

Experimental examination of early snowmelt-induced water stress in
Helianthella quinquenervis: effects on demographic vital rates

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I. Abstract

One of the consequences of global climate change is earlier snowmelt in high elevation environments. In the Colorado Rocky Mountains, early snowmelt leads to a longer growing season and may also cause water stress in plants that utilize snowmelt as a main early-season water resource. This creates the potential to see both positive and negative effects of early snowmelt on subalpine plant species. Here we conducted a direct manipulation of snow removal to test two separate and non-mutually exclusive hypotheses; one) that early snow melt may have negative effects on growth and reproduction via frost damage and water stress, and two) that early snow melt may have positive effects on growth and reproduction via a longer growing season. We examined *Helianthella quinquenervis*, a plant species known to respond to early snowmelt by flowering earlier, with our control plots containing plants that are part of a long-term demographic study. The snow removal plots were snow-free for 13 days prior to the control plots, were consistently drier, and showed higher levels of plant water stress. Despite evidence of water stress, plants in the snow removal plots were larger in height than control plants, and this height difference was consistent throughout the duration of our experiment until all plants ceased growing for the season. Consistent with the growth response, plants in the snow removal plots exhibited a greater probability to reproduce, while simultaneously suffering a greater rate of frost damage to flowering stalks. We saw an increase in susceptibility to damage by spring frost due to the early initiation of flower buds in snow removal plots relative to the controls. While the growth and frost damage responses are consistent with long-term trends for this species, the probability of flowering was the opposite. This suggests that long-term data including year-to-year transitions in vital rates may not always be captured in a one-year experimental manipulation. This study shows that climate change is likely to exert a complex combination of positive and negative effects on plant vital rates.

II. Introduction

Global climate change has been shown to have significant effects on ecosystems worldwide, including higher temperatures and earlier snowmelt (Walther et al. 2002, Dunne et al. 2003, Inouye 2008). As the climate continues to warm, spring snowmelt will continue to advance (IPCC), and these changes will be more pronounced in temperate ecosystems (Steltzer et al. 2009). One of the results of earlier snowmelt is a longer growing season, which can lead to a host of ecological consequences including: increased soil temperature, increased sun exposure, and reduced soil moisture, causing water stress in plants and perhaps limiting productivity (Lambrecht et al. 2007). At the same time, a longer growing season may be beneficial for plants, providing them with longer timeframes for growth within a season (Starr et al. 2000) In order for species to survive such changes they must adapt to a changing environment (Doak and Morris 2010).

Climate change also has a strong effect on phenology. Changes in phenology, the timing of biological life phases, are one of the strongest bio-indicators of the direct effects of climate change (Caradonna et al. 2014). There is now a significant body of literature showing global phenological

advances across many taxa (Parmesan 2007). These phenological shifts have complex and dynamic effects on ecosystems that are poorly understood, yet have substantial impacts on the mechanisms that drive population dynamics (Wolkovich et al. 2014). Despite the increased interest in phenology there is a paucity of research examining the demographic consequences of earlier flowering. Establishing a connection between changes in phenology and population dynamics are difficult to quantify, partly due to the fact that phenological and population dynamics are seldom researched together in the same system (Post 2013).

In this study we took advantage of well-known flowering phenology and climate relationships to examine how early snowmelt affects the growth and reproduction of *Helianthella quinquenervis* (Aspen Sunflower). We explored two hypotheses concerning the ways in which *H. quinquenervis* is affected by early snowmelt: 1) negative effects could include plant water stress and frost damage to flowering stalks, and 2) positive effects could manifest through a longer growing season and additional resources available to allocate to reproduction and growth. Snow removal experiments are a common way to investigate the consequences of climate change (Wipf and Rixen 2010).

In this experiment we examined how early snowmelt affects growth and reproduction in this species, investigating the evidence for both negative and positive effects of early snowmelt. We examined the direct effects of early snowmelt on plant water stress and the demographic vital rates of *H. quinquenervis*. Demographic vital rates include recruitment, survival, growth, and reproduction. This study focuses on growth and three aspects of reproduction: the proportion of flowering plants, proportion of frost damaged stalks, and the number of flowers per plant.

