Interactions between *Ribes sanguineum* and *Symphotrichum chilense* in the context of drought-conscious restoration

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ABSTRACT

Planting of native species is a common strategy in restoration. When selecting plants for restoration projects, it is important to take into account how they will interact and how these interactions are affected by ecosystem factors. In particular, urbanized ecosystems in California are greatly impacted by water availability. To assess impacts of water availability on plant interactions in the context of an urban riparian restoration project, I examined the growth of *Ribes sanguineum* (red flowering currant) and *Symphotrichum chilense* (common aster) in a greenhouse study under 3 different watering regimes and compared their relative growth rates. I also compared a series of *R. sanguineum* plants at two different restoration sites to identify effects of sun exposure on growth under field conditions. Competition was observed much more than facilitation among plants in the greenhouse study, among both plants of the same species and of different species. Relative growth rates and leaf count comparisons suggest that resource availability had an effect on overall growth, especially in the case of *S. chilense*. *S. chilense* plants were able to crowd out *R. sanguineum* plants, while *R. sanguineum* individuals may have been adversely affected by insufficient space for growth. Additionally, *R. sanguineum* plants in recently restored areas showed significantly higher leaf counts, flower counts and plant heights under high-sunlight conditions than under low-sunlight conditions. These findings suggest that it is feasible to grow *R. sanguineum* and *S. chilense* together for low-water restoration projects as long as minor precautions are taken to prevent detrimental competition.

KEYWORDS

Common aster, red flowering currant, novel ecosystems, Strawberry Creek, restoration ecology

INTRODUCTION

Ecological restoration projects consist of efforts to bring degraded areas back to their natural states through deliberate human intervention, particularly using techniques such as bioremediation (removal of harmful substances from the ecosystem) and establishment of plants which are suited to the area in question. Specifically, replacing invasive species with natives is often an important goal of restoration projects (Funk et al. 2008). Novel ecosystems, which contain species compositions or abundances previously not observed in a given biome (Hobbs et al. 2006), are often sites of restoration efforts and can be considered to remain novel ecosystems even after these efforts if it is not possible to return to the true natural condition (Miller and Bestelmeyer 2016).

One of the most important aspects of conducting a restoration project is selecting the proper plant species to use in the area in question. Understanding which organisms are best suited to a particular area is crucial to the success of any given restoration, and is often difficult in urbanized areas due to the absence of a natural analog for the site. It is also necessary to establish ecosystems which are resilient to changes in abiotic factors such as water availability, particularly in California where precipitation varies heavily from year to year (Dettinger et al. 2011). Changes in abiotic factors on a longer time scale must also be taken into account when selecting restoration species as they have the potential to affect restoration projects (Chapple et al. 2017). California's ongoing drought in particular poses a considerable danger to many of its ecosystems. This drought, whose severity is unparalleled compared to other recent dry periods (Robeson 2015), has affected humans and ecosystems by drastically reducing water availability across the state (Dettinger et al. 2011). Plant water stress levels have increased markedly, resulting in reduction of plant ground cover in many ecosystems (Potter 2015). The unpredictability of drought severity over time is of particular concern for restoration projects (Chapple et al. 2017) as plants' responses to water availability can vary Ecological restoration projects using native vegetation are one possible strategy for drought mitigation (Vaughn et al. 2011), and their effectiveness at reducing water use is highly contingent upon the makeup of the ecosystem in the context of its historical usage.

The Strawberry Creek watershed on the University of California, Berkeley campus is a novel ecosystem which has been highly impacted by human activities dating back to the founding of the university and has undergone extensive restoration in recent decades (Charbonneau and

Resh 1992). Anthropogenic changes to the ecosystem have involved introduction of invasive species such as ivy and eucalyptus as well as pollution such as toxic runoff from sewer lines (Charbonneau 1987). Restoration of the riparian area began in 1987 and has continued to the present, largely through participation of students and other community members (Charbonneau and Resh 1992, Purcell et al. 2007).

In addition to water availability, sunlight availability is particularly relevant in the areas adjacent to Strawberry Creek due to the abundance of invasive and introduced overstory vegetation not seen in native ecosystems nearby (Purcell et al. 2007). Assessing the impacts of shading on restored plant communities is thus also important when considering the direction to pursue in restoration projects.

One major aspect of resilience and ecosystem health lies in biodiversity, which must be achieved based on selecting a range of possible coexisting plants when considering restoration of novel ecosystems since degraded ecosystems are often low in diversity due to factors such as prevalence of invasive species. Biodiversity is important for establishing ecosystem resilience through sustainable use of different resources and protection against invasive species (Funk et al. 2008). Assessing plant niches on a community scale can thus allow predictions of community success and stability (Funk et al. 2008). Due to the aforementioned level of human influence on the watershed in question (which is commonly seen among urban streams and watersheds; Walsh et al. 2005) it is necessary to gauge the efficacy of growing different plants together in the context of their use in restoration projects with increased levels of diversity. With this added diversity, it is possible to establish healthier, more resilient ecosystems in previously degraded areas.

