ELEMENTA
Science of the Anthropocene

Jones, JM, et al. 2022. Microbial community response to drought depends on crop. *Elem Sci Anth*, 10: 1. DOI: https://doi.org/10.1525/elementa.2021.00110

RESEARCH ARTICLE

Microbial community response to drought depends on crop

Jennifer Marie Jones[1,*], Emma Lauren Boehm[2], Kevin Kahmark[1,3], Jennifer Lau[2], and Sarah Evans[1,4]

Growing season drought can be devastating to crop yields. Soil microbial communities have the potential to buffer yield loss under drought through increasing plant drought tolerance and soil water retention. Microbial inoculation on agricultural fields has been shown to increase plant growth, but few studies have examined the impact of microbial inoculation on plant and soil microbial drought tolerance. We conducted a rainout shelter experiment and subsequent greenhouse experiment to explore 3 objectives. First, we evaluated the performance of a large rainout shelter design for studying drought in agricultural fields. Second, we tested how crop (corn vs. soybean) and microbial inoculation alter the response of soil microbial composition, diversity, and biomass to drought. Third, we tested whether field inoculation treatments and drought exposure altered microbial communities in ways that promote plant drought tolerance in future generations. In our field experiment, the effects of drought on soil bacterial composition depended on crop type, while drought decreased bacterial diversity in corn plots and drought decreased microbial biomass carbon in soybean plots. Microbial inoculation did not alter overall microbial community composition, plant growth, or drought tolerance despite our efforts to address common barriers to inoculation success. Still, a history of inoculation affected growth of future plant generations in the greenhouse. Our study demonstrates the importance of plant species in shaping microbial community responses to drought and the importance of legacy effects of microbial inoculation.

Keywords: Soybean, Corn, Inoculum, Bacteria, Plant, Legacy effects, Interactions, Rainout shelter

Introduction

Climate change is altering precipitation patterns, with many places experiencing longer and more frequent dry periods (Intergovernmental Panel on Climate Change, 2012). The increased frequency of droughts will likely decrease plant and crop growth (Li et al., 2009; Lesk et al., 2019) and alter soil microbial communities (Clark et al., 2009; Hawkes et al., 2011; Hueso et al., 2012; Bouskill et al., 2013). Although drought stress can disrupt plant and microbe interactions (Kaisermann et al., 2017), plant–microbe associations can increase plant drought tolerance by altering plant root architecture and plant physiology (Bacteria: Ngumbi and Kloepper, 2016, Fungi: Quiroga et al., 2017; Pavithra and Yapa, 2018; Bahadur et al., 2019). In addition, soil microbes can retain soil moisture and thus increase moisture availability for plants by producing extracellular polymeric substance (EPS; Schimel, 2018). Because microbes can influence both plant physiological responses to drought and mitigate the effects of drought by manipulating the soil environment plants experience, understanding when such effects are most likely to occur is critical for predicting plant drought response.

Drought can alter microbial community composition and both microbe and plant physiology. Drought can decrease microbial community diversity (Bouskill et al., 2013; Naylor et al., 2017; Naylor and Coleman-Derr, 2018; Veach et al., 2020, but see Hawkes et al., 2011) and increase the abundance of drought tolerant taxa, such as Actinobacteria (Naylor et al., 2017; Santos-Medellín et al., 2017; Moreno-Espindola et al., 2018; Ochoa-Hueso et al., 2018; Preece et al., 2019) and monoderm or Gram-positive bacteria (Xu et al., 2018; Xu and Coleman-Derr, 2019). Drought can also decrease microbial biomass (Hueso et al., 2012; Alster et al., 2013, but see Naylor and Coleman-Derr, 2018; Schimel, 2018) and alter the expression of microbial drought stress tolerance strategies, such as osmolyte and EPS production, which can delay soil drying (Schimel, 2018). Like microbes, plants also decrease

[1] W.K. Kellogg Biological Station, Michigan State University, Hickory Corners, MI, USA
[2] Department of Biology, Indiana University, Bloomington, IN, USA
[3] Great Lakes Bioenergy Research Center, Michigan State University, Hickory Corners, MI, USA
[4] Department of Integrative Biology, Michigan State University, East Lansing, MI, USA

* Corresponding author:
Email: jones514@msu.edu

growth under drought and alter their physiology to better tolerate drought, which can lead to changes in plant nutrient uptake and decreases in plant photosynthetic rate and crop yield (Farooq et al., 2009).

Plants can alter root growth and microbial communities and sometimes do so in ways that increase plant drought tolerance. Plant species select for different microbial communities via changes in root exudation (Sasse et al., 2018) and root morphology (Naylor and Coleman-Derr, 2018), both of which are altered by drought. Under drought, plants can alter root exudate profiles to attract beneficial microbes (Williams and de Vries, 2019) and increase the amount of carbon they release from their roots through root exudates (Henry et al., 2007), though this depends on the severity of drought (Reid, 1974). Finally, plants can respond to drought by increasing root biomass and root depth (reviewed in Fang and Xiong, 2015). Therefore, crops with different rhizosphere microbes and root architecture, such as corn and soybeans (Swain et al., 2013), will likely differ in drought response.

Although plants can alter soil microbes, microbes also can affect plant drought tolerance through rhizosphere microbes' connections with plant roots and bulk soil microbes' roles in shaping soil properties important for plant growth. Rhizosphere bacteria can alter root architecture of plants to increase water and nutrient uptake in soils, increase water content of plants during drought, and increase the production of plant osmolytes (Ngumbi and Kloepper, 2016). Mycorrhizal fungi can increase drought tolerance in plants, including crops such as corn and soybean (Quiroga et al., 2017; Pavithra and Yapa, 2018; Williams and de Vries, 2019). Free-living bacteria and fungi can also improve soil properties for plant drought tolerance by delaying drying through EPS production (Schimel, 2018) and increasing soil organic matter (Kallenbach et al., 2015; Lefèvre et al., 2017). Soil organic matter can decrease crop yield loses due to drought (Robertson et al., 2014) but does not always lead to increases in soil water holding capacity (Minasny and McBratney, 2018). In addition to specific mechanisms though which microbes can aid plant drought tolerance, increased microbial diversity can lead to increased multifunctionality in the soil (Wagg et al., 2019, but see Maynard et al., 2017), which can lead to increased plant growth (Lankau et al., 2022) and plant drought tolerance (Prudent et al., 2020).

Such microbial responses to drought, combined with microbial effects on plant drought tolerance, have the potential to cause persistent legacy effects, which we define as differences in plant growth or other traits when plants are grown in soil communities with a history of different inoculations or environmental conditions. Inoculation can change soil microbial communities to influence plant growth after the inoculated plants are gone (Moore et al., 2022) and increase plant growth in new plants grown in soil that previously had inoculated plants (Buchenau et al., 2022). Legacies of drought can alter bacterial community composition (Evans and Wallenstein, 2013; Meisner et al., 2018), leading to increased drought tolerance of future plant generations by selection for drought tolerant taxa (Bouskill et al., 2013) or decreased drought tolerance by destabilizing bacterial community networks (de Vries et al., 2018) or reducing microbial driven ecosystem functions (Kaisermann et al., 2017). For example, drought legacy can alter microbial communities in ways that decrease future plant growth (Kaisermann et al., 2017) or promote plant growth under drought (Lau and Lennon, 2012).

The link between microbial communities and crop yield has led to a large body of literature investigating the addition of microbes to soil to improve crop growth, with mixed effectiveness. In greenhouse experiments, many studies have shown that plant drought tolerance can be improved by microbial inoculum (Sarma and Saikia, 2013; Ortiz et al., 2015; Ghorchiani et al., 2018; Takács et al., 2018; Shirinbayan et al., 2019) and increased soil microbial diversity (Prudent et al., 2020). However, few studies have demonstrated successful microbial inoculation in the field (Kaminsky et al., 2019). This is because variation in field environmental conditions makes microbe establishment unpredictable and decreases the strength of relationships between plants and microbial inoculation (Forero et al., 2019). In field conditions, microbes in inocula may overlap functionally with existing microbes, decreasing inoculum establishment (Kaminsky et al., 2019). Additionally, the inoculum must come in contact with either plant roots or soils to be effective (Malusá et al., 2012), which can be difficult in agricultural fields where application of inoculation treatments cannot interfere with typical planting practices. Studying diverse microbial inocula and different application methods may increase the effectiveness of microbial inocula for improving plant growth in field conditions.

One important challenge to studying drought in agricultural fields is designing rainout shelters that can reduce rain and allow for active farm management without altering microclimatic factors (Beier et al., 2012). For example, roofing materials for shelters must be strong enough to withstand high winds while transparent enough to allow light for plants to grow (Beier et al., 2012). Many other rainout shelter designs are fixed in place (Fay et al., 2000; Kant et al., 2017), but we needed a removable shelter design to allow for typical crop management (Kundel et al., 2018). Thus, designing and testing rainout shelters that meet these criteria was a first goal of this study in addition to our scientific questions.

Our primary scientific aim was to understand the effects of drought and microbial inoculation on plant growth and soil microbial communities. Using a field and greenhouse experiment, we tested 3 hypotheses: (1) Crop affects the response of soil microbial composition, diversity, and biomass to drought. (2) Soil microbial inoculation can increase crop drought tolerance through the mechanism of increasing soil microbial diversity. (3) Inoculation and drought exposure will lead to greater plant drought tolerance in future generations (legacy effects). To test the first 2 hypotheses, we used a rainout shelter to exclude rain during the growing season in corn and soybean fields inoculated with 2 different microbial communities to soils and roots (**Figure 1**). To test the third hypothesis, we grew corn and soybean plants in the greenhouse with

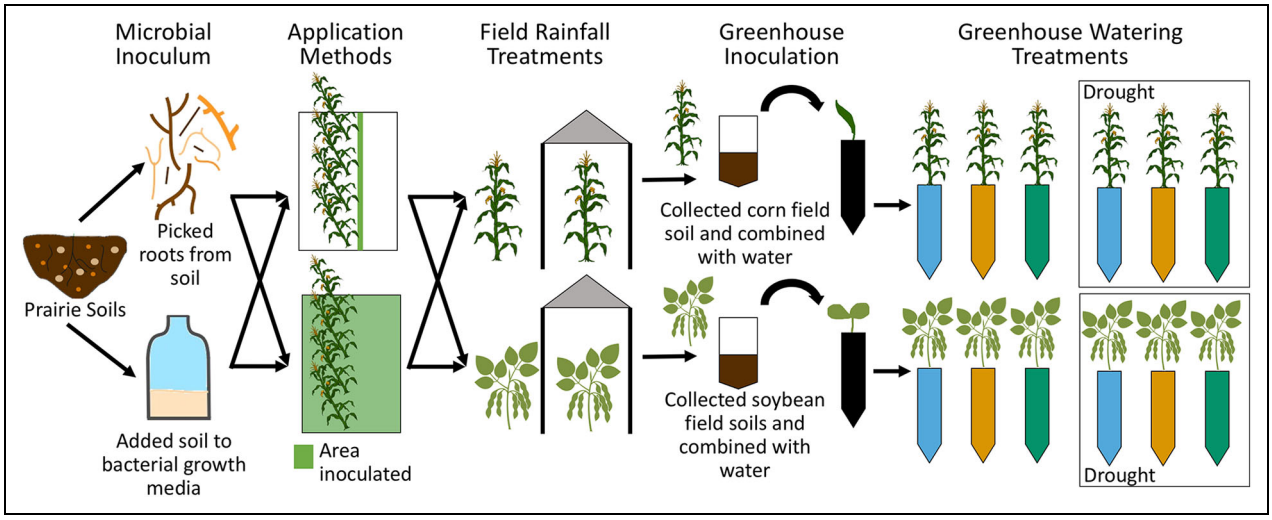

Figure 1. Experimental design. Diagram of the inoculum types, application methods, and rain and watering treatments in the field and greenhouse experiments. Corn plant image: Martin, P. Corn Plant. http://www.phillipmartin.com/. Accessed September 22, 2022.

inoculated soils collected from both rain treatments in the field experiment.

