Journal of Arid Environments 164 (2019) 46–52

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Seed bank community and soil texture relationships in a cold desert

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ARTICLE INFO

Keywords:
Plant communities
Seed banks
Soil texture
Drylands
Cheatgrass
NMDS

ABSTRACT

Sustainable dryland management depends on understanding environmental factors driving the composition of current and future ecological communities. While there has been extensive research on aboveground plant communities, less is known about belowground soil seed bank communities. In the Colorado Plateau of the western United States, we simultaneously explored aboveground and belowground plant communities and how they varied across sites with similar climate but contrasting soil textures. We found that aboveground vegetation and belowground seed bank community composition each varied significantly among sites. We also observed marked aboveground-belowground compositional dissimilarity across sites, suggesting that the two spatially-associated communities may respond differently to the same environmental gradient. Lastly, we found that abundances of cheatgrass (*Bromus tectorum*) – one of the region's major exotic invasive plants – varied strongly with soil texture, a finding with implications for invasive species management. From our results, we highlight two general patterns for dryland managers. First, we show that aboveground and belowground plant communities can respond to the same environmental variation in a strongly divergent manner. Second, the data underscore a large potential role for soil texture and its associated factors in mediating plant community responses to a range of environmental conditions.

1. Introduction

Successful management of ecological resources depends upon knowledge of environmental factors that drive plant community composition (Lavorel and Garnier, 2002; McNaughton, 1983). Accordingly, the suite of factors that structure spatial and temporal patterns for plant communities are among the most extensively studied in ecological research, extending back to the beginnings of the field itself (Grime, 2001). Research investigating why certain plants grow and survive where they do has focused primarily on the aspects of the system that are most readily observable: the plant communities growing above the soil surface. However, less attention has been placed on the plant seeds that lie dormant within the soil, yet this seed bank makes up a substantial component of many plant reproduction strategies and represents the potential future of aboveground plant communities (Grime, 1981; Thompson and Grime, 1979; Vandvik et al., 2016; Warr et al., 1993).

Serving as both short- and long-term plant seed repositories within an ecosystem, soil seed banks can provide valuable information about past, present, and future plant communities (Thompson, 2000). We know from seed bank research that, in general, the composition of soil seed banks depends largely on species abundances in the current system and on climate, soil, seed traits, as well as a variety of other interacting environmental and physiological factors that can influence a seed bank's characteristics and fates (Thompson, 2000; Thompson and Grime, 1979). For example, as climates shift, species that once thrived aboveground in a given area may no longer be successful, and may move toward more hospitable climates in other locations. This can also create new opportunities for species to establish, and such losses and gains of species result in altered community composition. The increased abundance of new species, those not yet widespread in the aboveground vegetation, often occurs because new species' seeds were already present in the seed bank, providing a future source for recruitment under favorable conditions as they arise (Vandvik et al., 2016). Given the importance of soil seed banks as resources for restoration, adaptation, and invasive species management (Faist et al., 2013), it is critical to investigate how seed banks respond to the range of dynamic environmental factors (Faist et al., 2015; Faist and Collinge, 2015; Hopfensperger, 2007).

Climate is not the only factor controlling seed banks and their success. Soil texture is a vital environmental component influencing the distribution and structure of aboveground and belowground plant

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https://doi.org/10.1016/j.jaridenv.2019.01.008
Received 28 September 2018; Received in revised form 30 December 2018; Accepted 9 January 2019

communities (Benvenuti, 2007). Soil texture and other edaphic characteristics regulate the availability of water, which subsequently affects the system's productivity (e.g., Noy-Meir, 1973), as well as the cycling of key soil nutrients, particularly in dryland ecosystems (Chung et al., 2017; Dexter, 2004; Schlesinger et al., 1995). Soil texture can also directly influence the composition of soil seed banks through its effects on the horizontal and vertical movements of seeds (Chambers and MacMahon, 1994). Soil bears the legacy of the system's management and past anthropogenic disturbances – such as the degradation of stabilizing biological soil crusts – which can have lasting effects on soil texture via accelerated erosion processes (Belnap and Gillette, 1998). Soil texture can additionally play interactive roles in mediating the effects of other anthropogenic disturbances, such as those of cattle grazing on soil organic carbon (McSherry and Ritchie, 2013).

