

Invasive plant benefits a native plant through plant-soil feedback but remains the superior competitor

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Abstract

Plant soil feedback (PSF) occurs when a plant modifies soil biotic properties and those changes in turn influence plant growth, survival or reproduction. These feedback effects are not well understood as mechanisms for invasive plant species. *Eragrostis lehmanniana* is an invasive species that has extensively colonized the southwest US. To address how PSFs may affect *E. lehmanniana* invasion and native *Bouteloua gracilis* growth, soil inoculant from four sites of known invasion age at the Appleton-Whittell Audubon Research Ranch in Sonoita, AZ were used in a PSF greenhouse study, incorporating a replacement series design. The purpose of this research was to evaluate PSF conspecific and heterospecific effects and competition outcomes between the invasive *E. lehmanniana* and a native forage grass, *Bouteloua gracilis*. *Eragrostis lehmanniana* PSFs were beneficial to *B. gracilis* if developed in previously invaded soil. Plant-soil feedback contributed to competitive suppression of *B. gracilis* only in the highest ratio of *E. lehmanniana* to *B. gracilis*. Plant-soil feedback did not provide an advantage to *E. lehmanniana* in competitive interactions with *B. gracilis* at low competition levels but were advantageous to *E. lehmanniana* at the highest competition ratio, indicating a possible density-dependent effect. Despite being beneficial to *B. gracilis* under many conditions, *E. lehmanniana* was the superior competitor.

Keywords

Below-ground interactions, black grama, invasion ecology, Lehmann lovegrass, plant competition, plant invasion, soil microbiota

Introduction

Plant-soil feedbacks (PSFs; Bever et al. 1997) are interactions between a plant and the biotic and abiotic components of soil that affect plant growth, reproduction, and survival. One plant can create a PSF that affects itself, other conspecifics, or other co-occurring species. Positive PSFs result in increased growth, reproduction, or survival from increases in nutrient availability by arbuscular mycorrhizal fungi or mineralizing microbes (Klironomos 2002), while negative feedbacks result in decreased growth, reproduction, or survival from increases in herbivores, parasites, or pathogens (Bever et al. 1997; Petermann et al. 2008). Plant-soil feedback interactions may affect biodiversity and ecosystem functioning (Mack and Bever 2014), species coexistence (van der Putten et al. 2013), community dynamics (Teste et al. 2017), and competition (Kulmatiski et al. 2008).

Plant-soil feedback and competition are not always independent processes and should not be considered separately (Casper and Castelli 2007). Understanding such interactions is essential for the management and restoration of invaded grassland ecosystems (Wolfe and Klironomos 2005; Eviner and Hawkes 2008). Furthermore, PSFs may change over time (Bartelt-Ryser et al. 2005). For example, Reynolds et al. (2003) determined that positive PSFs influenced early successional communities, resulting in homogenization while negative PSFs resulted in increased diversity. Plant-soil feedback effects may remain after removal of the invasive species, limiting the growth of native species by creating a biotic legacy effect that influences successional changes (Kardol et al. 2007) or the restoration of native species (Kardol and Wardle 2010).

Eragrostis lehmanniana (Lehmann lovegrass), is an invasive, perennial C4 bunchgrass that reproduces both sexually and asexually. It was introduced into the United States from South Africa (Cox 1992) as part of efforts to restore degraded rangelands. A seed production program initiated by the USDA-Soil Conservation Service in 1937 led to extensive seeding in northern Mexico, west-Texas, New Mexico, and Arizona (Cox et al. 1982). The only area with extensive documentation of *E. lehmanniana* population expansion is Arizona where *E. lehmanniana* had established on approximately 145,000 hectares in Arizona by 1986 (Cox and Ruyle 1986). It is now known to have formed large monospecific stands in many areas of Arizona and New Mexico. Many of these areas were formerly dominated by the native grass species, *Bouteloua gracilis* (blue grama), a drought tolerant perennial C4 grass of high forage value (Gould 1951).

The expansion of *E. lehmanniana* in the southwestern United States is likely a result of several factors. In addition to the ability to increase tiller production in response to drought (Fernández and Reynolds 2000), *E. lehmanniana* produces great quantities of wind and water-dispersed seeds (Sumrall 1990). Fire is ineffective for control because canopy burning increases *E. lehmanniana* seedling establishment (Biedenbender and Roundy 1996). Even though only one genetic line was introduced into the U.S., and therefore *E. lehmanniana* has limited genetic diversity, it shows a high degree of phenotypic plasticity (Schussman et al. 2006). While phenotypic plasticity, prolific reproduction, and positive response to fire contribute to the success of *E. lehmanniana*

in the U.S., interactions with below ground biota may also facilitate invasion via PSF. In addition, many invasive plant species competitively suppress natives (Levine et al. 2003), and while *E. lehmanniana* likely can competitively suppress native rangeland grasses, few studies have experimentally explored the importance of *E. lehmanniana* competition on community structure that results from *E. lehmanniana* invasion.

