

RESEARCH ARTICLE

Sympatric soil biota mitigate a warmer-drier climate for *Bouteloua gracilis*

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Funding information

McIntire-Stennis Cooperative Forestry Research Program, Grant/Award Number: 2014-32100-06014; U.S. Bureau of Land Management, Grant/Award Number: L17AC00031

Abstract

Climate change is altering temperature and precipitation, resulting in widespread plant mortality and shifts in plant distributions. Plants growing in soil types with low water holding capacity may experience intensified effects of reduced water availability as a result of climate change. Furthermore, complex biotic interactions between plants and soil organisms may mitigate or exacerbate the effects of climate change. This 3-year field experiment observed the performance of *Bouteloua gracilis* ecotypes that were transplanted across an environmental gradient with either sympatric soil from the seed source location or allopatric soil from the location that plants were transplanted into. We also inoculated plants with either sympatric or allopatric soil biotic communities to test: (1) how changes in climate alone influence plant growth, (2) how soil types interact with climate to influence plant growth, and (3) the role of soil biota in mitigating plant migration to novel environments. As expected, plants moved to cooler-wetter sites exhibited enhanced growth; however, plants moved to warmer-drier sites responded variably depending on the provenance of their soil and inoculum. Soil and inoculum provenance had little influence on the performance of plants moved to cooler-wetter sites, but at warmer-drier sites they were important predictors of plant biomass, seed set, and specific leaf area. Specifically, transplants inoculated with their sympatric soil biota and grown in their sympatric soil were as large as or larger than reference plants grown at the seed source locations; however, individuals inoculated with allopatric soil biota were smaller than reference site individuals at warmer, drier sites. These findings demonstrate complicated plant responses to various aspects of environmental novelty where communities of soil organisms may help ameliorate stress. The belowground microbiome of plants should be considered to predict the responses of vegetation more accurately to climate change.

KEYWORDS

adaptation to climate change, allopatric, microbiome, plant migration, plant-soil feedback, provenance, sympatric

1 | INTRODUCTION

Plant populations are being confronted with emerging novel environments throughout the world. Climate change alters plants' abiotic environments in situ, by creating novel environments as warmer

temperatures and more variable precipitation patterns emerge in most regions (Kharin et al., 2013; Sillmann et al., 2013). Additionally, land use change, including land conversion to agricultural fields, challenges restoration efforts by altering soil conditions, including the community composition of soil biota (Koziol et al., 2021; Wubs

et al., 2016). One of the possible responses of plant populations to novel climates is dispersal to environments that are more like those they are adapted to (Aitken et al., 2008; Roberts & Hamann, 2016). Plant species distributions have already demonstrated an upward shift or “lean” in elevation in response to warming (Breshears et al., 2008; Feeley et al., 2011). However, as plants migrate upslope over generations, they may be exposed to novel abiotic and biotic soil factors that are unlike the evolutionary environment of their progenitors (Bucharova, 2017; Bucharova et al., 2016; Butterfield et al., 2016).

Plant populations in the process of shifting their distributions may experience similar climatic conditions but dissimilar edaphic conditions (Bowker et al., 2012; Hoopes & Hall, 2002; Sanderson et al., 2015). In many regions, a complex history of geological processes leads to a mosaic of widely different soil parent materials that change at scales ranging from meters to kilometers. Distinct parent materials give rise to soils with distinct physical and chemical properties. Novel edaphic environments are generated not only by changes in the abiotic soil environment but also by changes in the composition of soil biotic communities. Assisted plant migration and ecosystem restoration efforts rarely consider the roles of plant-associated microbes such as co-adapted symbionts and other biotic associates (Bagchi et al., 2014; Müller, Horstmeyer, et al., 2016; Müller, van Kleunen, & Dawson, 2016). Plant populations used in restoration and assisted migration efforts may need to establish interactions with communities of soil biota with which they have no history of co-occurrence. While the effects of novel climatic environments on plants are being widely explored, few studies are able to separate the relative influence of climate from the influence of both abiotic and biotic properties of the soil.

Plant populations may become strongly locally adapted to their environment and often perform best in climates and soil environments that resemble their evolutionary environment compared to novel environments (Byars et al., 2007; Pregitzer et al., 2010, 2013). The roles of soil biota in influencing plant growth are widely documented, ranging from beneficial effects of root symbionts such as mycorrhizal fungi, negative effects of pathogens, and a variety of influences arising from complex soil food webs (Johnson & Graham, 2013; Paz et al., 2015; Pineda et al., 2010; Smith et al., 2010). Plants and soil biota originating from the same environment generally interact in a more mutually beneficial way than plants interacting with novel soil biota (Gehring et al., 2017; Johnson et al., 2010; Koziol et al., 2021; Rúa et al., 2016). Evidence suggests that biotic interactions are often the product of coevolution, thus plants and their associated sympatric soil biota often perform better as a whole when the environment is most similar to that in which the interaction evolved (Brockhurst & Koskella, 2013; Hoeksema et al., 2010, 2018; Piculell et al., 2008; Rúa et al., 2016). Just as abiotic environmental factors are a selective agent in plant evolution, they may also be selective of the interactions among plants and soil biota.

Numerous soil organisms, including mycorrhizal fungi and plant growth promoting rhizobacteria, are known to offset environmental stress in plants (Revillini et al., 2016; Rubin et al., 2017; Sanchez-Díaz & Honrubia, 1994). These organisms are often the most beneficial when they help provide the most limiting resource in an ecosystem (Bárzana

et al., 2012; Ruiz-Lozano & Azcón, 1996; Ruth et al., 2011). This suggests that soil microbes may facilitate plant growth in novel environments where limiting resources such as water become more limiting; likewise, soil biota may be less important to plants in cases where the most limiting resource becomes less limiting such as cooling and wetting of previously water-limited regions (Revillini et al., 2016). Field studies that utilized environmental gradients of limiting resources and also manipulated the origin of soil biota are uncommon; however, some studies simulated environmental gradients in greenhouse trials or other controlled environments and demonstrated that the benefits of soil biota are greater in sympatric pairs of soil biota and plants that originate from the same site (Nuske et al., 2021; Remke et al., 2020).

We conducted a 3-year field experiment along an elevational gradient to study plant responses to novel environments. In our study system, water is generally considered a limiting resource, water availability covaries with elevation, and there are numerous abrupt edaphic boundaries, given the geologic diversity of the region. *Bouteloua gracilis* was chosen as our research plant because populations of this broadly distributed C₄ grass are documented to be locally adapted to their abiotic environments (Wood et al., 2015), and also because a recent greenhouse experiment demonstrated its local adaptation to its communities of mycorrhizal fungi and associated soil organisms by showing a strong mutualistic response to sympatric but not allopatric soil biota (Remke et al., 2020). Individuals from two populations of *B. gracilis* in the middle of the elevation gradient were grown from seed and then planted into four novel sites that were approximately 2 and 3°C warmer to simulate warming and 2 and 3°C cooler to simulate plant migration to cooler environments. Seedlings from the two *B. gracilis* populations were grown at all six sites (two source sites and four transplant sites) with all possible combinations of living soil organisms, hereafter referred to as inoculum, and soil. Sympatric biotic soil communities were generated when plants and inoculum were from the same site and allopatric biotic soil communities were generated when plants were grown with inoculum from the transplant sites. Likewise, sympatric soil conditions were those in which plants were grown in the same soil that the seed originated and allopatric soil conditions were generated when plants were grown in soils from the transplant site (Figure 1). This experimental design allowed us to simultaneously manipulate the biotic and abiotic components of soil across a climate change gradient to uncouple the relative importance of locally adapted soil biota to plant responses to novel environments. Plant shoot and root biomass, seed mass, and specific leaf area (SLA) were measured to assess the responses of plant growth, reproduction, and leaf morphology to interactions among climate, soil, and soil biota. Our experimental design specifically tests four hypotheses:

- H1** *Plant performance will increase when moved to cooler-wetter environments and decrease when moved to warmer-drier environments.*
- H2** *Plant performance will be higher in sympatric soil compared to allopatric soil.*