Methods

Study site and experimental design

This experiment was conducted at the Kellogg Biological Station Long Term Ecological Research (KBS LTER) site in southwest Michigan (42° 24′ N, 85° 24′ W, elevation 288 m). Average rainfall is 1,005 mm/yr, and average annual temperature is 10.1°C (Robertson and Hamilton, 2015). The field study was conducted in the weather station and lysimeter field at the KBS LTER main site. This field has had a corn-soybean-winter wheat rotation since 2012, with soybeans planted in the previous year. The field was divided in half, with corn planted on one half and soybean on the other. Corn (Pioneer P0306 AM) was planted on May 15, 2019, with 76 cm row spacing at 31,000 seeds/acre (approximately 6 seeds/m). Soybeans (Pioneer P22T69 R) were planted on June 6, 2019, with a 38 cm row spacing at 160,000 seeds/acre (approximately 14 seeds/m).

We created 4 large plots: an ambient rain plot and a drought plot, each in a corn planting and soybean planting. We covered drought plots with a rainout shelter designed to impose drought on agricultural systems. The rainout shelters aimed to block 100% of the rain for 8 weeks to resemble the 2012 growing season drought in Michigan which decreased soybean yields by 50% (Robertson et al., 2014). Adjacent control plots in both the corn and soybean plantings were uncovered and received ambient rain (89 mm during the 8-week period). After the emergence of both corn and soybean crops, we installed rainout shelters from June 28, 2019, to August 26, 2019. To account for differences in crop height between corn and soybean, the shelters had side post heights of 8.5′ for corn and 4.5′ for soybean. Because we anticipated rain intrusion under shelter up to 1 m from the outside perimeter, especially in corn, we used a large shelter footprint of 24′ × 26′, allowing at least a 0.75-m buffer between the shelter edge and our corn and soybean sampling area. The corrugated roofing panels (Amerilux Greca Lexan) allow approximately 90% light transmittance above 385 nm. A gutter and hose network spanning the length of each shelter was installed to allow any rain collected from the roof to be diverted outside the plot. For more details about materials used for the rainout shelter construction, see Supplementary Files.

We created 1 × 0.5 m subplots for inoculation treatments (see below) centered on a row of corn or soybean plants (Figure S1). Subplots were separated from one another by 25 cm. Subplots in rainout shelters were at least 0.5 m from the edge of the rainout shelter, with higher distances from the edge on the south and west sides of the rainout shelter, which we expected to have greater rain infiltration because heavy summer rainstorms in southwest Michigan usually come from the southwest (Figure S2).

The inoculation treatments were applied to subplots within each of the 4 large rain treatment plots (corn drought, corn ambient rain, soybean drought, and soybean ambient rain). We organized the subplots into 4 blocks designed to capture variation in rain infiltration across the rainout shelter. There were 36 subplots in each larger rain plot: 4 microbial inocula (whole soil liquid inoculum, sterile whole soil liquid inoculum, root inoculum, sterile root inoculum) × 2 inoculation application methods (plant-focused and subplot application) × 4 blocks, plus an additional control subplot in each block that just received water. The full experiment has a total of 144 subplots: each of the 36 subplots in 2 crops (corn and soybean) × 2 rain treatments (drought and ambient rain).

Inoculum creation and application methods

We developed microbial inocula originating from both soil and roots to test the effect of different diverse microbial communities on plant–microbial interactions under

drought, and we applied the microbial inocula using plant-based and whole-plot applications to test the effect of different application locations on inoculation success (**Figure 1**). We inoculated plots with microbes from prairie soil and from roots. In May 2019, we collected the top 15 cm of prairie soil from a restored prairie at the Kellogg Bird Sanctuary in Kalamazoo County, MI. We made our whole soil inoculum using bacterial growth media by adding 2 g of sieved restored prairie soil to 200 ml of either high (LB) or low (R2A) nutrient media to grow a more diverse microbial community for inoculation (Kaminsky et al., 2019). We combined equal parts R2A and LB culture and diluted the culture to a final concentration of 8.3×10^9 cfus/ml using R2A media. We applied 20 ml of inocula to each inoculation plot (more than a standard amount of cells used in field experiments: Bai et al., 2003; Zhang et al., 2003; Berger et al., 2018). We also made inoculum that targeted root taxa by separating roots from prairie soil during sieving and applying 15 g ($\pm$0.25 g) of fresh roots to each inoculation plot. We also treated plots with "sterile controls" to control for the effect of added nutrients, carbon, and sterile cells on crop growth and soil microbial communities. We killed the microbes in the inocula by heat-treating half of the inoculum in an oven >90°C at least for 3 h. For whole soil liquid inoculum, we found no colonies after 24 h of growth in LB media, verifying that our heat treatment had killed the microbes in the inoculum.

We applied the inocula to the subplots using 2 different methods to test whether inoculation nearer to plants was more effective. We applied each inoculum described above near the plant (applied approximately 3 cm to the east of the seedlings) or across the whole plot (applied evenly 0.5m^2 area, 0.25 m on either side of the plants for 1 m length).

Soil sampling

A network of soil moisture and temperature probes was installed in 2 transects for each drought plot. Each transect contained 5TM soil moisture/temperature sensors (Decagon, Pullman, WA) connected to several EM50-series data loggers (Decagon, Pullman, WA), see Supplementary Files for more information.

Soil samples were collected 1–2 days before inoculation, 1 week after inoculation, and 6 weeks after the rainout shelter had been set up. To sample the soils, we used a 1.25-cm diameter soil core to take three 10-cm cores from random locations in each subplot and then pooled for further analyses. Soil samples were kept on ice and stored in the freezer until the sample processing. Soil was sieved with a 2-mm sieve, and a sample was taken for DNA extraction and microbial biomass assays.

We analyzed microbial biomass carbon (C) and nitrogen (N) using K_2SO_4 extraction with chloroform fumigation on 6 g of soil for each fumigated and unfumigated extractions (Brookes et al., 1985). We ran the samples on a TOC (TOC-Vcph carbon analyzer, Shimadzu, Kyoto, Japan). We corrected microbial biomass C and N by dividing values by .45 for carbon (Wu et al., 1990) and .54 for nitrogen (Brookes et al., 1985). Out of 144 plots, we excluded only 2 samples from analysis of extractable organic carbon (EOC) and microbial biomass C that had a microbial biomass C of less than -200 μgC g^{-1} soil.

DNA extractions and sequence processing

We extracted DNA from 0.15 ml of soil from each sample and from whole soil inoculum (20 μl) and root inoculum (0.15 cm^3). We extracted the samples using the MagAttract PowerSoil DNA kit (Qiagen, Germantown, MD, USA) for Kingfisher Flex (Thermo Scientific, Waltham, MA, USA) using the manufacturer's protocol, with an added 2-step binding process. We then sent DNA extractions to the Research Technology Support Facility Genomics Core at Michigan State University to complete library preparation of bacterial 16 S v4 region using dual-indexing (Kozich et al., 2013), and sequence the amplicons using 2 lanes on Illumina MiSeq v2 Standard 500 cycle to output 2×250 bp reads.

We used USEARCH v11 for sequence processing (Edgar, 2010). We merged paired reads, trimmed reads to 250 bp, and screened quality with a maxEE score of 1 (which retained 99% of reads). We clustered sequences into OTUs (operational taxonomic units) at 97% similarity and removed chimeras using default settings of UPARSE (Edgar, 2013). We then classified OTUs using the Silva v.123 database (Quast et al., 2013) and SINTAX classifier using USEARCH (Edgar, 2016). OTUs with single reads were removed for a final sequence read count of 11,488,657 across 25,434 OTUs and 440 samples (8,150–43,179 reads per sample). Analysis on bacterial community composition was done on relative abundance data of raw reads. For a more detailed methods description, see Supplementary Files.

Plant measurements

We used a MultispeQ v 2.0 (PhotosynQ Inc., East Lansing, MI, USA) to measure relative chlorophyll of one leaf per inoculation plot after 8 weeks of rain treatments were applied. We avoided spots or damage on leaves for our readings and held the MultispeQ level to take measurements. We harvested 3 soybean plants from each subplot on October 7 and harvested one ear of corn from the center of each subplot on October 29, 1–2 months after the rainout shelters were removed. We then dried the samples for more than 1 week at 60°C. For soybeans, we separated beans from pods and weighed the beans for all 3 plants and then averaged the bean mass per plot. For the corn, we removed and weighed the kernels.

Greenhouse experiment

To test whether rain treatment and microbial inoculation in the field affected subsequent plant growth, we manipulated water availability on greenhouse grown plants (drought or control) and inoculated plants with field soils collected from the above experiments in a factorial design: 2 greenhouse watering treatments $\times$ 2 field rain treatments $\times$ 3 field inoculation treatments (root live plant-focused inoculation, whole soil live plant-focused inoculation, and field control). In the fall of 2019, we planted 144 corn and 144 soybean seeds from the same

commercial seed source used in the field experiment in individual 25-cm deep, 6.4-cm wide pots (Stuewe & Sons, Tangent, OR, USA) in the Indiana University Greenhouse. All seeds were planted into steam sterilized (121°C) potting soil, and plants were spaced to minimize potential contamination between pots and were randomly assigned to inoculation and watering treatments.

We inoculated greenhouse plants using soils collected from the field experiment in September 2019. Bulk soil was collected from the following inoculation treatments in the field experiment: root live plant-focused inoculation, whole soil live plant-focused inoculation, and control (no inoculation) within both the ambient and drought plots (field rain treatment). We included these treatments because we thought these would be the most successful inoculations. We created each inoculum by mixing 10 mL (approximately 8 g, based on samples from adjacent field plots) of soil with 40 mL of water using a falcon tube, and then applied 5 mL of inoculum to the base of each assigned seedling approximately 6 days postgermination and again approximately 13 days postgermination. To simulate drought, we watered ambient plants with approximately 250 mL of water every 3 days, and we watered drought plants once per 6–10 days or when there were signs of severe drought stress (i.e., wilting, dropping leaves).

We recorded leaf count, chlorophyll content, and height 17–23 days postgermination and again 30–42 days postgermination. We used a chlorophyll meter (SPAD-502, Konika Minolta, Osaka, Japan) to measure the amount of chlorophyll of the youngest, fully expanded leaf of each individual plant. We measured height from the base of the plant (without touching the soil to avoid microbial cross-contamination) to the topmost node. We also measured specific leaf area (SLA), a trait associated with plant drought tolerance (Poorter et al., 2009), near the end of the experiment for corn plants. We harvested aboveground and belowground biomass after approximately 7 weeks for corn and approximately 9 weeks for soybeans, when some plants showed signs of becoming root bound. For the soybean plants, we counted the number of nodules. All above- and belowground biomass was weighed after drying at 65°C for at least 72 h.

Data analysis

We analyzed volumetric water content (VWC) from soil sensors to assess soil drying under the rainout shelters. To account for sensor variation, we first calculated the difference in VWC from the original date loggers were installed (7/2/2019) to the dates of interest (7/3–8/9/2019). We used the difference from initial VWC for all statistical analyses. We analyzed the difference between sensors inside the shelter (defined as greater than 1 m from the edge of the shelter) and outside the shelter (defined as outside the shelter or less than or equal to 1 m from the edge of the shelter) using a linear model for each day the sensors were in the field.

