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RESEARCH ARTICLE

Grassland Research

Inoculation with native grassland soils improves native plant species germination in highly disturbed soil

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Abstract

Background: Grasslands are globally imperiled, facing continued threats from anthropogenic disturbances. Seeding remains a common grassland restoration method, and yet, is typically met with limited success, partially because soils of degraded systems inhibit the germination of native species.

Methods: We assessed the germination success of 16 native grassland species sown in soils collected from a degraded grassland converted into a nonnative warm-season perennial grass, *Bothriochloa ischaemum,* and areas previously subjected to the eradication of this nonnative species. Our objectives were as follows: (1) determine native seed germination in soils collected from *B. ischaemum* or eradication control sites, compared to germination in native grassland soil, and (2) assess if native soil inoculation improves germination, compared to germination in degraded soils without inoculation.

Results: Germination of native species was exceedingly low when seeded into soil dominated by *B. ischaemum,* or in soil previously treated with combinations of herbicide and prescribed fire, relative to native grassland control. However, amendments with native grassland soil resulted in germination equivalent to native grasslands, alleviating the negative influences of degraded soils.

Conclusions: Our results highlight the role of native soil in improving the germination of desirable plant species following intensive management and soil degradation. Our research may improve restoration outcomes for managers focused on the conservation and restoration of grasslands.

KEYWORDS

Bothriochloa ischaemum, invasive species, restoration, soil inoculation

INTRODUCTION

Grasslands, among the largest terrestrial biomes, are currently under high conservation concern as they provide as many as 33 important ecosystem services (Zhao et al., 2020), including the primary source of meat and dairy products, at least one-third of the global carbon storage of all terrestrial ecosystems, food sources for declining pollinators, soil erosion and flood control, aquifer recharge, and climate regulation (Sala et al., 2017). As the world's human population is projected to reach 10.9 billion by 2100 (United Nations, 2019), global food demand is predicted to double (Lal et al., 2016), and increased demands for meat and dairy production will require diverse and highly productive grasslands (Sanderson et al., 2004; Schaub et al., 2020), and yet, much of the world's grasslands face large-scale loss or degradation resulting from anthropogenic factors such as conversion to cultivated crops, droughts exacerbated by climate change, over-grazing, and introduction of invasive species (Torok et al., 2021; Y. Zhang et al., 2019). Clearly, meeting the demands of global food security will require successful restoration of degraded lands, including developing improved methods, as current practices frequently fail to regain forage production, biodiversity, and other ecosystem attributes of historical intact grasslands.

Current restoration methods often not only fail to reinstate native biodiversity but can also unexpectedly exacerbate the loss of native grassland (NG) ecosystem services. For example, practices such as topsoil removal to remediate high nutrient loads and undesirable seed banks often result in high levels of erosion and inadvertent removal of beneficial soil organisms (Torok et al., 2011). Nonnative plant species have often been introduced as erosion control agents and can aggressively establish on degraded sites, as many nonnatives are characterized by traits such as rapid biomass production and exceptionally high reproduction and germination success (Duell et al., 2021). However, establishing a monoculture is clearly not a path forward to increasing biodiversity; in fact, invasive species have been reported to be one of the main causes of biodiversity loss (Vitousek et al., 1997). Non-native species also often alter soil biotic and abiotic properties (Castro-Diez et al., 2019; Duell et al., 2022; Vila et al., 2011), negatively influence fire regimes (Brooks et al., 2004), or interfere with the establishment of desirable native species (Pearson et al., 2018), ultimately compromising restoration of native biodiversity and ecosystem services. In fact, invasive species have been considered the most critical barrier to restoration success (D'Antonio & Meyerson, 2002), and removing nonnative species is one of the most common restoration interventions (D'Antonio et al., 2016; Weidlich et al., 2020).