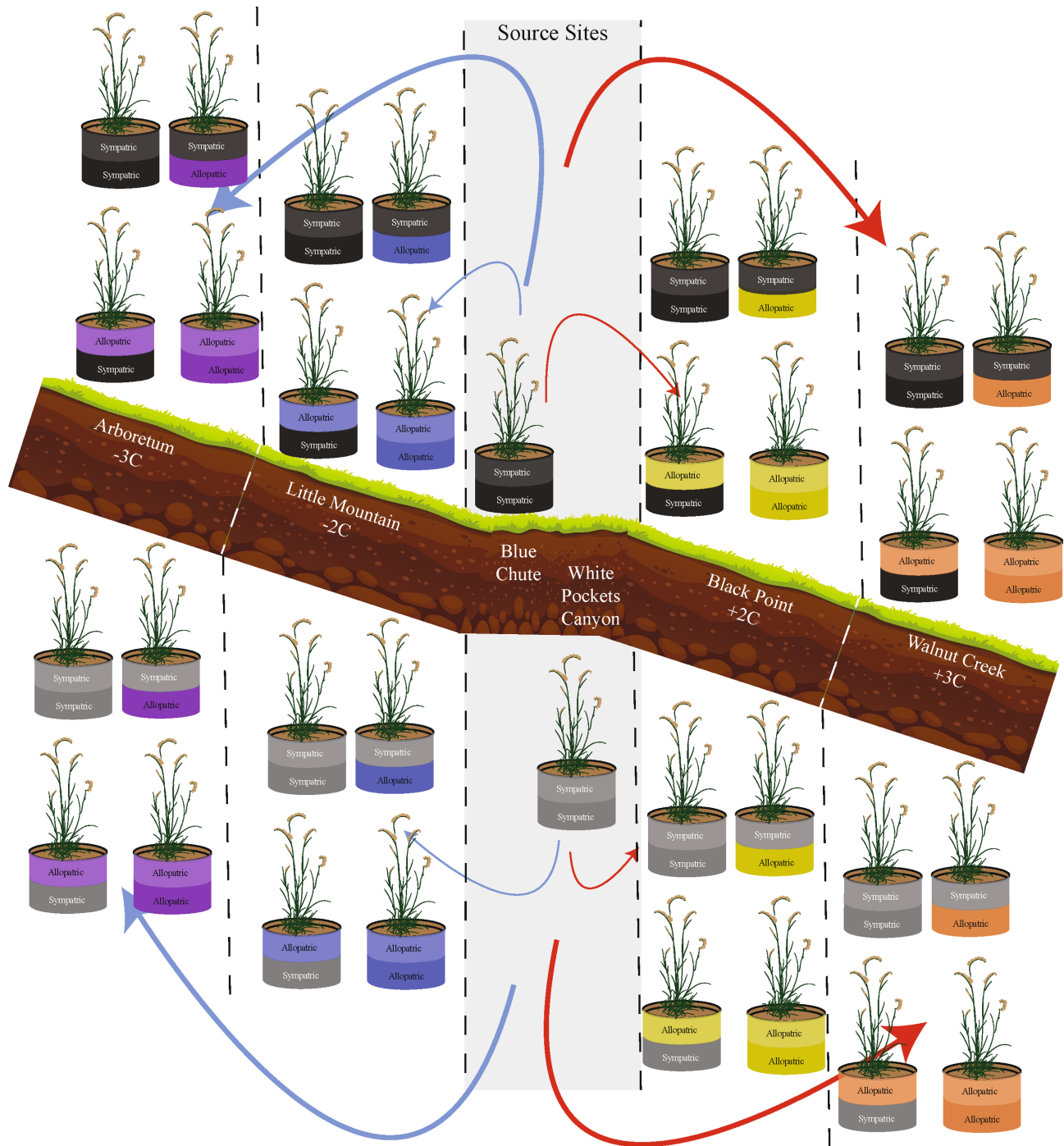


FIGURE 1 Conceptual diagram depicting the experimental design. The top half of the figure represents treatment units associated with the Blue Chute population where the bottom half represents treatment units associated with the White Pockets Canyon population. Each treatment unit consists of a plant and then the source of soil biota where sympatric soil biota are neutral colors (shades of gray) and allopatric colors are colored based on the site of which they came from. Sympatric soils represent darker shades of grey and allopatric soils are represented by darker shades of color for each site. There were 34 treatment combinations with 10 replicates each resulting in 340 treatment units. Soil inoculum was only 1 cm of live soil and was not equal to the amount of background soil used.

H3 Plant performance will be higher when inoculated with sympatric soil biota compared to allopatric biota, and this response will be observed in plants transplanted to warmer-drier environments but not in those transplanted to cooler-wetter environments.

H4 Plant performance will be highest when plants are simultaneously grown in sympatric soil and inoculated with sympatric soil biota, and this response will be observed in plants transplanted to warmer-drier environments but not in those transplanted to cooler-wetter environments.

These hypotheses expand on concepts outlined by the stress gradient hypothesis (Callaway et al., 2002), the microbe exacerbation-mitigation continuum (David et al., 2018), and the law of the minimum (Johnson et al., 2010). Importantly, in this region soil water tends to be a limiting resource, so this experiment functionally expands a drought experiment to a wider water availability gradient where we expect selection for soil microbial communities with increased mutualistic function at warmer-drier sites compared to cooler, wetter sites (Remke et al., 2021).

2 | MATERIALS AND METHODS

2.1 | Elevation gradient and collection of materials

This study was conducted at six different sites within the Southwest Experimental Garden Array (SEGA) (<https://sega.nau.edu/home>) in Northern Arizona, which is a collection of experimental sites situated across a climate gradient spanning 6°C. Detailed information about each site is listed in Table 1. Two sites in the middle of the gradient with abundant *B. gracilis*, Blue Chute (BC) and White Pockets Canyon (WPC), were selected as the source populations for seeds, thus allowing us to manipulate climate in both a warming and cooling direction. The BC and WPC seed sources represent two replicate populations of our study species. The Seeds of Success protocol (https://www.blm.gov/sites/blm.gov/files/program_nativeplants_collection_quick%20links_technical%20protocol.pdf) was used to collect seeds of *B. gracilis*. Soil was collected from the same two source sites to be used for the sympatric soil treatment, and from the four transplant sites to be used for the allopatric soil treatment (Figure 1; Table S1).

Live rhizosphere 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 two transplant

sites where *B. gracilis* was absent, live soil was collected from the rhizosphere of the dominant plant community of the site instead. Soil subsamples within each site were pooled together and mixed. We justify homogenizing inoculum from each site because we were interested in *B. gracilis* responses to the average soil biotic communities 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. At each sampling location, background soil was collected along the same three transects by carefully digging into bare soil away from plants at depths between 0 and 60 cm. Background soil within each site was homogenized and steam sterilized at 125°C twice for 24 h.

2.2 | Design and preparation of experimental units

We used Steuwe and Sons 7.8 L tree pots (model TP812) as experimental units. This pot size was selected to accommodate multiple years of growth of *B. gracilis* without getting pot-bound. Experimental units were planted into the two seed source sites to create sympatric reference plants or into the four possible transplant sites with warmer or cooler climates. Four combinations of soil and inoculum relative to each plant population and transplant site were generated (Figure 1). This design created three types of novel edaphic environments to compare to the fully sympatric reference plants and uncouple the abiotic and biotic components of the edaphic environment: sympatric inoculum and allopatric soil (SA), allopatric inoculum and sympatric soil (AS), and allopatric inoculum and allopatric soil (AA; Figure 1). Each treatment combination was replicated 10 times at each transplant site for each of the two plant populations, and 10 sympatric reference units were planted at the

TABLE 1 Detailed site descriptions for each study site including basic soil and climate information. All climate information is derived from PRISM Climate Group, Oregon State University

Site	Code	Source or transplant	Latitude	Longitude	Elevation (m)	Precipitation (mm)
Walnut Creek	WAL +3°C	Transplant	34.92	-112.84	1567	397
Black Point	BP +2°C	Transplant	35.68	-111.48	1566	152
Blue Chute	BC	Source reference	35.58	-111.97	1930	478
White Pockets Canyon	WPC	Source reference	36.61	-112.41	2057	443
Little Mountain	LM -2°C	Transplant	36.58	-112.36	2276	502
Arboretum	ARB -3°C	Transplant	35.16	-111.73	2179	556

two seed source sites. This resulted in 170 experimental units for each of the two *B. gracilis* populations and a total of 340 experimental units (Figure 1; Table S1).

Each experimental unit, was filled with 7.5 L of sterilized background soil and then covered with a 2 cm thick band (0.45 L) of living inoculum soil. *Bouteloua gracilis* seeds were sprinkled onto inoculum soil at a density of 20 seeds per pot and covered with 1 cm of sterilized background soil. Later, seedlings were thinned to one plant per mesocosm. Seedlings were grown in the greenhouse from November 2014 until late April 2015 under a standard nursery watering regime that maintained soil that was damp to the touch. This meant watering approximately every 48–72 h to ensure that the seedlings did not experience drought stress that could induce premature mortality.