The date of snowmelt is strongly related to *H. quinquenervis* flowering phenology (Iler et al. 2013). One consequence of earlier flowering in response to early snowmelt is an increased risk of frost damage (Inouye 2001) and a decrease in the probability of flowering (Iler, unpublished). Recent demographic modeling has shown that in years of earlier snowmelt *H. quinquenervis* exhibits a lower probability of flowering and a lower population growth rate, which has implications for species persistence and supports the longer growing season-drought hypothesis (Iler, unpublished). In contrast, the longer growing season may also cause plants to begin photosynthesizing earlier, allowing them to grow more and allocate a greater quantity of resources to reproduction (Kruger and Volin 2006). Consistent with this idea, early snowmelt also leads to increased growth in large plants (Iler, unpublished).

We conducted a direct manipulation experiment by removing snow from six plots adjacent to long-term demography plots. Based on previous research, we predicted that consequences of an earlier snowmelt could have severe consequences to virtually all of *H. quinquenervis*' demographic vital signs, as the species has been shown to be water limited (Valpine and Harte 2001). Building on knowledge from long-term observations and subsequent demographic modeling, we expected to see reduced growth as measured by plant size and reduced probability of flowering in the treatment plots (Iler, unpublished). We also expected to see lower soil moisture and higher leaf water pressure in the snow removal plots relative to control plots. This

study informs our understanding of the demographic vital rates (reproduction & growth) and the long-term implications for the future persistence of *H. quinquenervis* in the face of climate change.

III. Methods

A. Field Site

Ecosystems at higher elevations and latitudes have been shown to experience greater temperature shifts (IPCC), affecting snowmelt, soil moisture, length of the growing season, and plant phenology (Walther et al. 2002, Dunne et al. 2003). For these reasons the Rocky Mountain Biological lab (RMBL), located in the West Elk Range of the Colorado Rocky Mountains, provides a uniquely suited environment to conduct experiments to further understand species-level reactions to climate change. This research was conducted in Maxfield Meadow, down valley from the Gothic town site at the location of the existing long-term *H. quinquenervis* demography plots (Fig. 1).

B. Study Species

Helianthella quinquenervis is a long lived perennial sunflower indigenous to the western United states found between 2743-3505 m in elevation and is common in the meadows surrounding RMBL (Inouye and Taylor 1979). The plant is characterized by multiple vegetative clumps arising from a single, “often contorted root mass” (Inouye and Taylor 1979).

C. Experimental Design & Sampling Procedures

The six treatment plots measured 2.5m x 1.5m. Snow removal began on 9 May 2014 and was conducted over two days; at that time the depth of snowpack measured an average of 73 cm in the treatment plots and 69 cm in the controls. The plots were cleared of snow with an additional .25m on all sides (to allow for edge effect of the melting snowpack) for a total 3m x 2m dimension of snow removal. After the initial clearing there was additional snowfall; this was subsequently cleared on 13 May 2014. Before the second removal took place, the total snowfall was measured at an average depth of 84.5 cm across the treatment plots. On 24 May three of the long-term (or control) plots were recorded as being 100% snow free, and all six plots were snow free on 28 May. Thus the treatment plots were clear of snow for at least thirteen days ahead of first clear ground recorded on the control plots. Additional control plots that are the same size of the treatment plots were also established at the same site for the leaf water pressure (LWP) and soil moisture measurements so they do not disturb the long-term demography project (Fig. 2).

We measured response variables related to detection of water stress, growth, and reproduction: plant height, soil moisture, plant size, LWP, and total number of plants in flower including total number of flowers per plant. The height, LWP, and soil moisture were measured in weekly intervals. The count of flowering plants, aborted stalks and number of flowers were assessed during a one time census during the second half of July. Once the July weather pattern favored afternoon thundershowers we stopped recording LWP because of the confounding effects contributed by cloud cover.

Soil moisture was recorded using a TDR100 volumetric soil meter (Spectrum Technologies, Inc., Aurora, IL) with three samples across the long axis of each plot once weekly. These readings were averaged for each plot for analysis. Originally we had planned to record gravimetric soil moisture however we changed to a volumetric measurement so we do not have data for the first week of the study period. Measurements were taken in the mid-morning (0800-0900 hrs), but due to scheduling conflicts for weeks five and six measurements were taken in the evening (1900-2000 hrs). During the seventh week it was raining heavily on the day we were to record data, so sampling was postponed for one day. It is not expected that the difference in scheduling should have any impact on the data (Rutgers, personal communication).