To analyze the effect of crop, rain treatment, and inoculation treatment on soil moisture (using gravimetric soil moisture), relative chlorophyll, microbial biomass C, microbial biomass N, EOC, and extractable organic nitrogen, we used linear mixed effects models with crop, rain treatment, and inoculation treatment as fixed effects and block as a random effect (lme4 package in R version 4.0.3). Model selection was then completed using AICc (second-order Akaike information criterion) using the dredge command (MuMin package in R). We evaluated the significance of fixed effects using Type III tests with Satterthwaite approximation for degrees of freedom via the R lmerTest package. Then, we used the R emmeans package with a Tukey adjustment to assess pairwise differences for significant interactions. We also used the same linear mixed effects models to analyze kernel mass and soybean seed mass except that separate tests were done on kernel mass and soybean seed mass. We removed one sample based on potential incorrect soil moisture data.

In our analysis of bacterial community composition, we accounted for existing spatial variation, because bacterial community composition significantly differed between rain plots before inoculation and rain treatments were applied (Table S1). We analyzed changes in bacterial community composition across crop, rain treatment, and inoculation treatment using a partial distance-based redundancy analysis (dbRDA, *dbRDA* command in *vegan*) with plot location (as *x* and *y* coordinates) as conditional factors in our models to account for existing spatial variation and model selection (*ordistep* command in vegan). We also analyzed how rain treatment affected the pairwise Bray Curtis dissimilarity in soil bacterial communities within crops and between crops. We analyzed the difference in mean dissimilarity between ambient and drought plots using a *t* test for corn soils, soybean soils, and the dissimilarity between corn and soybean soils. We also accounted for existing spatial variation in bacterial diversity, because bacterial diversity differed between rain treatments in soybean plots (Table S1). Therefore, we compared percent difference in bacterial diversity from before inoculation to after 6 weeks of rain treatment using a linear mixed effects model with block as random effects.

To explore hypothesized shifts in bacterial taxa based on known drought tolerant taxa, we separately analyzed the 10 bacterial phyla and unclassified bacteria that accounted for more than 1% of the relative abundance of reads in the dataset. Combined, these phyla accounted for more than 95% of the relative abundance in the full dataset. We analyzed the community composition of each phyla separately using dbRDA analysis using the methods described above. We also analyzed the relative abundance of each phylum using a linear mixed effects model with inoculation, crop, and rain treatment as fixed effects and block as a random effect. We selected models via AICc using the dredge command in MuMin package in R.

To analyze the results from the greenhouse experiment, we constructed linear mixed models to test the effect of the greenhouse watering, field rain treatment, field inoculation treatment, and their interactions on plant traits (lme4 package in R). In our models, we included rack number as a random factor to account for variation across the greenhouse environment and subplot the inocula was collected from (unique inoculum) nested within field block from which the soil samples originated

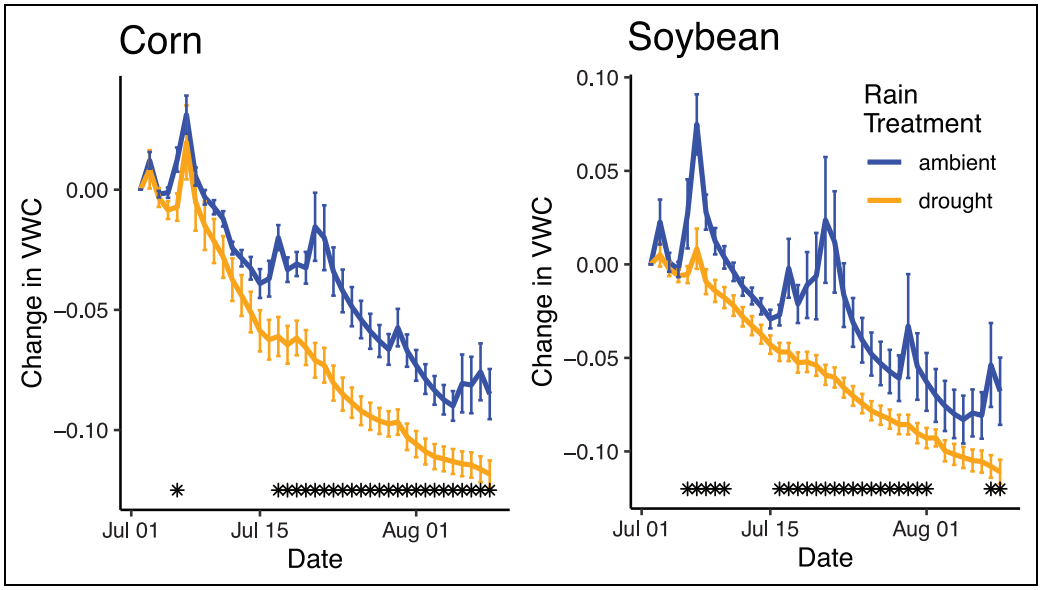

Figure 2. Volumetric water content decreased under drought treatment. Change in volumetric water content (VWC, mean ± standard error bars) from the day of sensor installation (July 2) in drought (>1 m from the edge of the shelter) treatments and ambient rain (outside of shelter or <1 m from the edge of the shelter) in corn and soybean fields. Shelters were installed on June 28.

as a random factor to account for non-independence within blocks. Though initial models included all possible interactions of fixed effects, we only included significant interactions in the final model to improve overall model convergence. We used AICc for model selection, and used the emmeans package with a Tukey adjustment to assess pairwise differences for significant interactions.

Caveats

While our statistical analyses appropriately tested for inoculation effects, field rain treatment effects and particularly rain × crop interaction effects should be interpreted cautiously because the rain treatments were not replicated within each crop type. There was only a single drought plot and a single ambient precipitation plot in the corn planting and a single drought plot and a single ambient precipitation plot in the soybean planting (Figure S1). As a result, our ability to extrapolate the effect of rain treatment or crop type effects are limited. Even though we accounted for spatial variation within field rain treatment in our analyses, spatial variation in plot location could have also contributed to observed effects.

Results

Soil moisture under rainout shelters

The rainout shelters reduced soil VWC at distances greater than 1 m from the edge of the rainout shelter (Figure S3). The intrusion of rain from the side of the shelters depended on the rain event. After 6 mm and 34 mm rain (on July 2 and July 6, respectively), the soil moisture increased at the sensors placed 1.8 m from the shelter edge (Figure S4). All other rain events did not increase soil moisture at these sensors (Figure S4). Soil moisture under shelters became consistently and significantly lower than ambient in corn and soybean fields around July 17 (19 days after the shelters were installed; **Figure 2**). During the period that VWC was measured (July 2 to August 9), soil under the rainout shelter had lower VWC than soil outside or at the edge of the shelter for 25 days in the corn field and 24 days in the soybean field. For these days, the shelter decreased VWC by an average of 3.5% ($SD = 0.9\%$) in the corn field and 4.0% ($SD = 1.6\%$) in the soybean field.

The effect of rain treatment on soil moisture also depended on crop, with drought reducing soil moisture more in soybean fields than in corn fields (rain × crop interaction: $F = 37.13$, $P < 0.001$). At the last census, corn fields had lower soil moisture than soybean fields in both ambient rain and drought plots. Overall, crop explained 33% of the variation in moisture at the last census.

Effects of drought on seed mass, chlorophyll, and soil microbial biomass C and N

Rain treatment altered seed mass and soil organic carbon and nitrogen differently in corn and soybean plots (crop × rain interactions; **Table 1**). The drought treatment decreased seed biomass in soybean plants ($P = 0.01$) but not corn plants ($P > 0.05$, **Figure 3A**). Chlorophyll concentrations were higher in soybean plants than corn plants, but only in ambient rain (crop × rain interaction; **Table 1**). The rain treatment did not significantly alter relative chlorophyll in either corn or soybean plants (**Figure 3B**).

Soil microbial biomass C and N and extractable organic C and N were affected by rain treatment and crop. Microbial biomass C was lower in drought than ambient rain plots in the soybean field but not corn field (crop × rain interaction; **Table 1**; **Figure 3C**). Microbial biomass N was lower in drought than ambient rain plots averaged across both crops (but not significantly different for each crop individually) and was higher in the soybean than corn

Table 1. Crop and rain treatments effect crop and soil carbon and nitrogen measurements

Treatment	Relative Chlorophyll	Extractable Organic C	Extractable Organic N	Microbial Biomass C	Microbial Biomass N
Crop	63.87***	0.20	21.94**	21.38***	82.97***
Rain	0.65	32.43***	17.60***	16.60***	5.99*
Crop × rain	15.37***	5.14*	13.12***	15.24***	–

Explaining relative chlorophyll, microbial biomass C and N, and extractable organic C and N after shelters were applied using a linear mixed effects model with crop, rain treatment, and inoculation (not listed) as fixed effects and block as a random effect. Dashes indicate variables were removed during model selection. *F* values are reported.

*$P < 0.05$. **$P < 0.01$. ***$P < 0.001$.

field (**Table 1**; **Figure 3D**). EOC was higher in drought plots than ambient plots in soybean fields, but did not differ in corn fields (crop × rain interaction; **Table 1**; **Figure 3E**). In contrast, extractable organic nitrogen was higher in corn drought plots than ambient plots but did not differ in soybean fields (crop × rain interaction; **Table 1**; **Figure 3F**).

Drought effects on bacterial communities

Rain treatment and crop altered bacterial community composition (rain × crop interaction, **Table 2**; adjusted $R^2 = 0.06$, **Figure 4A**). Drought made corn and soybean bacterial communities more similar; that is, it decreased the pairwise dissimilarity of corn versus soybean communities (*t* test: 18.28, $P < 0.001$; **Figure 4B**). Even though, drought increased pairwise dissimilarity of bacterial composition within corn and soybean soils (corn: $t = -12.53$, $P < 0.001$; soybean: $t = -17.50$, $P < 0.001$; **Figure 4B**). Because crop influenced soil moisture, which could explain the crop differences in bacterial community composition, we also analyzed the effect of soil moisture on bacterial community composition. We found that while soil moisture had a significant effect on bacterial community composition, soil moisture only explained 1% of variation (dbRDA: $F = 2.89$, $P < 0.001$, $R^2 = 0.012$).

To further understand how the communities responded to drought and crop, we separately analyzed the composition and relative abundance for each dominant bacterial phyla. Rain by crop interactions explained community composition for all 10 phyla with a relative abundance of >1% and unclassified bacteria (Table S2). Relative abundances were higher in corn than soybeans for Actinobacteria, Chloroflexi, Firmicutes, Proteobacteria, and unclassified bacteria, while Acidobacteria, Bacteroidetes, Gemmatimonadetes, and Verrucomicrobia relative abundances were higher in soybeans than corn (Figure S5; Table S3). Across both crops there were similar bacterial phyla responses to precipitation: Actinobacteria, Chloroflexi, Firmicutes, and Proteobacteria were enriched in drought plots, while Acidobacteria, Bacteroidetes, Gemmatimonadetes, and Planctomycetes were enriched in ambient plots (Figure S5; Table S3).

Bacterial diversity responded to drought in the corn field but not soybean field (rain × crop interaction; **Table 2**). Overall, bacterial diversity was higher in soybean plots (mean ± *SE*, 6.74 ± 0.024) than corn plots (6.55 ± .024) at the end of the experiment. Because bacterial diversity differed across plots before experimental manipulations were applied, we analyzed the change in bacterial diversity between the initial and final sampling. While bacterial diversity decreased through the experiment for all treatments (**Figure 4C**), diversity decreased more in drought than ambient rain in corn plots, but not soybean plots (**Table 2**; **Figure 4C**).

