Effects of early snowmelt and climate warming on *Valeriana edulis* and the insects that depend on it

Student: Alice Theibault

Mentor: Ian Billick

Full Time Independent Research

Summer 2014

Abstract

Global climate change can disrupt ecosystems by impacting the interactions between organisms. I investigated the impact of early snowmelt and warming on the dioecious perennial herb *Valeriana edulis*, as well as their indirect effects on the aphid species *Aphis valerianae* and the ants that tend the aphids. The study was conducted in a field that had been partially buried by an avalanche, with the avalanche standing as a proxy for a later snowmelt scenario, and open-top chambers were placed around the bases of half the plants in the experiment to simulate climate warming. Aphids were then placed on the plants and their colonies and interactions with ants were observed over the course of several weeks. I also collected data on the plants' growth the first, second, and last week of the experiment. I found was that snowmelt had the biggest impact on the plants' growth and their ability to maintain aphid colonies and attract ants. Sex of the plants also impacted interactions in the system, independently of snowmelt. Warming the plants had no statistically-significant impacts on the plants or their interactions with the insects, though it did seem to have an impact on the total number of ants. These results suggest that changes in snowmelt will be a major driver of changes to ecosystem interactions in the Rocky Mountains.

Introduction

Global climate change is having far-reaching effects on biotic communities across the world. Warming climates are projected to cause a shift of lower-elevation species toward higher elevations and tropical species toward the poles, as well as a slew of other environmental changes (Parmesan 2006, Inouye 2008). One of the ways climate change can alter ecosystems is by disrupting interactions between organisms (Toby Kiers et al. 2010).

Many studies have shown that interactions between species may change or break down in different environmental conditions. Toby Kiers et al. (2010) proposed that in a changing environment, mutualisms may break down if the costs to either partner outweigh the benefits. A study of ant-plant interactions in Mexico (Rico-Gray et al. 1998) showed that a number of factors influence interactions between ants and plants, from temperature and precipitation to vegetation heterogeneity and the abundance of nectar, though they did find that ants tended to interact with plants less in drier and cooler habitats overall. The effects of the mutualisms themselves on the host plants of the ants and aphids are similarly variable—Styrsky and Eubanks (2007) have shown that whether mutualisms between hemipterans and ants have positive impacts on plants (by keeping away other, more devastating herbivores) or negative impacts (caused by parasitism of the hemipterans) depends on a variety of environmental factors, including the relative rates of herbivory, the species of hemipteran and ant, the characteristics of the host plant (positive interactions more strongly outnumbered negative interactions in woody species than herbaceous ones), and even the latitude.

Because ant and treehopper mutualisms are more common in lower-elevation areas with warmer and drier climates (Olmstead and Wood 1990), the rate of mutualisms between ants and some hemipterans may actually increase as the climate warms and higher-elevation habitats become more accessible to ants. The treehopper *P. modesta*, which employs maternal care to attract ants, remains with its offspring because it is semelparous owing to the high elevation and harsh climates where it is found, whereas treehoppers that live in more mild climates are more likely to be iteroparous and abandon their young to lay more eggs (Billick et al. 2001). As a result, higher temperatures may lead to greater iteroparity among treehoppers and thus less maternal care, which could affect their relationship with ants. A study by Marquis, et al. (2014) showed that mutualisms between ants and aphids can buffer the effect of warming on plants, but that warmer temperatures led to greater levels of infestation by pest aphid species and a reduction in carnivores which could control aphid populations. However, few studies have been done on how climate change affects the interactions between ants and aphids, and their host plants, in the field.

For this study I investigated the impacts of climate change on the plant *Valeriana edulis*, as well as the indirect effects of these changes on ant-aphid interactions. V*aleriana edulis* is a perennial dioecious flowering herb found in alpine meadows. The plant has separate sexes with slightly different ecologies, and shows greater female bias in sex ratios in higher elevations (Soule 1981). The plant serves as a host to the aphid species *Aphis valerianae*, and the ants that tend these aphids. A recent study found that female plants host more aphids than male plants, and also produce more nectar and flowers more attractive to ants (Petry et al. 2013). A study of *V. edulis* plants at a 2,900 m alpine meadow (Mooney et al. 2012) demonstrated that although both male and female plants are capable of comparable direct defenses against herbivory, females are superior at indirect defense, with many more carnivores and ants tending aphids found on female plants than male ones. For this experiment, I hypothesized that the plants subject to the early snowmelt and warming treatments will undergo greater stress, and thus become less attractive to aphids and ants. I also predict that the difference will be greater in female plants than male plants, since females are more successful in cooler, wetter climates (Soule 1981).

Methods

This study was conducted in a subalpine meadow just north of Gothic, in the southern Colorado Rocky Mountains, at an elevation of approximately 3,000 meters. This meadow is located beside a parking lot at the Judd Falls trailhead. This meadow was partly buried by an avalanche, which provided a useful proxy for measuring the effect of early and late snowmelt, with the part of the field that was buried representing a late snowmelt scenario and the field that was not buried representing early snowmelt.

