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Plant responses to soil biota depend on precipitation history, plant diversity, and productivity

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Abstract

Soil biota are critical drivers of plant growth, population dynamics, and community structure and thus have wide-ranging effects on ecosystem function. Interactions between plants and soil biota are complex, however, and can depend on the diversity and productivity of the plant community and environmental conditions. Plant–soil biota interactions may be especially important during stressful periods, such as drought, when plants can gain great benefits from beneficial biota but may be susceptible to antagonists. How soil biota respond to drought is also important and can influence plant growth following drought and leave legacies that affect future plant responses to soil biota and further drought. To explore how drought legacies and plant community context influence plant growth responses to soil biota and further drought, we collected soils from 12 grasslands varying in plant diversity and productivity where precipitation was experimentally reduced. We used these soils as inoculum in a growth chamber experiment testing how precipitation history (ambient or reduced) and soil biota (live or sterile soil inoculum) mediate plant growth and drought responses within an experimental plant community. We also tested whether these responses differed with the diversity and productivity of the community where the soil was collected. Plant growth responses to soil biota were positive when inoculated with soils from less diverse and productive plant communities and became negative as the diversity and productivity of the conditioning community increased. At low diversity, however, positive soil biota effects on plant growth were eliminated if precipitation had been reduced in the field, suggesting that diversity loss may heighten climate change sensitivity. Differences among species within the experimental community in their responses to soil biota and drought suggest that species benefitting from less drought sensitive soil biota may be able to compensate for some of this loss of productivity. Regardless of the plant species and soil origin, further drought eliminated any effects of soil biota on plant growth. Consequently, soil biota may be unable to buffer the effects of drought on primary productivity or other ecosystem functions as extreme events increase in frequency.

KEYWORDS
bacteria, community structure, drought, extreme events, global climate change, grasses and grasslands, legacy effects, mycorrhizas, pathogens, soil microbes, species richness, stability

INTRODUCTION

In a changing climate, the diversity and functioning of ecological communities will depend on their ability to withstand those changes, including an increasing frequency and severity of droughts for many regions (Harrison & LaForgia, 2019; Ukkola et al., 2020; Zhang et al., 2019). Community responses will depend on the tolerances of the individual species within those communities and of the other organisms with which they interact (Allison & Goulden, 2017; Harrison & LaForgia, 2019; Stone et al., 2010). For plants, some of the most important interactions are with soil biota, which can negatively or positively affect their growth and, through strong effects on seedling growth, their fitness (Bever et al., 2012). The reverse is also true, however, as soil biota communities are shaped by the current and previous generations of plants growing in that soil (Fitzpatrick et al., 2018; Wubs & Bezemer, 2018). The specificity of the responses of both plants and soil biota to these interactions means that they can be important drivers of plant population dynamics and, consequently, plant diversity and ecosystem functioning (Klironomos, 2002; Yang et al., 2018). Both plants and soil biota, however, are sensitive to environmental changes, including drought (Allison & Martiny, 2008; Revillini et al., 2016; Smith et al., 2010). As such, plant responses to soil biota (hereafter soil biota responses or SBR) and the associated broader ecosystem effects may depend on the plant community as well as any current and legacy effects of drought mediated through the soil (Bennett & Klironomos, 2019; van der Putten et al., 2016; Wubs & Bezemer, 2018).

Drought effects on plant growth may be linked to certain microbial groups, like arbuscular mycorrhizal fungi or plant growth promoting bacteria (Revillini et al., 2016), yet these soil biota also vary extensively in their responses to drought (De Vries & Shade, 2013; Fuchslueger et al., 2016; Lozano et al., 2021; Schimel, 2018). Consequently, previous droughts may have a lasting effect on the soil biome potentially resulting in decreased growth and increased mortality in response to future drought and thus altering plant community dynamics (Kaisermann et al., 2017; Nguyen et al., 2018; Wilschut & van Kleunen, 2021). A recent meta-analysis suggests that drought may enhance the benefits plants receive from soil biota (Beals et al., 2020), although the ubiquity of such changes is uncertain as drought effects likely depend on the composition of both the plant community and soil biome (Beals et al., 2020; Kaisermann et al., 2017; Lozano et al., 2021; Rasmussen et al., 2020).

Plant diversity has been highlighted as a key driver of multiple ecosystem processes, including driving the assembly of the soil biome and its response to drought (Bennett et al., 2020; Chen et al., 2019). Diverse plant communities often have more beneficial biota, fewer antagonistic biota, and a higher fungi to bacteria ratio, which can enhance nutrient retention (Bennett et al., 2020; Maron et al., 2011; Schnitzer et al., 2011; Waring et al., 2013). Consequently, soil biota from diverse plant communities are thought to promote plant growth. Further, diverse plant communities can have more drought tolerant soil biomes that may improve plant growth following drought (Bennett et al., 2020), although the mechanism remains unclear. Nonetheless, this suggests that SBRs should become more positive as plant diversity increases and be less affected by drought legacies, especially in drought stressed systems.