Inoculation effects on bacterial community composition and crop yield

The bacterial community composition differed across the whole soil inoculum, root inoculum, and the inoculated soil (PERMANOVA, $F = 12.87$, $P < 0.001$; Figure S6). The whole soil inoculum had 150 OTUs with the highest number of OTUs belonging to the Proteobacteria (58 OTUs). The root inoculum included 4,311 OTUs with the highest number of OTUs also belonging to the Proteobacteria (1,370 OTUs).

Soil bacterial community composition did not differ after microbial inoculation, either 1 week after inoculation (**Table 3**) or after rain treatments were applied (**Table 2**). However, inoculation significantly altered bacterial diversity 1 week after inoculation in corn plots only (**Table 3**). The live root plant-focused application inoculation resulted in a larger decrease in diversity than 2 heat-treated inoculations (root sterile plant-focused (contrast $P = 0.001$) and whole soil sterile plant-focused (contrast $P = 0.022$; Figure S7). Inoculation did not significantly alter diversity after rain treatment for either crop (**Table 2**).

At harvest, inoculation did not affect plant seed mass (inoculation removed from model during model selection).

Inoculation and drought legacy effects on crop growth

In soybean plants grown in the greenhouse with soils treated from the field experiment, greenhouse drought had the strongest effect on reductions in above- and belowground biomass. However, the magnitude of this drought effect depended on field inoculation (greenhouse watering treatment × field inoculation treatment: aboveground biomass *F* value = 3.21, $P < 0.05$; belowground

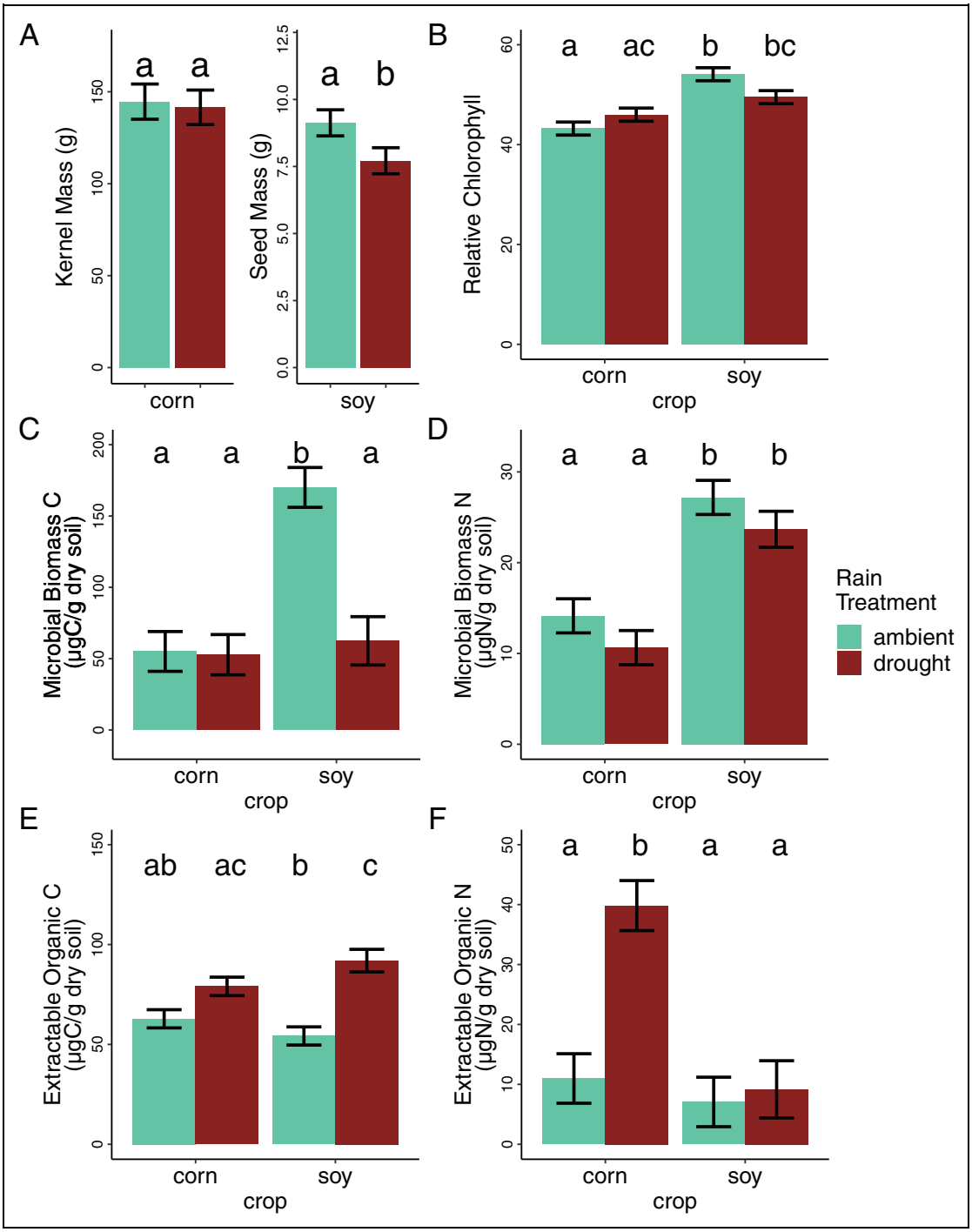

Figure 3. Rain treatment effects on crop growth and soil carbon and nitrogen differed between crops. Mean and standard error bars of (A) corn kernel mass and soybean seed mass, (B) relative chlorophyll, (C) microbial biomass carbon (µgC/g dry soil), (D) microbial biomass N (µgN/g dry soil), (E) extractable organic carbon (µgC/g dry soil), and (F) extractable organic nitrogen (µgN/g dry soil). Letters indicate significant difference ($P < 0.05$).

biomass F value = 6.98, $P < 0.05$). For aboveground biomass, the significant interaction was driven by plants grown in soils with whole soil inoculum having higher aboveground biomass than plants grown in inoculum from field control treatment (no inoculation) in ambient watering greenhouse conditions ($P = 0.07$; **Figure 5A**). For belowground biomass, plants grown in whole soil inoculum had higher belowground biomass than those grown in root inoculum, but only under greenhouse drought conditions ($P = 0.04$; **Figure 5B**). Greenhouse drought treatments reduced average leaf number (F value = 672, $P < 0.05$), average height (F value = 266, $P < 0.05$), nodule number (F value = 120, $P < 0.05$), and increased average chlorophyll content (F value = 110, $P < 0.05$; Table S4). No other statistically significant effects aside from greenhouse watering treatment were detected on leaf number, height, or average chlorophyll content; however, nodule number strongly correlated with both

Table 2. Rain treatment and crop, but not inoculation, altered bacterial communities and diversity

	Community Composition		Change in Diversity	
			Corn	Soybean
Treatment	**Sum of Sqs**	***F***	***F***	***F***
Inoc.	0.72	0.99	5.99***	—
Rain	0.19	2.09**	5.73*	—
Drop	0.30	3.30***		
Inoc. × Rain	0.77	1.06	—	—
Inoc. × Crop	0.70	0.96		
Rain × Crop	0.79	8.71***		
Inoc. × Rain × Crop	0.69	0.95		

Explaining bacterial community composition after 6 weeks of shelter installation using a partial dbRDA and percent change in diversity (from before inoculation treatment to after shelter installation) using a linear mixed effects model with crop, rain treatment, and inoculation treatment (Inoc.) as fixed effects and block as a random effect in the mixed effects model and *x* and *y* plot coordinates as conditional variables in the dbRDA. Gray boxes indicate variables were not examined. Dashes indicate variables were removed during model selection.

*$P < 0.05$. **$P < 0.01$. ***$P < 0.001$.

aboveground biomass ($r = 0.69$, $P < 0.05$) and belowground biomass ($r = 0.55$, $P < 0.05$).

Greenhouse drought also reduced above- and belowground biomass in corn plants, but unlike soybean, the magnitude of the greenhouse drought effect was independent of field inoculation type, field rain treatment, and interactions (greenhouse watering treatment: aboveground biomass, $F = 516.30$, $P < 0.05$; belowground biomass, $F = 156.58$, $P < 0.05$). Inoculating plants with microbes that originated from an ambient field rain treatment led to a marginally significant increase in SLA only in the greenhouse drought treatment (F value = 3.53, $P = 0.055$; Figure S8). Drought also reduced average leaf number ($F = 126$, $P < 0.05$), average height ($F = 224$, $P < 0.05$), and increased average chlorophyll content ($F = 33.8$, $P > 0.05$; Table S4). No other statistically significant effects aside from greenhouse watering treatment were detected on leaf number, height, or average chlorophyll content.

Discussion

We assessed the impact of drought and inoculation on crop growth and soil bacterial communities using a rainout shelter study in the field and in the greenhouse. We found support for our first hypothesis that crop species alters microbial responses to drought. Crop and drought interacted to affect bacterial community composition and diversity, and microbial biomass. Microbial community responses to drought may have differed across crops because drought occurred at different stages in the crop's phenology. These effects should be interpreted cautiously, however, given the lack of replication of field rain × crop treatments. Contrary to our second hypothesis, inoculation had almost no immediate effect on crop growth or bacterial communities, despite testing multiple inoculation methods. However, legacies of inoculation had crop and environment-specific effects on corn and soybean plants, partially supporting our third hypothesis. These historical effects did not overwhelm the dominant effect of greenhouse (contemporary) drought on plants.

Rainout shelters induced drought and reduced plant growth

We found that our rainout shelters successfully decreased soil moisture >1 m from the edge of the shelter, showing that our rainout shelter design can effectively induce drought in agricultural fields. Our rainout shelter was also strong enough to withstand the weather and the design is movable by tractor so that regular management can be completed for agricultural fields, which has been a challenge in previous rainout shelter designs (Beier et al., 2012; Kundel et al., 2018). While another design used a portable automated retractable rainout shelter design in agricultural fields (Fay et al., 2000), simpler, smaller rainout shelters are advantageous because they may be less costly to produce and as a result could allow for randomized and more replicated treatments.

The drought that we induced impacted crops differently. Drought decreased soybean seed mass, but not corn seed mass. It is unlikely that these different responses across crop reflects differences in physiological drought tolerance because in our greenhouse study, drought decreased plant growth in both crops. Instead, we attribute this difference to the different phenology of the plants when the drought was applied. Planting, flowering, fruiting, and harvest occur at different times for corn and soybeans, and 1-month decreases in precipitation are most detrimental in July for corn and August for soybeans (Zipper et al., 2016). Our rainout shelter began decreasing VWC on July 17 and shelters stayed on until August 26, likely including key drought sensitivity for soybeans but not corn. It is also possible that differences in root

