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RESEARCH ARTICLE

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Sympatric pairings of dryland grass populations, mycorrhizal fungi and associated soil biota enhance mutualism and ameliorate drought stress

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Abstract

1. There is evidence that the distribution of ecotypes of plants and their symbiotic arbuscular mycorrhizal (AM) fungi and other associated soil biota may be structured by the availability of essential soil nutrients; and that locally adapted partnerships most successfully acquire limiting nutrients. This study tests the hypotheses that plant genotypes are adapted to the water availability of their local environment, and this adaptation involves associations with local soil biota, including AM fungi.
2. We grew semi-arid *Bouteloua gracilis* ecotypes from relatively wet and dry sites, with either sympatric or allopatric soil inoculum under moderate and extreme soil drying treatments to examine (a) how varying degrees of water limitation influence grass responses to soil biota and (b) the relationship between AM fungal structures and the responses.
3. Under extreme soil drying, the dry site ecotype tended to perform better than the wet site ecotype. Both ecotypes performed best in either drying treatment when inoculated with their sympatric soil biota. Sympatric pairings produced more AM fungal hyphae, arbuscules and dark septate fungi. Extreme soil drying tended to accentuate these apparent benefits of sympatry to both plants and fungal symbionts, relative to the moderate drying treatment.
4. Our findings support the hypothesis that AM symbioses help *Bouteloua gracilis* ecotypes adapt to local water availability. This conclusion is based on the observations that as water became increasingly limited, sympatric partnerships produced more AM fungal hyphae and arbuscules and fewer vesicles. The abundances of hyphae and arbuscules were positively correlated with plant growth, suggesting that in sympatric pairs of plants and AM fungi, allocation to fungal structures is optimized to maximize benefits and minimize the costs of the symbioses. This provides strong evidence that co-adaptation among plants and their associated AM fungi can ameliorate drought stress.
5. *Synthesis*. Our study documents the role of locally adapted soil borne plant symbionts in ameliorating water stress. We found a relationship between AM fungal structures in roots and plant performance. Generally, plants and fungi from the same site resulted in more positive effects on plant growth.

KEYWORDS
arbuscular mycorrhizas, *Bouteloua gracilis*, climate change, co-adaptation, drought, local adaptation, soil organisms

1 | INTRODUCTION

Plants are often locally adapted to their abiotic environment (Leimu & Fischer, 2008; Richardson et al., 2014; Smith et al., 2012) and to their local biotic environment, including soil biota (Gehring et al., 2006; Johnson et al., 2010; Waller et al., 2016). Plants respond variably to soil biota, in part because soil biota can both enhance and inhibit plant growth and survivorship via the activities of beneficial mycorrhizal fungi, harmful pathogenic fungi, saprotrophic fungi, a suite of bacterial species and food webs of soil fauna (van Grunsven et al., 2009; Hendriks et al., 2015; van der Putten et al., 2013). In turn, plants can shape soil communities, for example by evolving features that attract beneficial biota such as mycorrhizal fungi or repel detrimental biota such as pathogens (Venturi & Keel, 2016). Plant associations with arbuscular mycorrhizal (AM) fungi are known to facilitate soil nutrient and water acquisition as well as buffer against a variety of stresses (Reininger & Sieber, 2012; Rowe et al., 2007; Stahl & Smith,). There is evidence that, like their plant partners, these fungal symbionts may also be adapted to the abiotic and biotic environments (Ji et al., 2013; Johnson et al., 2010; Stahl et al., 1990).

Many AM fungal species have a nearly global distribution (Davison et al., 2015) demonstrating physiological variation within species (Ehinger et al., 2012) that may display differing functional attributes contingent upon the environmental context (Antoninka et al., 2015; Hoeksema et al., 2010; Johnson et al., 1997; Revillini et al., 2016). Mycorrhizas from resource limited and stressful environments tend to show greater mutualistic function (Revillini et al., 2016), reminiscent of the stress-gradient hypothesis in that greater abiotic stress favours more beneficial interactions (Callaway et al., 2002). Additionally, AM fungi and plants that originated from a common location and potentially share a co-evolutionary history, tend to have a greater mutualistic function (Ji et al., 2013; Johnson et al., 2010). We call this the sympatric advantage hypothesis (Remke, Hoang, et al., 2020). Some evidence suggests that plants and co-occurring soil microbes, including mycorrhizal fungi, rapidly adapt to changes in the environment and thus co-adaptation creates greater mutualistic function (Lau & Lennon, 2011, 2012; Vurukonda et al., 2016). Thus, mycorrhizal function is documented to vary based on both environment and provenance of symbionts (Johnson et al., 2010). The need for a better understanding of the mechanisms of these joint influences is becoming increasingly poignant as climate change modifies the abiotic environments of plants and their fungal partners, for example by enhancing soil drying and diminishing water availability.

The functional equilibrium model might serve as a reasonable expectation of the outcome of increasing environmental stresses in water-limited environments. This model predicts that plant allocation of photosynthate and biomass varies to optimize acquisition of the most limiting resource (Briske & Wilson, 1980; Johnson, 2010; de Vries et al., 2012). When a soil resource such as phosphorus or water is added to a resource-limited system, the need for mycorrhizal delivery of that resource diminishes (Johnson et al., 1997; Ladwig et al., 2012). As a result, plants invest less in root exudates and fungal symbionts (Orwin et al., 2010). Simultaneously, fungi allocate less to resource harvesting (hyphae) and exchange (arbuscules) structures and more to storage structures (vesicles; Johnson et al., 2003). This shift in allocation to different AM fungal structures may be one possible manifestation of a shift in mycorrhizal function to less mutualistic symbioses (Johnson & Grahm, 2013). Conversely, decreasing the supply of the limiting soil resource can increase the mutualistic function of mycorrhizas and allocation to arbuscules and hyphae.

Water is a limiting soil resource in nearly half of the world's terrestrial ecosystems (Prăvălie, 2016). Mycorrhizal fungi are known to contribute to vascular plant water balance both directly and indirectly. Mechanisms for this are observed as active water uptake and delivery (Ruth et al., 2011), passive water delivery (Allen et al., 1981), improved plant nutritional status and size (Augé, 2001, 2004), and plant hormonal regulation of stomata (Augé et al., 2015). It follows that plant available water is a soil resource that influences mycorrhizal function (i.e. location on the mutualism–parasitism continuum). The increased frequency and severity of drought in many drylands predicted by many climate change scenarios suggest the potential for increasing the importance of AM mutualisms in the future (van der Putten et al., 2016). Studies have documented that plants and associated soil organisms are co-adapted in native grasslands and perform best when grown together in nutrient limited systems (Johnson et al., 2010). Given the importance of mycorrhizas to plant water balance, the importance of co-adaptation among plants and AM fungi in a water limited system should be evaluated. We sought to determine the interactive effects of provenance and soil drying regimes on mycorrhizal function and elucidate how patterns of fungal allocation to resource harvesting and exchange structures versus storage structures are associated with mycorrhizal function.

