

Climate Change Affects *Boechera stricta* Genotypes Through Local Maladaptation

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Abstract

As environments continue to change, plant communities will increasingly be pressured to adapt to their environment to maintain fitness levels. The most common release of climatic stressor result in range shifts and changes in phenology for plants. *Boechea stricta*, a perennial forb native to a range of elevations in the Rocky Mountains in the western United States, has been study species for adaptation responses from climate change. Already, it has been documented that local maladaptation has occurred for this wild mustard species. Low elevation species adapted *B. stricta* was recorded to do better along an entire elevation gradient than its locally adapted counterparts. This study inquires if, by manipulating snowfall to mimic historic levels, we can reverse the maladaptation in *B. stricta*, and see locally adapted mustards do better than either high or low adapted genotypes. We found that we were able to restore local adaptation of *B. stricta* for all sites in our snow addition treatment. In addition, we saw a continued shift in optimum source elevation to lower elevation genotypes. However, with notably high mortality rates among all gardens on all treatments, more than one climatic factor needs to be changed for there to be any lasting impact on these local adaptations.

Key Words: *Boechea stricta*, climate change, elevation, germination

Climate Change and Plant Adaption

Rapid environmental changes are significantly altering necessary plant processes such as phenology and germination rates (Anderson, Lee, & Mitchell-Olds 2011, Pearson & Dawson 2003). Plants are responding to climate change in patterns that can be seen largely through changes in phenology and range shifts (Parmesan 2006). These changes in phenology and range shifts affect the specific local adaptations of certain plants. As temperatures continue to rise and precipitation rates decrease, plants are pressured to adapt as fast as possible to the changing environment to maintain their fitness levels. One of the consequences of environmental change is the movement of species to higher elevations when the climate they are adapted for is displaced (Jump et al. 2005). This movement is harmful to the biodiversity of elevational gradients. As better adapted plants move up a mountain, they can compete with plants that are not as well adapted when the temperatures rise. In this case, more plant populations will move along an increasing elevational gradient to alleviate climatic stressors (Davis & Shaw 2001).

As environmental variation increases, phenotypic plasticity could help plants assimilate to their new climate or support their range shifts. Understanding plastic responses is crucial for predicting and managing the effects of climate change on native species as well as crop plants. Though scientists argue whether plasticity or adaption is more important for maintaining plant fitness in the face of rapid climate change, phenotypic plasticity can provide a buffer against rapid climate change and assist rapid adaption (Lande 2009, Chevin et al. 2010).

Members of the Brassicaceae family have become increasingly important for ecological research over the past two decades (Verkerk et al., 2009). Some plants in the Brassicaceae, such as *Boechea stricta*, show high levels of heritable within-species variation (Rushworth et al. 2011, Prasad et al. 2012).

Hence, they provide rich opportunities to investigate how natural selection may act to maintain natural phenotypic and genetic variation. To date, the ecological and evolutionary processes that maintain natural diversity have remained unknown or poorly understood (Pierterse and Dicke 2007).

In a study done on *B. stricta* by the Anderson lab at RMBL, observations of local maladaptation were found, even under control conditions. They found a negative linear relationship between fitness and elevation of origin of *B. stricta*. These observations of maladaptation motivated the snow addition project. The experiment is designed to test whether we can detect patterns more consistent with local adaption under conditions that were less affected by climate change, as opposed to the patterns shown in Figure 2. By comparing seed germination in snow addition to control treatments, we can test whether climate change has already disrupted local adaptation. In addition, by comparing snow addition + control to snow removal, we can test whether local maladaptation will become more severe as climatic conditions continue to rapidly change.

Methods

Study Organism

Boechnera stricta (Brassicaceae) is a native mustard species inhabiting a broad range of elevations in the Rocky Mountains of North America (Anderson et al. 2015). Because it is primarily self-pollinating and has variation in different habitats, *B. stricta* is an exceptional study organism for understanding the role of environment on phenotypic plasticity through adaptation.