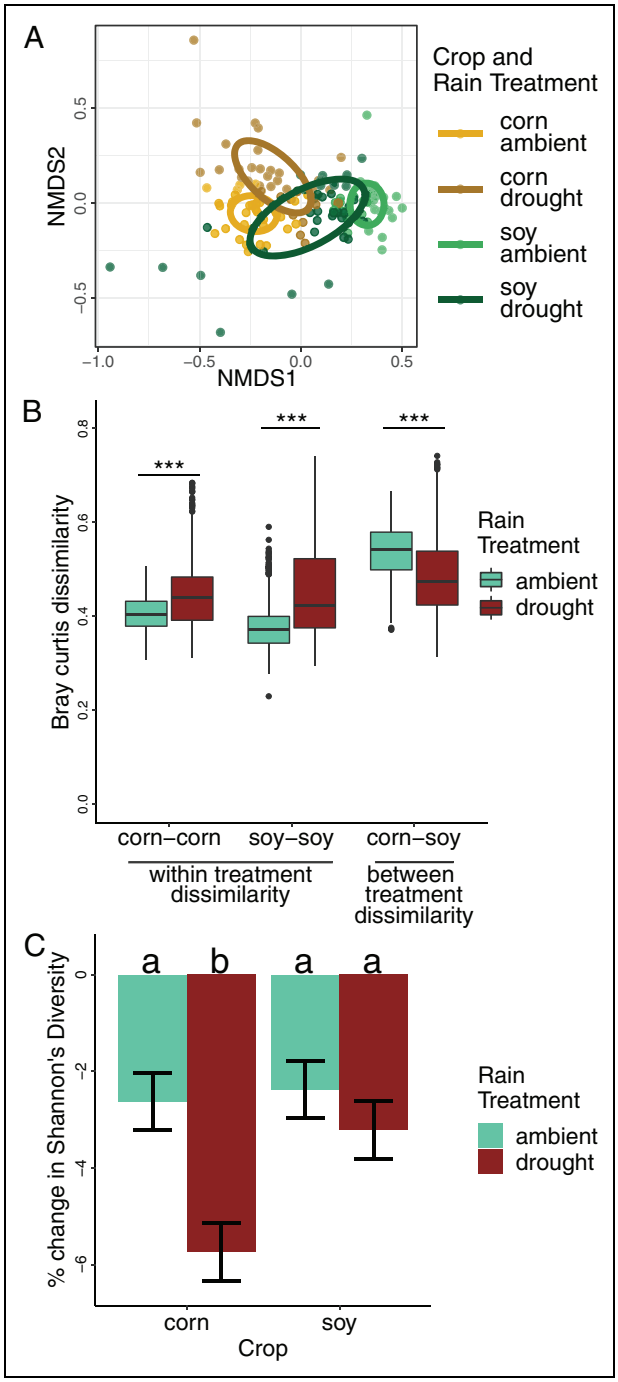

Figure 4. The responses of bacterial community composition and diversity to rain treatment depended on crop. (A) NMDS ordination (stress = 0.14) of bacterial community composition and standard deviation ellipses of samples taken 6 weeks after shelters applied. (B) Bray Curtis dissimilarity (median, 25 and 75 percentile). (C) Percent change in Shannon's diversity (mean ± standard error bars) from before inoculation to after rain treatments were applied. Letters indicate significant difference ($P < 0.05$).

structure, which may not be fully realized in a greenhouse, could account for the differences in drought response. Corn has deeper roots than soybeans, leading to soil moisture at greater depths and over longer time periods affecting corn growth (Swain et al., 2013).

Crop shaped effect of drought on microbial communities

While plant species and drought are known to independently impact bacterial communities in roots and soils, fewer studies assess the effect of drought on bacterial communities across plant species. In this study, we found that crop altered the response of bacterial community composition, bacterial diversity, and microbial biomass C to drought (**Figure 4**). This may have been due to differing crop physiological responses (discussed above) or differing nutrient dynamics of the crops and surrounding soils (e.g., soybean less N-limited as an N-fixing legume). Crop roots also could have differed in their impact on soil pore structure, thus altering the availability of water for microbes under dry conditions (Fischer et al., 2015; Tecon and Or, 2017).

No consistent pattern has been described for how drought alters bacterial diversity and microbial biomass (Naylor and Coleman-Derr, 2018; Schimel, 2018). Our study suggests that the variation in previous studies may be due in part to plant-modulated responses of soil microbial communities to drought. Indeed, other studies have found that plant presence (Koyama et al., 2017; Santos-Medellín et al., 2017; Veach et al., 2020) and composition (Fitzpatrick et al., 2018; Fahey et al., 2020) affect microbe responses to drought. Interestingly, the magnitude of effect we observed in bulk soil communities in the field setting are similar to other studies in rhizosphere and root communities (Santos-Medellín et al., 2017) and in greenhouse experiments (Preece et al., 2019). The magnitude of drought effect on diversity we observed is also similar to other experimental drought manipulations in the field (Yuste et al., 2014) and greenhouse (Veach et al., 2020).

While plant species clearly altered microbial drought response, crop effects on microbial communities were smaller under drought, demonstrated by higher pairwise community dissimilarity under drought in within-crop comparisons (**Figure 4B**). The sizes of pairwise dissimilarity effects that we observed are similar to what has been found in other research on drought (Osburn et al., 2021) and crop variation (Hao et al., 2021). When plants are under drought stress, plants can decrease the carbon released from their roots, in favor of allocating carbon to maintenance and stress tolerance (Hasibeder et al., 2015). The decrease of carbon exudates from stressed plants may decrease the plant's impact on soil bacteria (Henry et al., 2007; Ruehr et al., 2009). Even when the plants continue to send exudates into the soil, drought can decrease the accumulation of exudates in microbial biomass (Karlowsky et al., 2018), potentially due to decreased microbial growth under drought (Schimel et al., 2007) or the lack of water decreasing the availability of those exudates to soil microbes (Tecon and Or, 2017). Consistent with the accumulation of exudates in the soil, we found increased EOC under drought in soybean soils only (**Figure 3E**). However, the EOC increase we observed is more likely a result of microbes dying and releasing carbon, because we saw a decrease in microbial biomass C during drought in soybean soils (48.4 μgC/g dry soil without fumigation efficiency correction; Figure S9) that

Table 3. Inoculation did not affect bacterial communities or diversity 1 week after application

	Community Composition				Change in Diversity	
	Corn		Soybean		Corn	Soybean
Treatment	Sum of Sqs	*F*	Sum of Sqs	*F*	*F*	*F*
Rain	0.22	1.89**	0.13	1.29	5.73***	–
Inoc.	0.94	1.02	0.85	1.09	4.00*	–
Rain × Inoc.	0.85	0.91	0.76	0.98	–	–

Explaining bacterial community composition and change in diversity 1 week after inoculation in corn and soybean fields separately using dbRDA (community composition) and linear mixed effects models (diversity) with rain treatment and inoculation (inoc.) as fixed effects and plot *x* and *y* coordinates as conditional variables in dbRDA and block as a random effect in linear mixed effects models. Dashes indicate variables were removed during model selection.

*$P < 0.05$. **$P < 0.01$. ***$P < 0.001$.

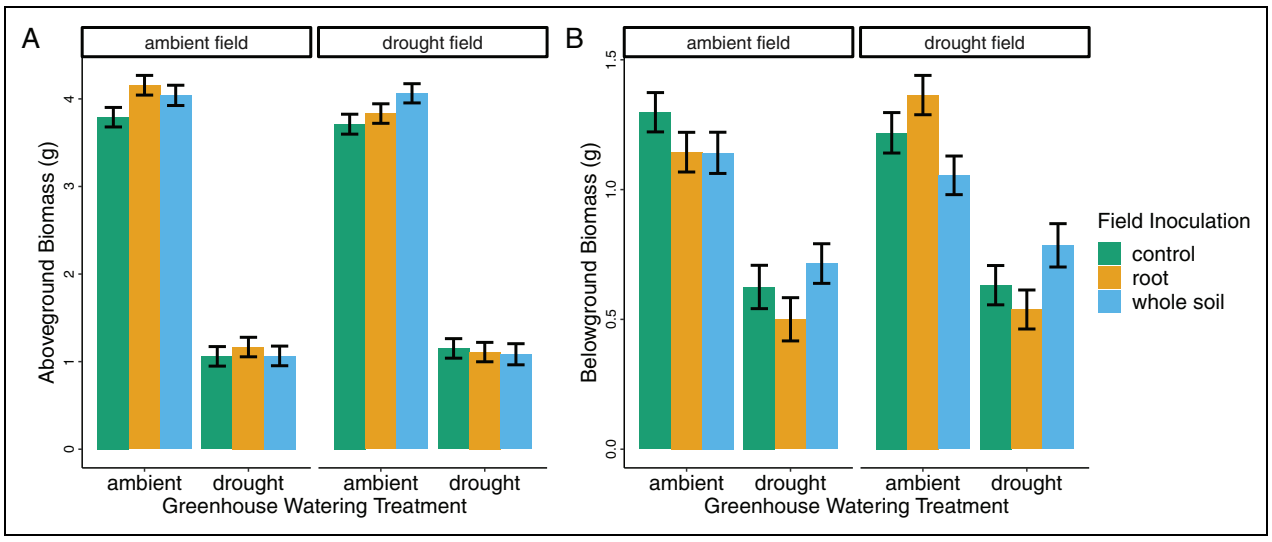

Figure 5. Field inoculation by greenhouse watering treatment interactions in soybean biomass. Mean and standard error bars of aboveground (A) and belowground (B) biomass of soybean across field inoculation treatment and greenhouse watering treatment.

was slightly larger than the EOC increase (37.7 µgC/g dry soil). Still, some EOC could have been derived from soluble C destabilization under rewetting (Homyak et al., 2018). Further data would be needed to determine the cause of the increase in EOC and decrease in microbial biomass in drought in soybeans soils.

Alternatively, it is possible that the increased distance in bacterial community composition we observed in our study is not caused by changes in the influence of plants on soil communities but is instead due to an increase in drought tolerant taxa (e.g., Naylor et al., 2017). In other words, strong selection for drought tolerant microbial taxa in both corn and soybean soils led to convergence in community composition across crops. We found that drought increased the relative abundance of known drought tolerant bacterial taxa in both crops in magnitudes similar to previous studies (Naylor et al., 2017; Ochoa-Hueso et al., 2018). Interestingly, we found that the phyla that were enriched in corn soils were also enriched under drought. The effect of drought on the relative abundance of bacterial phyla found in this study are largely consistent with the growing evidence that monoderm (Gram-positive) bacteria increase in relative abundance under drought, while diderm bacteria (Gram-negative) decrease under drought (Xu and Coleman-Derr, 2019). We found that Actinobacteria, Chloroflexi, and Firmicutes, which are predominantly monoderm lineages, increased under drought across both crops. However, we also found that Proteobacteria, a phylum primarily made up of diderm taxa, increased under drought across both crops. While Actinobacteria is well-known as a drought tolerant lineage (Santos-Medellín et al., 2017; Moreno-Espindola et al., 2018; Ochoa-Hueso et al., 2018; Preece et al., 2019), the responses of many other bacterial phyla are less consistent. For example, Proteobacteria can increase (Bouskill et al., 2013; Acosta-Martínez et al., 2014; Moreno-Espindola et al., 2018) and decrease (Bachar et al., 2010; Yuste et al., 2014; Naylor and Coleman-Derr, 2018) under drought. Acidobacteria, which decreased with drought in this experiment, has been shown to increase

(Yuste et al., 2014) and decrease (Barnard et al., 2013; Santos-Medellín et al., 2017; Moreno-Espindola et al., 2018) under drought. Overall, we found shifts in bacterial community composition and the relative abundance of phyla consistent with previous research on drought.

Microbial inoculation did not immediately affect bacterial composition or plant growth

We found no immediate effect of microbial inoculation on bacterial communities, plant traits, or microbial response to drought. We only found that the root live inoculum applied directly to the plants decreased bacterial diversity more than 2 other treatments in corn. Inoculation success is often limited in soils because microbes in inocula must compete with the existing soil microbial community (Kaminsky et al., 2019), come in contact with the plant, and survive in a new and stressful environment (Malusá et al., 2012). We attempted to overcome these barriers by testing several inoculation approaches, including 2 inoculum compositions (root and whole soil) and 2 application areas (a root-focused and soil-focused inoculation) to aid in establishment. Given how difficult successful microbial inoculation is, future studies must examine the conditions necessary for inoculum survival and establishment to meet growing interest in microbial inoculation (Malusá et al., 2012). Community characterization with 16 S amplicons is also just one way of characterizing changes in microbial dynamics; inoculation may have had other effects that are relevant to plant and microbial function, as our greenhouse study suggests.