Interactions between plants of the same or different species can have major effects on overall characteristics of the ecosystem, and understanding how they function in specific cases can aid in designing robust ecosystems for restoration purposes. These interactions manifest in most cases as either facilitation, where presence of existing individuals assists the establishment and growth of new individuals, or as competition, where the struggle for resources results in some individuals having more success in establishment, growth and propagation than others (Bertness and Callaway 1994). In general, facilitation occurs in high-stress environments while competition occurs in low-stress environments, a phenomenon characterized by the stress gradient hypothesis (Bertness and Callaway 1994). However, this hypothesis does not adequately explain all interactions between plants, which are site-specific and often nonlinear (Kawai and Tokeshi 2007, Martorell et al. 2015). It is thus important to examine how *Ribes sanguineum* and *Symphotrichum chilense*, two drought-tolerant plants native to California coastal areas and used extensively in Strawberry Creek restoration projects, interact in relation to their candidate restoration sites in order to consider their potential to be planted together as a low-intensity means of increasing biodiversity in human-dominated California landscapes.

The overall goal of this study was to determine if and how *R. sanguineum* and *S. chilense* affect each other's growth in the context of a drought-conscious restoration project. In order to answer this question, I posed two sub-questions: (1) Do *R. sanguineum* and *S. chilense* follow the stress gradient hypothesis with respect to facilitation and competition when grown in sites with differing exposure to sunlight? (2) What effect, if any, does difference between soil moisture and available sunlight levels have on plant growth? Assuming the stress gradient hypothesis applies in this situation, I predicted that the overall trend would show a correlation between increasing stress on plants and a tendency toward facilitative interactions among individuals (both interspecific and intraspecific). To answer these questions, I grew plants in a greenhouse under various watering regimes and with different interactions taking place and calculated their relative growth rates. I also compared leaf counts, flower counts and heights of *R. sanguineum* plants from a previous restoration project along the creek to determine whether sunlight affected their overall growth.

METHODS

Study System

Greenhouse study: interactions and water availability

The first portion of the study took place in a greenhouse in the Oxford Tract at the University of California, Berkeley. Red flowering currant (*R. sanguineum*) and California aster (*S. chilense*) were planted under various treatments consisting of watering regime and interaction type. Both of these plants are native to the western United States and grow mainly in coastal areas. *R. sanguineum* grows as a small deciduous shrub while *S. chilense* is a perennial herb. *R. sanguineum* is able to live in multiple habitat types along Strawberry Creek and has been specifically recommended for restoration projects in the area (Kaplow and Cloud 1988). Similarly, both plants have been used extensively in the UC Berkeley Department of Environmental Health and Safety's ongoing Demonstration Garden and other restoration efforts in recent years (Purcell et al. 2007). Plants were obtained from the Watershed Nursery in Richmond, California; *S. chilense* individuals were in slightly larger containers than *R. sanguineum* individuals when purchased, but plants were otherwise very similar in size and age.

Field study: effects of sunlight availability

The second portion of the study took place in two restoration sites near Strawberry Creek on the University of California, Berkeley campus (37.8719° N, 122.2585° W). The sites were selected since a large number of *R. sanguineum* plants are present from a previous restoration project roughly one year ago; one site experiences a high degree of sunlight as it faces south and has a relative lack of nearby overstory species while the other faces west and is highly shaded by nearby trees.

The area surrounding Strawberry Creek has been dominated by introduced plants as well as other human impacts such as erosion and rerouting of the creek since the construction of the university campus, with restoration initiatives dating back to 1987 (Charbonneau and Resh 1992). Restoration has been successful in restoring the creek to a healthier state (Berkeley EH&S n. d.). The Strawberry Creek Ecological Stabilization Project was the most recent of these initiatives and was completed in 2015 in order to reinforce a delicate section of the creek's banks (Berkeley EH&S n. d.).

There is a great amount of variation between levels of shade directly adjacent to the creek, and main tree species in the area include coast live oak (*Quercus agrifolia*), blue gum eucalyptus (*Eucalyptus globulus*) and coast redwood (*Sequoia sempervirens*). *Quercus agrifolia* is the only locally native tree species in the area; *Eucalyptus globulus* and *Sequoia sempervirens* were both deliberately planted in this area as ornamental vegetation.

Treatment Methods

Greenhouse study

Plants were placed in a series of 1-gallon pots and grown in a greenhouse. 3 different water level treatments (high, medium and low) were used on blocks of plants arranged on benches. The high-water treatment group received water three times per week, the medium-water treatment group received water twice per week, and the low-water treatment group received water once per week. Each pot received roughly 1.1 liters of water per watering session (calculated based on volume of pot between soil level and top of pot). The interaction treatment groups consisted of conspecific individuals of each species planted together, heterospecific individuals planted together, and individuals of each species planted alone (Fig. 1). Individuals within a treatment group were planted 10 centimeters apart within the same container. Pots were rearranged every week in order to control for any spatial discrepancies in greenhouse conditions. Leaf counts were collected and used to calculate relative growth rates of each plant. Baseline leaf counts were recorded before planting, and leaves were counted twice between February and April 2017 at one-month intervals. Height measurements were also taken at the end of the study. In addition, I measured soil moisture for each pot at the end of the study.

