

Plant-Soil Feedbacks of the Invasive *Centaurea Solstitialis*

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ABSTRACT

There is increasing interest in how plant-soil feedback systems may contribute to plant invasions, and in particular, the enemy-release hypothesis. In this experiment, I conducted a greenhouse experiment to assess the existence and nature of plant-soil feedbacks of *Centaurea solstitialis*. I planted individuals of *C. solstitialis* in sterilized soil, in soil that had never hosted *C. solstitialis*, and in soil that had hosted a variety of densities of *C. solstitialis*. I also planted individuals of the grass *Avena fatua* (a common competitor of *C. solstitialis* in California grasslands) in the same soil categories for comparison. I measured germination, plant height, and root, shoot, and total biomass, and used several statistics to test for plant-soil feedbacks. I found that *C. solstitialis* had higher shoot and total biomass when grown in sterilized soil than when grown in soil that had previously hosted *C. solstitialis*, which suggests a possible negative plant-soil feedback. This would imply that the enemy-release hypothesis may not explain the invasiveness of *C. solstitialis*. Inconsistencies between this study and previous studies are likely the result of spatial and temporal variation of the influence of plant-soil feedback on plant growth, which should be investigated further.

KEYWORDS

invasion ecology, enemy-release hypothesis, California grasslands, plant-soil interactions, greenhouse experiment, Yellow starthistle,

INTRODUCTION

A plant-soil feedback (PSF) is a system where plants impact the soil in a way that has consequences for their own growth. PSFs are defined by two phenomena- one in which plant activity affects an aspect of soil quality, and another in which that aspect of soil quality affects plant growth. PSFs can be either positive (encouraging plant growth) or negative (inhibiting plant growth) and can impact both the plant that initiated the PSF and neighboring plants. Over the past two decades, PSFs have gained a lot of attention in research. (Ehrenfeld et al. 2005, Van der Putten et al. 2013). PSFs can help us understand many dynamics in plant biology, such as diversity and interspecific competition (Fukami and Nakajima 2013, Dias et al. 2104), and in particular, dynamics in invasion ecology.

Much of the literature concerning PSFs published in the last few years has focused on the role that PSFs of invading plants may play. (Lee et al. 2012, Bozzolo and Lipson 2013, Maron et al. 2014). The enemy-release hypothesis proposes that invasive species often outcompete native species because they are less impacted by inhibitive PSFs (Lee et al. 2012, Maron et al. 2014). This hypothesis is largely consistent with the PSF literature (Kulmatiski et al. 2008). PSFs may also play roles in invasion ecology outside of that proposed by the enemy-release hypothesis; for example, one invasive plant may encourage its growth by increasing nitrogen in the nearby soil (Lee et al. 2012). Ultimately, the PSFs of any specific invasive weed have to be examined for knowledge of PSFs to be of any use to management of that weed.

Centaurea solstitialis, a widespread invasive weed in North America also known as the yellow starthistle, is considered one of California's highest-priority weeds (Pitcairn et al. 2006, Julia et al. 2006); it has become California's most common weed, covering 14.3 million acres of California land in 2006 (Pitcairn et al. 2006). Because it is poisonous to horses and cattle are unwilling to graze it, *C. solstitialis* reduces the usefulness of rangelands it invades. (Pictairn et al. 2006). Through these damages to rangelands, along with loss of wildlife habitat, and decreases in water quality control, *C. solstitialis* can result in serious economic loss (Julia et al. 2006). The range of *C. solstitialis* in California is only expected to increase (Pitcairn et al. 2006), and *C. solstitialis* will likely only become more competitive as the world's climate changes (Dukes et al. 2011) Biocontrol agents which have been introduced have probably done all they can to halt the spread of *C. solstitialis* (Gutierrez et al. 2005), meaning more active and educated management

practices will be required to address the issue. It has already been established that the *C. solstitialis* has PSF's (Batten et al. 2006), but the details of the nature of those PSFs, such as their direction, impacts on other plants, and thresholds, have not.

In this project I sought to address the nature of PSF's of the *C. solstitialis*, asking three questions: whether or not PSF's of the *C. solstitialis* are present, whether are they positive or negative, and whether or not they are only active above or below certain thresholds. Following the literature and enemy-release hypothesis, I predicted that I would find negative PSF's. In order to address these questions, I collected biometrics of *C. solstitialis* and another rangeland plant, *Avena fatua*, grown in soil which had previously fostered different densities of *C. solstitialis*

METHODS

With this experiment, I sought to explore possible density-dependent plant-soil feedbacks of *C. solstitialis* by measuring biometrics of plants grown in soils which had hosted varying densities of *C. solstitialis*. The experiment was a greenhouse experiment, conducted at the Oxford Tract at UC Berkeley. The methods of this experiment were based on those of a previous experiment conducted by Pierre Mariotte, and are similar to those conducted to establish plant-soil feedbacks for other plants.

