

Tests for Elevational Gradients in Herbivore Abundance and Plant Resistance in the Rocky Mountain Ecosystem

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ABSTRACT

Community interactions are shaped by the species' traits dependent on an array of biotic and abiotic factors, yet relatively little is understood about the importance of these factors. Plants have been shown to adapt based on *in situ* herbivore pressure and abiotic conditions. As herbivore density is theorized to decrease with elevation, plant resistance to herbivores should thus decrease in response. We surveyed grasshopper communities to document changes in herbivore abundance along an elevational gradient and quantified associated shifts in plant palatability through feeding bioassays with grasshoppers. We related grasshopper abundance to elevation at the community level by surveying at 10 sites along an elevational gradient of 488m and related plant palatability to elevation at the species level through feeding bioassays in the lab. In congruence with the decrease in herbivore abundance with elevation, we observed that high elevation plants experienced almost double the herbivore damage as their low elevation counterparts. Our results suggest that high elevation plant communities are less resistant to herbivores and that this shift in palatability may thus be an outcome of the relaxation to local herbivore density and changes in abiotic conditions associated with elevation.

INTRODUCTION

Herbivores play an essential role in plant evolution¹; many phenotypic plant traits have evolved as defenses against herbivores^{1,2,11}. Herbivory is the most common multicellular interaction on earth,¹ more than half of the planet's multicellular diversity is composed of plants and herbivores, thus herbivory plays a fundamental role in global ecosystem function and biodiversity. Despite the fact that every plant has developed herbivore defense traits³, studies show plant investment in defense is highly variable both within^{1,3,11} and among^{1,3,4,11} plant species. Herbivore defense is costly to plants¹, thus plants are expected to efficiently allocate their energy between their investment in defense and other functions such as growth, competition, and reproduction, based on the amount of herbivory they experience^{1,11}.

Since insects are ectothermic, it is presumed that their abundance and levels of herbivory will decrease at higher elevations^{5,6} where they face harsher temperatures¹³. With these theories in mind, we predict that elevational gradients in herbivore density should result in parallel gradients in plant resistance. Specifically, plants are predicted to invest less in herbivore resistance at higher elevation because of the decrease in herbivore abundance, whereas plants at lower elevation are expected to have adapted to higher levels of herbivory with stronger resistance.

Elevational gradients provide natural experiments to study variance in plant resistance based on changes in biotic and abiotic factors such as herbivore density, nutrient availability and physical stress⁵. However, despite previous observations of herbivore density decreasing with elevation, and the prediction that plant defense should in turn decrease, evidence has been equivocal, based upon two proposed mechanisms. First, the resource availability hypothesis (RAH) states that the cost of herbivorous damage is high when resources are limited^{1,2}. Thus at higher elevations where resources are scarce, according to the RAH, plants should invest more in defense¹. Second, plant adaptations to harsh physical conditions (ie. extreme winds create tougher leaves) may result in traits that indirectly make plants less palatable to herbivores⁷. Whether high elevation is associated with lower plant resistance, or higher plant palatability, will thus depend on the influence of not only herbivory, but also resource availability and other abiotic stressors¹¹. Since relatively little is understood about the interactions and the effects of these factors along elevational gradients, additional case studies are required and encouraged to arrive at a general understanding of these processes.

In this study, we documented patterns of herbivore density and plant resistance along an elevational gradient of 488m around the Rocky Mountain Biological Laboratory in Colorado, USA to determine if these conditions decrease with elevation. Specifically, we tested for an elevational gradient in grasshopper density by conducting surveys at 10 sites along the elevational gradient, and in plant palatability by conducting grasshopper feeding bioassays in the lab. This study contributes valuable insight as climate warming is expected to drive insect herbivores upslope⁸, thus it is more important now than ever to understand the community-level interactions along elevational gradients and how local adaptations may have effects on such. This study is merely a first exploration of these questions regarding the Rocky Mountain ecosystem and we encourage future studies to focus on the role of herbivory, plant defense, and other multi-dimensional environmental factors in these highly complex communities along elevational gradients.

METHODS

Study System

We selected ten rocky meadow sites in the East River Valley in Colorado, USA (Fig. 1). Grasshoppers (*Orthoptera: Caelifera*) are useful herbivores to study as they are dietary generalists⁹, abundant in Rocky Mountain ecosystems, and span along a wide range of elevations. We surveyed a natural variety of grasshopper species and used *Melanoplus borealis* for our feeding trials. Our focus was set on the plant species *Erigeron speciosus*, *Fragaria*

virginiana, *Helianthella quinquenervis*, *Potentilla pulcherrima*, and *Delphinium nuttallianum*, as they are abundant and widely dispersed in the East River Valley.

Grasshopper Abundance Surveys

We conducted grasshopper inventory surveys along an elevational gradient of 488 m (from 2872m to 3360m). This difference in elevation encompasses a natural variety of conditions for plants such as herbivore density, resource availability and abiotic stress, although this study only focuses on herbivore density. Within each of our 10 meadow sites, we randomly selected 2 plots that had similar microenvironments in regards to vegetation cover, vegetation height, and rock presence for each date we surveyed. We surveyed each site 4 times between June 29, 2021 and July 28, 2021 so we could incorporate changes in abundance over time into our analysis. To survey for grasshopper abundance, we consistently swept an insect net over the vegetation of two 4m² plots for 3 minutes, recorded the total number of grasshoppers we caught and their individual lengths, which we used as an indicator of biomass, then returned the grasshoppers to the site at which they were collected. Surveys were conducted no earlier than 10:00am to avoid the concern that grasshoppers were not active in cooler, wet conditions. These methods allowed us to define patterns of herbivore density along the elevational gradient.

Feeding Bioassays

We conducted two feeding experiments to test the effects of plant elevation on herbivory. The feeding experiments were conducted using *Melanoplus borealis* and the five plant species *Erigeron speciosus*, *Fragaria virginiana*, *Helianthella quinquenervis*, *Potentilla pulcherrima*, and *Delphinium nuttallianum*. For each trial, we used 1/2 inch circular disks from leaves that were previously undamaged and came from a plant that had little overall herbivore damage. We assume that the leaves with more herbivore damage are less defended against herbivores, and that those with less damage have developed resistance.