First, I haphazardly selected sixty plants on each side of the field. Only plants that flowered this year were used in the experiment. I assembled open-top chambers in the shape of a hexagon out of fiberglass, held together by twist ties. I collected temperature data from Friday, July 18th until Thursday, July 24th from a group of plants with and without chambers to ensure that the chambers increased the temperature near the base of the plants. Pairs for this experiment consisted of two *V. edulis* plants that were close to one another. I randomly assigned treatments by flipping a coin. Once the chambers were placed around the plants, I hammered stakes into the ground inside of loops on each side of the chamber to hold them in place. The pairs were assigned and the chambers were set up on June 29th, 2014. Shortly afterward, I placed numbered tags around the inflorescences of each plant to identify them in case any flags went missing. Two pairs of plants (561 and 588, and 563 and 589) were located in an area that had melted out earlier; these plants were included in the avalanche zone because they had ever been buried by the avalanche.

On the third of July I measured the plants along their longest axis, and the height of their tallest inflorescence. I performed the measurements using a meter stick. I also recorded the date, time, and weather conditions on the days the measurements took place. I repeated this measurement on July 10th and one final time on July 27th. Four plants were excluded from analysis because I could not determine whether they comprised just one plant or several plants. By the time I measured the plants for a third time, several of the plants had had part of all or their inflorescences removed; their inflorescent heights were also excluded from analysis.

To create colonies of aphids to place on the plants during the study, I tied mesh bags around *V. edulis* stalks that already had large amounts of aphids on them, and allowed the aphids to collect in the bags for several days.

I transferred aphids to each of the plants over the course of four(?) days. I peeled back the mesh bags over the inflorescences and cut the inflorescences using shears, placing them in a small cooler to shelter the aphids from the sun. I transferred ten aphids at a time to each of the plants using a paintbrush. I only transferred aphids that were medium or large-sized and dark gray, including winged adults, or that were large and light gray. Most plants received a mixture of each of these kinds of aphids. Each day I placed aphids on ten plants one side of the field and five on the other side, alternating treatments so that each side received the same total amount of aphids at the same time. Aphids were placed on several parts of the inflorescent stalk, including the stem and flowers, but only occasionally on the leaves.

On July 11, I scraped the aphids off any plants that already had established aphid colonies of ten individuals or more, replacing them with aphids from the cooler and placing the removed aphids in the cooler so I could transplant them elsewhere. However, because this technique was so destructive and time-consuming, for the next three days I simply made a note of plants with established aphid colonies and added ten more aphids of any size to them. A colony was considered to have "ten or more" aphids if it had many aphids in multiple age classes, as well as if it simply had ten adults. If a plant or inflorescent stalk had fewer than ten aphids, I added aphids until it had ten in total. If a plant had an inflorescent stalk with aphids that numbered less than ten, I placed the aphids on that stalk.

When surveying the plants, I first made a note of how many of the plants' inflorescent stalks had aphids on them, and then I counted the number of ants on the stalks above the first juncture with flowers, dividing them into one of five functional species: *Dolicoterines*, *Myrmicines*, *Formica fusca*, *Formica rufa*, and *Camponotus*. I then made a note of the relative amounts of aphids on each inflorescence, and recorded the amounts as a letter, with A= no aphids, B= 1 to 5 aphids, C=5 to 25 aphids, and D=>25 aphids. I also noted any spiders I saw on the plants, as well as anything else unusual about them, such as herbivore damage or the presence of other insects.

To measure differences in ambient temperature in control and treatment plots, I left Hobo temperature probes at the base of thirteen plants on the early snowmelt side of the field, close to the front. These probes recorded data from July 18th to July 24th. The average difference in temperature between the warming chambers and ambient temperature was 1.18 degrees (personal calculations).

I used two-way ANOVAs to determine the effects of early snowmelt, warming and sex, and their interactions on the plants. The response variables used in the analysis were the plants' growth along their longest axis, growth of tallest inflorescence, the size and average size of aphid colonies on the plants for the first and second week, and the total number of ants.

To determine whether climate change impacted the interaction between aphids and ants, I performed two-way ANOVAs that crossed aphid colony sizes with both the avalanche and warming treatments. I also performed a linear regression analysis with aphid colony size as the independent variable and number of ants as the dependent variable. All statistical tests were performed in JMP, version 11 (SAS).

Results

Of all the ANOVA's conducted, three of them—proportion growth of tallest inflorescence, average aphid colony size, and total ant number—yielded statistically significant results (Table 1). The snowmelt treatment had statistically significant ($P<0.05$) effects on growth of the plants' tallest inflorescences as well as on average aphid colony size and number of ants. The inflorescences of plants grown in the avalanche zone grew 1.72 times as much as those of plants not in the avalanche zone. Plants that had been impacted by the avalanche demonstrated smaller aphid colony sizes but approximately 4.88 times the number of ants (Table 2a).