Inoculation had small effects on future plant growth

Although we did not observe changes in community composition as a result of inoculation in the field, a history of inoculation altered future plant growth in the greenhouse. However, the direction of responses was difficult to interpret. We expected that a history of inoculation and drought would lead to greater crop growth under drought. However, we found little evidence that microbial legacies of previous drought affect plant growth, and the legacy effects of field inoculation treatments were greenhouse watering- and crop-dependent. For example, few microbial legacy effects on corn were detected, and for soybean belowground biomass, inoculation only affected plants in the greenhouse drought treatment, but for soybean aboveground biomass, inoculation only affected plants in the greenhouse ambient treatment.

It is somewhat surprising that legacy effects of inoculation were detected given limited evidence that our field inoculation treatments altered microbial community composition; however, these differences between results in the field and greenhouse experiments also may have been due to environmental differences between field and greenhouse settings. Biotic and abiotic differences between field and greenhouse settings can influence plant–microbe interactions. For example, greenhouse experiments often lack soil fauna that may alter plant–microbe interactions (Bezemer et al., 2013; Kuťáková et al., 2018), and greenhouse experiments often lack an existing microbial community, reducing competition for microbes and increasing inoculum establishment (Kaminsky et al., 2019). Abiotic factors such as high nutrient availability from sterilized soil used in greenhouse experiments may make beneficial microbes parasitic (de Deyn et al., 2004). As we aim to identify the role of microbes and microbial inoculation in plant drought response, field studies will be necessary to confirm the importance of microbes in altering plant drought tolerance.

Conclusion

In this study, we demonstrated the successful use of rainout shelters to impose drought in agricultural fields. In this rainout shelter experiment, crop altered responses of soil microbial communities to drought. Although these results should be interpreted cautiously because of the limited replication of field drought treatments, this finding indicates that interactions between plants and microbes likely alter microbial responses to drought. We found that inoculation did not alter crop growth to plants it was applied to, but inoculation had small effects on crops in the greenhouse grown with microbes from previously inoculated soils. This suggests that inoculation may have altered microbial functions via mechanisms other than the changes in microbial diversity and composition that we examined and illustrates the importance for studying legacy effects of inoculation. Overall, we argue that future studies on the importance of microbial communities and inoculation to drought tolerance should incorporate measurements of inoculation legacy effects in field experiments.

Data accessibility statement

Sequence data are available in the NCBI Sequence Read Archive under the BioProject ID PRJNA82367. Data and R scripts for analysis are publicly available at Environmental Data Initiative's Data Portal at https://doi.org/10.6073/pasta/42dc991ce0f931d06ead9b65bb3dc505.

Supplemental files

The supplemental files for this article can be found as follows:

Supplemental Methods, Figures S1–10, and Tables S1–4 can be found in the Jones et al. Supplementary Materials.docx.

Acknowledgments

We thank Holly Vander Stel, Emily Burgess, Rémy Van Geersdaële, Andrew Kelley, Stephanie Clark, Jamie Smith, Tayler Ulbrich, Nick Haddad, Hope Meyers, and Sarah Johnson for support in the field and lab. We thank Allyson Mettler and Nicole Hardy for assisting with greenhouse work. We also thank Joe Simmons, Mark Hammond, Lisa Duke, and Stacey Vanderwulp for providing critical resources and technical support for this project. We acknowledge that field and lab work for this project were completed at Michigan State University and Kellogg Biological station which occupies the ancestral, traditional, and contemporary Lands of the Anishinaabeg—Three Fires Confederacy of Ojibwe, Odawa, and Potawatomi peoples.

For our greenhouse experiment, we wish to acknowledge and honor the Miami, Delaware, Potawatomi, and Shawnee people, on whose ancestral homelands and resources Indiana University Bloomington is built. This is KBS Contribution Number 2316.

Funding

Support for this research was provided by the NSF Long-Term Ecological Research Program (DEB 1832042 and 1637653) at the Kellogg Biological Station AgBioResearch.

Competing interests

The authors declare no competing interests.

Author contributions

Substantial contributions to conception and design: JJ, EB, KK, JL, SE.

Acquisition of data: JJ, EB, KK.

Analysis and interpretation of data: JJ, EB, KK.

Drafting the article or revising it critically for important intellectual content: JJ, EB, JL, SE.

Final approval of the version to be published: JJ, EB, KK, JL, SE.

References

Acosta-Martínez, V, **Cotton, J**, **Gardner, T**, **Moore-Kucera, J**, **Zak, J**, **Wester, D**, **Cox, S.** 2014. Predominant bacterial and fungal assemblages in agricultural soils during a record drought/heat wave and linkages to enzyme activities of biogeochemical cycling. *Applied Soil Ecology* **84**: 69–82. DOI: http://dx.doi.org/10.1016/j.apsoil.2014.06.005.

Alster, CJ, **German, DP**, **Lu, Y**, **Allison, SD.** 2013. Microbial enzymatic responses to drought and to nitrogen addition in a southern California grassland. *Soil Biology and Biochemistry* **64**(C): 68–79. DOI: http://dx.doi.org/10.1016/j.soilbio.2013.03.034.

Bachar, A, **Al-Ashhab, A**, **Soares, MIM**, **Sklarz, MY**, **Angel, R**, **Ungar, ED**, **Gillor, O.** 2010. Soil microbial abundance and diversity along a low precipitation gradient. *Microbial Ecology* **60**(2): 453–461. DOI: http://dx.doi.org/10.1007/s00248-010-9727-1.

Bahadur, A, **Batool, A**, **Nasir, F**, **Jiang, S**, **Mingsen, Q**, **Zhang, Q**, **Pan, J**, **Liu, Y**, **Feng, H.** 2019. Mechanistic insights into arbuscular mycorrhizal fungi-mediated drought stress tolerance in plants. *International Journal of Molecular Sciences* **20**(17): 4199. DOI: http://dx.doi.org/10.3390/ijms20174199.

Bai, Y, **Zhou, X**, **Smith, DL.** 2003. Enhanced soybean plant growth resulting from coinoculation of *Bacillus* strains with *Bradyrhizobium japonicum*. *Crop Science* **43**(5): 1774–1781. DOI: http://dx.doi.org/10.2135/cropsci2003.1774.

Barnard, RL, **Osborne, CA**, **Firestone, MK.** 2013. Responses of soil bacterial and fungal communities to extreme desiccation and rewetting. *ISME Journal* **7**(11): 2229–2241. DOI: http://dx.doi.org/10.1038/ismej.2013.104.

Beier, C, **Beierkuhnlein, C**, **Wohlgemuth, T**, **Penuelas, J**, **Emmett, B**, **Körner, C**, **Boeck, H**, **Christensen, JH**, **Leuzinger, S**, **Janssens, IA**, **Hansen, K.** 2012. Precipitation manipulation experiments—Challenges and recommendations for the future. *Ecology Letters* **15**(8): 899–911. DOI: http://dx.doi.org/10.1111/j.1461-0248.2012.01793.x.

Berger, B, **Patz, S**, **Ruppel, S**, **Dietel, K**, **Faetke, S**, **Junge, H**, **Becker, M.** 2018. Successful formulation and application of plant growth-promoting *Kosakonia radicincitans* in maize cultivation. *BioMed Research International* **2018**(4): 1–8. DOI: http://dx.doi.org/10.1155/2018/6439481.

Bezemer, TM, **Putten, WH**, **Martens, H**, **Voorde, TFJ**, **Mulder, PPJ**, **Kostenko, O.** 2013. Above- and below-ground herbivory effects on below-ground plant–fungus interactions and plant–soil feedback responses. *Journal of Ecology* **101**(2): 325–333. DOI: http://dx.doi.org/10.1111/1365-2745.12045.

Bouskill, NJ, **Lim, HC**, **Borglin, S**, **Salve, R**, **Wood, TE**, **Silver, WL**, **Brodie, EL.** 2013. Pre-exposure to drought increases the resistance of tropical forest soil bacterial communities to extended drought. *ISME Journal* **7**(2): 384–394. DOI: http://dx.doi.org/10.1038/ismej.2012.113.

Brookes, PC, **Landman, A**, **Pruden, G**, **Jenkinson, DS.** 1985. Chloroform fumigation and the release of soil nitrogen: A rapid direct extraction method to measure microbial biomass nitrogen in soil. *Soil Biology and Biochemistry* **17**(6): 837–842. DOI: http://dx.doi.org/10.1016/0038-0717(85)90144-0.

Buchenau, N, **van Kleunen, M**, **Wilschut, RA.** 2022. Direct and legacy-mediated drought effects on plant performance are species-specific and depend on soil community composition. *Oikos* **2022**(5). DOI: http://dx.doi.org/10.1111/oik.08959.

Clark, JS, **Campbell, JH**, **Grizzle, H**, **Acosta-Martìnez, V**, **Zak, JC.** 2009. Soil microbial community response to drought and precipitation variability in the Chihuahuan Desert. *Microbial Ecology* **57**(2): 248–260. DOI: http://dx.doi.org/10.1007/s00248-008-9475-7.

de Deyn, GB, **Raaijmakers, CE**, **Putten, WHVD.** 2004. Plant community development is affected by nutrients and soil biota. *Journal of Ecology* **92**: 824–834.

de Vries, FT, **Griffiths, RI**, **Bailey, M**, **Craig, H**, **Girlanda, M**, **Gweon, HS**, **Hallin, S**, **Kaisermann, A**, **Keith, AM**, **Kretzschmar, M**, **Lemanceau, P**, **Lumini, E**, **Mason, KE**, **Oliver, A**, **Ostle, N**, **Prosser, JI**, **Thion, C**, **Thomson, B**, **Bardgett, RD.** 2018. Soil bacterial networks are less stable under drought than fungal networks. *Nature Communications* **9**(1): 1–12. DOI: http://dx.doi.org/10.1038/s41467-018-05516-7.

Edgar, RC. 2010. Search and clustering orders of magnitude faster than BLAST. *Bioinformatics* **26**(19): 2460–2461. DOI: http://dx.doi.org/10.1093/bioinformatics/btq461.

Edgar, RC. 2013. UPARSE: Highly accurate OTU sequences from microbial amplicon reads. *Nature Methods* **10**(10): 996–998. DOI: http://dx.doi.org/10.1038/nmeth.2604.

Edgar, RC. 2016 Sep 8. SINTAX: A simple non-Bayesian taxonomy classifier for 16 S and ITS sequences. *bioRxiv*: 1–20. DOI: http://dx.doi.org/10.1101/074161.

Evans, SE, **Wallenstein, MD.** 2013. Climate change alters ecological strategies of soil bacteria. *Ecology Letters* **17**(2): 155–164. DOI: http://dx.doi.org/10.1111/ele.12206.

Fahey, C, **Koyama, A**, **Antunes, PM**, **Dunfield, K**, **Flory, SL.** 2020. Plant communities mediate the interactive effects of invasion and drought on soil microbial communities. *ISME Journal* **14**(6): 1396–1409. DOI: http://dx.doi.org/10.1038/s41396-020-0614-6.

Fang, Y, **Xiong, L.** 2015. General mechanisms of drought response and their application in drought resistance improvement in plants. *Cellular and Molecular Life Sciences* **72**(4): 673–689. DOI: http://dx.doi.org/10.1007/s00018-014-1767-0.

Farooq, M, **Wahid, A**, **Kobayashi, N**, **Fujita, D**, **Basra, SMA.** 2009. Plant drought stress: Effects, mechanisms and management. *Agronomy for Sustainable Development* **29**(1): 185–212. DOI: http://dx.doi.org/10.1051/agro:2008021.

Fay, PA, **Carlisle, JD**, **Knapp, AK**, **Blair, JM**, **Collins, SL.** 2000. Altering rainfall timing and quantity in a mesic grassland ecosystem: Design and performance of rainfall manipulation shelters. *Ecosystems* **3**(3): 308–319. DOI: http://dx.doi.org/10.1007/s100210000028.