Leaf water pressure (LWP) was measured with a “pressure bomb” (PMS instruments, Inc., Corvallis, OR). A single leaf was sampled from five plants per plot each week. Plants were randomly selected by throwing a rock into the plot and sampling the nearest plant. Sample leaves were between 6-10 cm, but more importantly had to have a stem diameter not in excess of 2.5 mm, the limit of the testing instrument. When plants lacked morphologically compatible leaves to sample, the next nearest eligible plant was measured. When a plant was selected but was unable to be successfully measured there were no more than two attempts to make a measurement before moving to an alternate plant. Plants were marked to ensure that plants were only sampled once. Leaf samples were collected and after being dried in a 65C° oven for 24 hours were weighed. We also conducted one sample of pre-dawn LWP measurement to verify expected physiological patterns, that plants should have lower pre-dawn LWP relative to mid-day samples of LWP. Due to number of plants and time available during the pre-dawn time interval, only three plants were sampled per plot. During the fourth week of the experiment, the July monsoon weather pattern became dominant and confounded our attempts to make accurate LWP measurements. The process of sampling all plots took approximately eight hours (divided evenly over two days during peak afternoon). Due to the duration of the measurement process and the variable cloud cover we decided that it was no longer possible to record meaningful data on LWP.

A height census was conducted weekly. Both the height and size (the number of clumps of the plant or leaves if there is only a single clump) were recorded. The height recorded was the tallest leaf from a non-flowering clump. A clump is essentially an aboveground meristem, following Dr. Inouye’s protocol for assessing plant size. Plants in the long-term plot were previously labeled with aluminum labels, and the treatment plots were labeled in a similar manner during the LWP measurements. Each week the same sixty plants from each treatment were measured (10 plants per plot).

On July 17th and 18th the annual demography census was conducted on the long-term demographic plots that served as our controls. The treatment plots were censused in the same way the following week. All plants were cataloged and the number of clumps, flowering stalks, aborted stalks, and flowers per stalk were recorded.

D. Statistical Analysis

The unit of replication is the plot (N=6 plots per treatment). The response variables that we analyzed were: plant size (height and number of clumps), volumetric soil moisture, LWP, the

percentage of plants that invested in flowering (i.e., the number of plants having either undamaged or aborted flowering stalks, or both/ the total number of plants), percentage of plants with aborted stalks, percentage of plants with undamaged flowering stalks, and average total flowers per plant. Dry leaf biomass was recorded as a covariate to LWP. There were no significant effects of dry leaf biomass on LWP, so it was not included in the analysis of LWP.

A series of t-tests were used to evaluate the difference in soil moisture, LWP, percentage of plants that flowered, percentage of plants with aborted stalks, and average number of flowers per plant that reproduced between the snow-removal and control plots. The data was analyzed for normalcy, heteroscedasticity, and constant error structure confirming the assumptions for a t-test. In cases where there was not normal variance this was taken into account for the t-test with the Welch correction for unequal variance. Height was analyzed by repeated measures ANOVA to examine evidence for differences in growth rate: a height by week interaction. Height was a continuous response variable, treatment and weeks were categorical predictors, and plot was the repeated measure. Residuals from the model were determined to be normal using a Shapiro-Wilk test. The open source statistics suite 'R' was used for analysis of all data.

IV. Results

Soil moisture followed an expected pattern until the beginning of the monsoon rain season, which began during our fourth week of the experiment, but only after we had taken data for that week (Fig 2). Soil moisture in the snow removal treatment was significantly or marginally significantly lower than the control plots in weeks 2, 3, and 6. While the other weeks were not significant, the treatment plots were consistently drier than the controls (Table 1).

Leaf water pressure was significantly different between treatments for only the first week, however the third week was marginally significant (Fig 3a; Table 2). Despite the non-significant results the treatment plots consistently demonstrated a higher LWP. The predawn measurements were, as expected, considerably lower than the mid-day samples but did not exhibit a significant difference between treatments (Fig 3b).