Field site

This experiment ties into a larger field study of threshold dynamics of invasive weeds in California. The site of that field study is located at the Sierra Foothills Research Extension Center, or SFREC, (39°14'N, 121°18'W), a rangelands ecosystem research center 60 miles northeast of Sacramento. The field site is divided into plots which were seeded to varying degrees with invasive weeds to establish density gradients of each weed, ranging from zero individuals per square meter to 10,000 individuals per square meter. Both inside and outside of the plots, the site is completely dominated by the invasive grass *Avena fatua*.

Seed and soil collection

I obtained my experimental inputs of soil and seeds of *C. solstitialis* from the SFREC field site. I collected the *C. solstitialis* seedheads by removing them from live plants in areas of high *C. solstitialis* density at the SFREC in late August 2014. At that time I also dissected the seedheads to gather the seeds. *A. fatua* seeds were purchased in bulk from Pacific Coast Seeds Inc., which collected them from Northern California, so that the effects of *C. solstitialis* on both itself and plants it could potentially displace could be investigated. *A. fatua* is also invasive to North America, and covers many California grasslands and often co-exists with the *C. solstitialis*. To reduce disturbance to the field experiment, the bulk of the soil for my experiment was collected by shovel from areas outside the borders of the field plots, and then autoclaved at the Oxford Tract in late August 2014. I then collected soil inoculum with a spoon and measuring cup from 32 different *C. solstitialis* plots representing a range of *C. solstitialis* density (zero individuals seeded per square meter to 48 individuals seeded per square meter), and from three high-density *C. solstitialis* areas outside of the field experiment. I sampled from the high-density areas because poor *C. solstitialis* recruitment that year left me with few truly high-density plots in the field experiment; to collect this soil I simply collected soil from as close to directly underneath the individuals in thick *C. solstitialis* patches as possible. To collect the soil inoculum, I mixed and bagged soil from the top 5 centimeters of five different spots within each square meter plot. There were 35 bags of soil, one from each plot sampled, and these bags of soil inoculum were kept on ice until they were ready to be added to the greenhouse experiment.

Greenhouse set-up

To provide as much control over the experiment as possible, I conducted the experiment in a greenhouse. I set up the greenhouse experiment in late August 2014. This experiment consisted of 250 1.5-inch diameter cone pots. I added sterilized soil and three *C. solstitialis* seeds to half of these cones; to the other half I added sterilized soil and three *A. fatua* seeds. From each bag of soil inoculum (corresponding to a particular field plot) I added 20 g of soil each to three *C. solstitialis* cones and three *A. fatua* cones. Forty control cones (twenty for each species) had no soil inoculum added to them.

Management and harvest

To allow time to show differences in growth, the seeds were allowed to grow for fourteen weeks before being harvested for biometrics. After planting, I watered the cones three times a weekly, and during the growing period I monitored the plant heights and germination. After a period of learning to identify the plants, I began to remove plants so that there was only one individual in each cone. After one month, I re-planted two seeds each in each pot which had not yet germinated, so that I would have enough plants at harvest time for meaningful results. After fourteen weeks, I took a final measurement of height from soil level to the top of the highest stem for each plant, in centimeters, and removed them from the cones. I cleaned each plant of soil clinging to the roots, dried them in the heating oven overnight, and separated the root and shoot biomass. I weighed the root and shoot biomasses separately for each plant, in grams, and then took the sum for total biomass.

Data analysis

I ran a series of statistics using R 3.1.2 to test for plant soil feedbacks. I used chi-squared tests and analyses of variance to test for differences in plant germination and growth between individuals grown in soil of three different backgrounds (sterilized soil, soil which has hosted *C. solstitialis*, and soil which has not hosted *C. solstitialis*). I then used linear regressions and logistic regressions to test the effects of *C. solstitialis* density, as a stand in for the severity of a *C. solstitialis* invasion. I also tested effects density by using analyses of variance and comparing between low, medium, and high *C. solstitialis* densities. For the analyses of variance and linear regressions, I used the biometrics height, root biomass, shoot biomass, and total biomass.

RESULTS

Means testing for feedbacks

I used chi-squared tests and analyses of variance to test for the presence of any plant-soil feedbacks. I separated the individuals into those grown in sterilized soil, those grown in soil which had hosted *C. solstitialis* in the field, and those grown in soil which had never hosted *C. solstitialis*. Using chi-squared tests, I tested for differences in germination rates between these three groups, and using analyses of variance, I tested for differences in plant height (cm), root biomass (mg), shoot biomass (mg) and total biomass (mg) between the three groups. The chi-squared tests (Table 1) did not produce significant results for *C. solstitialis* ($X^2=4.527$, $p=0.104$) or *A. fatua* ($X^2=1.708$, $p=0.426$).

Table 1. Results of chi-squared tests on germination.