Plant productivity may also influence soil biota and thus plant SBRs. Productive communities may contain fewer beneficial biota, such as arbuscular mycorrhizal fungi, as they are less necessary when soil resources are not limiting (Johnson, 2010). Pathogens may also become more abundant as the fast-growing species typical of productive environments allocate fewer resources towards defense (Reich, 2014). Consequently, soil biota from productive communities should reduce plant growth relative to biota from less productive communities. How these interactions affect soil community responses to drought is unclear; however, productive plant and microbial communities may be less well adapted to drought (Ochoa-Hueso et al., 2018; Paruelo et al., 1999; Schimel, 2018). A history of reduced precipitation may thus have stronger effects on soil biota from productive areas thus reducing negative effects of soil biota on plant growth. Soils from unproductive communities are likely to be resistant to drought, especially if productivity is water limited (Schimel, 2018). These soils also tend to contain microbes promoting plant drought tolerance and may thus increase plant growth during and after drought (Bennett & Klironomos, 2019; Revillini et al., 2016).

Plant responses to soil biota are often dependent on the plant species as well as the environmental and community contexts (Baxendale et al., 2014; Bennett & Klironomos, 2019; Harrison & Bardgett 2010). Different components of plant communities therefore likely will possess divergent responses to drought and drought-conditioned soil biota, which may complicate predictions of drought effects on community structure and function (Batbaatar et al., 2021; van der Putten et al., 2016). Understanding how drought affects SBRs and the consequences for plant communities therefore requires studying how these factors alter plant survival and growth within a community context.

To explore how plant diversity and productivity alter SBRs and whether these SBRs differ with precipitation history and current drought, we conducted a two-phased experiment. In the first phase, we experimentally reduced precipitation in the field using rain-out shelters (hereafter “precipitation history”) deployed in 12 Canadian grasslands belonging to an international drought experiment (DroughtNet). For the second phase of this experiment, we collected soils from both ambient and reduced precipitation plots to test whether precipitation history altered SBRs in a growth chamber experiment. We seeded pots with five common grassland plant species and inoculated them with a small amount of either live or sterilized field soil, using the difference as an indicator of SBRs (Brinkman et al., 2010). Additionally, we subjected half the pots in the growth chamber experiment to a drought episode to determine how precipitation history and soil biota affected plant growth responses to drought. As the grassland sites used vary naturally in plant species richness (4.0–18.0 species/m^2) and productivity (33.6–492.3 g/m^2), we also tested whether precipitation history, SBRs, and their effect on plant drought responses differed with species richness and productivity among sites. We hypothesized (see Appendix S1: Figure S1 for a graphical depiction):

1. When fully watered, soils from diverse plant communities would promote positive SBRs overall while minimizing any drought legacies relative to soils from less diverse communities.
2. Under drought, soils from diverse communities would improve plant growth responses to drought relative to soils from less diverse communities, thereby strengthening the positive relationship between diversity and SBRs.
3. When fully watered, plant productivity would be negatively associated with SBRs overall but that the negative feedbacks at high productivity would be neutralized by drought legacies.
4. Under drought, soil biota from unproductive communities would enhance plant growth irrespective of any drought legacy, but negative SBRs at high productivity would also be neutralized.

We did, however, expect variation among species within the growth chamber experiment.

METHODS

Field sampling

Soils for this experiment were collected from 12 grassland sites covering the extent of the Great Plains in Canada (Table 1). All sites are part of the Drought-Net experiment, an international coordinated drought experiment. At each site, there were both control plots and drought plots where rainout shelters were used to reduce precipitation by ~50%. Shelters were erected in 2016 for all sites except one that was erected in 2017 (Brookdale). These two treatments (hereafter precipitation history) were replicated between three and five times at each site for a total of 98 field plots (Table 1). Soils for the growth chamber experiment were collected from undisturbed areas in all control and reduced precipitation plots at each site in late July or early August 2019. We collected 250 ml of soil from five haphazardly placed soil cores sampled to 15 cm depth per plot. Soils were placed on ice immediately and shipped to the University of Saskatchewan within 2 days of collection. Once received, the soils were refrigerated at 4°C until use (maximum 10 days).