The field experiment was initiated in early May, 2015 when 30 cm × 30 cm × 90 cm deep holes were dug in the ground at each transplant site and whole experimental units, including the pots, were placed into the holes without disturbing the plants or soils in the pots such that the soil level inside and outside of each pot was approximately equal. Pots were used in the field to maintain the mesocosm as a whole unit to ensure soil abiotic and biotic properties remained manipulated for the duration of the experiment. Removing the pot would have allowed roots to explore multiple soil types, confounding the soil variable of this experiment. At this point, plants were 6 months old and fairly similar in size. This age of plant had enough matured roots to withstand some stress by manipulating climates. This was the initiation of the novel climates with transplant sites that are approximately 2°C (BP) and 3°C (WAL) warmer, and 2°C (LM) and 3°C (ARB) cooler compared to the source sites (Figure 1; Table 1). Ten experimental units were similarly planted back into their site of origins at BC and WPC. These units represented the climate and sympatric soil and inoculum environments that the seed sources were adapted to and were used as a frame of

reference for all other treatments. All field plantings were completed on consecutive days.

2.3 | Measurements of plant performance

Plant performance was measured at the end of the third growing season in November 2017. At the time of harvest, some plant mortality had been observed and the experiment was harvested at a time where dead plants still had remaining aboveground biomass and decomposition had not yet begun. This allowed us to analyze biomass across all treatment units regardless of observed mortality in the field. Seeds were removed from plants whenever they were observed during the duration of the experiment, dried at 60°C for 24 h, and weighed. All remaining aboveground biomass was clipped, dried, and weighed. Soil was carefully cleaned from roots by soaking and wet sieving, and clean roots were dried and weighed.

SLA is the ratio of leaf area to leaf mass and it has been shown to decrease with drought stress in a variety of plant species (McCoy-Sulentic et al., 2017). Under drought conditions, plants tend to produce leaves with lower SLA to conserve resources. At the time of harvest, we collected green leaves to measure SLA using dry leaves as outlined in Garnier et al. (2001). All leaves were collected at 09:00 on the day of sampling and were rehydrated for 6 h in a dark room prior to measurements using WinRHIZO (Regent Instruments) to calculate leaf area.

2.4 | Statistical analysis

Four-way repeated measures ANOVA were used to compare the effects of climate (i.e. transplant site), plant origin, soil inoculum

Minimum annual temperature (°C)	Maximum annual temperature (°C)	Diffusion coefficient (cm ² s ⁻¹)	Soils	Soil parent material	Plant community	<i>Bouteloua gracilis</i> present at site
3	22	0.091	Agrids, sandy loam	Alluvial		Yes
5	21	0.091	Orthents, loamy sand	Basalt	Saltbrush shrubland	No
0.9	19	0.112	Ustalfs, clay loam	Basalt	Piñon-Juniper woodland	Yes
4.0	19.0	0.121	Agrids, gravelly loam	Limestone	Piñon-Juniper woodland	Yes
1	17	0.133	Ustolls, loam to gravelly clay loam	Limestone	Ponderosa pine forest	No
-1	16	0.126	Ustolls sandy clay loam	Basalt	Ponderosa pine forest	Yes

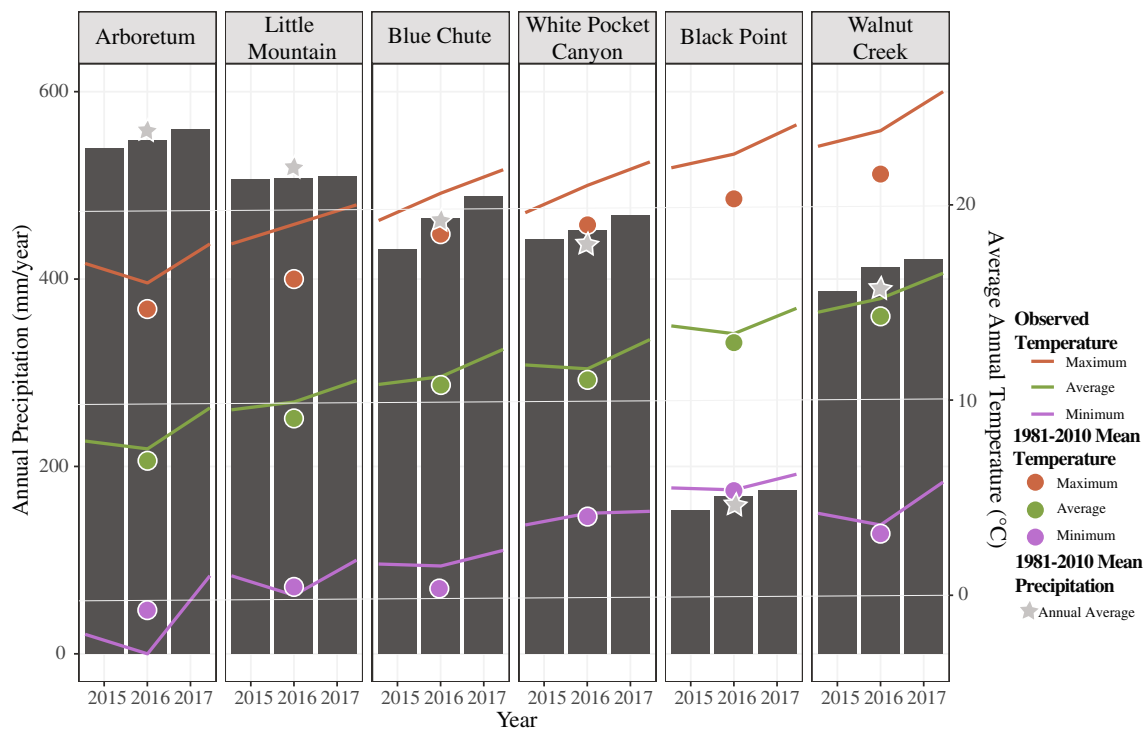


FIGURE 2 Observed and 1981–2010 average annual precipitation (mm) and temperature (°C) for the study period of 2015–2017. Red, green, and purple lines represent observed annual mean daily maximum, average, and minimum temperature, grey bars represent observed annual precipitation (mm). Red, green, and purple dots represent 1981–2010 average annual maximum, average, and minimum annual temperatures and grey stars represent 1981–2010 annual average precipitation.

origin, and soil origin on plant response variables. We used the four transplant sites as climate factors (i.e. +2, +3, -2, -3°C), the two plant populations for plant origin factors, sympatric versus allopatric soil biota for the soil inoculum factor and sympatric versus allopatric soil for the soil origin factor. All factors were included as fixed effect factors because we specifically selected these sites and controlled for these variables. This model was repeated for plant biomass, root:shoot ratio, SLA, and seed mass. The reference site was left out of the analysis to maintain a balanced design. 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). All data sets met all of the assumptions and no transformations were made. We compared mean and variation of each individual treatment combination to the reference site and other treatment combinations to detect overlapping 95% confidence intervals of each treatment to the all sympatric reference site. This approach utilized the reference site as a baseline and answers the question of whether plant performance varied with treatment. In each figure, if variance of individual treatments overlaps the variance of the fully sympatric reference site, then we conclude that there is no difference in plant performance for that variable. Specifically, if a treatment has reduced growth relative to the reference site, it indicates a negative effect of the treatment and if a treatment is greater than the reference site then the treatment had an advantageous effect. Data are publicly available in the data dryad online database (<https://doi.org/10.5061/dryad.gtht76hq9>).

3 | RESULTS

3.1 | Climate manipulations

During this 3-year study, the elevation gradient generated the desired temperature range. The two seed source sites had average temperatures of 12°C throughout the duration of the study and temperature increased by an average of 2.1 and 3.2°C, respectively, at the +2 and +3°C sites and decreased by an average of 1.8 and 2.8°C at the -2 and -3°C sites (Figure 2). Interestingly, all sites experienced slight increases in average annual temperature each incremental year of the 3-year study period. In general, warm sites had lower precipitation, however, the -2°C site was much drier than the -3°C site or any other site (Figure 2). Sites had near 30-year (1981–2010) average (PRISM) annual precipitation, and minimum and average mean daily temperature, but mean maximum daily temperature was higher during the study period compared to the 30-year average. We also calculated the diffusion coefficient of water vapor at each site based on average summer time temperature according to Smith and Geller (1979): there was a small range in the diffusion coefficient with slight increases at higher elevations.