In Fall 2016, the Anderson lab planted 17,755 seeds representing 100 genotypes from 50 populations that reflect the extent of the distribution of *Boechnera stricta* in Gothic Valley. Approximately 3550 seeds were planted in each of five established gardens spanning an elevational gradient (Estess 2540m, Peanut Mine 2710m, Gothic 2884m, Schofield 3133m, and North Pole 3340 m) (Figure 1.). They planted the seeds into grids that were subsequently placed in one of three treatments in each garden: control (ambient snowpack), early snow removal, or delayed snowmelt. The early snow removal treatment was imposed by shoveling snow from above designated grids prior to the natural onset of snowmelt (Figure 3). The delayed snow melt treatment was imposed by placing large, bottomless barrels above grids, which collect more snow, delay snow melt, and maintain increased soil moisture relative to ambient conditions.

Statistical Analysis

All statistical analyses were done in SAS, a statistical program. We summarized the total number of seeds planted and germinated for each garden and treatment, sources elevation, garden elevation, and created a dataset with that information. With the data collected, Germination Success was calculated by taking the total number of germinants in a grid divided by the total number of seeds planted in that grid. In addition, the Elevational Difference was calculated. This was done by taking the source elevation of the *Boechnera stricta* genotype and subtracting the garden elevation from it. We then

ran a logistic regression, modeling germination success as a function of treatment, garden, garden by treatment, linear and quadratic effects of elevational difference, and treatment by elevational difference (Table 1). The model included random effect for planted genotype nested within source population. We used a binomial distribution with a logit link in Proc Glimmix. We then noted the Germination Success for each Garden by Treatment pair (Table 2, Figure 2). A Tukey's post-hoc test was then run to view comparisons between Treatments and Gardens.

Results

For our hypothesis, we were testing to see if the differences in garden and treatment resulted in a difference of seed germination success. We ran a logistic regression on the data that we received using the methods outlined above (Table 1). We found that the effect of treatment varied by garden. Specifically, we found that germination success was increased by Snow Addition treatment in Estess, Peanut Mine, and Gothic gardens. Germination success was decreased in North Pole and Schofield garden. Snow removal treatment increased the germination success in North Pole and Schofield, and decreased success in Estess, Peanut Mine, and Gothic gardens. As a result, we were able to support our hypothesis that seed germination success would have been significantly different between the different gardens and treatments.

In addition, we found significant linear and quadratic interactions between elevational difference and treatment. For snow addition, there is a quadratic relationship with elevational difference ($t_{1382} = -4.06$, $p < 0.0001$, Figure 3). Under our control treatment, there was no statistical indication of a linear or quadratic relationship with elevational difference in our model (Figure 4). Under the Snow Removal treatment, there is also a quadratic relationship with elevational difference ($t_{1382} = -5.97$, $p < 0.0001$, Figure 5).

Discussion

Our results show that seed germination success can vary along an elevational gradient dependent on climate through snow removal, ambient, and snow addition treatments. The climate surrounding an organism, like *Boechera stricta*, can depict the survival, fitness, and, thus, the local adaptation of the organism. In our case, the treatments given to the *B. stricta* plants had heavy impact on their seedling germination and survival rates in all of our gardens. Specifically, Figure 2 shows the relationship between seedling germination success of *B. stricta* and garden by treatment. Snow addition to the plots increased the germination for our lower elevation gardens (Estess, Peanut Mine, and Gothic), but it decreased germination success in the upper gardens (Schofield & North Pole). For the lower gardens, this was expected. The snow addition increases the snow, delays snowmelt, and increases soil temperature which are all indicative to plant success through increased intake of water by the plant. However, the inhibition of germination success at our high elevation gardens was unexpected. We hypothesize that this may be due to differences in seed dormancy rates between the elevations.

With higher elevation may come lower seed dormancy rates, which could in turn decrease the germination of seeds as growing season is postponed.

In terms of local adaptation, we saw significant linear and quadratic interactions between elevational difference and treatment. For our Snow Addition treatment, Figure 3 shows a quadratic relationship primarily centered around an elevational difference of 0. This peak germination success relationship is demonstrative of local adaptation. This indicated that the local genotypes have a fitness advantage over both the lower elevation and higher elevation genotypes. Conversely, the control treatment shown in Figure 4 has no significant linear relationship between germination success and elevational difference. This means that across all gardens, no genotypes for specific elevations had an increased fitness over others. In addition, our snow removal treatment in Figure 5 showed a quadratic relationship. However, the peak elevational difference is shifted left indicating that genotypes from lower elevations have a fitness advantage over both local and higher elevation genotypes. As our snow removal treatment is meant to simulate climatic changes, we expected that the lower elevation genotypes would have a fitness advantage over higher elevation genotypes. This relationship is indicative of range shifts of plants to higher elevations to alleviate climatic stressors.