As yet, we lack an understanding of the role of plant-mediated soil biotic changes, such as PSF, and their effects on interspecific competition in *E. lehmanniana* invasions in native grasslands. *Eragrostis lehmanniana* invasion may be increasing in part because of PSF, and PSF mediated competition. However, little is known about *E. lehmanniana* PSF, so it is equally possible that these feedbacks could be negative and ultimately limit *E. lehmanniana* invasion. Interspecific competition may also play a role in *E. lehmanniana* invasion, but how PSF influences interspecific competition is not yet understood. Evaluating the influence of PSF on competitive interactions between *E. lehmanniana* and native grasses will enhance understanding of PSF effects on plant competition and supply information that may be invaluable for rangeland restoration in the U.S. southwest.

The goal of this study was to evaluate the roles of competition and PSF in *E. lehmanniana* invasion over an invasion chronosequence. To address this goal, we determined how *E. lehmanniana* PSFs vary over time since invasion and affect competitive interactions between *E. lehmanniana* and the native grass *B. gracilis*. Three questions framing this study were: 1) How does the age of established populations of *E. lehmanniana* affect the strength and direction of *E. lehmanniana* PSF on itself and on *B. gracilis*? 2) How do PSFs created by *E. lehmanniana* affect *B. gracilis* growth? 3) How do PSFs created by *E. lehmanniana* affect competition between *E. lehmanniana* and *B. gracilis*? We predicted: 1) PSF benefits of *E. lehmanniana* to itself and conspecifics would dissipate as time since invasion increased, 2) PSFs created by *E. lehmanniana* would reduce *B. gracilis* biomass production, and 3) PSFs created by *E. lehmanniana* would provide an advantage to *E. lehmanniana* in competitive interactions with *B. gracilis*.

Methods

Study area

The Appleton-Whittell Research Ranch (Fig. 1) is managed by the National Audubon Society as a cooperative effort among the National Audubon Society, The Research Ranch Foundation, Bureau of Land Management, The Nature Conservancy, Resolution Copper Company, and the U.S. Forest Service (Kennedy and Robinett 2013). Located near Sonoita, Arizona in Madrean mixed grass prairie, grazing has been excluded from the 8000 acres since 1968 (Kennedy and Robinett 2013).

According to Breckenfeld and Robinett (2001), on the Appleton-Whittell Research Ranch, loamy upland ecological sites occur as mesa tops and fan terraces with neutral to slightly acid pH. A six-inch clay horizon is covered by one to three inches of gravelly



Figure 1. Loamy upland sampling sites at Appleton-Whittell Audubon Research Ranch, Sonoita, AZ, USA. Inset shows location of Appleton-Whittell Audubon Research Ranch in Arizona, USA. Dates are the estimated dates of Lehmann lovegrass (*Eragrostis lehmanniana*) invasion. Map data 2021 Google.

sandy loams. *Bouteloua* species dominate areas not invaded by nonnative *Eragrostis* species. Native grasses include *Bouteloua gracilis*, *B. curtipendula* (sideoats grama), and *B. chondrosioides* (sprucetop grama) and are mixed with *Aristida* (threeawn), *Lycurus setosus* (wolftail), *E. intermedia* (plains lovegrass), and *Bothriochloa barbinodis* (cane beardgrass) (Breckenfeld and Robinett 2001).

Inocula collection

Soil inocula were collected from four loamy upland sites (Fig. 1, Table 1) on the Appleton-Whittell Research Ranch (AWRR) in Sonoita, AZ in 2017 (Fig. 1) on October 23, 2017. Three of these sites had been invaded by *E. lehmanniana* and one site was uninvaded. *E. lehmanniana* invaded these sites in 1949, 1985–2001, and 2003–2006. Ranges of invasion ages are based on best estimates from staff at the AWRR. At each invaded site, we collected 50 ml soil samples from 0–10 cm immediately below the root crown for each of 60 *E. lehmanniana* plants. Crown circumference of each plant was recorded. A hand trowel, sterilized with 70% ethanol solution between samples, was used to collect soil and transfer soil to 50 ml Falcon centrifuge tubes. In the uninvaded site, we collected 50 ml soil samples from the rhizosphere of 60 *B. gracilis* plants using a sterilized hand trowel. A total of 240 soil samples were collected and stored in

Table 1. Locations of loamy upland soil sample collection sites at Appleton-Whittell Audubon Research Ranch, Sonoita, AZ, USA.

Site	North American Datum 1983	Universal Transverse Mercator (UTM)	
	Latitude / Longitude	Easting	Northing
Uninvaded	31.571065, -110.492825	547152	3495008
2003–2006	31.580104, -110.489865	545463	3494981
1985–2001	31.591461, -110.498605	547515	3495289
1949	31.575366, -110.492261	547712	3496438

an insulated cooler for transportation and kept at 26 °C for 30 days before use. Because soils were dry when collected, storage at room temperature was unlikely to lead to any rapid biological transformations. This storage temperature approximated the historical mean monthly temperature at the sample collection site when samples were collected. Any potential increase in soil respiration due to the difference in temperature was prevented by lack of available moisture (Conant et al. 2004).