To examine mycorrhizal functioning and fungal allocation across different environmental and co-adaptation scenarios, we grew two populations of a C4 perennial grass *Bouteloua gracilis* with locally occurring (sympatric) or novel (allopatric) soil organisms. The populations were sourced from semi-arid environments at two elevations in close geographic proximity, with strongly contrasting precipitation (28 cm vs. 43 cm mean annual precipitation). We hypothesized that more severe limitation of soil moisture will favour stronger mycorrhizal mutualisms at the drier site compared to the wetter site. The experimental plants were maintained under moderate (more gradual) or extreme (more abrupt) soil drying conditions to simulate the natural environmental stress caused by

limited soil moisture at the wetter and drier sites respectively. This experimental design allowed us to simultaneously test predictions of two complementary, non-exclusive hypotheses: sympatric advantage and functional equilibrium, and their interactions, as they relate to mycorrhizal function.

Sympatric advantage hypothesis 1 Plants and sympatric soil biota are more likely to engage in effective mutualism because of a shared history of co-adaptation. If true, we predict that plants grown with sympatric soil biota will be larger and more tolerant of soil drying compared to allopatric pairings.

Functional equilibrium hypothesis 1 Predicts that symbiotic root-associated microbes will provide a greater advantage when water is more limiting, and that plant growth and tolerance of soil drying is associated with greater AM fungal allocation to structures that facilitate acquisition and exchange of the most limiting soil resource (hyphae and arbuscules) and less allocation to storage structures (vesicles). We further hypothesize that optimal allocation is one of the mechanisms in which sympatric advantage is expressed. If true, we predict that better plant growth and tolerance of drying will be positively associated with acquisition and exchange structures, and greater allocation to these structures will be found in sympatric pairings.

Testing these hypotheses will help generate a useful framework for predicting the responses of mycorrhizal symbioses to increasingly water-limited environments. If predictions are supported, it would suggest that maintenance or re-creation of sympatric pairings of plants and soil organisms may be important for successful ecological restoration, forestry, assisted plant migration and other applications.

2 | MATERIALS AND METHODS

2.1 | Sources of plants, soil and inoculum

Seeds and soil were collected from two sites within 25 km of one another, but with very different annual precipitation. The wetter site (hereafter 'wet site') was a semi-arid grassy understorey of a piñon-juniper woodland on the west side of the Kaibab Plateau (Coconino County, Arizona, USA) at an elevation of 2,064 m with approximately 43 cm of precipitation annually (PRISM Climate Group). The drier site (hereafter 'dry site') was a semi-arid grassland adjacent to an alluvial drainage on the east side of the Kaibab Plateau at an elevation of 1,710 m with an average of 28 cm of precipitation annually (PRISM Climate Group). The soils at both sites are derived from Kaibab Limestone and the wet site soils are composed of argids while the dry site soils are a mosaic of orthents and calcids.

Bouteloua gracilis seed was collected from the two sites using the Seeds of Success protocol (https://www.blm.gov/sites/blm.gov/files/program_nativeplants_collection_quick%20links_technical%20protocol.pdf). Live soil inoculum was collected from the rooting zone of *B. gracilis* along three 100 m transects established from a random origin (azimuths of 0°, 90° and 270°) at the wet and dry sites. Soil subsamples within each site were pooled together and mixed. We justify homogenizing inoculum from each site because we were interested in seedling responses to average soil biotic conditions across sites, rather than within a single site or extrapolating to a broader geography than our sampling sites (a 'type C' design; Gundale et al., 2017, 2019). Inoculum soil was refrigerated 2 weeks until its use in the experiment. The abundance of different soil organisms in the two inoculum soils was determined using phospholipid fatty acid (PLFA) and neutral lipid fatty acid (NLFA) analysis. Lipids were extracted from 5 g of freeze-dried inoculum soil by vortex mixing in a one-phase mixture of citrate buffer, methanol and chloroform (0.8:2:1: v/v/v, pH 4.0). The biomass of AM fungi was estimated from the NLFA 16:1 ω5: 20:1 ω9 and 22:1 ω13, biomass of other fungi was estimated from 18:2 ω9:12c, and biomass of bacterial groups was estimated from signature PLFAs for Gram positive and Gram negative bacteria (Olsson et al., 1995). This analysis indicated that the soil inoculum from the wet and dry sites had similar abundances of various fungal groups, including AM fungi, and bacteria (Table S1).

The community composition of soil fungi in wet and dry inoculum treatments were compared before and after the experiment. Samples of soil were collected and DNA was extracted from 0.5 g of soil using a PowerSoil DNA Extraction Kit (MO BIO Laboratories, Inc.). Genomic DNA was normalized to 2 ng/μl, diluted 10-fold and amplified in triplicate PCR using the universal ITS general eukaryotic primer WANDA and the AM fungal-specific primer AML2 for the small subunit (SSU) rRNA gene (Dumbrell et al., 2011; Lee et al., 2008). Purified products were quantified with PicoGreen fluorescence. Indexing PCR was completed using 8 bp dual indexed WANDA and AML2 primers. Indexed PCR products were purified using a 1,1 carboxylated magnetic bead solution, quantified and combined into a final sample library. The library was purified, concentrated and quantified using quantitative PCR against Illumina DNA standards on an Illumina MiSeq System (Illumina, Inc.) running in paired end 2 × 300 bp mode. Forward reads were trimmed to 250 bp to remove low quality tails and demultiplexing was carried out using a minimum quality threshold of q20 and default parameters in QIIME 1.9.1 (Caporasso et al., 2010) Taxonomy was assigned to sequences using BLAST with 90% similarity and an E-value $< 10^{-4}$, against the online MaarjAM database (http//maarjam.botany.ut.ee; Öpik et al., 2010). Taxa that made up <1% of relative abundance were labelled as 'other', otherwise species were recorded to the genus level for community comparisons. Many species remained unidentified or classified only to order or family.

2.2 | Experimental design

Mesocosms were prepared with all four possible combinations of plant and inoculum origin, two sympatric combinations (inoculum

and plants from the wet site, or inoculum and plants from the dry site) and two allopatric combinations (inoculum from the dry site with plants from the wet site, or inoculum from the wet site with plants from the dry site). These treatments were further crossed with two levels of water availability to mimic the severity of water limitation at the two source sites. To generate a frame of reference for the performance of plants without sympatric or allopatric soil organisms under the soil drying regime that most closely resembles their home site, we created two sterile inoculum treatments in which plants from the wet site were grown with sterile soil under a moderate drying regime and plants from the dry site were grown in sterile soil under extreme drying conditions. Each combination of plant ecotype, inoculum origin and drying regime was replicated nine times, resulting in 72 mesocosms, plus, the two sterile inoculum treatments replicated nine times for a total of 90 experimental units.