Our first feeding experiment, which we will refer to as the multi-species experiment, allowed 16 low elevation grasshoppers to feed on three leaf disks of each plant species from high (3360m) and low elevation (2872m) for a total of 10 leaves with 3 leaf disks each for 30 leaf disks total. Each grasshopper was in its own cafeteria tray and each trial was monitored and photographed as it progressed. We extracted herbivory data after the equivalent of approximately 5 leaf disks had been consumed. In addition, we measured leaf dry matter content (LDMC) and leaf mass area (LMA) of every leaf used in our first feeding experiment to see if elevation had an effect on these traits.

In our second feeding experiment, which we'll refer to as the single-species experiment, we tested the effect of elevation more directly. For this experiment, we used 50 grasshoppers, 25 from high elevation (3360m) and 25 from low (2886m), and each had the option to feed on one leaf from high elevation (3360m) and one from low elevation (2872m) of a single plant species for 6 leaf disks total. Each plant species was in 10 trials, 5 each with high-

and low-elevation grasshoppers. We pulled data from the single-species trials 17 hours after their start.

Statistical Analyses

Grasshopper surveys: To test for the effect of elevation on grasshoppers, we modeled grasshopper abundance and total biomass as dependent upon the fixed effects of elevation and survey date, with site included as a random effect to account for the fact that we were returning to the same sites. The residuals of these analyses met assumptions of normality.

Feeding trials: We modeled the percent of herbivory for the multi-species experiment as dependent upon the fixed effects of plant species, elevation, and their interaction, with the cafeteria tray included as a random effect. For the single-species experiment, we modeled the percent of herbivory as dependent upon the fixed effects of plant species, plant elevation, grasshopper elevation and the interactions of each of these effects, with cafeteria tray included as a random effect. In both analyses, the dependent variable herbivory was log +1 transformed to meet assumptions of normally distributed residuals.

Leaf traits: To test for the effects of elevation on plant leaf traits we modeled LDMA and LMA as dependent upon plant species, elevation and their interaction. The residuals of these analyses met assumptions of normality.

All statistical analyses were conducted using the "car" package in R 4.1.0 (R Core Team, 2021).

RESULTS

Grasshopper Surveys: We observed significant effects of elevation on grasshopper abundance ($P = 0.044$) and biomass ($P = 0.049$) from the grasshopper inventory surveys. The total number of grasshoppers decreased with elevation (slope = -0.014 , std. error = 0.007) (Fig. 2), as did their biomass (slope = -0.132 , sd. error = 0.06) (Fig. 3). Survey date had significant effects on grasshopper abundance ($P = 0.006$) and biomass ($P = 0.022$) where the number of grasshoppers (slope = -0.143 , sd. error = 0.052) and their biomass (slope = -1.027 , sd. error = 0.45) decreased as time progressed (Fig. 4).

Feeding trials: The effect of plant elevation on herbivory was not significant in the multi-species experiment ($P = 0.49$). The effect of plant species was significant ($P < 0.001$), showing that grasshoppers are making choices and have clear preference for the plant species they consume (Fig. 5). The interaction between plant species and elevation was significant from the multi-species experiment ($P = 0.0438$), but this varied among species whether that meant high or low elevation (Fig. 5). *Erigeron speciosus* was the most preferred species with herbivory at 41.8% for high elevation and 77.8% for low. *Helianthella quinquenervis* was second most preferred with herbivory at 51.9% for high elevation and 36.7% for low. Third most preferred was *Potentilla pulcherrima* with herbivory at 5.77% for high elevation and 12.9% for low. *Fragaria virginiana* was fourth most preferred with herbivory at 9.31% for high elevation and 7% for low. Lastly, *Delphinium nuttallianum* faced no herbivory.

The single-species experiment demonstrated a significant effect of plant elevation on herbivory ($P = 0.0013$) (Fig. 6). Grasshoppers consumed almost double the amount of high elevation leaves than their low elevation counterparts. The effect of plant species was marginally significant ($P = 0.0513$), with patterns of plant choice aligning to those from the first feeding trial (Fig. 7). High elevation grasshoppers consumed significantly more than those from low elevation ($P = 0.0048$) (Fig. 8). The interaction of plant species and plant elevation was not significant ($P = 0.86$). The interaction of plant species and grasshopper elevation was not significant ($P = 0.58$). The interaction of plant elevation and grasshopper elevation was not significant ($P = 0.19$). Finally, the interaction of plant species, plant elevation, and grasshopper elevation was not significant ($P = 0.53$).

Leaf traits: The effects of elevation alone on LDMC and LMA were not significant ($P = 0.73$, $P = 0.12$, respectively) (Fig. 10–11). The effects of plant species on LDMC and LMA were significant (both had P values < 0.001) (Fig. 10–11). For LDMC, the interaction between elevation and species was not significant ($P = 0.74$) (Fig. 10). For LMA, the interaction between elevation and species was significant ($P = 0.002$) with elevation resulting in both increases and decreases among species (Fig. 11).

DISCUSSION

As predicted by theory, we observed decreases in grasshopper abundance and plant resistance with elevation. Grasshopper count and biomass decrease significantly with elevation. The multi-species experiment clearly showed grasshoppers' plant preference, but the results were inconclusive on elevational difference in resistance. However, the effect of plant elevation was clear from the single-species experiment, which was designed to better detect these effects, with herbivory being nearly double for high vs. low elevation leaves. The effect of plant species was marginally significant and aligned with plant preference from the multi-species experiment. Grasshopper elevation had a significant effect on herbivory; high elevation grasshoppers consumed more than low elevation grasshoppers, but we do not have supporting evidence to draw a conclusion for why this may be. Since the effect of elevation was not significant for LDMC or LMA, we can assume that these traits did not affect grasshopper preference. Since grasshoppers were given the option to feed on plant leaves from both high and low elevation, we can infer that the leaves with more herbivorous damage are less resistant to herbivores. Thus, high elevation plants are less resistant. These results align with the decrease in herbivore abundance at higher elevations since plants are expected to allocate their resources effectively between defense and other functions based on the amount of herbivory they experience. We can infer that the lower resistance shown by high elevation plants is a result of their adaptive relaxation to *in situ* herbivore density. Since climate warming is expected to drive insect herbivore communities up-slope, these findings provide critical insight as to how the local adaptation of plants may inhibit a rapid response to changes in community composition brought by climate change.