Inoculum and bulk soil preparation

One half of the soil samples from each of the four locations was randomly selected to be used as “live” inoculum. The remainder was sterilized by autoclave for use as “sterile” control inoculum for the PSF experiment. A local sandy loam soil collected from the Chihuahuan Desert Rangeland Research Center near Las Cruces, NM was used as the growing media. We collected 0–20 cm of the soil surface and then double steam pasteurized the soil in a Heavy Duty Pro-Grow Soil Sterilizer at 88–93 °C over 48 consecutive hours with mixing at 24 h. Soil was added to the soil sterilizer in layers, with each layer being wetted initially and at 24 h after the start of pasteurization, when soil was mixed for the second round of pasteurization.

Experimental design

We conducted a two-phase plant-soil feedback experiment (Fig. 2, Brinkman et al. 2010). *Eragrostis lehmanniana* conditioned soil microbial communities in Phase 1. Growth of *B. gracilis* and *E. lehmanniana* indicated response to microbial communities in Phase 2. We used a randomized complete block design with five levels of competition, four invasion times, two soil treatments (living and sterile), four plants per pot, and six replicates for a total of 240 pot-level experimental units. On November 25, 2017, three percent inoculum was added to 97 % pasteurized sandy loam field soil to create a total of 1L of medium per pot. The use of soil inoculum isolates the effect of soil biota from other soil properties (Brinkman et al. 2010). Each pot was inoculated with one soil sample collected from one plant. Treatment with live, non-autoclaved *B. gracilis* inoculum yielded a single uninvaded treatment, and treatments with live, non-autoclaved *E. lehmanniana* inoculum from three invaded sites yielded three invaded treatments.

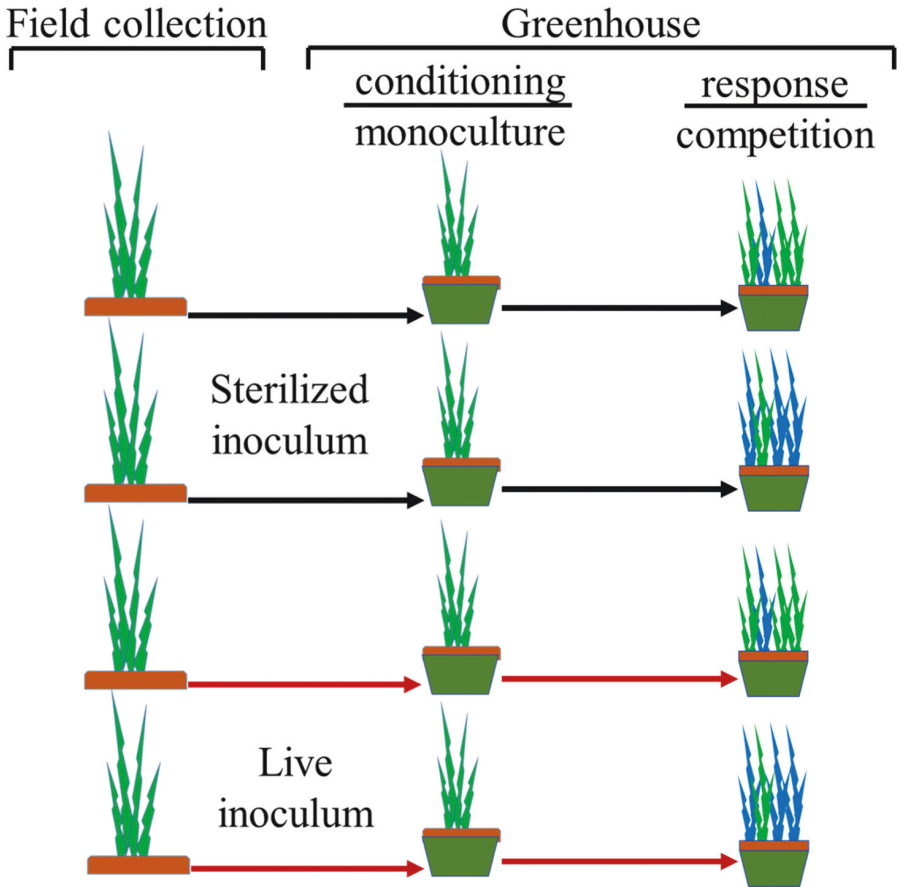


Figure 2. Experimental design for plant-soil feedback experiment based on Brinkman et al. (2010) combined with de Wit and van der Bergh (1965) replacement series for plant competition experiment.

Greenhouse experiment – conditioning phase

In Phase 1, the conditioning phase, all pots were seeded with *E. lehmanniana*. Because a high amount of plant biomass was desired to facilitate the proliferation of soil microbes from minimal inoculum, *E. lehmanniana* was seeded at a high density (100–150 seeds per pot). This resulted in approximately 50 to 75 plants per pot. While there were different numbers of *E. lehmanniana* plants per pot, this likely did not affect biomass produced, as the density was high enough to ensure the effect of the law of constant final yield (Weiner and Freckleton 2010). To provide time for the microbial community from the inoculant to proliferate throughout the soil, plants were grown for 12 weeks during the conditioning phase. After 12 weeks, all aboveground biomass was harvested by clipping at soil level, oven-dried at 60 °C for 48 h, and weighed. The pots were air-dried at ambient greenhouse temperature for two weeks to ensure that *E. lehmanniana* plants were dead prior to Phase 2.

