

Great Basin Native Forb Responses to Competition with Cheatgrass and Elevated Soil Nutrients

Marena Disbro, Dr. Elizabeth Leger & Dr. Sarah Barga

University of Nevada, Reno, Department of Natural Resources and Environmental Science

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Abstract: The Great Basin Desert is among the most difficult places for successful ecological restoration due to the repeated effects of fire, aridity and invasive plants. The goal of this research was to determine whether four local populations of two native annual forb species, *Microsteris gracilis* and *Layia glandulosa*, differed in the capacity to survive competition with cheatgrass (*Bromus tectorum*) and whether soil nutrients affected outcomes. Seeds were collected in the spring of 2016 and planted in two phases in the fall, allowing for maximum germination. Factorial treatments included a competition treatment, with either a single forb or cheatgrass seed sown alone or together, and a soil nutrient treatment, with either no nutrient addition (low) or the addition of fertilizer pellets (high). Plants were harvested, dried and weighed in March of 2017. Biomass and flower production were compared across treatments. The two forb species had declining performance in competition with cheatgrass, especially under high nutrient conditions, where cheatgrass grew larger. Neither species exhibited population-level variation in reproductive response to any treatment, but *L. glandulosa* populations varied in biomass responses to soil nutrient availability. Though the presence of cheatgrass competition and high soil nutrients affected all forb populations negatively, one *L. glandulosa* population was able to respond to increased soil nutrients, indicating that some populations may serve as better sources for restoration.

Introduction

The Great Basin Desert has experienced devastating effects from the invasion of cheatgrass (*Bromus tectorum*), since it was first introduced into the western United States in the late 1890s. Cheatgrass, originating from Europe, northern Africa, and southwest Asia (Zouhar, 2003), has since formed monocultures on at least 40 million hectares of land in the Great Basin (Evans et al., 2001). Cheatgrass has been able to outperform native species in this system by taking advantage of ephemeral resources and reliably reproducing in both wet years and drought years (Mack & Pyke, 1983; Rice et al., 1992). In addition, cheatgrass is largely responsible for rapidly increasing fire frequencies in the Great Basin (Zouhar, 2003), thereby facilitating the transition of native plant communities into landscapes dominated by exotic annuals, such as cheatgrass (Chambers & Wisdom, 2009). The best combative strategy against further invasion is through restoration

efforts, particularly revegetation and rehabilitation of degraded sites (Shinneman & Baker, 2009).

There is a growing body of evidence that native early-successional species, and annual forbs in particular, have the ability to persist in invaded areas and even outcompete invasive species in arid systems (Abella et al., 2011; Abella et al., 2012; Leger et al., 2014; Uselman et al., 2014). Some native, annual forbs may be able to serve critical roles in the re-establishment of native vegetation in disturbed areas (Leger et al., 2014; Uselman et al., 2014). Additionally, native forbs are integral for healthy ecosystems as they provide support for many ecosystem services such as providing wildlife food and habitat, increasing biodiversity of native flora and fauna, and encouraging landscape resiliency after disturbance (Shaw et al., 2012; Barak et al., 2015). However, information is currently lacking for most native forbs regarding their ability to grow and reproduce while in competition with introduced species.

Soil nutrients are crucial for plant growth and productivity, especially for desert annual forbs, with nitrogen often a limiting resource for plants in the Great Basin Desert (Farrior et al., 2013). Recently, desert ecosystems have experienced elevated levels of soil nitrogen as a result of unsustainable land use practices, increased pollution and atmospheric deposition (Brooks, 2003). While higher soil nutrient availability may benefit some native species, desert ecosystems are also susceptible to invasive plant species that are able to efficiently exploit soil resources, allocating it to biomass and seed production. This leads to invasive plant species with greater plant biomass and fecundity than natives (Evans, 2001). Plants that display strategies for enhancing their competitive outcomes, such as efficient soil nutrient uptake and consumption, are likely to outperform their neighbors (Tabassum & Leishman, 2016). Research indicates that invasive species in the Great Basin, such as cheatgrass, possess such strategies and are expected to continue invading and dominating the Great Basin Desert (Brooks, 2003; DeFalco et al., 2003). However, information is lacking with regards to how native species vary in their ability to utilize soil nutrients and whether these differences may lead to variation in their ability to compete with cheatgrass when soil nutrients are more abundant (Booth et al., 2003; James, 2008).

