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Authors: Larson, Jennifer L., Venette, Robert C., and Larson, Diane L.

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Conservation Issues

Restoration for Resilience: The Role of Plant–Microbial Interactions and Seed Provenance in Ecological Restoration

Jennifer L. Larson,[1,3] **Robert C. Venette,**[2] **and Diane L. Larson**[1]

[1]U.S. Geological Survey, Northern Prairie Wildlife Research Center, Minnesota Field Station, 1561 Lindig Street, St. Paul, MN 55108
[2]U.S. Department of Agriculture – Forest Service, Northern Research Station, 1561 Lindig Street, St. Paul, MN 55108

[3]Corresponding author: jllarson@usgs.gov; 651-649-5042

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ABSTRACT

With global efforts to restore grassland ecosystems, researchers and land management practitioners are working to reconstruct habitat that will persist and withstand stresses associated with climate change. Part of these efforts involve movement of plant material potentially adapted to future climate conditions from native habitat or seed production locations to a new restoration site. Restoration practice often follows this plant-centered, top-down approach. However, we suggest that restoration of belowground interactions, namely between plants and arbuscular mycorrhizal fungi or rhizobia, is important for restoring resilient grasslands. In this synthesis we highlight these interactions and offer insight into how their restoration might be included in current grassland restoration practice. Ultimately, restoration of belowground interactions may contribute to grassland habitat that can withstand and respond to future climate uncertainties.

Index terms: prairie restoration; seed sourcing; species interactions; resilience

INTRODUCTION

Value of Interactions in Resilience

Over the last century humans have played a primary role in the loss of natural habitat through conversion of millions of acres of grassland to agriculture and other land uses, but there are now abundant efforts to restore the once expansive grassland ecosystems. The Temperate Grasslands Conservation Initiative highlighted the need for conservation and protection of temperate grasslands (Henwood 2010) while the United Nations General Assembly declared 2021–2030 the UN Decade of Ecosystem Restoration (UNEP 2019), which included a focus on grasslands (UNEP and FAO 2020). For successful restorations, "ecological resilience," or the ability of an ecosystem to absorb some amount of disturbance while remaining in a stable state (Holling 1973), deserves greater attention. The value of species interactions in ecosystem resilience has recently gained traction as an essential component in ultimately restoring a degraded landscape to its original state (Mateos 2019). However, due to limited time and resources, grassland restoration practice often follows a top-down approach focused primarily on replacing the plant community. Abiotic (e.g., compost, biochar) and biotic (e.g., arbuscular mycorrhizal fungi [AMF], rhizobia) soil amendments as an element of site preparation can be included in restoration but are not the norm (Beyhaut et al. 2014; Bauer et al. 2020; Koziol et al. 2020). A more nuanced approach to restoration that includes consideration of both plant species and belowground interactions could lead to better establishment and persistence of these grasslands into the future.

In this synthesis, we focus on specific belowground interactions (plant–AMF, plant–rhizobia) and offer insight for practitioners to consider when developing plans for grassland restoration. We also highlight how restoring belowground interactions may influence additional interactions that can contribute to (pollination) or counteract (herbivory) successful plant establishment. While there are numerous other interactions (e.g., antagonistic) that play a role in successful grassland restoration, we focus on restoration of belowground interactions recently highlighted in the literature. Subsequently, we offer suggestions on how to incorporate the restoration of these key interactions in reconstruction of degraded grasslands, to create a system more resilient to biotic and abiotic stressors, primarily related to climate change.

Restoration as Typically Practiced: Attention to Plant Species and Provenance

Plant species translocations (i.e., moving plant material from one part of a species' range to another, usually as seed; Vitt et al. 2016) are often used to restore grassland habitats. Common species are planted to create habitat structure, such as during a revegetation, and rarer or at-risk species are typically planted for conservation or to enhance biodiversity. The success of a translocation is difficult to quantify (Menges 2008), with estimates of successful population establishment ranging from 16% to 92% depending on the response variable measured and length of monitoring (Godefroid et al. 2011; Guerrant 2012). Much of the literature surrounding plant translocations in grassland habitats is focused on genetic provenance. Genetic provenance refers to the source of the original, wild population of the plant material used (Broadhurst et al. 2008; Breed et al. 2013, 2018; Aavik and Helm 2017; Bucharova 2017), and is often seen as a key determinant of successful translocation.

