fieldwork. Altogether, camera-based research is suitable for investigating the phenological responses of plants in response to climate change.

5. Conclusion and future research

This study suggests that small-scale variations in snowmelt timing, ground surface temperature, and soil moisture impact the flowering phenology and seed set of *D. octopetala* at Finse, southern Norway.

Based on my findings and previous literature, snowmelt timing may have a major impact on the flowering phenology of *D. octopetala* in the future if it is associated with warmer temperatures during the prefloration interval. If temperatures increase in the prefloration interval due to climate, *D. octopetala* may have an earlier flowering onset or vice versa; if temperatures do not increase during the prefloration interval, the risk of frost damage is higher. This can harm the phenological development and seed set of *D. octopetala*. On the other hand, earlier snowmelt timing results in longer growing seasons, giving more time to complete their plant phenology. Future research is needed to understand the potential impact of climate warming on the phenological shifts of *D. octopetala*.

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Appendix

Appendix 1

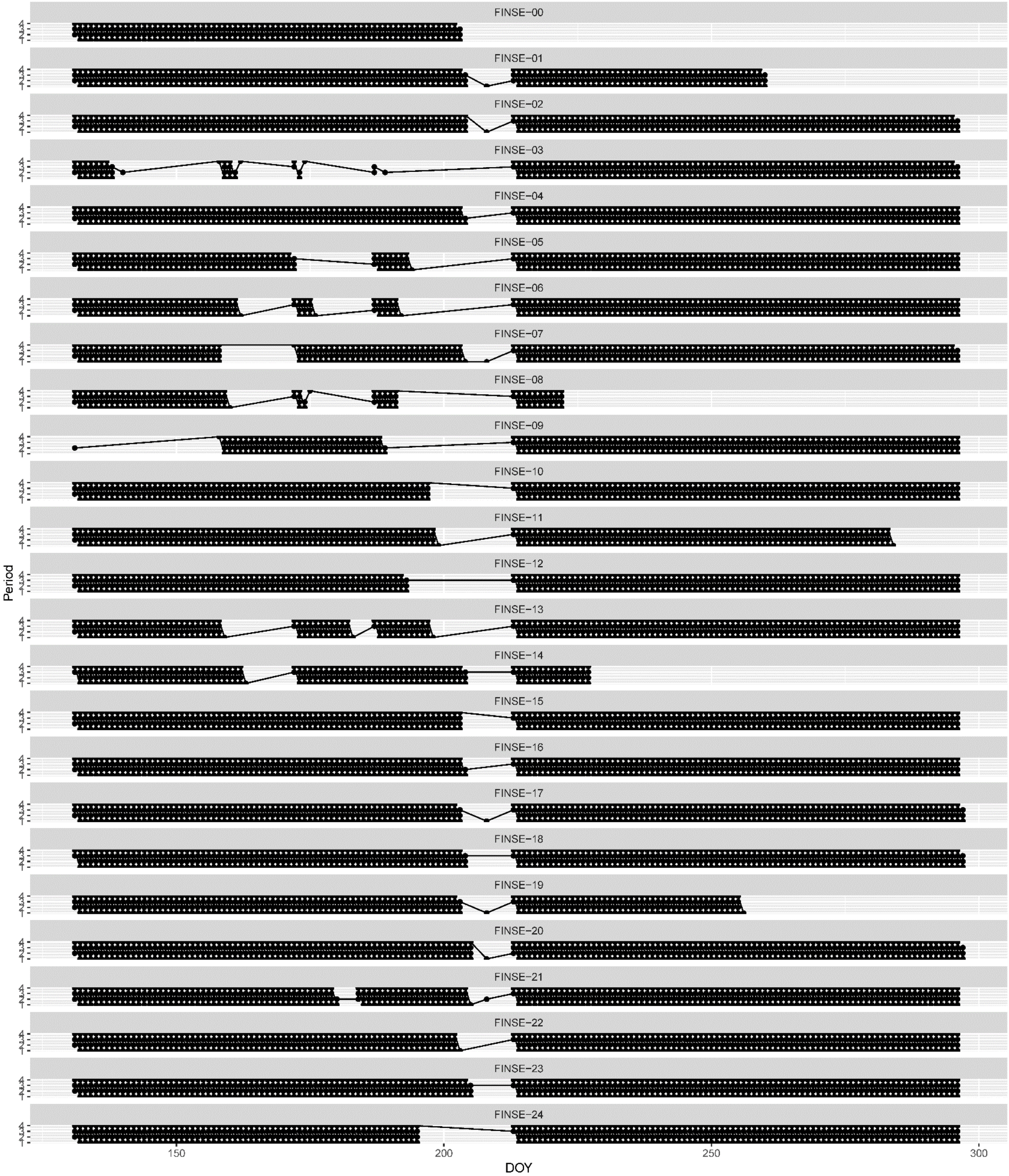

Figure 1: Camera overview of the image recording where the gaps in the recording differ in duration or frequency among plots.

