THESIS

EFFECTS OF EARLY SNOWMELT ON PLANT PHENOPHASE TIMING AND DURATION ACROSS AN ELEVATION GRADIENT

Submitted by

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ABSTRACT

EFFECTS OF EARLY SNOWMELT ON PLANT PHENOPHASE TIMING AND DURATION ACROSS AN ELEVATION GRADIENT

Plant phenology is an important indicator of the effects of climate change, yet the relative importance of both the drivers of plant phenology and the importance of individual phenophases in how plants respond to climate change is not well understood. Here we assess the impact of early snowmelt, a critical climate perturbation in mountain regions, on the timing and duration of individual plant phenophases across an elevation gradient in Crested Butte, Colorado. We observed a sequence of plant phenophases, new leaves, full leaf expansion, first open flower, and full leaf color change at five sites at distinct elevations (2774 m, 2957 m, 3167 m, 3475 m, 3597 m) across three mountain life zones (montane, subalpine, and alpine) in 2017 and 2018. In the spring of 2018, we used solar radiation absorbing fabric to accelerate the timing of snowmelt and observed the differences in timing for early snowmelt plots relative to control plots. The two study years had different snowmelt timing with 2018 being much earlier than 2017, so we analyzed the data to evaluate the effect of year using unmanipulated plots only, and, separately the snowmelt manipulation, on phenophase start dates and durations. Phenophase timing was advanced at nearly all sites in 2018 and responses in duration were variable. The snowmelt manipulation did not shift the timing of phenophases at the lowest elevation in our elevation gradient and the effect of the experiment on the timing of phenophases decreased as elevation increased. Even though snowmelt was significantly accelerated in the manipulation plots in 2018 at the lowest elevation the timing of

phenophases were not advanced. This may indicate a threshold beyond which early snowmelt no longer advanced leaf emergence. Earlier snowmelt in mountain regions can shift the timing and duration of plant growth, though not consistently, which will have consequences on how plants affect the movement of water and retention of nutrients and metals in mountain watersheds.

ACKNOWLEDGMENTS

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INTRODUCTION

Phenology is the study of the timing of life cycle events and is driven by abiotic and biotic processes. Plant life cycle events, called phenophases, occur sequentially, one after another throughout the life cycle (Li et al. 2016). Most phenological research has examined the impact of changing climate on individual phenophases (e.g., Iler et al. 2013, Diez et al. 2012). Less research has been conducted on the influence of changing climate on the timing and duration of season-long sequences of phenophases relative to one another (Post et al. 2008, Li et al. 2016). This type of information can help in determining the relative importance of environmental and organismal cues for individual phenophases.

Each phenophase plays a different role in the plant life cycle (Li et al. 2016). The timing of plant emergence and senescence determines the duration of season-long primary production. The timing of flowering and other reproductive life cycle events influences community and population dynamics (Diez et al. 2012). Collectively, these life cycle events influence environmental processes at local and global scales through the development of the plant canopy, the turnover of carbon and nutrients, and the moderation of climate (Richardson et al. 2013). While all the phases serve a specific purpose, they cannot be truly separated from each other.

Plant phenology is inherently associated with geography and seasonality and thus is variable across spatial and temporal scales. This leads to some mechanisms, environmental or organismal, being more influential phenological drivers than others depending on location or time of year. Plants themselves influence the timing of life cycle events, for example through evolved constraints on leaf lifespan or duration of growth (Post et al. 2008). Together, these cues and constraints reduce risk of growing or flowering at the wrong time, when damage might occur, and growing at times when resources are more available. The complex interaction of environmental and organismal mechanisms is a critical gap in understanding how plant phenology may change with changing climate.

Plants have evolved phenological strategies that may include when certain phenophases occur, as well as how long they occur. Plant species are adapted to live in habitats from seasonally snow-covered regions to the tropics that vary in the duration of the year when plant growth is possible, due to light and temperature, as well as snow cover constraints. For example, plants have evolved winter chilling requirements which are influential for cueing plants to enter and emerge from dormancy (Vitasse et al. 2018). Plants may be sensitive to or 'perceive' drivers such as rain depending on their taxonomy or rooting depth which can determine access to water at depth or dependence on rain (Chmura et al. 2019).

Environmental mechanisms also play a key role in plant phenology (Jerome et al. 2021). Photoperiod (proportion of light hours to dark hours in a day) and winter chilling can serve as cues for plant phenophase transitions, helping to keep plants from growing too early in the season or protecting against frost damage and variable spring climate (Richardson et al. 2013). Temperature cues and the accumulation of heat are essential in emergence and accumulating biomass because they signal appropriate times to grow and are critical for processes like photosynthesis (Chmura et al. 2019). The timing, duration, frequency, and form of precipitation also play a role in driving plant phenophases. For example, snow may inhibit plants from growing, and melt water or rain can provide water resources at critical periods of the plant life cycle (Steltzer et al. 2009, Petraglia et al. 2014, Wipf et al. 2009).

Climate change has altered many of the environmental mechanisms that drive plant phenology, and, in mountain regions, this includes altered snow regimes (Steltzer et al. 2009). The timing, amount, and persistence of snow is a critical aspect of how mountain regions function (Seastedt et al. 2004). Mountain regions are characterized by elevation gradients across which the timing of snowmelt and amount of snow is variable. For plant phenology, the timing of snowmelt and snow accumulation constrains the plant growing season (Petraglia et al. 2014). In high snow areas, snow cover generally persists past the minimum photoperiod requirement for plant emergence (Keller and Korner 2003). Snow insulates soil throughout the winter which keeps it at a temperature suitable for plants to stay dormant (Steltzer et al. 2009). Snow provides a steady input of water to soils that is used by plants during the spring and long after (Hammond et al. 2019). However, the timing of snowmelt in mountain regions has been advancing, and plant phenology has been shown to be advancing with it (Iler et al. 2013, Wadgymer et al. 2018). Other studies have observed the impact of early snowmelt on the timing of the onset of the growing season (Wipf et al. 2009, Petraglia et al. 2014) and flowering (Iler et al. 2013, Inouye et al. 2008). However, the relative importance of early snowmelt phenomena for the timing and duration of plant phenophase sequences is still unclear. Additionally, the ways in which early snowmelt affects phenology across elevation, one of the most critical environmental gradients in mountain regions, is also not well understood.

To identify the impact of early snowmelt on the timing and duration of sequential plant phenophases within a growing season we observed the timing of plant phenophases at five sites across an elevation gradient over two years in relation to an experimental early snowmelt manipulation. Our main objectives were to a) accelerate the timing of snowmelt, b) observe the differences in timing and duration of new leaves, full leaf expansion, first open flower, and full leaf color change between snowmelt accelerated plots and control plots at each elevation, c) identify the influence of the snowmelt manipulation on the timing and duration of phenophases at each elevation. We aimed to answer the questions:

- How does earlier snowmelt affect the timing of plant phenophases across elevation?
- How does earlier snowmelt affect the duration of plant phenophases across elevation?

METHODS

2.1 Study Area

This study was done in the East River and Washington Gulch valleys in the West Elk Mountains near Crested Butte, Colorado. The East River is a main tributary of the Gunnison River that contributes significant water inputs to the Colorado River in Grand Junction, Colorado. The area has an average low temperature of about -8°C and an average high temperature of about 11°C. The area receives between 640 and 1320 mm of precipitation (Table 1). The lower boundaries of the watershed (2774 m to 3000 m) include evergreen forest, high mountain meadow, and shrubland (Artemisia tridentata, Potentilla fruticosa, Salix spp., Symphoricarpos rotundifolius, etc.). The upper boundaries of the watershed (3000 m to 4000 m) include evergreen forest, high mountain meadow, mesic, high elevation shrubland (Salix spp., Vaccinium caespitosum), and alpine tundra vegetation. Snow accumulation begins between October and November and persists until May to June.

Table 1. Mean annual climate variables for study sites. Temperature and precipitation from PRISM. Snow persistence is the mean annual percent of time with snow cover between Jan 1 and Jul 3 from 2001-2020 (Hammond 2020).

Elevation (m)	Temperature (C)	Precipitation (mm)	Snow Persistence (%)
2774	1.83	638	65
2957	2.09	901	71
3167	1.18	1135	79
3475	0.05	1210	88
3597	-0.71	1320	94

2.2 Sites and Plots

We established five monitoring sites at distinct elevations (Figure 1). The sites were chosen to be representative of distinct life zones in both climate and plant community. The lowest two sites were located at the lower and upper boundaries of the montane life zone at 2774m (LM) and 2957m (UM); the middle and second highest sites were located at the upper and lower boundaries of the subalpine life zone at 3167m (LSA) and 3475m (USA), and the highest site was in the alpine life zone at 3597m (ALP) (Figure 1). Based on the definitions in Moore et al. (2015), the alpine and subalpine sites are in the persistent snow zone, and the montane sites are in the transitional snow zone. All sites were N/NE facing and were established in meadow and grassland vegetation with the top edge of the plots situated at the crest of a hillslope. At the lower four sites, six 10m X 14m plots were established in pairs. Each pair was similar in vegetation composition and cover. One plot within each pair was designated as an experimental early snowmelt plot and one as a control plot. At the highest site, three 10m X 14m plots were established for monitoring without a snowmelt manipulation. Within each of the 10m X 14m plots two 1m X 1m subplots were established for phenological observations. Figure 2 shows the typical layout of plots at each site.