Consistent with past studies, we found a decrease in grasshopper abundance with elevation, although it appears factors aside from elevation may be at play here. Our highest elevation site in North Pole Basin (3360m) had lower grasshopper abundance than our low

elevation sites, as expected, but higher abundance than the other 4 high elevation sites north of Schofield Pass. We know temperature is one of the leading abiotic factors to affect insect herbivore development, dispersal, range, and survival¹², so it is expected that the grasshoppers would be less abundant at our high elevation sites¹³. However, biotic factors such as plant community composition and predation¹⁷, as well as other abiotic factors such as precipitation, wind current and velocity, and nutrient availability have also been shown to affect grasshopper dispersal and abundance along elevational gradients.¹² For example, Prinster et. al. observed that the abundance of dispersing grasshoppers along a gradient declined 4-fold from their low to high elevation sites and increased with warmer conditions and when wind flow patterns were mild or in the downslope direction¹². In addition, water availability has been shown to have an effect on herbivore dispersal and consumption¹⁶. In their study of herbivory along an elevational gradient in New Guinea, Sam et. al. found that vegetation at the climatically most favorable elevations where water is abundant, and temperatures are still relatively warm, suffers the maximum amount of herbivorous damage, and that the damage changes seasonally, reflecting the water availability¹⁶. With that in mind, we can guess that the water availability, or the snowmelt, stream, and lake system, at North Pole Basin plays a factor in the herbivore pressure, but further supporting data are required to reach this consensus. Thus, we know grasshoppers are less abundant at higher elevations, but we do not have enough supporting evidence to draw any conclusions as to why and encourage more case studies on the biotic and abiotic factors that influence grasshopper dispersal.

The feeding bioassays revealed clear, consistent grasshopper preference for plant species, demonstrating that our cafeteria method worked. Although our two feeding bioassays differed in outcome, collectively these results suggest that high elevation plants have lower resistance to herbivores. The nature of the first, multi-species experiment makes it hard to detect plant elevation effects since the grasshoppers had so many options, but the strong preferences among species mirrors that of the second, single-species experiment where we indeed found significant effects of elevation within plant species. Descombes et.al. address concerns of grasshoppers' local adaptation to plant selection by using larvae of the African cotton leafworm (*S. littoralis*) in their feeding bioassays⁵, but our high and low elevation grasshoppers demonstrated the same preferences, eliminating this potential conflict. In addition, other studies indicate LDMC and LMA as leaf traits that matter. Although LDMC has previously been shown to have positive correspondence to leaf toughness¹⁴, which in turn makes leaves less palatable to chewing insect herbivores, we found no consistent variation in means of LDMC and LMA for high vs. low elevation leaves. Our results support the findings of Descombes et. al., that leaf variables such as leaf toughness (represented by LDMC and SLA) were not associated with plant palatability. We did find a significant effect of the interaction between plant species and elevation on LMA, but whether it was regarding a high or low elevation leaf was variable, so this does not apply to our question.

Both high and low elevation grasshoppers preferred high elevation plants over low, but the high elevation grasshoppers consumed significantly more than their low elevation counterparts. We do not have enough supporting information to draw any concrete conclusions on why this may be, but we can say that all of our grasshoppers were relatively the same size and that those from high elevation were behind phenologically and were not winged

adults (Fig. 9). Ibanez et. al. suggest that functional traits of grasshoppers may affect their plant preference; for example, they found that the incisive strength of grasshoppers was positively correlated to the toughness of the leaves they preferred¹⁵. So, future studies on the functional traits of multiple grasshopper species could provide more definitive insight to this discrepancy in grasshopper consumption along elevational gradients.

Consistent with theory and our elevation survey results, we observed a decrease in plant resistance with elevation. Similarly, Pellissier et. al. found that on-site plant resistance to herbivores is a combination of short-term responses to temperature and the cumulative effect of long-term adaptive responses to local herbivory pressure¹³. Although many studies of plant and insect herbivore dynamics along elevation have shown similar patterns to ours, recent studies have rightfully questioned this paradigm, stating that it oversimplifies highly complex community dynamics that are constantly adapting to an array of biotic and abiotic factors along elevational gradients¹¹. For example, it is not entirely clear if the decrease in plant resistance we found at higher elevations is a result of the decrease in herbivore pressure or rather the plants' phenotypic adaptations to climate variation that have indirect consequences for herbivores. To understand this, we'd need to look further into the plant adaptations that could affect herbivores and to evaluate whether those traits may be expected to be a response to elevation. Although our results were consistent and valuable, since this was a first exploration of these questions in the Rocky Mountain ecosystem, we recognize the relative simplicity of this study and encourage future research to embrace the complexities of multi-dimensional environmental factors at play, such as biotic and abiotic stress and resource and water availability, to better understand elevational gradients and what they may look like in the era of climate change.