Mesocosms were constructed from 21 L plastic containers (43 cm × 28 cm × 18 cm) with six 0.3 cm diameter holes drilled into the bottom for drainage. In order to remove the effects of any variation in soil physical and chemical characteristics at the two different sites, we created a sterilized common soil using a 1,1 mixture of soil from the two sites that was steam sterilized at 125°C for 48 hr. Our experimental design matches type C in Gundale et al. (2017), because unique and variable sub-populations of plant subjects (a random draw of seeds collected from a site) are confronted with one of two soil biota conditions that represent the gamma diversity of each site, and the same background soil condition. This design is preferred when the goal is to detect differences among two or more groups of subjects, and when within-site or regional spatial variation is not a focus (Cahill et al., 2017; Gundale et al., 2017; Gundale et al., 2019). Each mesocosm was filled with approximately 15 L of sterilized soil and topped with a 1-cm thick band of either live or sterilized (dead) inoculum soil. *Bouteloua gracilis* seed was sprinkled onto the inoculum soil at a rate of 60 seeds per mesocosm and later thinned to 10 seedlings per mesocosm. Mesocosms were placed in fully randomized spatial locations to account for microclimatic variation within the glasshouse.

2.3 | Watering treatments

Initially, all mesocosms were watered three times each week for 8 weeks and then they were watered twice per week for 4 weeks before starting the drying treatments. Each watering event brought the mesocosms to field capacity to ensure adequate moisture for plant establishment. Rather than simulate an unrealistically abrupt transition from abundant moisture to dry conditions, we simulated a more gradual transition based on per cent of field capacity. These transitions simulate what a plant may experience during the growing seasons as soil moisture diminishes after snowmelt or summer monsoons. Mass at field capacity was estimated by weighing 10 randomly selected containers 24 hr after watering. Then, the mass of one randomly selected container was measured every other day, until a soil mass threshold indicated it was time to water again to field capacity. For the moderate drying treatment, we used an initial threshold of 60% of mass at field capacity. For the extreme drying treatment, we used an initial threshold of 40%. After each sequential watering, we decreased both of these threshold percentages by 5%. This both gradually decreased the amount of water available to the plants and increased the length of time between watering events. Eventually, we reached permanent wilting point (approx. −1.5 MPa) in both treatments resulting in at least 90% mortality after 8 months when the experiment was terminated.

2.4 | Plant performance

Every 2 weeks, we measured plant height in all containers and the percentage of plant tissue that was green was monitored to estimate the length of time until plant senescence. Greenness was based on ocular estimates of colour. No plants produced inflorescences. At the termination of the experiment, all above-ground biomass was clipped, dried at 60°C for 24 hr and weighed. Root biomass was sampled by taking four soil cores (5 cm diameter and 18 cm deep). Roots were cleaned, dried and weighed and the weight of roots per volume of core was used to estimate root biomass in the total volume of the mesocosm.

2.5 | AM fungal performance

Soil and root materials obtained from destructive harvesting at the end of the experiment were analysed from all 90 mesocosms. A 10-g subsample of fresh root material was refrigerated until it could be examined for root colonization by fungi. Root samples were cleared with 5% KOH and stained with ink in vinegar (Vierheilig et al., 1998). Colonization by AM fungi and other root endophytes was determined using the gridline intersect method at 200× magnification (McGonigle et al., 1990). Mycorrhizal root colonization was distinguished as arbuscules, vesicles and hyphae; dark septate endophytes (DSEs) were also quantified.

The soil-borne (external) hyphae of AM fungi were extracted from the soil cores after root removal, using the methods of Sylvia (1992), and quantified using a gridded eyepiece graticule in an inverse compound microscope at 250× magnification. At points where hyphae intersected gridlines, hyphae were counted, and counts were converted to length of hyphae per gram of soil. Hyphae of AM fungi were distinguished from other fungal hyphae based on their morphology and colour.

2.6 | Statistical analysis

Soil biota effect was calculated to quantify plant biomass responses to AM fungi and other soil organisms relative to plants grown in the absence of living inoculum. Each *B. gracilis* population was compared

to the average value of plants of the same population grown with sterile inoculum under the moisture regime most similar to the site of origin of the plant material.

$$\text{Soil biota effect} = \frac{\mu_{\text{living}} - \mu_{\text{sterile}}}{\sqrt{\frac{(n_{\text{sterile}} - 1)SD^2_{\text{sterile}}}{(n_{\text{living}} - 1)SD^2_{\text{living}}}}}$$

where μ is the mean final plant biomass, n is the sample size and SD is the standard deviation of the treatment of interest.

Three-way repeated measures ANOVA was used to compare the effects of plant origin, soil inoculum origin and drying regime on plant height and time until senescence over 13 time points that span 24 weeks. Three-way ANOVA was used to compare the effect of the same three factors on final plant biomass, soil biota effect, density of external AM hyphae and per cent root length colonized by AM fungi and DSEs. Differences within groups were determined using Tukey's HSD test. Sterile controls were excluded from all ANOVA models. Linear regressions were used to determine relationships between soil biota effect and density of external AM hyphae, and per cent root length colonized by different AM fungal structures and DSEs. Model assumptions were checked using the Shapiro–Wilk test of normality and the Levene's test of heterogeneity of variance. All statistics were conducted in R (version 3.3.1).

3 | RESULTS

3.1 | Plant responses

Bouteloua gracilis ecotypes from the wet and dry sites differed in their responses to moderate and extreme drying. Ecotypes tended to grow taller and stay green longer when grown under the watering regime most similar to their site of origin (Figure 1). Plants grew significantly larger and were more tolerant of drying when grown with sympatric soil organisms compared to allopatric soil organisms. Plants from the dry site inoculated with their sympatric soil organisms consistently grew 1.5× taller than those grown in sterile soil or inoculated with allopatric soil organisms (Figure 1a; $F = 82.9$, $p < 0.001$). Plants from the dry site tended to be no larger under