Higher establishment success of material with a local provenance is typically assumed (Broadhurst et al. 2008; Breed et al. 2013, 2018; Aavik and Helm 2017; Bucharova 2017) because some evidence shows that locally sourced plants do better than those that are distantly sourced (e.g., Bucharova et al. 2017; but see Bischoff et al. 2010). This success could be due to the presence of appropriate mutualistic interaction partners including arbuscular mycorrhizal fungi (Koziol and Bever 2016; Koziol et al. 2020) and nitrogen fixing bacteria (Beyhaut et al. 2014; Grman et al. 2020). However, even when seed is sourced locally, failure of conservative species (e.g., those that are most reliant on pristine habitat; see Bauer et al. 2018) to establish can occur (Larson et al. 2018), possibly due to disruptions in the soil microbial community as a result of land use prior to the restoration (Harris et al. 2006; Pugnaire et al. 2019). Subsequent reestablishment of the grassland plant community could be limited by recovery of interactions between the desired plants and their corresponding soil microbiota (Ramalho et al. 2017; Mateos 2019). Often missing from restorations and reconstructions is planning for interactions necessary to support resilient communities and ecosystems (Bucharova 2017).

In many cases, grassland reconstruction practitioners lack resources and expertise to include soil microbial restoration into project planning (Beyhaut et al. 2014; Farrell et al. 2020b; Grman et al. 2020). The focus of restoration efforts is often a specific suite of plants based on historical, reference, or desired conditions, but consideration of soil microbes is not routine (Farrell et al. 2020b). For instance, in a study on a semi-arid grassland restoration, Farrell et al. (2020a) found that soil microbial communities were more closely associated with plant cover, soil organic matter, and pH than with specific plant species. With disturbance or other degrading processes such as climate change, ecosystem processes including nutrient cycling, plant growth promotion, and environmental buffering (Neher 1999) may not be able to support these historical vegetation communities (Hobbs et al. 2009). These legacy effects could result in a mismatch between the desired plant community and the new soil microbial community at a given restoration site (Farrell et al. 2020b). Studies set across grassland restorations of varying ages showed mixed results in assessment of the transition toward microbial community composition in undisturbed, remnant systems. Herzberger et al. (2015) suggested the net effects of microbial communities on plants to be similar in restoration and remnant grasslands after 20 y, while Jangid et al. (2010) found that the microbial community was not fully restored after 30 y. Failure of certain plant species to establish may be due to lack of necessary mutualist symbionts (Larson and Siemann 1998; Grman et al. 2020) as indicated by this lengthy recovery process. Management plans that include restoration of these interactions essential to species establishment and persistence may bring us closer to the goal of self-sustainable grassland ecosystems (McAlpine et al. 2016; Heinen et al. 2020).

Belowground Plant–Microbe Interactions: A Focus on Arbuscular Mycorrhizal Fungi and Rhizobia

Arbuscular Mycorrhizal Fungi: Arbuscular mycorrhizal fungi can directly benefit plant fitness under certain environmental conditions by allowing greater access to water and limiting mineral resources (Smith and Read 2010), moderating negative effects of root herbivory (Vannette and Rasmann 2012), and providing disease resistance (Delavaux et al. 2017). In exchange, the infected plant provides photosynthetically derived carbohydrates (Smith and Read 2010). Plants differ in ability to reduce carbon allocated to AMF "cheaters" in situations where there is little benefit of infection to the plant (e.g., high phosphorus soils; Grman 2012) and many native prairie species are sensitive to AMF community composition (Koziol and Bever 2016). Local adaptation between plants and mycorrhizae can occur, and this adaptation may be more important than that of mycorrhizae to soil (Johnson et al. 2010; Rúa et al. 2016). AMF species did better in studies when the fungus and host were sourced from the same local area (e.g., Baoming et al. 2010; Johnson et al. 2010), but plant hosts showed greater variability in their response to local versus nonlocal AMF (e.g., Klironomos 2003). In a meta-analysis, Rúa et al. (2016) found that geographic origins of plants and fungi were always significant predictors in describing plant response to AMF inoculation; the effect of AMF inoculation was greater when the plant, AM fungal partner, and soil were all naturally sympatric, compared to when they came from different geographic origins. However, they also found evidence that locality overlap between plant–soil or fungal partner–soil was enough to mend any decrease in plant performance that came from a nonlocal third component. In a recent study on effects of AMF provenance on nonlocal prairie plant establishment, Bauer et al. (2020) found that plant community biomass was greater when AMF and soil were from the same location; interestingly, this benefit was greater in early-successional species that tended to have lower responses to the presence of AMF. Results from both studies could have profound ramifications for prairie restorations taking place on former agricultural fields, as is happening in the upper midwestern United States. Work with AMF in grasslands suggested that restoring a local fungal community may improve establishment and growth for at least some native plant species (Middleton et al. 2015). This, along with the evidence provided above, indicated that combining sympatric AMF–soil *or* sympatric plant–soil combinations could result in greater establishment success, even when a locally adapted third partner is unavailable.