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FIGURES AND TABLES

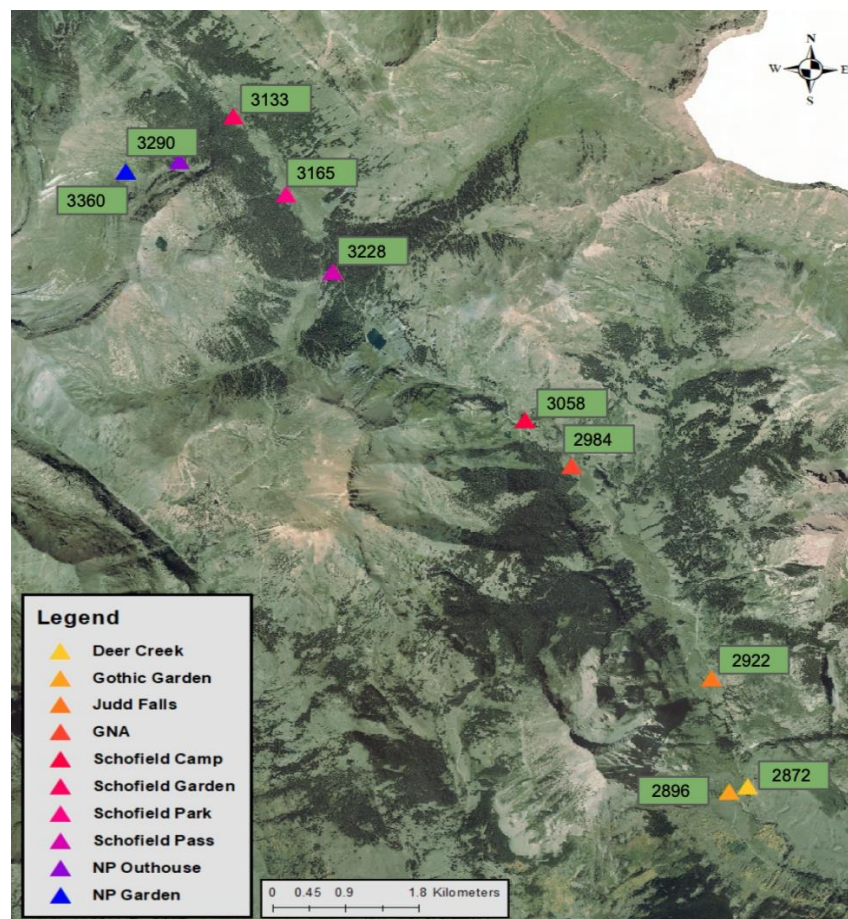


Figure 1. Vicinity map of field sites with their corresponding elevation in meters. Map points are color-coded with purple as the highest elevation and yellow the lowest elevation.

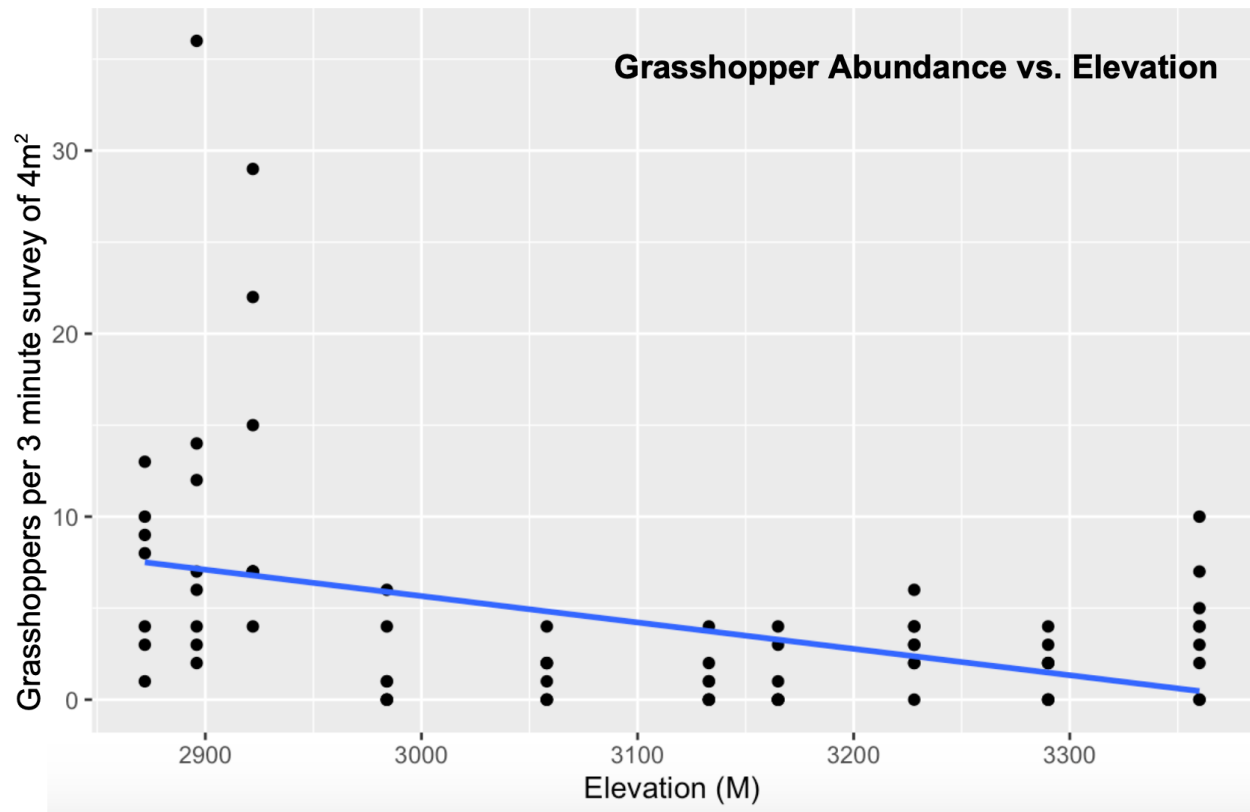


Figure 2. Grasshoppers per 3 minute sweep net survey of 4m² plot as dependent on elevation (P= 0.044). Survey site is included as a random effect. Grasshopper abundance decreases with elevation (slope = -0.014, std. error= 0.007).

