

**Effects of abiotic and biotic stress on plant fitness and herbivore defense in
*Boechera stricta***

Allison Carter, UNC-Chapel Hill

RMBL Program: Independent Research and Course

Mentors: Lauren Carley & Tom Mitchell-Olds, Duke University

Abstract

Abiotic and biotic factors influence plant fitness by altering the physical environment and resource availability. According to the stress gradient hypothesis, increasing physical stress in an environment increases positive plant-plant interactions and decreases negative interspecies interactions. I investigated how variance in abiotic stress modifies interactions between the wildflower *Boechera stricta* and its heterospecific plant neighbors. I also tested how heterospecific neighbor density may affect insect herbivory due to associational defenses. I conducted a common garden experiment where the density of neighbor vegetation naturally varied across microsites and rainout shelters were used to manipulate soil moisture. I collected data on *B. stricta* survival, fecundity, and insect herbivory under these varying combinations of drought and neighbor density. I also performed a potted plant experiment with *B. stricta* to isolate the relationship between neighbor vegetation density, herbivore defense, and plant fitness. From early season data in the common garden, I found a significant positive relationship between neighboring vegetation density and survival in *B. stricta*. I also found a significant positive relationship between neighboring vegetation and total fitness in *B. stricta* planted in 2015, suggesting facilitation. Consistent with the stress gradient hypothesis, plants in the rainout plots showed greater facilitation than those in the control plots. However, I found no significant interaction between neighboring vegetation and abiotic conditions (permissive vs. drought-stressed environments). From the potted plant experiment, I found a significant negative relationship between herbivory and neighboring vegetation, indicative of associational defenses. I also found an indirect negative relationship between neighboring vegetation and reproductive output, providing evidence for competition. Finally, I found genetic variation in these plant-plant interactions; of the two genotypes I tested, one experienced greater competitive effects of neighbors (evidenced by a stronger decrease in reproduction with increasing neighbor density), while the other benefited more from neighbors through associational defenses. Genotypic differences in the strength and direction of ecological interactions with neighbors indicates that the stress-gradient hypothesis may not be sufficient in understanding plant responses to stress.

Introduction

Both biotic and abiotic stressors influence plant fitness in a particular environment. Abiotic stressors, such as drought or climate change, have been shown to increase facilitative interactions among plants (Liancourt et al., 2005). However, effects of plant-plant interactions on plant fitness are not as well studied (Smit et al., 2009). Interspecific biotic interactions can be positive or negative. Positive, or facilitative, interactions increase average plant fitness whereas negative, or competitive, interactions decrease average plant survival and reproduction by limiting access to resources (Brooker et al., 2008). The relative impact of facilitative and competitive interactions depends in part on abiotic stress (Maestre et al., 2009). The stress-gradient hypothesis (**Figure 1**) offers a model to conceptualize how interspecific interactions are

mediated by abiotic and biotic factors. According to this hypothesis, as physical stress or consumer pressure increases in an ecosystem, interspecific interactions are expected to result in facilitation (Bertness and Callaway, 1994). This may be due to two mechanisms: (1) neighbor plant amelioration, in which plants improve the abiotic environment of their neighbors, and/or (2) associational defenses, in which protection is gained by an organism from living in association with another species (Hunter and Aarssen, 1988). That is, neighboring plants have the ability to protect an individual plant from drought, herbivory, and/or extreme climate. However, in less stressful conditions with more mild consumer pressure, stronger competitive interactions are predicted to occur where less competitive plants are expected to have lower fitness and are more susceptible to herbivory (Hunter and Aarssen, 1988). The net sum of these positive and negative plant-plant interactions have implications for species coexistence and community structure; for example, stronger competitive interactions can result in a decrease in biodiversity (Price et al., 1980).

Due to frequent changes in abiotic factors, such as climate, water availability, and temperature, the relative strength of facilitative and competitive interactions also changes over time (Leverett, 2017). The questions arise: How does variation in abiotic stress modify interactions between plants and their neighbors? How might neighboring plant density affect herbivore defense? Investigating the role of biotic and abiotic factors in influencing positive and negative interactions will help us better understand the balance between them as well as their potential effects on focal species and communities (Leverett, 2017).

In addition, local adaptation of specific genotypes can also confer advantages to individuals, regardless of the magnitude of biotic and abiotic stress. That is, due to selective pressures, individuals of the same population may vary in their responses to stress (Espeland and Rice, 2007). *Boechera stricta*, a plant from the mustard family, provides a useful model for studying plant-plant interactions; it is a short-lived, common, widespread perennial wildflower native to the Rocky Mountains, USA, where it occupies a diverse range of ecological niches spanning elevational and latitudinal gradients which vary widely in abiotic and biotic stress. Furthermore, its well-characterized anti-herbivore defenses (secondary metabolites called glucosinolates; Anderson and Mitchell-Olds, 2011; Prasad et al. 2012) provide good resources for testing the importance of genetically-controlled vs. associational defenses. In this study, I explored the plant-plant interactions that occur between *Boechera stricta* and neighboring plant species in order to determine how these interactions may affect fitness and herbivore defense in this species. Specifically, I tested the following hypotheses:

1. More stressful abiotic conditions will lead to increased facilitative plant interactions, whereas less stressful abiotic conditions will lead to increased competitive plant interactions between *Boechera stricta* and its neighboring plants.

2. A higher density of neighboring plants will confer greater associational defenses (less insect herbivory) in focal plants, whereas a lower density of neighboring plants will confer less associational defenses (greater insect herbivory) of *Boechnera stricta* individuals.