0 0	0 1	1 1
0	1	

Figure 1. Example of a block of treatment groups (not to scale). 1s and 0s denote plants of each species. Each treatment was placed in a separate pot and the ordering of the pots and location of each treatment group was changed weekly. Three of these blocks were present for each water treatment.

Field study

To estimate growth of *R. sanguineum* plants as a result of sunlight availability, I collected measurements of leaf counts, flower counts and heights of all plants in the two sites. Though it was not possible to calculate relative growth rates since no baseline data was available, plants were of similar sizes when initially planted (D. Chapple, personal correspondence). Leaf counts and heights were collected as a means of examining overall plant size and biomass, while flower counts were collected to compare reproductive potential.

Data analysis

Greenhouse study

In order to analyze the data from this study, I conducted a two-way analysis of variance using type of interaction (inter/intraspecific or none) and water level (coded as "high," "moderate" or "low") as categorical variables and relative growth rate (based on leaf counts for the purposes of this study) as the response variable. I selected this test due to the presence of two categorical variables and under the assumption that the data fits the requirements for use of a parametric test. Relative growth rate was calculated for each month interval between measurements using the following equation: $RGR = (\ln LC_2 - \ln LC_1) / (t_2 - t_1)$ where LC_1 represents leaf count at the beginning of the month interval, LC_2 represents leaf count at the end of the interval, and t_1 and t_2 represent the beginning and end of the interval (in days) respectively (adapted from Pérez-Harguindeguy et al. 2013). The ANOVA test was conducted using the R statistical software (R Development Core Team 2016) in the RStudio environment (RStudio Team 2015) and using the Rcmdr graphical interface (Fox and Bouchet-Valat 2017). Since baseline data was missing for some of the *R. sanguineum* plants, relative growth rates for these individuals were calculated using data from the first leaf count as LC_1.

Field study

The field study was analyzed using a Mann-Whitney-Wilcoxon test as the data did not seem to come from the normal distribution. Leaf counts, flower counts and heights of plants in each group were compared using this test run in R (R Development Core Team 2016) using RStudio (RStudio Team 2015) and Rcmdr (Fox and Bouchet-Valat 2017).

RESULTS

Relative growth rates in greenhouse

I found that overall higher relative growth was seen in plants with no interactions and that water availability had a positive relationship with growth on a broad scale (Figs. 2 and 3). ANOVA tests showed a statistically significant relationship between growth and interaction type (*R. sanguineum:* p = 0.0632, *S. chilense:* p = 0.0413) as well as growth and watering regime (*R. sanguineum:* p = 0.0100, *S. chilense:* p = .0000) for both plant species, though there was not a statistically significant relationship between watering regime and interaction type. *R. sanguineum* had a high level of variation between both categorical variables, with heterospecific treatments seeing the least growth in all cases. Under high and medium water conditions solitary plants had the highest relative growth rates, while there was not a significant difference between relative growth rates among the low-water plants (though several conspecific plants did have considerably higher relative growth than both heterospecific and solitary plants). *S. chilense* showed a much more consistent trend between water availability and growth, though there was a much larger difference between low and medium water than between medium and high water. Interaction type had the greatest effects in the low-water group; all conspecific *S. chilense* individuals with low water availability died in the second month of the study while no other plant mortality was observed.