The warming treatment had no statistically significant effects on any of the dependent variables in the study, though its effect on total number of ants came closest to being significant. Plants not subjected to the warming treatment had 1.51 times the number of ants of those that were warmed (Table 2b).

Sex significantly impacted growth of the plants, numbers of aphids, and number of ants. Females demonstrated higher levels of growth along their longest axis and higher numbers of ants and aphids for both survey weeks (Table 2c).

Interactions between these factors were never statistically significant. Interactions that had close to statistically significant effects included the effect of snowmelt and sex on percent growth of tallest inflorescence, and the effect of warming and sex on growth of the aphid colonies (Table 4).

Linear regression analysis reveals no statistically significant correlation between aphid colony size and ant number, either in the first or second week. However, the slope of the regression lines did vary with treatment—the correlation between aphid number and ant number was greater in plants buried by the avalanche, and in those not subject to the warming treatment (Figures 1 and 2).

Discussion

In this study, I sought to determine the effects of early snowmelt and warming on the dioecious perennial herb *Valeriana edulis*, and on the ants and aphids that the plant interacts with. I found that snowmelt, moreso than warming, impacted the plants' growth and their ability to attract aphids and ants. I also found a strong effect of sex, both on growth and on the amount of aphids and ants found on the plants.

The plants that had been buried by the avalanche experienced a greater proportion of growth over the course of the experiment. However, the plants that had not been buried flowered and produced seeds earlier (personal observations). This is in line with the research by Inouye (2008), which demonstrated that plants alter their phenology in accordance with different snowmelt scenarios, and that earlier snowmelt leaves plants more vulnerable to frost damage. Frost damage in turn reduces growth (Wipf et al. 2009). Because June is a relatively dry month in the Rocky Mountains (Dr. John Harte, personal correspondence) the plants may also be dependent on snow to provide them with water, and may suffer increased water stress in years with earlier snowmelt. Plants buried by the avalanche also many more ants, possibly because they were healthier and so more desirable as food. However, these same plants seemed to have smaller aphid colonies. Other studies have shown that the presence of tending ants may actually reduce the size of aphid colonies (Petry et al. 2012) but it is unclear in this system whether the ants respond to smaller numbers of aphids, or whether they themselves reduce the size of the aphid colonies.

Warming, by contrast, had little direct or indirect effect on the aphids, but did reduce the total number of ants found on the plant. There was no interaction between warming and snowmelt. In the dry highlands of Zapotitlán, Mexico, which have a temperature regime fairly close to that of the Rocky Mountains in the summer, temperature was found to have the most significant impact on ant-plant interactions, moreso than precipitation or the interaction between the two. However, since Zapotitlán is located in the tropics and temperatures there do not drop below freezing (Rico-Gray et al. 1998), it likely does not experience snow, and so the plants and ants would be used to a different water regime than the ones in the Rocky Mountains and may be impacted differently by water. It is possible that the lack of more extensive warming impacts on the system is a result of the relatively small amount of warming the chambers provided. Perhaps a more dramatic temperature difference would impact the plants more strongly.

Initially, I had expected that female plants would suffer more from the effects of early snowmelt and warming than males, and would thus not perform as well, since they survived better in cooler and wetter climates (Soule 1981). However, no statistically significant interactions between sex and treatments were found, even though studies have shown that hotter and drier climates are more male-friendly (Soule 1981). Furthermore, females consistently attracted more aphids and ants, as did the female plants in the study by Mooney et al. (2012), which did not incorporate climate change Potentially, there is a threshold temperature or moisture level outside of which females become disadvantaged, and this site has not reached this threshold yet. Alternatively, since ant-tending interactions with aphids have been shown to buffer against the effects of climate change (Marquis et al. 2014), the females' ability to attract more ants and aphids may make them less vulnerable than their natural habitat preferences would suggest.

Plants subjected to the early snowmelt and warming regimes generally had less strong relationships between the ants and aphids found on them, though the relationship was not statistically significant in either study. Further studies may be necessary to determine whether there are significant interactions between a plant's colony size and temperature or snowmelt in the amount of ants a plant can attract. Since early snowmelt and warming impact the presence of ants on a plant, but plants subjected to these treatments still had aphids, the aphids may cause greater stress to the plant in a warmed world, since they will continue to feed on the plants but no longer attract as many ants to keep away predators (Styrsky and Eubanks 2007).

This experiment demonstrates clearly that climate change stands to have impacts on systems of interactions between insects and plants. However, early snowmelt and warming seem to impact the system independently, and to differing degrees. The fact that earlier snowmelt created so many significant differences in the performance of the plants and insects suggests that snow cover and snowmelt date, moreso than warming temperatures, could exert changes on the ecological communities of the Rocky Mountains.