Rhizobia: The plant–rhizobia symbiosis forms when chemical signaling by rhizobia initiate host plant formation of root nodules, where the bacteria eventually reside and convert atmospheric nitrogen into plant-available ammonia (Stefan et al. 2018). Plants, in turn, recognize signals from beneficial rhizobia in the early stages of the symbiosis (Heath and Tiffin 2009). Interactions between plants and rhizobia show specificity at the level of species and genotype (Wang et al. 2018). Despite these efforts from both plant and rhizobia to form a successful partnership, incompatibility can occur even in later stages of symbioses development, with nodules that are unable to fix nitrogen (Graham 2005; Wang et al. 2018). The specificity of the relationship is highlighted in recent work by Grman et al. (2020), which showed restored prairies may lack rhizobia that could enhance growth of native prairie legumes. Sympatric rhizobia convey the benefit to the host plant of increased fitness (Parker 1995), greater biomass production (Grman et al. 2020), and more successful establishment (Parker et al. 2006). Furthermore, Grman et al. (2020) found no evidence that spontaneous recovery of suitable rhizobia had occurred in restored prairie soils. Grman et al. (2020) and Beyhaut et al. (2014) both suggested that practitioners work with local universities to isolate and culture rhizobial strains for restoration purposes. Previous work by Graham (2005) and Tlusty et al. (2004) highlighted potential avenues for future collaborations.

Initial work by Tlusty et al. (2004) identified possible strains to use in restoration practice, and Graham (2005) provided additional guidance as to why native rhizobia might surpass commercial inoculant in efficacy. Possible shortcomings of commercial inoculant identified by Graham (2005) included inappropriate application, inoculant with rhizobia of lesser quality, unfavorable soil environment at seeding, and past fertilization practices that may be suboptimal for nodulation and nitrogen fixation to occur. Inappropriate application of rhizobia can occur when inoculant is applied at rates too low to induce nodulation of the host plant. These concerns could apply in application of local rhizobia strains as well. Rhizobia that are of inoculant (i.e., high) quality should have the following characteristics: form effective nodules with the target legume, persist in the soil, tolerate extreme soil temperatures and pH, and are culturable (Keyser et al. 1992). Soil environments in which low rainfall, extreme temperatures, high soil nitrate, heavy soil metals, and biocides occur may be uninhabitable for all but a few isolates of rhizobia (Zahran 1999). Furthermore, inoculant-grade rhizobia must undergo extensive testing (Graham 2005), which is outside the range of work for many restoration practitioners. Collaboration between researchers and land managers may be well worth the effort to generate inoculant-grade rhizobia appropriate for grassland restorations, especially if the end result promotes habitat with a highly diverse plant community that includes legumes.

Migration of Plants, AMF, and Rhizobia

The ability of plants to migrate and persist beyond their current range may be limited by the lack of suitable symbiotic partners in adequate densities for the interaction to successfully establish (Stanton-Geddes and Anderson 2011). Before deciding to transport AMF or rhizobia from one part of a plant's range to another, it is necessary to understand how these symbionts disperse naturally.

