

INTRASPECIFIC VARIATION IN SANDBERG BLUEGRASS (*POA SECUNDA*)'S RESISTANCE TO
ANNUAL GRASS INVASION

BY

EMILY COOK

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ANNUAL GRASS INVASION

Approved: 

Lauren Hallett

Exotic species pose a threat to many ecosystems within the western U.S. The annual grass species known as cheatgrass (*Bromus tectorum*) is a prevailing invader in the Great Basin. Cheatgrass invasion in combination with a change in fire regime and climate exacerbate large fires in the region, contributing to loss of native plant species. Seeding of native perennial grass species has been adopted as a management strategy for post-fire rehabilitation. Native grass species are known to have high variability in traits across climate and space. Knowing this, some populations may be better at resisting invasion to cheatgrass than others. This study explores how water availability and intraspecific variation in traits affects the native Sandburg bluegrass' (*Poa secunda*) capacity to resist invasion by cheatgrass. I hypothesize that (1) *P. secunda*'s resistance to cheatgrass will decline with reduced water availability, but *P. secunda* populations from warm and arid source environments will have a smaller decline than those from cooler and wetter environment, (2) that the *P. secunda* populations from warmer, drier areas will be shorter in height, have lower SLA, and higher LDMC and (3) that *P. secunda* populations with greater trait plasticity will better resist invasion to cheatgrass. Seeds from five populations of *P. secunda* within the Great Basin were collected and sown in monocultures and in competition with cheatgrass in a greenhouse. I evaluated relationships between several leaf and plant traits with a wet and dry treatment. Significant trait variation was found among populations and between wet and dry treatments. These findings suggest that using seeds that are locally adapted to a restoration area can be beneficial to plant fitness and resistance to invasion. Considering traits connected with disturbance and invasion is valuable to restoration work in the region.

Intraspecific Variation in Sandberg Bluegrass (*Poa secunda*)'s Resistance to Annual Grass Invasion

Environmental Science Honors Thesis
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Introduction

Background

Exotic species pose a threat to many ecosystems across the western U.S. An example of this is the annual grass species known as cheatgrass (*Bromus tectorum*), a prevailing invader in the Great Basin. The Great Basin has hosts of native plant and animal species. However, cheatgrass invasion in combination with a change in fire regime and climate exacerbate large fires in the region. These factors contribute to loss of native plant species and native perennial grasses in particular, which are excellent at resisting cheatgrass invasion (Billings 1990). Restoration efforts in the Great Basin aim to reestablish native species where successful restoration is achieved when native plants are able to resist invasion by cheatgrass (Funk et al. 2008). A prominent question for restoration within the Great Basin is what to look for when choosing native plants. This study explores how within species trait variation may create an advantage for native grasses in competition with cheatgrass in a region where shifting climate may alter water availability.

Shifts in fire regimes are one obstacle preventing successful restoration. Cheatgrass has quickly altered the fire regime in western North America by increasing fuel continuity (Brooks et al. 2004). This in turn has led to an increase in fire frequency and size (Brooks et al. 2004). Cheatgrass tends to replace native grass stands following disturbance, particularly following fire, and its early senescence results in fine and continuous layers of fire fuels. This results in catastrophic megafires (100,000 acres). Previously, low-intensity fires were utilized by the Paiute people to reduce fire fuel (McAdoo et al. 2013), but Euro-American settlement has since largely suppressed fire, leading to greater amounts of fuel (Kimmerer and Lake 2001). This change in fire management paired with a shift in climatic conditions make the current Great Basin grasslands even more susceptible to cheatgrass invasion.

Similarly, shifting climate conditions may favor cheatgrass establishment. Climate is highly variable across time and space in the Great Basin. The mean annual precipitation was approximately 10.5 inches between 1980 and 2010 in the northern Great Basin (Davies et al. 2016) but fluctuates from lows of approximately 5.6 inches to highs of around 16.8 inches over the years (PRISM 2015). Spring and summers in the future are predicted to be hotter and drier in the Great Basin, as well as an expected extension of fire season, while winters are predicted to increase in precipitation (Germino et al. 2016). Native plant species are well adapted to these variable environments. Perennial life history trait is one of the adaptations to this fluctuating environment. Cheatgrass is a winter annual, whose germination occurs in early fall and winter due to increased precipitation (Mack and Pyke 1983). An increase in temperature and altered precipitation due to climate change are likely to further shift the range of favorable conditions for cheatgrass (Bradley et al. 2016), which is well adapted to wet winters and dry summers. This shift in germination window creates advantageous conditions for cheatgrass to expand and invade ecosystems which were previously resistant to invasion, particularly if increased precipitation occurs during crucial germinating and growth periods for cheatgrass (Germino et al. 2016).

As the Great Basin becomes more prone to cheatgrass establishment, restoration strategies that target effective competitors are more likely to be successful long term. Cheatgrass are excellent competitors with native species due to its early germination, accelerated growth, and high reproductions (Germino et al. 2016). These traits make cheatgrass a serious concern to ecologists and managers who must manage ecosystems in a way that makes them resilient to disturbances and resistant to invasion (Germino et al. 2016). To prevent further invasion of cheatgrass, and more large wildfires in the Great Basin, seeding of native perennial grass species has been adopted as a management strategy for post-fire rehabilitation and to establish new populations. However, for restoration to be successful long term, perennial grasses must be able to resist the invasion of cheatgrass.