While many researchers have explored species-level variation in performance in invaded arid systems (e.g. Abella et al., 2012; Herron et al., 2013), very little is known about the degree of population-level variation exhibited by desert forbs. Variation among populations is largely controlled by exposure to varying environmental factors, such as year-to-year differences in climate or spatial variation in soil nutrients (Ackerly et al., 2000), and could result in populations that are adapted to their specific local environmental conditions (Meyer et al., 1995; Wright et al., 2006). For example, *Collinsia sparsiflora*, an annual forb native to California, has displayed population-level variation in its ability to grow on two different soil types (Wright et al., 2006) and populations of *Penstemon* differed in the timing of germination depending on environmental characteristics such as elevation (Meyer et al., 1995). Desert plants may have a higher propensity for local adaptation due to their lack of adaptations for long-range seed dispersal (Fillner & Shmida, 1981), leading to infrequent transfer of genetic material across populations, and thus populations will differ in their responses to disturbance and competition.

Identifying appropriate restoration species will require an understanding of how native species respond to multiple stressors, which can include both competition with invasive species and higher nutrient availability (Abella et al., 2012). This study investigates how the growth and reproduction of two native annual forbs are affected by both nutrient availability and competition with

cheatgrass, asking whether these species exhibit population-level differences in their performance. Two annual forbs were selected for this experiment, *Microsteris gracilis* (Hook.) Greene (slender phlox) and *Layia glandulosa* (Hook.) Hook. & Arn. (tidytips). Both species are known to be important food sources for Greater sage-grouse (*Centrocercus urophasianus*), a species of particular conservation concern in the Great Basin and beyond (Gregg & Crawford, 2009; Pennington et al., 2016). Both forb species were observed to be prevalent in cheatgrass-invaded sites throughout the Great Basin. The factorial experimental design of this study includes both a competition treatment and a nutrient addition treatment, in an effort to test the separate and combined effects of resource availability on the capacity of these native forbs to grow with and potentially suppress cheatgrass. In order to identify whether there were population-level differences in the growth and reproduction of these forbs when competing with cheatgrass, seeds were collected from four populations for each species. We asked whether a) competition with cheatgrass, b) nutrient addition, or c) both competition and nutrient addition affect the performance of the focal species, asking the following research questions:

- 1) How is the growth and reproduction of native annual forbs affected by the above experimental treatments?
- 2) Are there population-level differences in the ability of forbs to grow and reproduce when experiencing our different experimental treatments?
- 3) How is the growth and reproduction of cheatgrass affected by nutrient availability?
- 4) Are there differences in cheatgrass response to competition with different forb species?

We hypothesized that *L. glandulosa* and *M. gracilis* would exhibit a positive response in biomass and flower production to high nutrient conditions. We predicted that both native forbs would exhibit population-level variation in their response to treatments but would generally decline in performance when exposed to competition with cheatgrass, with greater reductions under conditions of greater nutrient availability. Finally, we expected cheatgrass to exhibit differences in response to competition with different native forb species.

Methods

Natural History Background

The native species studied here differ in their seed dispersal ability and reproductive strategies, which may affect population differentiation. *M. gracilis* can self-pollinate, resulting in less genetic diversity (Grant & Grant, 1965; Levin, 1978), while *L. glandulosa* is incapable of self-pollinating and requires out-crossing to produce viable seeds. *M. gracilis* is ballistically dispersed, meaning

that ripe seeds are enclosed in a capsule that bursts and catapults seeds within the vicinity of the parent plant (Levin, 1978), while *L. glandulosa* has a feather-like pappus that enables wind dispersal, leading to greater dispersal distances than *M. gracilis*.

Seed Collection

Seeds were collected from four populations for each species: *B. tectorum*, *L. glandulosa*, and *M. gracilis* (Table 1). Seeds were collected on two occasions at each location, late May and early June of 2016, with the exception of only collecting once from the Dutch John population of *M. gracilis* in Winnemucca, NV along Dutch John Creek. The Hoge Rd. populations were collected off of Hoge Rd, Reno NV. The Patagonia populations were collected on a hiking trail behind the Patagonia warehouse in Reno, NV, and the Hidden Valley populations were collected from Hidden Valley Regional Park in Reno, NV. The Susileen population of *L. glandulosa* was collected on Susileen Rd. in Reno, NV. Collecting seeds at multiple points in time creates a more representative sample of the seeds from the entire

population, given that the timing of seed maturation may be staggered across individuals within a population. Cheatgrass seeds from all populations were mixed to create a sample that would be representative of diversity across all sites, to avoid confounding competition treatments with any population differences in cheatgrass. All seeds were cleaned and stored in a dry, room temperature environment until sowing.