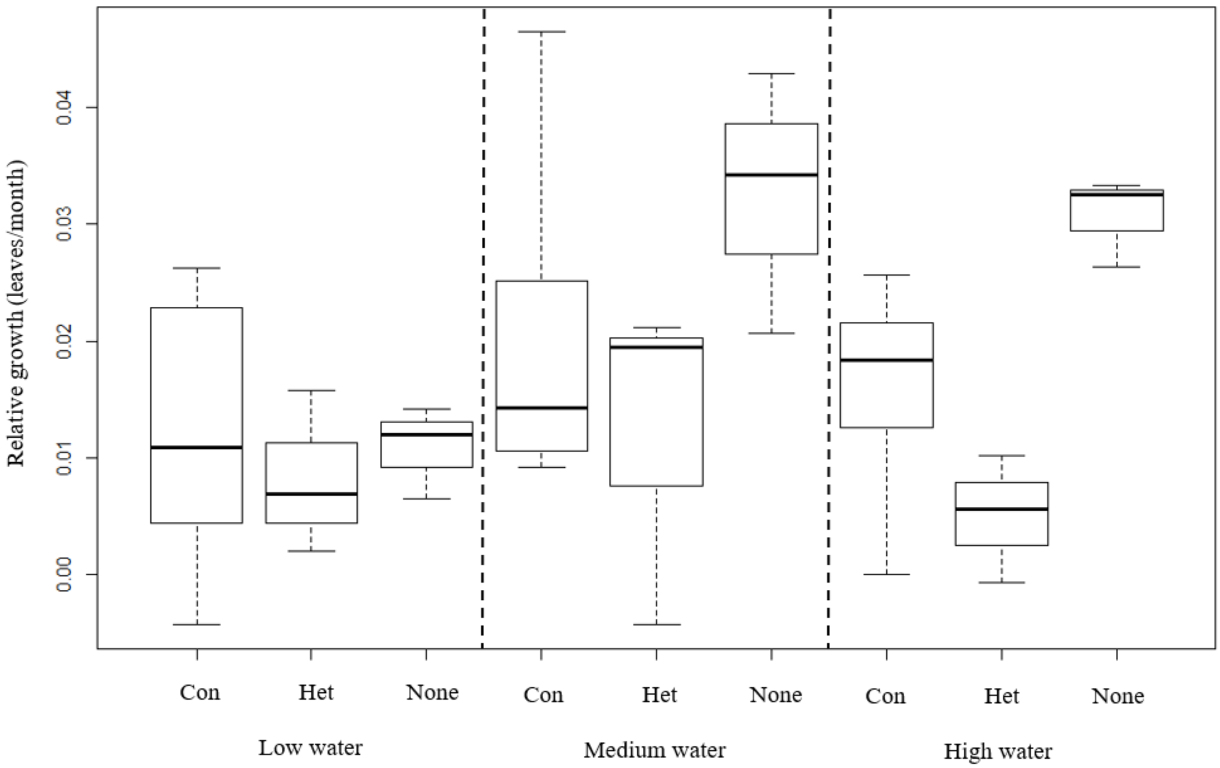

Figure 2. Relative growth rates of *R. sanguineum* in greenhouse. Boxplots showing distributions of relative growth rate measures for conspecific ("con"), heterospecific ("het"), and no interactions ("none") and for low, medium and high moisture levels. A two-way ANOVA test showed significant relationships between relative growth rates and both interaction type ($F = 5.491$, $p = 0.0632$) and watering regime ($F = 3.064$, $p = 0.0100$), but no relationship between the two categorical variables ($F = 1.090$, $p = 0.3818$).