Germination	<i>C. solstitialis</i>		<i>A. fatua</i>	
	Yes	No	Yes	No
Sterilized	18	2	19	0
No <i>C. solstitialis</i>	5	4	8	1
<i>C. solstitialis</i>	68	28	90	6

Before running analyses of variances, I tested that the data for each biometric matched the assumptions of the test, normal distributions within groups and homogeneity of variances between groups. I used Shapiro-Wilk tests to test the normality of each group and Bartlett tests to test the homogeneity of variances. In each case, for both plant species and all three biometrics, the untransformed data did not match all of these criteria, but at least one transformation of the data did. For all *A. fatua* biometrics and *C. solstitialis* height, this was the base-ten logarithm. For *C. solstitialis* biomass, the square root provided the best match for the criteria. I ran analyses of variance on both the transformed data and untransformed data, and found the results were very similar between cases. As such, the results for the untransformed data are provided here. I disregarded individuals which did not germinate for the purposes of the analyses of variance. The *A. fatua* data yielded no significant results for any biometric (Figure 1;

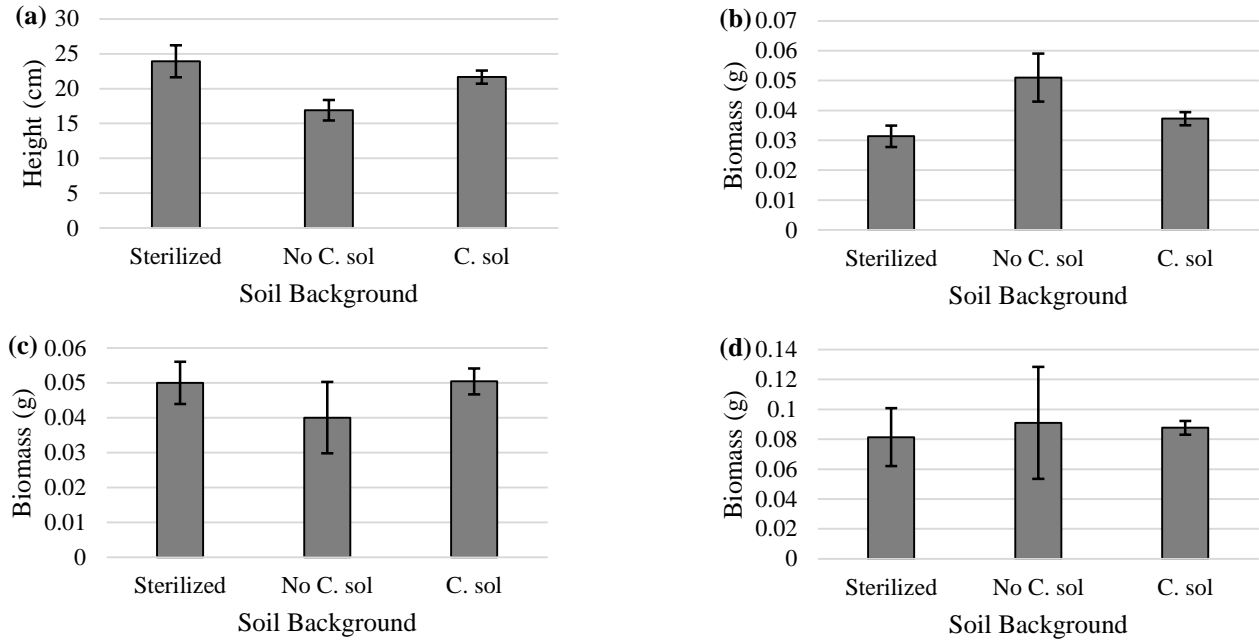


Figure 1. Differences in *A. fatua* growth between different soil treatments. There were no significant differences for (a) height or (b) root biomass, (c) shoot biomass, or (d) total biomass.