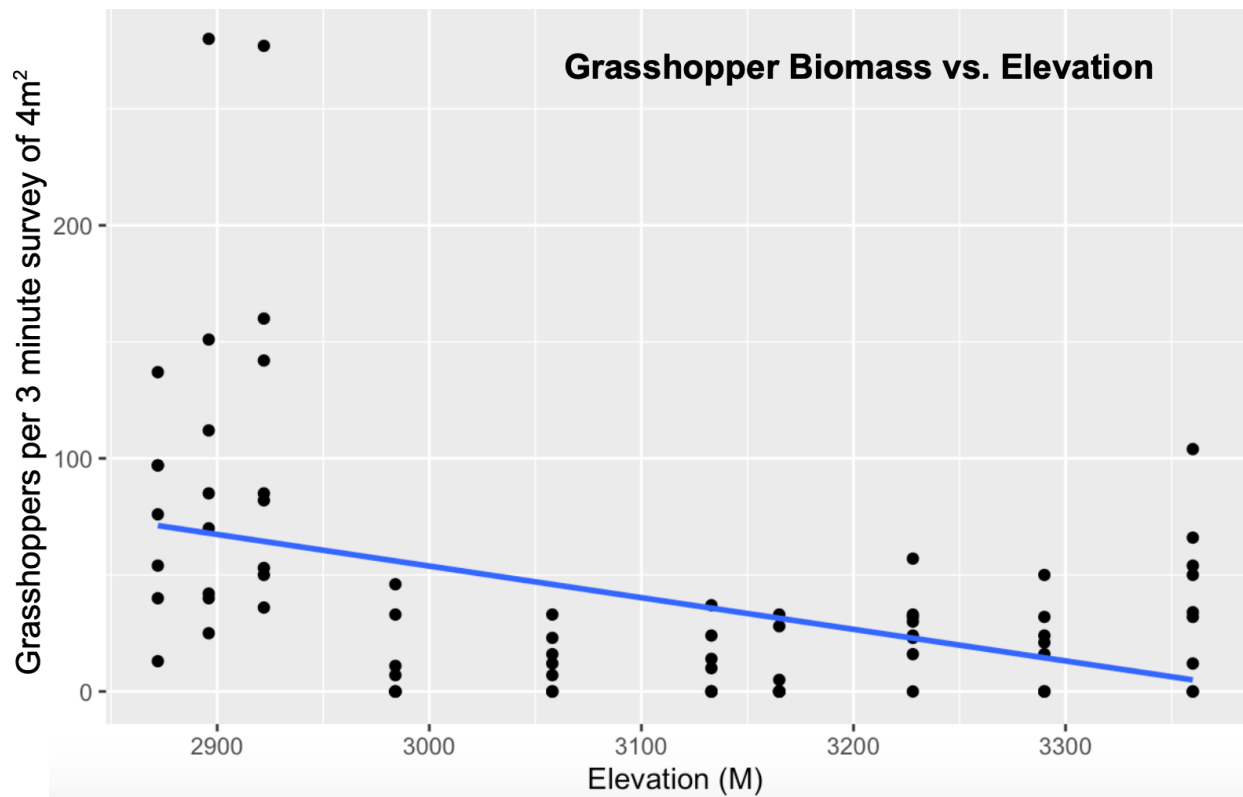


Figure 3. Total length (biomass) of grasshoppers per survey date as dependent on elevation ($P=0.049$). Site is included as a random effect. Grasshopper lengths decrease with elevation (slope= -0.132 , std. error= 0.06).

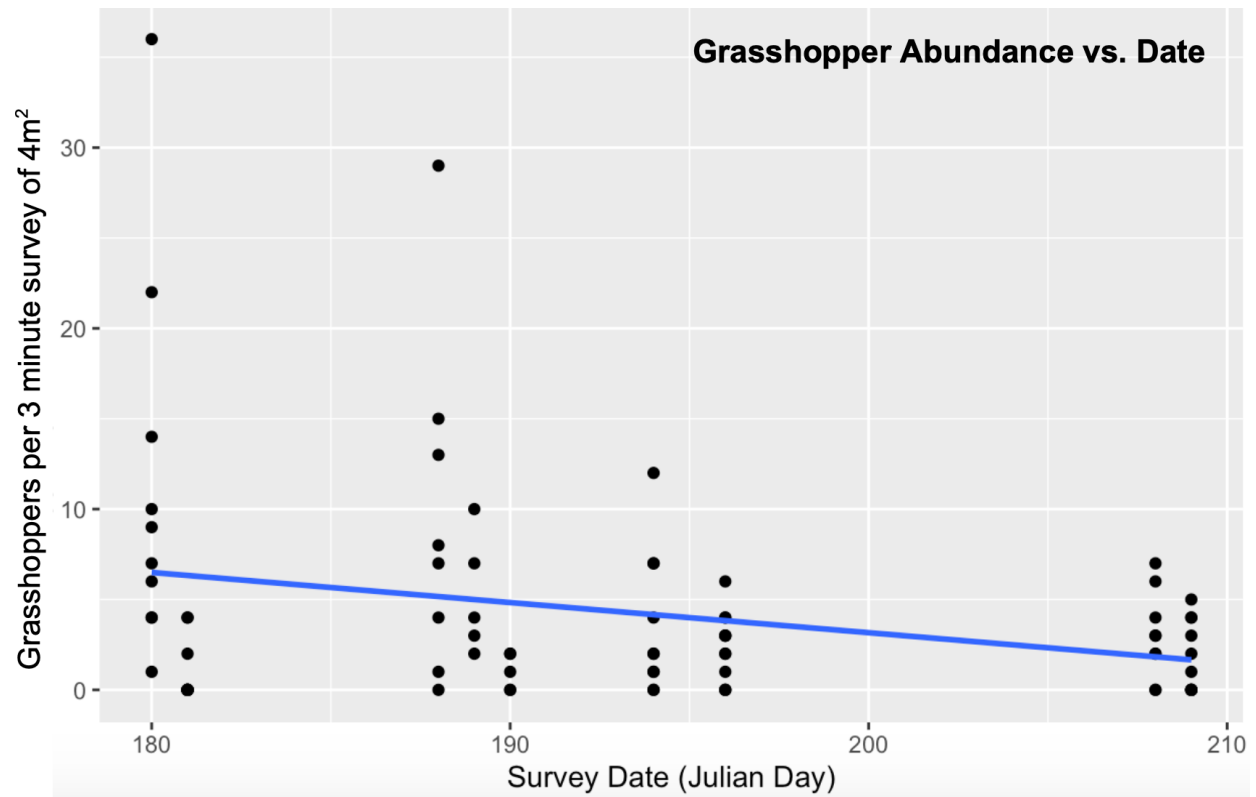


Figure 4. Grasshopper abundance is shown relative to survey date (Julian date calendar)($P=0.006$). Number of grasshoppers decreased with time (slope= -0.143 , std. error= 0.052).