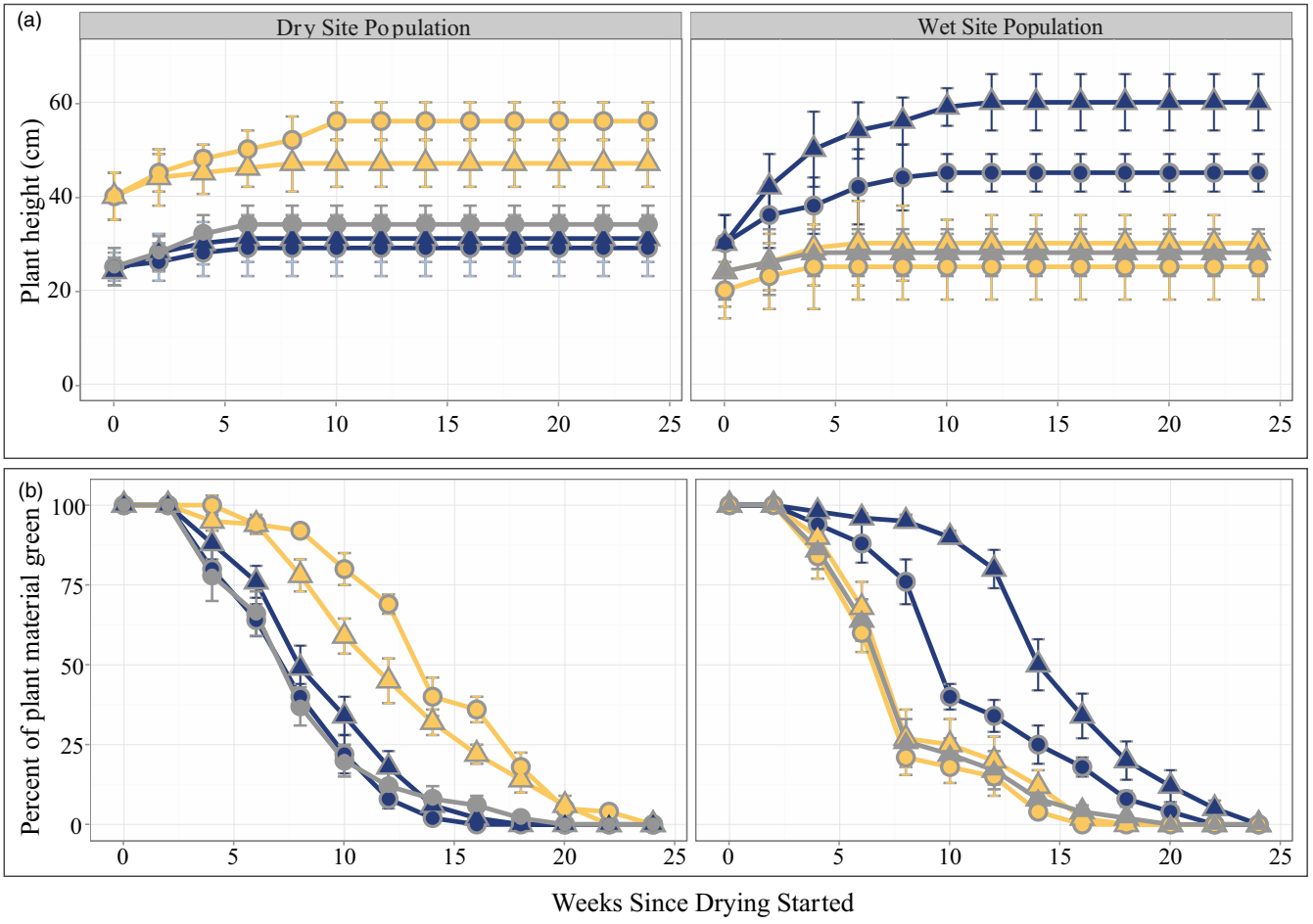

FIGURE 1 Plant height (a) and per cent green plant material (b) plotted against time since initiation of drying treatments for different treatments and plant populations. Dark symbols represent soil biota from the wetter site and lighter colours represent soil biota from the drier site; graphs on the left side represent the plant population from the dry site, and those on the right represent the plant population from the wet site. Grey symbols represent plants grown with sterile inoculum. Triangles represent moderate drying treatments and circles represent extreme drying treatments

extreme drying treatments relative to the moderate drying treatments (Figure 1a; $F = 1.23$, $p = 0.08$). Plants from the wet site grew 1.7× more when inoculated with their sympatric soil organisms relative to allopatric soil organisms (Figure 1b; $F = 87.4$, $p < 0.001$); however, plants grown under moderate drying were 1.2× larger than plants grown under extreme drying (Figure 1b; $F = 4.87$, $p = 0.03$). Plants grown with allopatric soil organisms were no taller than those grown in sterile controls for plants from the dry population (Figure 1a; $F = 0.10$, $p = 0.56$) as well as for plants from the wet population (Figure 1b; $F = 0.12$, $p = 0.55$). Plants paired with their sympatric soil organisms maintained green tissue 3–4 weeks longer into the drying events than those grown in sterile soil or grown with allopatric soil organisms (Figure 1b; $F = 128.4$, $p < 0.001$). Sterile controls stayed green up to 2 weeks longer than plants that were grown with allopatric soil organisms (Figure 1b).

There were no main effects of plant population ($F = 2.22$, $p = 0.14$), or watering treatment ($F = 0.60$, $p = 0.44$) on plant biomass, however, there was a significant effect of inoculum source ($F = 10.15$, $p < 0.001$) and an interaction between plant origin and soil inoculum ($F = 8.79$, $p < 0.001$; Table S3). Tukey's HSD shows that plants grown with sympatric soil organisms were consistently larger than allopatric pairings (Figure 2). Although not statistically significant, the total biomass of plants from the dry site tended to be higher when grown under extreme drying than under moderate drying, in contrast, there was no difference in plants from the wet site being grown under moderate drying or extreme drying when grown with their sympatric soil biota (Figure 2).

In both *B. gracilis* populations, the soil biota effect was positive for sympatric inoculum and negative for allopatric inoculum, and this effect was exacerbated in plants from the wet site grown in extreme drought (Figure 3). The dry site population exhibited a more positive response in sympatry and a less negative response in allopatry compared to the wet site population. There was no effect of drought treatment alone.

3.2 | Fungal responses

The biomass of microbial groups was similar in the initial soil inoculum from the wet and dry sites, as indicated by the PFLA and

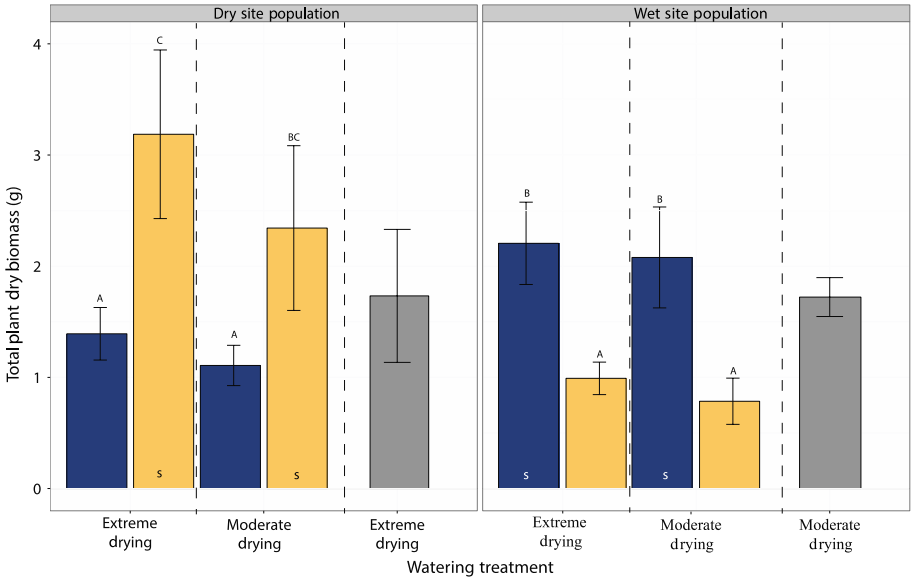

FIGURE 2 Total plant biomass in mesocosms at the termination of the experiment. Comparison of plants inoculated with soil biota from the dry site (lighter bars) and from the wet site (dark bars) grown under extreme and moderate drying treatments for 32 weeks. Plants grown with sterile inoculum are indicated by grey bars. Different letters within each figure indicate significant different means according to Tukey's HSD. The letter 's' in the bars represents sympatric pairings of plants and soil biota