Using repeated measures ANOVA, clumps did not differ significantly by week (p-value: 0.98). The lack of change in number of plant clumps is informative because it shows that while clump size differs from year to year (Iler, unpublished), it does not change within one growing season. Therefore height is the appropriate metric for growth in this study. The weekly height census showed a significant difference in height between treatment and control plots, indicating that plants in snow removals were taller than plants in controls, and this height difference was significant every week, until plants stopped growing (Fig. 4; Table 3). Using a piecewise regression we observed growth stopped at the end of the fourth week (breakpoint identified as 3.7 weeks for treatment, and 4.7 weeks for control; see Fig. 4). There was no significant difference between the slopes of the regression lines for the first four weeks (p-value: 0.26). Slopes for both regression lines for weeks 5-7 were essentially flat (0.15 cm/week for the treatment verses 0.001cm/week for the control).

In terms of flowering, the treatment plots contained on average a lower percentage of successfully flowering plants and a higher rate of aborted stalks (Table 5; Fig. 5a & 5b). However when evaluating plants that made a reproductive effort (all plants with either successful and aborted stalks) we saw a marginally higher rate of reproduction in the snow removal plots (Fig. 5c). The average number of flowers per flowering plant was not significantly different between treatments ($t = 0.57$, $p\text{-value} = 0.58$; control: 3.1 ± 1.0 flowers per plant (± 1 SEM), snow removal: 2.7 ± 1.0 flowers per plant.)

V. Discussion

If climate change continues to advance the date of snowmelt and thus spring conditions in the East River valley as expected (Inouye 2008) these findings present implications for the demography of *H. quinquenervis*. The snow removal treatment plots showed a significantly higher level of frost damage, which ultimately has negative effects on fecundity. The snow removal plots enjoyed a longer growing season, potentially having positive effects on growth and reproduction, but at the same time this also exposed them both to an extended period of water stress and potential frost damage which may result in negative effects. Our results confirmed that the plants in the snow removal plots were exposed to water stress in several weeks of the experiment. Finally, the snow removals plots, despite the increased water stress, showed a greater probability of making a reproductive effort, however the increased frost damage made them ultimately less successful in flowering.

Collectively soil moisture and leaf water pressure both showed the expected results consistent with drought conditions. This is expected as one of the consequences of a longer growing season is reduced soil moisture (Starr et al. 2000). The snow removal treatments had reduced soil moisture, but this effect varied across weeks (Fig. 4). The soil moisture oscillated in weeks five through seven as expected after the initiation of the rainy season. This pattern of soil moisture for weeks 5-7 concurs with the recorded rainfall during those weeks. The rainfall on week four occurred after we recorded our data (Table 6). Interestingly, we saw statistically significant differences in soil moisture in week six even after considerable rain. It is worth noting that with the exception of week 7 (which had a rainfall event the day prior to measurements), even after considerable rainfall, the treatment plots continued to show a water deficit (Fig. 3). This shows that the deficit from water input is persistent. This highlights a subtle difference between early snowmelt and snow removal: in an early snowmelt event, the water content of the snowpack would have contributed to the hydrological cycle; in this experiment, the snow was removed and thus deprived the system of water it would have received.

Similar to the soil moisture data, the plants in the treatment plots continued to exhibit higher water stress through the duration of data collection (Fig. 4). This is expected as *H. quinquenervis* has been shown to be water limited (Valpine and Harte 2001), and also as expected one of the consequences of a longer growing season are physiological changes to plants (Starr et al. 2000). Our predawn measurements showed that intraday change in LWP varies considerably and that this is consistent with other studies (Donovan et al. 1996). As such it is important to sample across all plants during similar environmental conditions.

The treatment plots had a two-week head start on their growth effort; accordingly the treatment plots were consistently taller than the controls until they stopped growing (Fig. 4). Plants stopped growing during the fourth week of measurements. These results suggest that plants, which get an early start as a result of the early snowmelt, do not reach a larger size within the growing season, but are instead bigger at an earlier date. Similar growth rates between treatments shows that despite the difference in water stress, the plants growth in terms of rate of change in height is unaffected (growth rate is consistent between treatments). These findings are consistent with other studies of alpine habitats which have shown that different snow melt dates do not result in measurable difference in plant growth rates (Jonas et al. 2008).