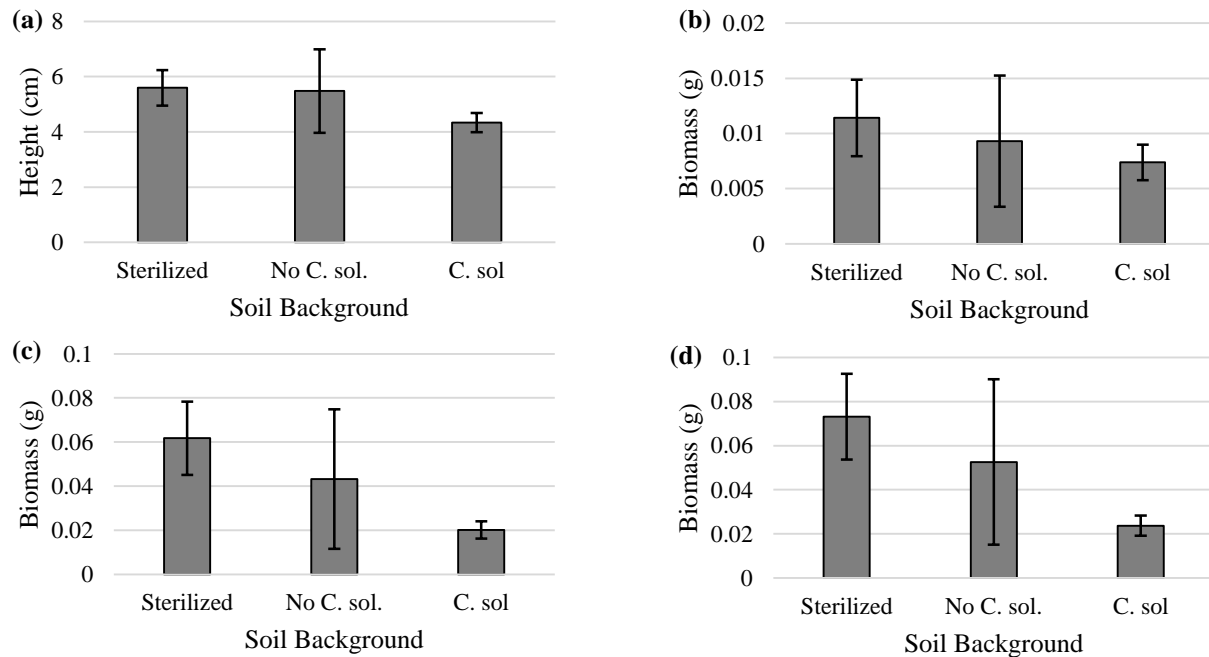


Figure 2. Differences in *C. solstitialis* growth between different soil treatments. There were no significant differences for (a) height or (b) root biomass, but (c) shoot biomass and (d) total biomass were higher for sterilized soil than soil with a history of hosting *C. solstitialis*.

height $F(2, 114)=1.782$, $p=0.173$; root biomass $F(2, 114)=2.6$, $p=0.0787$; shoot biomass $F(2, 114)=0.349$, $p=0.706$; total biomass $F(2, 114)=0.152$, $p=0.859$). This was also true of *C. solstitialis* (Figure 2) height ($F(2, 88)=1.517$, $p=0.225$) and root biomass ($F(2, 77)=0.647$, $p=0.526$). However, I did find significant results for shoot biomass ($F(2, 77)=5.771$, $p=0.00462$) and total biomass ($F(2, 87)=6.282$, $p=0.00283$). In both cases, biomass of individuals grown in sterilized soil was greater than of those grown in soil which had previously hosted *C. solstitialis*.

Regression analysis

I used regression analysis to test for relationships between the *C. solstitialis* density in the field plots and plant growth in the greenhouse experiment. I used a logistic regression to test for a relationship between density and germination, and linear regressions to test for relationships between density and the aforementioned biometrics. The logistic regressions (Figure 3) did not produce significant results for *C. solstitialis* ($p = 0.1109$) or *A. fatua* ($p = 0.332$).

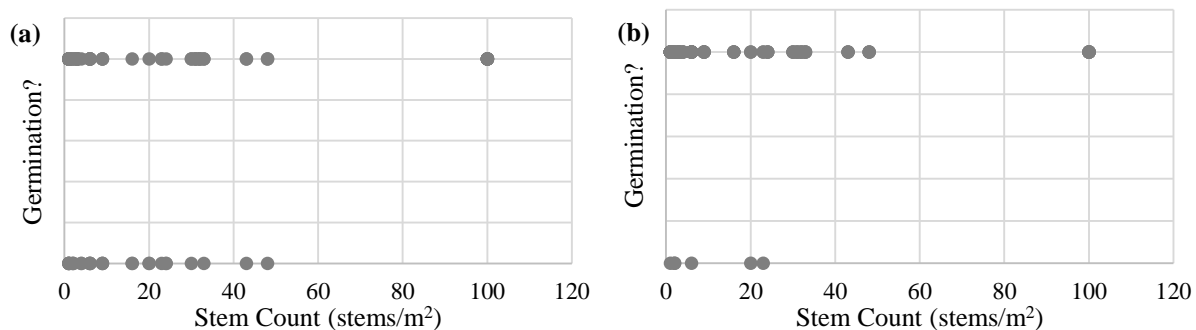


Figure 3. Germination rates by density. Germination for (a) *C. solstitialis* and (b) *A. fatua*, with no significant relationship with density for either.