Methods

Study species and genotypes: *Boechnera stricta* is a flowering, self-pollinating plant in the mustard family, Brassicaceae. It is an exemplary model system for ecological genomics as a perennial plant with a tractable genome that occupies a variety of ecologically distinct habitats in the Rocky Mountains in the western USA (Rushworth et al., 2011). I used potted *B. stricta* plants and a common garden containing known genotypes to address my study questions. The two focal genotypes in each experiment were near-isogenic lines (NILs), which have nearly identical genetic makeups except for the specific location controlling variation in defensive chemical (glucosinolate) profile. *Boechnera stricta* shows high levels of heritable within-species variation in glucosinolates (Anderson and Mitchell-Olds, 2011). The trait most well characterized regarding herbivore defense is BC-ratio, which represents the percent of total glucosinolates derived from valine and isoleucine (branched-chain amino acids) vs. methionine (Prasad et al. 2012). In some prior studies, plants with a high BC-ratio, or the branched-chain genotype, have been found to have more effective defensive chemistry than plants with a low BC-ratio, when grown in common gardens near the Rocky Mountain Biological Laboratory (RMBL) in Colorado (Carley et al., *unpub.*).

Common garden experiment: To test how the magnitude and direction of plant-plant interactions vary under different conditions, I used rainout shelters to increase variation in abiotic stress in the Mitchell-Olds common garden in Schofield townsite, CO (**Figure 11**). In the common garden, *B. stricta* plants are planted at 10-cm intervals directly into the native vegetation matrix in a randomized, complete block design with 50 plants per block. The genotypes in the common garden include two cohorts of the glucosinolate near-isogenic lines (NILs), one planted in 2015 and the other in 2016. Rainout shelters that decreased soil moisture by 25.7% (**Figure 2**) were placed over half of the garden blocks during the growing season in 2017 and were re-established in late May 2018. I utilized both cohorts of BC-ratio NILs for a total initial sample size of 2300 plants. At the beginning and end of the field season (two data collection points), I measured neighbor vegetation density as well as *B. stricta* survival, fecundity, and insect herbivore defense in both the rainout and control conditions. I measured neighbor vegetation density by recording percent vegetation cover within a 5-cm radius of each *B. stricta* individual. I estimated insect herbivory by visually estimating percent leaf area removal on each individual. Ultimately, fecundity will be measured as the product of the number and size of fruits per individual. However, because late-season censuses were only recently completed and analyses of those data are ongoing, early-season fecundity was estimated as a binary variable of whether or not each

individual produced any flowers or fruits. I calculated total fitness by multiplying survival and fecundity for each plant. Throughout the experiment, I also measured soil moisture approximately every other day at three points per garden block, and added water to control plots for the first four weeks, to account for the low precipitation and snowmelt in the early season (16.69 inches in rainfall this year vs. an average of 25.81 inches from the past 5 years; barr, “Gothic Weather”). I used regressions to determine whether the effects of neighbor density on *B. stricta* fitness components were positive (indicating facilitation) or negative (indicating competition). I also tested whether the slope of this relationship was modified under more permissive vs. more drought-stressed environments, directly testing the stress gradient hypothesis.

Potted plant experiment: Since data collected from the common garden was largely correlational, an additional experiment was done to test for a potential causal relationship of neighboring vegetation on insect herbivory and plant fitness. In the Gothic townsite (**Figure 11**), I conducted a potted plant experiment in a randomized complete block design. 100 vernalized, juvenile *B. stricta* glucosinolate NILs were sent to RMBL via mail from the Duke University greenhouse in Durham, NC. I transplanted the 97 surviving individuals into 4x4 inch pots filled with Miracle Grow Potting Mix soil (0.21 N: 0.11P: 0.16K; The Scotts Company, LLC, Marysville, Ohio). I dug up a 2X2-foot turf plot of vegetation outside of the Gothic Research Center and planted the vegetation within a 5 cm radius of each potted plant at 0, 25, 50, 75, or 100% neighbor density. To control for differences in neighbor identity, age, and size, the turf plot contained predominantly (>95% cover) *Poa pratensis* (Poaceae). *P. pratensis* (Kentucky bluegrass) is an herbaceous perennial species that is invasive to Colorado. After 3 weeks, I recorded survival, reproduction, and insect herbivory for each plant. I measured these fitness components using the same methods described above for the common garden experiment. I used regressions to determine whether there is a relationship between neighbor density and insect herbivory or fitness in *B. stricta*, as well as to test for genotypic differences in these relationships.

Results

Common garden experiment: Due to this year’s dry conditions (16.69 inches in rainfall this year vs. an average of 25.81 inches from the past 5 years; barr, “Gothic Weather”), both the rainout shelter and control plots experienced relatively stressful abiotic conditions (barr, “Gothic Weather”). Consistent with facilitation, I found a significant positive relationship between neighboring vegetation density and overwinter survival for *B. stricta* planted in both 2015 ($P=0.0002$; **Figure 3A**) and 2016 ($P=0.0001$; **Figure 3B**) (**Table 1**) in the common garden. However, there was no significant interaction between neighboring vegetation and stress treatment (rainout vs. control) for either cohort (2015: $P=0.142$, **Figure 3A**; 2016: $P=0.154$, **Figure 3B**) (**Table 1**). I found a marginally significant positive relationship between neighboring vegetation and fecundity in *B. stricta* planted in 2015 ($P=0.100$; **Figure 4A**), but not for those

planted in 2016 ($P=0.486$; **Figure 4B**) (**Table 2**). I also found no significant relationship between neighboring vegetation and fecundity under rainout vs. control treatments for either cohort (2015: $P=0.487$, **Figure 4A**; 2016: $P=0.181$, **Figure 4B**) (**Table 2**). Indicative of facilitation, I found a significant positive relationship between neighboring vegetation and total fitness of plants from 2015 ($P=0.036$; **Figure 5A**), but not for those planted in 2016 ($P=0.796$; **Figure 5B**) (**Table 3**). I found no significant relationship between neighboring vegetation and total fitness under rainout vs. control treatments environments for either cohort (2015: $P=0.6578$, **Figure 5A**; 2016: $P=0.169$, **Figure 5B**) (**Table 3**). With late-season data, I will analyze the relationships between neighboring vegetation, survival, reproduction, and insect herbivory.