3.2 | Plant biomass

Variance in total plant biomass was strongly related to site (proxy for climate; $F = 15.712$, $p < .0001$) and to interactions among many

TABLE 2 Summary of the ANOVA results for each factor and interaction terms between factors for all the response variables the model was repeated for. Only *p*-values are included to highlight patterns within the results, significance values of .05 were used to determine significant difference

Factor	Total biomass	Shoot biomass	Root biomass	Specific leaf area	Seed mass
Plant source	.294	.446	.307	.090	.216
Soil source	.244	.237	.493	.891	.640
Inoculum source	.146	.462	.066	.815	.232
Site	.000001	.000001	.000001	.013	.106
Plant×soil	.000001	.00081	.001	.892	.177
Plant×inoculum	.000001	.00014	.00001	.025	.725
Soil×inoculum	.000001	.000001	.000001	.055	.963
Inoculum×site	.000005	.00018	.00025	.355	.801
Plant×site	.0131	.0006	.0055	.157	.0087
Soil×site	.0258	.119	.502	.257	.754
Plant×soil×inoculum	.396	.318	.753	.928	.445
Plant×soil×site	.969	.577	.282	.030	.237
Plant×inoculum×site	.0478	.471	.0026	.810	.093
Soil×inoculum×site	.379	.042	.412	.350	.663
Plant×soil×inoculum×site	.388	.254	.788	.415	.034

of the experimental factors (Table 2, Table S2). Mean total biomass was highest at the cooler-wetter sites ARB and LM, and lowest at the warmer-drier sites BP and WC (Figure 3). There were several strong two-way interactions: soil×inoculum ($F = 26.9$, $p < .0001$), plant population×inoculum ($F = 21.5$, $p < .0001$), plant population×soil ($F = 15.9$, $p < .0001$), and inoculum×site ($F = 9.4$, $p < .0001$). These results indicate that the soil biota in the inoculum treatments function differently in different abiotic environments and in the two plant populations. Total biomass of plants grown at the two cooler-wetter sites were consistently as large or larger than the total biomass of the reference plants grown at the source sites. In contrast, total biomass of plants grown at the warmer-drier sites were only as large as the reference plants when they were grown in sympatric inoculum or both sympatric soil and inoculum (SA and SS in Figure 3). In one case, WPC population grown at BP, plants grown in allopatric inoculum and sympatric soil were as large as the reference plants.

Predictors of variance in root (Table S3) and shoot (Table S4) biomass generally mirrored the patterns for total biomass, except that the strongest predictor of root biomass was the soil×inoculum interaction ($F = 29.4$, $p < .0001$), and the strongest predictor of shoot biomass was the plant genotype×inoculum interaction ($F = 14.9$, $p < .0001$).

Interestingly, there were no significant treatment effects on root:shoot ratios (Table S5) suggesting that the biomass responses arise from differences in total biomass rather than preferential plant allocation to aboveground or belowground structures (Figure 3).

3.3 | Seed mass

There were no main effects of the treatments on cumulative seed mass; however, there was a significant plant×site interaction (Table 2, Table S5; $F = 3.94$, $p = .0087$). Also, there was a significant four-way plant×soil×inoculum×site interaction ($F = 4.40$, $p = .03$;

Figure 4; Table S6). Seed mass was not consistently higher in the cooler-wetter sites compared to the reference site. Seed mass of the BC population in the SA treatment at ARB and the WPC population in the SS treatment at LM were smaller compared to the reference. In contrast, at the hottest driest site (Walnut Creek, +3°C), seed mass met or exceeded the reference site in all of the treatments in the BC population and in all but the AA treatment in the WPC population (Figure 4).

3.4 | Specific leaf area

Site was the strongest predictor of SLA ($F = 7.0$, $p = .013$), followed by plant×inoculum ($F = 5.1$, $p = .025$), soil×inoculum interactions ($F = 3.7$, $p = .05$), and a three-way plant×soil×site interaction ($F = 3.0$, $p = .03$; Table 2, Table S7). In all cases, the SLA was larger in plants transplanted to cooler sites compared to the reference plants (Figure 5). At three of the four transplant sites, the SLA of plants grown in sympatric soil with sympatric inoculum had a similar SLA as the reference plants. The exception was BC plants growing at WC, the +3°C site, where all of the treatments had lower SLA compared to the reference plants.

4 | DISCUSSION

There is growing concern that climate change is altering environmental conditions to such an extent that many plants are becoming maladapted in their current geographic distribution, and they may be unable to disperse or adapt rapidly enough to keep pace with changing environmental conditions (Krause et al., 2015). To effectively address this concern, a more mechanistic understanding of the factors that influence plant performance in natural environments is

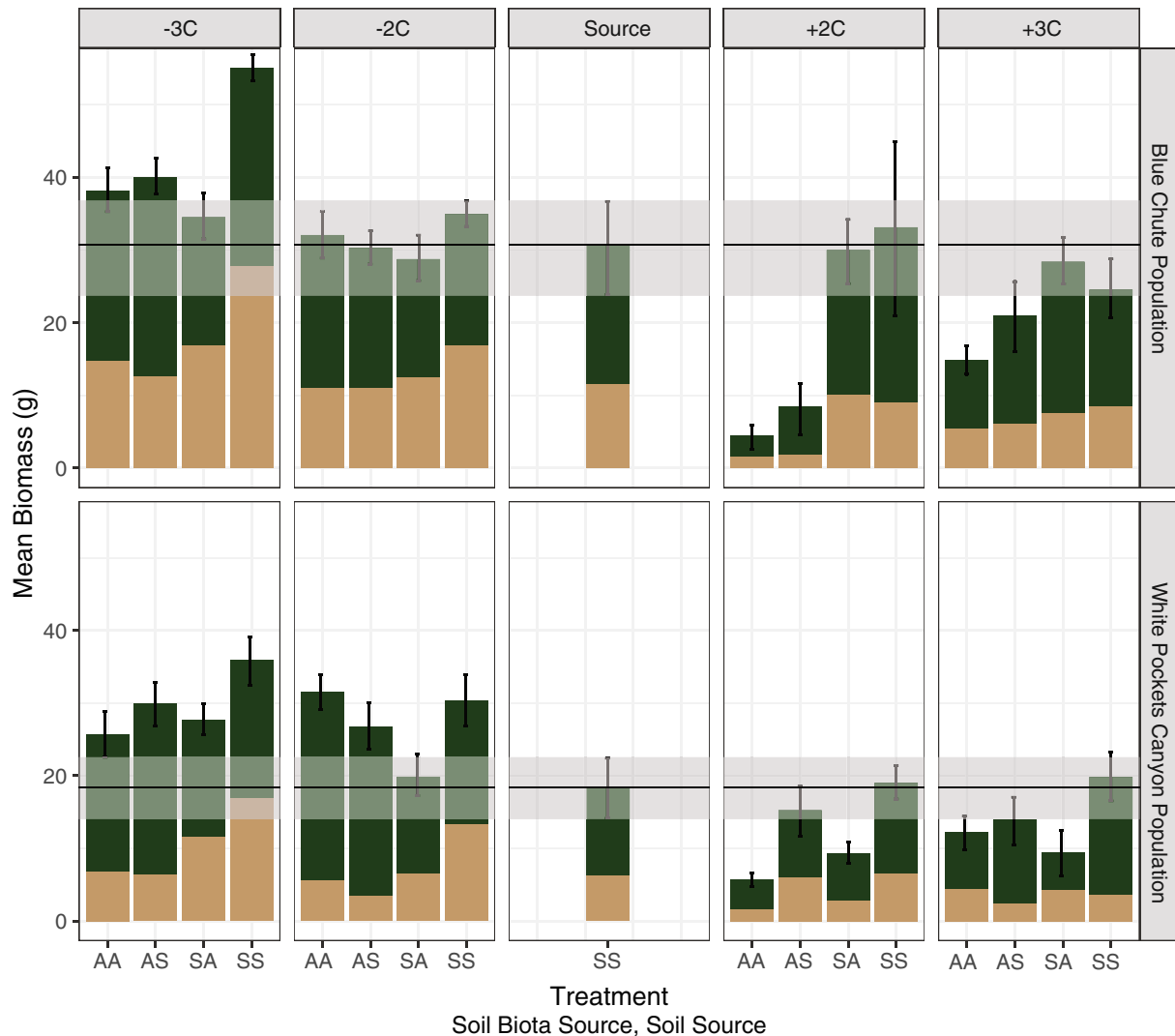


FIGURE 3 Mean total final biomass after 3 years of growth of two populations of *Bouteloua gracilis*. Dark green bars represent shoot biomass and light brown colors represent root biomass. AA represents allopatric inoculum and allopatric soil, AS represents allopatric inoculum and sympatric soil, SA represents sympatric inoculum and allopatric soil, and SS represents sympatric inoculum and sympatric soil. Black horizontal line represents the mean of the plants grown at the source site for baseline comparisons. Horizontal grey bars represent the 95% confidence interval of the reference site treatment, where black error bars represent 95% confidence intervals for each treatment.

required. Native plants are adapted to local climate as well as soil properties and biotic communities, and the direct and interactive effects of all these factors should be considered when developing protocols to address climate change (Bucharova, 2017). The factorial experimental design of our 3-year field experiment allowed us to uncouple the direct and interactive effects of climate, soil abiotic properties, and soil biotic communities on the performance of two populations of *B. gracilis*, a dominant C_4 grass species in North American rangelands. Reference plants grown at the site of their seed origin in their sympatric soil with sympatric biotic communities were used as the benchmark to compare with transplants that experienced a novel climate.