As with the analyses of variances, before conducting linear regressions, I tested various transformations of the data to see how well they match the assumptions of linear regression. I used Shapiro-Wilk tests to test both the data themselves and their residuals for normality. As before, in all cases there was a transformation which matched the criteria better than the untransformed data. These transformations were the same as those most appropriate for the analyses of variance. Just as before, I found that the results of the linear regression of the untransformed data were very similar to those of the transformed data, and so the results for the untransformed data are presented

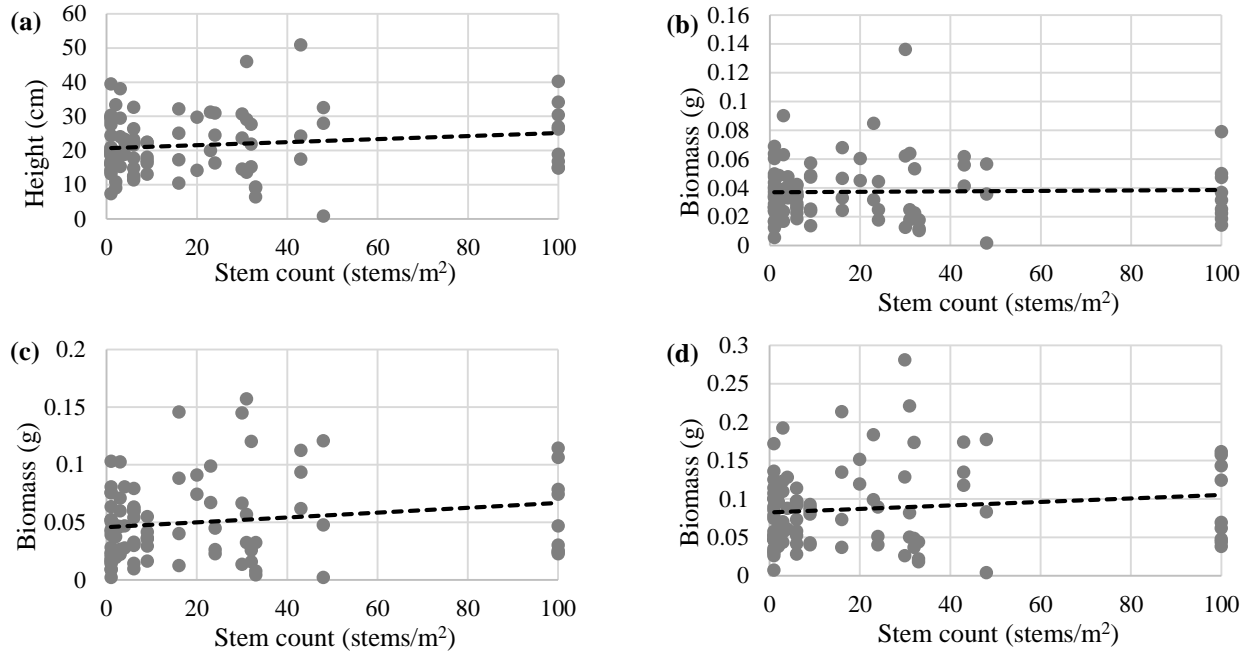


Figure 4. Relationship between *A. fatua* growth and *C. solstitialis* density. No significant relationship was found for (a) height, (b) root biomass, (c) shoot biomass, or (d) total biomass.