Appendix 2

Table 1: Overview of *D. octopetala* plots at different elevations with respective camera ID numbers at Sanddalsnuten, Finse. The total count of flower classes, seed set , and prefloration interval are included in each plot.

Elevation	Camera ID	Bud	Opening bud	Open flower	Withered flower	Seed development	Open seed capsule	Seed set (%)	Prefloration interval (days)
Low	Finse-13	27	10	14	29	34	27	100	39
Low	Finse-21	18	16	10	12	15	0	0	33
Low	Finse-22	12	5	3	9	0	0	0	38
Low	Finse-23	9	2	1	2	0	0	0	43
Low	Finse-24	4	3	2	4	3	2	50	40
Middle	Finse-00	1	1	1	1	0	0	0	No open flower
Middle	Finse-02	2	1	1	1	0	0	0	57
Middle	Finse-03	1	1	0	1	1	1	100	No open flower
Middle	Finse-04	4	1	1	0	0	0	0	46
Middle	Finse-05	1	0	0	0	0	0	0	No openflower
Middle	Finse-06	6	2	0	5	0	0	0	No openflower
Middle	Finse-07	4	3	3	6	3	3	75	75
Middle	Finse-08	16	5	1	3	0	0	0	54
Middle	Finse-09	16	12	5	4	6	5	31	39
Middle	Finse-10	0	0	0	0	0	0	0	No openflower
Middle	Finse-11	20	15	9	18	11	10	59	47
Middle	Finse-12	19	8	3	7	5	5	26	49
Middle	Finse-14	6	5	3	4	2	0	0	62
Middle	Finse-15	14	8	3	18	6	7	50	59
Middle	Finse-16	4	1	0	2	0	0	0	No openflower
High	Finse-01	37	6	7	7	4	1	5	45
High	Finse-17	6	2	1	1	0	0	0	46
High	Finse-18	56	26	28	43	31	17	30	33
High	Finse-19	2	2	1	2	0	0	0	49
High	Finse-20	3	1	1	2	0	0	0	54

Appendix 3

Table 2: Overview of the coordinates to the *D. octopetala* plots, including snowmelt timing, temperature- and soil moisture before and after snowmelt from the TMS-4 loggers. The temperature and soil moisture measurements for Camera ID with the name Finse-01 is an average value from the other Camera ID at the same elevation because this TMS-4 logger disconnected.

Elevation	Camera ID	Coordinates	Snow-melt timing (DOY)	Ground surface temperature before snowmelt	Ground surface temperature after snowmelt	Soil moisture before snowmelt	Soil moisture after snowmelt
Low	Finse-13	60.61390; 7.51889	137	-1.56 °C	6.56 °C	0.154	0.346
Low	Finse-21	60.61399; 7.51929	151	-1.46 °C	6.96 °C	0.200	0.292
Low	Finse-22	60.61398; 7.51901	137	-4.26 °C	7.21 °C	0.123	0.242
Low	Finse-23	60.61386; 7.51902	138	-2.50 °C	6.83 °C	0.143	0.308
Low	Finse-24	60.61391; 7.51867	145	-1.34 °C	6.58 °C	0.183	0.277
Middle	Finse-00	60.61451; 7.51936	142	-4.19 °C	6.59 °C	0.121	0.201
Middle	Finse-02	60.61444; 7.51968	140	-3.94 °C	6.57 °C	0.154	0.236
Middle	Finse-03	60.61441; 7.51975	139	-2.14 °C	7.13 °C	0.056	0.081
Middle	Finse-04	60.61434; 7.52007	139	-2.09 °C	6.77 °C	0.166	0.192
Middle	Finse-05	60.61434; 7.51979	136	-3.81 °C	6.50 °C	0.114	0.198
Middle	Finse-06	60.61431; 7.51980	123	-6.14 °C	6.86 °C	0.082	0.253
Middle	Finse-07	60.61426; 7.51991	140	-8.18 °C	4.98 °C	0.110	0.210
Middle	Finse-08	60.61427; 7.52007	133	-4.95 °C	6.27 °C	0.110	0.203
Middle	Finse-09	60.61423; 7.52010	146	-5.12 °C	6.87 °C	0.158	0.246
Middle	Finse-10	60.61436; 7.51950	136	-1.90 °C	6.87 °C	0.104	0.206
Middle	Finse-11	60.61425; 7.51971	135	-2.61 °C	6.56 °C	0.111	0.153
Middle	Finse-12	60.61422; 7.51983	134	-3.31 °C	6.39 °C	0.118	0.114