Greenhouse Experiment

Phase 1 (early planting)

On October 2, 2016, we filled 640 pots (Ray Leach - 158 ml Cone-tainers) with soil local to the Reno, NV area, and placed them into trays with 80 pots per tray. High nutrient treatments were given four pellets of fertilizer (Osmocote Smart-Release Plant Food Plus Outdoor and Indoor Food - 15% N, 9% P₂O₅, 12% K₂O) per pot. Both treated and untreated pots were watered for five days to increase soil water content and to allow nutrients to release from the fertilizer pellets into the soil prior to planting.

Table 1. Distance between sites and sample sizes for treatments for A) *Layia glandulosa*, B) *Microsteris gracilis*, and C) *Bromus tectorum*.

	Distance (Km)						Sample Sizes for Nutrients/Competition (Early Planting:Late Planting)			
	1->2	1->3	1->4	2->3	2->4	3->4	Low/No	Low/Yes	High/No	High/Yes
A) <i>Layia glandulosa</i>										
1. Hoge Road	15.0	9.1	8.0				5:3	3:6	1:7	0:6
2. Hidden Valley				16.8	11.1		9:3	10:7	5:6	1:0
3. Patagonia						5.7	0:1	2:1	1:5	0:2
4. Susileen							3:3	3:1	1:3	1:4
B) <i>Microsteris gracilis</i>										
1. Dutch John	316.1	309.2	318.4				3:3	2:4	6:9	4:10
2. Hidden Valley				15.0	16.8		0:2	0:0	3:11	2:7
3. Hoge Road						9.1	2:0	1:0	8:11	4:9
4. Patagonia							1:1	2:5	8:8	4:10
C) <i>Bromus tectorum</i>										
	Sample Sizes for Competition Species/Nutrients (Early Planting:Late Planting)									
	<i>M. gracilis</i> /Low		<i>M. gracilis</i> /High		<i>L. glandulosa</i> /Low		<i>L. glandulosa</i> /High			
	14:34		5:8		18:15		2:12			

To quantify differences in soil nutrients in the low and high soil nutrient treatments, 20 pots were filled with soil at the beginning of the experiment, 10 of which were given four fertilizer pellets, and were watered along with the pot planted for experimentation. At the end of the experiment, soil from these pots was sent to A & L Western Agricultural Lab in Modesto, CA (www.al-labs-west.com) for analysis of soil nutrient composition, including: nitrogen, phosphorus, and potassium. All of these nutrients increased with the addition of the fertilizer pellets. The soil samples contained 3 ppm of nitrogen in low nutrient and 52 ppm in high nutrient treatments, 18 ppm of phosphorus (weak bray) in low and 21 ppm in high, and 291 ppm potassium in low and 334 ppm in high.

On October 7, 2016 all seeds were sown and factorial treatments assigned (control, competition, and nutrient modification). Control treatments for forbs were represented by a single forb seed planted in the center of a pot without fertilizer pellets. Each forb species was represented by 20 individuals from each population, resulting in a total of 80 forb individuals per treatment, though not all individuals germinated (Table 1). Competition treatments were sown with one cheatgrass seed and one forb seed approximately ½ inch apart in the center of a pot. Nutrient modification treatments were sown with either one forb seed alone or one forb seed sown with one cheatgrass seed assigned to either high or low soil nutrients. After treatments were applied, pots were re-distributed among trays, maintaining equal representation of all populations and treatments within each tray. For the first month, plants were watered every day on a mist setting, to avoid seed displacement, and trays were randomly re-distributed along the greenhouse tables every week.