Following eradication of invasive plant species, seeding with desirable native species remains the most common method of revegetating landscapes (Palma & Laurence, 2015), and yet, reseeding is typically met with limited success, suggesting that soils previously occupied by nonnative species have properties that inhibit germination of desirable native species. Invasive plants can create legacy effects, including disruption and alteration of native soil microbial communities, which often persist for many years following removal (Grove et al., 2012; Jordan et al., 2008). For example, invasive plant species may accumulate soil pathogens that negatively affect the growth of local native plant species (Mangla et al., 2008), disrupt beneficial arbuscular mycorrhizal **(AM)** fungal communities (Q. Zhang et al., 2010), or produce allelopathic root exudates that inhibit germination of native grasses (Greer et al., 2014). However, restoration efforts typically focus exclusively on the removal of nonnative plant species under the assumption that removal of the nonnatives will result in the desired restoration outcomes (Quirion et al., 2018). While previous research indicates that failing to address belowground alterations is likely responsible for the poor results of many restorations (Grove et al., 2012, 2015; Jordan et al., 2008), few studies have examined the germination of native species in invaded or herbicide-treated areas compared to germination in corresponding native soils, or if the use of soil inoculation might improve germination in degraded soil further impacted by invasive species and herbicide or prescribed fire.

In our current greenhouse study, we assess germination of native plant species in soils collected from a degraded grassland that was converted to a nonnative warm-season perennial, *Bothriochloa ischaemum* (L.) Keng monoculture. The site was subjected to herbicides and prescribed fire to experimentally assess specific eradication management practices. Successful restoration of this site is exceedingly difficult as *Bothriochloa* spp. have been shown to exert direct and indirect effects on native soil, plant, and animal communities (Bhandari et al., 2018; Duell et al., 2022; Gabbard & Fowler, 2007; Hickman et al., 2006; Koziol et al., 2021), and soil legacy effects of herbicides used to control invasive plants have been known to limit native plant establishment (Cornish & Burgin, 2005; Lekberg et al., 2017). The specific objectives of our study are to (1) determine the effects of *B. ischaemum* and eradication control management on native plant germination, relative to germination **in NG** soil, and (2) assess if native soil inoculation improves germination success of 16 species of **NG** grasses and forbs, compared to germination in degraded soils without inoculation. Based on minimal success following seeding with native species at the study site, we hypothesized that germination of native plants seeded into degraded soils will be significantly reduced, relative to germination in native soils. Based on previous studies that reported substantial increases in native plant survival and acceleration of plant community succession following amendments with native soil (e.g., Koziol & Bever, 2017; Koziol et al., 2020), we further hypothesized that inoculation with native soil amendments can substantially improve germination of native species seeded into degraded soil, compared to noninoculated soils.

MATERIALS AND METHODS

Site description and previous experimental treatments

Soil for our current germination study was collected from plots of a previous field experiment conducted at the Marvin Klemme Range Research Station (35° 22' N, 99° 04' W) in western Oklahoma, USA (Robertson et al., 2013). This area receives an average of 75 cm of precipitation annually, with an average annual temperature of 26°C (Brock et al., 1995). The research station has been managed for the past ~30 years by low to moderate cattle grazing intensity and is dominated by native warm-season perennial grasses; however, several areas of near-monotypic stands of *B. ischaemum* are also present. The experiment conducted by Robertson et al. (2013) assessed single, multiple, and combined treatments of herbicides and prescribed fire applied in a factorial experiment utilizing a random block design to test the efficacy of various control methods on *B. ischaemum.* Treatments with glyphosate were applied in early (May 18), middle (August 2), or late (September 1) throughout the growing season. Glyphosate (Roundup WeatherMAX; Monsanto) was applied at a rate of 2.125 kg a.i. ha^{-1} (mixed with 0.232 g of ammonia sulfate) using an R&D EXD-203s bicycle sprayer with 11 002 AirMix 110° fan nozzles approximately 20-25 cm above the vegetation. The early herbicide treatment was applied when *B. ischaemum* had formed five true leaves (Robertson et al., 2013). Prescribed fire was only applied mid-season, between early- and late-season herbicide applications.