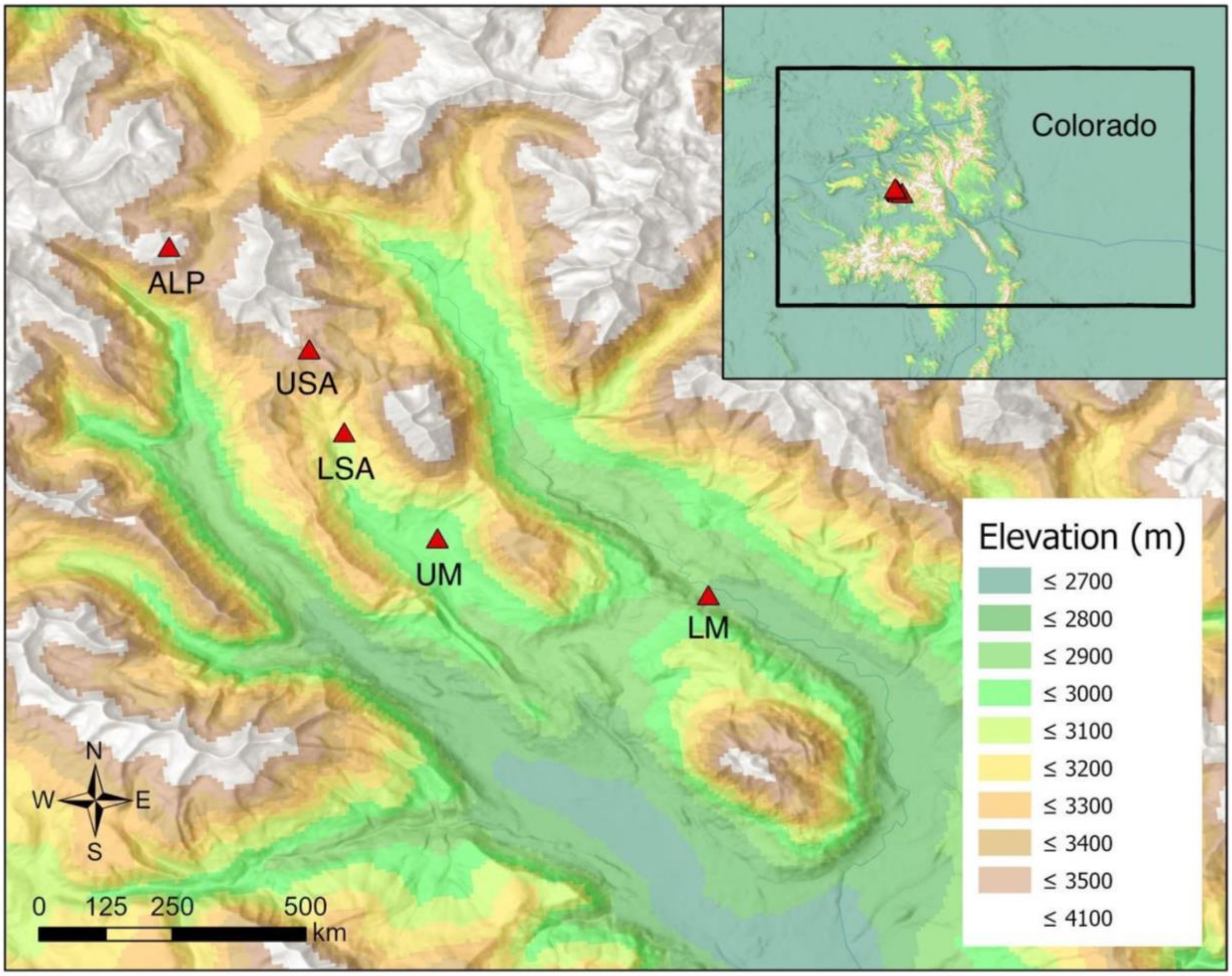


Figure 1. Locations of sites in the East River Valley. From lowest to highest elevation: Lower Montane (LM), Upper Montane (UM), Lower Subalpine (LSA), Upper Subalpine (USA), and Alpine (ALP).

2.3 Phenology Observations

Phenology observations were performed for all 1m X 1m plots at all sites in 2017, prior to the snowmelt manipulation, and in 2018 when snowmelt was manipulated. Nearly all species within a plot were cataloged and observed, and there were typically 20 - 40 species observed at each site. Phenology events observed were new leaves, where new clustered leaves were emerged from the soil; full leaf expansion, where at least one leaf in a cluster of new leaves was pulled apart from the rest and completely open and showing most of its surface area; first open flower, where a flower bud’s petals were pulled apart and reproductive organs exposed; and full leaf color change, where at least one leaf was completely changed from green to yellow, red, or purple (Figure 3). The start date of a phenology event was recorded for a species when at least one individual in a subplot had exhibited the phenophase. Plant phenology was observed 2-3 times a week during the early growing season (from the first date that the lowest site was snow free until most of the species had flowered at the highest sites) and 1-2 times a week during the later growing season when plants were transitioning to senescence.

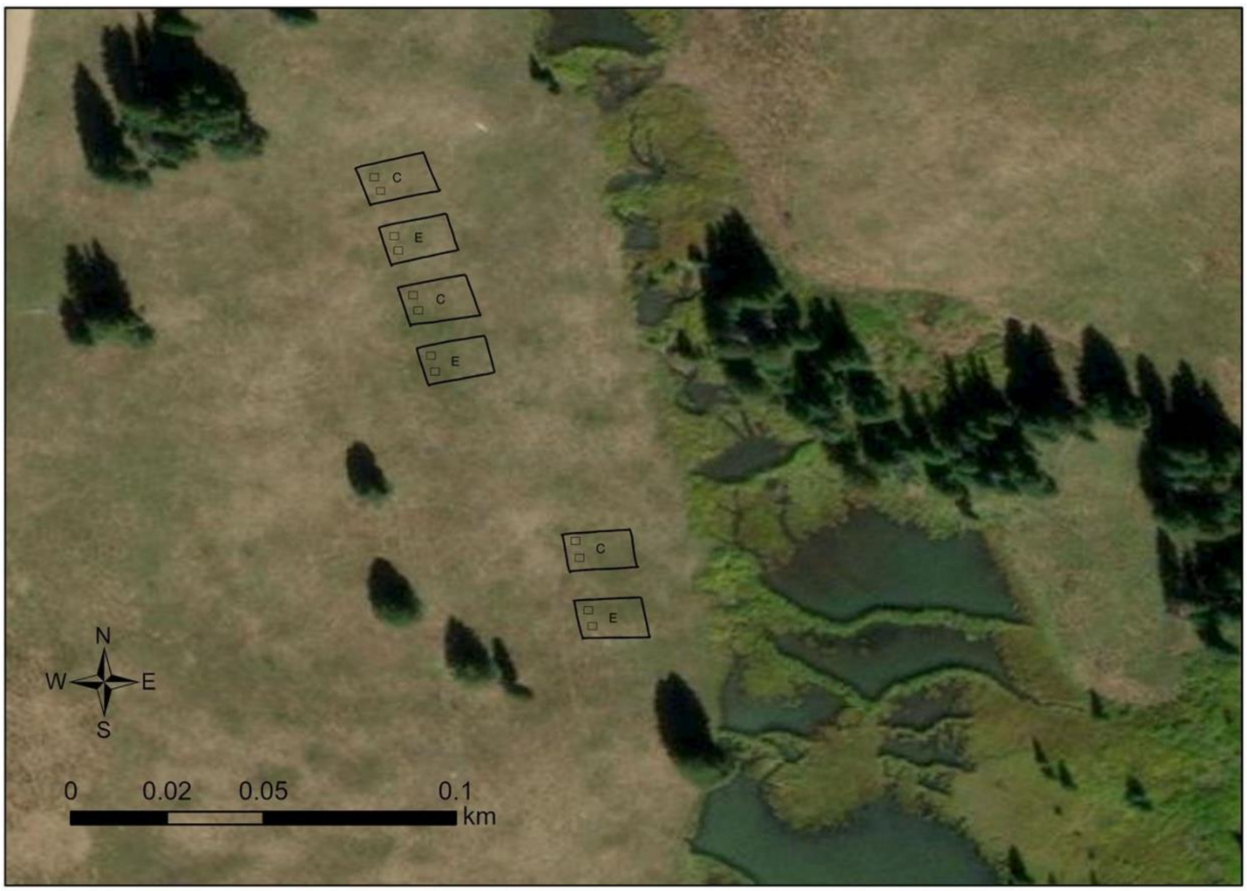


Figure 2. Example plot design. At each site where a snow manipulation was implemented there were six 10mX14m plots paired together into a control and treatment (early) block. Within each larger plot there were two 1mX1m subplots where phenology observations were taken on all species.