Climate change is affecting more than just one variable in an environment. It does not change just the snow levels, but also the rain levels and temperature. We accounted for snowfall in our experiment, which produced early germination success in the snow addition treatment—achieving results that supported our hypothesis. However, across all gardens and treatments we found record high mortality rates among seedlings. This is to say that one year of heavy snow will not have a lasting impact on local adaptation. We hypothesize that there needs to be a change in more than just one climatic factor to have enduring results on these local adaptations. In the future, studies should be done with added treatments manipulating other factors in addition to those discussed in this paper. Seeing the interaction between increased soil temperature, increased rainfall, and increased snowfall would be imperative to resolving maladaptation in plants.

Literature Cited

Anderson, Jill T., and Zachariah J. Gezon. "Plasticity in functional traits in the context of climate change: a case study of the subalpine forb *Boechera stricta* (Brassicaceae)." *Global change biology* 21.4 (2015): 1689-1703.

Chevin, L-M. et al. (2010) Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLoS Biol.* 8, e1000357

Davis, Margaret B., and Ruth G. Shaw. "Range shifts and adaptive responses to Quaternary climate change." *Science* 292, no. 5517 (2001): 673-679.

Jump, Alistair S., and Josep Penuelas. "Running to stand still: adaptation and the response of plants to rapid climate change." *Ecology Letters* 8, no. 9 (2005): 1010-1020.

Lande, R. (2009) Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. *J. Evol. Biol.* 22, 1435-1446

Parmesan, Camille. "Ecological and evolutionary responses to recent climate change." *Annu. Rev. Ecol. Evol. Syst.* 37 (2006): 637-669.

Pearson, Richard G., and Terence P. Dawson. "Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful?." *Global ecology and biogeography* 12.5 (2003): 361-371.

Pieterse CMJ, Dicke M (2007) Plant interactions with microbes and insects: from molecular mechanisms to ecology. *Trends Plant Sci* 12 564–569

Prasad, Kasavajhala VSK, Bao-Hua Song, Carrie Olson-Manning, Jill T. Anderson, Cheng-Ruei Lee, M. Eric Rushworth, Catherine A., et al. "Boechera, a model system for ecological genomics." *Molecular ecology* 20.23 (2011): 4843-4857.

Verkerk R., Schreiner M., Krumbein A., Ciska E., Holst B., Rowland I., Schrijver R.D., Hansen M., Gerhäuser C., Mithen R. et al. (2009) Glucosinolates in *Brassica* vegetables: The influence of the food supply chain on intake, bioavailability and human health. *Mol. Nutr. Food Res.* 53: S219–S265