To test our hypotheses regarding plant diversity and productivity effects on SBRs and drought responses (Appendix S1: Figure S1), we estimated vascular plant community composition as percent cover and harvested aboveground biomass for each plot in mid to late July 2019, at its peak. Using the percent cover data, we counted the number of species to estimate species richness per square meter per plot; however, the size of quadrats used differed among investigators, with percent cover data collected using a 1.0-m^2 quadrat at five sites and using a 0.25-m^2 quadrat at seven sites. To get site level estimates for species richness per treatment, we averaged richness estimates across all replicates for sites using the 1.0-m^2 quadrat. At sites using 0.25-m^2 quadrats, we used the total number of species for sites with four replicates or the average species richness across all possible combinations of four plots for sites with five replicates. We tested whether the sampling scale for species richness influenced the effect of species richness on SBRs, we initially included it as a factor in the analyses. As we found no significant effects of sampling scale on the diversity relationship (see Appendix S1: Tables S4 and S5), we excluded scale from subsequent analyses to minimize model complexity. Biomass was harvested by clipping all live plants to the soil surface in different subplots measuring either 0.2 or 0.1 m^2. These samples were dried, weighed, and then converted to dry live herbaceous biomass per square meter. Biomass estimates were then averaged within treatments at the site level for an estimate of productivity in the ambient and reduced moisture treatments.

TABLE 1 Site locations from which soil inocula were collected, average species richness and standing biomass for each of the sites, and the number of replicates per control and drought treatment at that site.

Site	Latitude (°N)	Longitude (°W)	Species richness (species/m^2)	Biomass (g/m^2)	No. replicates
Biddulph	51.9	106.7	6.3	98.8	3
Brookdale	50.1	99.9	10.8	200.1	5
Kernen	52.2	106.5	11.7	165.3	3
Kinsella	53.0	111.6	13.0	274.8	5
Matador	50.7	107.7	10.7	117.8	3
Mattheis	50.9	111.9	6.0	33.6	5
Onefour	49.0	110.4	9.0	62.2	4
Oyen	51.6	110.5	10.0	231.7	4
Sangudo	53.8	114.8	4.0	493.3	4
Stavely	50.2	113.9	18.0	220.8	4
Swift Current	50.3	107.8	13.2	102.1	5
Twinriver	49.0	112.3	15.0	147.6	4

Growth chamber experiment

The growth chamber experiment consisted of two factorial treatments (soil sterilization by additional drought) that were crossed with the field precipitation treatments in a factorial design. For this experiment we kept all soils from the 98 field plots (49 control, 49 reduced precipitation) to use as inocula. To prepare the inocula, each of the field collected soils were split in half, with one half sterilized by autoclaving twice at 121°C. We use soil sterilization to examine the effect of soil biota; however, we recognize that changes in soil structure and increases in nutrient availability can result from these treatments (Dietrich et al., 2020). These 196 different inocula were then split again, so that we could inoculate two pots, one for the control and one for the additional drought treatment (392 pots total; see following paragraphs for treatment details). Each 1 L pot was filled with autoclave sterilized background soil (same method as inocula) before mixing in 40 ml of the inocula prior to seeding. The background soil was a 1:1 v/v mixture of topsoil and sand that ended up being primarily sand (90%) with low soil nutrient content (6.5% carbon, 8.9 ppm phosphorus, 11.2 ppm nitrogen).

To seed the pots, we selected five plant species that belonged to different functional groups or plant families: *Pascopyrum smithii* is a C_3 grass, *Bouteloua gracilis* a C_4 grass, *Vicia americana* a legume, *Geum triflorum* belongs to the Rosaceae, and *Achillea millefolium* belongs to the Asteraceae. We refer to these species hereafter by their genus. All species are common throughout the northern Great Plains, although not all species were present at each site. To each pot, we added 10 seeds per species for 50 seeds total. Seeds were sourced commercially from either Brett Young (*Pascopyrum*, *Bouteloua*, *and Vicia*) or Blazing Star Wildflower Seed Company (*Achillea*, *Geum*). The pots were then arranged in a randomized complete block design in a Conviron GR-118 growth chamber. The chambers were set to an 18:6 h light:dark cycle with an average temperature of 24°C and humidity of 13%. The pots were fertilized once with 0.5 g Plant-Prod 20-20-20 fertilizer (equivalent to 5 kg N/ha).

For the drought treatment portion of the growth chamber experiment, control pots were watered to capacity with tap water approximately every second day. For the drought treatment, the plants were continuously watered as above for 8.5 weeks after seeding then received no water until the leaves of most plants turned brown (10 days post treatment), after which they were watered again for two additional weeks before the experiment was ended.

From each pot, we collected data on both germination and plant biomass. At 4 weeks, we recorded the number of individuals per species per pot to estimate germination success. After ending the experiment, we collected live and dead shoot biomass from each pot, with live shoot biomass harvested by species. We then washed the roots free of soil over a 2 mm sieve. All samples were dried for at least 72 h at 60°C, then weighed.