2.4 Snowmelt Manipulation

Snowmelt manipulation was conducted in the spring of 2018. We used 10m X 14m, black, 50% shade garden tarps to accelerate snowmelt in the plots that were designated for the experiment. The tarps were placed directly on each of the experimental early snowmelt plots and allowed to rest over the plot while absorbing solar radiation and melting the snow below. This method of melting snow mimics the reduced albedo caused by dust deposition which is the most common cause of early snowmelt in these areas. This method also ensures that no snowmelt water is removed from the plot itself. The goal was to advance snowmelt timing by about 10 days between the experimental early snowmelt plot and the control in each pair. The timing of deployment was assessed on a site-by-site basis. We used the snow depth as an indication of when to deploy tarps at each site, aiming for 1-2m depth depending on the lower and upper elevation boundaries, respectively. Paracord was woven through the tarps from corner to corner in an 'X' pattern. At the end of the paracord, wooden dowels were attached with about 2 meters of slack extending from the tarp corners. The dowel and the slack were then dropped into a hole in the snow about a meter out from the corner and buried to secure the tarp to the surface and allow for an even melt across the plot (Steltzer et al. 2009, Leonard et al. 2020). Once deployed, the tarps remained in place until snow cover was around 20 cm or 80% of the plot was completely snow free. At this point, the tarps were removed, and remaining snow was allowed to melt out naturally to avoid any damage or shading to vegetation within the plots (Figure 4, Table 2).

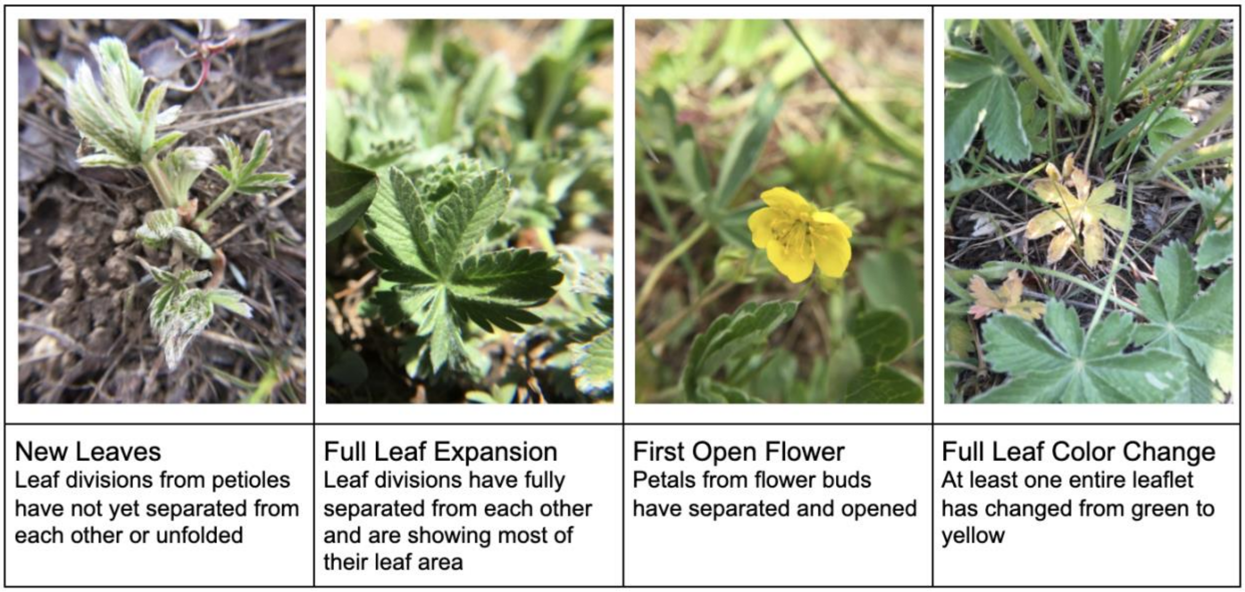


Figure 3. Example sequence of phenological observations for one species, Potentilla pulcherrima. New leaves is the first phase observed, followed by full leaf expansion, first open flower, and full leaf color change.

2.5 Data Analyses

The two different years of the study varied in snowmelt timing. Therefore, we performed two separate analyses for the effect of the year and the effect of the treatment on the timing and duration of phenophases. The analysis for the effect of the year compares the differences in the timing and duration of phenophases between the control plots in 2017 and the control plots in 2018. The analysis for the effect of the treatment compares the differences in the timing and duration of phenophases between the control plots in 2018 and the experimental early snowmelt plots in 2018.

To determine whether each phenophase differed in timing or duration between years or between the control and the early snowmelt plots, we developed mixed statistical models. These were created using the lme4 package along with the emmeans package in R to compare groups. We ran a model for each phenophase comparing the control plots in 2017 and 2018 and the treatment plots and control plots in 2018. This allowed us to assess the effect of the extremely early snowmelt year and the effect of the snowmelt manipulation separately. In each phenophase model the interaction between site, treatment, and year were fixed effects. We included random effects for the blocks, plots, and subplots to account for variation introduced in the design of the experiment. Each pairwise test comparing groups was a type III ANOVA with Kenward-Roger's method.

Table 2. Snowmelt manipulation implementation.

Elevation (m)	Date Tarps Applied	Snow Depth When Applied (cm)	Tarps Removed
2774	3/19/18	53	4/16/18
2957	3/26/18	88	4/27/18
3167	4/10/18	125	5/5/18
3475	5/5/18	182	5/29/18

Figure 4. Snowmelt manipulation plot with tarp on (left) and off (right) after the snow had melted.

RESULTS

3.1 Snowmelt Manipulation

This study was conducted over a pair of consecutive snow years that varied in snow condition and snowmelt timing (Table 3). This allowed us to observe the effect of a naturally low snowpack and early snowmelt year (2018) combined with a successful experimental early snowmelt manipulation. The timing of snowmelt was 21 to 38 days earlier in 2018 compared to 2017 with the greatest advances seen at the higher elevations. Historical data show that only two other years (2002 and 2012) have had earlier snowmelt dates than 2018. The experimental snowmelt manipulation in 2018 advanced the date of snowmelt in our plots even further. Snowmelt was 7 days earlier in the experimental plots compared to the control plots in 2018 at 2774m, 8 days earlier at 2957m and 3167m, and 17 days earlier at 3475m (Figure 5). There was no experimental manipulation of snowmelt at 3597m.

Table 3. There are two Natural Resource Conservation Survey snow telemetry (SNOTEL) sites near the study area: Butte (3097 m) and Schofield Pass (3261 m). Table includes snow conditions in study years (2017-2018) compared to the 1986-2021 average at both SNOTEL stations.

Butte Snotel #380					
Variable	Temperature (C)	Winter Precipitation (mm)	Peak SWE (mm)	DOYsf	Summer Precipitation (mm)
1986-2021 mean	2.4	650	390	140	164
2017	4.3	765	541	147	157
2018	5	409	257	126	96

Schofield Pass Snotel #737					
Variable	Temperature (C)	Winter Precipitation (mm)	Peak SWE (mm)	DOYsf	Summer Precipitation (mm)
1986-2021 mean	0.8	1216	964	162	263
2017	2.2	1425	1265	168	132
2018	2.8	795	729	149	71

3.2 Timing

New leaves and full leaf expansion were significantly advanced in 2018 compared to 2017 (p-value = <0.0001), and the greatest advances were at the highest two sites where the advance in snowmelt was also greatest. However, when the timing of new leaves and full leaf expansion are normalized by the advance in timing of snowmelt, the pattern changes. For new leaves, the greatest advances were at 3167 m; for full leaf expansion, the greatest advances were at 2774 m, followed by 3167m (Figure 6, Table 4). Figure 7 demonstrates the high correlation between day of year snow-free and the timing of new leaves and full leaf expansion in control plots between 2017 and 2018.