Tables and Figures

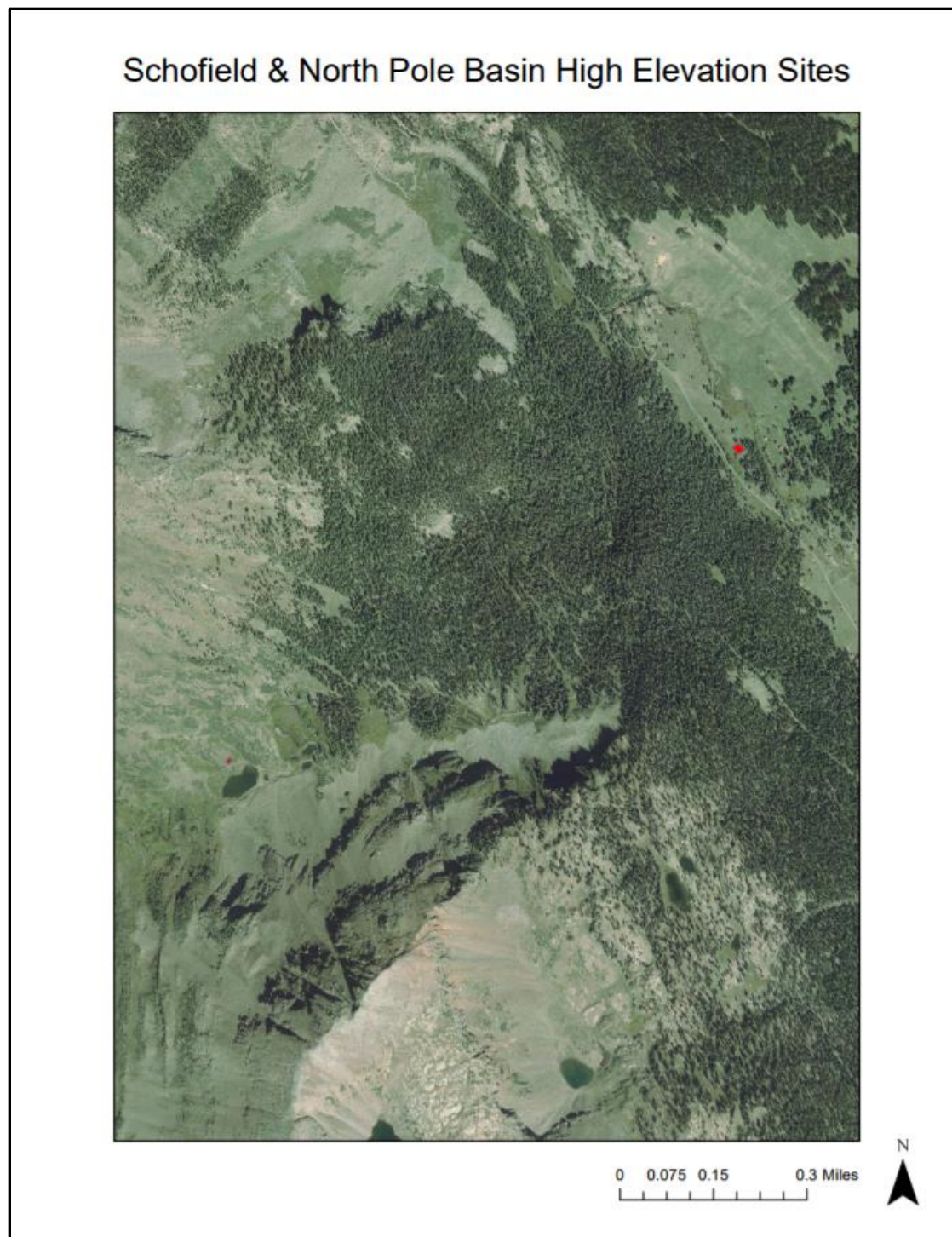


Figure 1. Map of North Pole Basin and Schofield common garden sites denoted by red markers.

Effect	Numerator degrees of freedom	Denominator degrees of freedom	F-value	p-value
Treatment	2	1382	6.72	0.0012
Garden	4	1382	64.48	<.0001
Garden × Treatment	8	1382	30.08	<.0001
Linear Elevational difference	1	1382	2.33	0.127
Quadratic elevational difference	1	1382	38.78	<.0001
Linear Elevational difference×Treatment	2	1382	4.8	0.0084
Quadratic elevational difference×Treatment	2	1382	6.39	0.0017
Genotype nested within population			$\chi^2=830.5$	<0.0001

Table 1.

garden	garden elevation (m)	treatment	Germination success	SE
Estess	2553	Addition	0.0357	0.0068
Estess	2553	Control	0.0122	0.0030
Estess	2553	Removal	0.0089	0.0024
Peanut Mine	2710	Addition	0.1635	0.0181
Peanut Mine	2710	Control	0.0598	0.0082
Peanut Mine	2710	Removal	0.0718	0.0094
Gothic	2890	Addition	0.0805	0.0089
Gothic	2890	Control	0.0652	0.0076
Gothic	2890	Removal	0.0543	0.0065
Schofield	3133	Addition	0.0508	0.0070
Schofield	3133	Control	0.0568	0.0079
Schofield	3133	Removal	0.0751	0.0098
North Pole	3340	Addition	0.0246	0.0050
North Pole	3340	Control	0.1050	0.0175
North Pole	3340	Removal	0.1335	0.0211