Potted plant experiment: Indicative of associational defenses, I found a significant negative relationship between herbivore damage and neighbor vegetation density ($P=0.0001$; **Figure 6**) (**Table 4**). Consistent with competition, there was a significant negative relationship found between height and neighbor vegetation density ($P=0.016$; **Figure 7**) (**Table 4**). I also found a significant positive relationship between the number of reproductive structures and height ($P<0.0001$; **Figure 8**) (**Table 5**). Thus, I found an indirect negative relationship between the number of reproductive structures and neighbor vegetation ($P=0.049$; **Table 6**). In testing for genotypic differences, I found a marginally significant negative relationship between the number of reproductive structures and the interaction of neighbor vegetation and NIL genotype ($P=0.145$; **Figure 9**) (**Table 6**). There was also a significant negative relationship found between herbivory and the interaction of neighbor vegetation and NIL genotype ($P=0.0008$, **Figure 10**) (**Table 6**).

Discussion

Variation in Plant-Plant Interactions Across Fitness Components: In response to similar levels of biotic and abiotic stress, interactions between *B.stricta* and its heterospecific neighbors varied across fitness components, including survival, reproduction, flowering, and herbivore defense. Consistent with the stress-gradient hypothesis, I found a facilitative effect of neighboring vegetation on plant survival and reproduction in the common garden under stressful conditions. Despite adding water to control plots to account for the lack of precipitation in the early season, the plants in both treatments experienced increased abiotic stress, which increased the frequency of facilitative interactions. My first hypothesis was supported in that plants in the rainout plots (more stressful condition) showed greater facilitation than those in the control plots (**Figure 3**). This is consistent with theoretical predictions (Bertness and Callaway, 1994) as well as empirical evidence that other fitness components were positively impacted by neighbors under stressful conditions such as with low precipitation and colder temperatures (Leverett 2017). In addition, due to increased abiotic stress, only a small percentage of plants in the common garden flowered (**Figure 4**). This may have brought about the stronger relative contribution of reproduction on total fitness in the early season (**Figure 5**). In future analysis, it would be interesting to study

how total fitness may be affected by neighboring vegetation when a wider range of total fitness is expressed across individuals. From the potted plant experiment, I found a causal relationship between neighboring vegetation and insect herbivory (**Figure 6**). I found that my second hypothesis was supported in that more neighboring vegetation conferred greater associational defenses on *B. stricta* individuals. However, these associational defenses did not necessarily confer higher fitness. I discovered that neighboring vegetation had an indirect negative effect on *B. stricta* fecundity, suggesting the presence of competitive interactions (**Figures 7 and 8**). This suggests that growth-defense trade offs may have occurred in which *B. stricta* experienced reduced fecundity, while herbivore defense increased in stressful environments (Haugen, 2008). Future analysis should be done on late season census data from the common garden to further explore potential tradeoffs and relationships between neighboring vegetation, insect herbivory, and plant fitness.

Genotypic Differences in Plant-Plant Interactions: In order to determine how genetic variation in *B. stricta* defensive chemistry may moderate positive and negative interactions with neighbors, I explored the interaction between neighbor density and glucosinolate NIL genotype on herbivory and reproduction. Analyses for common garden plants are still ongoing. From the potted plant experiment, I found that reproductive output of the branched-chain glucosinolate genotype experienced greater reductions due to neighbor abundance (i.e., stronger competition) than that of the methionine genotype (**Figure 9**). Conversely, I found that the methionine genotype benefited more from neighbors through associational defenses than the branched-chain genotype (**Figure 10**). In past studies, the methionine genotype has been shown to have less effective defensive chemistry than that of the branched-chain genotype (Prasad et al. 2012). Thus, the plants of the methionine genotype may be more facilitated by neighbors because they offer associational defenses to these *B. stricta* plants. Conversely, plants of the branched-chain genotype may be in greater competition with neighbors since plants of this genotype already have strong defensive chemistry against herbivores. Future studies should further analyze genotypic variation in the strength and direction of ecological interactions with neighbors, especially in response to varying abiotic stress. With individual genotypic variation, the stress-gradient hypothesis may not be adequate to predict population- and community-level responses to abiotic and biotic stress (Noto and Shurin, 2016). That is, the same type of stress might not cause fitness consequences for all individuals in a specific environment. Thus, the maintenance of genotypic diversity within populations and species diversity within communities may be implicated by genotypic variation (Espeland and Rice, 2007). Further exploration should be done on how plants may be locally adapted to abiotic and biotic stress in their environments and how these adaptations could change over time.

Acknowledgements

I would like to thank my mentor, Lauren Carley, for her endless support and guidance in every step of the research process at RMBL. I would also like to thank Tom-Mitchell Olds for giving me the opportunity to conduct research in the Schofield Common Garden. I appreciate all of the help from Team Boechera research assistants, Nick Niezgoda and Tris Dodge, who assisted in potting plants, digging up turf, censusing plants, and starring in short films. I would also like to thank my fellow undergraduate, Kristin Schepke, for providing insight and support. In addition, I would like to thank everyone at the Rocky Mountain Biological Laboratory, especially Jennie Reithel, Rachel Steward, and Rosemary Smith, for helping me find my research sites and guiding me through the research process. Finally, I would like to thank my funders, the Rocky Mountain Biological Laboratory and the Morehead-Cain Foundation for granting me the opportunity to conduct research at the most magical place on Earth.