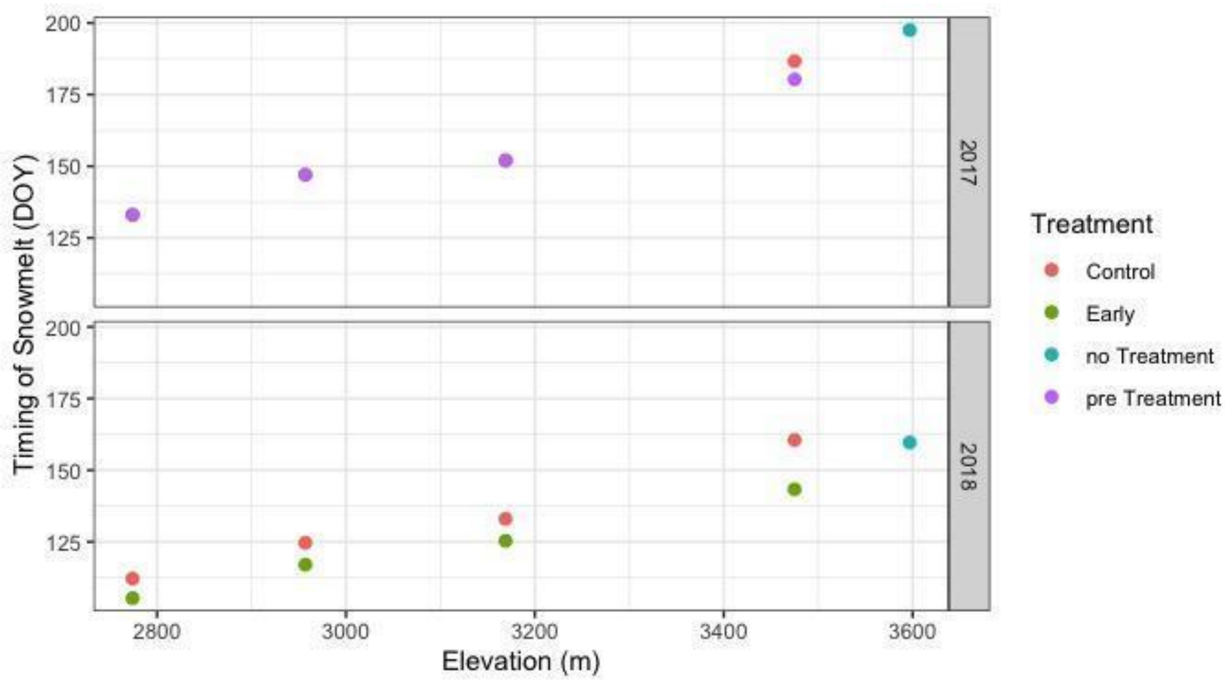


Figure 5. Snowmelt dates in 2017 (no snowmelt manipulation) and 2018 (with snowmelt manipulation). Red dots represent control plots, blue dots represent plots where there was no snowmelt manipulation, purple dots represent pre-treatment plots (designated as a treatment plot before manipulation year), and green dots are plots where there was a snowmelt manipulation. Dates of snowmelt for the lowest three sites in 2017 in 'control' and 'early' plots are the same.

While new leaves and full leaf expansion were advanced in the snowmelt manipulation plots compared to the control plots in 2018 for the highest three sites (2957 m, 3167m, and 3475 m), the lowest site (2774 m) showed no advance in timing. When normalized by the advance achieved in snowmelt timing, this pattern becomes stronger with little to no change in the timing of new leaves and full leaf expansion at the lowest site (2774 m) and increasing advance at the higher three sites (Figure 6, Table 4). Figure 8 shows the increased variation in the timing of new leaves and full leaf expansion in the experimental early snowmelt plots compared to the control plots.

First open flower was significantly advanced in 2018 compared to 2017 (p-value = <0.0001), and the magnitude of these advances increased with increasing elevation. When normalized by the number of days advance in snowmelt timing, the greatest advances were at 3167 m and 3475 m (Figure 6, Table 4). Figure 7 shows the increased variation in the timing of first open flower with day of year snow-free in control plots across years.

The change in the timing of first open flower between treatment and control plots in 2018 was not significant, apart from at 3597 m. While advances at 2957 m and 3167 m become more significant when normalized by the advance achieved in snowmelt timing, the advances at 2774 m do not (Figure 6, Table 4). Figure 8 shows the high amount of variation in first open flower associated with day of year snow-free in control and treatment plots in 2018.

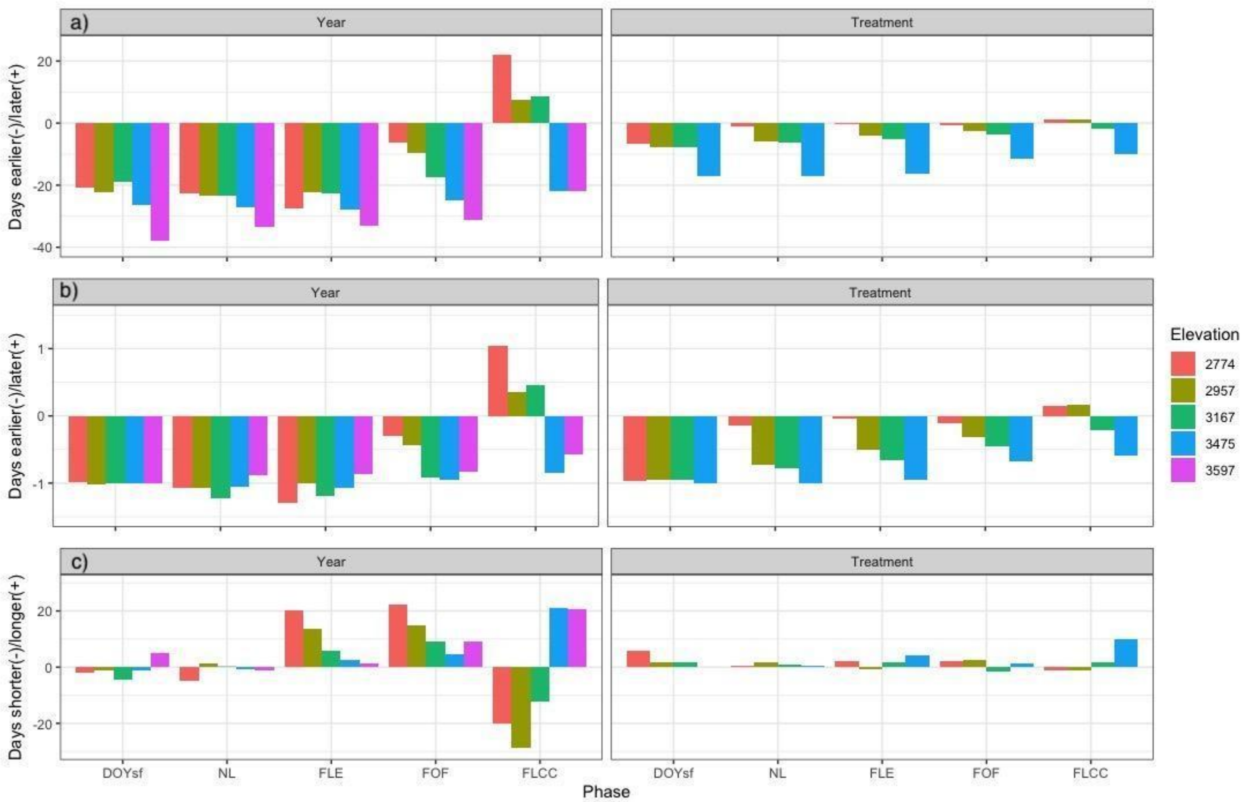


Figure 6. Number of days difference in timing (a and b) and duration (c) for all phenophases at all elevations. Panel a) shows raw statistical results and panel b) shows the statistical results for timing normalized by the number of days advance in day of year snow free (DOYsf). The year effect is calculated as the timing of phenophases in control plots in 2018 - the timing of phenophases in control plots in 2017. The treatment effect is the timing of phenophases in experimentally early plots in 2018 - the timing of phenophases in control plots in 2018.

Full leaf color change was delayed at 2774 m, 2957 m, and 3167 m and advanced at 3475 m and 3597 m in 2018 compared to 2017. When normalized by the year advance in snowmelt timing, the greatest delay in full leaf color change was at 2774 m followed by 3167 m and 2957 m. The greatest advance was seen at 3167 m followed by 3597 m (Figure 6, Table 4). Figure 7 demonstrates the low correlation between full leaf color change and day of year snow-free in control plots in 2017 and 2018.

Full leaf color change showed little to no change in timing between the treatment and control plots in 2018, except for at 3475 m where it was advanced (Figure 6). Figure 8 shows the low correlation between the timing of full leaf color change and day of year snow-free between control and treatment plots in 2018.

Table 4. Statistical results of mixed models. All bolded numbers are significant to at least alpha = 0.05; most are significant to alpha <0.0001.