Table 2

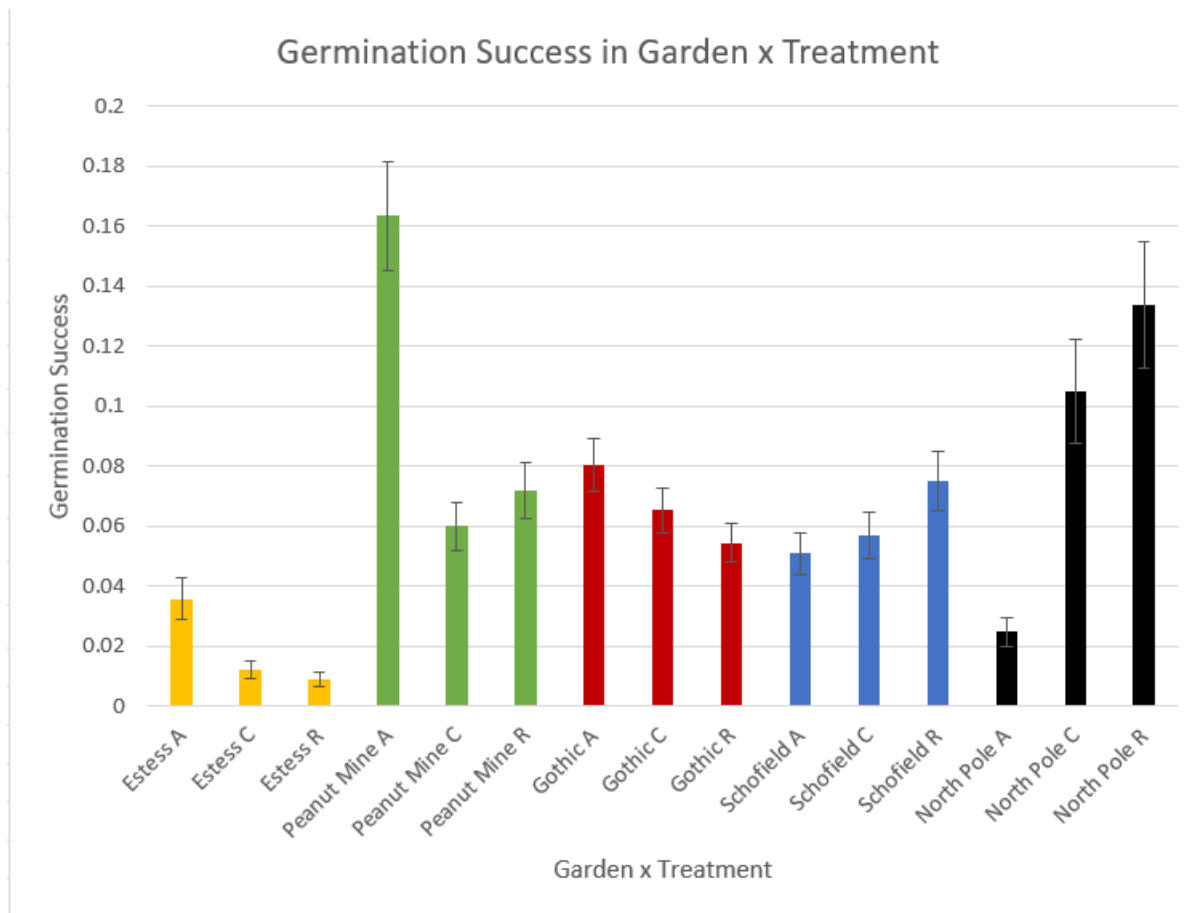


Figure 2. The relationship between Garden by Treatment and Germination Success. The logistic regression done in SAS shows a significant relationship between Garden by Treatment and Germination Success.