Greenhouse experiment – response phase

In Phase 2, we used a replacement series design (de Wit and Van den Bergh 1965) to determine competition effects between species, and the effects of site, defined by *E. lehmanniana* invasion age, on competition. This design, common in plant competition studies, holds plant density constant and varies the relative proportion of two species, A and B. If species A is the superior competitor, the relative yield of species B in competition with species A will be less than when species B is grown in monoculture. Likewise, the relative yield of species A will be higher in competition with species B than it would be when grown in monoculture. In our experiment, plant density was held constant at four plants per pot while one of five ratios, 0:4, 1:3, 2:2, 3:1, 4:0, of *E. lehmanniana* and *B. gracilis* was randomly assigned to each pot from Phase 1, stratified by site. Treatments were divided equally among five blocks. Each pot was divided into four sections using wooden popsicle sticks cut to fit in the pot. This ensured seeds from the two species remained separate for germination. Approximately 25 *E. lehmanniana* and *B. gracilis* seeds were sown in the randomly assigned section of the soil surface. Preliminary germination trials indicated *Bouteloua gracilis* seeds needed three more days for germination than *E. lehmanniana* seeds (data not shown). Therefore, *B. gracilis* seeds were sown three days prior to *E. lehmanniana* so all plants would emerge simultaneously. Two weeks after emergence, when it was possible to identify seedling species, seedlings were thinned so that each pot contained only four equidistant plants. Phase 2 plants were grown for 12 weeks at which time the aboveground biomass was harvested and dried as described for Phase 1.

In both phases, pots were watered daily to maintain a moist growth environment. Pots were fertilized once between Phase 1 and Phase 2 with 20 ml Miracle-Gro Water Soluble All Purpose Plant Food (24-8-16).

Plant-soil feedback

Plant-soil feedback values were calculated using above-ground biomass per pot in each phase. We had six replicates for each level of competition, inoculum, and invasion age. Within each set of matching combinations of competition and invasion age, we randomly paired each of six sterile pots with one of the six live pots to calculate one PSF value for each pair of pots. This resulted in a total of six PSF values for each factor and treatment following Petermann et al. (2008). Plant-soil feedback values were calculated using untransformed biomass values as:

$$\text{PSF} = \ln \left(\frac{\text{biomass live inoculum}}{\text{biomass sterile inoculum}} \right) \quad (1)$$

whereas biomass was the above-ground plant material in a single pot. This formula was chosen based on recommendations in Brinkman et al. (2010) so all feedback scores were symmetrical around zero. Feedbacks are described from the plant perspective and

aligned with common usage in PSF research (Brinkman et al. 2010; van der Putten et al. 2016). Positive and negative PSF values indicate higher and lower biomass production with live inoculum, respectively.

Replacement series and relative yield

Relative yield (RY) and relative yield total (RYT) were calculated according to de Wit and Van den Bergh (1965):

$$RY = \left(\frac{Y_x}{Y_m} \right) \quad (2)$$

$$RYT = \left(\frac{Y_{ix}}{Y_{im}} \right) + \left(\frac{Y_{jx}}{Y_{jm}} \right) \quad (3)$$

where Y_x is yield in mixture and Y_m is yield in monoculture for relative yield and where i and j are *E. lehmanniana* and *B. gracilis*, respectively, for relative yield total. Relative yields instead of absolute yields were used because the biomass produced by the two species were qualitatively very different (Jolliffe 2000).

Statistical analysis – invasion chronosequence and plant-soil feedback

In the response phase, PSFs were analyzed as a function of species, site, and competition as fixed effects, block as random effect, and all two- and three-way interactions of fixed effects using a linear mixed-effects model with PSF as a normally distributed response variable. Conditioning phase biomass and crown circumference were evaluated as covariates but were not significant and were removed from the model. Data were subset for specific comparisons when an interaction term was significant. In addition, data from monocultures were analyzed as a function of species and site as fixed effects, block as random effect, and factorial interactions of all fixed effects using a linear mixed-effects model with PSF as the response variable. Data were then subset by species and analyzed as a function of site as a fixed effect and block as a random effect using a linear mixed-effects model with PSF as the response variable. When significant differences in mean PSF were detected among site and treatment, we used post hoc testing using Tukey's Honest Significant Difference (H.S.D., $p < 0.05$) to identify treatments with different effects.

Statistical analysis – competition with and without plant-soil feedback

Lovegrass-grama competition without PSF was analyzed using paired t-tests that tested the null hypothesis that the actual relative yield was equal to the expected relative yield at each competition ratio and for each species. To test if *E. lehmanniana* PSF

provided an advantage to *E. lehmanniana* in competitive interactions with *B. gracilis*, we analyzed the significance of the difference between mean relative yield in sterile vs living soil for a given *E. lehmanniana* : *B. gracilis* ratio using the same linear mixed-effects model and Tukey H.S.D *post hoc* tests with relative yield as the gamma-distributed response variable.