The rates of aborted stalks were significantly higher in the snow removal plots which confirms that earlier snow melt exposes plants to greater risk of frost damage as observed in observational studies (Inouye 2008). This suggests that the frost damage pathway is an important factor in population dynamics via negative effects on fecundity. The temperature data used here for reference were recorded by Billy Bar's RMBL weather station, which is located approximately 2km from our study site and at a slightly higher elevation. Local topography, aspect slope and local events of cold air drainage can affect temperature (Inouye 2008). That having been said, the June minimum temperature had 10 days where below freezing temperatures were recorded, the last occurring on 20th June. Eight of the 10 days where below freezing temperatures were recorded happened prior to 15th June. This weather data, despite being recorded a slight distance from the research site, concurs with our results showing that the snow removal plots were exposed to a much greater durations when frost events can occur.

With regard to the decision to flower, we found the opposite of our expectations. In contrast to the long-term observational data, plants experiencing early snowmelt conditions exhibited a higher percentage of flowering compared to control plants. These results suggest that the magnitude of soil moisture reduction and increase in leaf water potential were insufficient to cause *H. quinquenervis* enough water stress to reduce its reproductive effort. One possible explanation for this is that the treatment plants had the benefit of a longer growing season, which our growth results support. Threshold flowering sizes are common in perennial plants (Wesselingh et al. 1997). Plants in snow removals were larger than plants in controls up through the end of week four (10 July), and therefore could have potentially reached a threshold flowering size earlier than the controls (Fig. 4). The long-term growth data are also consistent with this interpretation: larger plants are more likely to reproduce than smaller plants and exhibit increased growth under early snowmelt conditions (Iler, unpublished). Thus, if more *H. quinquenervis* plants can reach a threshold flowering size when snowmelt is early, as our data suggest, then more plants may be able to reproduce. However, these results contrast with the observational pattern of a reduced probability of flowering when snowmelt is early. Long-term data include year-to-year transitions in vital rates that may not be captured in a one-year experimental manipulation. In summary despite the additional water stress that they had to withstand during our manipulation, the longer growing period could ultimately be a larger factor in the reproductive decision.

VI. Conclusion

We have shown through a direct manipulation which simulated early snowmelt that *H. quinquenervis* even under increased water stress shows a higher likelihood to begin the reproductive effort, simultaneously exposing itself to greater risk of frost damage and aborted flowering stalks. This experiment did not confirm Iler's demographic model, however it did confirm experimentally for the first time that an earlier beginning of the reproductive effort results in increased risk of frost damage to flowering stalks during years of early snowmelt. Furthermore, the negative effects from frost damage on *H. quinquenervis* appear to outweigh the benefits of a longer growing season shown in the percentage of plants that successfully flowered, because frost damage occurs after the decision to flower. The treatment plots used for this experiment will remain in place and continue to be investigated to examine evidence for one year lag-effects of early snowmelt.

VII. Acknowledgements

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VIII. Literature Cited

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IX. Tables and Figures

Table 1. Soil moisture t-test results (weeks 2-7)

	Mean (log transformed)		Standard Error		df	t	P value	
	Treatment	Control	Treatment	Control				
Week 2	1.6	1.9	0.05	0.07	10	2.39	0.038	**
Week 3	1.5	1.6	0.08	0.02	5.97	2.00	0.092	+
Week 4	1.4	1.5	0.10	0.06	10	0.84	0.421	
Week 5	2.4	2.4	0.06	0.08	10	0.68	0.513	
Week 6	2.0	2.1	0.04	0.03	10	2.58	0.027	*
Week 7	3.0	3.1	0.04	0.07	10	0.43	0.676	

Table 2. Leaf water pressure t-test results (weeks 1-3 and predawn)

	Mean		Standard Error		df	t	P value	
	Treatment	Control	Treatment	Control				
Week 1	187.8	150.2	10.5	11.8	10	-2.39	0.038	*
Week 2	191.5	177.5	18.0	12.7	10	-0.64	0.537	
Week 3	225.2	197.9	9.7	9.8	10	-1.98	0.076	+
Predawn	66.5	55.9	4.6	4.3	21	-1.68	0.107	