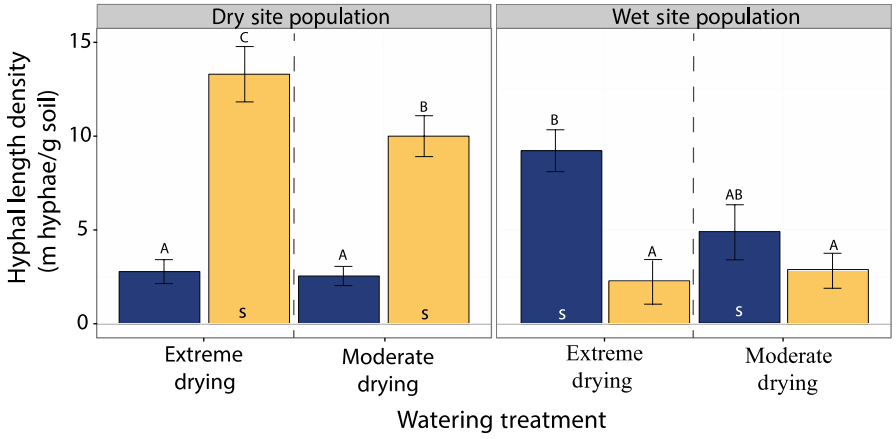

FIGURE 3 External hyphal length density at the end of the experiment in soils from mesocosms inoculated with soil biota from the dry site (lighter bars) and the wet site (dark bars) and grown under moderate and extreme drying treatments. Different letters within each figure indicate significant different means according to Tukey's HSD. The letter 's' in the bars represents sympatric pairings of plants and soil biota

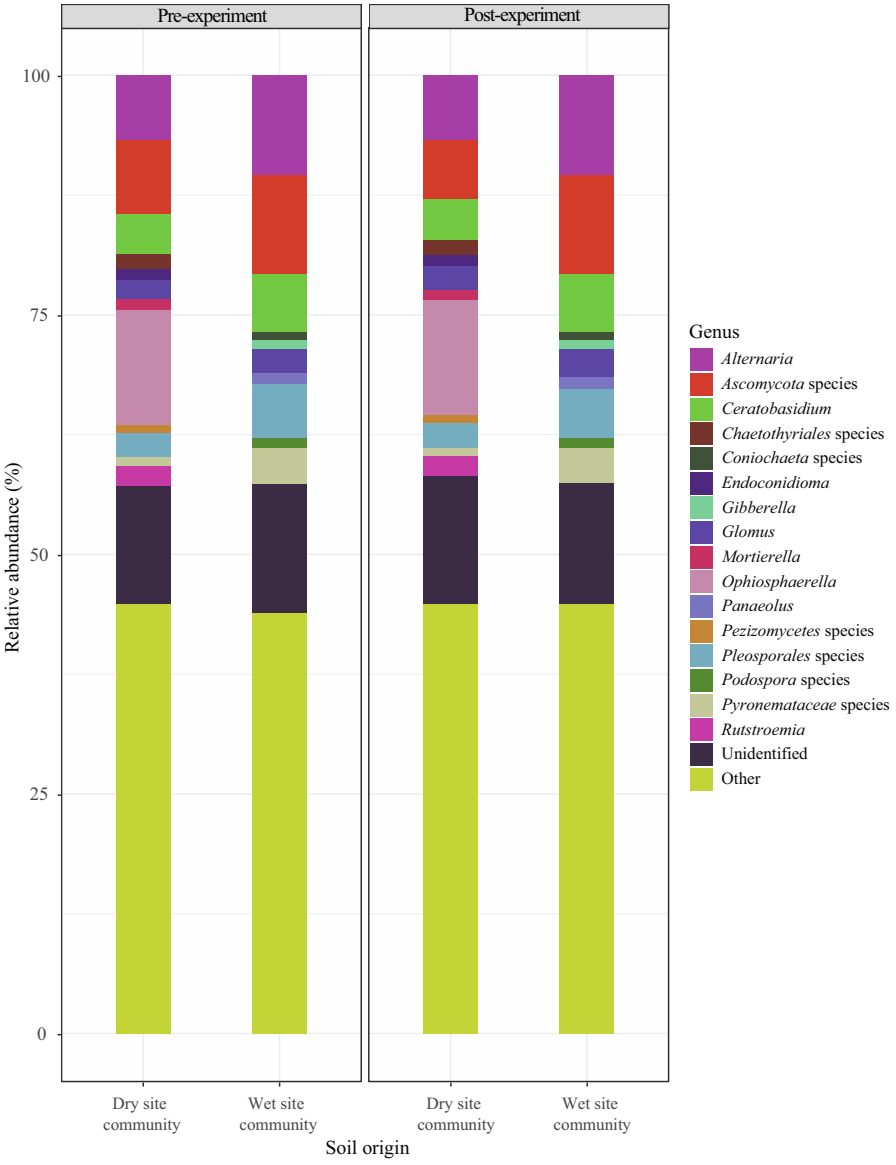

FIGURE 4 Relative abundance (%) of soil fungi based on sequencing of ITS general fungal primer WANDA amplicons in the soil inoculum before the experiment started (unalerted inoculum) and from the mesocosms at the termination of the experiment. Taxa with less than 1% abundance were grouped into the category 'other' and taxa that could not be matched to genus were labelled at the finest resolution that could be matched, or if they could not be matched to an order, they were labelled as 'Unidentified'

NFLA analysis (Supplemental Information Tables S1 and S2). In contrast, the composition of the fungal communities in the wet and dry soil inoculum was different, and these differences persisted from the beginning to the end of the experiment (Figures 4 and 5). The density of external AM fungal hyphae in the soil responded to watering treatment ($F = 10.49$, $p < 0.001$), plant origin ($F = 5.99$, $p = 0.017$) and provenance ($F = 13.65$, $p < 0.001$). Mesocosms with sympatric pairings of plants and soil inoculum consistently had more external AM fungal hyphae than allopatric ones ($F = 75.41$, $p < 0.001$). The highest density of external AM fungal hyphae was observed in mesocosms with both *B. gracilis* and soil inoculum from the dry site that were grown under the extreme drying treatment (Figure 3). Under the moderate drying treatment, sympatric pairs of plants and inoculum from the dry site population produced nearly two times more external hyphae than pairs from the wet site (Figure 3; Table S4).