		Year Effect		Treatment Effect	
		Timing	Duration	Timing	Duration
Phase	Elevation (m)	Year effect (days advanced (-)/delayed (+))	Year effect (days shorter (-)/longer (+))	Treatment effect (days advanced (-)/delayed (+))	Treatment effect (days shorter (-)/longer (+))
DOYsf	2774	**-20.8**	**-1.8**	**-6.8**	6
DOYsf	2957	**-22.3**	**-1.1**	**-7.7**	1.8
DOYsf	3167	**-19.0**	**-4.3**	**-7.7**	1.6
DOYsf	3475	**-26.2**	-1.1	**-17.2**	0.0
DOYsf	3597	**-37.8**	**5.0**		
NL	2774	**-22.6**	**-4.8**	-1.0	0.7
NL	2957	**-23.5**	**1.3**	**-5.8**	**1.8**
NL	3167	**-23.3**	0.2	**-6.3**	1.1
NL	3475	**-27.2**	-0.6	**-17.1**	0.7
NL	3597	**-33.5**	-1.3		
FLE	2774	**-27.3**	**20.2**	-0.2	2
FLE	2957	**-22.1**	**13.7**	-4.0	-0.7
FLE	3167	**-22.6**	**5.8**	**-5.3**	1.7
FLE	3475	**-27.7**	2.7	**-16.2**	**4.1**
FLE	3597	**-33.1**	1.3		
FOF	2774	**-6.4**	**22.2**	-0.7	2.3
FOF	2957	**-9.5**	**14.8**	-2.5	2.7
FOF	3167	**-17.3**	**9.1**	-3.6	-1.5
FOF	3475	**-24.9**	4.6	**-11.4**	1.1
FOF	3597	**-31.3**	**9.1**		
FLCC	2774	**21.9**	**-19.9**	1.0	-1.0
FLCC	2957	**7.6**	**-28.7**	1.3	-1.3
FLCC	3167	**8.7**	**-12.3**	-1.7	1.7
FLCC	3475	**-21.9**	**20.9**	**-10.0**	**10.0**
FLCC	3597	**-21.8**	**20.8**		

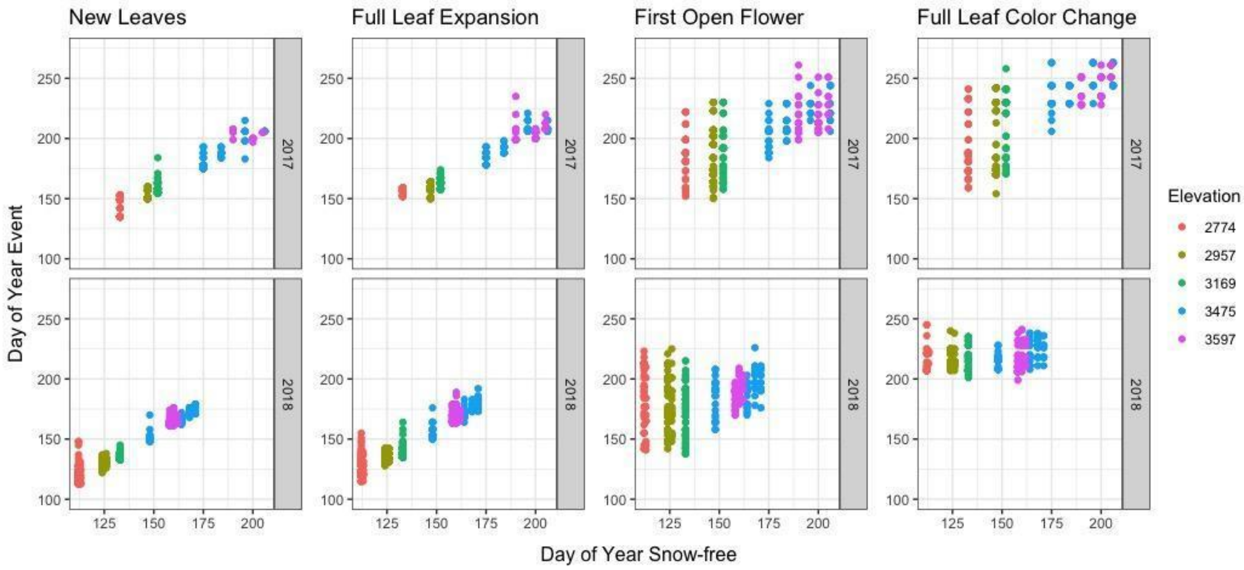


Figure 7. The effect of year on the relationship between the timing of phenophases and the day of year snow free. Data includes control plots in 2017 and 2018.

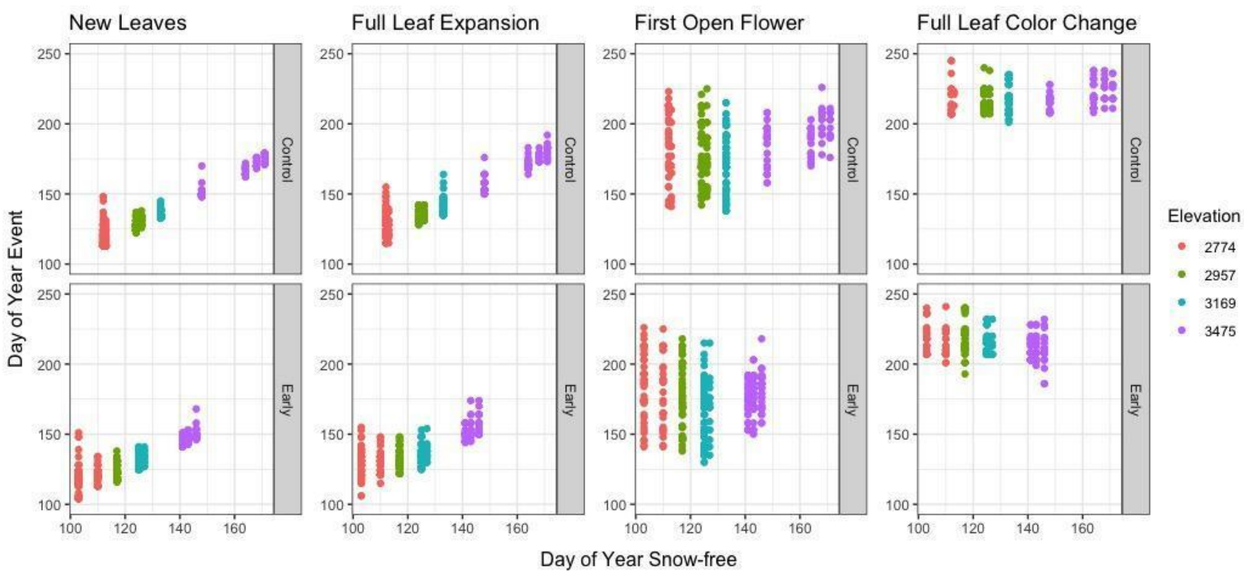


Figure 8. The effect of the treatment on the relationship between the timing of phenophases and the day of year snow free. Data includes control and treatment plots in 2018.

3.3 Duration

The period between snowmelt and new leaves and between new leaves and full leaf expansion was not significantly different in 2018 compared to 2017. However, the period between full leaf expansion and first open flower and between first open flower and full leaf color change was significantly longer. These extensions in duration were greatest at the lowest elevations and decreased with increasing elevation (Figure 6, Table 4). Figure 9 shows how start dates of phenophases varied across species in 2017 and 2018.

While no durations were significantly different in the treatment plots compared to the control plots in 2018, the period between snow free and new leaves was longer (Figure 6, Table 4). When normalized by the advance in snowmelt timing, the lack of advance in new leaves at 2774 m is notable (although not statistically significant). Figure 10 shows how start dates of phenophases varied across species in control and treatment plots in 2018.