Statistical analyses

To test for treatment effects on plant growth, we ran four similarly structured mixed models. Two of these models focused on community level responses: total biomass (live shoots, dead shoots, and roots; square-root transformed to normalize the residuals) and the root mass fraction (root biomass/total biomass). We use total plant biomass as a representation of overall productivity. We include the root mass fraction as changes in root allocation can be mediated by microbes under drought (Wilschut & van Kleunen, 2021) and can influence plant responses to drought (Liu et al., 2018). To examine differences among species, we ran two additional models using the shoot biomass of the two most abundant species (*Pascopyrum* and *Vicia*). Other species were excluded from these species-level analyses due to lower germination and biomass. For each model, we used a mixed model in the R package *lme4* (Bates et al., 2015) with significance determined using F tests and Kenward-Roger estimate of degrees of freedom in the R package *car* (Fox & Weisberg, 2019). Precipitation history, soil sterilization, and the drought treatment were included as factorial fixed effects, and field plot identity nested within site as random effects. We also included seedling number as a fixed effect (or species-specific seedling numbers for the single-species models) to account for any variation due to germination rates. For *Vicia*, we excluded four pots where it did not germinate. There were no treatment effects on germination (Appendix S1: Table S1). We initially ran models that included the starting year of the experimental site as a factor interacting with the other experimental treatments; however, we found no effect of start year on our results (see Appendix S1: Tables S2 and S3), so we excluded this factor to simplify our analyses. We also ran models using just shoot or root biomass; however, these models did not differ qualitatively from the total biomass models, so are not considered further (Appendix S1: Table S2).

We ran additional models using site level data to test how plant community productivity and diversity in the field altered soil biota effects on plant growth and response to drought in the growth chamber experiment. Plant productivity at the field experiment sites ranged from 33.6 to 492.3 g/m^2 and species richness from 4.0 to 18.0 species/m^2, with no relationship between the two community characteristics among sites (see Appendix S1: Figure S2). Previous research using a subset of these sites also found no effect of drought on plant diversity and inconsistent effects on productivity (Batbaatar et al., 2021), suggesting that precipitation history, diversity, and productivity effects on SBRs may be evaluated independently. We calculated the treatment averages of total biomass, the root mass fraction, as well as *Pascopyrum* and *Vicia* biomass by field site. Using these average values, we estimated the SBR for each variable as the log response ratio (log[live/sterile soils]; Hedges et al., 1999) as these ratios represent positive and negative effects symmetrically around zero (Brinkman et al., 2010). Due to high mortality of *Vicia* following the current drought (69% of pots had no living *Vicia* plants), we focus on SBRs in continuously watered pots only for that species. These site-averaged estimates of SBRs were then included as response variables in five separate mixed models conducted using the *lme4* and *car* packages in R as before (Bates et al., 2015; Fox & Weisberg, 2019). We used the square root transformed (to reduce the influence of outliers) site averaged field estimates of species richness and biomass in the ambient precipitation and drought field plots for each site as predictor variables. Both variables were included in factorial interactions with precipitation history and current drought, but not each other. Current drought was excluded from *Vicia* models, however. We included site identity as a random effect. Due to the complexity of these models, we used backwards selection to remove terms that increased the AIC$_c$ score of the model. Only terms that included richness or biomass were removed from the model as we considered precipitation history and current drought to be structural to the study. All data can be found on figshare (Lundell et al., 2022).

RESULTS

Overall, the growth chamber drought treatment reduced total plant biomass (Figure 1a; $F_{1,255.4} = 31.86$, $p < 0.001$), while reducing root allocation ($F_{1,257.7} = 5.01$, $p = 0.026$, Figure 1b). Soil sterilization reduced total plant growth ($F_{1,257.7} = 6.99$, $p = 0.009$), but not if there was a history of reduced precipitation (Figure 1a; interaction term $F_{1,260.5} = 4.11$, $p = 0.044$). Neither precipitation history nor soil sterilization increased plant growth responses following subsequent drought or affected root allocation (Appendix S1: Table S2).