Root colonization by different fungal structures was highly responsive to watering treatment ($F = 4.01$, $p = 0.04$), however,

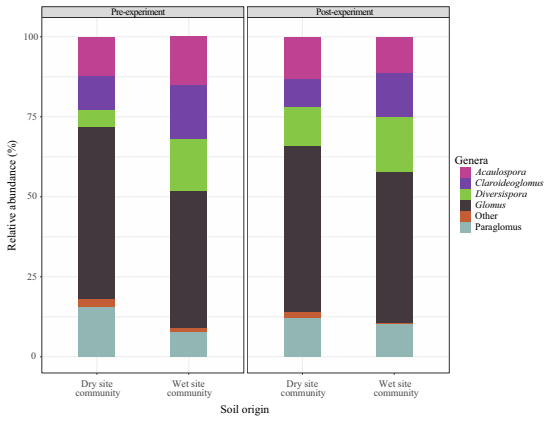

FIGURE 5 Relative abundance (%) of arbuscular mycorrhizal fungal genera based on sequencing of the small subunit of the rRNA gene in the soil inoculum before the experiment started (unalerted inoculum) and from the mesocosms at the termination of the experiment. Taxa with <1% abundance and taxa that could not be matched to genus were grouped into the category 'other'

not to provenance ($F = 0.61$, $p = 0.43$) or plant origin ($F = 0.04$, $p = 0.84$). Mycorrhizal fungal hyphae inside plant roots showed similar patterns as the hyphae outside plant roots with approximately 2.5× greater colonization in extreme drying treatments in sympatric pairings than in allopatric pairings in extreme drying (Figure 6). In general, there was 10% more root length colonized by hyphae in sympatric pairings regardless of drought treatment (Figure 3; Table S5). Furthermore, sympatric pairings had three to four times more arbuscular colonization compared to allopatric pairings in moderate and extreme drought respectively (Figure 6; Table S6). In contrast, vesicular colonization was more than twice as high in allopatric pairings compared to sympatric pairings. The highest colonization by fungal vesicles was observed in allopatric pairings of the wet population grown under extreme drying (Figure 6; Table S7). In the dry site *B. gracilis* population, provenance of the inoculum did not influence colonization by DSEs but in the wet site population it did, with significantly higher colonization in sympatric pairings (Figure 6; Table S8). There was a strong positive relationship between the soil biota effect and the abundance of external and internal hyphae and arbuscules, and a strong negative relationship with root length colonized by vesicles (Figure 7). There was no significant linear relationship between the soil biota effect and colonization by DSEs.

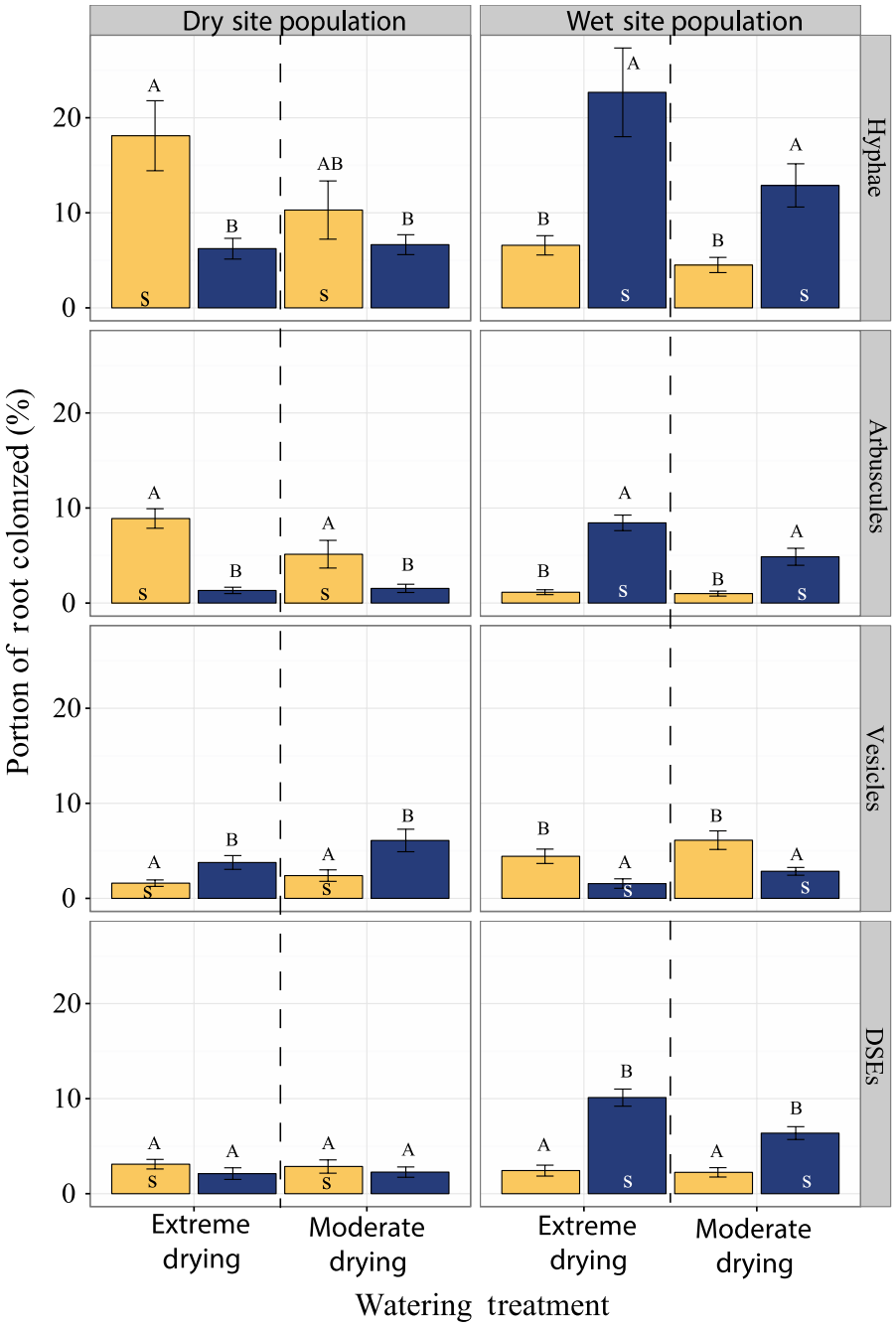

FIGURE 6 Percentage of plant root length colonized by hyphae, arbuscules, vesicles and dark septate endophytes (DSEs) in the dry site (light bars) and wet site (dark bars) populations of *Bouteloua gracilis* grown with extreme and moderate drying. Different letters within each figure indicate significant different means according to Tukey's HSD. The letter 's' in the bars represents sympatric pairings of plants and soil biota