As a biome particularly sensitive to climate and human land use changes (Maestre et al., 2012), drylands are in need of a holistic understanding of the controls over their full plant communities (i.e., aboveground and belowground), as well as how those communities respond to changes in environmental conditions (Safriel and Adeel, 2005). Dryland systems make up 41% of the world's land area, and their spatial extent is increasing, thus their role in global function should not be underestimated (Safriel and Adeel, 2005). In particular, studies of dryland plant communities have proven fundamental to understanding current functional dynamics of soil seed banks (Pake and Venable, 1996; Thompson, 2000; Tielbörger and Valleriani, 2005). Nevertheless, soil seed banks in arid environments often have characteristic functions that contrast with those in other biomes, a distinction that requires further investigation (Hopfensperger, 2007; Thompson, 2000). Furthermore, dryland plant communities are already undergoing shifts in aboveground composition due to factors including climate change (Brown et al., 1997; Munson et al., 2011) and the spread of non-native species (Bryce et al., 2012; Knapp, 1996). However, changes in soil seed banks may not demonstrate the same spatial and temporal behaviors as their aboveground counterparts. Understanding the central drivers of soil seed banks may be particularly important for dryland managers seeking to control widespread invasion by problematic species, such as cheatgrass (*Bromus tectorum*) within semiarid regions of the western United States (Getz and Baker, 2008; Knapp, 1996; Rice and Dyer, 2001).

This study set out to address these important knowledge gaps by examining the relationships between aboveground and belowground dryland plant communities across a soil texture gradient. We framed our research around two main questions. First, how variable are plant communities spanning gradients of soil texture within a given climate and ecosystem type? Second, what is the relationship between aboveground and belowground plant community patterns at a given site and across sites that experience similar climate but that span a soil texture gradient? Through better understanding the drivers of plant community dynamics, both above- and belowground, we hope to provide useful information aiding resource managers and stakeholders in reaching management goals for our current dryland landscapes, as well as predicting and managing for how plant communities may respond to future change.

2. Methods and materials

2.1. Site characterization

We conducted our study at a series of three sites co-located within the northwestern Salt Valley section of Arches National Park near Moab, Utah, USA (Fig. 1). All of our field sites are located within the Semiarid Benchlands and Canyonlands ecoregion of the Colorado Plateau (Bryce et al., 2012). Mean annual temperature for the area is 14.1 °C and mean annual precipitation is 216 mm (mean temperature and precipitation are from the Arches National Park Headquarters weather station, 1980–2012). Due to their close proximity to one another (the two farthest sites are ~4.4 km apart), we suggest sites have experienced near-identical climatic conditions, characterized by cold winters and hot summers with variable monsoonal precipitation (Bryce et al., 2012). Weather stations at each site were beyond the scope of this project and due to the sites' proximity and similar topographic position and aspect, temperature and precipitation are likely highly similar across the sites, which were selected to keep climatic conditions consistent yet to vary edaphic properties. Thus, we propose that any differences in climate across these adjacent sites would be modest relative to the potential for soils' control over plant patterns. That said, we cannot rule out small-scale climatic variation among sites. Though the study area's location within Arches National Park precludes many current anthropogenic impacts (e.g., there is no current livestock use), the region has a significant history of grazing, with sheep grazing permitted within the study area as recently as 1982 (National Park Service Southeast Utah Group archives).

Our three sites were selected for their distinct edaphic characteristics, which have been assessed as part of previous and ongoing field studies at the sites (Chung et al., 2017; McHugh et al., 2017). Based on their soil texture, the three sites were designated as Sandy Loam, Loamy Sand, and Sand, representing a gradient of increased sand content and decreased silt and clay content (Supplementary Table 1). Gradients in soil chemistry reflect the gradient in soil texture, with lower pH, soil organic carbon (C), and soil nitrogen (N) corresponding to higher sand content (Supplementary Table 1; Chung et al., 2017).