Works Cited

Billick, Ian, Ryan Brown, and Jennifer S. Reithel. 2005. Importance of Fertilization of Host Plants to Ant Tending and Growth Rates in *Glaucopysche lygdamus* (Lepidoptera: Lycaenidae). Annals of the Entomological Society of America 98(4): 491-495.

Billick, Ian and Kirk Tonkel. 2003. The Relative Importance of Spatial Vs. Temporal Variability in Generating a Conditional Mutualism. Ecology 84(2): 289-295.

Inouye, D. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. Ecology 89(2): 353-362.

Marquis, Michael, Israel Del Toro, and Shannon L. Pelini. 2014. Insect mutualisms buffer warming effects on multiple trophic levels. Ecology 95(1): 9-13.

Mooney, Kailen A., Aleshia Fremgen, and William K. Petry. 2012. Plant sex and induced responses independently influence herbivore performance, natural enemies, and aphid-tending ants. Arthropod-Plant Interactions 6: 553-560.

Olmstead, K.L. and T.K. Wood. 1990. Altitudinal Patterns in Species Richness of Neotropical Treehoppers (Homoptera: Membracidae): The Role of Ants. Proceedings of the Entomological Society of Washington 92(3): 552-260.

Parmesan, Camille. 2006. Ecological and Evolutionary Responses to Recent Climate Change. Annual Review of Ecology, Evolution, and Systematics 37: 637-669.

Petry, William K., Kayla I. Perry, Aleshia Fremgen, Sarah K. Rudeen, Mitchell Lopez, John Dryburgh, and Kailen A. Mooney. 2013. Mechanisms underlying plant sexual dimorphism in multi-trophic arthropod communities. Ecology 94(9): 2055-2065.

Petry, William K., Kayla I. Perry, and Kailen A. Mooney. 2012. Influence of macronutrient imbalance on native ant foraging and interspecific interactions in the field. Ecological Entomology 37: 175-183.

Rico-Gray, Victor, José G. García-Franco, Mónica Palacios-Rios, Cecilia Díaz-Castelazo, Victor Parra-Tabla and Jorje A. Navarro. 1998. Geographical and Seasonal Variation in the Richness of Ant-Plant Interactions in Mexico. Biotropica 30(2): 190-200.

Soule, Judith Dingle. 1981. Ecological Consequences of Dioecism in Plants: A Case Study of Sex Differences, Sex Ratios and Population Dynamics of *Valeriana Edulis* Nutt. PhD dissertation. Michigan State University.

Styrsky, John D. and Micky D. Eubanks. 2007. Ecological consequences of interactions between ants and honeydew-producing insects. Proceedings of Royal Society B 274: 151-164.

Toby Kiers, E., Todd M. Palmer, Anthony R. Ives, John F. Bruno, and Judith L. Bronstein. 2010. Mutualisms in a changing world: an evolutionary perspective. Ecology Letters 13(12): 1459-1474.

Wipf, S., Veronika Stoeckli, and Peter Bebi. 2009. Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. Climatic Change 94: 105-121.

Tables

Table 1: 2-way ANOVAs testing effects of early snowmelt, warming, sex, and their interactions

a) Proportion growth along longest axis

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	0.6521275	0.108688	1.6662
Error	108	7.0449678	0.065231	**Prob > F**
C. Total	114	7.6970953		0.1362

b) Proportion growth of tallest inflorescence

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	20.581128	3.43019	8.4511
Error	83	33.688526	0.40589	Prob > F
C. Total	89	54.269654		<.0001*

c) Number of aphids Week 1

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	89.4214	14.9036	1.2003
Error	108	1340.9612	12.4163	Prob > F
C. Total	114	1430.3826		0.3117

d) Number of aphids Week 2

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	138.9053	23.1509	1.8974
Error	108	1317.7555	12.2014	Prob > F
C. Total	114	1456.6609		0.0877

e) Total colony growth

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	56.89017	9.48169	1.4940
Error	108	685.40548	6.34635	Prob > F
C. Total	114	742.29565		0.1870

f) Average number of aphids Week 1

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	11.106253	1.85104	2.9420
Error	108	67.951347	0.62918	Prob > F
C. Total	114	79.057601		0.0107*

g) Average number of aphids Week 2

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	11.351747	1.89196	3.0794
Error	108	66.354543	0.61439	Prob > F
C. Total	114	77.706290		0.0080*

h) Average colony growth

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	3.535497	0.589249	1.1149
Error	108	57.081276	0.528530	Prob > F
C. Total	114	60.616773		0.3585

i) Total number of ants

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	478.3098	79.7183	9.1525
Error	108	940.6815	8.7100	Prob > F
C. Total	114	1418.9913		<.0001*

Table 2: Means, F-ratios, and P-values of 2-way ANOVAs testing effects of a) early snowmelt, b) warming, and c) sex. Statistically significant P-values are labeled with *.