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Tables

Table 1. Statistical summary of logistic regressions testing the effect of neighbor vegetation density and stress treatments (rainout shelters vs. control plots) on *B. stricta* survival in a common garden.

Model Effect	2015 Cohort				2016 Cohort			
	Estimate	Std. Error	Z value	P value	Estimate	Std. Error	Z value	P value
Vegetation	0.010	0.003	3.064	0.002**	0.028	0.007	3.842	0.0001 ***
Water Treatment [Rainout]	-0.145	0.197	-0.739	0.460	0.113	0.283	0.401	0.688
Vegetation × Water Treatment [Rainout]	0.007	0.005	1.470	0.142	0.014	0.010	1.426	0.154

** significance level of 0.001

*** significance level of <0.001

Table 2. Statistical summary of logistic regressions testing effect of vegetation and stress treatments on *B. stricta* fecundity in a common garden.

Model Effect	2015 Cohort				2016 Cohort			
	Estimate	Std. Error	Z value	P value	Estimate	Std. Error	Z value	P value
Vegetation	0.017	0.010	1.645	0.100	-0.030	0.042	-0.697	0.490
Water Treatment [Rainout]	-0.137	0.840	-0.163	0.870	-4.275	2.870	-1.490	0.136
Vegetation x Water Treatment [Rainout]	-0.012	0.017	-0.696	0.487	0.088	0.066	1.338	0.181

Table 3. Statistical summary of logistic regressions testing effect of vegetation and stress treatments on *B. stricta* total fitness in common garden.

Model Effect	2015 Cohort				2016 Cohort			
	Estimate	Std. Error	Z value	P value	Estimate	Std. Error	Z value	P value
Vegetation	0.020	0.010	2.098	0.0359 *	-0.011	0.041	-0.259	0.796
Water Treatment [Rainout]	-0.256	0.810	-0.316	0.752	-3.86	2.758	-1.399	0.162
Vegetation x Water Treatment [Rainout]	-0.007	0.016	-0.443	0.658	0.087	0.063	1.376	0.169

* significance level of 0.01

Table 4. Statistical summary of linear regression testing the effect of vegetation on *B. stricta* herbivory and height in potted plants.

Model Effect	log(Average Leaf Area Damage)				Height			
	Estimate	Std. Error	t value	P value	Estimate	Std. Error	t value	P value
Vegetation	-0.007	0.002	-3.907	0.0001 ***	-0.018	0.007	-2.45	0.016 *

* significance level of 0.01

*** significance level of <0.001

Table 5. Statistical summary of linear regression testing the effect of height on the number of reproductive structures in *B. stricta* potted plants.

Model Effect	Number of fruits + flowers			
	Estimate	Std. Error	t value	P value
Height	1.532	0.128	11.989	< 2e-16 ***

*** - significance level of <0.001

Table 6. Statistical summary of linear regressions testing effects of vegetation and genotypes on *B. stricta* number of reproductive structures and herbivory in common garden.

Model Effect	Number of fruits+flowers				log(Average Leaf Area Damage)			
	Estimate	Std. Error	t value	P value	Estimate	Std. Error	t value	P value
Vegetation	-0.043	0.022	-1.995	0.049*	-0.001	0.003	-0.404	0.687
Genotype [SS: Methionine]	-1.424	1.867	-0.763	0.448	0.552	0.217	2.547	0.013 *
Vegetation x Genotype [SS: Methionine]	0.044	0.030	1.469	0.145	-0.012	0.003	-3.448	0.0008 ***

* - significance level of 0.01

*** - significance level of <0.001

Figures

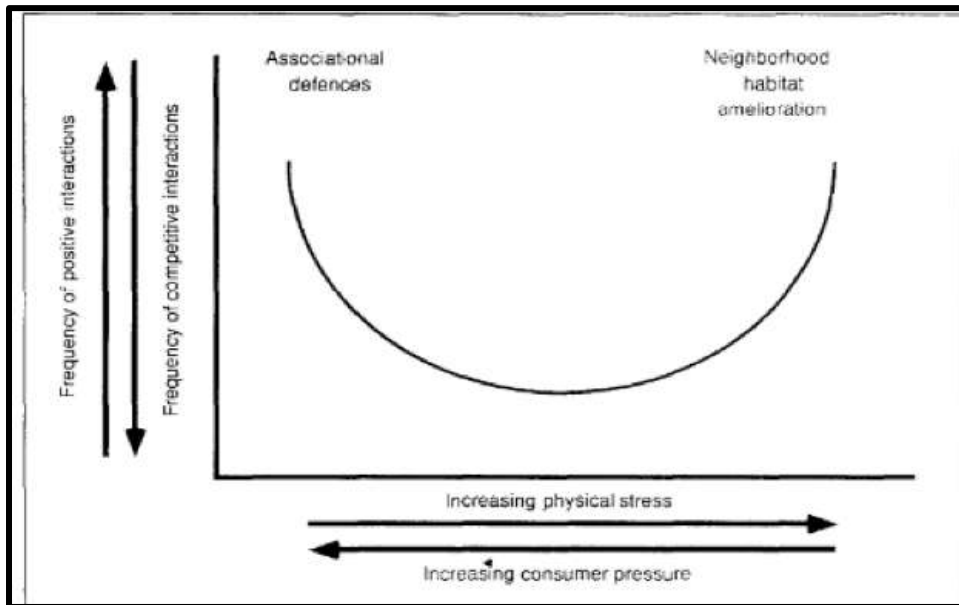


Figure 1. Stress Gradient Hypothesis (adapted from Bertness and Callaway, 1994). As physical stress or consumer pressure increases in a particular environment, associational defences and neighborhood plant amelioration increases in frequency. Conversely, as physical stress or consumer pressure decreases, the frequency of competitive interactions increases.