2.2. Vegetation assessment and soil sampling

All aboveground plant data and seed bank soil collection occurred on July 20th, 2017, approximately at peak biomass following the flowering stage of most local annual herbaceous plant species. At each of the three sites, seven sampling plot locations were sequentially selected at random. Each plot was laid out as a circle 10 m in diameter ($78.54\ m^2$). At the center of each plot, a 1.5 × 1.5 m quadrat was placed and used to visually estimate percent cover of all aboveground plants, which we identified down to the finest possible taxonomic resolution. Cover estimates included a ‘catch-all’ category for all late-successional biological soil crust mosses and lichens known to be ecologically important to the areas surrounding our study. For a more complete representation of species located in the study area, we recorded the presence or absence of all aboveground plants within the full 10 m plot (Supplementary Table 2). Due to the timing of sampling, vegetation assessments included both alive and dead plant taxa identifiable within the plots. Within each quadrant of the 1.5 × 1.5 m quadrat at plot center, soil seed bank samples were collected from within 50 cm of plot center. Each soil sample consisted of six individual soil cores extracted at random to a depth of 5 cm, using a 2.54 cm diameter soil corer and homogenized to the subplot level ($n = 4$ per plot). To avoid the inclusion of debris in the seed bank sample, the top litter layer of the soil was lightly removed prior to collection, if present.

Soil water holding capacity was also assessed for each of the three sites (Supplementary Table 1). Water holding capacity was assessed by saturating soil collected from 0 to 10 cm depth collected outside of the plots of each site with deionized water. Samples were allowed to drain until there was no standing water and no water drained from the bottom (~30 min). Samples were then weighed, dried at 105 °C for 48 h, and reweighed (Reed et al., 2011).

2.3. Soil seed bank identification

After field collection, soil seed bank samples were kept in a cool dark location at approximately 40 °C for cold storage and stratification, to reduce loss of viability and aid in germination, for approximately 5 months (Baskin and Baskin, 1998). To initiate germination using the standard greenhouse emergence method (Faist et al., 2015; Gross, 1990) the soil samples were maintained by plot and subplot in

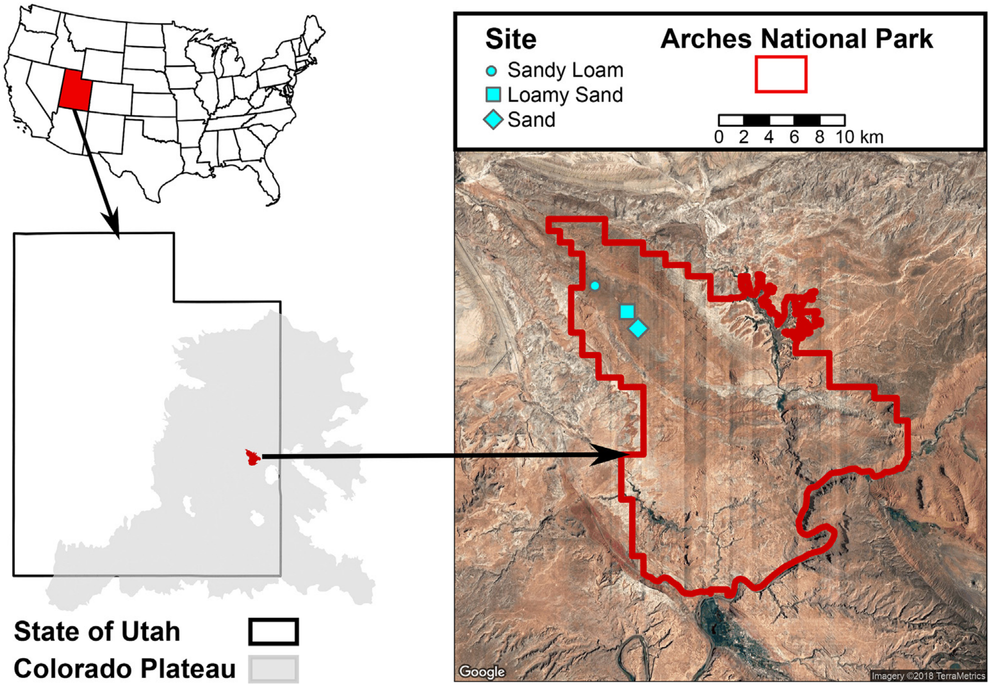

Fig. 1. Site locations in Arches National Park, Utah, Colorado Plateau, USA.