Soil collection/preparation

Soil from the previous field experiment by Robertson et al. (2013) was collected from replicate plots *(n* = 4) subjected to the following treatments: (1) early herbicide and late herbicide (EL) resulting in 63% *B. ischaemum* cover, (2) early-season herbicide, mid-season burn, and late-season herbicide (EBL) resulting in 10.5% *B. ischaemum* cover, (3) early-season herbicide, mid-season herbicide, and late-season herbicide (EML) resulting in 10% *B. ischaemum* cover, and (4) experimental control (no herbicide or burn) with >90% *B. ischaemum* cover *(Bi).* Soil from adjacent NG (0 *B. ischaemum* cover) was collected to serve as the restoration reference (control) site. Soil was collected from six random areas across each treatment plot to a depth of 15 cm using a hand trowel. Soil of each treatment was homogenized, transported to Oklahoma State University greenhouse facilities, and sieved through a 10 mm sieve to remove large plant roots, rhizomes, rocks, and coarse debris. Soils used in the germination experiment were collected in April, 1 year following the conclusion of the herbicide treatments applied for Robertson et al. (2013). Soils were analyzed by the Oklahoma State University Soil, Water and Forage Analytical Laboratory. To test for differences in nutrients among soils, a one-way analysis ofvariance **(ANOVA)** was utilized, with soil source as the main effect. There were no significant differences in the nutrient composition of soil collected from the different experimental treatments (i.e., soil sources) ($p = 0.5$), with soils containing 9mgkg^{-1} plant-available P (Mehlich test 3), 14.9mgkg^{-1} NH_4, and 8.5 mgkg^{-1} NO_3, and a pH of 6.7.

Germination study design

To determine seed germination in soil influenced by *B. ischaemum* or by previous experimental treatments to eradicate *B. ischaemum,* four replicate plastic greenhouse seedling flats (25.0 cm length x 25.0 cm width x 5.08 cm depth without individual seedling cells or humidity domes) were filled with 1.5kg (dry weight) offield-collected, sieved soil from each of the 5 previous soil sources (EL, EBL, EML, *Bi,* and NG) for each of16 plant species (Table 1). To determine the influence of NG soil amendment, four additional replicate flats for each of the 16 plant species were filled with 1.0kg ofsoil from each ofthe 5 soil sources (EL, BBL, EML, *Bi,* and NG) topped with 0.5kg (dry weight) of freshly collected NG soil distributed evenly across the soil surface. The volume of native prairie soil amendment was selected to maintain consistent volumes of total soil used across all treatments. Therefore, the complete experimental design consisted of640 flats (5 soil sources x 2 **NG** amendments [+/-] x 16 plant species x 4 replicate flats). An additional four flats containing NG soil, without added seeds, were randomly placed throughout the greenhouse to confirm the absence ofcontamination from nonintentional seed sources.

We selected 16 NG species including 8 warm-season grasses, 2 cool-season grasses, and 6 forbs purchased from local seed distributers, Johnston Seed Company and Sharp Brothers Seed (Table 1). No source was able to provide all 16 plant species. Seeds were cold-moist stratified as required to break seed dormancy. Seeds were surface-

TABLE 1 Complete list of plant species, along with associated taxonomic families, broad functional groups, and life histories used in the seed germination experiment

Functional group	Species	Family	Growth habit
Warm-season grasses	*Andropogon gerardii* Vitman	Poaceae	Perennial
	Bouteloua curtipendula (Michx.) Torr.	Poaceae	Perennial
	Eragrostis trichodes Wood	Poaceae	Perennial
	Leptoch/oa dubia (Kunth) Nees	Poaceae	Perennial
	Panicum virgatum L.	Poaceae	Perennial
	Schizachyrium scoparium (Michx) Nash	Poaceae	Perennial
	Sorghastrum nutans (L.) Nash	Poaceae	Perennial
	Sporobolus compositus (Poir.) Merr.	Poaceae	Perennial
Cool-season grasses	*Elymus virginicus* L.	Poaceae	Perennial
	Pascopyrum smithii (Rydb.) A. Love	Poaceae	Perennial
Forbs	*Chamaecrista fasciculata* (Michx.) Greene	Fabaceae	SL perennial
	Croton texensis (K.lotzsch) **Milli.** Arg.	Euphorbiacaeae	Perennial
	Erigeron strigosus Muhl. ex. Wild.	Asteraceae	Perennial
	Gaillardia pulchella Foug.	Asteraceae	SL perennial
	Linum sulcatum Riddell	Linaceae	SL perennial
	Ratibida co/umnifera (Nutt.) Wooron & Stand!.	Asteraceae	SL perennial