As predicted by our first hypothesis (H_1), regardless of soil or inoculum treatments, plants transplanted to cooler-wetter sites had higher total biomass and SLA than those transplanted to lower elevation warmer-drier sites (Figures 3 and 5; Table 2). This finding is

contrary to a recent meta-analysis of mostly mesic elevation gradients showing that plants transplanted to lower elevations generally experience less stress compared to plants moved to higher elevations (Midolo & Wellstein, 2020). This discrepancy likely reflects different limiting growth factors in our gradient compared to those that were included in the meta-analysis. Our elevation gradient is located in a prevailingly water-limited region. Upward transplantation on our gradient is likely to alleviate soil moisture limitation due to greater precipitation, but even more importantly, lower potential evapotranspiration due to cooler temperatures. In contrast, the gradients of Midolo and Wellstein (2020) were in mountains, mostly in more mesic regions than ours, where cold temperatures may become limiting at higher elevations, and where water-limitation is a lesser factor at lower elevations. We believe that downward transplantation to warmer and drier regions is a reasonable simulation of expected climate change in our region, wherein warming trends have

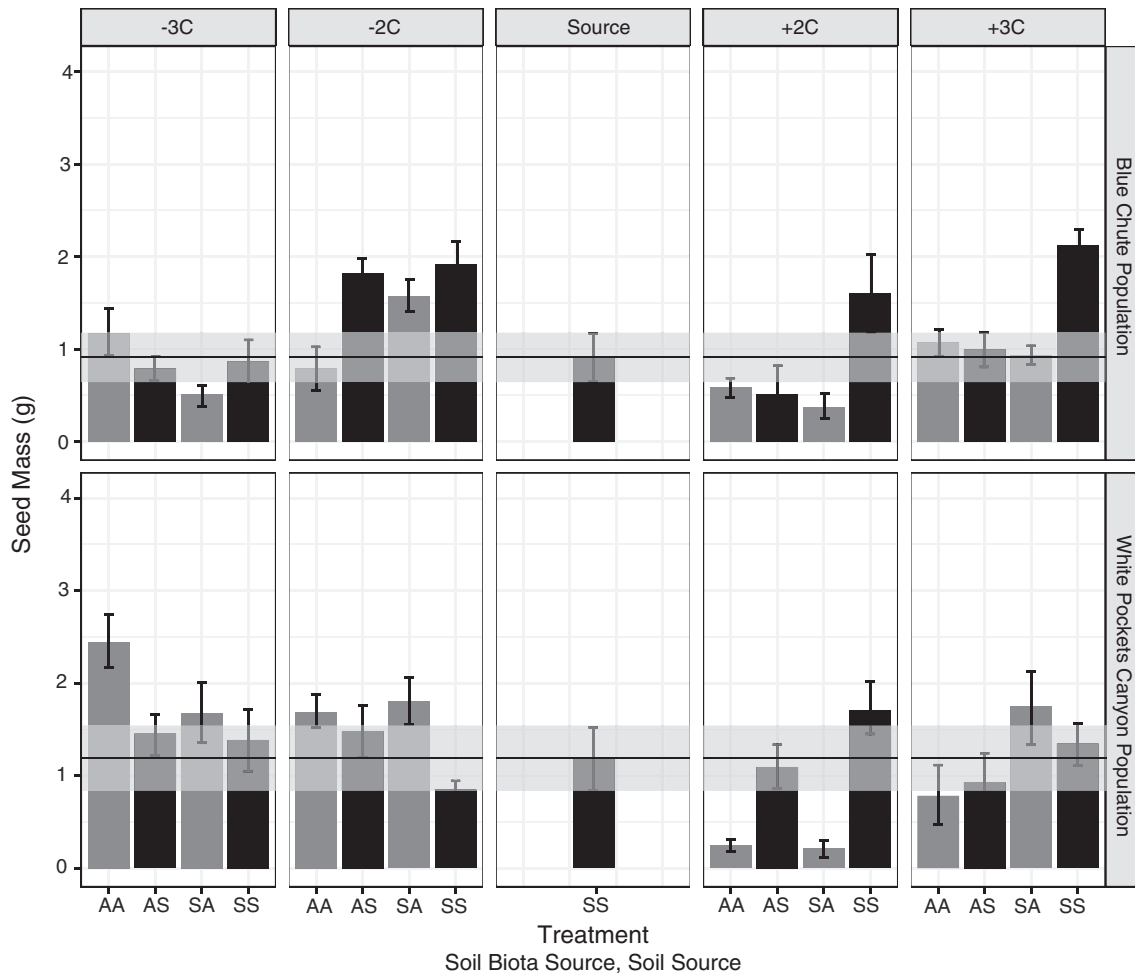


FIGURE 4 Total seed mass (g) produced for the 3-year study of *Bouteloua gracilis* for each study site and population. Dark colors represent plants grown in their sympatric soil and light colors represent plants grown in allopatric soil. AA represents allopatric inoculum and allopatric soil, AS represents allopatric inoculum and sympatric soil, SA represents sympatric inoculum and allopatric soil, and SS represents sympatric inoculum and sympatric soil. Black horizontal line represents the mean of the plants grown at the source site for baseline comparisons. Horizontal grey bars represent the 95% confidence interval of the reference site treatment, where black error bars represent 95% confidence intervals for each treatment.

already been a major driver of drought conditions and are projected to continue doing so (Gonzalez et al., 2018).

As global temperatures rise, due to climate change, plant populations will either adapt in situ, migrate to new locations via seed dispersal, go locally extinct, or be artificially migrated somewhere as either a climate mitigation strategy or augmented restoration strategy to avoid diminished growth and population viability. Natural migration or human-assisted movement may result in situations where plant materials cross edaphic boundaries and experience novel edaphic conditions. Numerous studies have demonstrated that plants are locally adapted to their soil environment (Fischer et al., 2014; Pregitzer et al., 2010; Rúa et al., 2016). Our second hypothesis (H_2) predicted superior plant performance in sympatric soils, but we observed no main effects of soil source. In contrast to our prediction that allopatric soils would reduce plant growth and fitness relative to sympatric soils, we found that only one soil, at the +2°C site, had significant negative effects on plant growth for one of the plant populations (Figure 5). Highly contingent interactive

effects of soil provenance with site, plant genotype, or both were the only lines of evidence that supported our second hypothesis, and in all other cases, evidence suggests that novel soils alone had minimal influence on plant growth. It is important to note that soils at the +2°C site are coarse-textured, poorly weathered and very well-drained orthents, and thus the soil effect could be related to soil water holding capacity (e.g., Bowker et al., 2012).

Beyond these highly contingent soil effects, we did find numerous cases where soil biota interactions strongly influenced plant growth. Similar to abiotic soil properties, there is evidence that plants are locally adapted to soil biota, including mycorrhizal fungi (Ji et al., 2013; Rúa et al., 2016). Plant microbiomes can either mitigate or exacerbate stress, but because antagonistic relationships would diminish the persistence of a plant species in stressful environments, plants with stress-mitigating microbiomes are expected to prevail over time (David et al., 2018). Our third hypothesis (H_3) predicted that we would detect superior performance of plants inoculated with sympatric compared to allopatric biota. Furthermore, H_3 predicted