individual pots and spread in a thin layer (~0.5 cm) over a substrate of sand/gypsum mix. Samples were monitored daily to ensure that soil moisture was maintained. Watering was applied overhead through a fine mist nozzle so as not to disturb the integrity of the soil during the germination process but allow for water to percolate through the soil column. The first round of germination was in place for ~60 days, then soils were quickly dried down and the topsoil seed bank layer was moved to a bed of potting mix (Miracle-Gro Potting Mix) for an additional ~60 days, as maintaining adequate soil moisture in the sand mixture was difficult as spring temperatures increased. This method of wetting and drying also served as a process to cause a new 'flush' of germinants and has been successfully implemented in other seed bank trials (Faist et al., 2013; Faist and Collinge, 2015).

During both repeat trials, germinants were monitored a minimum of 3x per week and the study was ultimately terminated after > 2 weeks had passed with no new germination observed. Germinants were noted as either monocots or dicots at initial germination and identified to the highest resolution of taxonomic capabilities possible. If no clear characteristics were present, individuals were grown out until characteristics appeared. Due to a high level of mortality at the cotyledon stage, a number of species remained in either the "monocot" or "dicot" category. However, our four dominant seed bank species (*Vulpia octoflora, Bromus tectorum, Plantago patagonica and Sporobolus* sp.) were identifiable at the initial germination stage and comprised approximately 83% of total germinants in the study (N = 402). Other less abundant germinants included *Sphaeralcea* spp., unidentified species in the family Asteraceae, two unknown but distinct dicot species, and other unknown dicots and monocots. Greenhouse temperatures were monitored daily and maintained an average low of 13.6 °C and an average high of 37.4 °C. To provide a final assessment of seeds released from the seed bank, we manually sorted through a subset of the soil seed bank samples and only a small amount of seed hulls and non-viable seeds were found.

2.4. Community metrics & analyses

Metrics of aboveground plant diversity were calculated for each site. Species richness (R) was calculated as the total number of species present in each site, while Shannon-Wiener indices (H) were calculated using the relative cover. Evenness (E) was a combination of the two (E = H/ln(R)). To assess the relationship between edaphic properties and plant community composition, we constructed distance matrices of Bray-Curtis dissimilarities and conducted permutational multivariate analyses of variance (PERMANOVAs) in the statistical software R (Oksanen et al., 2018; R Core Team, 2016). For aboveground plants, dissimilarities in relative species abundance were calculated using cover estimates for the quadrat at each plot's center. For belowground plants (i.e., the seed bank community), the abundances and dissimilarities were based on the relative number of unique plant taxa that survived germination.

For our aboveground and belowground comparisons at each site, our data were limited to only the dominant species that could be positively identified within the germinated soil seed bank. These four species included three monocots (*Vulpia octoflora, Bromus tectorum, and Sporobolus* sp.) and one dicot (*Plantago patagonia*). For each plot, we calculated Sorensen's Index of Similarity between above and belowground communities based on the relative abundances of these four species. Finally, we compared above versus belowground community composition across all sites by assessing the correlations between their corresponding distance matrices (Mantel test).

Cross-site variation in soil texture and chemistry (Supplementary Table 1) was assessed using a multivariate General Linear Model. Data were tested for assumptions of normality and homoscedasticity; if either assumption was violated, data were ln-transformed to eliminate assumption violation prior to statistical analyses. Tukey's *post hoc* analyses were used to assess variance among specific sites.