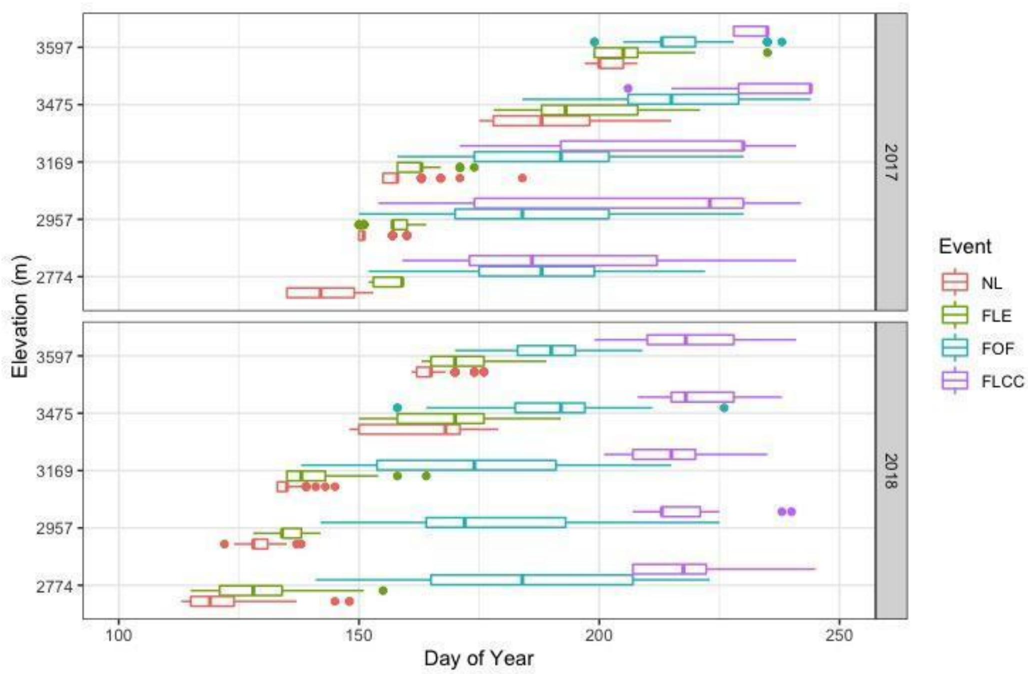


Figure 9. Phenophases in sequence for control plots in 2017 and 2018. The start date of each phenophase is the earliest date that was observed for a species at that site. The end date is the last date that the phenophase was observed for a species at that site.

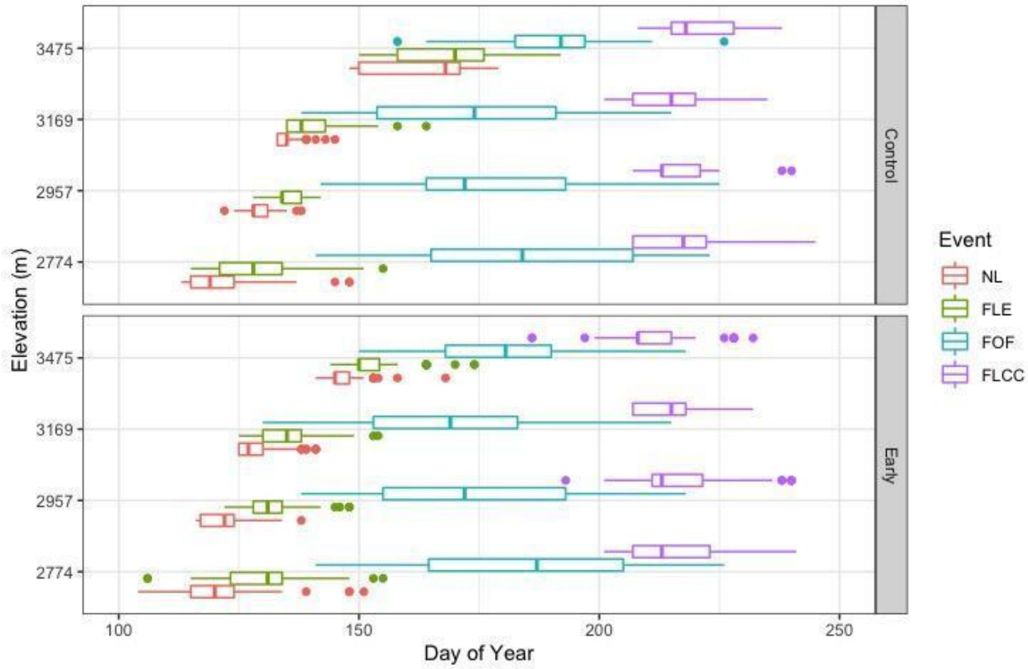


Figure 10. Phenophases in sequence for control and treatment plots in 2018. The start date of each phenophase is the earliest date that was observed for a species at that site. The end date is the last date that the phenophase was observed for a species at that site.

DISCUSSION

4.1 Timing

2017 and 2018 were extremely different snow years, and this is an important aspect of how the timing and duration of phenophases changed. Nearly all phenophases were advanced and most to a significant degree by this year effect, which is consistent with other studies that observed variability in the timing of plant phenophases across years (Iler et al. 2013, Wadgymar et al. 2018, Yu et al. 2010, Meng et al. 2016). In addition, the early snowmelt manipulation in 2018 advanced the timing of snowmelt in treatment plots even further than those in the control plots. However, the effect of the early snowmelt manipulation on the timing of phases was not as large as the differences between years.

Appearance of new leaves and full leaf expansion saw the greatest advances due to the year effect, and both phenophase start dates were highly correlated with the day of year that plots were snow-free. Some increased variability in phenophase start dates is evident in the relationship between the timing of new leaves and full leaf expansion and the timing of snowmelt for both the year analysis and the treatment analysis. This may suggest that as the timing of snowmelt becomes increasingly early the influence of other phenological drivers becomes more significant for cueing these two phases. For example, the treatment analysis showed that at the lowest site, where snowmelt timing was pushed even further than the advance due to the year, new leaves and full leaf expansion did not advance at all. In a study of early snowmelt and temperature effects on phenophase timing in the arctic tundra, Livensperger et al. (2016) found that while early snowmelt significantly advanced phenophase timing regardless of temperature the rates of advance in timing were less and thus may have been inhibited by temperature or some other driver. Our results indicate that the advance in snowmelt timing may have been great enough that plants did not advance their emergence timing any more in the treatment compared to the control because a threshold in some other phenological cue had been met.

In mountain regions and other seasonally snow-covered environments, snowmelt determines the timing of plant phenophases such as leaf emergence and expansion (Iler et al. 2013, Wipf et al. 2009, Cornelius et al. 2013) (Figure 7, Figure 8). This makes sense given that snowmelt is the primary, if not the main, water resource in mountain regions. Shifts in the timing of these phases ensures that water resources are available to be used during a critical period when investment is being directed to vegetative structures that support reproductive processes. However, if these phases continue to advance with advancing snowmelt timing the period between water resources provided by snowmelt and the onset of summer rains increases and thus, leaves plants vulnerable to periods of low water resource elsewhere in the season (Sloat et al. 2015) (Figure 11a). However, it is an increasing risk to emerge and grow earlier as spring weather can be highly variable in temperature. The lack of advance that we observed between experimentally early plots and control plots in 2018 both divorces these phases from a critical water source while also possibly protecting from exposure to low temperatures and frost damage (Inouye et al. 2008) (Figure 11e).

While flowering was significantly advanced in 2018 compared to 2017, the high variation in timing of first open flower associated with snowmelt dates suggests that this phenophase may be more driven by other climate variables than snowmelt compared to early phenophases like new leaves and full leaf expansion. Slower rates of advance in flowering have been observed in relation to earlier snowmelt (Iler et al. 2013, Wadgymar et al. 2018). This suggests that flowering timing may be inhibited by some other phenological cue such as a certain amount of accumulated heat, some minimum photoperiod length, or it could be associated with a water availability cue like rain elevating soil water content (Meng et al. 2016, Wang et al. 2014) (Figure 11d).