Table 3. Plant height t-test results (weeks 1-7)

	Mean height (cm)		Standard Error		df	t	P value	
	Treatment	Control	Treatment	Control				
Week 1	20.7	15.6	0.60	0.66	10	-5.71	< 0.001	***
Week 2	23.0	18.1	0.56	0.79	10	-5.04	< 0.001	***
Week 3	24.8	21.6	0.56	0.66	10	-3.74	0.004	**
Week 4	26.2	23.5	0.84	0.67	10	-2.56	0.029	*
Week 5	26.9	25.7	0.95	0.96	10	-0.89	0.395	
Week 6	26.5	25.9	0.70	1.01	10	-0.48	0.645	
Week 7	26.9	25.7	0.95	0.96	10	-0.89	0.395	

Table 4. Repeated measures ANOVA of Difference in plant height (examining only weeks 1-4)

	DF	Sum Sq	F	P value	
Week	3	2087	32.766	< 0.001	***
Treatment x Week	3	124	1.316	0.269	
Residuals	452	14193			

Table 5. Comparisons of reproduction between treatments.

Response variables	Mean Percentage [^]		df	t	P value	
	Treatment	Control				
% of Plants Flowering	5%	17%	10	4.49	0.001	**
% with aborted stalks	58%	32%	10	-3.66	0.004	**
% with Reproductive effort	59%	36%	10	-1.90	0.087	+

[^] non-transformed values

Table 6. Rainfall during weeks 1-7

	Rainfall (inches)
Week 1	0.0
Week 2	0.0
Week 3	0.0
Week 4	0.67
Week 5	0.11
Week 6	0.26
Week 7	1.59