There was considerable variation among species in their establishment and responses to the soil inocula. While *Pascopyrum* and *Vicia* were nearly ubiquitous (100% and 99% of pots with 40.7% and 47.7% germination, respectively), *Bouteloua* only established in 52% of pots (12.9% germination) and *Geum* and *Achillea* were rare (6% and 9% of pots and 0.6% and 1.5% germination, respectively). *Pascopyrum* also comprised most of the live biomass at the end of the experiment (81%), followed by *Vicia* (17%) and *Bouteloua* (2%). Both *Geum* and *Achillea* comprised <0.1% of biomass. Growth of the two most common species responded differently to the treatments. Treatment effects on *Pascopyrum* largely mirrored the overall biomass responses, which reflects the fact that *Pascopyrum* comprised 80% of live biomass. *Pascopyrum* biomass declined with drought ($F_{1,256.4} = 37.45$, $p < 0.001$). There was also a marginal interaction between precipitation history and soil sterilization, where sterilization reduced growth in soils that received full

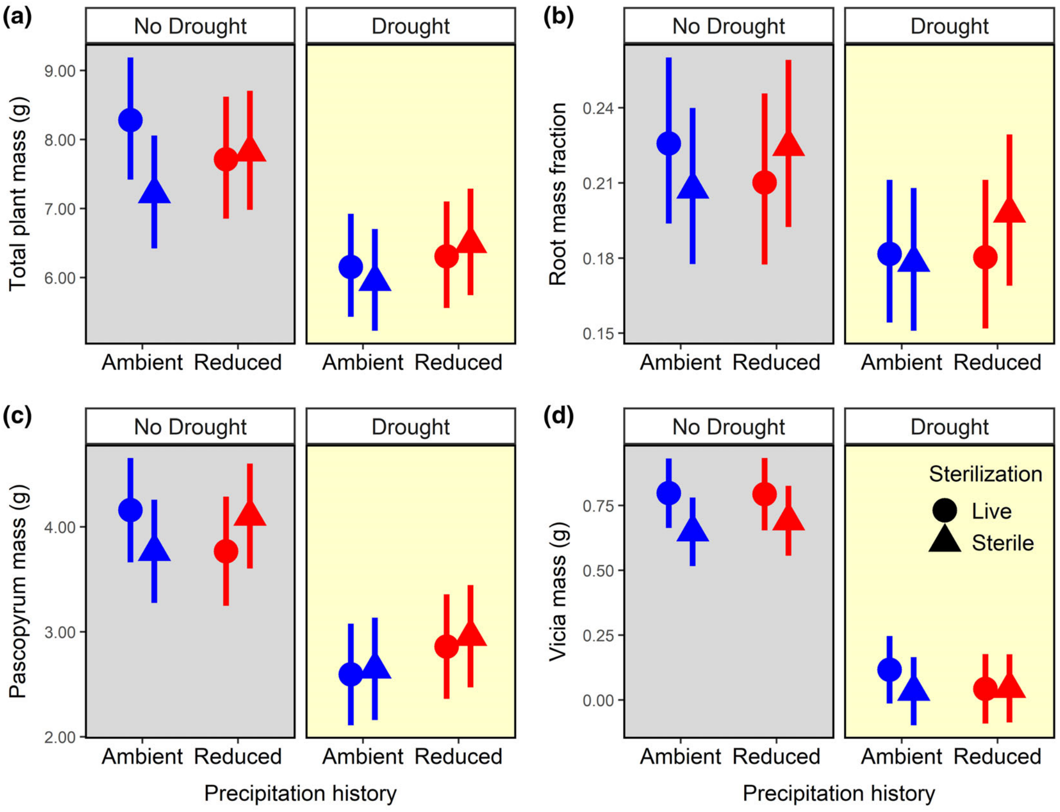

FIGURE 1 Interaction plots showing the effects of precipitation history (blue, ambient; red, reduced), soil sterilization (circles, live; triangles, sterile), and subsequent drought (gray panels, control; yellow panels, drought) on growth and biomass allocation. Shown are treatment effects on (a) total biomass (live shoots + roots + dead shoots), (b) the root mass fraction (roots/[live + dead shoots]), and the live shoot biomass of the two most frequent species, (c) *Pascopyrum smithii* and (d) *Vicia americana*. Points denote means and error bars 95% confidence intervals as estimated by mixed models.

precipitation in the field, but increased growth in soils that had experience reduced precipitation (Figure 1d; $F_{1,260.9} = 3.69$, $p = 0.056$). *Vicia* was nearly eliminated from drought treated pots ($F_{1,257.2} = 98.84$, $p < 0.001$; Figure 1e) and grew poorly in sterile soils ($F_{1,261.6} = 4.52$, $p = 0.034$) but experienced no significant effects of precipitation history (Appendix S1: Table S2).

Total biomass SBRs varied with both site productivity (Figure 2b; $F_{1,10.6} = 10.73$, $p = 0.008$) and species richness, although the relationship with species richness was dependent on precipitation history ($F_{1,40.8} = 5.37$, $p = 0.026$; Figure 2a). SBRs went from positive to neutral as productivity increased independently of any other conditions (Appendix S1: Table S4). In soils that had ambient precipitation, species richness had a negative effect on SBRs, whereas the relationship was positive in soils that had reduced precipitation, resulting in strong differences in SBRs between ambient and reduced precipitation histories in low species richness sites.