One promising candidate is Sandberg bluegrass (*Poa secunda*), a perennial native grass species. They grow in a large spatial range, from Mexico to south-central Canada (NRCS Plant Guide). In the Great Basin, *P. secunda* is often used for post-fire rehabilitation - they grow in a large spatial range from warmer, drier deserts in Nevada to cooler, moister deserts in Oregon. Native grass species are known to have high variability in traits across climate and space (Baughman et al. 2019). Knowing this, some populations of *P. secunda* may be better at resisting invasion to cheatgrass than others.

One approach to selecting suitable seed for restoration may be to select specific traits that are appropriate to the region and similar to competitive invaders (Funk et al. 2008). At regional or smaller scales, intraspecific trait variation can vary significantly within species for traits such as specific leaf area (SLA) and leaf dry matter content (LDMC) (Roybal and Butterfield 2019). Additionally, seed mass can have considerable effects on germination, whose timing can be a strong predictor of plant survival (Leger and Baughman 2015). Since it is known that plants and native grasses show intraspecific variation among populations (Bucharova et al. 2016; Baughman et al. 2019), the question of which population will be most successful to introduce as seed arises. Using seeds that are locally adapted to the restoration area can be beneficial to plant fitness (Bucharova et al. 2016), as well as their performance and survival in the context of disturbance and invasion (Leger and Baughman 2015). The seeds used should be able to perform effectively in the environmental conditions, resist competitive invasive species, and withstand periodic wildfire (Leger and Baughman 2015). Thus, considering traits connected with disturbance and resistance to invasion is valuable to restoration work in the region (Leger et al. 2019).

Due to the wide array of traits that a plant may display the question of which traits to measure becomes important. For example, plant size (measured by height), seed size (measured by mass), and leaf structure (measured by specific leaf area or leaf dry-matter content) are commonly considered pertinent due to their significant influence on plant performance and ease of measurement (Perez et al. 2013; Schroeder et al. 2016). It is helpful to note which traits we expect to be variable, and how those traits may affect a plant's ability to perform. Both dry biomass weight and SLA are important components to determining relative growth rate, which is a suggestive indicator of plant productivity, particularly in the context of how a plant responds to stress and disturbance (Perez et al.) such as drought. Plant height is expected to be highly variable within and across species (Perez et al. 2013). Plant height can be suggestive of a plant's ability to compete, along with its potential lifespan and fecundity. (Perez et al. 2013). SLA can often be more variable within species than LDMC (Roybal and Butterfield 2019), and we expect species from resource rich environments to have higher SLA than those from resource poor environments. LDMC often correlates negatively with relative growth rate and positively with

leaf lifespan. Leaves with high LDMC are often somewhat robust, and more resistant to physical vulnerabilities like wind or hail. Leaves with high LDMC tend to be linked with productive, highly disturbed environments. Finally, seed mass is expected to be variable. Stored resources in large seeds usually help young seedlings survive and establish during environmental stress (i.e., drought). Additionally, smaller seeds tend to be buried deeper in the soil, which aids in their longevity in seed banks (Perez et al. 2013).

Seedling traits may affect the ability of a native grass to resist invasion by cheatgrass in the future if conditions are warmer and drier. The environmental condition that selects the subset of species in the community may shift towards native grass exclusion and cheatgrass invasion as the climate in the Great Basin becomes drier (Funk et al. 2008). Previous studies have shown that populations of a native perennial grass (*Elymus elymoides*) from arid environments germinated faster than populations from cooler environments (Leger et al. 2019). Because cheatgrass has early fall germination, native plants with early emergence will be able to better compete with cheatgrass and resist invasion.

Hypotheses

This study explores how water availability and intraspecific variation in traits affects a native grass' capacity to resist invasion by cheatgrass. We will examine which populations, and which traits, are correlated with resistance. (1) I hypothesize that *P. secunda*'s resistance to cheatgrass will decline with reduced water availability, but *P. secunda* populations from warm and arid source environments will have a smaller decline than those from cooler and wetter environments. (2) I hypothesize that the *P. secunda* populations from warmer, drier areas will be shorter in height, have lower SLA, and higher LDMC. (3) I hypothesize that *P. secunda* populations with greater trait plasticity will better resist invasion to cheatgrass.

Methods

This study uses a greenhouse experiment at the University of Oregon with a cheatgrass competition treatment on five populations of *P. secunda*. *P. secunda* seeds were collected across a latitudinal range within the Great Basin from June to July 2019 (Burns, OR; Steens, OR; Water Canyon, NV; Reno, NV; Butte Valley, CA). Cheatgrass seeds were collected June 2019 from Burns, Oregon. Each population of *P. secunda* was sown both in monocultures and in competition with cheatgrass in 7x7x7 cm pots with eight replicates (6 *P. secunda* populations x 2 competition treatments x 8 replicates = 96 total) in November 2020. Monocultures of *P. secunda* were sown as a control. Fifty seeds of cheatgrass seeds were sown with 25 seeds of *P. secunda* in competition pots, and 25 seeds of *P. secunda* were sown in monocultures per pot. Each pot was filled with mixed soil (3:1 ratio of soil collected in the field: vermiculate) and seeds were sown ¼ in. deep. Wet trays were watered 2 L per tray (12 pots per tray) twice per week, while dry trays were watered 0.5 L per tray twice per week. Other species that germinated from the collected soil were removed. The wet treatment is established by the average monthly precipitation level in Butte Valley, CA (approximately 3 inches). The dry treatment is established by the average monthly precipitation level in Winnemucca, NV from November to April (approximately 0.8 inches). Soil moisture levels were tracked weekly using a Terros 10 soil moisture sensor (METER Group, Inc). Temperatures within the greenhouse were set to 65 F and artificial lights were on from 6 am to 6 pm.