Phase 2 (late planting)

A second round of sowing took place on November 9th and 10th. Pots without forb germination and pots with solely cheatgrass germination were removed from every tray. All removed pots were then re-sown with their respective treatment and randomized in the same fashion as in round one. Plants from phase-1 were kept in separate trays for the following four weeks and watered every other day, while plants from phase-2 were watered every day. At the beginning of December, pots from both phases of planting were combined and watered on an every-other day schedule for the duration of the experiment. In late January, the number of trays was doubled and the pots were spread randomly among each tray to provide extra room for above ground biomass.

Data Analysis

On March 10th all aboveground biomass was collected, labeled, and placed in individual 5 x 7 coin envelopes to be dried for two days in a drying oven at 48°C. Biomass was then weighed and the number of flowers per plant were counted for inclusion in the

analyses. Additionally, the biomass and flowers of all cheatgrass that were involved in the competition treatment were measured to determine differences in the competitive effects on cheatgrass among the forbs. Analysis of variance (ANOVA) was used to compare performance within and among populations of forbs, as well as differences in the performance of cheatgrass in response to nutrient addition and competition with both native forbs (Table 2). Because planting took place in two phases, planting date was incorporated as a variable in the analyses. All data were analyzed using program R (R Development Core Team, 2016). The *car* package was used to analyze the percent change in trait values for the factorial treatments using type 2 ANOVAs (Fox & Weisberg, 2011), the *agricolae* package to perform Tukey's tests for significant differences in mean values between groups (de Mendiburu, 2016), and the *ggplot2* package to create figures 2, 3, and 4 (Wickham, 2009).

Results

Native forb responses to competition and nutrient treatments (Question 1)

Our predictions were supported in that both *L. glandulosa* and *M. gracilis* plants were smaller and produced fewer flowers when exposed to cheatgrass competition ($P < 0.001$), and were larger and produced more flowers when nutrient levels were high ($P < 0.001$) (Table 2, Fig. 1, Fig. 2). For both *L. glandulosa* and *M. gracilis* there was a significant interaction between competition and nutrient addition (*L. glandulosa* – $P < 0.01$, *M. gracilis* – $P < 0.001$) (Table 2) where plants differed more dramatically in size in response to nutrient availability when there was a lack of competition. *L. glandulosa* exhibited no interaction between nutrient addition and competition on the number of flowers produced. In contrast, *M. gracilis* exhibited a significant interaction between nutrient addition and competition, where plants differed more dramatically in flower production in response to nutrient availability when there was a lack of competition ($P < 0.001$) (Table 2, Fig. 2B).

Native forb population-level responses to competition and nutrient treatments (Question 2)

Our predictions for the existence of population-level variation in response to our treatments was partially supported for *L. glandulosa* but unsupported for *M. gracilis* (Table 2). Populations of *L. glandulosa* did not vary in their response to competition with cheatgrass but did vary in biomass in response to nutrient availability ($P < 0.05$) (Table 2). The Hidden Valley, Hoge Road, and Patagonia populations of *L. glandulosa* exhibited a much greater difference in biomass in response to differences in soil nutrient availability. In contrast, the Susileen population exhibited much less variation in biomass

Table 2. ANOVA table of results for biomass and flower response to each factor and interaction (indicated with “.”), including degrees of freedom (df; numerator, denominator), F values, and P values, with “NS” indicating $P > 0.05$.

	df	Biomass		Flowers	
		F value	P	F value	P
A) <i>Layia glandulosa</i>					
Planting Date	1,85	7.22	<0.01	6.37	<0.05
Nutrients	1,85	69.71	<0.001	23.50	<0.001
Competition	1,85	64.07	<0.001	16.38	<0.001
Population	3,85	1.52	NS	1.26	NS
Nutrients:Competition	1,85	9.87	<0.01	2.55	NS
Nutrients:Population	3,85	3.53	<0.05	1.73	NS
Competition:Population	3,85	0.32	NS	0.27	NS
Nutrients:Competition:Population	3,85	1.60	NS	0.40	NS
B) <i>Microsteris gracilis</i>					
Planting Date	1,121	13.60	<0.001	14.74	<0.001
Nutrients	1,121	33.41	<0.001	12.46	<0.001
Competition	1,121	243.38	<0.001	137.69	<0.001
Population	3,121	0.25	NS	0.49	NS
Nutrients:Competition	1,121	41.56	<0.001	16.07	<0.001
Nutrients:Population	3,121	0.79	NS	1.27	NS
Competition:Population	3,121	0.89	NS	0.15	NS
Nutrients:Competition:Population	2,121	1.05	NS	0.12	NS
C) <i>Bromus tectorum</i> vs. native forbs					
Planting Date	1,102	23.59	<0.001	33.58	<0.001
Species	1,102	0.23	NS	0.01	NS
Nutrients	1,102	60.25	<0.001	11.50	<0.001
Species:Nutrients	1,102	0.01	NS	0.36	NS

relative to nutrient availability, relative to the other populations (Fig. 2A). Neither *L. glandulosa* nor *M. gracilis* exhibited population-level variation in flower production in response to competition with cheatgrass or nutrient addition.