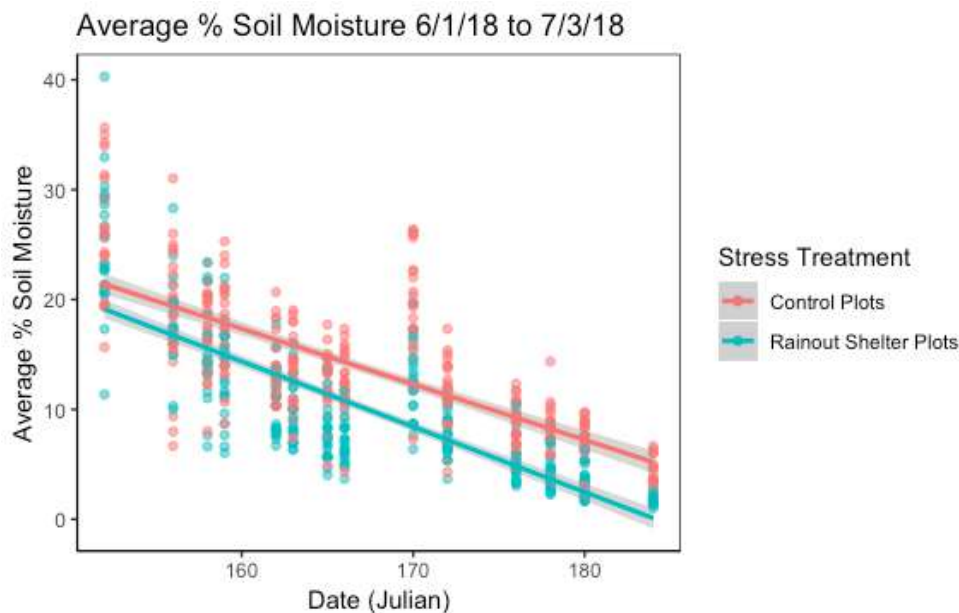


Figure 2. Reduction in Percent Soil Moisture by Rainout Shelters in the Common Garden. Least-squared mean for control: 13.88%; for rainout shelter: 10.31%. Percent soil moisture was reduced by 25.7% ($P = 2 \times 10^{-16} ***$).

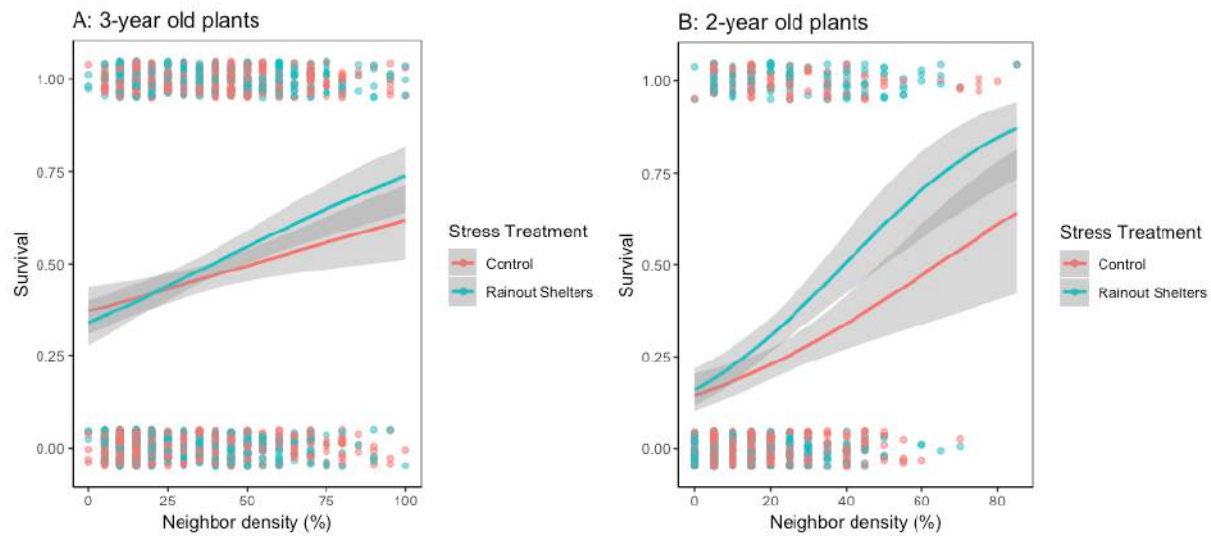


Figure 3. Survival vs. Neighbor Vegetation Density for Different Stress Treatments in Common Garden. As neighbor vegetation density increases, survival increases. Facilitative interactions present for both treatments. Panel A, three-year old plants: neighbor density: $P=0.002^{**}$, neighbor density*stress: $P=0.142$. Panel B, two-year old plants: neighbor density: $P=0.0001^{***}$, neighbor density*stress: $P=0.154$.