Note: These species are commonly used in restoration seedings in grasslands of central North America. This experiment was conducted 1 year following the conclusion of the field experiment conducted by Robertson et al. (2013), and was conducted at greenhouse facilities at Oklahoma State University in Stillwater, OK, USA.
Abbreviation: SL, short-lived.

sterilized by soaking in a 7% sodium hypochlorite solution for 10 min and then rinsing thoroughly with distilled water (Duell et al., 2021). Twenty surface-sterilized seeds of each plant species were sown along one of five 1.0 cm deep furrows in soils of each seedling flat (100 seeds total for each flat), maintained in a 20--25°C greenhouse, and watered regularly. Each flat contained 100 seeds of a single species planted into a single soil source. Flats were arranged in a randomized complete block design, blocked by replicate number. Once a seed germinated, species identity was confirmed, the individual was recorded, removed from the flat, and discarded. The study was concluded after 12 weeks, at which time, no additional seedlings had been observed for 7 days. Germination was quantified as percent germination.

Statistical analyses

Before data analysis, residuals were tested for normality and homogeneity of variances, using Shapiro-Wilk and Levene's tests, respectively. To test the effects of soil source and soil inoculation on germination within species, generalized linear mixed models (GLMM) were conducted, with soil source and soil inoculation as fixed effects, block as a random effect, and a gamma error distribution due to the skewed nature of the data, using the R package *lme4* (Bates et al., 2011). Soil inoculation was treated as a binary factor based on whether the flat received native prairie amendments. Pairwise post hoc comparisons were conducted using linear contrasts on estimated marginal means (adjustment method: Tukey) using the package R *emmeans* (Lenth, 2018). Due to the lack of differences in germination of native seeds among EL, EBL, and EML soil sources, all data from these soil sources were combined (hereafter referred to as "Treated").

As clear germination patterns emerged within functional groups, data were combined and analyzed by broad functional group (warm-season grasses, cool-season grasses, and forbs), relative to germination success in NG soil. For combined functional group data, a small constant (0.001) was added to each germination value to create positive values for all samples (i.e., true zeros occurred due to no germination recorded), after which all data were log-transformed for the purpose of standardization. The resulting data residuals were negatively skewed, and therefore, GLMMs were conducted in a manner identical to the methods described above. All statistical analyses were conducted in base R-software version 4.1.2 (R Core Team 2021).

RESULTS

Native species germination was very low when seeded into soil dominated by *B. ischaemum* or in soil previously treated with various combinations of herbicide and prescribed fire to eradicate *B. ischaemum* (Treated), relative to the NG control (Table 2). There was no interaction between soil source and soil inoculation for any of the 16 native species (Supporting Information:

TABLE 2 Relative germination of 16 native species commonly used in restoration seedings in grasslands of central North America (see Table 1 for complete species names)

Functional group	Species	*Bi*	*Bi*, amended	Treated	Treated, amended
Warm-season grasses	*Andropogon gerardii*	-88.9*	-31.0	-65.0*	-23.7
	Bouteloua curtipendula	-100.0*	-100.0*	-64.1*	+12.8
	Eragrostis trichodes	-100.0*	-60.4	-47.9	+9.9
	Leptochloa dubia	-67.9*	-10.4	-66.3*	-34.9
	Panicum virgatum	-100.0*	-52.0	-80.5*	-4.8
	Schizachyrium scoparium	-44.4	+50.0	-42.6*	+18.5
	Sorghastrum nutans	-70.4*	+8.6	-44.8*	+18.5
	Sporobolus compositus	-90.5*	-35.4	-80.6*	+10.2
Cool-season grasses	*Elymus virginicus*	-89.4*	-41.2	-71.8*	-43.5*
	Pascopyrum smithii	-95.6*	-73.9	-75.4*	-42.0
Forbs	*Chamaecrista fasciculata*	-80.0*	-42.8	-72.3*	-55.7
	Croton texensis	-95.8*	-64.2*	-81.7*	-2.4
	Erigeron strigosus	-90.6*	+12.5	-84.4*	-51.0
	Gaillardia pulchella	-95.1*	-34.1*	-47.9*	+7.3
	Linum sulcatum	-11.6	+8.9	-24.9	-26.4
	Ratibida columnifera	-77.3*	-16.9	-43.4*	+1.2

Note: Values represent percent differences in germination relative to native prairie soils (control). Seeds were sown into the following soil treatments: (1) native prairie (control [data not shown]), (2) dominated by ***Bothriochloa ischaemum*** (Bi), (3) dominated by ***B. ischaemum*** with native prairie soil amendment (***Bi,*** amended), (4) dominated by ***B. ischaemum*** and treated with various combinations of herbicide and prescribed fire (Treated), and (5) dominated by ***B. ischaemum*** and treated with various combinations of herbicide and prescribed fire with native prairie soil amendment (Treated, amended).