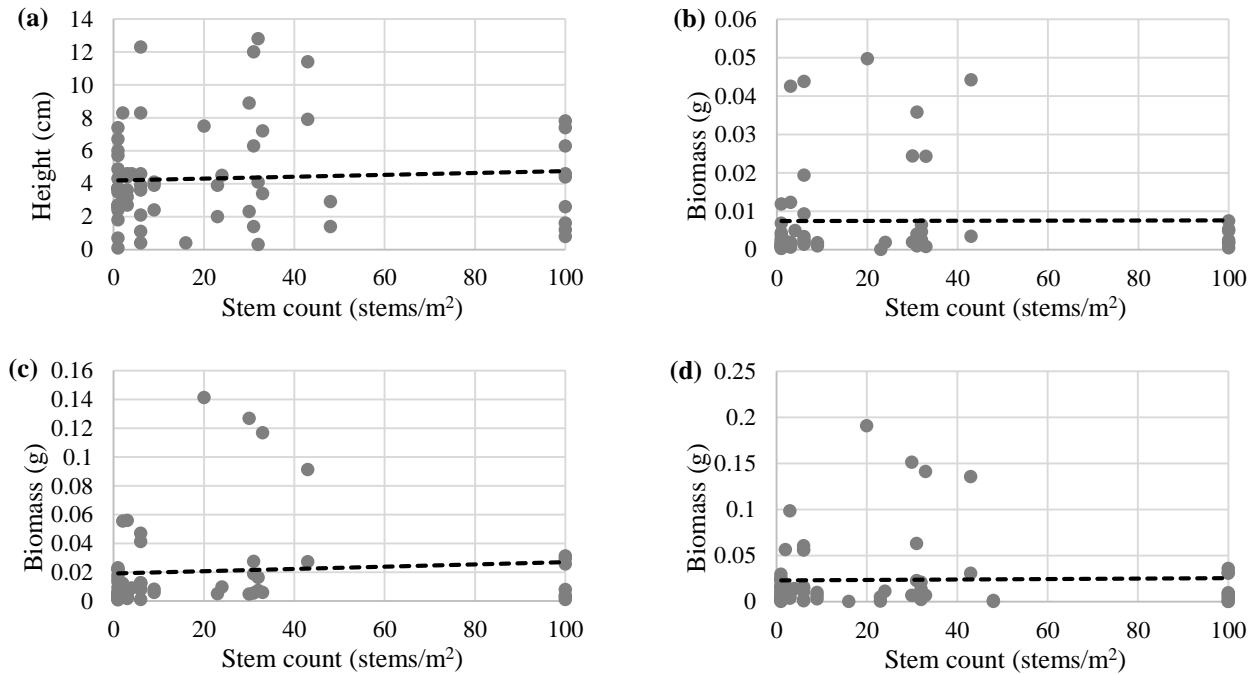


Figure 5. Relationship between *C. solstitialis* growth and *C. solstitialis* density. No significant relationship was found for (a) height, (b) root biomass, (c) shoot biomass, or (d) total biomass.

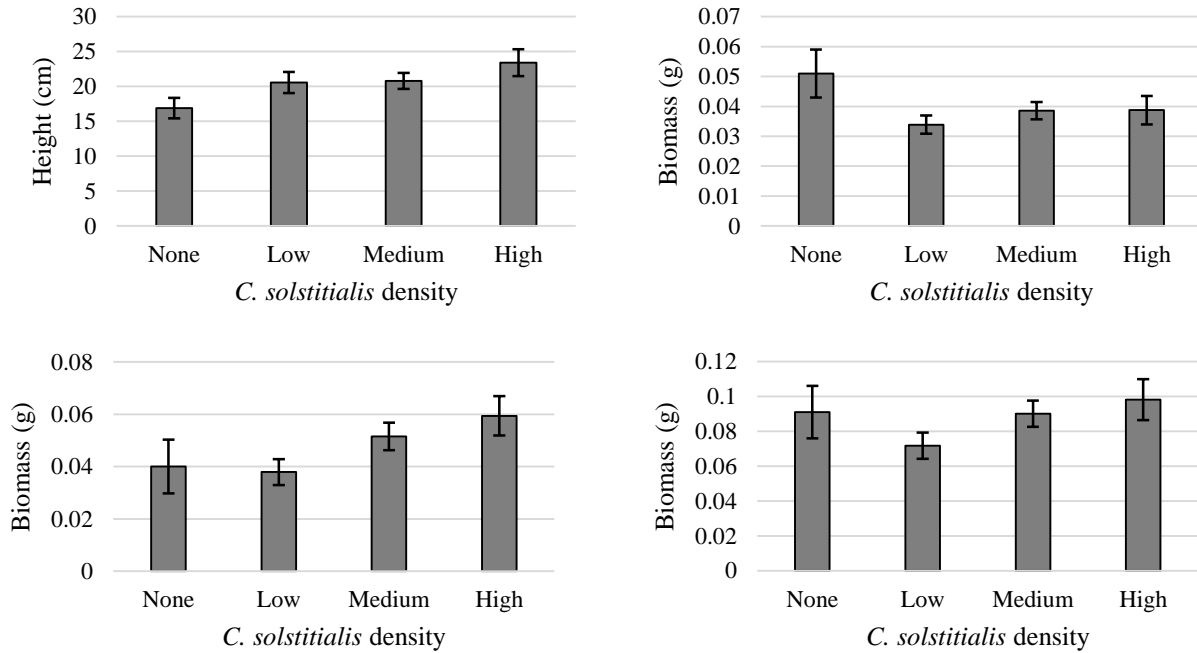


Figure 6. Differences in *A. fatua* growth between *C. solstitialis* density groups. No significant differences were found for (a) height, (b) root biomass, (c) shoot biomass, or (d) total biomass.