3. Results

3.1. Diversity and community composition across the soil texture gradient

Both aboveground and belowground plant communities varied significantly across sites with different soil textures and chemical properties. A total of 18 distinct taxa were identified within aboveground plot quadrats across all sites (26 taxa within the full presence-absence plots). The highest species richness was observed at the finest textured

Table 1
Aboveground plant diversity metrics at each site along a soil texture gradient.

	Sandy Loam	Loamy Sand	Sand
Richness (R)	15	12	14
Shannon Diversity (H)	1.963388	1.420826	2.168676
Evenness (E)	0.7250190	0.5717823	0.8217617

site (Sandy Loam), whereas the greatest Shannon diversity and evenness was observed at the coarsest textured site (Sand; Table 1). Our PERMANOVA analyses confirmed observed differences in cover-based aboveground community composition between the sites (p = 0.001; Fig. 2), with no significant variation among plots (p = 0.220). Similarly, soil seed bank communities of each site were distinct from one another (p = 0.019; Fig. 3), but they also varied among the plots at each site (p = 0.032).

3.2. Similarity between cover and soil seed bank

Comparisons between the aboveground plant cover and relative soil seed bank abundance of the four dominant species indicate low similarities between aboveground and belowground communities at each site. Similarity between aboveground and belowground composition was highest at the Sandy Loam site, where the mean Sorensen's Index within individual plots was 0.268. Mean Sorensen's indices were 0.107 at the Loamy Sand site and 0.115 at the Sand site. Aboveground plot composition across sites was also poorly correlated with belowground composition across sites (Mantel test statistic r = 0.1934). The observable patterns in the aboveground and belowground prevalence of the four dominant seed bank species further emphasized the community dissimilarities across all three soil textures (Fig. 4). Though percent cover and seed densities both varied across sites, those patterns generally did not align with one another.

4. Discussion

The clear differences in plant diversity and community composition aboveground and belowground across a soil texture gradient highlight the profound influence of edaphic characteristics in dryland ecosystems such as those on the Colorado Plateau. The soils with varying texture also maintained significant differences in water holding capacity and multiple metrics of soil fertility (Supplementary Table 1), showing that soil physical and chemical structure can have strong control over plant communities, above- and belowground. Indeed, the results shown here suggest that even relatively subtle differences in soil texture, and the edaphic factors that vary with texture, can have large control over soil seed banks, as has been observed in assessments of dryland aboveground plant community composition (Noy-Meir, 1973) and soil function (e.g., Cable et al., 2008). Such patterns are important, both because soil texture varies markedly within and across dryland ecosystems (English et al., 2005; McAuliffe, 1994; Schlesinger et al., 1995), and also because soil texture and chemistry are affected by anthropogenic activities such as grazing (Anderson et al., 1982; Belnap and Gillette, 1998).

In contrast with other observations from dryland ecosystems (Henderson et al., 1988; Hopfensperger, 2007), we observed a notable difference between the aboveground vegetation and the soil seed bank composition. A variety of factors could influence this deviation. For one, certain species may be more prolific seed producers, with seeds that can persist in the soil seed bank (Grime, 1981; Thompson and Grime, 1979; Vandvik et al., 2016) regardless of their contributions to cover, such as the small-statured *Plantago patagonica* (Venable, 2007). Additionally, although we timed collection to minimize collection of the current year's seeds, because of variation in when aboveground species drop their seeds, some of the current season's seeds may have been observed in the seed bank. This would have implications for the similarities, and differences, of the aboveground vegetation versus