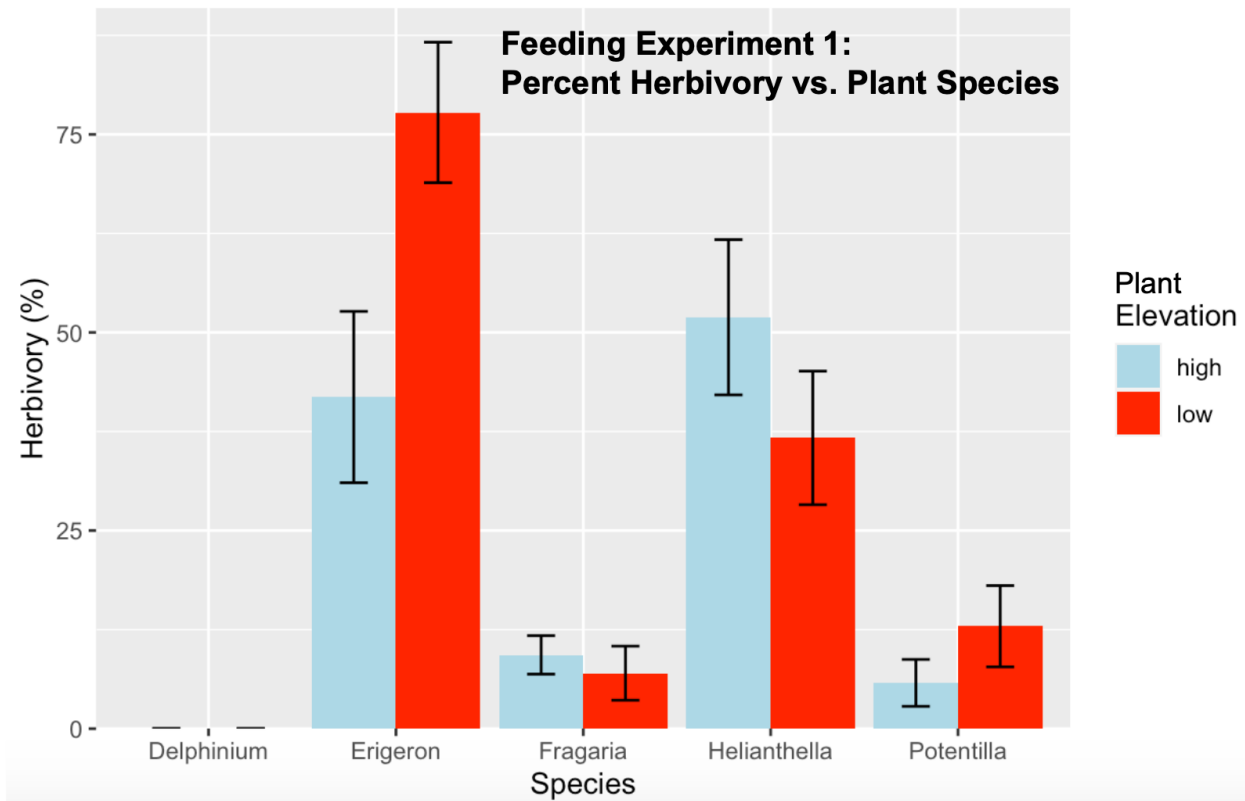


Figure 5. Herbivory (%) from the multi-species feeding experiment as dependent on plant species by elevation. High elevation refers to 3360m and low elevation refers to 2872m. The effect of plant elevation on herbivory is not significant ($P = 0.49$). The effect of plant species is significant ($P < 0.001$). The interaction of plant species and elevation is significant ($P = 0.0438$) but variable.

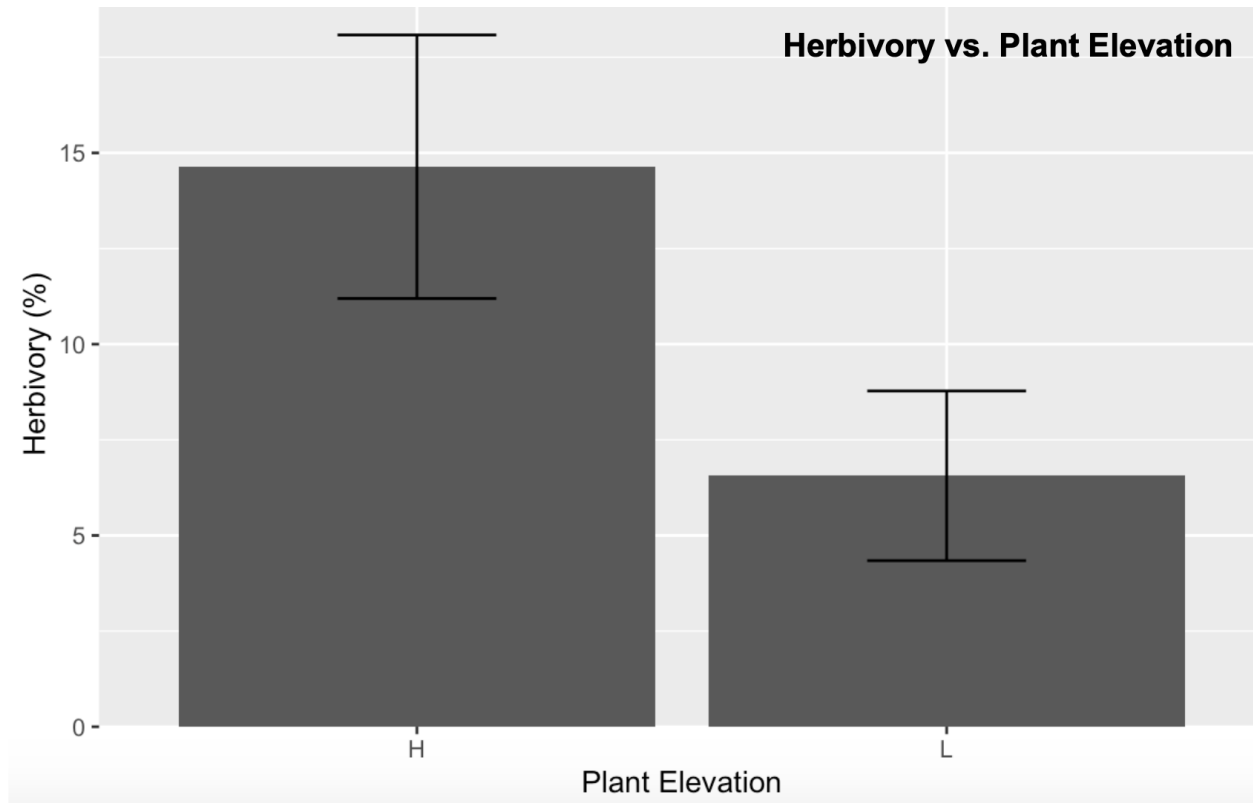


Figure 6. Percent of grasshopper herbivory from single-species feeding experiment as a function of plant elevation. H = high elevation (3360m) and L = low elevation (2872m). The effect of plant elevation is significant ($P= 0.0013$), demonstrating that high elevation plants are more palatable.