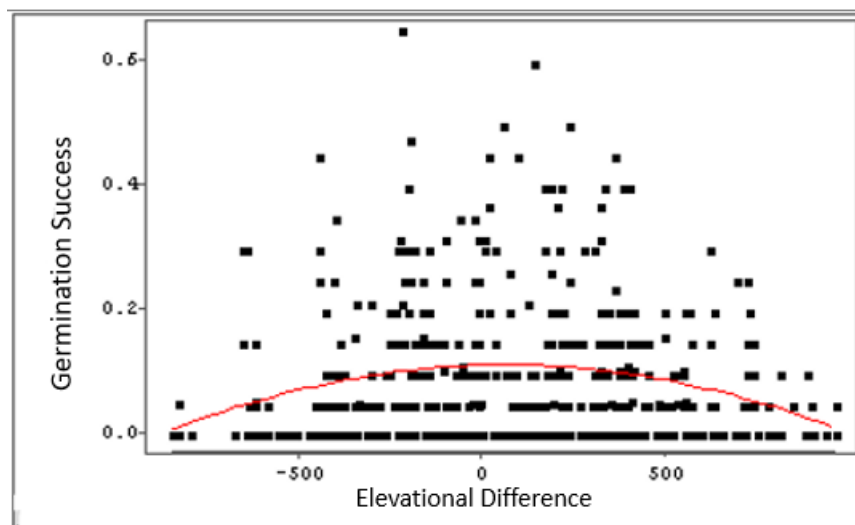


Figure 3. Shows the relationship between Elevational Difference and Germination Success. There is a significant quadratic relationship between Elevational Difference and Germination Success.

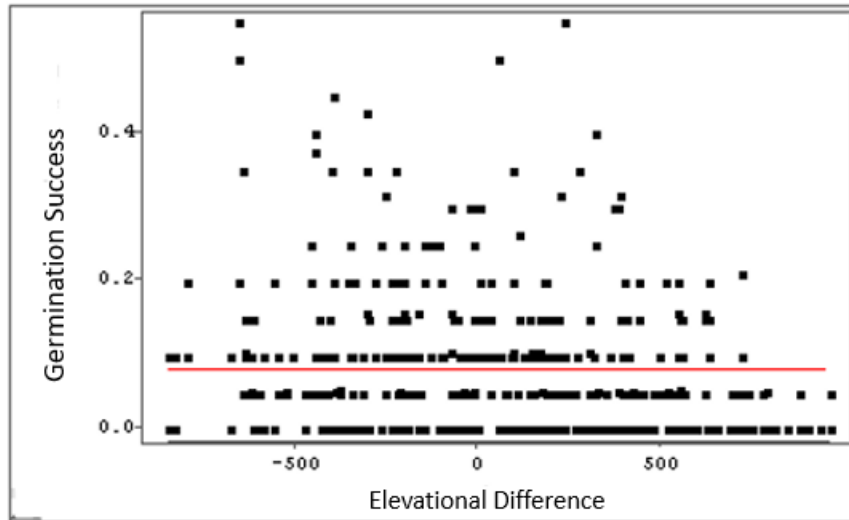


Figure 4. Shows the relationship between Elevational Difference and Germination Success. There is no significant relationship found between Elevational Difference and Germination Success.

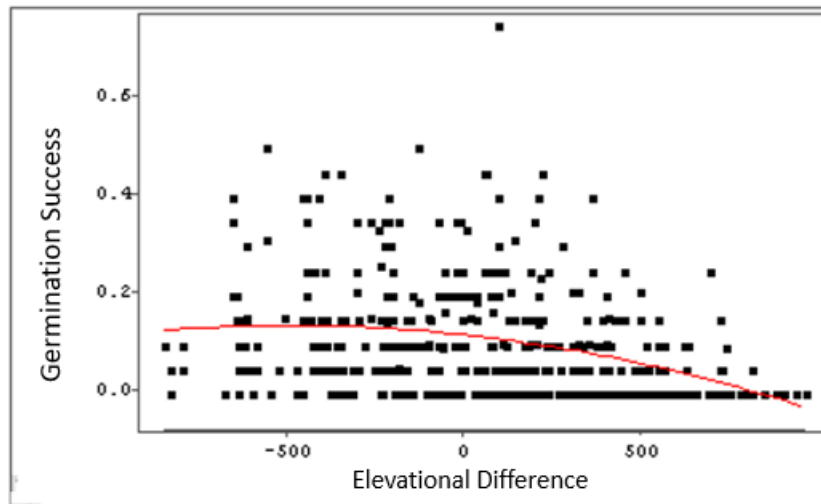


Figure 5. Shows the relationship between Elevational Difference and Germination Success. There is a significant quadratic relationship between Elevational Difference and Germination Success.