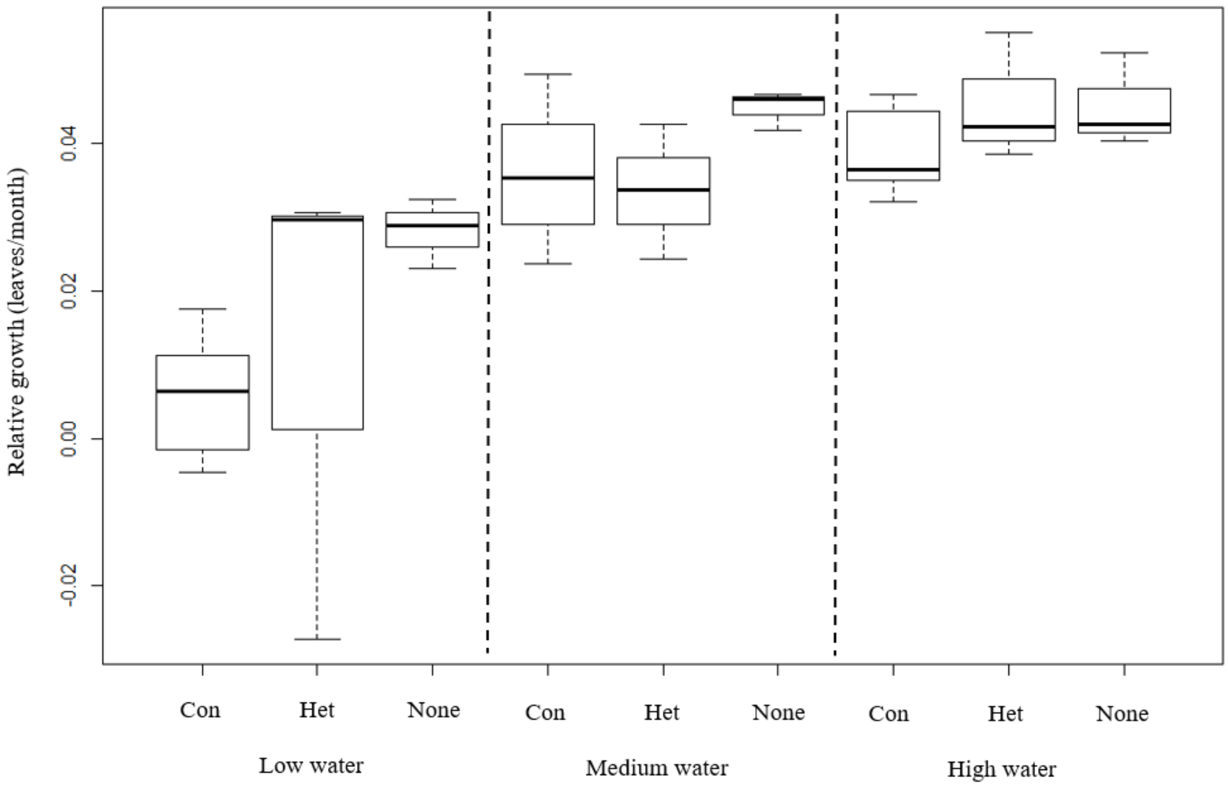

Figure 3. Relative growth rates of *S. chilense* in greenhouse. Boxplots showing distributions of relative growth rate measures for conspecific ("con"), heterospecific ("het"), and no interactions ("none") and for low, medium and high moisture levels. A two-way ANOVA test showed significant relationships between relative growth rates and both interaction type ($F = 3.596$, $p = 0.0413$) and water treatment ($F = 22.351$, $p < .0000$), but no relationship between the two categorical variables ($F = 0.754$, $p = 0.5642$).

Heights in greenhouse

In addition to calculating relative growth rates based on leaf counts, I measured heights of plants in the greenhouse at the end of the study. *S. chilense* plants with high water availability reached the largest heights, and generally were taller than *R. sanguineum* (especially in high-water heterospecific treatments). Height of *S. chilense* plants was shown to be greater under higher water levels while this was not the case with *R. sanguineum*, which had more variation in heights with the medium water treatment showing the highest values (Fig. 4). Similar to the relative growth rate data, a two-way ANOVA test found significant relationships between height and both interaction type (R. sanguineum: $F = 5.886$, $p = 0.0076$; S. chilense: $F = 2.958$, $p = 0.0689$) and water level (R. sanguineum: $F = 4.479$, $p = 0.0201$; S. chilense: $F = 20.380$, $p < 0.0000$) but no relationship between the two categorical variables (R. sanguineum: F = 1.888, p = 0.1414; S. chilense: F = 0.960, p = 0.4455).