Effects of nutrient availability on cheatgrass growth and reproduction (Question 3)

The growth and flower production of cheatgrass was significantly affected by nutrient availability, with cheatgrass plants growing 50-70% larger and producing 25-40% more flowers under high nutrient conditions ($P < 0.001$) (Table 2, Fig. 3A, Fig. 3B).

Cheatgrass responses to competition with native forbs (Question 4)

Our predictions for cheatgrass were unsupported as we did not observe variation in cheatgrass biomass or flower production when competing with either native forb species in competition treatments (Table 2, Fig. 3A, Fig. 3B).

Discussion

Because cheatgrass has an annual lifecycle and germinates in the winter, it has the ability to efficiently

consume ephemeral resources and therefore excels at outperforming native vegetation, (Mack & Pyke, 1983; Rice et al., 1992; Leger et al., 2014). This competitive advantage results in the formation of dense monocultures across the Great Basin (Evans et al., 2001). As predicted, both competition with cheatgrass and low soil nutrient availability resulted in declining performance for both forb species. Populations of *L. glandulosa* exhibited variation in biomass response to differences in soil nutrient availability. Finally, cheatgrass was found to be smaller and produced fewer flowers under low nutrient conditions, but its performance was not differentially affected by competition with either native forb species. Because cheatgrass experienced significant growth in biomass and flower production in response to high nutrient environments but was unaffected by native forb competition, elevated levels of soil nutrients are likely to enhance the success of this invasive weed, as has been seen in other systems (Brooks et al., 2003).

L. glandulosa and *M. gracilis* produced slightly contrasting responses in population-level variation, suggesting that these species may have different strategies for handling variation in soil nutrients. The results of this study support current research showing that

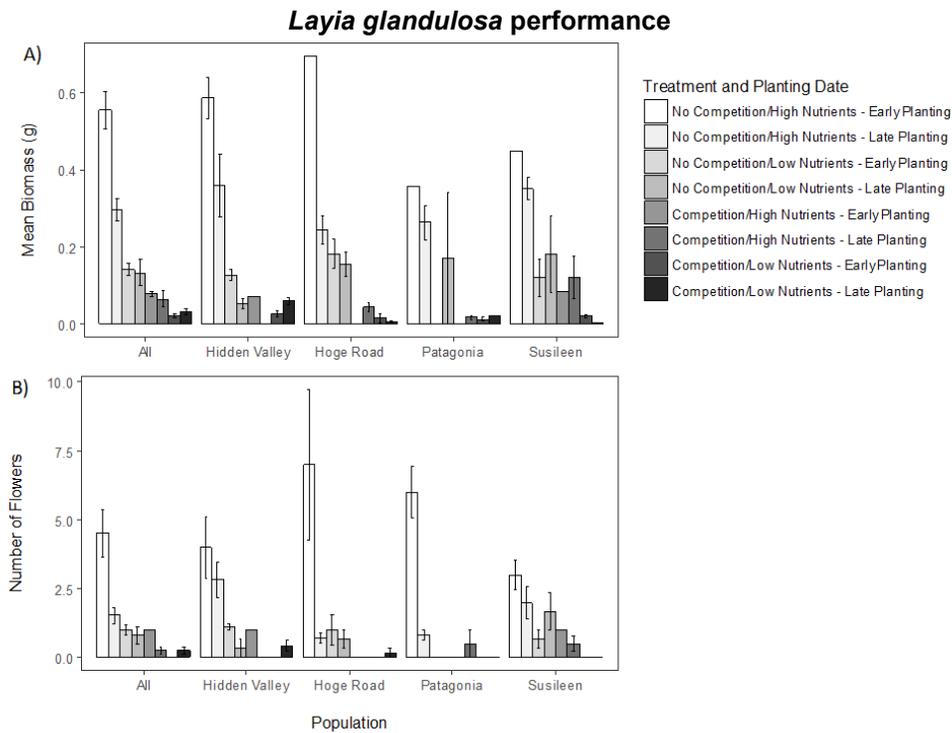


Figure 1. Mean biomass (A) and mean number of flowers (B) of *L. glandulosa* grown alone and in competition with cheatgrass under high and low nutrients. Error bars show the standard error across individuals.