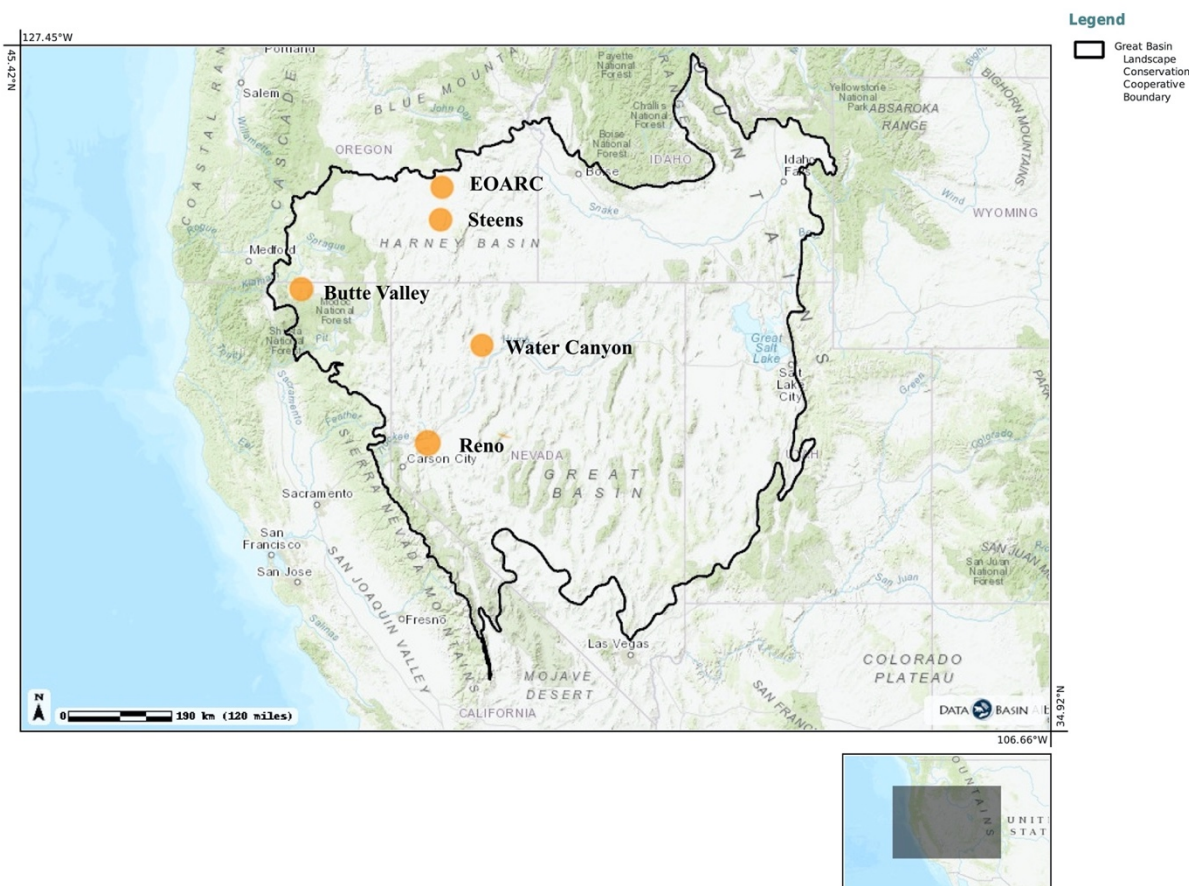


Figure 1. A map of sites where *P. secunda* seeds were collected (Burns, OR; Steens, OR; Water Canyon, NV; Reno, NV; Butte Valley, CA.) The boundary of the Great Basin outlined in black. Source: Conservation Biology Institute.

Traits

We began measuring traits when roots began to show from the bottom of the pots. We counted stems of *P. secunda* in January. We clipped aboveground biomass and dried them at 60° C for 48 hours to be weighed. We measured the fresh leaf and dry biomass weight, leaf surface area and height, and seed weight. We scanned leaves using a Canon scanner and used ImageJ to calculate surface area for each leaf. After leaves were scanned, they were placed in an oven to determine their dry mass. Up to five leaves from each pot were measured and averaged. Specific leaf area (SLA) is the area of a leaf divided by its dry mass (Perez et al. 2013). Leaf dry matter content (LDMC) is the oven-dry mass of a leaf divided by its fresh mass. Plant height is the shortest distance between the ground level and the upper limit of the selected leaf excluding an inflorescence (Perez et al. 2013). Ten replicates of 10 seeds were averaged to determine seed mass.

Analysis

All statistical analyses were calculated within RStudio (R Version 1.3.1093). We calculated means and standard errors of emergence and biomass as proxies for *P. secunda* resistance to cheatgrass. To test our first hypothesis, we compared the means and standard errors of emergence and biomass of *P. secunda* with and without competition in dry and wet conditions. We then calculated means and standard errors of traits (biomass, seed weight, height, SLA, LDMC). To test our second hypothesis, we compared the means and standard errors of traits by population. To test our third hypothesis, we calculated the coefficient of variation (CV) as a proxy for plant plasticity and ran a linear regression between the CV of the means of traits and the means of biomass.