Middle	Finse-14	60.61412; 7.52008	123	-5.96 °C	6.18 °C	0.165	0.278
Middle	Finse-15	60.61411; 7.52011	127	-6.55 °C	5.90 °C	0.110	0.255
Middle	Finse-16	60.61410; 7.51991	136	-5.75 °C	6.25 °C	0.134	0.192
High	Finse-01	60.61583; 7.52119	149	-6.26 °C	5.97 °C	0.101	0.188
High	Finse-17	60.61631; 7.51978	149	-3.46 °C	6.22 °C	0.141	0.252
High	Finse-18	60.61605; 7.52032	154	-2.18 °C	6.28 °C	0.188	0.355
High	Finse-19	60.61566; 7.52067	149	-2.52 °C	6.19 °C	0.155	0.292
High	Finse-20	60.61567; 7.52106	137	-5.82 °C	5.86 °C	0.109	0.206

Appendix 4

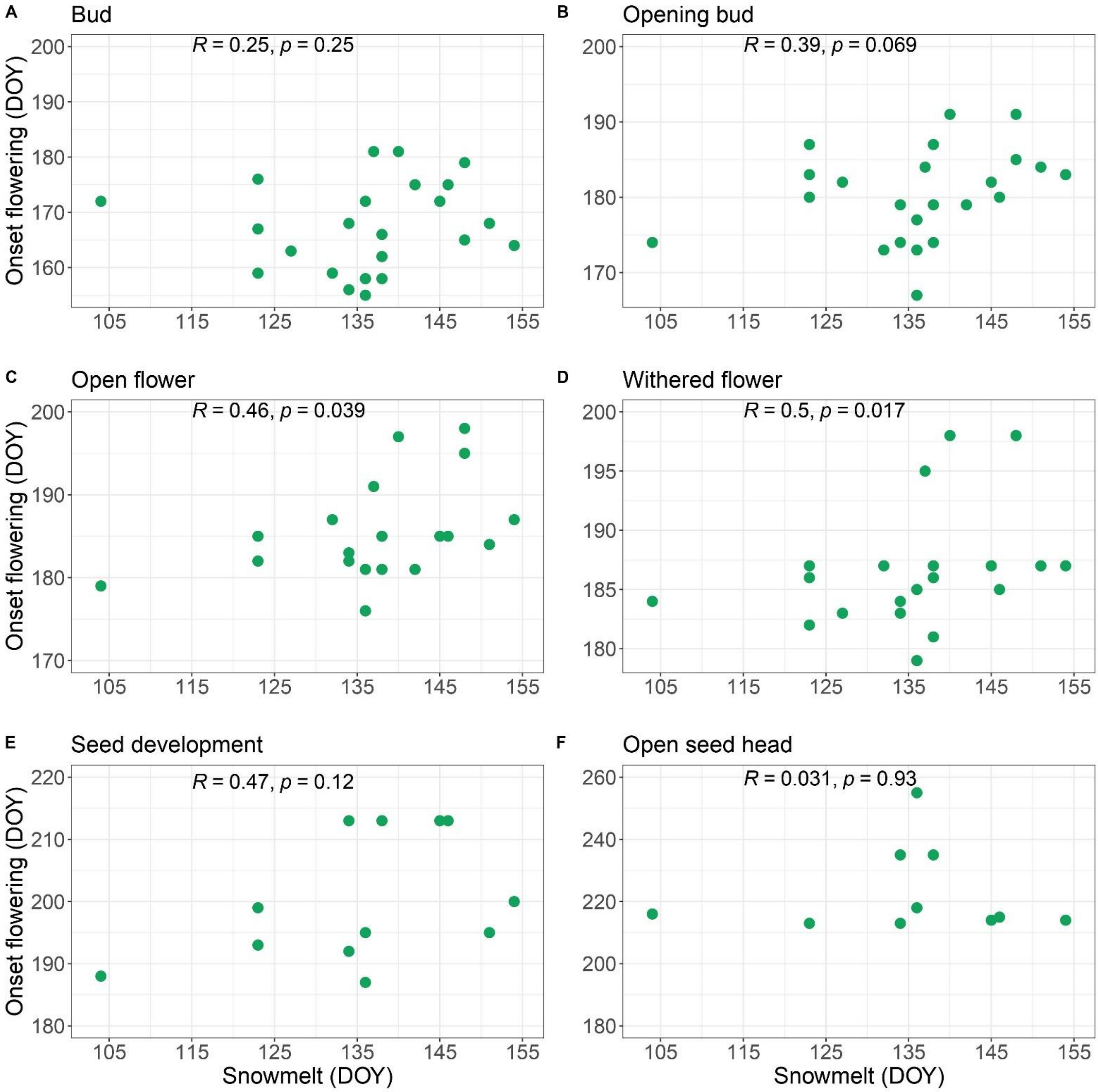

Figure 2: Correlation between snowmelt date and the onset of A) bud, B) opening bud, C) open flower, D) withered flower, E) seed development and F) Open seed head at Mt. Sanddalsnuten, Finse.

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