The root mass fraction SBR declined with productivity (Figure 2c; $F_{1,32.9} = 4.83$, $p = 0.035$), indicating that soil microbes from unproductive sites stimulated root allocation more than microbes from productive sites. There was a marginally significant interaction between productivity and drought where current drought masked any effect that microbes had on root allocation (Figure 2c; $F_{1,34.9} = 3.29$, $p = 0.078$; Appendix S1: Table S4).

SBRs differed among species. For *Pascopyrum*, SBRs were similar to those seen for total biomass, reflecting the dominance of *Pascopyrum* in the experiment. SBRs were more positive in soils lacking a drought legacy than in those with one ($F_{1,41.3} = 4.38$, $p = 0.042$; Figure 3a) and became increasingly negative as grassland productivity increased (Figure 3b; $F_{1,10.5} = 18.68$, $p = 0.001$). There was also a slight decline with species richness ($F_{1,30.9} = 3.34$, $p = 0.077$; Figure 3a) but, unlike total biomass, this relationship was not dependent on the precipitation history ($F_{1,41.7} = 2.32$, $p = 0.135$). Conversely, there was no significant effect of either precipitation history or soil origin on SRBs for *Vicia* (Appendix S1: Table S4 for full results).

DISCUSSION

Our results show that soil biota can enhance community productivity in cool temperate grasslands but that this

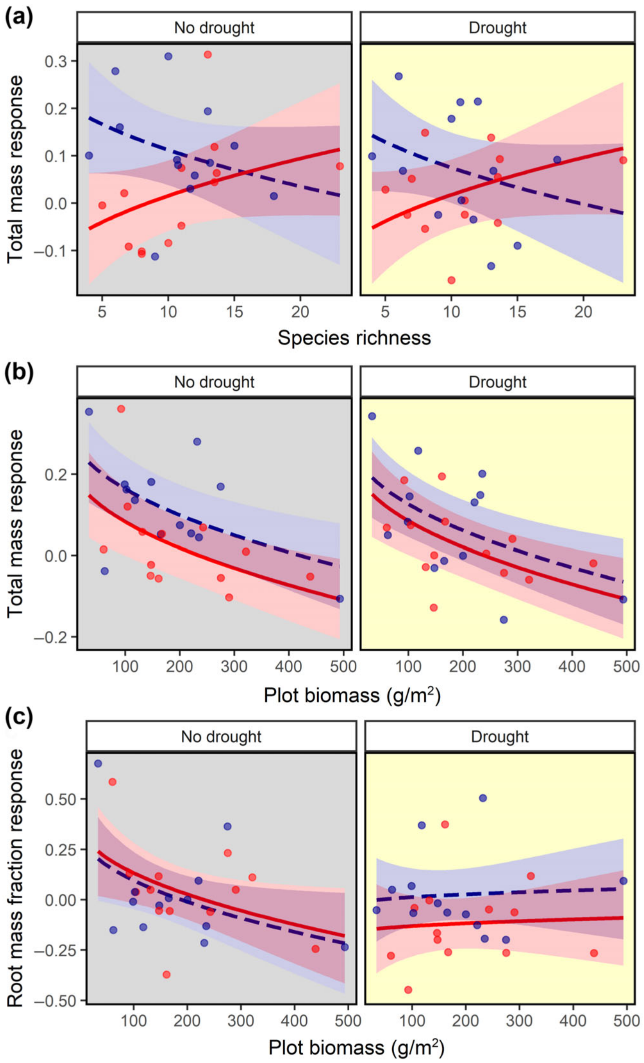

FIGURE 2 Plant responses to soil biota (SBRs) in terms of growth and biomass allocation as a function of precipitation history (ambient, blue; reduced, red), current drought, plant species richness, and plot biomass. SBRs are on a natural log scale and were calculated as log (live/sterile soils). Shown are the relationships between (a) species richness and total plant mass SBRs, (b) plot biomass and total plant mass SBRs, and (c) plot biomass and SBRs of the root mass fraction. Growth chamber drought is shown in yellow panels, whereas fully watered pots are shown in gray. Points represent partial residuals. Lines represent the model predicted relationship and bands the 95% confidence intervals for that relationship. Richness and productivity were back-transformed from the square root for the figures.

benefit may be neutralized by a history of reduced precipitation. Consequently, drought may have legacy effects on plant productivity and other ecosystem functions that persist after the drought has passed. The effects of soil biota, however, depended on the diversity and productivity of the conditioning community. Plant growth responses to soil biota (SBRs) became increasingly negative with the productivity of the site where the soil was collected but, contrary to our hypothesis, they also became increasingly negative with the plant species richness of the sites due to more positive SBRs in less diverse sites. The relationship with species richness, however, was muted when there was a history of reduced precipitation, potentially indicating that soil biota from less diverse communities are less tolerant of drought (Bennett et al., 2020). Regardless of precipitation history or soil origin, we did not find that soil biota increased plant growth following further drought, indicating that mediation of drought tolerance by soil biota, if present, has limits (Revillini et al., 2016).