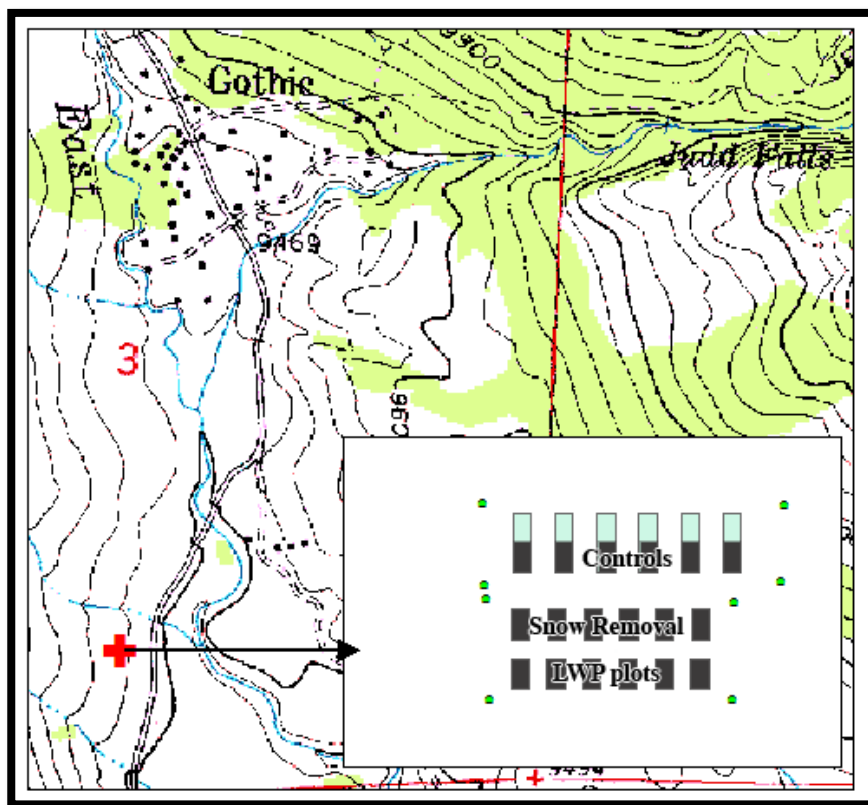


Fig 1. Area map and inset showing detail of experiment plots

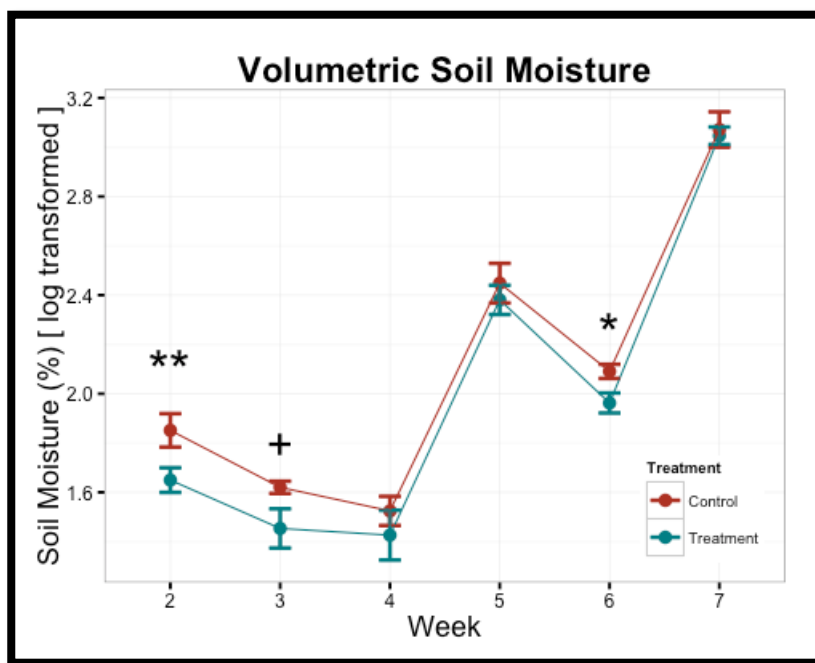


Fig 2. Effects of snow removal (Treatment) on volumetric soil moisture. Points are means and error bars ± 1 SEM ($n = 6$ plots). [Significance indicated by: + $p < 0.1$; * $p < 0.05$, ** $p < 0.01$ from two sample t-tests for each week.]

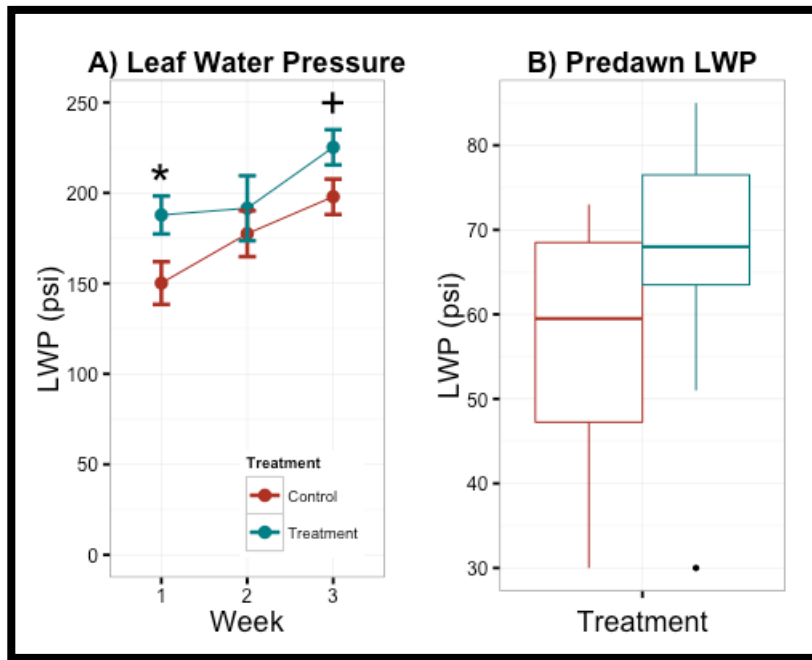


Fig 3. The effects of snow removal (Treatment) on leaf water pressure (LWP) in *H. quinquenervis*. A) Leaf Water Pressure by week. Mean values between treatment and control of plot means with Standard Error Bars. B) Predawn measurement of LWP. [Significance indicated by: + $p < 0.1$; * $p < 0.05$]