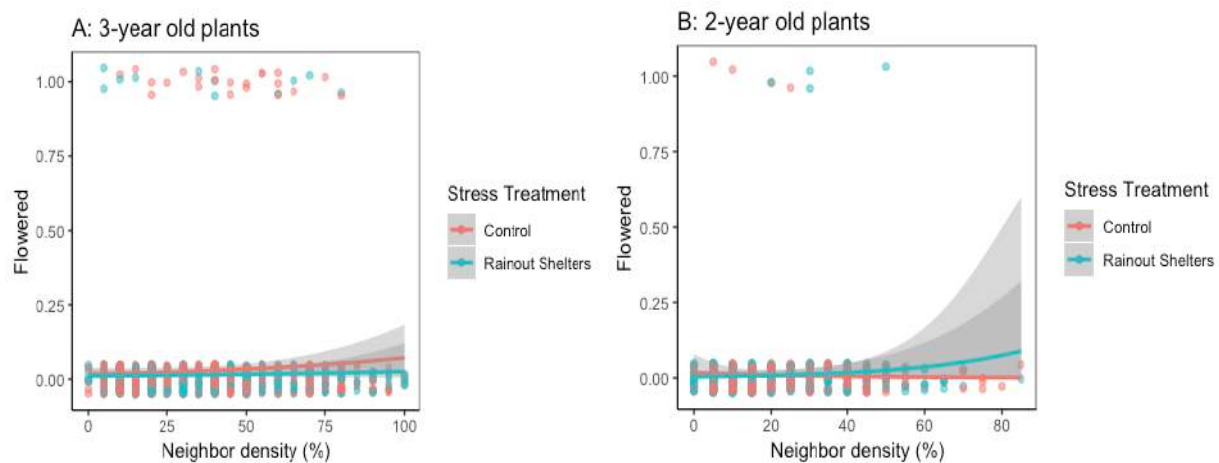


Figure 4. Flowering vs. Neighbor Vegetation Density for Different Stress Treatments in Common Garden. As neighbor vegetation density increases, slight increase in flowering. Facilitative interactions expected for both treatments. Panel A, three-year old plants: neighbor density: $P=0.100$, neighbor density*stress: $P=0.487$. Panel B, two-year old plants: neighbor density: $P=0.485$, neighbor density*stress: $P=0.181$.

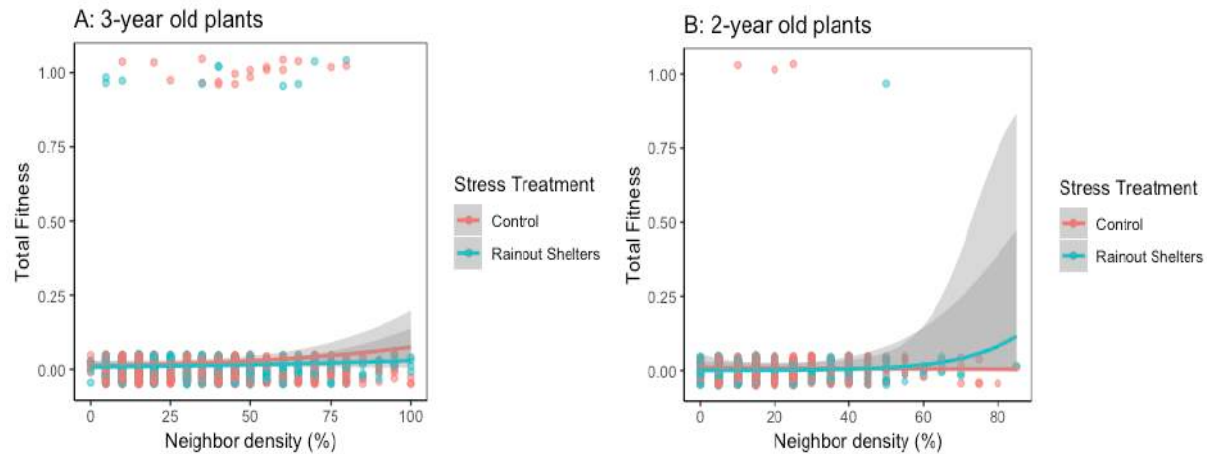


Figure 5. Total Fitness vs. Neighbor Vegetation Density for Different Stress Treatments in Common Garden. As neighbor vegetation density increases, slight increase in total fitness. Facilitative interactions expected for both treatments. Panel A, three-year old plants: neighbor density: $P=0.036^*$, neighbor density*stress: $P=0.685$. Panel B, two-year old plants: neighbor density: $P=0.796$, neighbor density*stress: $P=0.169$.

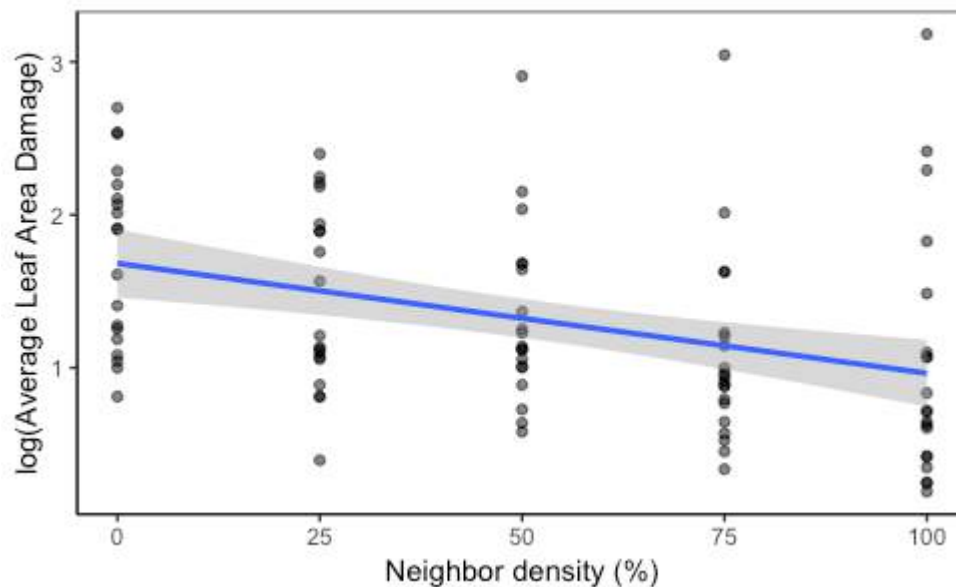


Figure 6. Potted Plants: Herbivory vs. Neighbor Vegetation Density. As neighbor vegetation density increases, the log of average leaf area damage decreases, indicating associational defenses. $r=-0.37^{***}$, $P=0.0002^{***}$