Results

Water Availability – Hypothesis 1

To investigate our first hypothesis that *P. secunda* resistance to cheatgrass will decline with reduced water availability we used emergence and biomass as proxy for *P. secunda*'s cheatgrass resistance. *P. secunda* showed germination in both presence and absence of cheatgrass (Fig. 2). Reno showed higher mean emergence stem count within the wet treatment than the dry treatment. However, all other populations of *P. secunda* showed no difference in mean stem survival counts by the water treatment with competition. Wet non-competition pots had the highest mean emergence stem counts in comparison with wet competition pots, dry competition, and dry no-competition pots. Within the dry treatment, non-competition pots showed higher emergence stem counts than competition pots in Reno and Butte Valley, while non-competition pots showed lower stem survival than competition pots for Water Canyon. Within the wet treatment, non-competition pots showed higher stem survival than competition pots in all populations except Reno.

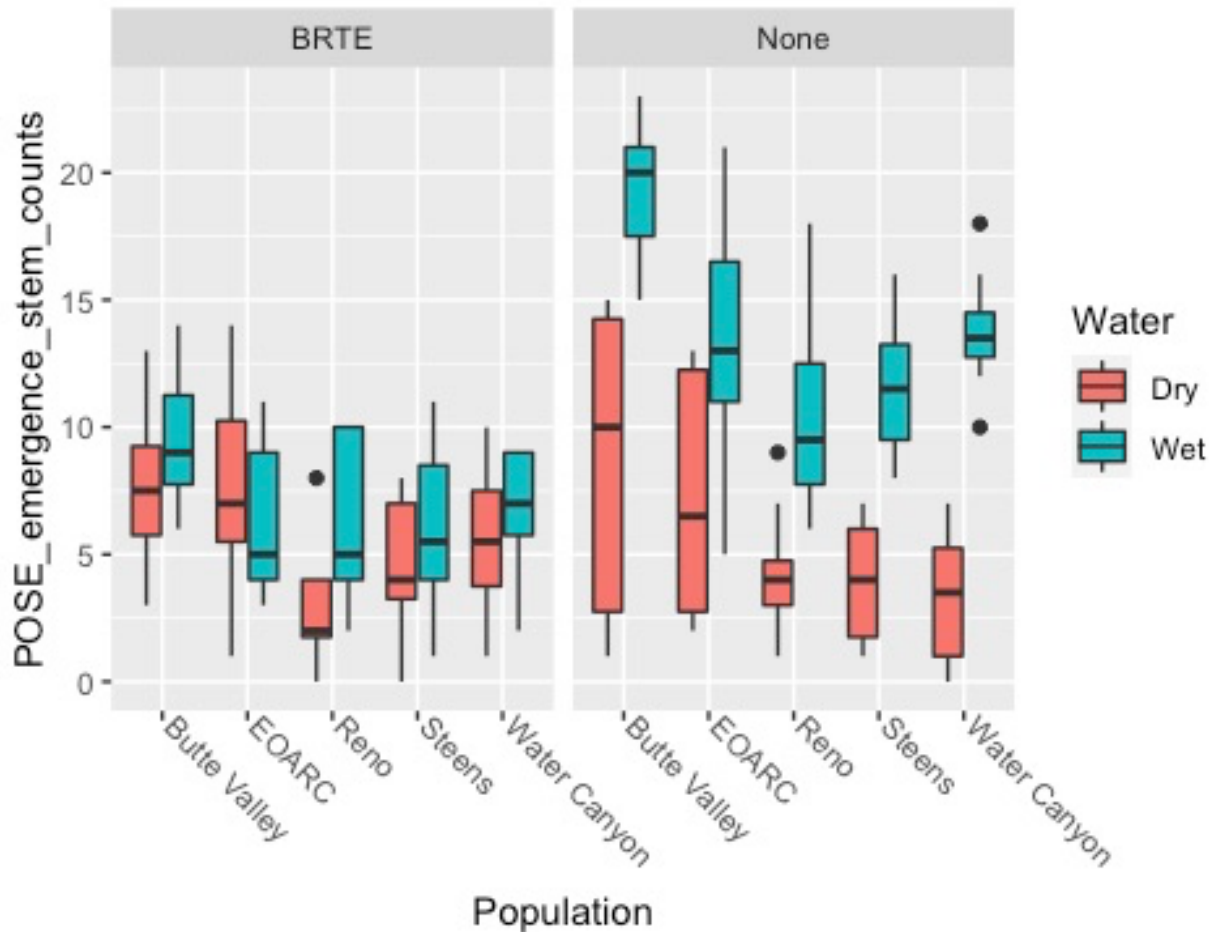


Figure 2. Emergence stem counts of *P. secunda* in competition and no-competition pots with a wet and dry treatment. All populations (excluding Reno) of *P. secunda* showed no difference in mean stem survival counts by the water treatment with competition.

All populations of *P. secunda* had a higher mean dry biomass weight in the wet treatment than the dry treatment in both competition and non-competition pots (Fig. 3). There was no difference in mean dry biomass weight in the wet, non-competition pots by population.