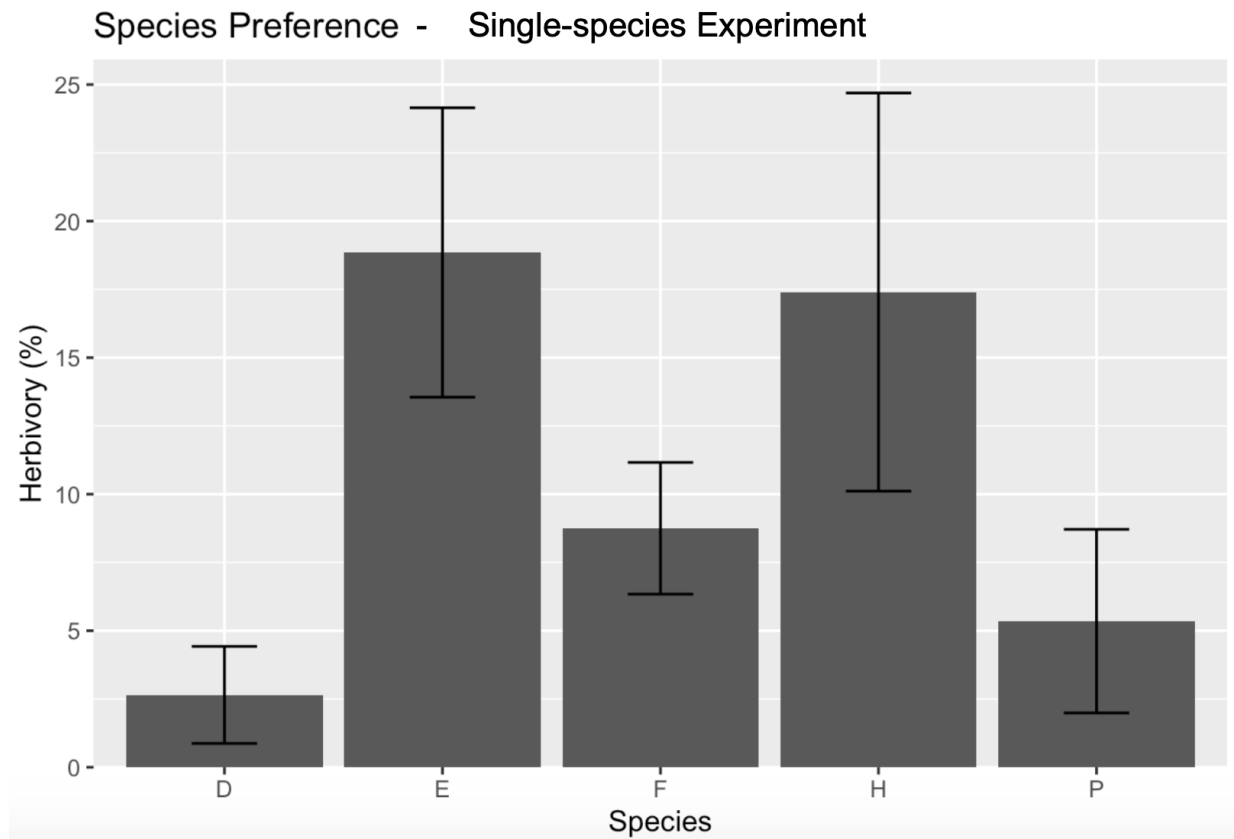


Figure 7. Percent herbivory as a function of plant species from the single-species feeding experiment. D = Delphinium, E = Erigeron, F= Fragaria, H = Helianthella, and P = Potentilla. The effect of plant species was marginally significant ($P= 0.0513$). Patterns of plant choice align to those from the first feeding trial (Figure 5).



Figure 8. Percent herbivory as dependent on grasshopper elevation ($P= 0.0048$). H = high elevation (3360m) and L = low elevation (2872m). High elevation grasshoppers consumed significantly more than low.

Feeding Experiment 2 *Orthoptera Caelifera*



Figure 9. Grasshoppers from the single-species feeding experiment separated by elevation.