*Significant reductions in germination (%) compared to seeds sown in native prairie soils, with significance assessed at $p \leq 0.05$.

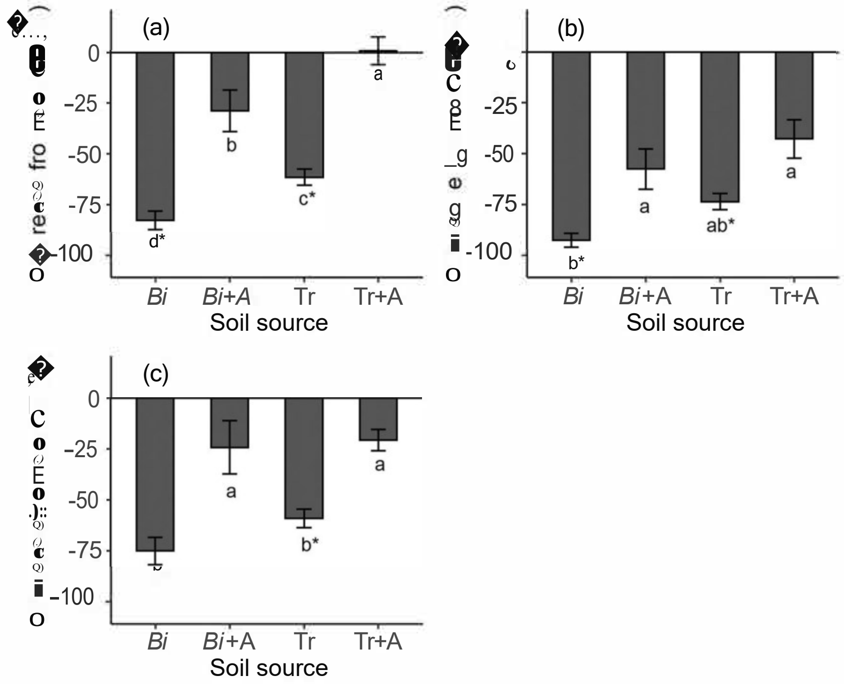

FIGURE 1 Relative germination of (a) warm-season grasses, (b) cool-season grasses, and (c) forbs when sown in soils collected from areas dominated by: *Bi, Bothriochloa ischaemum; Bi+A, B. ischaemum* amended with native prairie soil; Tr, *B. ischaemum* treated with various combinations of herbicide and prescribed fire; and Tr+A, *B. ischaemum* treated with various combinations of herbicides and prescribed fire amended with native prairie soil. Bars represent the relative differences in germination (%) from the native soil control (±SE). *Significant reductions in germination (%) compared to seeds sown in native prairie soils. Bars with different letters indicate significant differences among soil sources, with significance assessed at $p \le 0.05$.

Table SI). Germination of all native grasses, with the exception of *Schizachyrium scoparium,* and all native forbs, with the exception of *Linum sulcatum,* was significantly lower when seeded into soils previously dominated by B. *ischaemum,* relative to NG soils (Table 2). In contrast, the addition of NG soil alleviated the negative influence of the invasive warm-season grass, *B. ischaemum.* Furthermore, except for one grass *(B. curtipendula)* and two forb species *(Gaillardia pulchella; Croton texensis),* additions of native soil amendment to *B. ischaemum-dominated* soil ***(Bi,*** amended) was similar to germination in NG soil.

Germination of all native grasses, except for *Eragrostis trichodes,* and all native forb species was significantly lower when sown into soils dominated by *B. ischaemum* and treated for eradication of the invasive (Treated), compared to germination in NG soils (Table 2). Notably, only one species, *Elymus virginicus,* did not experience an enhancement in germination following addition of NG soil to soil previously treated for the eradication of ***B.*** *ischaemum* (Treated) (Table 2).