a) Avalanche

Dependent variable	Mean Y	Mean N	F-ratio	P-value
Proportion growth on longest axis	0.345754	0.255557	2.4772	0.1184
Proportion growth of tallest inflorescence	1.94235	1.12748	34.7224	<.0001*
Total number of aphids Week 1	3.92857	4.9322	1.3604	0.246
Total number of aphids Week 2	5.19643	5.52542	0.0124	0.9115
Total growth of colony	1.26786	0.59322	3.1894	0.0769
Average number of aphids Week 1	1.40417	1.86633	9.3867	0.0028*
Average number of aphids Week 2	1.80489	2.157	3.7287	0.0561
Average growth of colony	0.400723	0.290671	1.5898	0.2101
Total number of ants	4.7149	0.9661	39.2445	<.0001*

b) Warming

Dependent variable	Mean Y	Mean N	F-ratio	P-value
Proportion growth on longest axis	0.29274	0.305874	0.0083	0.9274
Proportion growth of tallest inflorescence	1.43084	1.47223	0.1732	0.6783
Total number of aphids Week 1	4.46429	4.42373	0	0.9952
Total number of aphids Week 2	5.64286	5.10169	0.234	0.6296
Total growth of colony	1.17857	0.67797	0.4386	0.5092
Average number of aphids Week 1	1.61548	1.66577	0.0005	0.9829
Average number of aphids Week 2	2.02819	1.94506	0.1962	0.6587
Average growth of colony	0.412713	0.279291	0.251	0.6174
Total number of ants	2.21429	3.33898	2.1122	0.149

c)

Sex

Dependent variable	Mean F	Mean M	F-ratio	P-value
Proportion growth on longest axis	0.263193	0.364971	4.6767	0.0328*
Proportion growth of tallest inflorescence	1.62355	1.05649	7.435	0.0131*
Total number of aphids Week 1	4.89189	3.63415	2.9108	0.0909
Total number of aphids Week 2	6	4.21951	6.8284	0.0103*
Total growth of colony	1.10811	0.58537	1.5299	0.2188
Average number of aphids Week 1	1.7756	1.39884	5.3062	0.0232*
Average number of aphids Week 2	2.16683	1.65833	10.8483	0.0013*
Average growth of colony	0.391227	0.259495	1.0771	0.3017
Total number of ants	3.28378	1.90244	5.1821	0.0248*

Table 3: Least-squared means of interactions between a) early snowmelt and warming, b) early snowmelt and sex, and c) warming and sex.

a)

Avalanche*Warming

Dependent variable	Least square mean N,N	Least square mean N,Y	Least square mean Y,N	Least square mean Y,Y
Proportion growth on longest axis	0.24904491	0.29843464	0.38197907	0.32339843
Proportion growth of tallest inflorescence	1.0137416	1.0026466	1.9888961	1.8704391
Total number of aphids Week 1	4.4440195	4.8577439	4.0464107	3.6410134
Total number of aphids Week 2	4.9929254	5.2100055	4.9534179	5.4023796
Total growth of colony	0.5489059	0.3522616	0.9070072	1.7613663
Average number of aphids Week 1	1.7590024	1.8659784	1.3920462	1.2783527
Average number of aphids Week 2	2.0212901	2.0982826	1.7325897	1.7924582
Average growth of colony	0.26228773	0.23230418	0.34054344	0.51410558

Total number of ants	1.2269826	0.4218389	4.8983801	4.0126574

b)

Avalanche*Sex

Dependent variable	Least square mean N,F	Least square mean N,M	Least square mean Y,F	Least square mean Y,M
Proportion growth on longest axis	0.21307826	0.33440128	0.30452915	0.40084835
Proportion growth of tallest inflorescence	1.3578317	0.6585565	1.9808803	1.8784548
Total number of aphids Week 1	5.6230827	3.6786807	4.0559708	3.6314532
Total number of aphids Week 2	6.5011117	3.7018192	5.5766262	4.7791713
Total growth of colony	0.8780291	0.0231385	1.5206554	1.147718
Average number of aphids Week 1	2.0118592	1.6131216	1.4958237	1.1745752
Average number of aphids Week 2	2.389452	1.7301206	1.9415089	1.583539
Average growth of colony	0.37759288	0.11699903	0.44568523	0.4089638
Total number of ants	1.3357599	0.3130616	5.2678384	3.6431991

c)

Warming*Sex

Dependent variable	Least square mean N,F	Least square mean N,M	Least square mean Y,F	Least square mean Y,M
Proportion growth on longest axis	0.28318636	0.34783761	0.23442105	0.38741202
Proportion growth of tallest inflorescence	1.633367	1.3692706	1.705345	1.1677407
Total number of aphids Week 1	4.8828775	3.6075526	4.7961759	3.70245813
Total number of aphids Week 2	5.5020213	4.4443219	6.5757166	4.0366685
Total growth of colony	0.6191438	0.8367693	1.7795407	0.3340872
Average number of aphids Week 1	1.8442533	1.3067953	1.6634295	1.4809015
Average number of aphids Week 2	2.1003024	1.6535774	2.2306585	1.6600823
Average growth of colony	0.2560491	0.34678207	0.567229	0.17918076
Total number of ants	3.7013816	2.4239811	2.9022167	1.5322796