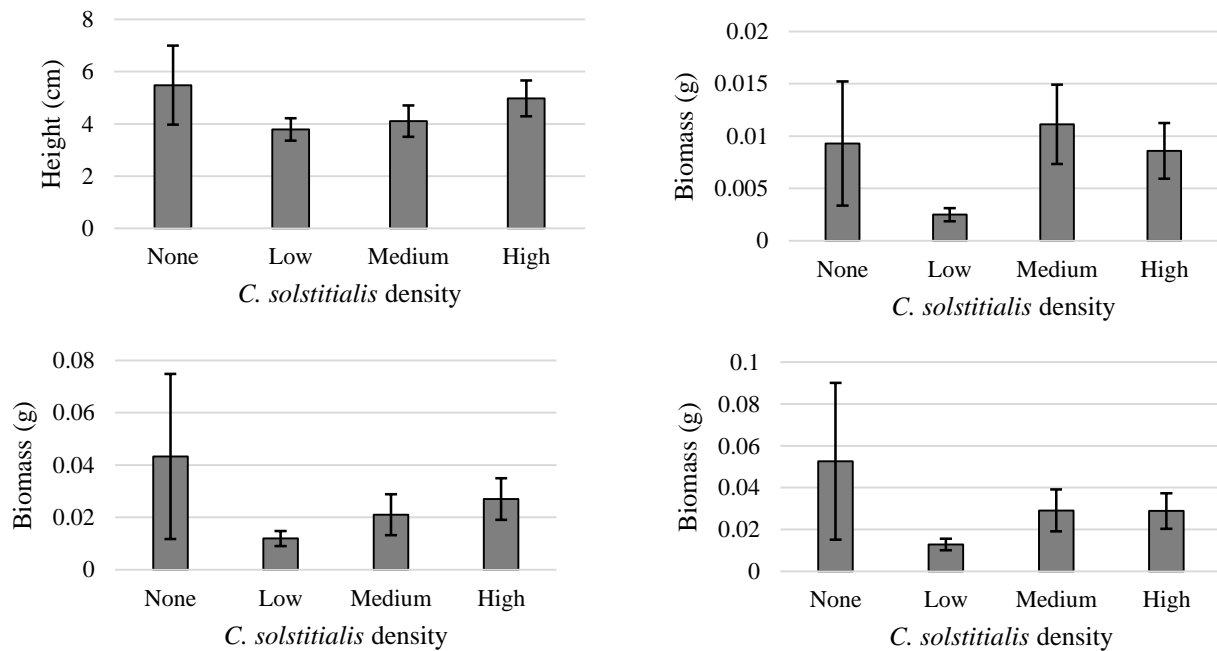


Figure 7. Differences in *C. solstitialis* growth between *C. solstitialis* density groups. No significant differences were found for (a) height, (b) root biomass, (c) shoot biomass, or (d) total biomass.

here. I found no significant results from the linear regressions for either *A. fatua* (Figure 4; height $R^2=0.0228$, $F(1, 88)=2.055$, $p=0.1552$; root biomass $R^2=5.549 \times 10^{-4}$, $F(1, 88)=0.0481$, $p=0.827$; shoot biomass $R^2=0.0312$, $F(1, 88)=2.838$, $p=0.0956$; total biomass $R^2=0.01613$, $F(1, 88)=1.443$, $p=0.2329$) or *C. solstitialis* (Figure 5; height $R^2=0.00393$, $F(1, 66)=0.2607$, $p=0.6113$; root biomass $R^2=3.598 \times 10^{-5}$, $F(1, 56)=0.00202$, $p=0.9644$; shoot biomass $R^2=0.00649$, $F(1, 56)=0.3655$, $p=0.5479$; total biomass $R^2=3.958 \times 10^{-4}$, $F(1, 66)=0.0261$, $p=0.8721$).

Means testing for density effect

I ran further analyses of variances to test for differences in plant growth between individuals grown in soil from high, medium, and low *C. solstitialis* density plots. In addition to the linear regressions, this was to test for specific thresholds for any plant-soil feedbacks. I defined low-density as one or two individuals of *C. solstitialis* in one plot, medium density as ranging from three to twenty individuals per plot, and high density as twenty or more individuals per plot. I also included a group for plots which had no *C. solstitialis*. I found no significant differences (Figure 6) between these groups for any biometric for either *A. fatua* (height $F(3, 113)=0.637$, $p=0.592$; root biomass $F(3, 113)=0.321$, $p=0.81$; shoot biomass $F(3, 113)=0.924$, $p=0.434$; total biomass $F(3, 113)=1.434$, $p=0.237$) or *C. solstitialis* (height $F(3, 69)=1.517$, $p=0.225$; root biomass $F(3, 59)=1.686$, $p=0.18$; shoot biomass $F(3, 59)=1.229$, $p=0.307$; total biomass $F(3, 69)=1.381$, $p=0.256$).

DISCUSSION

These results have implications for both the ecology of *C. solstitialis* and the enemy-release hypothesis. The goal of this study was to identify plant-soil feedbacks for this population of *C. solstitialis* and any thresholds for those feedbacks. I found differences in *C. solstitialis* between soil treatments which indicate a negative plant-soil feedback, but found no evidence of any relationship between that plant-soil feedback and *C. solstitialis* density. By examining these results in light of similar studies and the enemy-release hypothesis, conclusions can be drawn about new implications for the enemy-release hypothesis.