Contrary to our first hypothesis, soil inocula from less diverse communities increased plant growth more than soils from more diverse communities. Plant diversity cannot therefore be assumed to produce universally beneficial soil biota communities, as has previously been postulated (Bennett et al., 2020). Low plant diversity is associated with soils containing more bacteria than fungi (Bennett et al., 2020; de Vries et al., 2012), which also have more available inorganic nitrogen due to more rapid nutrient cycling (van der Heijden et al., 2008). C_3 grasses, like *Pascopyrum*, which dominated our experimental communities, are strong competitors for inorganic nitrogen in cool temperate grasslands and can effectively compete with (and as a result shape) the soil bacterial community for nitrogen (Bennett & Cahill, 2013; Piper, Lamb, & Siciliano, 2015; Piper, Siciliano, et al., 2015). These positive plant–soil feedbacks may keep plant diversity low and allow C_3 grasses to dominate these ecosystems. Communities dominated by species that benefit from a fungal food web, such as those dominated by slower growing (Baxendale et al., 2014) or mycorrhizal-dependent plant species (Hartnett & Wilson, 2002), may exhibit different responses to soils from low and high diversity sites. Given that C_3 grasses compose most of the biomass in cool temperate grasslands and tend to respond negatively or not at all to fungi (Bennett & Cahill, 2016; Hartnett & Wilson, 2002), our results may be typical of grasslands in the region; however, further tests with more grassland species would be required to confirm this hypothesis. Nevertheless, as we did not collect data on soil biota composition, this remains conjecture.

The positive SBRs exhibited in soils from less diverse sites became negative if precipitation was previously reduced, whereas precipitation history had no effects on SBRs in more diverse sites. This is consistent with part of our first hypothesis and previous results showing that soil biota from less diverse plant communities were more susceptible to drought than soil biota from diverse communities (Bennett et al., 2020; de Vries et al., 2012). If less diverse sites are dominated by bacteria, they may be more susceptible to drought than

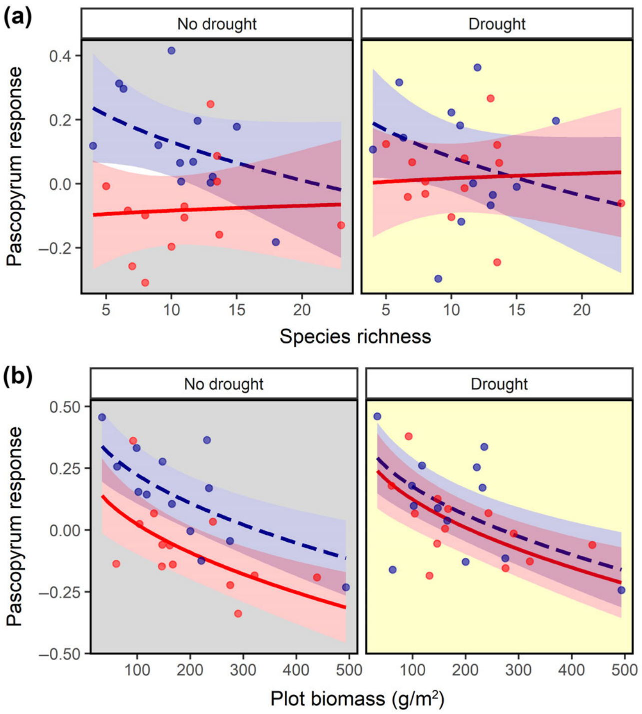

FIGURE 3 Responses to soil biota for *Pascopyrum smithii* as a function of (a) species richness and (b) biomass of the plots and precipitation history (ambient, blue; reduced, red). Growth chamber drought is shown in yellow panels, whereas fully watered pots are shown in gray. Points represent partial residuals. Lines represent the model predicted relationship and bands the 95% confidence intervals for that relationship. Richness and productivity were back-transformed from the square root for the figures.

fungi-dominated high-diversity sites and thus the benefits of these soils would be reduced (Bennett et al., 2020; de Vries et al., 2012; Evans et al., 2014). It is unlikely, however, that all bacteria and fungi will respond similarly (Lozano et al., 2021; Ochoa-Hueso et al., 2018). Indeed, some bacterial and fungal pathogens can increase under drought (Lozano et al., 2021, Ochoa-Hueso et al., 2018) and may contribute to negative SBRs under these conditions. The positive SBRs in less productive sites, however, suggest that pathogen contributions to SBRs may be limited in dry environments. Interestingly, drought effects on productivity in the field were independent of plant diversity (Appendix S1: Figure S1). This suggests that either SBRs are unimportant for drought tolerance in the field or that these responses are only important for younger plants, which can be more responsive to both beneficial and antagonistic species (Bennett & Cahill, 2016; Fenner, 1987). SBRs may thus exhibit lagged effects on plant community structure and function.