Table 4: F-ratios and P-values of interactions between a) early snowmelt and warming, b) early snowmelt and sex, and c) warming and sex. Statistically significant P-values are denoted with *.

a) Avalanche*Warming

Dependent variable	F-ratio	P-value
Proportion growth on longest axis	1.251	0.2658
Proportion growth of tallest inflorescence	0.1414	0.7078
Total number of aphids Week 1	0.3783	0.5398
Total number of aphids Week 2	0.0308	0.8609
Total growth of colony	1.2184	0.2721
Average number of aphids Week 1	0.5418	0.4633
Average number of aphids Week 2	0.0033	0.954
Average growth of colony	0.5488	0.4604
Total number of ants	0.0052	0.9425

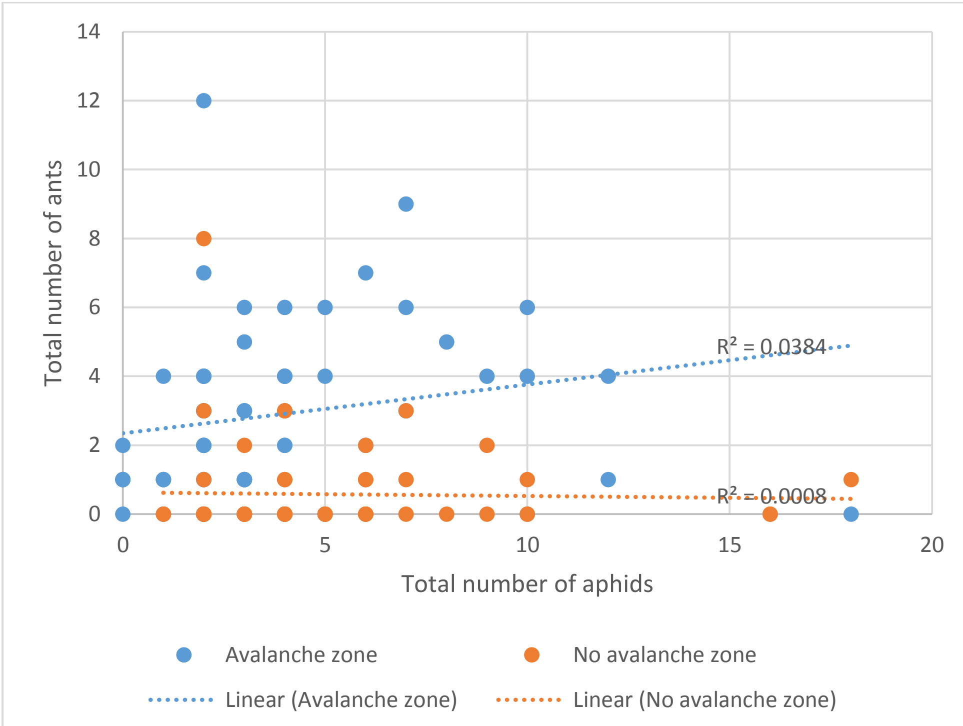
b) Avalanche*Sex

Dependent variable	F-ratio	P-value
Proportion growth on longest axis	0.0617	0.8043
Proportion growth of tallest inflorescence	3.5269	0.0639
Total number of aphids Week 1	1.1975	0.2763
Total number of aphids Week 2	2.114	0.1489
Total growth of colony	0.2356	0.6284
Average number of aphids Week 1	0.0614	0.8047
Average number of aphids Week 2	0.9515	0.3315
Average growth of colony	0.6104	0.4364
Total number of ants	0.2678	0.6059