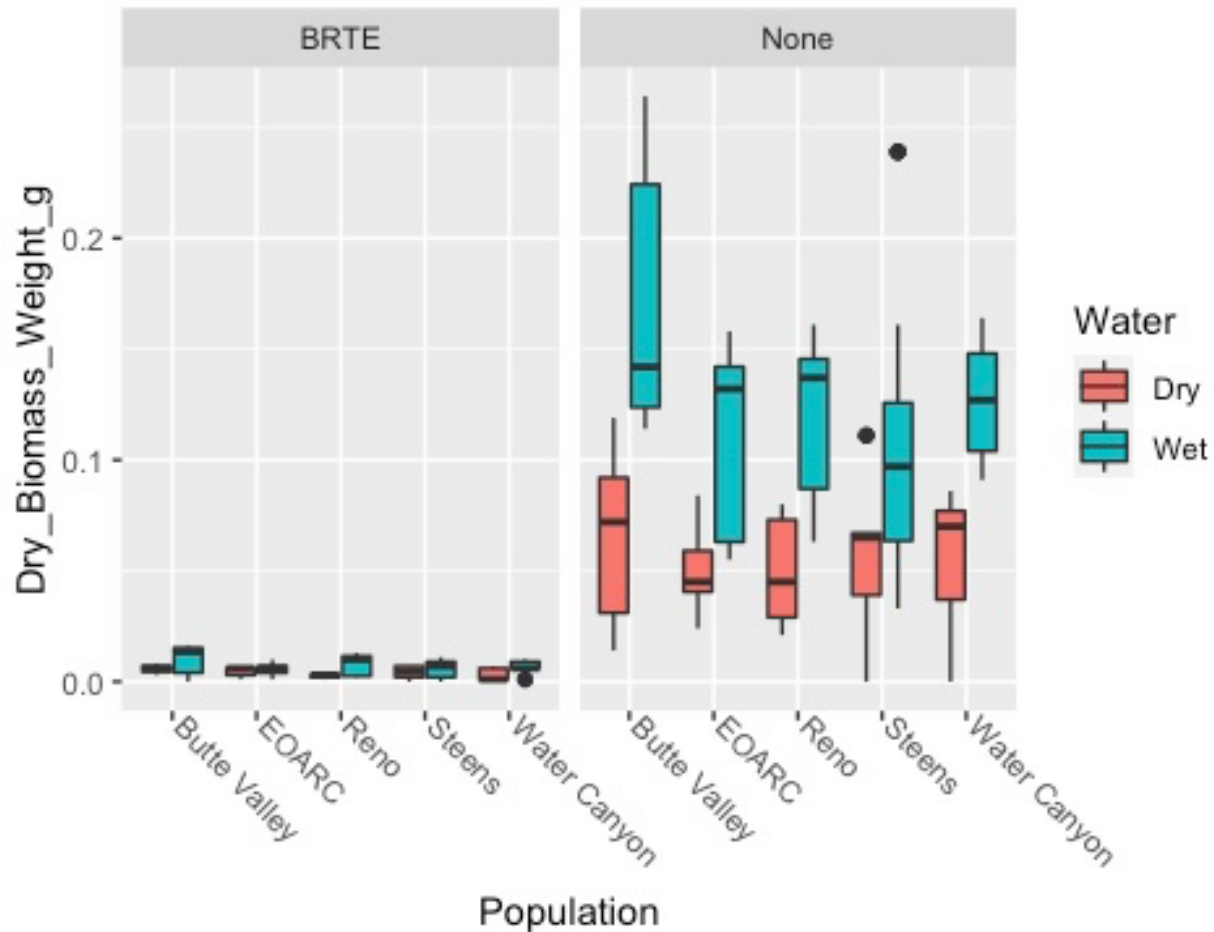


Figure 3. Mean dry biomass weight in competition and no-competition pots with a wet and dry treatment. All populations of *P. secunda* had a higher mean dry biomass weight in the wet treatment than the dry treatment in both competition and non-competition pots.

Variation in traits – Hypothesis 2

To address our second hypothesis, we found that *P. secunda* showed variation in traits across populations (Fig. 4). I hypothesized that the *P. secunda* populations from warmer, drier areas will be shorter in height, have lower SLA, and higher LDMC. For mean height EOARC showed the lowest mean height. Butte Valley, Reno, Steens, and Water Canyon showed no difference in mean height. For dry biomass weight, Butte Valley showed the greatest mean dry biomass weight. For leaf dry matter content (LDMC), Steens, Reno, and Butte Valley showed no difference in mean from each other, but Steens was greater than Water Canyon and EOARC, and Reno was greater than EOARC. For specific leaf area (SLA), all populations except Butte Valley showed no difference in SLA, but Butte Valley showed a lower SLA than EOARC, Reno, and Water Canyon. For seed weight, Butte Valley had the highest seed mass, while Steens had the lowest.