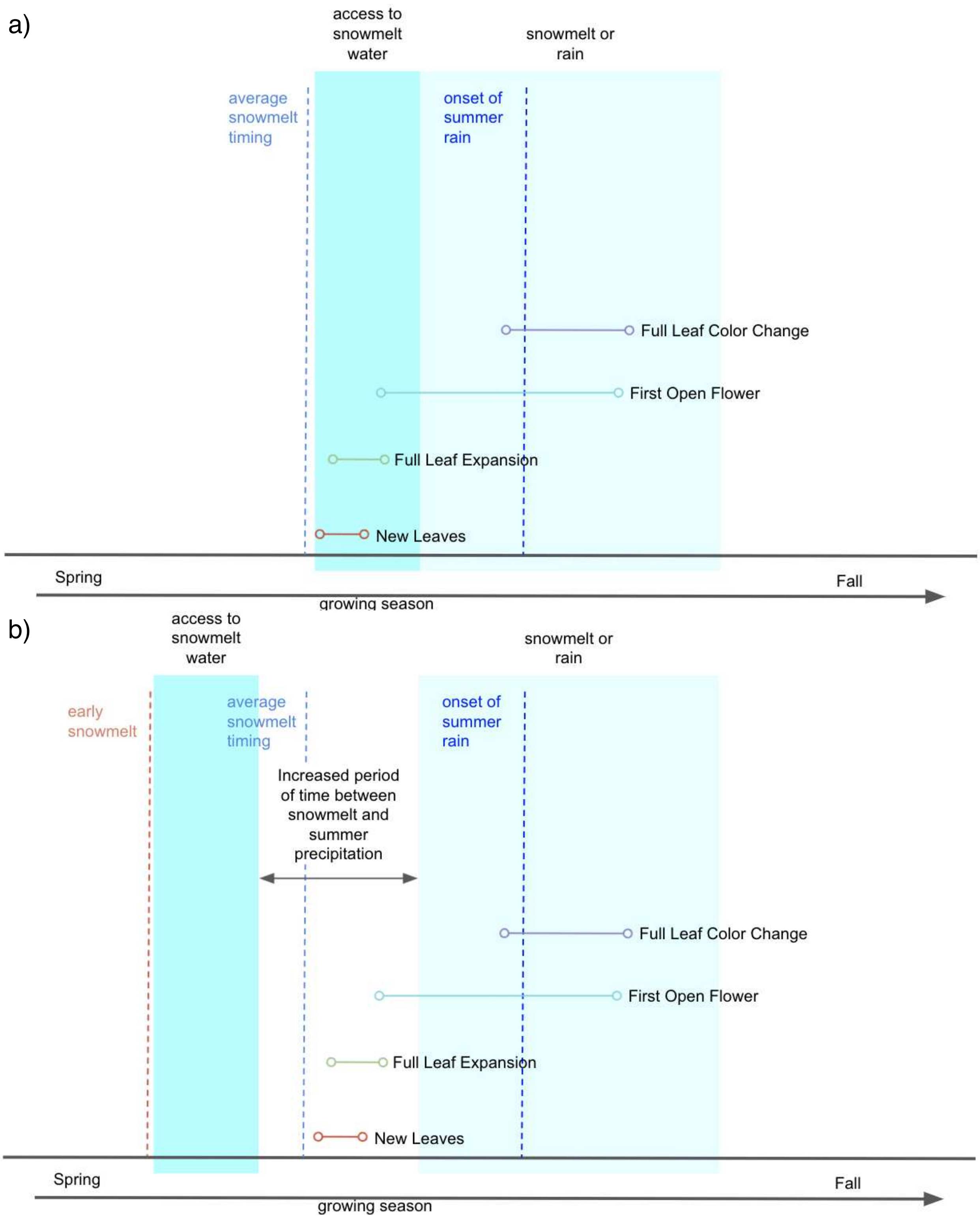
Early occurrence of vegetative phases and lesser shifts or no shifts in flowering can result in an increased period between plants using snowmelt water resources and water resources from summer rains. These shifts increase the possibility of aborted flower buds and unsuccessful reproductive phases. Flowering has been shown to be correlated with soil water content which suggests that this elongated period between water resources may have some part to play in why flowering didn't advance as much across the sites (Wang et al. 2014) (Figure 11c).

The timing of senescence at the lowest three sites was delayed in 2018 compared to 2017. Delayed senescence in response to temperature has been observed by other studies (Li et al. 2016). However, even though senescence was delayed in the early snow year, I found that full leaf color change was not highly correlated with day of year snow-free, so some other climate variable such as temperature or photoperiod (Richardson et al. 2013) is more likely to have caused changes in senescence timing between years.

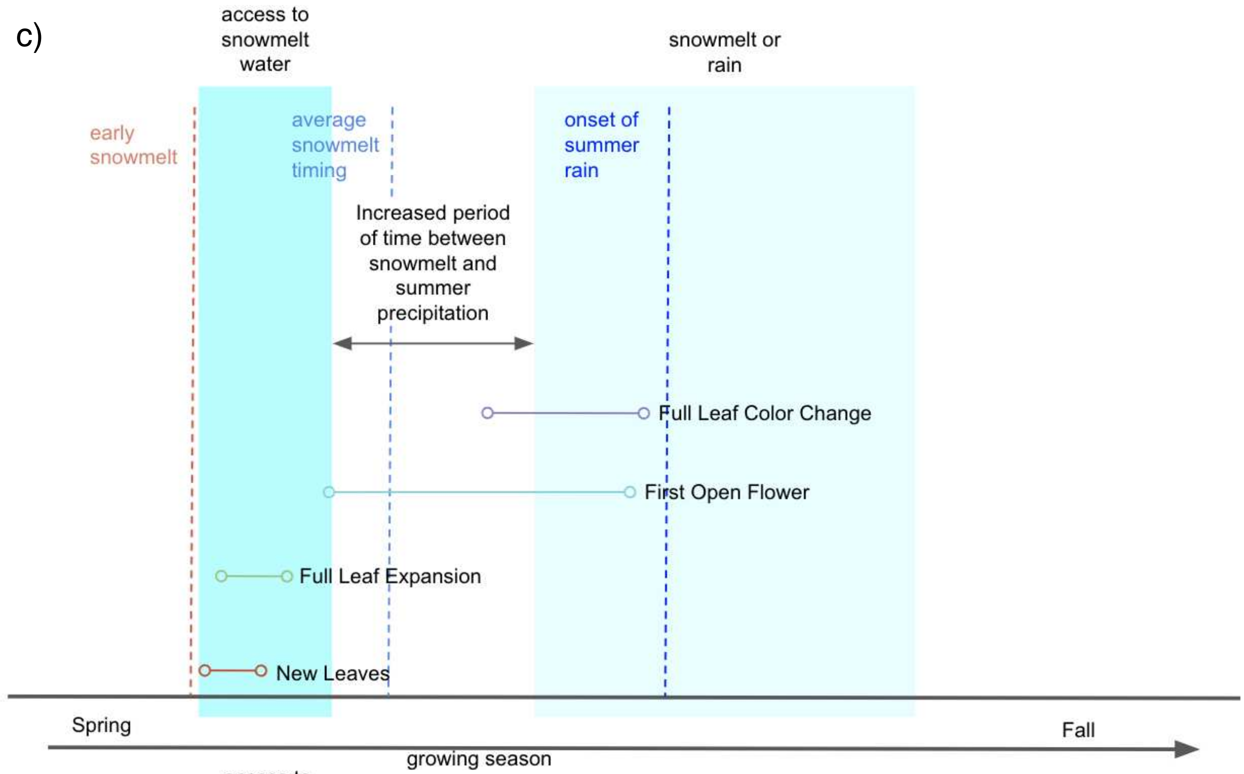
Our study shows that with extreme advances in timing of snowmelt it is possible for coupled phenological cues (timing of snowmelt, photoperiod, temperature) to be pulled apart from each other. The lack of advance in phenophase timing at the lowest elevation, 2774 m, is an example of possible phenological thresholds being met. While we generally found that early phenophases were driven by the timing of snowmelt, in a year where the timing of snowmelt was pushed farther than it may have ever been historically, these phases did not advance at all at the lower boundaries of our elevation gradient. These phenophases being decoupled from most of the water that is available for the season has consequences for primary production and the timing and amount of evapotranspiration occurring throughout the growing season.

4.2 Duration

The period between bare ground and new leaves and between new leaves and full leaf expansion were unchanged by the advance in snowmelt in 2018 compared to 2017. This lends further support to the result that snowmelt largely drives these early vegetative phenophases. However, the period between bare ground and new leaves in the treatment plots compared to the control plots in 2018 was 6 days longer. This further supports the interpretation that a threshold in some other driver was met beyond which plants could not advance the timing of new leaves.