All data were analyzed using IBM SPSS Statistics 25 (IBM, 2018). Validity of models was assessed with plots of fitted vs. residuals to check for constant variance and to ensure there were no negative fitted values. A Levene test and visual assessment of residuals were used to ensure homoscedasticity. Normal probability (Q-Q) plots were used to ensure the random effects were normally distributed. Wald chi-square statistics were calculated for linear mixed models using SPSS MIXED (IBM, 2018).

Results

Invasion chronosequence and plant-soil feedback

While conditioning biomass showed a weak, positive correlation to inoculum source-plant crown circumference ($r = 0.129$, $p = 0.016$), there was no evidence of relationship between source-plant crown circumference and above-ground biomass produced in the response phase. Therefore, crown circumference was excluded as a covariate for subsequent analyses. Neither *E. lehmanniana* nor *B. gracilis* response phase biomass was affected by *E. lehmanniana* conditioning phase biomass. Conditioning phase biomass was not correlated with response phase PSF for either species. Therefore, conditioning phase biomass was not included as a covariate for response phase analysis.

Plant soil feedbacks on *B. gracilis* in soil from the uninvaded area were significantly different from PSFs on *B. gracilis* in invaded soils ($F_{3,20} = 9.488$, $p < 0.001$, Fig. 3a). Plant-soil feedbacks developed in uninvaded soils were negative and resulted in decreased *B. gracilis* above-ground biomass. Plant-soil feedbacks on *B. gracilis* were positive in all invaded sites and resulted in increased above-ground biomass (Fig. 3a). Plant-soil feedbacks on *E. lehmanniana* were not significantly different from zero (Fig. 3b) over all invasion times.

Competition without plant-soil feedback

To evaluate competition independently of PSF, mean above-ground biomass per plant was evaluated across competition ratios for sterile treatments (Fig. 4), using pooled data from all sites. When grown in sterile soil inoculum, *E. lehmanniana* mean per plant biomass was equal across *E. lehmanniana* : *B. gracilis* ratios of 4:0, 3:1, and 2:2, yet increased at 1:3 ($F_{3,89} = 10.932$, $p < 0.001$, Fig. 4). In contrast, when grown in sterile soil inoculum, *B. gracilis* mean per plant biomass was equal across *E. lehmanniana* : *B. gracilis* ratios of 3:1, and 2:2, 1:3, and increased at 0:4 (Fig. 4, $F_{3,90} = 12.475$, $p < 0.001$).

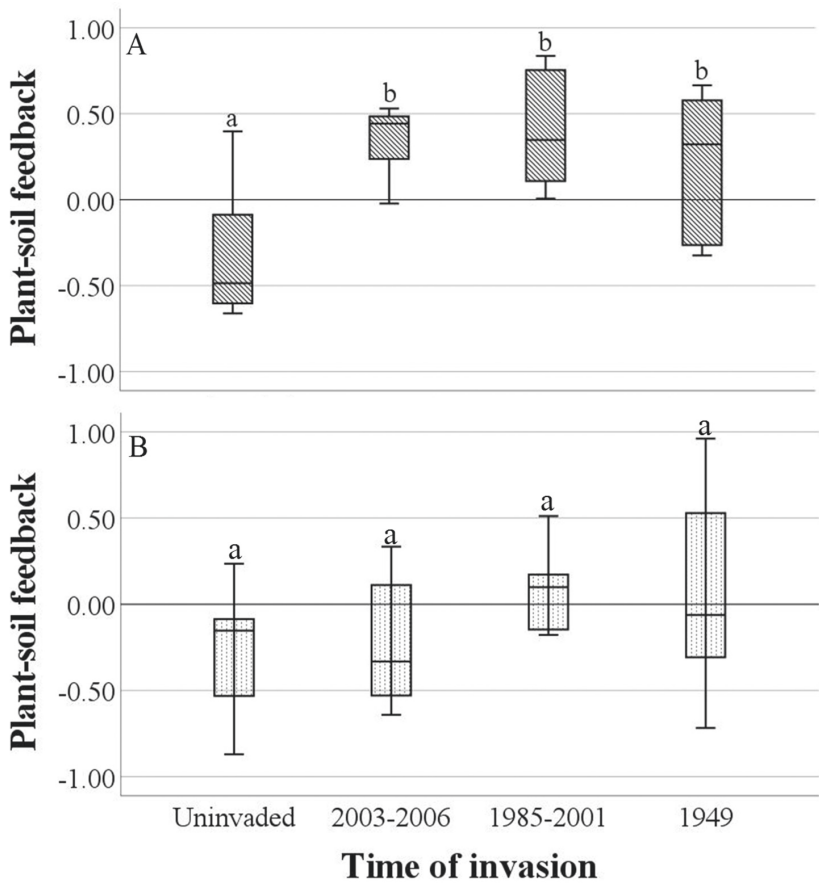


Figure 3. Plant-soil feedbacks for **A** *Bouteloua gracilis* and **B** *Eragrostis lehmanniana* monocultures grown in soils conditioned for 12 weeks by *E. lehmanniana*. Plants were grown for 12 weeks prior to harvesting in the response phase. Soil inoculum collected from sites of known lovegrass invasion times on Appleton-Whittell Audubon Research Ranch, Sonoita, AZ. (n = 6). Similar letters over the bars indicate no difference in plant-soil feedbacks between invasion times. The boxes represent 25–75% interquartiles. The bold black lines inside the box represent the medians. Top and bottom whiskers indicate the maximum and minimum values, respectively. Values greater than zero indicate that a species performed better on live soil than on sterile soil, and vice versa.