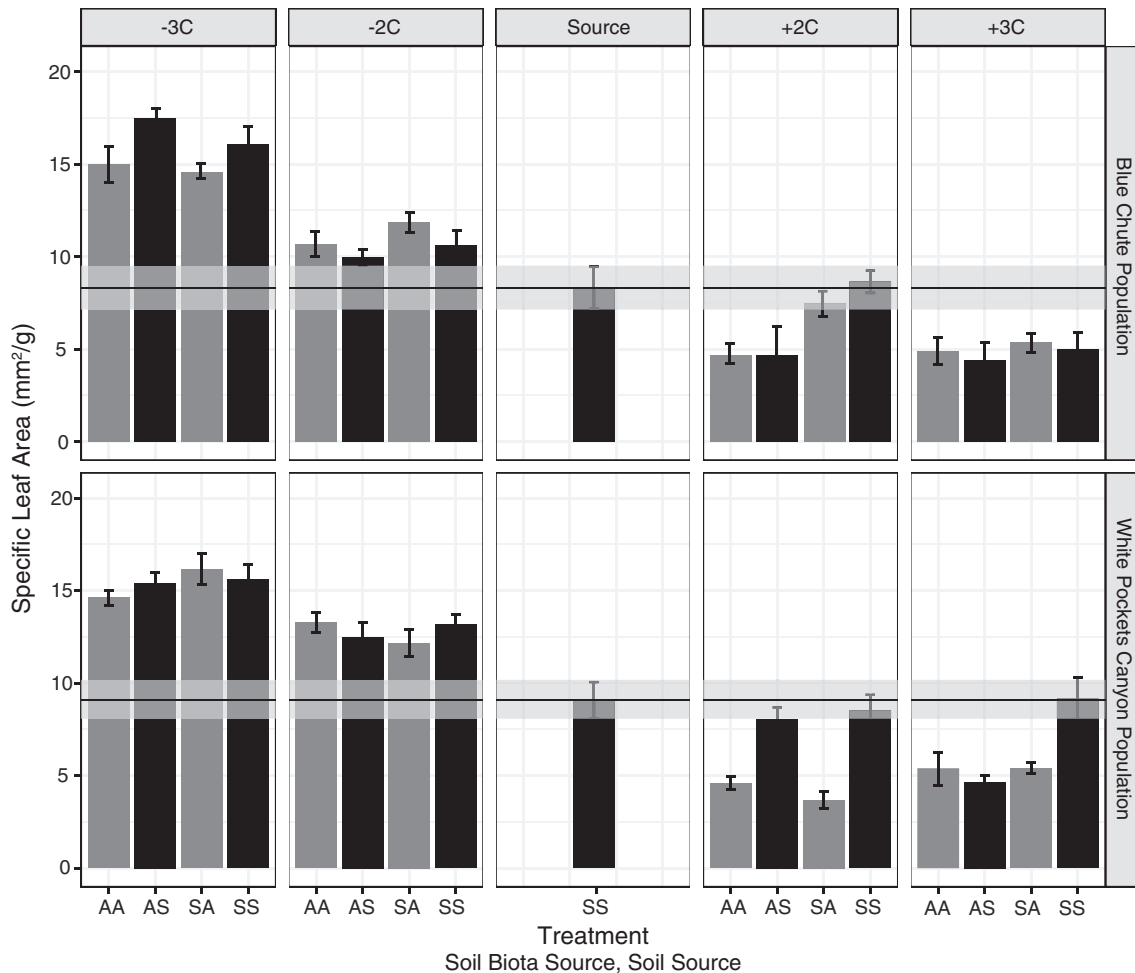


FIGURE 5 Specific leaf area ($\text{mm}^2 \text{g}^{-1}$) for *Bouteloua gracilis* for each study site and population. Dark colors represent plants grown in their sympatric soil and light colors represent plants grown in allopatic soil. AA represents allopatic inoculum and allopatic soil, AS represents allopatic inoculum and sympatric soil, SA represents sympatric inoculum and allopatic soil, and SS represents sympatric inoculum and sympatric soil. Black horizontal line represents the mean of the plants grown at the source site for baseline comparisons. Horizontal grey bars represent the 95% confidence interval of the reference site treatment, where black error bars represent 95% confidence intervals for each treatment.

that this would only be observed at the two warmer-drier environments where sympatric microbes would mitigate increased drought stress (Lubin et al., 2021; Remke et al., 2021; Revillini et al., 2016). In support of this hypothesis, there was a significant inoculum \times site interaction for plant biomass (but not SLA), and as expected, inoculum provenance was irrelevant for biomass gain in plants grown at the cooler-wetter sites, but it mattered for those grown at warmer-drier sites. However, at the two warmer-drier sites, there was not a consistent benefit of inoculum sympatry across both plant populations. Our findings demonstrate support evidence that biotic components of the environment can be a potential selection agent by influencing growth and fitness of plants, and also reveal that there are numerous interacting selection pressures in changing environments (van der Heijden et al., 2015). Significant interactions among the factors indicate that the influence of inoculum provenance on plant biomass is contingent on plant population, soil and climate.

Our hypothesis that sympatric soil and soil biota (H_4) combined would yield the greatest plant performance garnished the most

support. At warm-dry sites, plants grown with sympatric soil and soil biota were consistently among the largest and were always larger than plants grown with allopatic soil and soil biota. This generalization was also true for SLA in most cases. Further, one plant population experienced a >2 -fold boost in seed mass in both warm-dry sites, when grown in sympatric soil and inoculated with sympatric soil biota. The other plant population experienced enhanced seed production in one of the two warm-dry environments when grown with in sympatric soil and sympatric soil biota. This result suggests the potential for greater plant fitness when the biotic and abiotic elements of the plant's environment are kept intact, even as climate becomes more stressful. We observed additional support for this hypothesis even in cool-wet sites. In particular, plants of both populations grown at -3°C with sympatric soil and soil biota were larger than other treatments. The -3°C site is less stressful with regards to water availability but could be more stressful in different ways, like shorter growing seasons or colder temperatures. Our result may suggest that plant microbiomes also can mitigate these stresses, but

mainly in a soil environment like that of the source site. The interaction between biotic and abiotic components of soils could be among the strongest predictors of plant performance, and especially in a warmer-drier climate.

Overall, our findings support the microbial mitigation-exacerbation hypothesis (David et al., 2018; Revillini et al., 2016). These findings are consistent with a greenhouse study which demonstrated that during drought stress, sympatric plant-mycorrhizal pairings enhanced *B. gracilis* performance better than allopatric pairings (Remke et al., 2021). Other studies also show sympatric soil biota, including mycorrhizal fungi and rhizobacteria, can ameliorate drought stress on plants (Remke et al., 2020; Rubin et al., 2018). Since our study utilized whole soil inoculum, it is impossible to parse out which members of the soil microbial community are more active during drought treatments; however, subsequent molecular analysis shows consistent differences in the mycorrhizal fungal communities in our experimental *B. gracilis* that were inoculated with sympatric and allopatric soil biota, and that the original community in the inoculum was largely intact throughout the 3-year field experiment (Janouskova et al., *in review*). Specifically, the composition of the mycorrhizal fungal communities at the six sites differed from each other and diversity was higher in sympatric inoculum. Mycorrhizal fungal communities also differed in the two plant genotypes; but the composition of sympatric communities in both plant ecotypes was not significantly altered by transplantation alone. Only the combination of allopatric soil and transplantation to the two warmer sites was there a significant, but weak shift in the composition of the mycorrhizal fungal communities.

5 | CONCLUSIONS

Native plant populations are adapted to the physical, chemical, and biotic properties of their environment, and climate change may disrupt this adaptation (Anderson & Wadgymar, 2020). Plants and their sympatric soil biota may adapt to climatic novelty in situ, become maladapted to their original environment and go locally extinct, or migrate to new geographic locations with climatic conditions that match historical reference conditions. Migration may occur naturally or through human intervention (Vitt et al., 2016). Our findings suggest that interactions among plant traits, soil characteristics, and soil biota may influence the success of plant migration. Our 3-year field study demonstrates the importance of sympatric soil biota in facilitating growth of a late successional C_4 grass, *B. gracilis* in novel climatic conditions, which corroborates findings of a greenhouse study (Remke et al., 2021) and a field study involving *Pinus ponderosa* (Remke et al., 2020); however, there is likely variability across other plant species and functional groups. More field-based research is necessary to sufficiently understand these interactions. A recent study found no effect of inoculation of sympatric soil biota on the growth of *Pinus contorta* after two growing seasons (Wasyliw et al., 2022). This finding combined with other

studies implies that successional stage and plant functional groups could interact to determine the outcomes of inoculation (Wubs et al., 2016). Further, interactions with plants via competition or facilitation may also have indirect effects of soil biota on plant growth and may not be well captured in single species experiments (Lekberg et al., 2018). A better understanding of the many and complex interactions among plants and soil biota will enhance land management efforts where restoration of plant materials is necessary. Additionally, our study and others demonstrate complexities in controlled potted experiments, which help us articulate relevant ecological theory; however, to better translate these results to management actions, field trials of restoration applications of soil biota need to be initiated (i.e. Lubin et al., 2021; Wubs et al., 2016). The assisted migration of plant or soil microbial communities could also have unintended consequences by introducing new species or genetic material to an ecosystem and carries significant scientific uncertainty and also introduces challenging ethical considerations (Ahteensuu & Lehvävitra, 2014). Additionally, in circumstances where plants are exposed to novel microbial communities, it is important to understand the mechanisms of plant, or microbe mediated adaptation to novel biotic communities. Our study also focused on a widespread and abundant grass species: questions arise with plants that have restricted ranges such as narrow endemics, and of particular interest are the microbial communities associated with edaphic endemics. Nevertheless, a key takeaway from these studies is the conferred resistance to warming and drying offered by intact plant-soil biota interactions that suggests preservation of symbioses may result in higher resistance of plants to climate change compared to situations where these symbioses have been artificially severed.

ACKNOWLEDGMENTS

This work was supported by the McIntire-Stennis Cooperative Forestry Research Program (grant no. 2014-32100-06014/project accession no. 1001799) from the USDA National Institute of Food and Agriculture, and the Bureau of Land Management's Colorado Plateau Native Plants Program (Cooperative Agreement L17AC00031). MR was also supported by the NAU Genes to Environment extension of the NSF's IGERT program, Achievement Rewards for College Scientists (ARCS), and the ESA SEEDS program for supporting travel to conferences and excellent mentorship. We also thank Amy Whipple, Paul Henrich, Paul Flikkema, and all associated SEGA staff for site and technological maintenance. Phil Patterson provided endless support in germination and establishment of plants at the greenhouse. We also thank Katerina Smail and Tonny Hoang for support in site setup and takedown. Finally, numerous Grand Canyon Trust volunteers supported in project setup and data collection, and we thank the Grand Canyon Trust for research support through their volunteer program.