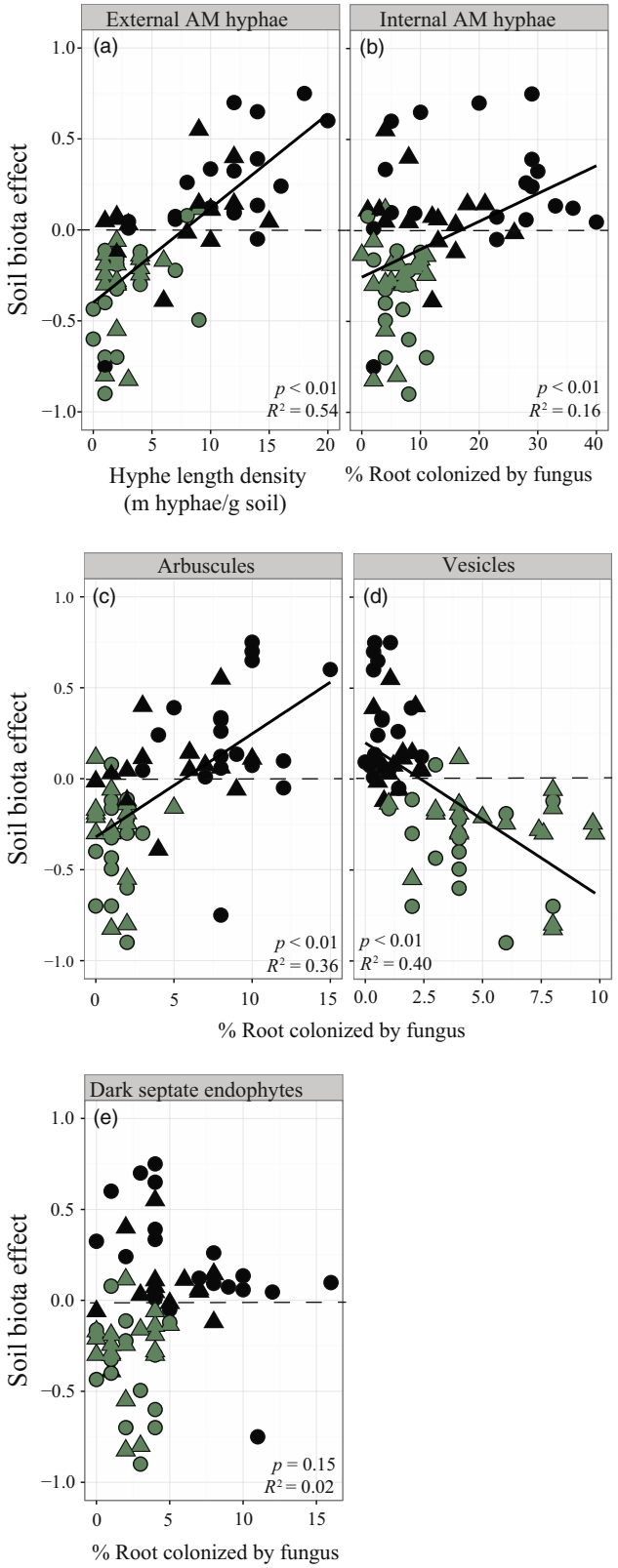

FIGURE 7 Soil biota effect plotted against external hyphal length density (m hyphae/ gram soil) (a), and per cent root length colonized by hyphae (b), arbuscules (c), vesicles (d), and dark septate endophytes (e). Dark symbols represent sympatric and light symbols represent allopatric pairings of plants and inoculum. Triangles represent the moderate drying treatment and circles represent the extreme drying treatment

4 | DISCUSSION

Our findings show evidence that success of *B. gracilis* is greatest in sympatric combinations of plants and their associated soil biota grown in the water regime under which they co-adapted. This suggests a gene × gene × environment interaction where the abiotic environment selects for specific phenotypes in multiple organisms (Hoeksema, 2010). When inoculated with sympatric soil organisms, the dry site population did best in terms of survival and height in the extreme drying and the wet site population survived longest and grew taller in the moderate drying treatment (Figure 1). In contrast, plants inoculated with allopatric soil biota performed similarly, or even worse, than plants grown with sterile inoculum, regardless of soil drying regime (Figure 1).

In contrast to height and survival, final biomass data supported the sympatric advantage hypothesis with no contingency on the environment (Figure 2). That biomass and survivorship exhibited different responses to drying treatments is not totally unexpected, as they are distinct facets of plant success; the largest or smallest plants are not always the most stress-tolerant. Height and biomass were expected to respond to our experiment similarly, but biomass was insensitive to drying treatment. *Bouteloua gracilis* generally grows in dense clumps with strong horizontal spread as opposed to predominately vertical growth, thus plants of similar height may have different biomasses.

4.1 | Environmental stress optimizes the sympatric advantage among plants and soil biota

Local adaptation in plants and soil micro-organisms has been shown to be driven by several abiotic factors such as climate (Hoeksema & Forde, 2008) and soil (Rúa et al., 2016), which are often linked to environmental stress. In our system, severe water limitation at the dry site may hypothetically have selected for sympatric soil biota that were more beneficial under extreme drying than moderate drying while sympatric soil biota from the wet site did not show this difference (Figure 8). The *B. gracilis* population from the dry site appears to have been selected for traits that best optimize the benefits of sympatric associations with soil biota and also minimize the detrimental effects of allopatric soil biota. Although both populations experienced growth depressions with allopatric soil biota, growth depression was significantly more negative in the population from the wet site (Figure 8).

One mechanism for the sympatric advantage is that antagonistic relationships are likely selected against (Hoeksema, 2010; Werner & Kiers, 2014). It is not known if antagonistic relationships are due primarily to the species composition of soil organisms, or the behaviours of different populations of the same plants and soil organisms. In either case, a longer shared history could reduce antagonism through either (a) increased abundance of mutualistic taxa at the expense of commensal or parasitic taxa (Bennett et al., 2017; Waller et al., 2016) or (b) altered gene frequencies or gene expression within either or both plant and microbial populations that enhance mutualistic behaviour (Hoeksema, 2010). An equally likely explanation of the sympatric

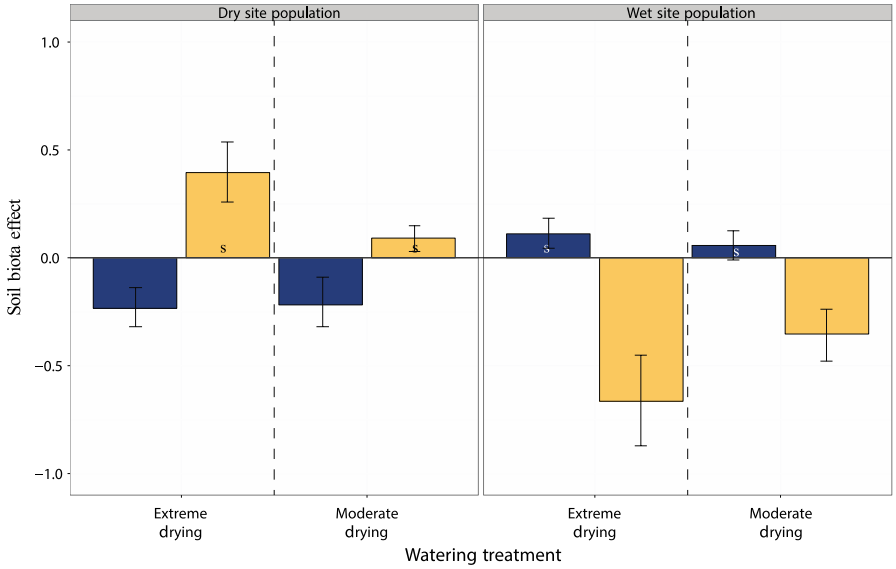

FIGURE 8 Soil biota effect for soil biota from the drier site (lighter bars) and soil biota from the wet site (dark bars) grown under moderate and extreme drying for wetsite and drysite plant populations. Error bars represent the 95% confidence interval for the soil biota effect. The letter 's' in the bars represents sympatric pairings of plants and soil biota

advantage is the positive selection of cooperative traits over many generations, reminiscent of the often highly specialized plant–pollinator interactions (Brundrett, 2002; Burdon & Thrall, 2009; Ehrlich & Raven, 1964). Such co-adaptation could hypothetically play out on a very local scale because one set of partners, the AM fungi and other soil organisms, are more dispersal-limited than their plant partners.