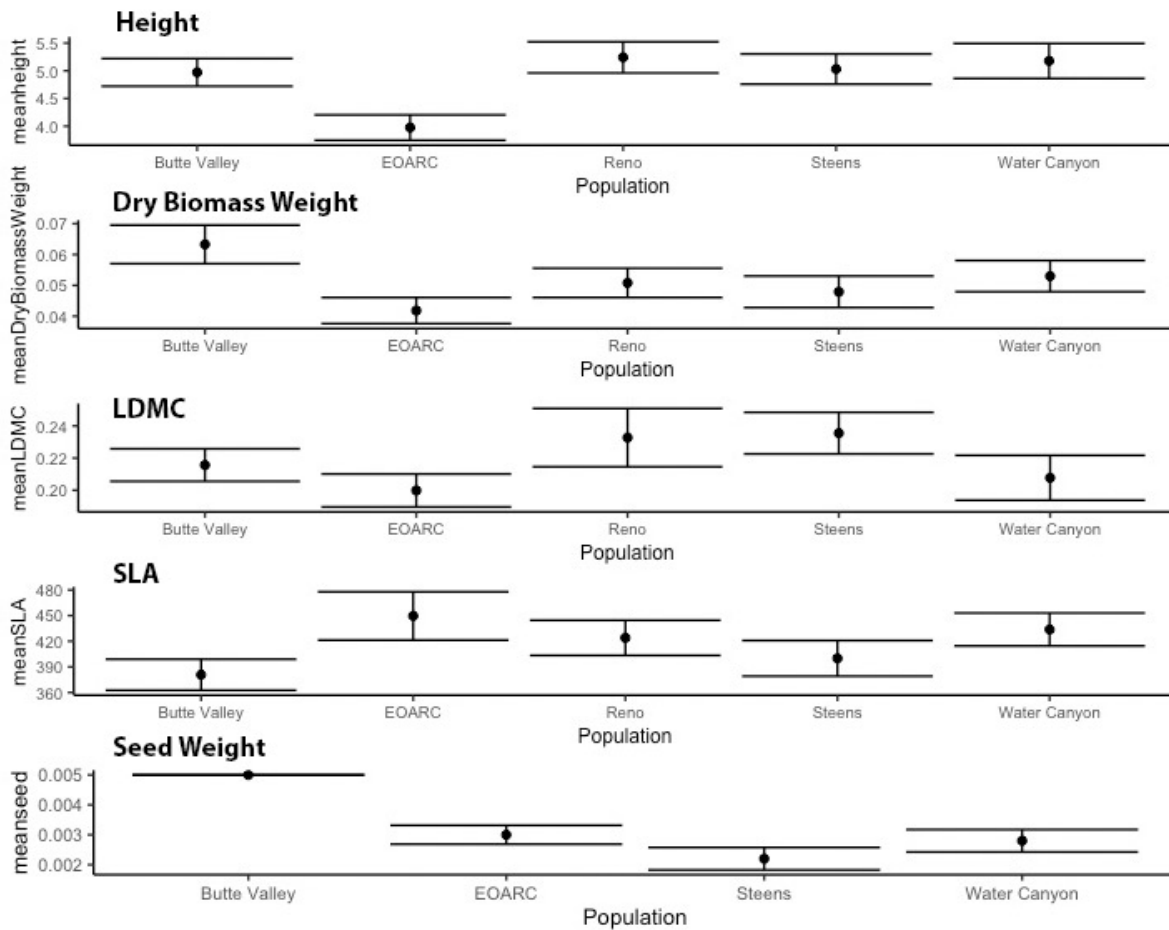


Figure 4. Mean and standard error by population for height, dry biomass weight, LDMC, SLA, and seed mass. *P. secunda* showed variation in traits across populations.

Plasticity and Resistance – Hypothesis 3

To address our third hypothesis, dry biomass weight shows high coefficient of variation (CV) and is the most plastic of traits measured (Fig. 5). Height, LDMC, and SLA show similar CV. Overall, there is no consistent pattern for which population has high CV across traits. Steens has high CV, while Reno and Water Canyon have relatively low CV for dry biomass weight. Water Canyon and EOARC have high CV for height. Reno and Water Canyon have high CV for LDMC. EOARC has high CV, while Reno and Water Canyon are relatively low for SLA.