When the native species were assessed as functional groups, amendment with native soil *(Bi+A;* Tr+A) significantly improved germination of each functional group (warm-season grasses; cool-season grasses; forbs), compared to germination in soil previously dominated by *B. ischaemum (Bi;* Treated). In fact, amending the soil degraded by *B. ischaemum* resulted in germination levels equivalent to germination in undisturbed NG soil (Figure la-c). Treatments to remove *B. ischaemum* did not influence germination of cool-season grasses or forbs (Figure 1 b,c), relative to sites not treated for removal of the invasive grass, while germination of warm-season grasses was significantly greater following implementation of eradication practices (Figure la). There was no effect of block on germination of any of the 16 native species. No seeds germinated in nonseeded control flats.

DISCUSSION

The two-sided challenge, a global requirement for greater food production versus globally reduced ecosystem services due to expanding grassland degradation, provides important opportunities to develop strategies to successfully restore degraded grasslands. One potential strategy for improved restoration outcomes is the incorporation of native soils combined with seeding NG species. An important and novel finding of our study is that the addition of NG soil substantially and significantly increased germination of 13 of 16 native grass and forb species seeded into degraded soils previously dominated by the nonnative grass, *B. ischaemum,* compared to germination in nonamended soil, and no grass or forb seeds experienced a decrease in germination following inoculation with native soil. Similarly, we observed a significant increase in germination of 15 of 16 grass and forb species following inoculation with NG soil, compared to germination directly into soil previously treated with herbicide and/or prescribed fire for the eradication of

B. ischaemum, with no evidence for a decrease in germination of any species following native soil inoculation. In terms of restoration, additions of a shallow layer of NG soil onto highly degraded soil not only improved germination but also allowed for similar germination success as was observed when seeding into nondisturbed native soil. This substantial increase in germination was consistent across almost all grass and forb species tested in our study.

Previous studies have reported that highly degraded soils, including those converted to nonnative invasive species, are characterized by dramatically altered soil conditions (Grove et al., 2012, 2015). Adverse effects of nonnative invasive species often persist long after removal due to legacy effects on soil microbial communities or production of allelopathic chemicals (Greer et al., 2014; Kalisz et al., 2021; Z. Zhang et al., 2021), resulting in reduced germination of native species (Bauer et al., 2012; Dorning & Cipollini, 2006; Z. Zhang et al., 2021). Furthermore, restoration strategies to eradicate nonnative plants often include mechanical or chemical removal of the invasive species, and these intensive management practices may also impede germination of native species (Hu et al., 2021; McManamen et al., 2018; Wagner & Nelson, 2014). While it is well documented that anthropogenic disturbances have adverse effects on soil microbial communities, the importance of re-establishing native microbial communities is seldom considered in ecological restorations (Koziol et al., 2021), and few studies have assessed effective strategies to enhance germination of desirable species in highly degraded soils.

If the soil community is drastically altered by disturbance (e.g., nonnative species, row crop agriculture, over-grazing) and no longer performs the same functions as nondisturbed soil, incorporating native soil communities may be critical to improving restoration outcomes. Indeed, the use of soil inoculation has been documented as a successful strategy to accelerate plant community succession, thereby improving restoration success (Koziol & Bever, 2017; Koziol et al., 2020). The benefit of native soil amendments is potentially twofold: (1) soil amendments may act as protective buffer against harmful allelochemicals or herbicide residuals remaining in the soils following nonnative species or chemical management or (2) native soil amendments may contain beneficial biota, such as mycorrhizal fungi, that directly improve establishment and survival of desirable species (Schmidt et al., 2020). These benefits are likely also the mechanisms enhancing germination observed in our study and suggest an important management step to include when seeding degraded grasslands.