Fischer, C, **Tischer, J**, **Roscher, C**, **Eisenhauer, N**, **Ravenek, J**, **Gleixner, G**, **Attinger, S**, **Jensen, B**, **de Kroon, H**, **Mommer, L**, **Scheu, S**, **Hildebrandt, A.** 2015. Plant species diversity affects infiltration capacity in an experimental grassland through changes in soil properties. *Plant and Soil* **397**(1–2): 1–16. DOI: http://dx.doi.org/10.1007/s11104-014-2373-5.

Fitzpatrick, CR, **Copeland, J**, **Wang, PW**, **Guttman, DS**, **Kotanen, PM**, **Johnson, MTJ.** 2018. Assembly and ecological function of the root microbiome across angiosperm plant species. *Proceedings of the National Academy Sciences of the Unites States of America* **115**(6): E1157–E1165. DOI: http://dx.doi.org/10.1073/pnas.1717617115.

Forero, LE, **Grenzer, J**, **Heinze, J**, **Schittko, C**, **Kulmatiski, A.** 2019. Greenhouse- and field-measured plant-soil feedbacks are not correlated. *Frontiers in Environmental Science* **7**: 3413–3418. DOI: http://dx.doi.org/10.3389/fenvs.2019.00184.

Ghorchiani, M, **Etesami, H**, **Alikhani, HA.** 2018. Improvement of growth and yield of maize under water stress by co-inoculating an arbuscular mycorrhizal fungus and a plant growth promoting rhizobacterium together with phosphate fertilizers. *Agriculture, Ecosystems and Environment* **258**: 59–70. DOI: http://dx.doi.org/10.1016/j.agee.2018.02.016.

Hao, J, **Chai, YN**, **Lopes, LD**, **Ordóñez, RA**, **Wright, EE**, **Archontoulis, S**, **Schachtman, DP.** 2021. The effects of soil depth on the structure of microbial communities in agricultural soils in Iowa (United States). *Applied and Environmental Microbiology* **87**(4): e02673-20. DOI: http://dx.doi.org/10.1128/aem.02673-20.

Hasibeder, R, **Fuchslueger, L**, **Richter, A**, **Bahn, M.** 2015. Summer drought alters carbon allocation to roots and root respiration in mountain grassland. *New Phytologist* **205**(3): 1117–1127. DOI: http://dx.doi.org/10.1111/nph.13146.

Hawkes, CV, **Kivlin, SN**, **Rocca, JD**, **Huguet, V**, **Thomsen, MA**, **Suttle, KB.** 2011. Fungal community responses to precipitation. *Global Change Biology* **17**(4): 1637–1645. DOI: http://dx.doi.org/10.1111/j.1365-2486.2010.02327.x.

Henry, A, **Doucette, W**, **Norton, J**, **Bugbee, B.** 2007. Changes in crested wheatgrass root exudation caused by flood, drought, and nutrient stress. *Journal of Environmental Quality* **36**(3): 904–912. DOI: http://dx.doi.org/10.2134/jeq2006.0425sc.

Homyak, PM, **Blankinship, JC**, **Slessarev, EW**, **Schaeffer, SM**, **Manzoni, S**, **Schimel, JP.** 2018. Effects of altered dry season length and plant inputs on soluble soil carbon. *Ecology* **99**(10): 2348–2362. DOI: http://dx.doi.org/10.1002/ecy.2473.

Hueso, S, **García, C**, **Hernández, T.** 2012. Severe drought conditions modify the microbial community structure, size and activity in amended and unamended soils. *Soil Biology and Biochemistry* **50**(c): 167–173. DOI: http://dx.doi.org/10.1016/j.soilbio.2012.03.026.

Intergovernmental Panel on Climate Change. 2012. *Managing the risks of extreme events and disasters to advance climate change adaptation. A special report of Working Groups I and II of the Intergovernmental Panel on Climate Change* (Field, CB, Barros, V, Stocker, TF, Dahe, Q, Dokken, JD, Ebi, KL, Mastrandrea, MD, Mach, KJ, Plattner, GK, Allen, SK, Tignor, M, Midgley, PM eds.). Cambridge, UK: Cambridge University Press.

Kaisermann, A, **de Vries, FT**, **Griffiths, RI**, **Bardgett, RD.** 2017. Legacy effects of drought on plant–soil feedbacks and plant–plant interactions. *New Phytologist* **215**(4): 1413–1424. DOI: http://dx.doi.org/10.1111/nph.14661.

Kallenbach, CM, **Grandy, AS**, **Frey, SD**, **Diefendorf, AF.** 2015. Microbial physiology and necromass regulate agricultural soil carbon accumulation. *Soil Biology and Biochemistry* **91**(C): 279–290. DOI: http://dx.doi.org/10.1016/j.soilbio.2015.09.005.

Kaminsky, LM, **Trexler, RV**, **Malik, RJ**, **Hockett, KL**, **Bell, TH.** 2019. The inherent conflicts in developing soil microbial inoculants. *Trends in Biotechnology* **37**(2): 140–151. DOI: http://dx.doi.org/10.1016/j.tibtech.2018.11.011.

Kant, S, **Thoday-Kennedy, E**, **Joshi, S**, **Vakani, J**, **Hughes, J**, **Maphosa, L**, **Sadler, A**, **Menidis, M**, **Slater, A**, **Spangenberg, G.** 2017. Automated rainout shelter's design for well-defined water stress field phenotyping of crop plants. *Crop Science* **57**(1): 327–331. DOI: http://dx.doi.org/10.2135/cropsci2016.08.0677.

Karlowsky, S, **Augusti, A**, **Ingrisch, J**, **Akanda, MKU**, **Bahn, M**, **Gleixner, G.** 2018. Drought-induced accumulation of root exudates supports post-drought recovery of microbes in mountain grassland. *Frontiers in Plant Science* **9**: 1593. DOI: http://dx.doi.org/10.3389/fpls.2018.01593.

Koyama, A, **Steinweg, JM**, **Haddix, ML**, **Dukes, JS**, **Wallenstein, MD.** 2017. Soil bacterial community responses to altered precipitation and temperature regimes in an old field grassland are mediated by plants. *FEMS Microbiology Ecology* **94**(1). DOI: http://dx.doi.org/10.1093/femsec/fix156.

Kozich, JJ, **Westcott, SL**, **Baxter, NT**, **Highlander, SK**, **Schloss, PD.** 2013. Development of a dual-index sequencing strategy and curation pipeline for analyzing amplicon sequence data on the MiSeq Illumina sequencing platform. *Applied and Environmental Microbiology* **79**(17): 5112–5120. DOI: http://dx.doi.org/10.1128/aem.01043-13.

Kundel, D, **Meyer, S**, **Birkhofer, H**, **Fliessbach, A**, **Mäder, P**, **Scheu, S**, **van Kleunen, M**, **Birkhofer, K.** 2018. Design and manual to construct rainout-shelters for climate change experiments in agroecosystems. *Frontiers in Environmental Science* **6**: 14. DOI: http://dx.doi.org/10.3389/fenvs.2018.00014.

Kuťáková, E, **Cesarz, S**, **Münzbergová, Z**, **Eisenhauer, N.** 2018. Soil microarthropods alter the outcome of plant-soil feedback experiments. *Scientific Reports* **8**(1): 11898. DOI: http://dx.doi.org/10.1038/s41598-018-30340-w.

Lankau, RA, **George, I**, **Miao, M.** 2022. Crop performance is predicted by soil microbial diversity across phylogenetic scales. *Ecosphere* **13**: e4029. DOI: http://dx.doi.org/10.1002/ecs2.4029.

Lau, JA, **Lennon, J.** 2012. Rapid responses of soil microorganisms improve plant fitness in novel environments. *Proceedings of the National Academy Sciences of the Unites States of America* **109**(35): 14058–14062. DOI: http://dx.doi.org/10.5061/dryad.qc537.

Lefèvre, C, **Rekik, F**, **Alcantara, V**, **Wiese, L.** 2017. *Soil organic carbon: The hidden potential*. Rome, Italy: Food and Agriculture Organization of the United Nations.

Lesk, C, **Rowhani, P**, **Ramankutty, N.** 2019. Influence of extreme weather disasters on global crop production. *Nature* **529**: 84–87. DOI: http://dx.doi.org/10.1038/nature16467.

Li, Y, **Ye, W**, **Wang, M**, **Yan, X.** 2009. Climate change and drought: A risk assessment of crop-yield impacts. *Climate Research* **39**: 31–46. DOI: http://dx.doi.org/10.3354/cr00797.

Malusá, E, **Sas-Paszt, L**, **Ciesielska, J.** 2012. Technologies for beneficial microorganisms inocula used as biofertilizers. *The Scientific World Journal* **2012**(1): 1–12. DOI: http://dx.doi.org/10.1100/2012/491206.

Maynard, DS, **Crowther, TW**, **Bradford, MA.** 2017. Competitive network determines the direction of the diversity–function relationship. *Proceedings of the National Academy Sciences of the Unites States of America* **114**(43): 11464–11469. DOI: http://dx.doi.org/10.1073/pnas.1712211114.

Meisner, A, **Jacquiod, S**, **Snoek, BL**, **ten Hooven, FC**, **van der Putten, WH.** 2018. Drought legacy effects on the composition of soil fungal and prokaryote communities. *Frontiers in Microbiology* **9**: 294. DOI: http://dx.doi.org/10.3389/fmicb.2018.00294.

Minasny, B, **McBratney, AB.** 2018. Limited effect of organic matter on soil available water capacity. *European Journal of Soil Science* **69**(1): 39–47. DOI: http://dx.doi.org/10.1111/ejss.12475.

Moore, JAM, **Abraham, PE**, **Michener, JK**, **Muchero, W**, **Cregger, MA.** 2022. Ecosystem consequences of introducing plant growth promoting rhizobacteria to managed systems and potential legacy effects. *New Phytologist* **234**(6): 1914–1918. DOI: http://dx.doi.org/10.1111/nph.18010.

Moreno-Espindola, IP, **Ferrara-Guerrero, MJ**, **Luna-Guido, ML**, **Ramirez-Villanueva, DA**, **Leon-Lorenzana, ASD**, **Gomez-Acata, S**, **Gonzalez-Terreros, E**, **Ramirez-Barajas, B**, **Navarro-Noya, YE**, **Sanchez-Rodriguez, LM**, **Fuentes-Ponce, M**, **Macedas-Jimenez, JU**, **Dendooven, L.** 2018. The bacterial community structure and microbial activity in a traditional organic milpa farming system under different soil moisture conditions. *Frontiers in Microbiology* **9**. DOI: http://dx.doi.org/10.3389/fmicb.2018.02737.

Naylor, D, **Coleman-Derr, D.** 2018. Drought stress and root-associated bacterial communities. *Frontiers in Plant Science* **8**: 69–76. DOI: http://dx.doi.org/10.3389/fpls.2017.02223.

Naylor, D, **DeGraaf, S**, **Purdom, E**, **Coleman-Derr, D.** 2017. Drought and host selection influence bacterial community dynamics in the grass root microbiome. *ISME Journal* **11**(12): 2691–2704. DOI: http://dx.doi.org/10.1038/ismej.2017.118.

Ngumbi, E, **Kloepper, J.** 2016. Bacterial-mediated drought tolerance: Current and future prospects. *Applied Soil Ecology* **105**: 109–125. DOI: http://dx.doi.org/10.1016/j.apsoil.2016.04.009.