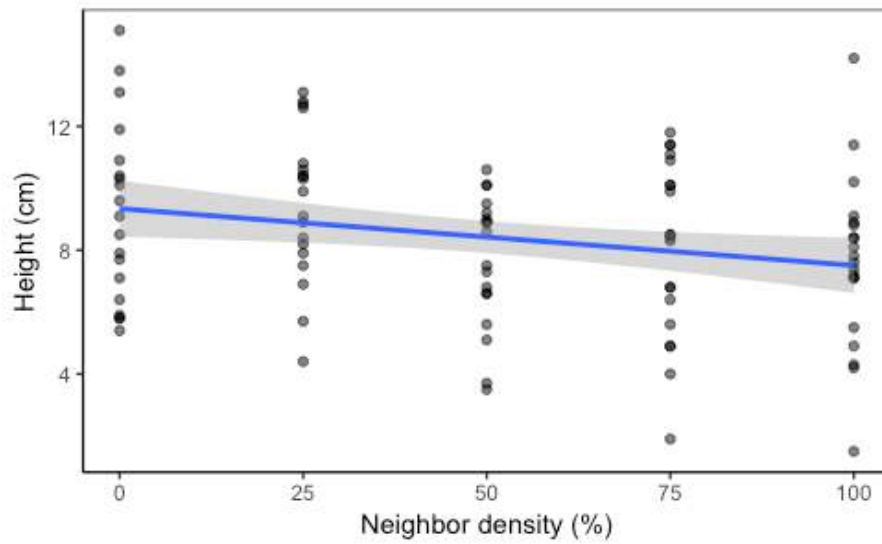


Figure 7. Potted Plants: Height vs. Neighbor Vegetation Density. As neighbor vegetation density increases, height decreases, indicating competition. $r=-0.24^*$, $P=0.02^*$

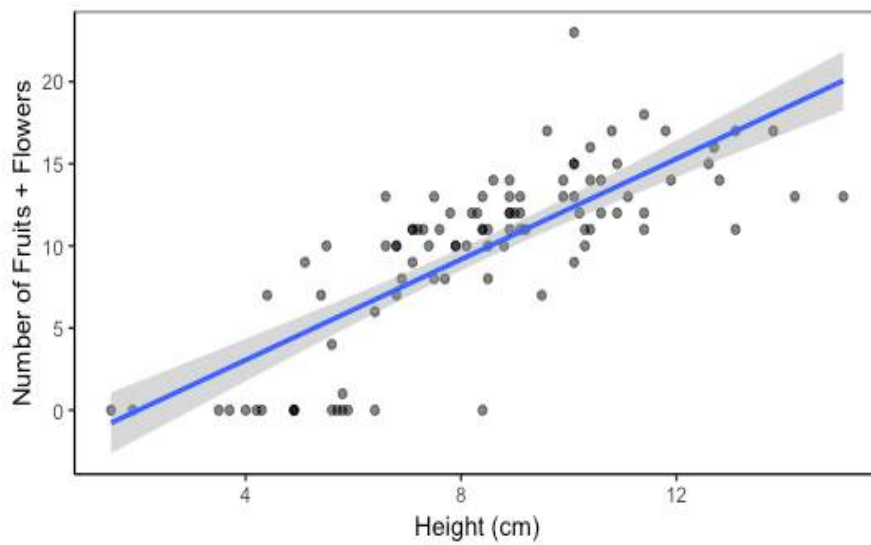


Figure 8. Potted Plants: Reproductive Structures vs. Height. As height increases, the number of fruits and flowers increases. $r=0.78^{***}$, $P < 2 \times 10^{-16}^{***}$

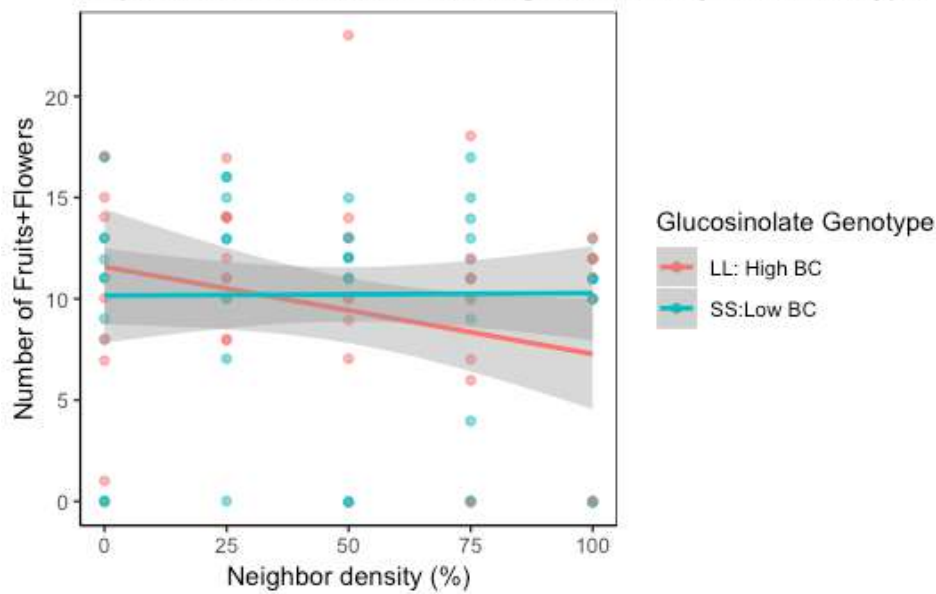


Figure 9. Potted Plants: Reproductive Structures vs. Neighbor Vegetation Density for Different Genotypes. SS, Low BC Genotype: As neighbor vegetation density increases, the number of fruits and flowers does not change. LL, High BC Genotype: As neighbor vegetation density increases, the number of fruits and flowers decreases, indicating competition. Neighbor Density: $P=0.0489^*$, Neighbor Density*Genotype: $P=0.145$.