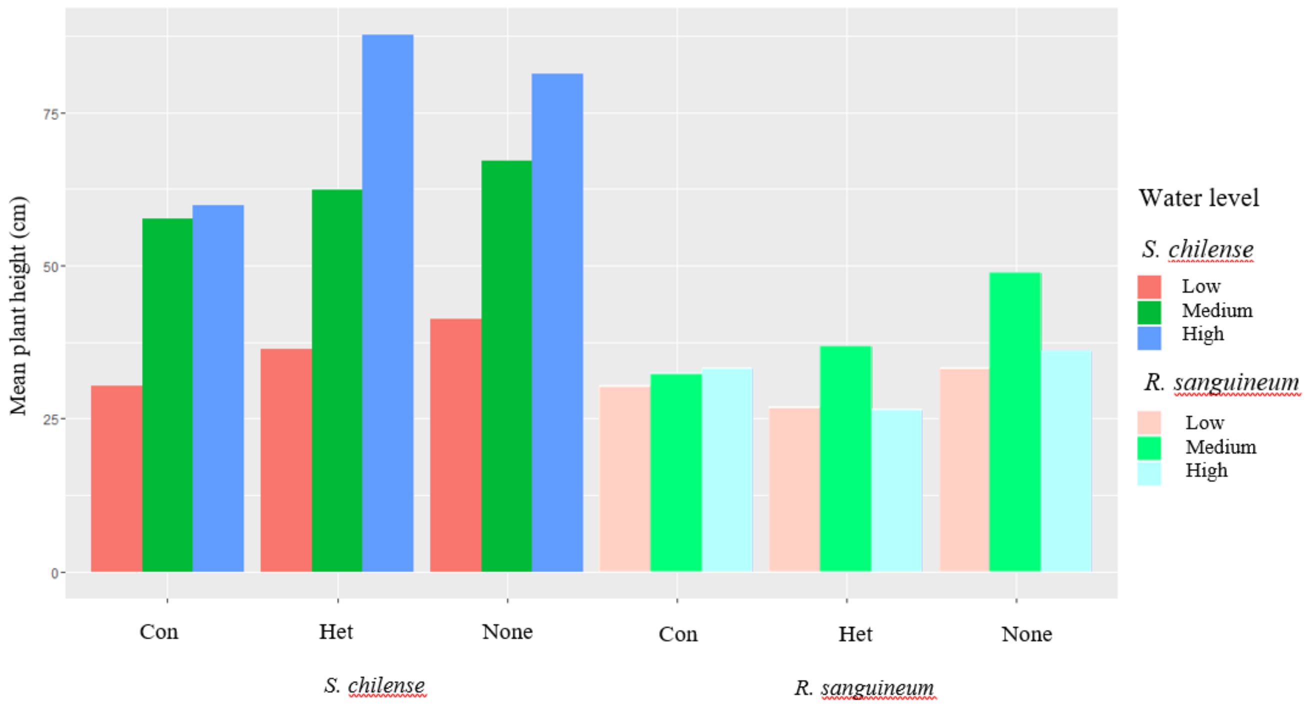

Figure 4. Heights of *R. sanguineum* plants. Mean plant heights at the end of the study by species, water level and interaction treatment. Similar to the relative growth rate data, a two-way ANOVA test found significant relationships between height and both interaction type (*R. sanguineum:* F = 5.886, p = 0.0076; *S. chilense:* F = 2.958, p = 0.0689) and water level (*R. sanguineum:* F = 4.479, p =0.0201; *S. chilense:* F = 20.380, p < 0.0000) but no relationship between the two categorical variables (*R. sanguineum:* F = 1.888, p = 0.1414; *S. chilense:* F = 0.960, p = 0.4455).

Moisture levels in greenhouse

Though moisture levels were collected as a means of testing whether the water treatments had an effect on actual soil moisture, due to the implementation of the methods this relationship was not seen (plants were watered on certain days of each week so measurements on any particular day would not properly reflect overall average moisture; measurements were taken on a day when no watering took place). Instead, soil moisture was highly correlated with interaction type. A two-way ANOVA test showed a strong relationship between interaction type and soil moisture level (F = 8.249, p = 0.0002) but no relationship between water level and soil moisture (F = 1.281, p = 0.2936), and a Tukey test showed that pots containing *S. chilense* individuals had significantly lower soil moisture than pots without asters (difference = -6.849, $p < .0000$).

Leaf counts, flower counts and heights in field

The Mann-Whitney-Wilcoxon test showed a statistically significant difference in heights (W = 105, p = 0.0293), leaf counts (W = 79, p = .0033), and flower counts (W = 93, p = .0022) between the two sites. Plants were noticeably larger and had a much higher number of flowers in the high sunlight site (Fig. 5), and the most heavily shaded plants in the low sunlight site were very short (less than 1 meter high) and had no flowers. Only two plants in the low sunlight site had any flowers while many of the plants in the high sunlight site had very high numbers of flowers. Most plants either had no flowers or a high number of flowers. Plants in the high sunlight site also were much larger in general, particularly those which were furthest from nearby trees. The high sunlight site also had a higher degree of overall vegetation, particularly considering plants other than *R. sanguineum*. Many plants of different species in this site grew very close together, including some whose branches overlapped to a high degree. Several of the *R. sanguineum* plants also grew very laterally, with little height but high leaf counts.

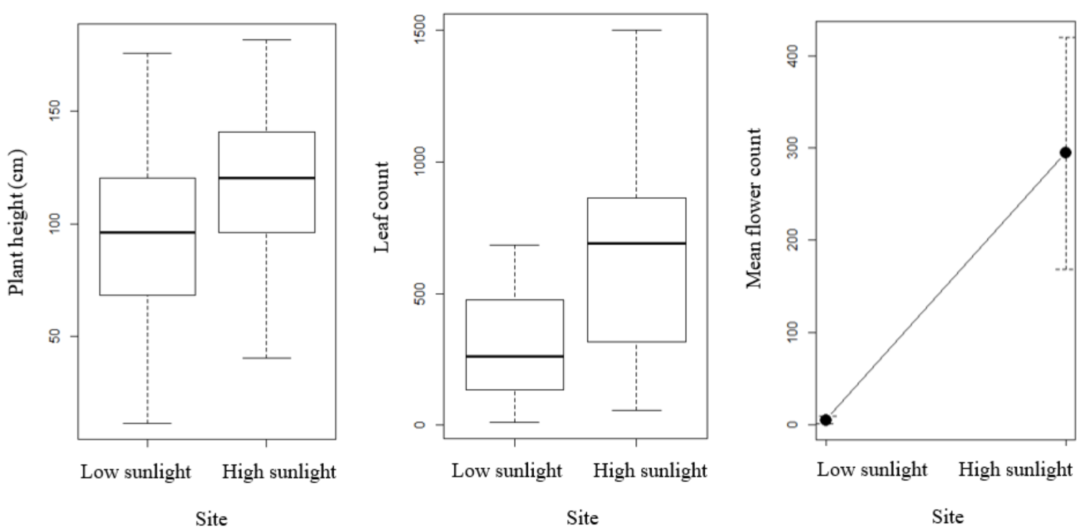

Figure 5. Comparisons of growth metrics between high and low sunlight sites. A. Distribution of leaf counts. B. Distribution of heights. C. Means of flower counts. Mann-Whitney-Wilcoxon tests showed significant differences between all metrics (height: W = 105, p = 0.0293; leaf count: W = 79, p = .0033; flower count: W = 93, p = .0022).