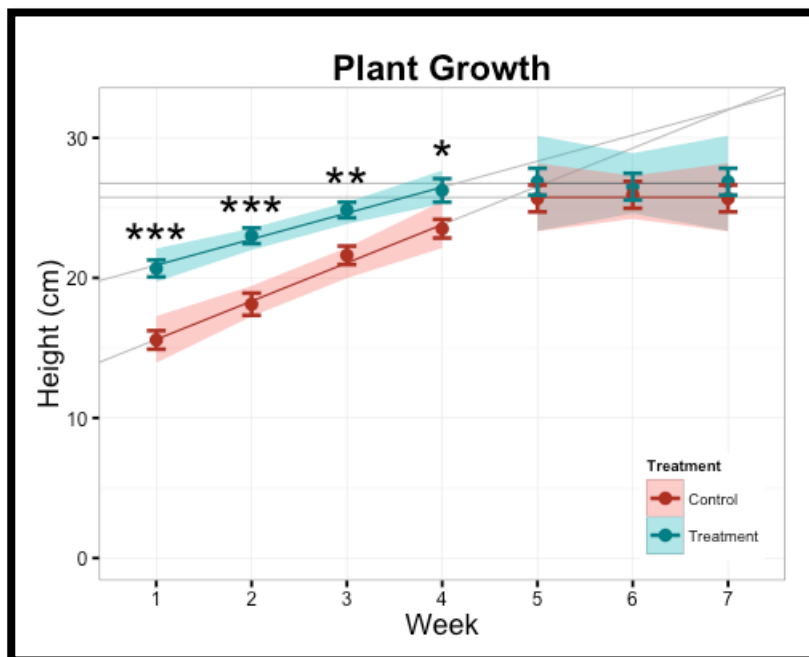


Fig 4. *Helianthella quinquenervis* height and difference in growth between snow removal (Treatment) and control plots. Points are mean values of height and error bars ± 1 SEM [Significance indicated by: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ from t-test for each week; slope of lines does not differ between treatments (ANCOVA, $P=0.27$).]

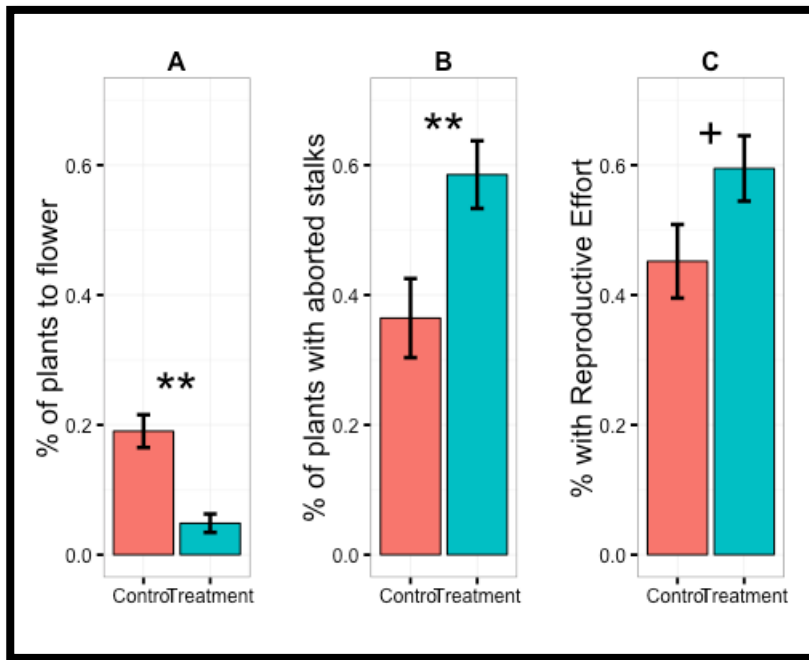


Fig 5. Comparison of mean A) Percentage of plants that produced undamaged flowers (the total number of plants with OK flowering stalks/the total number of plants), B) Percentage of aborted stalks (plants with aborted stalks/total number of plants), and C) Percent of plants that made a reproductive effort (the number of plants containing flowering stalks and aborted stalks divided by the total number of plants) between snow removal (Treatment) and control plots. Error bars represent ± 1 SEM [Significance indicated by: + $p < 0.1$, ** $p < 0.01$ from two-sample t-tests.]