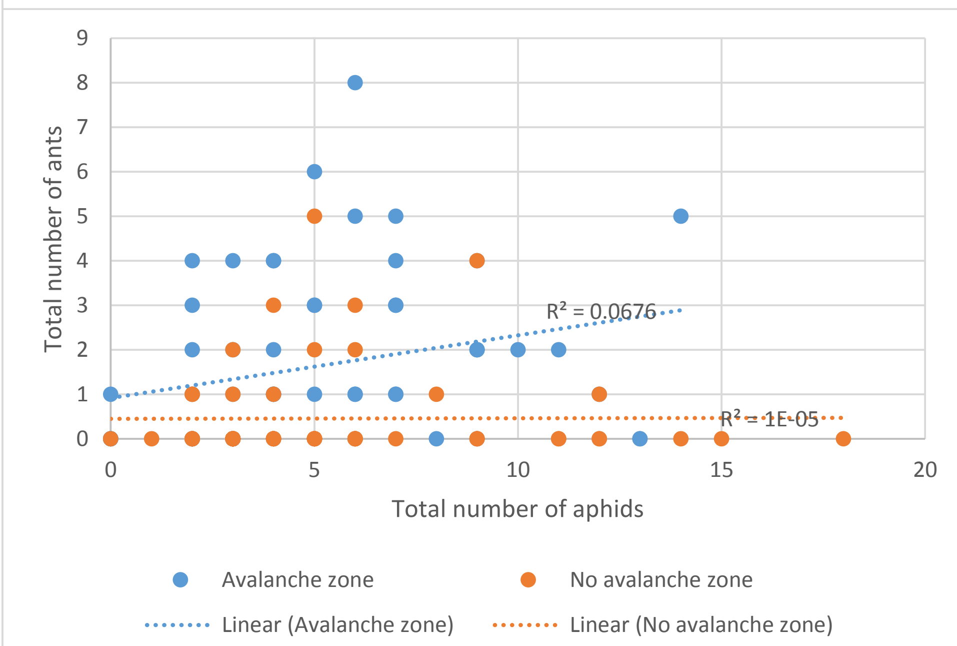
c) Warming*Sex

Dependent variable	F-ratio	P-value
Proportion growth on longest axis	0.7714	0.3817
Proportion growth of tallest inflorescence	0.8248	0.3664
Total number of aphids Week 1	0.0172	0.896
Total number of aphids Week 2	1.1596	0.2839
Total growth of colony	2.8101	0.0966
Average number of aphids Week 1	1.291	0.2584
Average number of aphids Week 2	0.161	0.689
Average growth of colony	2.7966	0.0974
Total number of ants	0.0063	0.9367

Figures

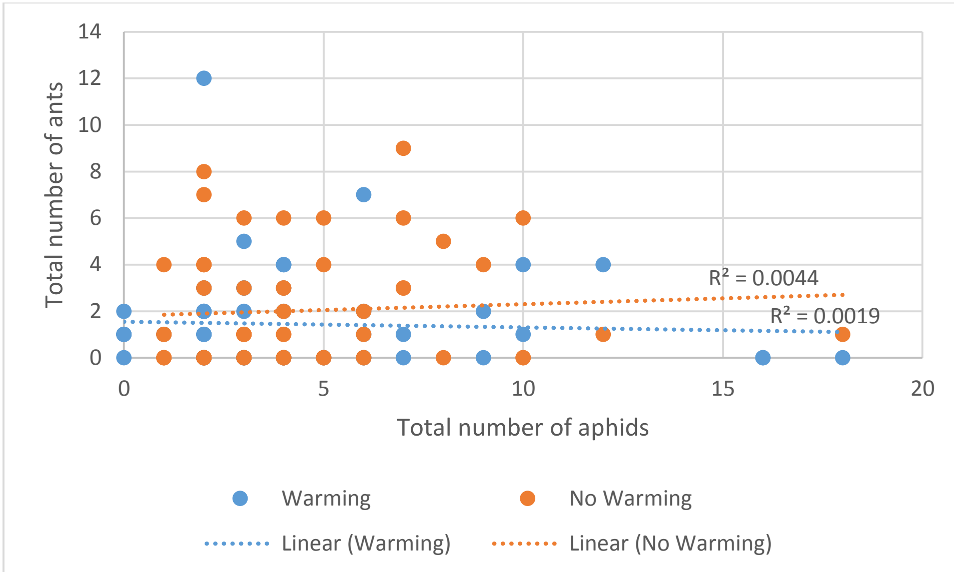


a)

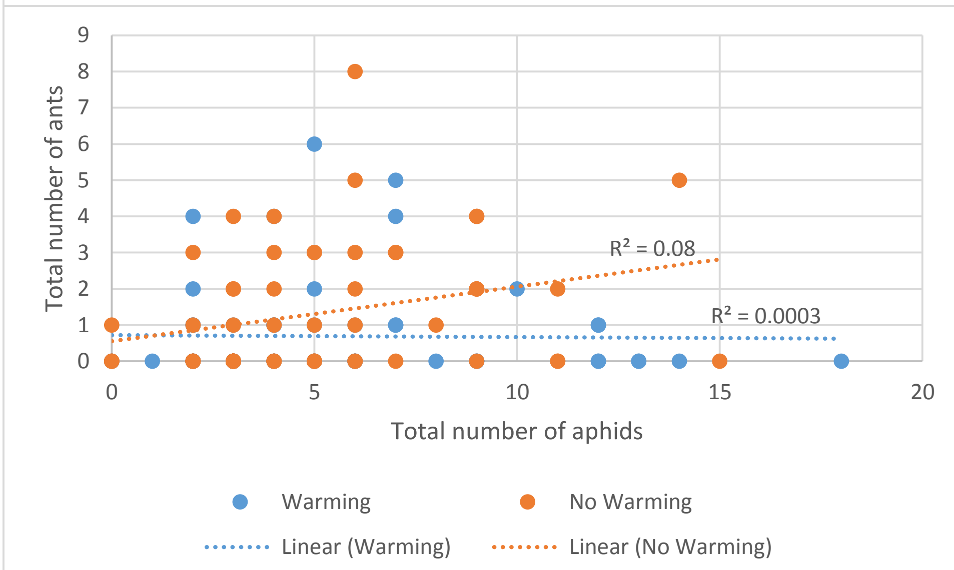


b)