4.2 | Extension of the functional equilibrium model to water limitation

Plants allocate photosynthate to AM fungal symbionts as an alternative strategy to investment in roots for acquiring soil resources, and this may buffer against stress caused by either nutrient or water limitation (Almaghrabi et al., 2012; Augé et al., 2015; Bever et al., 2009; Ji & Bever, 2016; Westoby, 1998). Compared to allopatric combinations, sympatric pairings of plants and inoculum produced greater growth of external and internal AM hyphae and arbuscules, and less root colonization by vesicles (Figures 3 and 4). This result is important because hyphae and arbuscules are involved in the acquisition and exchange of soil resources between AM fungi and their host while vesicles are fungal storage units that have been associated with less mutualistic or even parasitic AM symbioses (Johnson & Grahm, 2013; Lekberg et al., 2010). The functional equilibrium model suggests that plants invest in structures that most effectively help them forage for the most limiting resource (Bloom et al., 1985). The observed shift in relative allocation between resource harvesting and exchange structures versus storage structures suggests that the functional equilibrium model may be applied to allocation to fungal structures in AM symbioses (Johnson et al., 2003).

Support for functional equilibrium in AM symbioses has been documented in nutrient-limited systems (Johnson, 2010). Results of this study support the assertion that a functional equilibrium between plants and associated mycorrhizal fungi may also exist in water-limited systems. It is well understood that AM fungi can alter the water balance of their host plants both directly and indirectly, thus it is logical that the functional equilibrium model can incorporate water as a soil resource (Augé, 2001; Augé et al., 2015). Mycorrhizal hyphae in the soil can act as hollow tubes that transport water directly from soil pores to plant root tissue (Allen et al., 1981; Hardie, 1985). While this topic has been debated over the years, recent experimental evidence supports this claim (Ruth et al., 2011). Alternatively, AM fungi alter plant water balance by variety of indirect means. First, by improving plant nutritional status, mycorrhizas increase plant size, and thus, can contribute to increased root surface area for plant uptake of soil water (Ruiz-Lozano & Azcón, 1995). In our experimental system, water is obviously in limiting supply, but because phosphorous availability is influenced by soil moisture, we cannot rule out the possibility that plants and fungi are allocating resources toward P-foraging, and as a side effect benefiting from enhanced water access. Mycorrhizal fungi also are known to alter the hormonal status of their plant hosts and this can help plants regulate stomatal closure during periods of soil drying (Augé et al., 2015). Lastly, AM fungi can alter hydraulic conductivity in the soil through increased surface area and soil exploration (Bárzana et al., 2012). Combined, these mechanisms can have a profound influence on plant water balance in mycorrhizal plants compared to non-mycorrhizal controls (Augé, 2001). These influences make soil water a direct or indirect resource in the economic market between plant hosts and their associated AM fungi. When soil water is limiting, the functional equilibrium model would suggest that plants and their associated mycorrhizal fungi would invest in structures that optimize the foraging of soil moisture. For a plant that is highly mycorrhizal, this likely means increased investment to external hyphae to explore a greater soil pore volume for soil moisture, as we observed in our study. If, however, a plant is less mycorrhizal or is growing in a soil environment with greater soil water content, plants may alternatively invest in fine root growth rather than in their fungal symbionts.

The whole-soil inoculum used in our study contained complex communities of soil organisms, consequently, our observed inoculum effects arise from the interactions of plants with many

soil-dwelling micro-organisms, not only AM fungi. Although we acknowledge the potential roles of unmeasured soil organisms, the strong correlations between mycorrhizal structures and plant responses suggest that AM fungi are important drivers of the observed co-adaptation dynamics. Also intriguing in our results were patterns of DSEs being more prevalent in sympatric pairings from the wet site, however, the abundance of DSEs was not correlated with plant responses. Although the functions of DSEs in natural ecosystems are still relatively poorly understood, studies suggest that they tend to be more abundant in warmer, drier ecosystems and that they may reduce the pathogenicity of oomyctes (Newsham, 2011; Tellenbach & Sieber, 2012). Also, research shows that DSEs have a positive impact on plant growth in the absence of nitrogen fertilizer (Newsham, 2011). Our results cannot discern the role DSEs played in tandem with mycorrhizal colonization in facilitating plant growth, but we cannot eliminate the possibility that DSE were contributors.

5 | CONCLUSIONS

Moving forward, the frontier of this line of inquiry will be to determine to what degree the sympatric advantage is due to resource availability and to better understand the roles of the complex microbial communities that comprise the microbiome of plants. It will be equally important to determine how generalizable these patterns are across the landscape, a goal that will require multiple sites and a distinct experimental design (Cahill et al., 2017; Gundale et al., 2017, 2019; Reinhart & Rinella, 2016). Additionally, this study demonstrates the importance of having intact native plants and their associated soil biota to support and maintain resilient grassland systems These findings support work from others that have demonstrated greater mutualistic function when plant–soil biota relationships are intact (Johnson et al., 2010), and supports the idea that restoration of soil biota in tandem with native plant materials can steer plant communities towards desired conditions more rapidly (Koziol et al., 2018; Wubs et al., 2016). Furthermore, Duell et al. (2019) demonstrate that plant–microbe interactions become more variable under temperature extremes that do not match warm-season grasses of native environmental conditions, which suggest that the positive effect of plant–soil feedback may buffer plant growth against environmental extremes. Our study shows how AM fungal allocation, either within species or across species in the community, varies in sympatric versus allopatric plant–mycorrhizal pairings and provides evidence that fungal allocation, at least in part, determines their function. This work provides the foundation for the integration of a diversity of techniques from transcriptomics to community genetics to better understand the complex ecology of plant interactions with soil organisms (Hungate et al., 2015). It is plausible that both population- and community-level forces are interacting to determine mycorrhizal allocation and function across resource gradients, and a better understanding of these determinants of fungal allocation is an intriguing next step. Some studies, including Remke, Hoang, et al. (2020), have demonstrated that these patterns are likely to persist when soil resources are limited, however, patterns dissipate when soil resources are more abundant. For arid regions that are water limited, severe water stress from warming temperatures or prolonged drought might increase the importance and benefit of sympatric mycorrhizal associations in the future (Remke, Hoang, et al., 2020).

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AUTHORS' CONTRIBUTIONS

M.J.R. conceptualized the experimental design, conducted the experiment, was the lead on statistical analysis and led the writing of the manuscript; J.W. helped conduct the experiment and collected many samples, recorded data and assisted with analysis; N.C.J. provided intellectual input to the design of the experiment and assisted in interpretation of results; M.W. contributed to the field design of the experiment; M.A.B. assisted in the analysis of data and contributed to the design of the project.

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DATA AVAILABILITY STATEMENT

Data from this manuscript are available at Dryad Digital Repository https://doi.org/10.5061/dryad.bvq83bk74 (Remke, Johnson, et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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