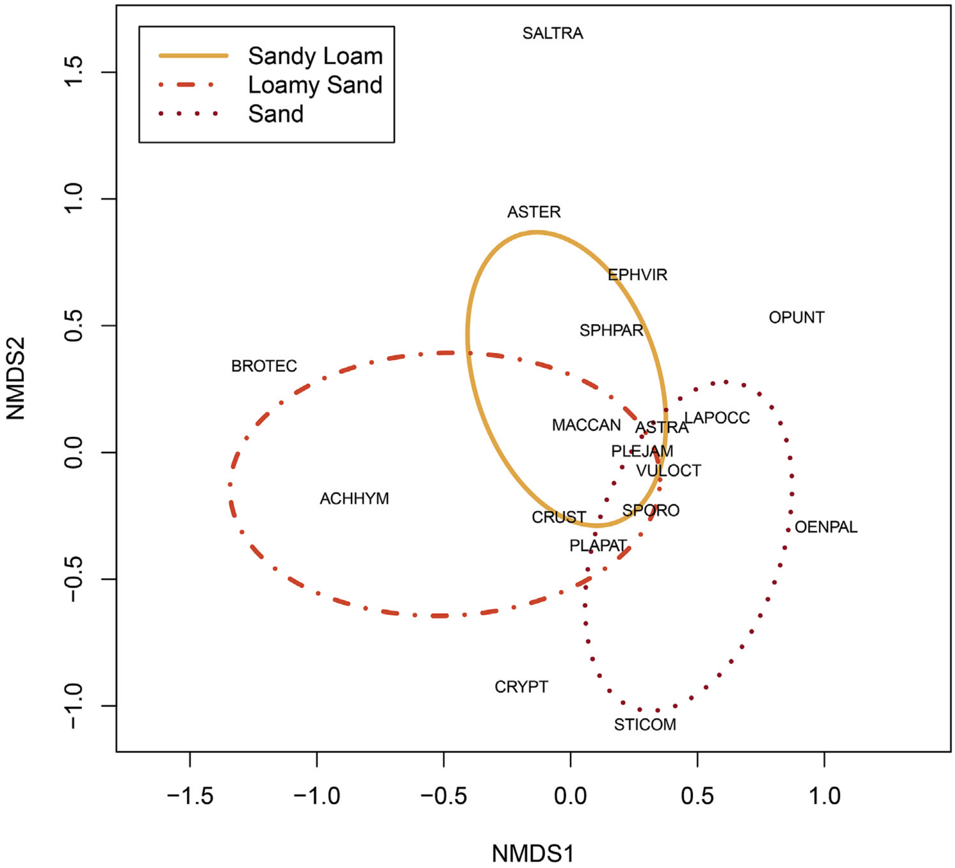

Fig. 2. Differences in aboveground community composition across all three sites, represented using non-metric multidimensional scaling (NMDS). Relative abundances were based on cover assessments within the quadrats of each plot. Standard error ellipses correspond to the three study sites with distinct soil textures. Text labels depict the codes used for the 18 identified plant taxa (Supplementary Table 2) and their proximity to one another represent their relatedness within the community. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