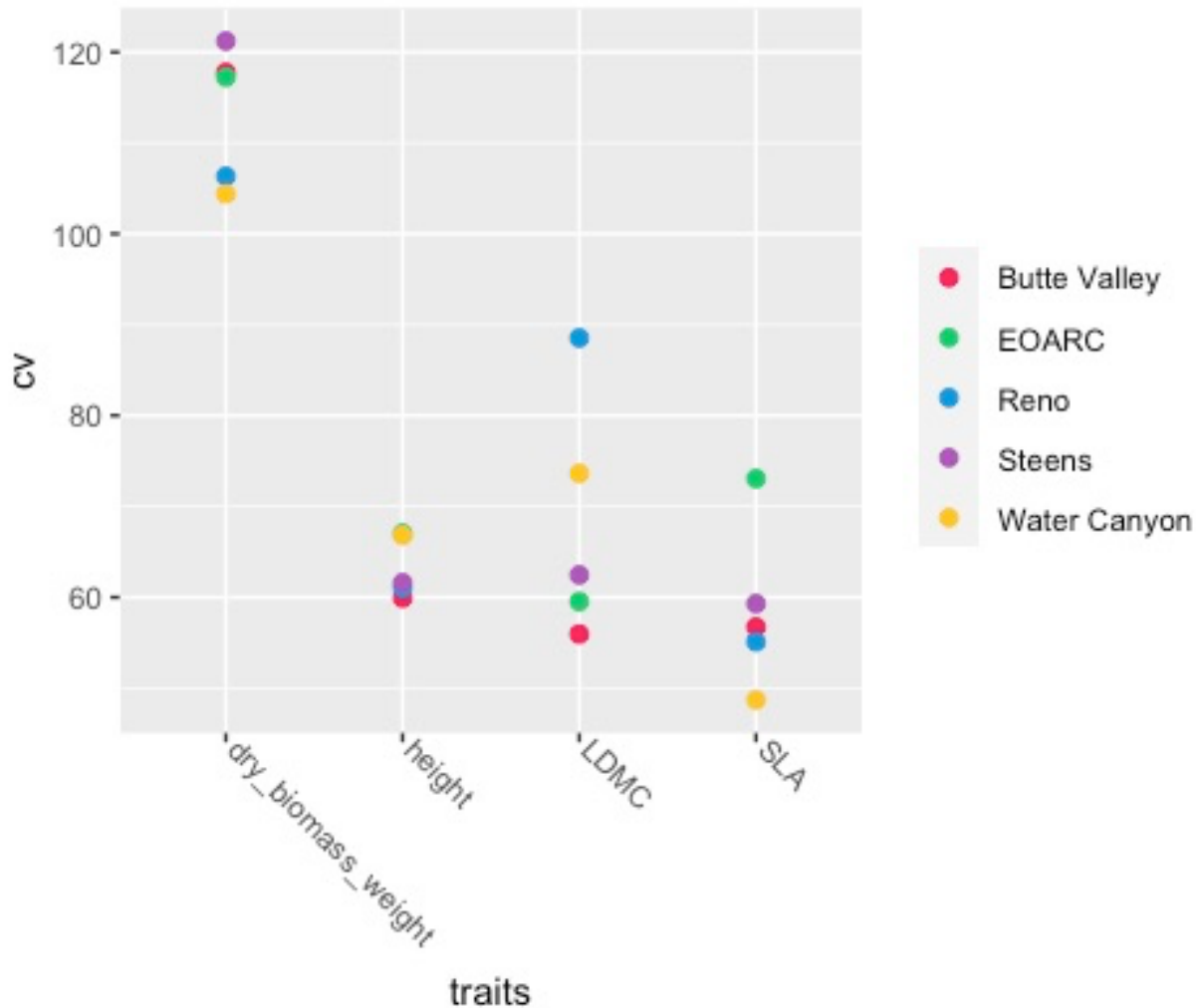


Figure 5. Coefficient of variance (CV) of dry biomass weight, height, LDMC, and SLA by population. There is no consistent pattern for which population has high CV across traits and the amount of plasticity by population varied by trait.

A negative correlation between dry biomass weight and height was found (R^2 value = 0.6033) with linear regression where lower CV of height is associated with higher dry biomass weight, and higher CV is correlated with lower dry biomass weight (Fig. 6). No correlation was found between dry biomass weight and CV of LDMC. A negative correlation between dry biomass weight and CV of SLA was found ($R^2 = 0.6339$) where lower CV of SLA is associated with higher biomass, and higher CV of SLA is associated with lower biomass. Butte Valley consistently shows lower values for CV of height, LDMC, and SLA; and EOARC consistently shows higher values for CV of height, LDMC, and SLA in comparison with the other populations.

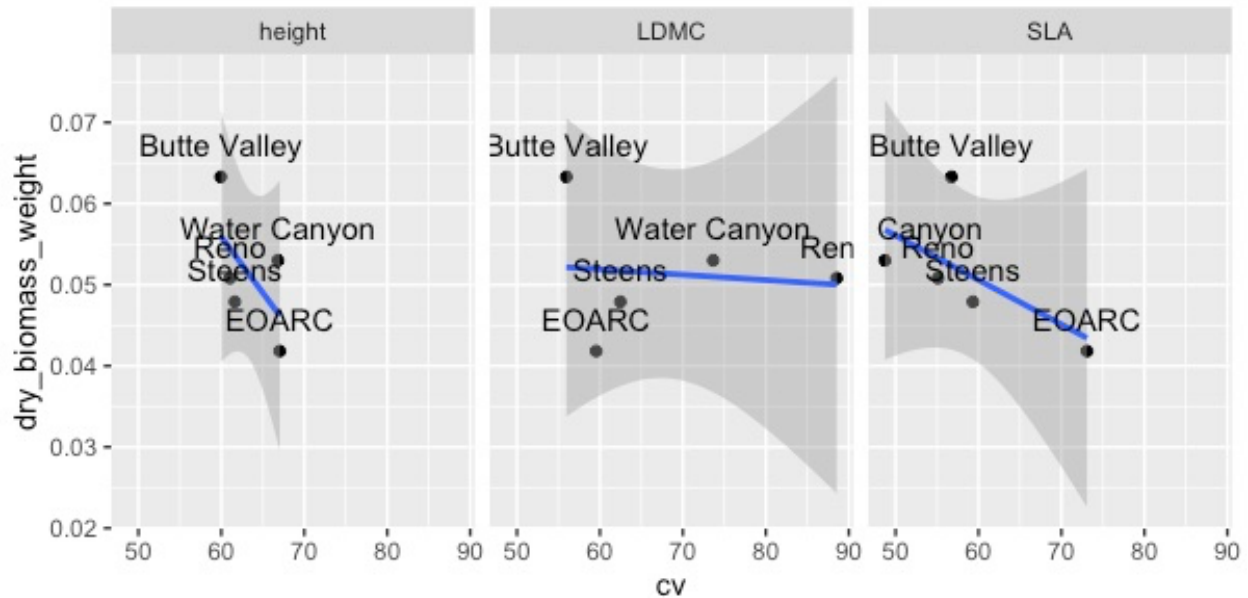


Figure 6. Linear regression between dry biomass weight of *P. secunda* and its coefficient of variance (CV) of height, LDMC, and SLA by population. Plasticity of height and SLA are negatively correlated with cheatgrass resistance of *P. secunda*. No correlation is found between plasticity of LDMC and cheatgrass resistance of *P. secunda*.