Plant-soil feedbacks

The difference in biomass between individuals of *C. solstitialis* grown in sterilized soil and soil from *C. solstitialis* plots indicates the presence of a plant-soil feedback. Because individuals grew larger in sterilized soil, this plant-soil feedback is probably caused by a soil pathogen, which is the most common mechanism of plant-soil feedbacks (Ehrenfeld et al 2005). Since there was no difference in growth between individuals grown in *C. solstitialis* plots and plots without *C. solstitialis*, this pathogen was likely present in the soil as a consequence of the *C. solstitialis*. However, since there was no difference between individuals grown in sterilized soil and in soil from plots without *C. solstitialis*, it is possible that there were additional general pathogens present in the soil as well. It is also possible that that lack of difference is the result of differences in sample size. In addition to the presence of a plant-soil feedback, these results also indicate the nature of the feedback.

This plant-soil feedback is a negative plant soil feedback, since *C. solstitialis* grew better in soils without a history of hosting *C. solstitialis*. Negative plant-soil feedbacks are much more common than positive ones (Kulmatiski et al. 2008), and negative plant-soil feedbacks for *C. solstitialis* have already been demonstrated (Andonian et al. 2011). This conclusion, at first glance, isn't particularly surprising. *C. solstitialis* is an annual forb. Forbs tend to be more negatively affected by plant-soil feedbacks, and annual plants tend to be significantly more negatively affected than perennial plants (Kulmatiski et al. 2008).

Since there was no difference in growth between individuals of *A. fatua* grown in soil of any of the three backgrounds, the pathogen or pathogens which caused the negative plant soil feedback must be species-specific pathogens of *C. solstitialis*. This is interesting because it suggests that the enemy-release effect does not apply to *C. solstitialis* in California soils. The enemy-release effect has been found to vary for *C. solstitialis* before, with populations in invaded California soils receiving the least negative plant-soil feedbacks while those in invaded Argentinian soils received even more negative plant-soil feedbacks than *C. solstitialis* in its native European ranges (Andonian et al. 2011). The enemy-release hypothesis hinges on non-native species having fewer "enemies" (less negative plant-soil feedbacks) and more mutualistic symbionts (more positive plant-soil feedbacks) in invaded soils (Callaway and Aschehoug 2000). This is largely consistent with the literature; non-native species receive less negative plant-soil

feedbacks, in general, than native species (Kulmatiski et al. 2008). Two aspects of *C. solstitialis* ecology in California could explain why it continues to suffer negative plant-soil feedbacks. First, species with large non-native ranges such as the *C. solstitialis* seem to benefit less from the effects of enemy-release and have more negative plant-soil feedbacks, perhaps since the more established a species is in a non-native soil, the more likely its pathogens have colonized the soil as well (Agrawal et al. 2005). Second, enemy-release is expected to be lower in the presence of native congeners whose pathogens can colonize the non-native species (Agrawal et al. 2005). Since *C. solstitialis* has likely been present in California for around a century and a half (Pitcairn et al. 2006), and there are other (also non-native) *Centaurea* species present in California, it is unsurprising that the enemy-release hypothesis would not apply particularly well to *C. solstitialis* in California.

The impact of density

What made this experiment different from other greenhouse plant-soil feedback experiments is that in this experiment I investigated the effect that plant density has on plant-soil feedbacks. Positive plant-soil feedbacks at high densities could be a mechanism for fast paced invasion, while negative plant-soil feedbacks at high densities could be a limiting factor for invasion and the growth of *C. solstitialis* patches. My results indicated that there were no effects of density on growth, that is, that the plant-soil feedback I found is not density-dependent.

Limitations

The effects of plant-soil feedbacks have been found to vary significantly between species, population, and year (Agrawal et al. 2005). Variation in the population of soilborne pathogens and above-ground herbivores from year to year may result in stronger years and weaker years for plant-soil feedbacks, and therefore range expansion (Agrawal et al. 2005). As a result, my results are likely to be fairly specific. My results are probably a poor predictor of plant-soil feedbacks for other species, for other populations of *C. solstitialis*, and in future years for my population of interest, though this might suffer from the least variation

Future Research and Conclusions

Since *C. solstitialis* suffers from negative plant-soil feedbacks in California soils, its spread should be, to an extent, limited by soilborne pathogens as most plants are. This relationship could be used to combat the invasion of *C. solstitialis* into California rangelands. Future research to that end would likely include identifying specific pathogens of *C. solstitialis* present in California soils. Greenhouse experiments are already common for identifying plant-soil feedbacks of invasive species, but are not commonly used for assessing the significance of plant density as in this experiment. Further experiments could address whether there is any relationship between plant-soil feedbacks and density for other invasive species of interest.

In California soils, *C. solstitialis* suffers from a negative, species-specific plant-soil feedback, which defies the enemy-release hypothesis. However, instead of refuting the enemy-release hypothesis, these results simply indicate how the enemy-release effect can weaken over time, and under certain ecological conditions, and illustrate how assessment of plant-soil feedbacks can be informed by a solid understanding of a population's ecological history.

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