Competition with plant-soil feedbacks

Data were pooled for each site because relative yield competition outcomes for each ratio did not vary across sites ($p > 0.05$). Live inoculum had little effect on relative yield of either species (Fig. 5), except at the highest (3:1) *E. lehmanniana*: *B. gracilis* ratio. *B. gracilis* yielded less than its hypothetical yield, as demonstrated by the yield line shifting to below the hypothetical expected yield line (Fig. 5). *Eragrostis lehmanniana* displayed the opposite trend with its relative yield shifted to above its hypothetical expected yield line (Fig 5). Across competition levels, relative yield total was only slightly less than expected for all sites combined.

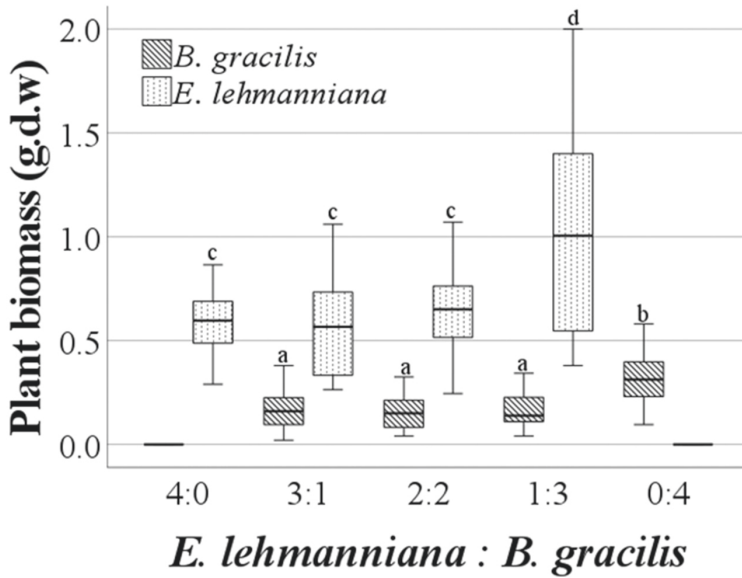


Figure 4. Median per plant above-ground *Bouteloua gracilis* and *Eragrostis lehmanniana* biomass (grams dry weight) produced in a replacement series competition experiment in soils conditioned for 12 weeks by *E. lehmanniana* with sterile inoculum. Plants were grown for 12 weeks prior to harvesting. Within species, significant differences among *E. lehmanniana* ($F_{3,89} = 10.932$; $p < 0.001$) and *B. gracilis* ($F_{3,90} = 12.475$; $p < 0.001$) biomass are represented by letters, with similar letters over the bars indicating no difference in mean biomass between competition ratios. The boxes represent 25–75% interquartiles. The bold black lines inside the box represent the medians. Top and bottom whiskers indicate the maximum and minimum values, respectively.

Discussion

The goal of this study was to evaluate the roles of PSF and competition in *E. lehmanniana* invasion into *B. gracilis* communities over time. We estimated net plant-soil feedbacks to determine the influence of *E. lehmanniana* invasion age on *B. gracilis* growth and competitive outcomes between the two species. Our results showed that *E. lehmanniana* invasion created interspecific PSFs that benefited *B. gracilis*. However, this effect was only present when *B. gracilis* was grown in soils conditioned with inocula from *E. lehmanniana* invaded communities. *Bouteloua gracilis* growth was inhibited when grown in soil conditioned by *E. lehmanniana* with inoculum from the native *B. gracilis* community, indicating that during the initial phases of an invasion, *B. gracilis* would suffer a negative PSF. Plant-soil feedbacks on *E. lehmanniana* were not significantly different from zero. Despite being beneficial through PSF to *B. gracilis* under many conditions, *E. lehmanniana* outcompeted *B. gracilis* over all competition levels. We found no significant differences in competition outcomes between live and sterile inoculum from *E. lehmanniana* populations of four invasion ages that would indicate PSF influences competition, apart from the highest ratio of *E. lehmanniana* to *B. gracilis*.