Ochoa-Hueso, R, **Collins, SL**, **Delgado-Baquerizo, M**, **Hamonts, K**, **Pockman, WT**, **Sinsabaugh, RL**, **Smith, MD**, **Knapp, AK**, **Power, SA.** 2018. Drought consistently alters the composition of soil fungal and bacterial communities in grasslands from two continents. *Global Change Biology* **24**(7): 2818–2827. DOI: http://dx.doi.org/10.1111/gcb.14113.

Ortiz, N, **Armada, E**, **Duque, E**, **Roldán, A**, **Azcón, R.** 2015. Contribution of arbuscular mycorrhizal fungi and/or bacteria to enhancing plant drought tolerance under natural soil conditions: Effectiveness of autochthonous or allochthonous strains. *Journal of Plant Physiology* **174**: 87–96. DOI: http://dx.doi.org/10.1016/j.jplph.2014.08.019.

Osburn, ED, **Badgley, BD**, **Aylward, FO**, **Barrett, JE.** 2021. Historical forest disturbance mediates soil microbial community responses to drought.

Environmental Microbiology **23**(11): 6405–6419. DOI: http://dx.doi.org/10.1111/1462-2920.15706.

Pavithra, D, **Yapa, N.** 2018. Arbuscular mycorrhizal fungi inoculation enhances drought stress tolerance of plants. *Groundwater for Sustainable Development* **7**: 490–494. DOI: http://dx.doi.org/10.1016/j.gsd.2018.03.005.

Poorter, H, **Niinemets, Ü**, **Poorter, L**, **Wright, IJ**, **Villar, R.** 2009. Causes and consequences of variation in leaf mass per area (LMA): A meta-analysis. *New Phytologist* **182**(3): 565–588. DOI: http://dx.doi.org/10.1111/j.1469-8137.2009.02830.x.

Preece, C, **Verbruggen, E**, **Liu, L**, **Weedon, JT**, **Peñuelas, J.** 2019. Effects of past and current drought on the composition and diversity of soil microbial communities. *Soil Biology and Biochemistry* **131**: 28–39. DOI: http://dx.doi.org/10.1016/j.soilbio.2018.12.022.

Prudent, M, **Dequiedt, S**, **Sorin, C**, **Girodet, S**, **Nowak, V**, **Duc, G**, **Salon, C**, **Maron, P-A.** 2020. The diversity of soil microbial communities matters when legumes face drought. *Plant, Cell & Environment* **43**(4): 1023–1035. DOI: http://dx.doi.org/10.1111/pce.13712.

Quast, C, **Pruesse, E**, **Yilmaz, P**, **Gerken, J**, **Schweer, T**, **Yarza, P**, **Peplies, J**, **Glöckner, FO.** 2013. The SILVA ribosomal RNA gene database project: Improved data processing and web-based tools. *Nucleic Acids Research* **41**(D1): D590–D596. DOI: http://dx.doi.org/10.1093/nar/gks1219.

Quiroga, G, **Erice, G**, **Aroca, R**, **Chaumont, F**, **Ruiz-Lozano, JM.** 2017. Enhanced drought stress tolerance by the arbuscular mycorrhizal symbiosis in a drought-sensitive maize cultivar is related to a broader and differential regulation of host plant aquaporins than in a drought-tolerant cultivar. *Frontiers in Plant Science* **8**: 1056. DOI: http://dx.doi.org/10.3389/fpls.2017.01056.

Reid, CPP. 1974. Assimilation, distribution, and root exudation of 14C by ponderosa pine seedlings under induced water stress. *Plant Physiology* **54**: 44–49.

Robertson, GP, **Gross, KL**, **Hamilton, SK**, **Landis, DA**, **Schmidt, TM**, **Snapp, SS**, **Swinton, SM.** 2014. Farming for ecosystem services: An ecological approach to production agriculture. *BioScience* **64**: 404–415. DOI: https://doi.org/10.1093/biosci/biu037.

Robertson, GP, **Hamilton, SK.** 2015. Long-term ecological research in agricultural landscapes at the Kellogg Biological Station LTER site: Conceptual and experimental framework. *The Ecology of Agricultural Landscapes: Long-term Research on the Path to Sustainability*: 1–32. Available at https://lter.kbs.msu.edu/wp-content/uploads/2015/04/Robertson-Hamilton-Ch1-Conceptual-and-experimental-framework-KBS-long-term-ecological-research-LTER-site-volume-synthesis-book-2015.pdf. Accessed 13 October 2022.

Ruehr, NK, **Offermann, CA**, **Gessler, A**, **Winkler, JB**, **Ferrio, JP**, **Buchmann, N**, **Barnard, RL.** 2009. Drought effects on allocation of recent carbon: From beech leaves to soil CO_2 efflux. *New Phytologist* **184**(4): 950–961. DOI: http://dx.doi.org/10.1111/j.1469-8137.2009.03044.x.

Santos-Medellín, C, **Edwards, J**, **Liechty, Z**, **Nguyen, B**, **Sundaresan, V.** 2017. Drought stress results in a compartment-specific restructuring of the rice root-associated microbiomes. *mBio* **8**(4): e00764-17. DOI: http://dx.doi.org/10.1128/mbio.00764-17.

Sarma, RK, **Saikia, R.** 2013. Alleviation of drought stress in mung bean by strain *Pseudomonas aeruginosa* GGRJ21. *Plant and Soil* **377**(1–2): 111–126. DOI: http://dx.doi.org/10.1007/s11104-013-1981-9.

Sasse, J, **Martinoia, E**, **Northen, T.** 2018. Feed your friends: Do plant exudates shape the root microbiome? *Trends in Plant Science* **23**(1): 25–41. DOI: http://dx.doi.org/10.1016/j.tplants.2017.09.003.

Schimel, J, **Balser, TC**, **Wallenstein, M.** 2007. Microbial stress-response physiology and its implications for ecosystem function. *Ecology* **88**(6): 1386–1394. DOI: http://dx.doi.org/10.1890/06-0219.

Schimel, JP. 2018. Life in dry soils: Effects of drought on soil microbial communities and processes. *Annual Review of Ecology, Evolution, and Systematics* **49**(1): 409–432. DOI: http://dx.doi.org/10.1146/annurev-ecolsys-110617-062614.

Shirinbayan, S, **Khosravi, H**, **Malakouti, MJ.** 2019. Alleviation of drought stress in maize (*Zea mays)* by inoculation with *Azotobacter* strains isolated from semi-arid regions. *Applied Soil Ecology* **133**: 138–145. DOI: http://dx.doi.org/10.1016/j.apsoil.2018.09.015.

Swain, S, **Wardlow, BD**, **Narumalani, S**, **Rundquist, DC**, **Hayes, MJ.** 2013. Relationships between vegetation indices and root zone soil moisture under maize and soybean canopies in the US Corn Belt: A comparative study using a close-range sensing approach. *International Journal of Remote Sensing* **34**(8): 2814–2828. DOI: http://dx.doi.org/10.1080/01431161.2012.750020.

Takács, T, **Cseresnyés, I**, **Kovács, R**, **Parádi, I**, **Kelemen, B**, **Szili-Kovács, T**, **Füzy, A.** 2018. Symbiotic effectivity of dual and tripartite associations on soybean (*Glycine max* L. Merr.) cultivars inoculated with *Bradyrhizobium japonicum* and AM Fungi. *Frontiers in Plant Science* **9**(1631): 1–14. DOI: http://dx.doi.org/10.3389/fpls.2018.01631.

Tecon, R, **Or, D.** 2017. Biophysical processes supporting the diversity of microbial life in soil. *FEMS Microbiology Reviews* **41**(5): 599–623. DOI: http://dx.doi.org/10.1093/femsre/fux039.

Veach, AM, **Chen, H**, **Yang, ZK**, **Labbe, AD**, **Engle, NL**, **Tschaplinski, TJ**, **Schadt, CW**, **Cregger, MA.** 2020. Plant hosts modify belowground microbial community response to extreme drought. *Msystems* **5**(3): e00092-20. DOI: http://dx.doi.org/10.1128/msystems.00092-20.

Wagg, C, **Schlaeppi, K**, **Banerjee, S**, **Kuramae, EE**, **van der Heijden, MGA.** 2019. Fungal-bacterial diversity and microbiome complexity predict ecosystem

functioning. *Nature Communications* **10**(1): 4841. DOI: http://doi.org/10.1038/s41467-019-12798-y.

Williams, A, **de Vries, FT.** 2019. Plant root exudation under drought: Implications for ecosystem functioning. *New Phytologist* **225**(5): 1899–1905. DOI: http://dx.doi.org/10.1111/nph.16223.

Wu, J, **Joergensen, RG**, **Pommerening, B**, **Chaussod, R**, **Brookes, PC.** 1990. Measurement of soil microbial biomass C by fumigation-extraction-an automated procedure. *Soil Biology and Biochemistry* **22**(8): 1167–1169.

Xu, L, **Coleman-Derr, D.** 2019. Causes and consequences of a conserved bacterial root microbiome response to drought stress. *Current Opinion in Microbiology* **49**: 1–6. DOI: http://dx.doi.org/10.1016/j.mib.2019.07.003.

Xu, L, **Naylor, D**, **Dong, Z**, **Simmons, T**, **Pierroz, G**, **Hixson, KK**, **Kim, Y-M**, **Zink, EM**, **Engbrecht, KM**, **Wang, Y**, **Gao, C**, **DeGraaf, S**, **Madera, MA**, **Sievert, JA**, **Hollingsworth, J**, **Birdseye, D**, **Scheller, HV**, **Hutmacher, R**, **Dahlberg, J**, **Jansson, C**, **Taylor, JW**, **Lemaux, PG**, **Coleman-Derr, D.** 2018. Drought delays development of the sorghum root microbiome and enriches for monoderm bacteria. *Proceedings of the National Academy Sciences of the Unites States of America* **115**(18): E4284–E4293. DOI: http://dx.doi.org/10.1073/pnas.1717308115.

Yuste, JC, **Fernandez-Gonzalez, AJ**, **Fernandez-Lopez, M**, **Ogaya, R**, **Penuelas, J**, **Sardans, J**, **Lloret, F.** 2014. Strong functional stability of soil microbial communities under semiarid Mediterranean conditions and subjected to long-term shifts in baseline precipitation. *Soil Biology Biochemistry* **69**: 223–233. DOI: http://dx.doi.org/10.1016/j.soilbio.2013.10.045.

Zhang, H, **Prithiviraj, B**, **Charles, TC**, **Driscoll, BT**, **Smith, DL.** 2003. Low temperature tolerant *Bradyrhizobium japonicum* strains allowing improved nodulation and nitrogen fixation of soybean in a short season (cool spring) area. *European Journal of Agronomy* **19**(2): 205–213. DOI: http://dx.doi.org/10.1016/s1161-0301(02)00038-2.

Zipper, SC, **Qiu, J**, **Kucharik, CJ.** 2016. Drought effects on US maize and soybean production: Spatiotemporal patterns and historical changes. *Environmental Research Letters* **11**(9): 094021. DOI: http://dx.doi.org/10.1088/1748-9326/11/9/094021.

How to cite this article: Jones, JM, Boehm, EL, Kahmark, K, Lau, J, Evans, S. 2022. Microbial community response to drought depends on crop. *Elementa: Science of the Anthropocene* 10(1). DOI: https://doi.org/10.1525/elementa.2021.00110

Domain Editor-in-Chief: Steven Allison, University of California Irvine, Irvine, CA, USA

Guest Editor: Moira Hough, Soil, Water and Environmental Science, The University of Arizona, Tucson, AZ, USA

Knowledge Domain: Ecology and Earth Systems

Part of an Elementa Special Feature: The World of Underground Ecology in a Changing Environment

Published: October 28, 2022 **Accepted:** September 1, 2022 **Submitted:** November 19, 2021