In an attempt to determine if AMF spores travel by air, Egan et al. (2014) measured air and soil across six different North American biomes composed of 18 ecoregions. Despite high AMF spore abundance in soils, spores were rarely found in air, indicating that air is an unlikely dispersal mode for AMF. Alternatively, Paz et al. (2021) found evidence to suggest that spore transport by wind and large animals was more effective than other dispersal agents, including invertebrates, water, and humans. Furthermore, Nielsen et al. (2016) measured the establishment of AMF communities on Peberholm, a newly constructed island between Denmark and Sweden. Here, they found AMF colonization was likely assisted by migratory birds, whose droppings contained all of the most abundant AMF taxa on the island. These taxa were present in similar relative abundances in collected plant roots. With a multitude of north–south flyways that span the Americas, transport by migratory birds could represent a possible opportunity for AMF dispersal. A recent review by Paz et al. (2021) suggested that future research should focus on determining commonality of co-dispersal of plant propagules and symbiotic AMF across ecosystems.

Legumes may be limited in their colonization and establishment potential without nitrogen-fixing symbionts (Parker et al. 2006; Stanton-Geddes and Anderson 2011; Bamba et al. 2016). This limitation can manifest in restoration of disturbed areas, where chemical or physical manipulation of the soil combined with lack of appropriate mutualistic partners has eliminated the *Rhizobia* species needed for successful establishment of legumes. Bamba et al. (2016) suggested that rhizobia associated with widespread legumes may distribute across a broad geographical range. For other less widely distributed rhizobia there are various means of potential dispersal and range expansion. Robertson and Alexander (1994) found that the symbiont *Azorhizobium caulinodans*, of the stem-nodulating plant *Sesbania rostrata*, disperses via precipitation runoff and wind-blown soil. Alternatively, rhizobia reach peanut (*Arachis hypogaea*) root zones by means of a fungal mycelia dispersal network, where rhizobia use the extensive vegetative structures of soil fungi for transport in soil (Zhang et al. 2020). These studies indicate that unless rhizobial symbionts are already present in future grassland reconstruction sites, practitioners may need to introduce appropriate rhizobia to facilitate legume transplantation into disturbed or expanded ranges.

Building Resilience: Including AMF and Rhizobia in Restoration Actions when Sourcing for Climate Change

Building resilience into restorations is not a new idea (Harris et al. 2006), and studies have suggested ensuring genetic diversity among and within plant species by sourcing outside of local provenance strategies. Breed et al. (2013) proposed increasing species genetic variability through a combination of a regional admixture strategy and a predictive strategy to achieve greater resilience. Regional admixture involves collecting seed from throughout a species' range, with no spatial bias toward the restoration site; the focus is to capture as much genetic variability as possible. Predictive strategy involves use of naturally occurring genotypes that have been experimentally determined to be adapted to predicted future climates. If these strategies are used in sourcing of plant seed, and these plants have AMF and/or rhizobia with which they interact, then it may prove beneficial to also source microbial symbionts in a similar manner. Wubs et al. (2018) proposed a related concept by inoculating soils with microbial communities from plant communities at different successional stages, with target native plant species benefiting from microbial inoculation with late-successional native heathland soils.

Heinen et al. (2020) provides an extensive overview of important elements to consider in conservation of interactions, which may translate well into restoration of interactions in grassland ecosystems. These elements include distributional range overlap of species, management that enhances naturally occurring interactions, and supporting reestablishment of interactions among naturally occurring species. In the context of sourcing seed adapted to potential climate change, and promoting interactions that facilitate long-term resilience, a comparison of the outcomes of local interactions with those from farther distances (that might be used in restoration) prior to restoration would be prudent. These actions will further the goal to both conserve what remains while facilitating shifts in adaptability, to create resilient ecosystems needing fewer management interventions to persist.