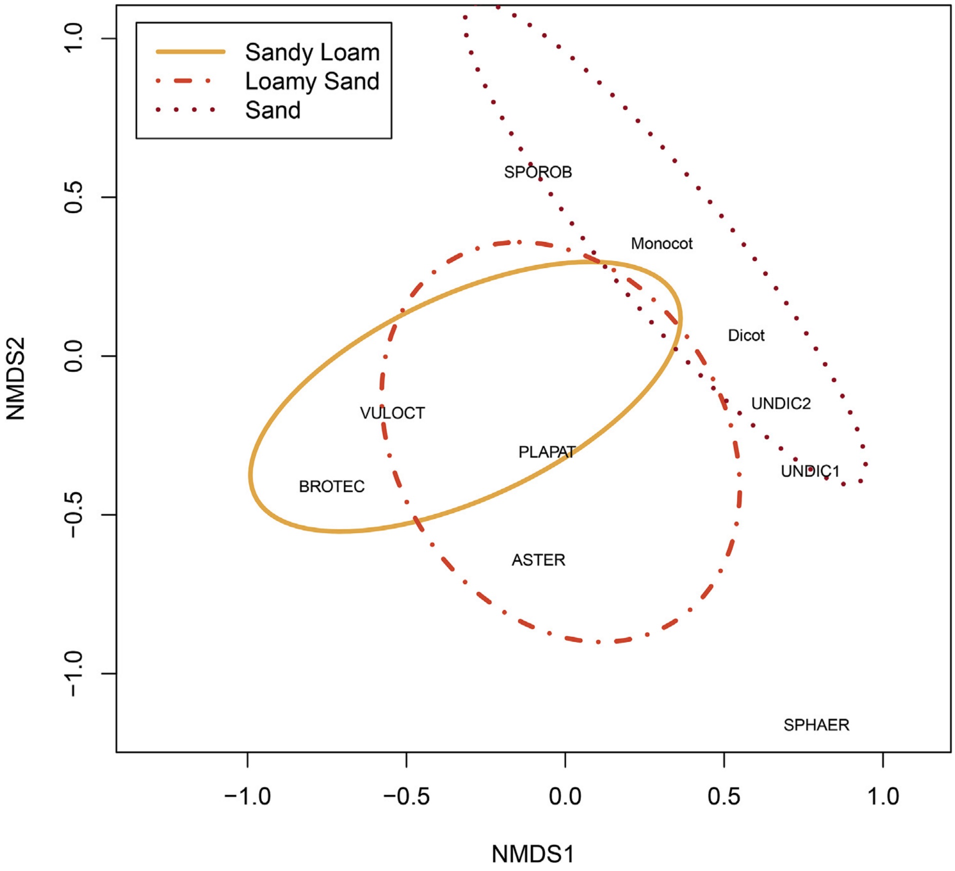

Fig. 3. Differences in belowground community composition across all three sites, represented using non-metric multidimensional scaling (NMDS). Community differences were based on relative abundances of soil seed bank germinants. Standard error ellipses correspond to the three study sites with distinct soil textures. Text labels depict the 6 plant taxa distinctly observed among seed bank germinants, as well as categories for unknown monocot and dicot species, respectively labeled 'Monocot' and 'Dicot'. The proximity of labels to one another represent their relatedness within the community. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

belowground seed bank community. If transient (i.e., the collection year's) seeds were collected in the seed bank and the same species was observed in the aboveground vegetation, we would expect similarities above- and belowground to be higher. However, understanding the role of seed inputs in seed bank composition across time remains difficult, as comparative seed bank studies are relatively rare (Hopfensperger, 2007). Looking just within our sites, the differences between aboveground and belowground communities could also be driven by interactions between soil texture, soil chemistry, and land use. These sites were grazed until the early 1980's (National Park Service Southeast Utah Group archives) and the legacy of that grazing almost certainly persists. Some of the cross-site variation between the plant species we observed aboveground versus those observed belowground could be related to how the system is responding to the removal of grazers, and how these responses vary with edaphic properties. Finally, some of the variation could be due to methodological constraints, because we were only able to make comparisons using our four dominant seed bank species. However, even with these constraints, alternate methods of quantifying aboveground relative abundance would still retain biases toward the species that produce more seeds. Regardless of the cause, these data point to the importance of elucidating the factors that control aboveground and belowground community composition in drylands, and underscore a strong role for soil texture and texture's interactions with hydrology and nutrient cycling.

Surprisingly, we found that patterns in the abundance of our system's major invasive species – cheatgrass – did not align in terms of overall belowground seed counts and aboveground cover. As with many other disturbance-tolerant, invasive species, cheatgrass produces numerous seeds that can persist within the seed bank (Smith et al., 2008). However, despite cheatgrass currently being prevalent aboveground at both our Sandy Loam and Sand sites, we observed fewer of its seeds in sites with sandier soils, with none being found at any of the Sand plots (Fig. 4). This supports the idea that soil characteristics, such as texture, may be acting as an additional filter limiting the spread of this invasive species (Miller et al., 2006). Thus, while climate and disturbance regimes still play major roles in predicting the susceptibility of a given site to invasion, these data highlight the utility of land managers further considering the role of soil when prioritizing invasive species management (Byers et al., 2002), and a predictive understanding of seed banks could be a powerful component of determining management options.