DISCUSSION

The results of the study support the argument that competition is an important factor in interactions between *R. sanguineum* and *S. chilense* as well as between individual *S. chilense* plants. Aside from the low water treatment, *R. sanguineum* plants were much more impacted by interaction types and did not show a clear trend between growth and water availability. *S. chilense* plant growth was much more contingent on water availability, with interaction type having a limited role in relative growth. Water availability did not seem to have any impact on plant interactions. A large difference was seen between the *R. sanguineum* plants in each site, with the higher-sunlight site showing far more flowers and leaves as well as greater heights than the lower-sunlight site.

Stress-gradient hypothesis

The stress-gradient hypothesis was not strongly supported by the data from the greenhouse study. Some possible evidence of facilitation was seen in the *R. sanguineum* plants (specifically, several of the conspecific *R. sanguineum* individuals had notably higher relative growth rates than heterospecific or solitary individuals), though the difference between the distributions within the low water treatment group was not statistically significant. By contrast, a great amount of competition was observed particularly among the heterospecific treatments with higher water levels and the conspecific *S. chilense* plants with lower water levels. In particular, *S. chilense* individuals with high water levels were able to crowd out the *R. sanguineum* individuals, greatly reducing their growth when compared to the solitary plants while not being affected to a great degree themselves. Additionally, competition was highly detrimental to the conspecific *S. chilense* individuals with low water levels; all of them experienced mortality and were in fact the only plants to die. This was further supported by the strong correlation between presence of *S. chilense* plants and soil moisture, which suggested that these plants used more water than *R. sanguineum* individuals.

Data from the greenhouse study also suggested that *R. sanguineum* was limited by space, possibly even more than by water availability. There was not a great degree of difference between relative growth rates in the medium and high water treatment groups, and barely any growth was observed in the second month of the study while a large level of growth occurred during the first month. This contrasts with the *R. sanguineum* specimens in the field, many of which had leaf counts exceeding 1000 after only one year of growth. This would suggest that the one-gallon pots were insufficient for development of roots, and may also explain the discrepancy between relative growth of conspecific and solitary plants since it may have been competition over space, not water, which caused conspecific plants to grow less. However, heterospecific growth was still most likely lower due to presence of *S. chilense*, which seemed to be able to take in water more effectively to the detriment of the *R. sanguineum* plants.

This is not consistent with the assumptions of the stress-gradient hypothesis, possibly since plants were already relatively established from the start of the study (as they were not grown from seed due to time and resource constraints) and also were of similar sizes to begin with so there could not be a clear emergence of “nurse plants” which sheltered or provided nutrients to smaller individuals (Noumi et al. 2015). This is more consistent with findings by Wright et al. (2014) which concluded that competition is generally a more dominant force than facilitation and that facilitation was more commonly seen in smaller plants. However, it is difficult to draw parallels based on scale due to the limited scope of my research and the fact that plant size is relative to planting conditions and characteristics of species examined. The nonlinear nature of my data is also consistent with Malkinson and Tielboerger (2010), whose revised framework for the stress-gradient hypothesis focuses largely on the importance of nonlinearity and complexity. However, it is difficult to assess the degree of nonlinearity due to the broad nature of the treatment groups; with only three water treatments and three interaction treatments there is not a high degree of granularity from which models can be developed. On a more general level, it has been found that many plant interactions cannot be adequately summarized by the stress-gradient hypothesis; Maestre et al. (2006) challenge the efficacy of this paradigm and suggest that many of the studies which support the hypothesis are too limited in their scope to provide compelling evidence. However, the study still suggests that these plants are relatively successful when grown together except under extreme conditions, which is important to note as a management issue even without taking into account characterizations of the interactions.

Resource availability

Relative growth rates, moisture levels and field data suggest that resource availability had a major effect on overall growth. The field study showed a large distinction between the sites with high and low sunlight availability, suggesting that restoration projects involving *R. sanguineum* must be developed with consideration given to the question of shading and aspect. The greenhouse study showed that water availability was also very important; a clear trend was seen between relative growth rates and watering regimes ($p < .1$ for *R. sanguineum* and $p << .01$ for *S. chilense*). In addition, in some cases water availability was shown to have a profound effect on interactions. The most pronounced example of this was that all conspecific *S. chilense* individuals in the low water treatment group died after roughly two months while all other plants (all interaction types and all water treatments) survived. Also, soil moisture was found to be much lower in pots containing *S. chilense* plants than in pots with only *R. sanguineum.* This suggests that *S. chilense* plants require large amounts of water and will suffer from mutually detrimental competition when planted together in low-water environments. The greater use of water is likely connected to the higher rates of growth, and may also relate to differing strategies for resource acquisition due to functional traits (Funk et al. 2008). Since *R. sanguineum* grows as a woody shrub while *S. chilense* is herbaceous this physiological difference could be a possible source of functional partitioning and growth strategies. Additionally, *R. sanguineum* may have grown less and used less water due to inadequate space for root growth within the pot, especially since *R. sanguineum* has a taproot structure (which would be limited by vertical growing space) while *S. chilense* grows roots as a rhizome mat which could allow for more lateral spread (Darrouzet-Nardi et al. 2006, Leng et al. 2013). This could also be explained by the idea that juvenile woody plants are less efficient than mature plants at using water (Donovan and Ehleringer 1992). By contrast, aboveground growth of *S. chilense* was able to outpace access to resources in the case of the low-water plants, resulting in mortality.