At the time of this article, we found no empirically proven methods in place for practitioners to concurrently restore both native grassland plants and AMF over large areas. Recent work indicates that the practice may be nearing implementation. Lubin et al. (2019) promoted a method of combining double rates of forb seeding and whole soil inoculation using nurse plants that were pre-inoculated by propagation in an 18% mixture of native prairie with sterile soil. By using this method, they increased seeded forb cover in mesocosm plots over what was achieved with either treatment alone. While this method might be beneficial on a smaller scale, practitioners would be advised to use care when removing even small amounts of soil from limited and potentially fragile native prairie fragments. Practitioners should be aware of the risk of introduction of pathogens or invasive soil microbes if a whole soil inoculum is used (Mawarda et al. 2020; Islam et al. 2021; Jack et al. 2021), even when using soil from areas considered native habitat. Koziol and Bever (2017) also used nurse plants and found that late successional plant species were dependent on specific AMF for establishment. With spread of mycorrhizal fungi in prairie occurring at rates of up to 2 m in a growing season (Middleton and Bever 2012; Middleton et al. 2015), practitioners could likely expect a less immediate and more heterogeneous effect.

An alternative to the use of nurse plants is broadcasting AMF and tilling it into soil at the time of seeding (Koziol et al. 2020). In this study, Koziol et al. (2020) tested a native mycorrhizal inoculum at seven densities recommended by both commercial and scientific studies. Native plant richness increased with increasing AMF densities, but inoculation levels recommended by commercial producers were too low to produce an effect. However, they also noted possible inefficiencies, compared to the use of nurse plants, with the broadcast-till method of application including (1) increased solar radiation exposure to AMF, which reduces infection rates (van de Staaij et al. 2001), and (2) inocula placement on soil prior to seed sprouting and roots to support AMF propagules. Future studies on application methods to increase AMF survival by increasing probability of contact between AMF propagules and roots may allow for lower concentrations of AMF application and decreased effort and cost to practitioners.

A review by Compant et al. (2010) found that plants in association with AMF had a generally positive response to potential climate change conditions of increased temperature and drought ranging from improved drought stress to increased extra-radical hyphal networks (thereby increased potential water acquisition) in warmed soils. We found only one study on AMF response to extreme rainfall events, which also are predicted under climate change; Walter et al. (2016) found that AMF root colonization and plant performance under extreme weather events, including heavy rain, was plant species specific. *Plantago lanceolata* had increased AMF under heavy rainfall and plant biomass was positively correlated with AMF colonization, whereas plant biomass of *Holcus lanatus* remained unchanged with lower AMF presence (Walter et al. 2016). Despite evidence of mainly positive effects of AMF on plant performance under the more extreme weather conditions predicted with climate change, a review by Walter (2018) indicated that less mycorrhizal infection may occur under drought and extreme waterlogging or flooding associated with heavy rain events. More recently, Lubin et al. (2021) found that plant species adapted to drier conditions benefited from AMF adapted to the same moisture regime; seeded species adapted to a wetter moisture regime did not benefit from inoculation with AMF sourced from a drier site. Taken together, this indicates that sourcing AMF from drier conditions in anticipation of altered soil moisture status due to climate change may best be paired with species already adapted to those drier conditions. Species associated with the wetter moisture regime coincided with early successional species, and drier sites with late-successional species (Lubin et al. 2021). Several studies have found AMF inoculation to be most beneficial to late-successional species (Koziol and Bever 2016; Bauer et al. 2018). Finding the closest possible match between AMF and plant partners to create successful interactions in grassland restorations will be challenging yet critical given future climate uncertainties.

Restored soils may lack appropriate rhizobia for native prairie legumes (Larson and Siemann 1998; Grman et al. 2020), suggesting that efforts to establish legumes could include soil amendments with associated symbionts. However, we found little indication that rhizobia amendments are included in current practice or that research to develop methods for soil application is underway. One exception was work done by Beyhaut et al. (2014) in which the authors tested several methods of inoculation including granular clay- and granular peat-based inoculants applied to sterile soil, sterile peat-based inoculants applied to seeds, and inoculated wheat seed as a cover crop. Rhizobia species and strains known to inoculate seven of ten species planted in their experiment were used in each of the treatments. Granular clay and wheat carrier treatments proved most effective, as indicated by higher richness and total legume counts compared to other treatments and an uninoculated control. To avoid destructive techniques associated with collecting whole plants to assess nodulation of legumes in the restoration, they collected soil cores and inoculated sterile seedlings of a subset of the species planted; the seedlings then "trapped" rhizobia from the soil. Using these methods, they determined that granular peat and wheat carrier treatments had the highest recovery rate of rhizobia used in the inoculation treatments. The authors further suggested use of rhizobia with broad host ranges to lower costs associated with inoculation.