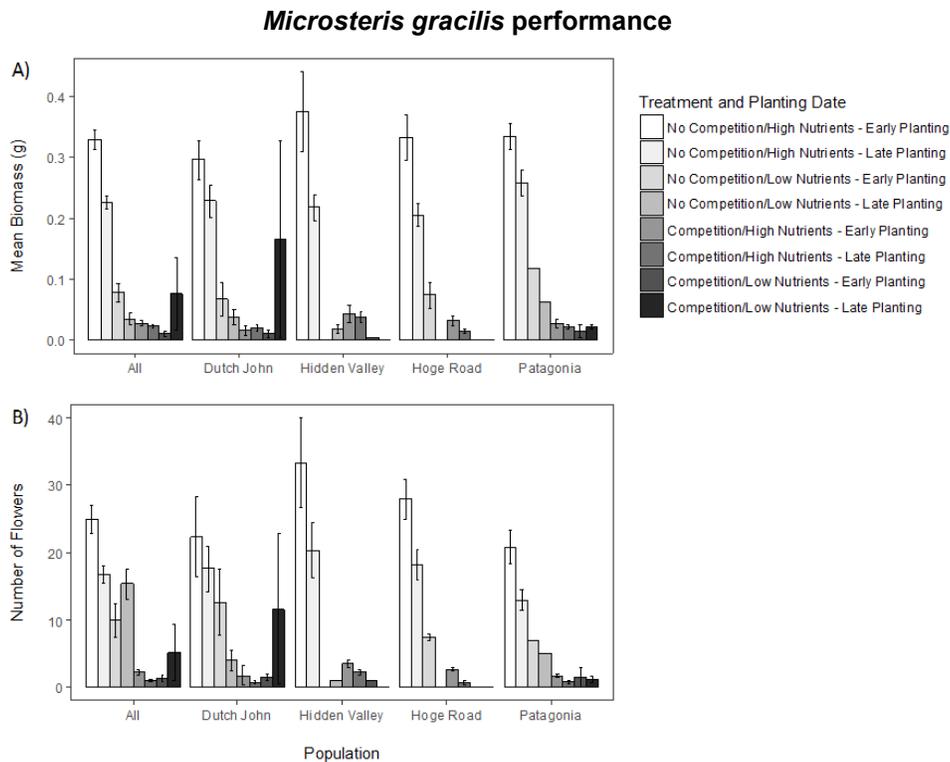


Figure 2. Mean biomass (A) and mean number of flowers (B) of *M. gracilis* grown alone and in competition with cheatgrass under high and low nutrients. Error bars show the standard error across individuals.