Our research demonstrates how vegetation cover and the soil seed banks may respond to the same environmental gradient - such as soil texture - but in a discordant manner. Ignoring the differential responses of these two major components of the plant community could lead to management mismatches, where actions based on existing vegetation and soil properties may not yield desired outcomes if the seed bank is not considered. Thus, an improved understanding of dryland seed banks would be of use. Furthermore, gradients of soil texture do not necessarily align with gradients of climate and other environmental factors that shape species distribution and community composition (Palm et al., 2007). Our results emphasize that efforts to predict ecological responses to shifting climate conditions should not only consider the substantial role that soil characteristics can play in mediating those responses – even within a single, distinct system – but also how interactions between soils, the soil seed bank, and its aboveground counterpart all help set the stage for the plant communities of the future.

Declarations of interest

The authors have no competing interests to declare.

Authorship contributions

JH wrote the majority of the manuscript and conducted the statistical analyses. SCR and AMF aided in writing the manuscript and

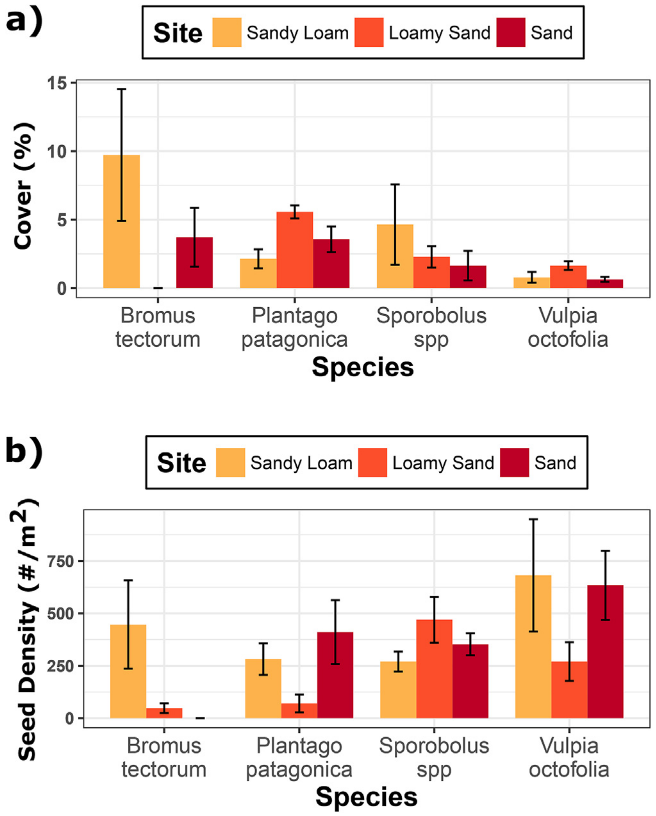

Fig. 4. Mean values of **a)** aboveground percent cover and **b)** belowground seed densities of the four dominant seed bank species at each site. Error bars correspond to one standard error for each site (n = 7 plots). Seed densities are the estimated number of seeds in 1 m^2 of the top 5 cm of soil that was sampled. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

statistical analyses. AMF designed the experiment and AMF and JH conducted the field work and soil collections. AMF led the greenhouse seed bank extraction efforts.

Acknowledgements

We are grateful to Adrienne Pilmanis of the Bureau of Land Management Colorado Plateau Native Plant program for ideas and support that helped shape and make this research possible. We also thank Paula (Peekay) Briggs of the National Park Service Southeast Utah Group for help accessing archived information about the sites' history, as well as to Matt Van Scoyoc and Laura Martin for help with permits and logistics. We thank Erika Geiger for assistance identifying aboveground communities and for help with field work, Robin Reibold for maintaining the sites, Megan Starbuck for performing water holding capacity analyses, and Taylor Sanchez and Chali Simpson for their help with the greenhouse seed bank efforts. We also thank Carla Roybal for valuable comments on a previous version of the manuscript. Finally, we would like to Nancy Huntly and the Utah State University Climate Adaptation Science Program for the opportunity to conduct this research. This work was supported by the Bureau of Land Management Colorado Plateau Native Plant Program, the Utah State University Climate Adaptation Science Program (National Science Foundation Award #1633756), the National Park Service Air Resources Division, and the U.S. Geological Survey Ecosystems Mission Area. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jaridenv.2019.01.008.

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