Interaction types

Relative growth rates suggest that *R. sanguineum* is strongly negatively affected by presence of *S. chilense*, especially when resource availability is high, while *S. chilense* are negatively affected by presence of conspecifics when resource availability is low. This may suggest that some niche partitioning takes place between these plants, and supports the idea that heterospecific growth is a legitimate planting strategy particularly if the focus is on growth of *S. chilense* as they definitely compete with each other in a mutually detrimental manner. Based on observations from the field study, it appears as though *R. sanguineum* is much more robust when space is not limited and can in fact crowd out *S. chilense* after extensive growth, so planting them close together will not necessarily prevent *R. sanguineum* from growing successfully. (Palmer et al. 1997). Other studies have shown that dissimilarity between species allows for a greater deal of facilitation and less competition due to niche partitioning, which allows for more successful restoration projects (Verdu et al. 2012, Martorell et al. 2015).

Limitations

Since the majority of this study only took place on a small scale within the greenhouse it is not possible to definitively apply the findings to a larger scale in a field setting. Only two plant species were examined, and interactions were limited to a maximum of two plants in one pot. It is therefore possible that more complex interactions take place at a larger scale when many plants are interacting (Maestre et al. 2009, Malkinson and Tielboerger 2010, Martorell et al. 2015); these effects would not have been revealed by this study. This is important to note as it means that these results cannot necessarily be extrapolated to larger sites. Similarly, since the study of interactions took place within the greenhouse it did not necessarily reflect field conditions (a field study was initially intended but was abandoned after high mortality resulting from severe weather). Specifically, planting conditions in the greenhouse were isolated and only a certain amount of space was available for each plant to grow laterally, both in terms of aboveground structures and roots. This led to the *S. chilense* plants growing mainly vertically with little lateral growth in the greenhouse while under field conditions they showed more horizontal growth than *R. sanguineum.* As mentioned previously, this also may have introduced a confounding variable in that the *R. sanguineum* plants ran out of space to grow after the first month of the study, particularly if they were lacking in vertical space for growth of taproots. The use of potting soil may also obscure an important factor in restoring urban landscapes where soil quality can be a particularly relevant concern (Pavao-Zuckerman 2008).

While the field study showed a statistically significant difference in plant growth metrics between sites, these comparisons only applied to *R. sanguineum* specimens and did not take interactions into account. Thus, while they provided important insight into the effects of shading on viability of *R. sanguineum* they did not offer information pertinent to restoration projects with biodiversity as a goal.

Recommendations for further research

Future research should mainly involve scaling the project up and examining more restoration-friendly species in a field setting to gain a better idea of how different species impact one another in this context. Experimental studies in the future should also take other resources into account; the field portion of this study showed that sunlight plays a major role as a limiting resource for *R. sanguineum* plants, and it would be beneficial to understand how nutrients are used by each plant species to determine whether niche partitioning takes place (Verdu et al. 2012, Martorell et al. 2015). To take field conditions into account while retaining experimental control over resource availability, treatment groups could have natural water sources supplemented or restricted as part of the design so that pre-established water levels could be held constant over time. Interactions could also be characterized in more depth, such as making comparisons among plants of differing growth stages. Additionally, if the study examined growth over a longer time period a greater degree of detail could be met through determining effects of seasonality and plant age (Vaughn and Young 2010, Wright et al. 2014). Another important point is that these field studies must be conducted under conditions which replicate site conditions where restoration will occur; adaptive management in actual restoration sites would be an ideal means of assessing how the plants would interact and grow in specific areas.

Broader implications and recommendations for management

In closing, these findings suggest that it is feasible to grow *R. sanguineum* and *S. chilense* together for low-water restoration projects in the Strawberry Creek watershed despite any negative effects seen in more extreme cases of interactions. Plants were able to coexist under low water conditions, making them good candidates for drought-conscious restoration. It is important to note that under field conditions plants would not be as close to one another as they were in the greenhouse study, so the issue of *S. chilense* individuals outcompeting each other over limited water would not be a major concern. One recommendation for creek restoration projects would be to plant individuals far enough apart that detrimental interactions and problems caused by insufficient space would be unlikely to happen, and to supplement *S. chilense* plants with water in situations of extreme drought. Since solitary plants did better overall than plants with any interactions, the evidence would suggest that giving each individual even a small buffer zone (regardless of whether nearby plants were of the same or different species) would promote more growth.

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