The addition of fertilizer in our experiment may have ameliorated negative PSF (Brinkman et al. 2010). Thus, it is possible that the positive PSF documented on

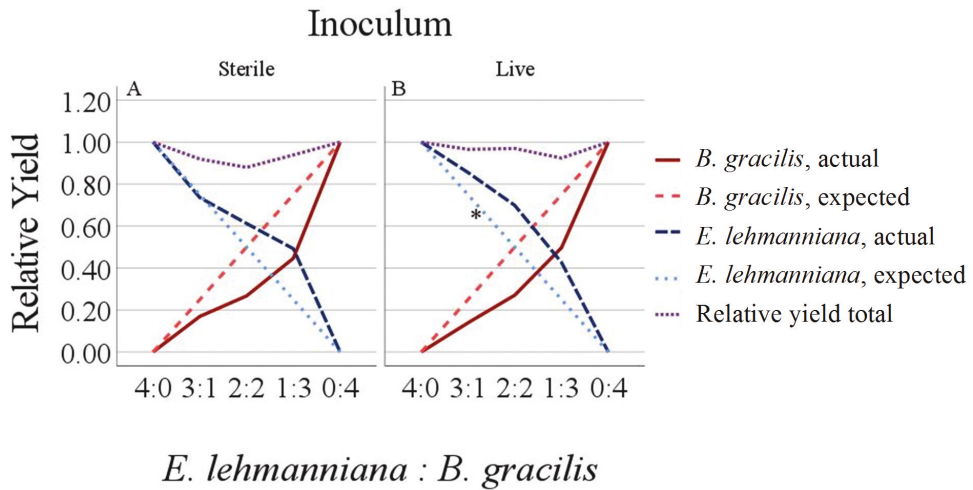


Figure 5. Replacement series competition study of relative yields of *B. gracilis* and *E. lehmanniana* across competition ratios grown in soil cultured with **A** sterile and **B** live inoculum. Soils were conditioned for 12 weeks by *E. lehmanniana*. Plants were grown for 12 weeks prior to harvesting in the response phase. Soil inoculum collected from sites of known lovegrass invasion times on Appleton-Whittell Audubon Research Ranch, Sonoita, AZ. The expected (hypothetical) lines represent the relative yield that would be expected if species did not compete with one another (e.g., the relative yield for a species A, planted with a competitor B, at A:B planting ratios of 0:4, 1:3, 2:2, 3:1 and 4:0 are 0, 0.25, 0.5, 0.75 and 1, respectively). If one species is outcompeted, it will yield less than expected and its curve will shift to below the expected line. The line for relative yield total will be convex for facilitation or concave for competition. The superior competitor will yield more than expected and its curve will shift to above its expected line. The asterisk indicates the proportion of *E. lehmanniana* at which plant soil feedbacks increased *E. lehmanniana* yield relative to yield in the sterile soil pots.

B. gracilis are the result of fertilization overcoming the negative affect of nutrient depletion as a feedback mechanism. Desert soils are often nitrogen poor (Peterjohn and Schlesinger 1991), and fertilizer addition can have great effect on plant growth especially in a greenhouse setting (Manning et al. 2008). Nutrient addition may also have decreased any positive feedback effects by reducing the benefit of microbes that assist in nutrient acquisition or increasing plant pathogen populations (Revillini et al. 2016). Nonetheless, we felt that fertilization was necessary after the conditioning phase where plants showed signs of nutrient deficiency. Further, fertilization increases plant-plant competition (Rajaniemi 2002) and facilitated the testing of *B. gracilis* – *E. lehmanniana* competition under the necessarily short time frame and limited growth space of a greenhouse PSF experiment (Forero et al. 2019).

Invasion chronosequence and plant-soil feedback

Though the mean *E. lehmanniana* PSF values indicated the potential for PSF to become more positive over time, the ages of established populations of *E. lehmanniana* did not significantly affect the strength and direction of *E. lehmanniana* PSF. Plant-soil feedbacks

effects on grasses are predominantly negative and 70 % of 329 experiments have resulted in negative PSF effects (Kulmatiski et al. 2008). Our mean *E. lehmanniana* intraspecific PSF effects ranged between -0.259 and 0.961, values higher than the -0.53 average for nonnative perennials reported by Kulmatiski et al. (2008). Diez et al. (2010) found that as invasive plant residence time and spread increased, PSFs became more negative; however, relatively few studies have evaluated PSF over decades of invasion residence time, as we have done. Many invasive plants develop greater negative PSF over time (Bever 2003; Reinhart and Callaway 2006). *Eragrostis lehmanniana* intraspecific PSFs were neutral across 68 years of invasion, suggesting this species may be unresponsive to soil microbiota.

Te Beest et al. (2009) suggested that the ability to increase plant performance in soils conditioned by heterospecifics may be a mechanism favoring invasion, especially for plants that easily disperse into new habitats via seed or propagule dispersal. *Eragrostis lehmanniana* PSFs were detrimental to *B. gracilis* in uninvaded soils. We hypothesize that once *E. lehmanniana* individuals become established they may condition the soil to the detriment of *B. gracilis*, facilitating further establishment and spread of *E. lehmanniana*. *Bouteloua gracilis* may subsequently respond positively to *E. lehmanniana* PSF, but the superior competitive ability of *E. lehmanniana* will negate any beneficial PSF effect on *B. gracilis*.