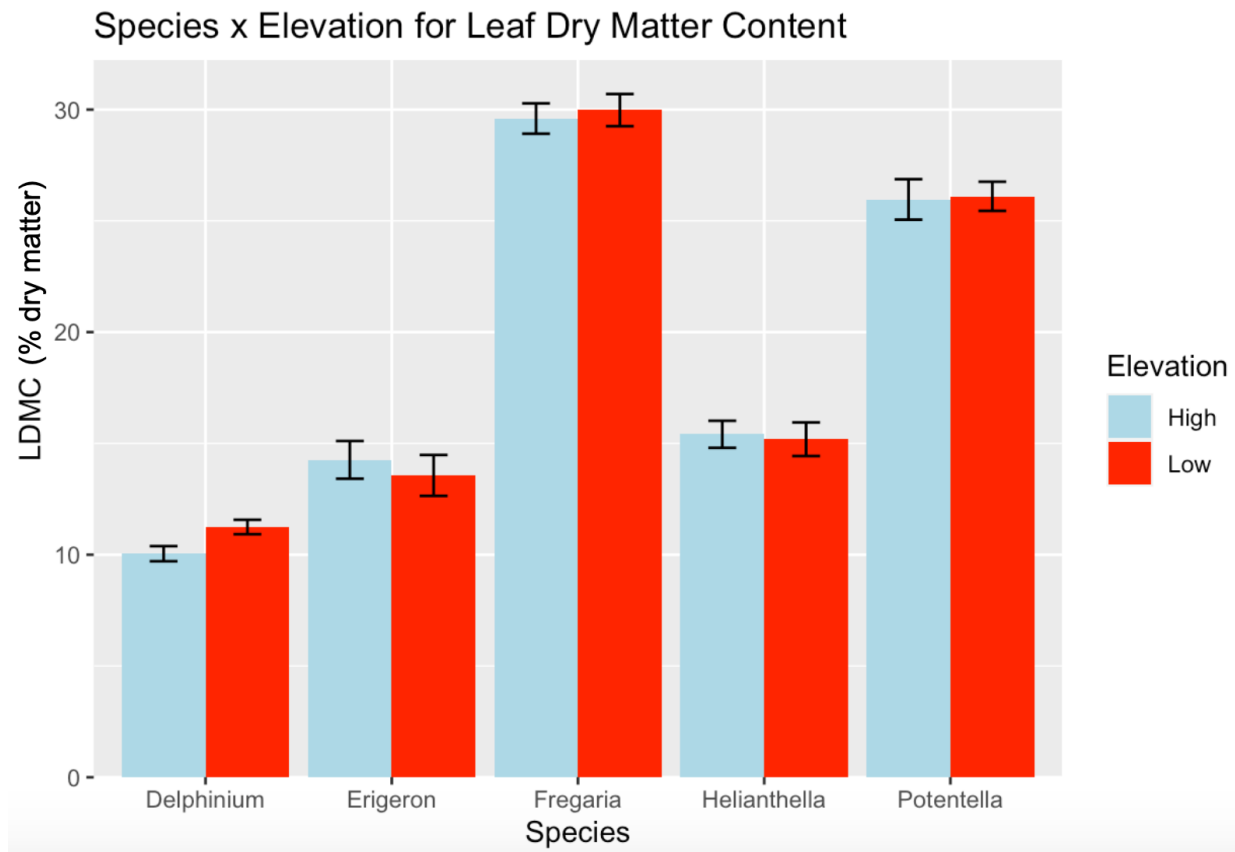


Figure 10. Leaf dry matter content (percent dry matter) for each plant species by elevation. The elevation effect on LDMC was not significant ($P = 0.73$). The elevation and species interaction was not significant ($P = 0.74$).

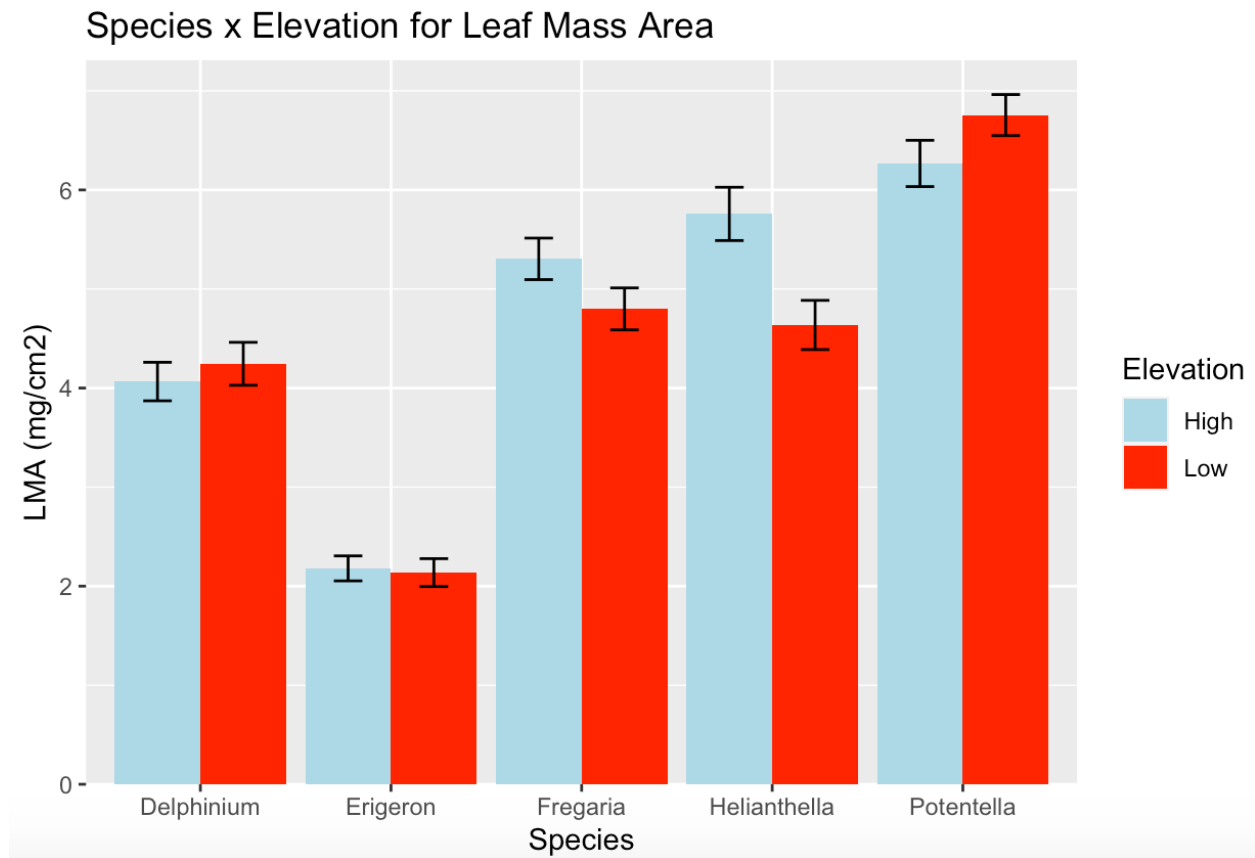


Figure 11. Leaf mass area (mg/cm^2) for each plant species by elevation. The effect of elevation on LMA was not significant ($P = 0.74$). The interaction of species and elevation was significant ($P = 0.002$).