CONFLICT OF INTEREST

The authors have no conflict of interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at <https://doi.org/10.5061/dryad.gtht76hq9>.

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REFERENCES

- Ahteensuu, M., & Lehv virta, S. (2014). Assisted migration, risks and scientific uncertainty, and ethics: A comment on Albrecht et al.'s review paper. *Journal of Agricultural and Environmental Ethics*, 27, 471–477. <https://doi.org/10.1007/s10806-014-9493-z>
- Aitken, S. N., Yeaman, S., Holliday, J. A., Wang, T., & Curtis-McLane, S. (2008). Adaptation, migration or extirpation: Climate change outcomes for tree populations. *Evolutionary Applications*, 1, 95–111.
- Anderson, J. T., & Wadgyar, S. M. (2020). Climate change disrupts local adaptation and favours upslope migration. *Ecology Letters*, 23, 181–192. <https://doi.org/10.1111/ele.13427>
- Bagchi, R., Gallery, R. E., Gripenberg, S., Gurr, S. J., Narayan, L., Addis, C. E., Freckleton, R. P., & Lewis, O. T. (2014). Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature*, 506, 85–88.
- B rzana, G., Aroca, R., Paz, J., Chaumont, F., Martinez-Ballesta, M., Carvajal, M., & Ruiz-Lozano, J. (2012). Arbuscular mycorrhizal symbiosis increases relative apoplastic water flow in roots of the host plant under both well-watered and drought stress conditions. *Annals of Botany*, 109, 1009–1017.
- Bowker, M. A., Mu oz, A., Martinez, T., & Lau, M. K. (2012). Rare drought-induced mortality of juniper is enhanced by edaphic stressors and influenced by stand density. *Journal of Arid Environments*, 76, 9–16.
- Breshears, D. D., Huxman, T. E., Adams, H. D., Zou, C. B., & Davison, J. E. (2008). Vegetation synchronously leans upslope as climate warms. *Proceedings of the National Academy of Sciences*, 105, 11591–11592.
- Brockhurst, M. A., & Koskella, B. (2013). Experimental coevolution of species interactions. *Trends in Ecology & Evolution*, 28, 367–375.
- Bucharova, A. (2017). Assisted migration within species range ignores biotic interactions and lacks evidence. *Restoration Ecology*, 25, 14–18.
- Bucharova, A., Durka, W., Hermann, J., H lzel, N., Michalski, S., Kollmann, J., & Bossdorf, O. (2016). Plants adapted to warmer climate do not outperform regional plants during a natural heat wave. *Ecology and Evolution*, 6, 4160–4165.
- Butterfield, B. J., Copeland, S. M., Munson, S. M., Roybal, C. M., & Wood, T. E. (2016). Prestoration: Using species in restoration that will persist now and into the future. *Restoration Ecology*, 25, 55–63.
- Byars, S., Papst, W., & Hoffmann, A. (2007). Local adaptation and co-gradient selection in the alpine plant, *Poa hiemata*, along a narrow altitudinal gradient. *Evolution*, 61, 2925–2941.
- Callaway, R., Brooker, R., Choler, P., & Kikvidze, Z. (2002). Positive interactions among alpine plants increase with stress. *Nature*, 417, 844–848.
- David, A. S., Thapa-Magar, K. B., & Afkhami, M. E. (2018). Microbial mitigation–exacerbation continuum: A novel framework for microbiome effects on hosts in the face of stress. *Ecology*, 99, 517–523.
- Feeley, K. J., Silman, M. R., Bush, M. B., Farfan, W., Cabrera, K., Malhi, Y., Meir, P., Revilla, N., Quisilyupanqui, M., & Saatchi, S. (2011). Upslope migration of Andean trees. *Journal of Biogeography*, 38, 783–791.
- Fischer, D., Chapman, S., Classen, A., Gehring, C., Grady, K., Schweitzer, J., & Whitham, T. (2014). Plant genetic effects on soils under climate change. *Plant and Soil*, 379, 1–19.
- Garnier, E., Shipley, B., Roumet, C., & Laurent, G. (2001). A standardized protocol for the determination of specific leaf area and leaf dry matter content. *Functional Ecology*, 15, 688–695. <https://doi.org/10.1046/j.0269-8463.2001.00563.x>
- Gehring, C. A., Hultz, C., Flores-Renter a, L., Whipple, A. V., & Whitham, T. G. (2017). Tree genetics defines fungal partner communities that may confer drought tolerance. *Proceedings of the National Academy of Sciences*, 114, 11169–11174.
- Gonzalez, P., Garfin, G. M., Breshears, D. D., Brooks, K. M., Brown, H. E., Elias, E. H., Gunasekara, A., Huntly, N., Maldonado, J. K., Mantua, N. J., Margolis, H. G., McAfee, S., Middleton, B. R., & Udall, B. H. (2018). Southwest. In *Impacts, risks, and adaptation in the United States: Fourth National Climate Assessment, volume II* (pp. 1101–1184). U.S. Global Change Research Program. <https://doi.org/10.7930/NCA4.2018.CH25>
- Gundale, M. J., Wardle, D. A., Kardol, P., & Nilsson, M. C. (2019). Comparison of plant–soil feedback experimental approaches for testing soil biotic interactions among ecosystems. *New Phytologist*, 221, 577–587. <https://doi.org/10.1111/nph.15367>
- Gundale, M. J., Wardle, D. A., Kardol, P., Van der Putten, W. H., & Lucas, R. W. (2017). Soil handling methods should be selected based on research questions and goals. *New Phytologist*, 216, 18–23. <https://doi.org/10.1111/nph.14659>
- Hoeksema, J. D., Bever, J. D., Chakraborty, S., Chaudhary, B. V., Gardes, M., Gehring, C. A., Hart, M. M., Housworth, E., Kaonongbua, W., Klironomos, J. N., & Lajeunesse, M. J. (2018). Evolutionary history of plant hosts and fungal symbionts predicts the strength of mycorrhizal mutualism. *Communications Biology*, 1, 116.
- Hoeksema, J. D., Chaudhary, B. V., Gehring, C. A., Johnson, N., Karst, J., Koide, R. T., Pringle, A., Zabinski, C., Bever, J. D., Moore, J. C., Wilson, G. W., Klironomos, J. N., & Umbanhowar, J. (2010). A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecology Letters*, 13, 394–407.
- Hoopes, M. F., & Hall, L. M. (2002). Edaphic factors and competition affect pattern formation and invasion in a California grassland. *Ecological Applications*, 12, 24–39.
- Janoušková, M., Remke, M., Johnson, N. C., Jana, A. B., Kolariková, R. Z., & Bowker, M. A. (in review). Moving together: Effects of inoculation with sympatric soil microbes on the composition of arbuscular mycorrhizal fungal communities. *Mycorrhizae*.
- Ji, B., Gehring, C. A., Wilson, G. W. T., Miller, R. M., Flores-Renter a, L., & Johnson, N. C. (2013). Patterns of diversity and adaptation in Glomeromycota from three prairie grasslands. *Molecular Ecology*, 22, 2573–2587. <https://doi.org/10.1111/mec.12268>
- Johnson, N., & Graham, J. H. (2013). The continuum concept remains a useful framework for studying mycorrhizal functioning. *Plant and Soil*, 363, 411–419.
- Johnson, N., Wilson, G. W., Bowker, M. A., Wilson, J. A., & Miller, M. R. (2010). Resource limitation is a driver of local adaptation in mycorrhizal symbioses. *Proceedings of the National Academy of Sciences*, 107, 2093–2098.
- Kharin, V., Zwiers, F., Zhang, X., & Wehner, M. (2013). Changes in temperature and precipitation extremes in the CMIP5 ensemble. *Climatic Change*, 119, 345–357.
- Kozioł, L., Bauer, J. T., Duell, E. B., Hickman, K., House, G. L., Schultz, P. A., Tipton, A. G., Wilson, G. W. T., & Bever, J. D. (2021). Manipulating plant microbiomes in the field: Native mycorrhizae advance plant succession and improve native plant restoration. *Journal of Applied Ecology*, 59, 1976–1985. <https://doi.org/10.1111/1365-2664.14036>
- Krause, C. M., Cobb, N. S., & Pennington, D. D. (2015). Range shifts under future scenarios of climate change: Dispersal ability matters for Colorado Plateau endemic plants. *Natural Areas Journal*, 35, 428–438. <https://doi.org/10.3375/043.035.0306>
- Lekberg, Y., Bever, J. D., Bunn, R. A., Callaway, R. M., Hart, M. M., Kivlin, S. N., Klironomos, J., Larkin, B. G., Maron, J. L., Reinhart, K. O., Remke, M., & van der Putten, W. H. (2018). Relative importance of competition and plant–soil feedback, their synergy, context