When sourcing seed from farther distances to account for limited seed availability or climate change (Larson et al. 2021), practitioners could employ a strategy partially outlined by Beyhaut et al. (2014) and Stanton-Geddes and Anderson (2011) in which seeds from the collection area are sterilized and germinated, and then paired with both soils or soil extracts from the collection area and from the proposed restoration area in a controlled common setting (greenhouse). Assessment of nodules (number, dry weight) can be performed, along with isolation of rhizobia within the nodules to determine if there are species differences and/or efficacy differences between rhizobia from the collection and restoration sites. If rhizobia from the restoration site are the same species, and comparable in compatibility as those from the collection site, one could anticipate that the associated plant species from the collection area would form a mutualism without further manipulation. If the given plant species lacks rhizobial symbionts in the restoration site soil, additional measures such as those suggested in Beyhaut et al. (2014) (e.g., soil-applied granular inoculant with the target rhizobia species) could be employed. While we concede that this is only one factor among many that contribute to successful plant establishment, and that other factors besides presence or absence limit rhizobia efficacy (Oldroyd et al. 2011; Stefan et al. 2018), providing access to appropriate symbionts may overcome a major obstacle for legumes not often taken into consideration with species translocations.

Quantification of Restored Plant–AMF or Plant–Rhizobia Interactions

There are several options land managers can use to assess AMF in prairie restorations that allow for flexibility in expertise and resources. Prior to any restoration implementation, an assessment of AMF taxa in the proposed restoration site compared to a nearby remnant or "ideal" will justify whether or not it is appropriate to restore AMF to the restoration site (Vahter et al. 2020; Guerra et al. 2021). If similar AMF taxa profiles exist in both locations, no further action to restore AMF may be necessary. If plant species found in remnants are lacking in the proposed restoration site, and efforts to incorporate AMF restoration are included in the restoration plan, practitioners could leave designated portions of the restoration site planted with the same seed mix throughout, but without AMF addition in order to compare plant performance. After plant establishment, plant performance measures including aboveground biomass, richness, and diversity of establishing plants can provide a useful assessment of whether or not AMF restoration provided anticipated benefits to the aboveground restoration effort (Koziol et al. 2020). Additional soil assessments of AMF taxa in the restoration compared to non–AMF addition plots as well as remnant soils can confirm if AMF amendment was successful and further help to explain any vegetation differences. Finally, plant root colonization of AMF can provide a relatively good proxy for whether or not an interaction is taking place (Caruso et al. 2012). This can be assessed via molecular methods (Rudgers et al. 2020; Paz et al. 2021), although these methods are in a constant state of improvement (Guerra et al. 2021). Land managers would likely need to form collaborations with university, federal, or other research staff to perform molecular assessments (Farrell et al. 2020), which would lead to a more accurate evaluation of the plant–AMF interaction potential in restored sites. In turn, it may be beneficial for research staff to reach out to interested land managers to collaborate on large-scale restorations on which to implement and test their methods at the landscape level.

As with AMF, there are several levels of monitoring that could determine the potential efficacy of rhizobial amendments with prairie restoration. Practitioners could determine whether or not rhizobial amendments are needed by comparing rhizobia present in the proposed restoration site with those found in nearby remnant prairie. To do so, one could perform "trapping" methods used by Beyhaut et al. (2014). To summarize, a representative composite of soil cores is taken from the restoration site and, if possible, the remnant site for comparison, to inoculate sterile soils, and pre-germinated seedlings of target legumes are grown for a 10 wk period. Presence or absence of nodules is recorded upon harvest, and nodule dry weight is measured. If no nodules form on the target legumes, rhizobial amendment might then be necessary. Similarly, if plants grown with extracts of restoration soil have fewer nodules and appear less robust (lower plant biomass, height, flowering) compared to those grown with remnant soil extracts, this also may indicate that rhizobial amendment could be of benefit. Further identification via genomic fingerprinting and subsequent culturing and propagation of rhizobia strains appropriate for the restoration could be accomplished through partnerships with researchers, as previously mentioned. The propagated rhizobia could then be applied to target plants grown in sterile soil and compared to control plants with no rhizobia applied. Measurements including nodule count and biomass, plant biomass, height, and flowering can be used to assess benefits of the selected strain of rhizobia.