Determining potential drivers of poor restoration outcomes is critical to the conservation of grasslands, and without identifying and understanding the mechanisms associated with restoration success or failure, restorations of degraded lands are likely to fail (Han et al., 2008); however, there is escalating urgency to evaluate the efficacy of novel conservation approaches under increasing anthropogenic demands (Hobbs et al., 2011). Given the growing recognition of the importance of soil microbiomes to native plant germination and establishment, successful restoration of native plant communities may require the re-establishment of native soil microbiomes (Wubs et al., 2018). However, inoculating with remnant NG soil is not practical for large-scale restorations, as collection and transfer of enough native topsoil are highly destructive to the very ecosystems that we are trying to restore and protect. To address these challenges, improved methods to re-establish soil microbiomes are currently being developed and there is much promise regarding the culturing of beneficial microbiota for landscape-scale applications (Koziol et al., 2021; Vahter et al., 2020). For example, out-planting "nurse" plants inoculated with local native soil or laboratory-cultured AM fungi from the same local grassland sites significantly improved restoration establishment of late-successional native grass and forb species (Koziol et al., 2021; Middleton & Bever, 2012), while minimizing the need for large quantities of native soil inocula to improve germination in large-scale restorations. As native soil inocula can spread as far as 2 m a year (Koziol & Bever, 2017), single plant inoculation and out-planting may restore altered soil microbiomes across large areas. These studies also provide mechanistic information, in that inoculation with whole soil, containing the entire suite of soil microbial communities, did not provide additional benefit as inoculating with isolated AM fungi, indicating that inoculation with this soil guild alone can improve restoration metrics, such as native plant germination and establishment. While commercial mycorrhizal fungal inocula have been promoted by some industries, these inoculations have generally been met with limited success (Aprahamian et al., 2016). Commercial AM fungal inocula often contain a single nonnative species that does not benefit native plants (Koziol & Bever, 2019), and diverse inocula promote grassland plant growth and diversity more effectively than commercial inoculum (Vogelsang et al., 2006). Additionally, native plant species and soil microbiomes are typically locally adapted, showing greater growth-promoting benefits when paired with "home" symbionts (Bauer et al., 2020; Johnson et al., 2010). Thus, the introduction of novel soil microbial communities will likely result in few added benefits for germination success or subsequent plant establishment. Our study clearly indicates that amending degraded soils with diverse native soil microbiomes improves native seed germination, potentially leading to establishment of diverse plant communities in degraded grassland soils.

We selected an exceptionally degraded grassland as our restoration model to confirm the benefits of native soil amendments. *B. ischaemum* has been reported to contain allelopathic properties, inhibiting the growth and survival of native warm-season grasses (Greer et al., 2014), and has been shown to significantly reduce biomass of native grasses (Wilson et al., 2012). This nonnative species produces large and persistent seed banks with a proportional decline of native grass and forb species present in the seed bank (Robertson & Hickman, 2012). If *B. ischaemum* eradication is not accomplished, the persistent seed bank allows complete reestablishment of the nonnative in as little as 2 years (personal observation). However, controlling this nonnative is challenging as *B. ischaemum* is physiologically similar to the native warm-season grasses of the United States, and common management practices used to control nonnative perennial grasses, including herbicide and prescribed fire, result in soil legacy effects known to limit native plant germination or establishment (Comish & Burgin, 2005; Lekberg et al., 2017). In this highly degraded grassland, we observed negligible germination of any grass or forb species sown directly into unamended soils. In fact, several species showed complete germination failure in nonamended soils. Considerable and consistent increases in germination of a wide array of NG species following inoculation with diverse soil microbial communities suggest that benefits of native soil amendments are likely to occur across less degraded soils.

Our results show that inoculation with NG soils can be a useful tool for enhancing restoration metrics, as none of the 16 grass and forb species tested were negatively affected by native soil amendments, and yet, almost all received substantial benefit. However, scaling up to large-area restorations remains unclear. Future research directions should include further developing methods to optimize the inclusion of NG soil or native AM fungal inoculation. To be used as an effective restoration tool that is not cost-prohibitive, techniques currently used for large-scale restoration operations, such as seed-drill or broadcast methods, may be modified to include re-establishing native soil microbiomes.

AUTHOR CONTRIBUTIONS

Eric B. Duell: Data curation; formal analysis; software; validation; visualization; writing-original draft. Karen **R. Hickman:** Conceptualization; data curation; funding acquisition; investigation; methodology; project administration; resources; supervision; writing-review and editing. **Gail W. T. Wilson:** Conceptualization funding acquisition; methodology; project administration; resources; supervision; writing-original draft; writing-review and editing.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data will be made available upon request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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