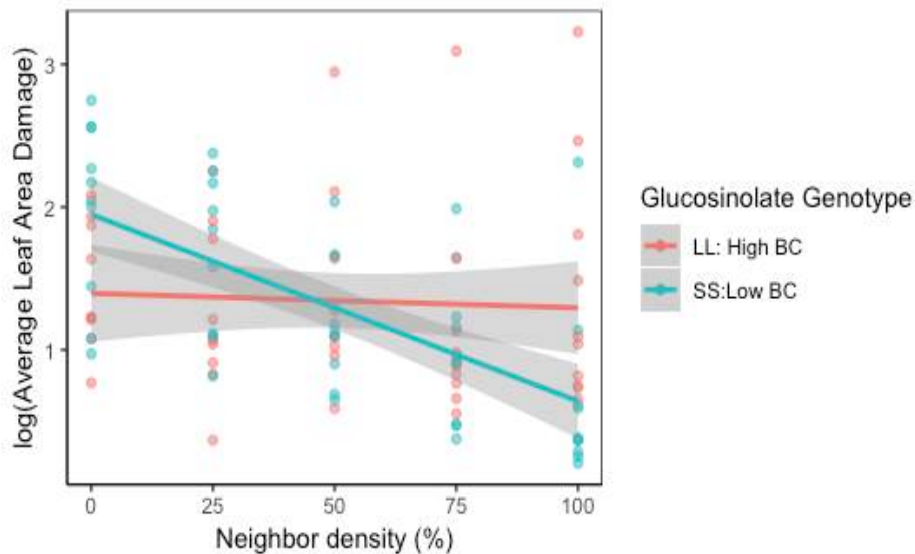
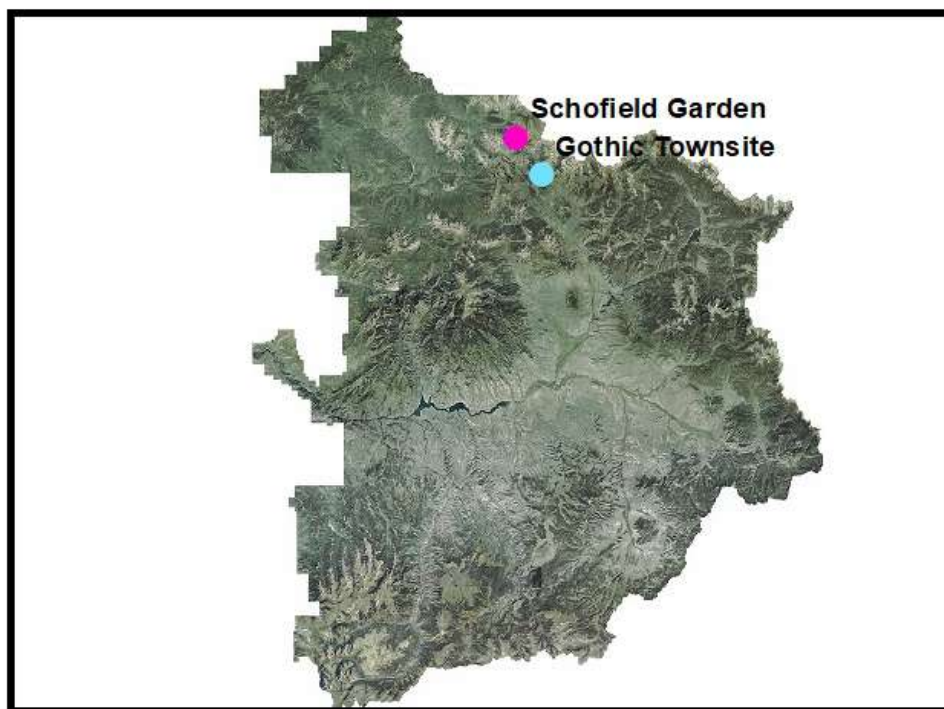
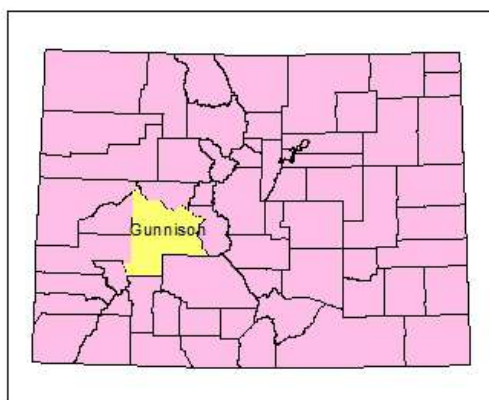


Figure 10. Potted Plants: Herbivory vs. Neighbor Vegetation Density for Different Genotypes. SS, Low BC Genotype: As neighbor vegetation density increases, the log of the average leaf area damage decreases, indicating the presence of associational defenses. LL, High BC Genotype: As neighbor vegetation density increases, the log of the average leaf area damage stays the same. Neighbor Density: $P=0.687^*$, Neighbor Density*Genotype: $P=0.000851^{***}$

Gunnison County Research Sites



Colorado



Schofield Common Garden



Author: Allison Carter
Mentor: Lauren Carley
PI: Tom Mitchell-Olds

Figure 11. Research Sites in Gunnison County, CO.