Discussion

I first hypothesized that *P. secunda*'s resistance to cheatgrass will decline with reduced water availability, but *P. secunda* populations from warm and arid source environments will have a smaller decline than those from cooler and wetter environments. We used emergence and biomass as proxies for cheatgrass resistance (where fewer stems emerged and lower biomass will relate to decreased resistance to invasion). When in competition with cheatgrass, our results show that there is no difference in emergence between wet and dry treatments except for in Reno (where emergence was greater in wet than dry). Water availability has an effect on emergence of *P. secunda* when it is not in competition with cheatgrass, but when it is in competition with cheatgrass, it is essentially the same as saying it is a drought year. This could suggest that when looking at emergence, water availability will not affect *P. secunda*'s ability to resist invasion to cheatgrass. Reno emergence may be greater than other populations here due to its climate being warmer and drier in comparison with other populations in this study. However, when looking at biomass, in both competition and non-competition pots, wet treatments have a higher mean dry biomass weight than dry treatments. There is no difference in mean dry biomass weight across populations within both dry and wet treatments. This suggests that resistance to cheatgrass will likely decline with reduced water availability since the wet treatments have a higher dry biomass than the dry treatments. Additionally, the wet treatments without competition have higher dry biomass weight than wet treatments with competition, showing that when in competition, *P. secunda* resistance declines. However, *P. secunda* populations from arid source environments did not have a smaller decline as those from cooler and wetter environments.

I hypothesized second that the *P. secunda* populations from warmer, drier areas will be shorter in height, have lower SLA, and higher LDMC. Our results show that *P. secunda* traits are

highly variable across populations and environments. For example, EOARC, Reno, and Water Canyon are comparatively warm and dry areas in the Great Basin. While EOARC was the shortest in height across populations, Reno and Water Canyon had similar height to those from wetter areas (Steens and Butte Valley) which we would not expect due to the gradient of temperature and precipitation. Knowing this, we cannot definitively say that populations of *P. secunda* from warmer, drier areas will always have shorter height. The variability in height, SLA, and LDMC across populations could be because there is high variability between traits and the environment which could not be captured within these five populations. Other environmental variables besides mean annual precipitation and mean annual temperature may also have a stronger relationship than we account for in this study. Alternatively, the environment in the greenhouse may have created optimal growth conditions which differ from how they would grow in the field.

Finally, I hypothesized that *P. secunda* populations with greater trait plasticity will better resist invasion to cheatgrass. We found that dry biomass weight is more plastic than the other traits (height, SLA, LDMC). Additionally, we found that there was no consistent pattern showing that a population had high variation across all traits, and the amount of plasticity by population varied by trait. These results show that there is no one population which has greater plasticity than another for all traits, but that some populations are more variable in one or two traits in comparison with others. Linear regressions between dry biomass weight and height, LDMC, and SLA shows the opposite of what we proposed, that increased CV (plasticity) will actually result in decreased dry biomass (proxy for resistance). This suggests that higher plasticity may not be an important factor for *P. secunda* in order to resist cheatgrass. Alternatively, this could mean that decreased biomass may actually be an advantage, particularly in locations which are especially prone to drought, as lower biomass can be correlated with reduced water loss. Butte Valley had relatively low plasticity in height, SLA, and LDMC, but as a population, it had relatively greater seed weight and dry biomass weight than other populations, and lower absolute height, LDMC, and SLA. Water Canyon, Steens, and Reno similarly had relatively low plasticity in height and SLA, and had intermediate means for dry biomass weight, height, LDMC, and SLA despite these three populations coming from largely differing and variable climates.

These results suggest that certain traits may be more important in different circumstances and environments. It is important to note that intraspecific trait variation can fluctuate quickly and is driven by both genetics and environmental conditions (i.e., soil or climate) (Roybal and Butterfield 2019). Environmental gradients in particular can drive responses from specific species (Roybal and Butterfield 2019) and certainly have influence on traits of *P. secunda*. Plants in this experiment were grown in a controlled environment, and our results may be limited due to the fact that traits may differ from plants grown in their natural habitats and environmental conditions (Tellez and Moller 2006). Variation among populations in this experiment may be because the traits we measured are more influenced by some other environmental condition besides water. In the greenhouse, the temperature, water availability and light were controlled, and we saw high emergence. In the field, we would expect fewer plants to emerge due to the variability in environment, where temperatures often reach below freezing within the germination window and seedling mortality is high. The controlled environment of the greenhouse may have optimized the traits we were studying, and in the field, we would expect to see smaller growth overall.

Another limitation to this study was that we only measured the traits of *P. secunda* both with and without competition but did not measure traits of cheatgrass itself. One approach to

selecting suitable seed for restoration may be to select specific traits in natives that are similar to invaders (Funk et al. 2008). Although cheatgrass traits can be found in literature (Griffith et al. 2014), if there is plasticity in those traits, the greenhouse could provide an optimal environment for it to grow and could show which traits are most similar or different to populations of *P. secunda*. This can be interesting research to follow up on in the future. Additionally, in this study we only looked at above ground traits. However, below ground traits, root traits, and variability in root traits are much less studied in other research but have been shown to influence seedling survival (Atwater et al. 2014; Leger and Goergen 2017), particularly in environments that are becoming warmer and drier due to their link to growth and drought tolerance (Harrison and LaForgia 2019). Measuring root length, density, and fine to course root ratio could offer further insights to this study in the context of variability in plant traits from different populations and a change in water availability.

Gaining knowledge around intraspecific trait variation, as well as climate-trait relationships has significant inferences for restoration ecology, predominantly for finding appropriate sources of seed for a variety of environmental conditions (Bureau of Land Management Staff 2015). Understanding how traits relate to specific environments will ensure that seeds have the appropriate traits for specific climates (Roybal and Butterfield 2019; Leger et al. 2019). Additionally, these findings can advise restoration choices in its relation to climate change, as plant species may become less adapted to their historic extent (Roybal and Butterfield 2019). Knowing how a plant will respond to climatic changes such as precipitation may make it easier to select plant populations which are known to respond positively. Finally, if these ideas can be applied in restoration, we may lower the risk for intense megafires, which are predicted to be larger and more frequent in the midst of changing climates and invasion.

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