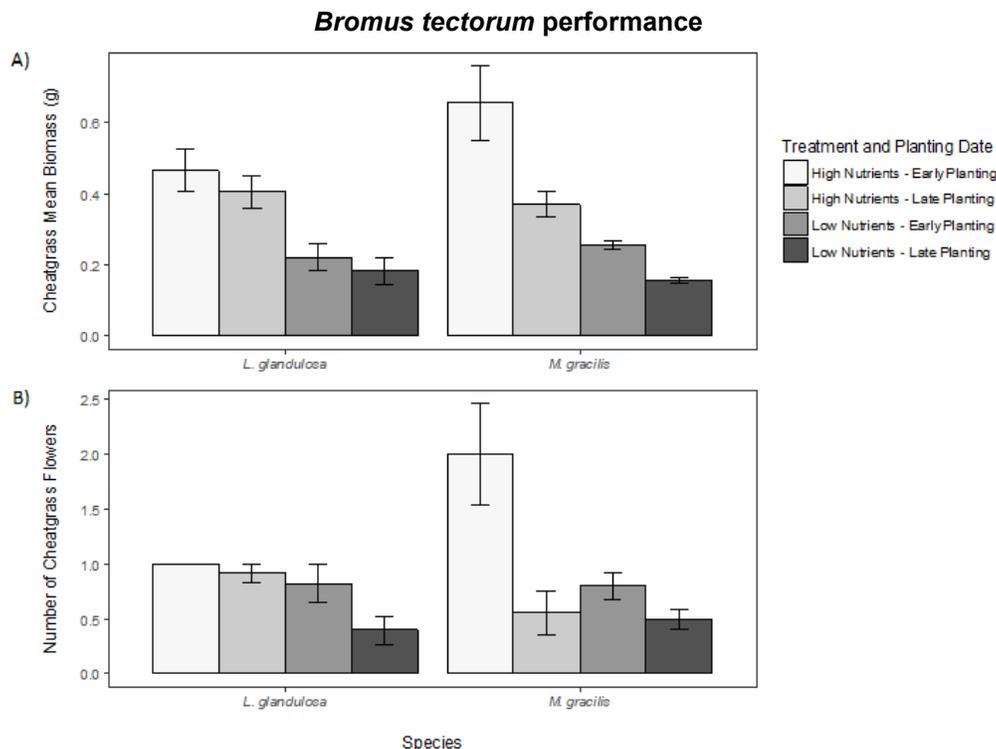


Figure 3. *Bromus tectorum* (cheatgrass) performance. Mean biomass (A) and mean number of flowers (B) of cheatgrass grown in competition with *L. glandulosa* and *M. gracilis* under high and low nutrient conditions. Error bars show the standard error across individuals.

nutrient addition enhances plant growth and reproduction for both native forbs and cheatgrass (Evans et al., 2001, Farris et al., 2013). These results also suggest that there are population-level differences in response to nutrient availability for *L. glandulosa*, which may lead to population-level variation in their ability to persist in disturbed systems.

Because nitrogen deposition is projected to negatively affect the Great Basin (Brooks, 2003), it is crucial that managers take into account the response of species and populations to enhanced levels of soil nutrients. This information may be used to select appropriate species, or populations, for restoration purposes. For example, though not statistically significant, the Hidden Valley population of *L. glandulosa* may be an appropriate seed source for areas with high levels of bare ground and high soil nutrient availability as it outperformed other populations in biomass production (Fig. 1A, Fig. 1B).

One goal was to determine how populations differed in competition with cheatgrass, with the hope of identifying promising populations for use in restoration. Though not statistically significant, the Susileen population of *L. glandulosa* may be an appropriate seed source for areas with high soil nutrient levels and cheatgrass, as it outperformed other populations in biomass production when experiencing both competition and high soil nutrient conditions (Fig. 1A, Fig. 1B). Further sampling of additional forb species populations could

identify populations that are more tolerant of competition with this highly-competitive species.

Differences in performance among populations may be the result of local adaptation to site-specific environmental conditions (Meyer et al., 1995, Wright et al., 2006) or to genetic drift (Loveless & Hamrick, 1984). Another explanation for differences in performance among populations may stem from spatial variation in the resources that were available to the parent plant, also known as maternal effects (Roach & Wulff, 1987). For example, maternal effects could influence the size and mass of offspring seeds potentially resulting in variation in performance (Roach & Wulff, 1987). Maternal effects were not controlled for in this study, but they could potentially have been factors contributing to the differences observed between *L. glandulosa* populations. One limitation must be addressed regarding the soil we used to conduct this experiment. Soil was only collected from one site in Reno, NV and may have differentially affected our plant populations.

This research supports the importance of selecting seed mixes that are sourced from populations of appropriate restoration species that are well adapted to site conditions, whether those conditions be enhanced levels of soil nutrients, intense invasions of exotic plant species, or other factors. Although there was no population-level variation for *M. gracilis* in response to competition or nutrient addition, previous research suggests that variation among populations does in fact

exist: *M. gracilis* exhibited population-level variation in seed germination in response to temperature and moisture cues (Barga et al., 2017). This research suggests that it may be important to test population performance prior to restoration, as native forb seeds are expensive and difficult to procure (Shaw et al., 2005). Finally, there is demand for research that can inform species selection and improve restoration success in the Great Basin (Oldfield et al., 2015). These results provide further support for the importance of considering both species and population-level responses to multiple environmental factors when formulating restoration protocols.

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