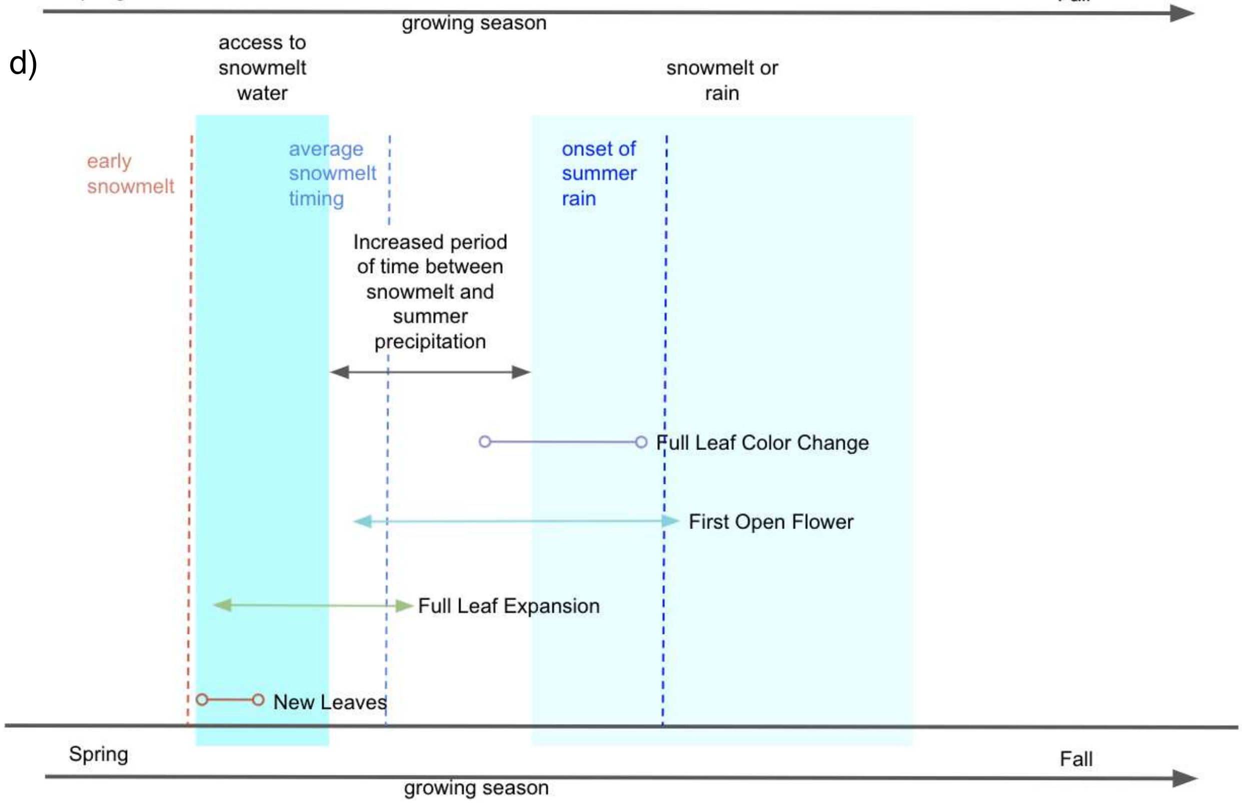

a)
access to snowmelt water
snowmelt or rain
average snowmelt timing
onset of summer rain
Full Leaf Color Change
First Open Flower
Full Leaf Expansion
New Leaves
Spring
Fall
growing season
b)
access to snowmelt water
snowmelt or rain
early snowmelt
average snowmelt timing
onset of summer rain
Increased period of time between snowmelt and summer precipitation
Full Leaf Color Change
First Open Flower
Full Leaf Expansion
New Leaves
Spring
Fall
growing season

c)



access to snowmelt water
snowmelt or rain
early snowmelt
average snowmelt timing
onset of summer rain
Increased period of time between snowmelt and summer precipitation
Full Leaf Color Change
First Open Flower
Full Leaf Expansion
New Leaves
Spring
Fall
growing season

d)



access to snowmelt water
snowmelt or rain
early snowmelt
average snowmelt timing
onset of summer rain
Increased period of time between snowmelt and summer precipitation
Full Leaf Color Change
First Open Flower
Full Leaf Expansion
New Leaves
Spring
Fall
growing season

e)

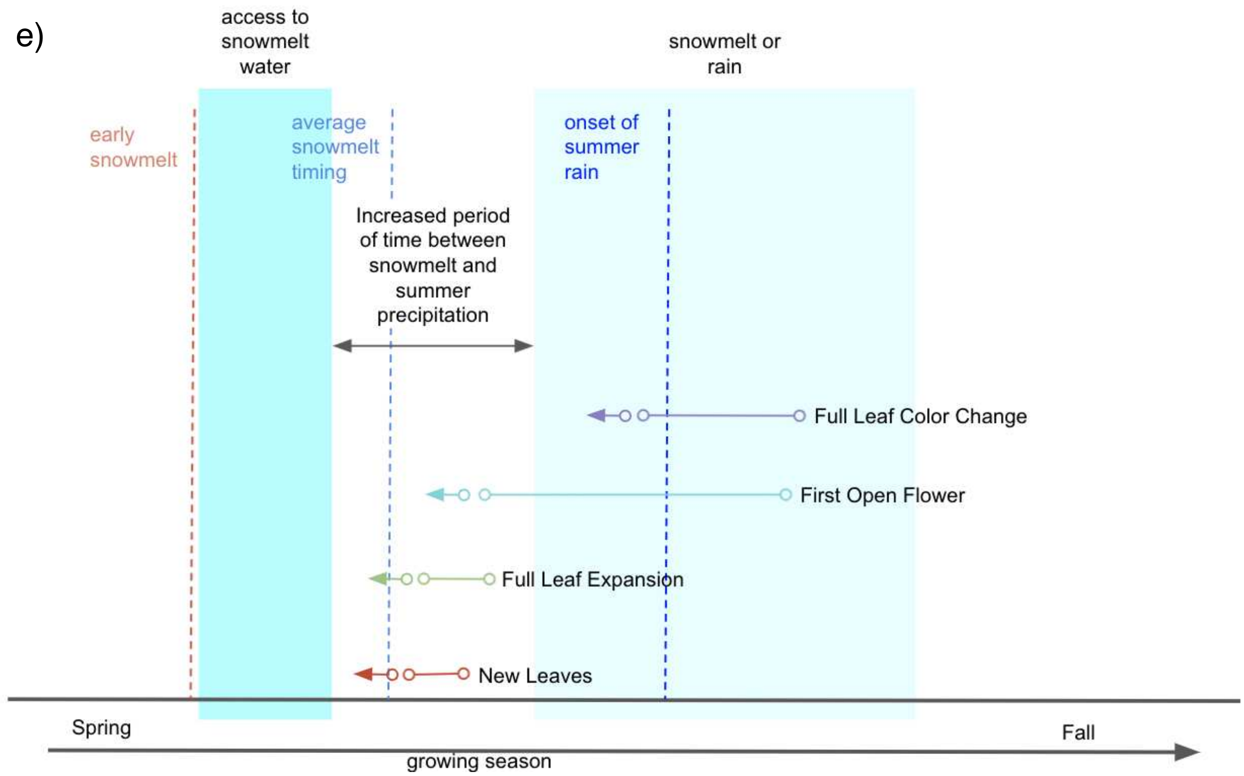


Figure 11. Conceptual diagrams of shifts in water sources and phenophase timing and duration. Panel a) shows a typical growing season where snowmelt water resources and summer rainwater resources are associated with each other. Panel b) shows how shifts in snowmelt timing produces a longer period when the source of water resources is uncertain and could be snowmelt, summer rain, or a lack of water. Panel c) shows shifts in phenophases with early snowmelt and the association of certain phenophases with longer periods of time where water source is not certain. Panel d) shows a situation in which some phenophases' durations are longer and more associated with periods of time when water source is not certain. Panel e) shows a situation in which phenophases do not advance with snowmelt and how this can result in phenophases not being associated with snowmelt water resources.

Interestingly, the duration of full leaf expansion and first open flower were significantly elongated in 2018 compared to 2017. Either there is some reason that these phenophases needed to take longer or the plants are unable to shift the timing of the following event during the season, making these phases last longer with earlier snowmelt. My results support the latter interpretation because the timing of first open flower and full leaf color change were less correlated with day of year snow free and thus the magnitude of shifts was not as great. In Post et al. (2016) that studied the effects of phenophase timing and duration on plant life histories, phenophase duration was found to be less plastic than that of phenophase timing which may explain the largely insignificant effect of the treatment on duration of phenophases.

While we found no significant change in phenophase duration associated with the snowmelt manipulation. However, the treatment effect cannot be completely separated from the year effect in this study. Thus, the changes in the duration between control and experimental early snowmelt plots in 2018 are in addition to the longer durations seen for full leaf expansion and flowering in the year effect. Lack of change in duration due to the experimental early snowmelt may be because duration is less plastic compared to timing or because the snowmelt manipulation was early enough that phases could not shift the duration any more than was produced by the year.

CONCLUSIONS

In this study we aimed to assess the impact of a critical climate perturbation in snow-dominated mountain regions, earlier snowmelt, on the timing of plant phenophase timing and duration. We were successfully able to accelerate the timing of snowmelt along an elevation gradient and observe the differences in timing between experimentally early snowmelt plots and naturally early snowmelt conditions. We found year-to-year variation has a significant impact on the timing of plant phenophases. In this example, the difference between a 'normal' snow year and a naturally early snowmelt year produced advances in emergence, growth, and flowering by 7 - 33 days. Results suggest that advances beyond this (with experimental early snowmelt manipulation) may be inhibited by thresholds in other phenological cues.

Our data show that the timing of early season phenophases are more driven by snowmelt timing than mid- and late season phenophases. Advances in snowmelt extend the growing season and have implications for water uptake in these systems. Alternatively, with extreme advances where phenological cues may become decoupled, these phases may be mismatched from critical water resource availability and therefore not advance as much with snowmelt. Because start dates of late season phases like flowering and senescence were less correlated with snowmelt timing, early snowmelt may result in longer periods between phenophases and increase the amount of exposure to drought conditions before reproduction.

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