Figure 1: Linear regression analysis of ant and aphid numbers in and out of the avalanche zone for a) Week 1 and b) Week 2

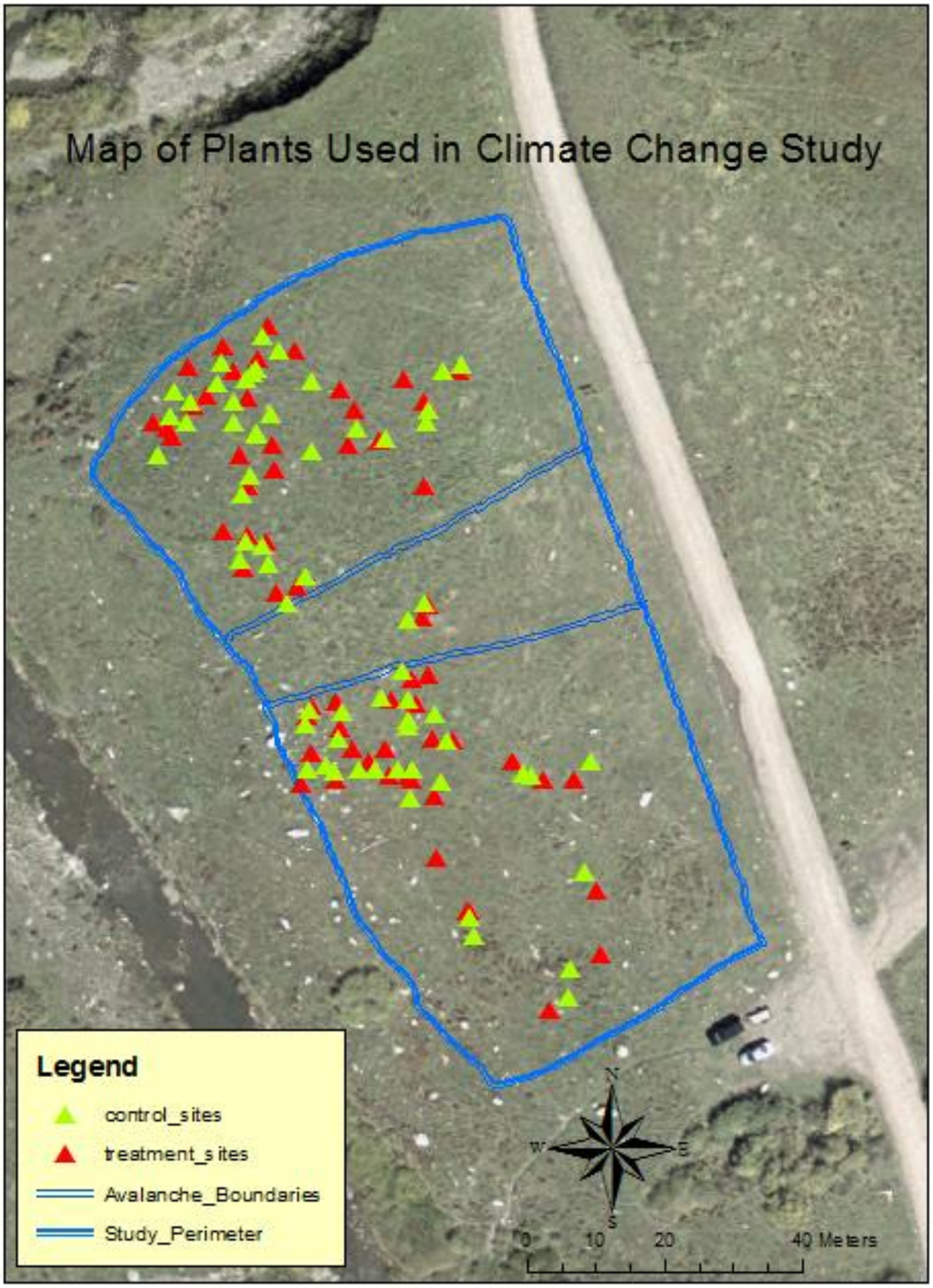


a)



b)

Figure 2: Linear regression analysis of aphid and ant numbers subject to warming and control treatments for a) Week 1 and b) Week 2



Map of Plants Used in Climate Change Study
Legend
control_sites
treatment_sites
Avalanche_Boundaries
Study_Perimeter
N
W
E
S
0
10
20
40 Meters