Many previous studies have shown that plants tend to perform better in soils conditioned by heterospecifics (Kulmatiski et al. 2008), and our results only partially support this idea. *E. lehmanniana* PSF conferred a benefit to *B. gracilis* in soils that were previously invaded by *E. lehmanniana*. However, in uninvaded soils, heterospecific feedbacks negatively affected *B. gracilis* performance. In a meta-analysis to determine the relative importance of competition and PSF, Lekburg et al. (2018) suggested that in resource-limited environments facilitative interactions are likely to be enhanced by PSFs. The combination of inter- and intraspecific PSF effects may potentially help maintain diversity and contribute to invasion resistance (Klironomos 2002; Reinhart et al. 2003; Te Beest et al. 2009). The ability to create monocultures despite beneficial interspecific PSF effects indicates that *E. lehmanniana* possesses other, more effective, traits for invasion, such as competitive ability.

Plant-soil feedback and competition

Though PSF can modify competitive interactions and vice versa (Casper and Castelli 2007), *Eragrostis lehmanniana* was a stronger competitor than *B. gracilis* regardless of PSF effects. Most exotic plant species exert a strong competitive effect against native plant species (Levine et al. 2003) and *E. lehmanniana* is no exception. Though *E. lehmanniana* competitively suppressed *B. gracilis*, competition between these two species reduced total relative yield, likely due to intraspecific competitive suppression by *E. lehmanniana*. Additional research is needed to fully understand the importance of this interaction in *E. lehmanniana* invasions.

Eragrostis lehmanniana PSFs affected competition only when at 75% *E. lehmanniana* density. At lower densities, the effects of competition were much greater than

PSF effects. Apart from the highest ratio of *E. lehmanniana* to *B. gracilis*, we found no differences in outcomes of competition between live and sterile inoculum from *E. lehmanniana* populations of four invasion ages that would indicate PSF influences competition. Similarly, when investigating how community context altered plant–soil feedback between the non-native invasive forb *Lespedeza cuneata* and co-occurring native prairie species, Crawford and Knight (2017) found that a beneficial intraspecific PSF effect had no effect on competitive outcomes. However, Lekberg et al. (2018) determined that at low densities, PSF was overwhelmed by the strength of competition. We found that PSF was overwhelmed at low *E. lehmanniana* density, yet influenced competition at higher density, indicating a density-dependent effect that likely contributes to the invasiveness of *E. lehmanniana*. Even without PSF, *E. lehmanniana* is the superior competitor in *E. lehmanniana*–*B. gracilis* interactions.

Wubs and Bezemer (2017) found that competitive hierarchies are altered by PSF if conditioned by a single species. However, if multiple species have conditioned the soil, plant evenness increases due to the PSF-induced similarity of competitive ability across species (Wubs and Bezemer 2017). Future research in this system should include individual and combined conditioning by *B. gracilis* as well as *E. lehmanniana* and should investigate the resultant competitive outcomes between the two species. Our results differ from Xue et al. (2018) who determined that PSF effects are enhanced by inter-specific competition. In our study, PSF influenced competition only in soils developed from the oldest site and only at high *E. lehmanniana* proportions.

Based on previous understanding (Casper and Castelli 2007), our results explain some variation within the PSF interactions at the seedling stage of *B. gracilis* and *E. lehmanniana*. Future research should attempt to quantify PSF interactions of these species over a longer growth period to determine if *E. lehmanniana* continues to provide a benefit via PSF to *B. gracilis* as plants mature and if competition outweighs this benefit. By utilizing soil inoculum from mature plants in established populations, our study helps develop the understanding of the changes in PSF potential over years of population habitation.

To further elucidate the function of PSFs in plant invasions, future research should include growth of *E. lehmanniana* in soil conditioned by heterospecific and conspecific individuals at varying plant densities. The mechanisms by which *E. lehmanniana* interacts with specific soil microorganisms also needs investigation. In addition, differences in biomass allocation resulting from soil conditioning by conspecifics and heterospecifics may influence reproduction and competitive ability, influencing range expansion (Te Beest et al. 2009) and have yet to be investigated in *E. lehmanniana*.

Conclusions

We rejected our prediction that PSF benefits of *E. lehmanniana* to itself and conspecifics would dissipate as time since invasion increased. Plant-soil feedbacks provided no benefit to *E. lehmanniana*, nor did this change over time. With respect to our

prediction that *E. lehmanniana* PSFs would inhibit *B. gracilis* biomass production, we determined that contrary to our prediction, *B. gracilis* benefited from PSFs under all conditions except uninvaded. Our third prediction that *E. lehmanniana* competition would be enhanced by PSF was only partially confirmed. Plant-soil feedback did not provide an advantage to *E. lehmanniana* in competitive interactions with *B. gracilis* at low competition levels but were advantageous to *E. lehmanniana* at the highest competition ratio, indicating a possible density-dependent effect.

Plant and soil-microbial communities are responsive to biotic and abiotic conditions that affect associated plants (Ehrenfeld et al. 2005). Conditions such as climate shifts, plant species assemblages, and herbicide use may change the diversity of associated mycorrhizae and microbial functional groups. These changes in turn affect both plant and community function. Determining the occurrence of PSFs in an exotic species such as *E. lehmanniana* is the first step in defining the functional significance of changes in the microbial community structure on invaded communities and ecosystems.

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