- dependency and implications for coexistence. *Ecology Letters*, 21, 1268–1281. <https://doi.org/10.1111/ele.13093>
- Lubin, T. K., Alexander, H. M., & Bever, J. D. (2021). Adaptation of plant-mycorrhizal interactions to moisture availability in prairie restoration. *Restoration Ecology*, 29, 1–11. <https://doi.org/10.1111/rec.13270>
- McCoy-Sulentich, M. E., Kolb, T. E., Merritt, D. M., Palmquist, E., Ralston, B. E., Sarr, D. A., & Shafroth, P. B. (2017). Changes in community-level riparian plant traits over inundation gradients, Colorado River, Grand Canyon. *Wetlands*, 37, 635–646. <https://doi.org/10.1007/s13157-017-0895-3>
- Midolo, G., & Wellstein, C. (2020). Plant performance and survival across transplant experiments depend upon temperature and precipitation change along elevation. *Journal of Ecology*, 108, 2107–2210. <https://doi.org/10.1111/1365-2745.13387>
- Müller, G., Horstmeyer, L., Rönneburg, T., van Kleunen, M., & Dawson, W. (2016). Alien and native plant establishment in grassland communities is more strongly affected by disturbance than above- and below-ground enemies. *Journal of Ecology*, 104, 1233–1242.
- Müller, G., van Kleunen, M., & Dawson, W. (2016). Commonness and rarity of alien and native plant species – the relative roles of intraspecific competition and plant-soil feedback. *Oikos*, 125, 1458–1466.
- Nuske, S. J., Fajardo, A., Nu, M. A., Wardle, D. A., Nilsson, C., Kardol, P., Smith, J. E., Peltzer, D. A., Moyano, J., & Michael, J. (2021). Soil biotic and abiotic effects on seedling growth exhibit context-dependent interactions: Evidence from a multi-country experiment on *Pinus contorta* invasion. *New Phytologist*, 232(1), 303–317. <https://doi.org/10.1111/nph.17449>
- Paz, H., Pineda-García, F., & Pinzón-Pérez, L. F. (2015). Root depth and morphology in response to soil drought: Comparing ecological groups along the secondary succession in a tropical dry forest. *Oecologia*, 179, 551–561.
- Piculell, B. J., Hoeksema, J. D., & Thompson, J. N. (2008). Interactions of biotic and abiotic environmental factors in an ectomycorrhizal symbiosis, and the potential for selection mosaics. *BMC Biology*, 6, 1–11.
- Pineda, A., Zheng, S.-J., van Loon, J. J., Pieterse, C. M., & Dicke, M. (2010). Helping plants to deal with insects: The role of beneficial soil-borne microbes. *Trends in Plant Science*, 15, 507–514.
- Pregitzer, C. C., Bailey, J. K., Hart, S. C., & Schweitzer, J. A. (2010). Soils as agents of selection: Feedbacks between plants and soils alter seedling survival and performance. *Evolutionary Ecology*, 24, 1045–1059.
- Pregitzer, C. C., Bailey, J. K., & Schweitzer, J. A. (2013). Genetic by environment interactions affect plant-soil linkages. *Ecology and Evolution*, 3, 2322–2333.
- Remke, M. J., Hoang, T., Kolb, T., Gehring, C., Johnson, N. C., & Bowker, M. A. (2020). Familiar soil conditions help *Pinus ponderosa* seedlings cope with warming and drying climate. *Restoration Ecology*, 28, 1–11. <https://doi.org/10.1111/rec.13144>
- Remke, M. J., Johnson, N. C., Wright, J., Williamson, M., & Bowker, M. A. (2021). Sympatric pairings of dryland grass populations, mycorrhizal fungi, and associated soil biota enhance mutualism and ameliorate drought stress. *Journal of Ecology*, 109, 1210–1223. <https://doi.org/10.1111/1365-2745.13546>
- Revillini, D., Gehring, C. A., & Johnson, N. (2016). The role of locally adapted mycorrhizas and rhizobacteria in plant-soil feedback systems. *Functional Ecology*, 30, 1086–1098.
- Roberts, D. R., & Hamann, A. (2016). Climate refugia and migration requirements in complex landscapes. *Ecography*, 39, 1238–1246.
- Rúa, M. A., Antoninka, A., Antunes, P. M., Chaudhary, B. V., Gehring, C., Lamit, L. J., Piculell, B. J., Bever, J. D., Zabinski, C., Meadow, J. F., Lajeunesse, M. J., Milligan, B. G., Karst, J., & Hoeksema, J. D. (2016). Home-field advantage? Evidence of local adaptation among plants, soil, and arbuscular mycorrhizal fungi through meta-analysis. *BMC Evolutionary Biology*, 16, 122.
- Rubin, R. L., Koch, G. W., Martinez, A., Mau, R. L., Bowker, M. A., & Hungate, B. A. (2018). Developing climate-smart restoration: Can plant microbiomes be hardened against heat waves? *Ecological Applications*, 28, 1594–1605. <https://doi.org/10.1002/eap.1763>
- Rubin, R. L., van Groenigen, K., & Hungate, B. A. (2017). Plant growth promoting rhizobacteria are more effective under drought: A meta-analysis. *Plant and Soil*, 416, 309–323.
- Ruiz-Lozano, J., & Azcón, R. (1996). Mycorrhizal colonization and drought stress as factors affecting nitrate reductase activity in lettuce plants. *Agriculture, Ecosystems & Environment*, 60, 175–181.
- Ruth, B., Khalvati, M., & Schmidhalter, U. (2011). Quantification of mycorrhizal water uptake via high-resolution on-line water content sensors. *Plant and Soil*, 342, 459–468.
- Sanchez-Díaz, M., & Honrubia, M. (1994). Impact of arbuscular mycorrhizas on sustainable agriculture and natural ecosystems. *Ecology*, 24, 167–178.
- Sanderson, L. A., Day, N. J., & Antunes, P. M. (2015). Edaphic factors and feedback do not limit range expansion of an exotic invasive plant. *Plant Ecology*, 216, 133–141.
- Sillmann, J., Kharin, V., Zhang, X., Zwiers, F., & Bronaugh, D. (2013). Climate extremes indices in the CMIP5 multimodel ensemble: Part 1. Model evaluation in the present climate. *Journal of Geophysical Research: Atmospheres*, 118, 1716–1733.
- Smith, S. E., Facelli, E., Pope, S., & Smith, A. F. (2010). Plant performance in stressful environments: Interpreting new and established knowledge of the roles of arbuscular mycorrhizas. *Plant and Soil*, 326, 3–20.
- Smith, W., & Geller, G. (1979). Plant transpiration at high elevations: Theory, field measurements, and comparisons with desert plants. *Oecologia*, 41(1), 109–122.
- van der Heijden, M. G. A., Martin, F. M., Selosse, M.-A. A., & Sanders, I. R. (2015). Mycorrhizal ecology and evolution: The past, the present, and the future. *New Phytologist*, 205, 1406–1423. <https://doi.org/10.1111/nph.13288>
- Vitt, P., Belmaric, P. N., Book, R., & Curran, M. (2016). Assisted migration as a climate change adaptation strategy: Lessons from restoration and plant reintroductions. *Israel Journal of Plant Sciences*, 63, 250–261. <https://doi.org/10.1080/07929978.2016.1258258>
- Wasyliw, J., Fellrath, E. G., Pec, G. J., Cale, J. A., Franklin, J., Thomasson, C., Erbilgin, N., & Karst, J. (2022). Soil inoculation of lodgepole pine seedlings alters root-associated fungal communities but does not improve seedling performance in beetle-killed pine stands. *Restoration Ecology*, 1–10. <https://doi.org/10.1111/rec.13663>
- Wood, T. E., Doherty, K., & Padgett, W. (2015). Development of native plant materials for restoration and rehabilitation of Colorado Plateau ecosystems. *Natural Areas Journal*, 34, 134–150.
- Wubs, J. E., van der Putten, W. H., Bosch, M., & Bezemer, M. T. (2016). Soil inoculation steers restoration of terrestrial ecosystems. *Nature Plants*, 2, 16107.

SUPPORTING INFORMATION

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

How to cite this article: Remke, M. J., Johnson, N. C., & Bowker, M. A. (2022). Sympatric soil biota mitigate a warmer-drier climate for *Bouteloua gracilis*. *Global Change Biology*, 00, 1–13. <https://doi.org/10.1111/gcb.16369>