The negative relationship between SBRs and productivity is partially consistent with our third hypothesis and suggests that the soil biota from productive communities are more antagonistic on average. Soil microbes can be of greater benefit in drier sites (Revillini et al., 2016), whereas pathogens can be more abundant and mobile in wetter sites (Garrett et al., 2006). Consequently, SBRs should become negative with increasing water availability (Beals et al., 2020; Bennett & Klironomos, 2018; De Long et al., 2019) and thus productivity, in the water-limited Great Plains (Knapp & Smith, 2001). Our results, however, focus only on the biotic component of soils. Increases in soil organic matter and nutrient availability in soils from productive communities, which were not captured by this experiment due to the small amount of soil inocula used, would still benefit plants (Cong et al., 2014) and may offset the negative effects of the soil biota. Interestingly, this relationship exhibited no legacy effects of reduced precipitation in contrast to our hypothesis, suggesting that plant diversity, rather than plant productivity, may be the primary mediator of drought effects on soil biota despite increased drought susceptibility of soil biota from mesic environments (Ochoa-Hueso et al., 2018).

Contrary to our second and fourth hypotheses, we found no evidence that further drought altered SBRs irrespective of soil origin and precipitation history. Any potential soil biota benefits were thus insignificant relative to the effects of the growth chamber drought, highlighting the limits of microbial drought mediation (Revillini et al., 2016). Previous studies have found that intense short-term droughts had stronger effects on grassland soils than sustained reductions in water availability (Hoover & Rogers, 2016). High mortality may have limited the ability of soil biota to respond to the growth chamber drought, whereas the sustained reduction in water in the field would have allowed some adaptation (De Vries & Shade, 2013), leading to a more nuanced drought legacy.

Soil biota responses of the root mass fraction were more muted than SBRs of total biomass, indicated by the lack of a mean response to soil sterilization or precipitation history. This runs contrary to recent results indicating that soil biota can alter biomass allocation (Wilschut & van Kleunen, 2021); however, SBRs of root allocation were negatively related to site productivity indicating that such effects may be site-specific and potentially driven by increasing pathogen to mutualist ratios (Garrett et al., 2006; Revillini et al., 2016). The growth chamber drought eliminated this relationship, suggesting that the responsible soil biota were susceptible to drought. Contrary to expectation (Liu et al., 2018), this change in root allocation does not seem to have influenced the community growth response to drought, as SBRs for plant biomass were not similarly affected.

Although community SBRs were driven by *Pascopyrum* in our experimental communities, SBRs differed for *Vicia*. As a legume, *Vicia* associates with rhizobium and mycorrhizal fungi (Graham, 2005; Reinhart et al., 2017), both of which can be important and may persist in soils with chronic water limitation (Revillini et al., 2016). That SBRs were typically positive but independent of soil origin suggests that *Vicia* may not be specific in its association with beneficial soil microbes. This suggests that subordinate species may be able to compensate for drought legacy effects if the dominant species relies on drought sensitive soil biota (Mariotte et al., 2015), which can result in altered plant composition as seen in the field for a subset of our sites (Batbaatar et al., 2021). That *Vicia* was strongly affected by drought in both live and sterile soils, however, suggests soil biota benefits are insufficient to allow persistence through drought. Plant community responses to extreme events are thus likely to be driven by the inherent drought tolerance of the constituent species more than any differences in their response to soil biota.

CONCLUSIONS

Repeated droughts are likely to affect both biodiversity and ecosystem functioning (Harrison & LaForgia, 2019; Zhang et al., 2019). Our results suggest that much of this response will be driven by the inherent drought tolerance of the plant species within that ecosystem. Longer term reductions in precipitation, as in our field experiment, may result in a more nuanced plant response that is mediated by changes in soil biota. These responses, however, are likely to depend on the plant community. Less diverse plant communities may be especially vulnerable to reduced precipitation, both because they may lack drought tolerant plant species (Wright et al., 2021) and because drought legacies may inhibit beneficial soil biota as we found. Primary productivity, however, is less likely to mediate the effect of precipitation history on plant responses to soil biota.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Lundell et al., 2022) are available in Figshare at https://doi.org/10.6084/m9.figshare.19735564.v3.

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SUPPORTING INFORMATION

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

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