Promoting Resilience in Grassland Restoration by Also Restoring Interactions

Farrell et al. (2020) suggested that research focused on the role that soil microbial communities play during ecological restoration is not generally routine. However, we found numerous examples of research focused on manipulating biotic soil conditions (e.g., inoculating with soil microbes) to promote restoration outcomes (Heneghan et al. 2008; Beyhaut et al. 2014; Grman et al. 2020; Vahter et al. 2020). Including restoration of soil microbial communities into ecosystem restoration can create conditions that ultimately increase successful establishment of a desirable plant community and the additional ecosystem services microbial communities can provide (Farrell et al. 2020).

Aboveground and belowground interactions with plants are not independent. A review by Barber and Gorden (2015) brings together multiple studies on how belowground interactions (nitrogen fixing bacteria, AMF, root herbivores) can influence floral traits that in turn may positively affect pollinator visitation and subsequent pollination potential. For example, AMF were found to increase nectar production, flower or inflorescence number, pollen production, and to a lesser extent flower size and nectar components including sugar, but this was context dependent (Gange and Smith 2005). In addition, in several studies that quantified pollinator visitation rates, plants infected with AMF had increased visitation. Wolfe et al. (2005) found that flower size and visitation by bumblebees and honey bees on *Chamerion angustifolium* increased, as did seed set, with infection of two AMF species compared to uninfected controls. Although, whether increased seed set was due to more effective pollinator activity or to the interaction with either AMF species could not be discerned, and germination rates did not differ between seeds of uninfected and infected plants. Furthermore, Middleton et al. (2015) found that *Ratibida pinnata* (Vent.)

Barnhart plants inoculated with native AMF experienced significantly less herbivory and grew larger 1 mo following herbivory, compared to those inoculated with commercial AMF and uninoculated controls. The increased growth potential of plants inoculated with native AMF may have been due to these plants experiencing less herbivory comparatively, or native AMF may have helped to facilitate a faster recovery with increased access to resources.

Grassland restorationists strive to create communities that require little recurring human intervention and resemble previous or remnant grasslands with respect to species composition, ecosystem function, or landscape physiognomy. Evidence does not support the suggestion that remnant grasslands are, or will be, resilient to the effects of climate change. Rather, substantial changes in species composition (e.g., Liu et al. 2018, Wüst-Galley 2021), ecosystem processes (e.g., Anderson 1991, Chen et al. 2014, Schuchardt et al. 2021), and geographic distribution (e.g., Jiménez-Garcia et al. 2021, Saintilan et al. 2021) of native and managed grasslands are anticipated as climate changes, particularly in response to altered precipitation. Thus, the translocation of grassland components, specifically AMF or rhizobia, is unlikely to confer resilience to a restoration site, but may be the first step in establishing plants adapted to future climate. Ultimately the goal is to create a plant community that supports and is supported by the interaction of species that are best suited to one another. From a pragmatic perspective, if restoration practitioners are able to provide AMF or nitrogen fixing bacteria from soil where seed was sourced, there is a greater likelihood of a successful belowground mutualistic interaction, which in turn can increase survival and persistence of plants translocated in anticipation of future climate change.

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Jennifer Larson is a Biologist with the U.S. Geological Survey and holds an MS in Resource Ecology and Management from the University of Michigan, Ann Arbor and a BS in Biology from the University of Minnesota, Minneapolis.

Robert Venette is a Research Biologist with the U.S. Department of Agriculture, Forest Service and Director of the Minnesota Invasive Terrestrial Plants and Pests Center at the University of Minnesota. He holds a PhD in Ecology from the University of California, Davis and a BS in Genetics and Cell Biology from the University of Minnesota, St. Paul.

Diane Larson is a Research Wildlife Biologist with the U.S. Geological Survey. She received her MA from the University of Colorado, Boulder and her PhD from the University of Illinois, Chicago.

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