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REPORT

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Traits of soil bacteria predict plant responses to soil moisture

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Abstract

Microorganisms can help plants and animals contend with abiotic stressors, but why they provide such benefits remains unclear. Here we investigated byproduct benefits, which occur when traits that increase the fitness of one species provide incidental benefits to another species with no direct cost to the provider. In a greenhouse experiment, microbial traits predicted plant responses to soil moisture such that bacteria with self-beneficial traits in drought increased plant early growth, size at reproduction, and chlorophyll concentration under drought, while bacteria with self-beneficial traits in well-watered environments increased these same plant traits in well-watered soils. Thus, microbial traits that promote microbial success in different moisture environments also promote plant success in these same environments. Our results demonstrate that byproduct benefits, a concept developed to explain the evolution of cooperation in pairwise mutualisms, can also extend to interactions between plants and nonsymbiotic soil microbes.

KEYWORDS
byproduct benefit, cooperation, drought, functional traits, plant–microbe interactions

INTRODUCTION

Plants and animals can adapt to a wide range of abiotic environments, but they often are not doing it alone. Instead, microbes can respond to abiotic environments in ways that help maintain plant and animal fitness via "microbial rescue" (sensu Mueller et al., 2020; also called "microbe-mediated adaptation" sensu Petipas et al., 2021). For example, cold exposure caused gut microbial community composition to shift in ways that promote cold tolerance in rodents (Chevalier et al., 2015), serpentine soil-adapted fungi promoted plant growth and phosphorus uptake in these phosphorus-limited soils (Doubková et al., 2012), and endophytic fungi from hotter, drier environments promoted plant growth in drought (Giauque et al., 2019). The microbial benefits from these examples and others (e.g., Allsup & Lankau, 2019; Fitzpatrick et al., 2018; Lau & Lennon, 2012; Yuan et al., 2019) may help diverse plant and animal populations persist in stressful environments, but why microbes provide these benefits remains unresolved.

A strong foundation of theory informs understanding of the evolution of cooperation between closely interacting pairs of species. However, explaining the host fitness-promoting effects of non-symbiotic, diffusely interacting species is more challenging because it is unclear how the fitness of these species could become correlated (Hawkes et al., 2020; Sachs et al., 2004). One potential driver of microbial rescue in such systems is byproduct benefits, which occur when the self-serving act of one species provides an incidental benefit to another species, with no direct cost to the provider (Sachs et al., 2004). Byproduct benefits can appear cooperative, but are not in the classic sense because classic

cooperation requires a cost to the provider species. Mechanisms that result in classic cooperation could also contribute to beneficial interactions between diffuse, non-symbiotic partners. For example, partner choice could contribute if hosts can selectively reward the most beneficial non-symbiotic microbes, and partner fidelity feedbacks could contribute if hosts can selectively transfer beneficial non-symbiotic microbes to their offspring. However, classic cooperation may be less likely to occur when potential interactors re-assemble each generation (Hawkes et al., 2020; Sachs et al., 2004).

Byproduct benefits also may commonly promote microbial rescue because microbial communities are functionally diverse, allowing for rapid changes in microbial traits in different environments due either to rapid evolution or to changes in microbial community composition (Elena & Lenski, 2003; Graves Jr et al., 2015). The traits expressed in these changed microbial communities could then incidentally affect plant or animal responses to the environment. For example, herbicide application could select for microbes that degrade herbicide, which could then reduce soil herbicide stress for plants.

Here we investigated whether byproduct benefits can explain microbial rescue. We tested whether self-beneficial microbial traits under drought or well-watered conditions benefit plants in these same environments, and found evidence that byproduct benefits may explain previous observations of microbial communities responding to stress in ways that promote plant stress tolerance.

METHODS

Experimental design overview

We grew individuals of the annual legume *Chamaecrista fasciculata* (*Chamaecrista* hereafter) under well-watered or drought-stressed conditions and inoculated pots with one of 14 phylogenetically diverse bacterial strains representing three phyla and 12 families that varied in biofilm production and optimum water potential ($N = [14$ microbial strains $+ 4$ sterile controls$] \times 2$ watering treatments $\times 5$ replicates $= 140$ plants; Appendix S1: Figures S1 and S2, Table S1). We measured the influence of each bacterial trait on plant growth, as well as several plant traits that commonly respond to drought: leaf chlorophyll concentration, specific leaf area (SLA), timing of reproduction, and size at reproduction. Drought can reduce chlorophyll concentration by decreasing the lability of nutrients in dry soils (Evans, 1989); early flowering is a common drought avoidance strategy; and lower SLA is associated with greater water use efficiency (Ackerly, 2004).

The design ensured that any benefit conferred by microbes could derive only from byproduct benefits, and not classic cooperation. Classic cooperation requires repeated interactions between partners ("partner fidelity feedbacks"), multiple partners to choose from ("partner choice"), or close relatedness between partners ("kin selection"; Sachs et al., 2004). We eliminated these possibilities by using bacterial strains that are naïve to *Chamaecrista* (strains were isolated from bulk soil in an area where *Chamaecrista* did not occur) and by inoculating single strains into sterilized soil, thereby preventing partner fidelity feedbacks and partner choice. If byproduct benefits occur, then we expect traits that are beneficial for microbes in drought and well-watered environments to benefit plants in those same environments.

Bacterial strains

The bacteria used in this experiment were isolated from bulk soils at the W.K. Kellogg Biological Station Long-Term Ecological Research site (KBS LTER, Hickory Corners, Michigan, USA). Strains had been previously sequenced using the 16S rRNA gene and characterized for a range of functional traits, including biofilm production and optimum water potential (Lennon et al., 2012). Strains with low optimum water potentials achieve maximum growth in dry environments, making low optimum water potential an adaptive bacterial phenotype under drought, and high biofilm production is generally adaptive under drought because it reduces desiccation stress (Lennon et al., 2012; Lennon & Lehmkuhl, 2016). Biofilm production was previously estimated using the Crystal Violet assay (O'Toole et al., 1999) and optimum water potential was estimated as the soil water potential at which a strain achieved maximum respiration rate (respiration rate strongly correlates with growth in these strains; see Lennon et al., 2012 for details). We selected 14 strains from this collection to maximize variation in biofilm production and optimum water potential. Therefore, although the traits correlated positively across the full collection of strains (Lennon et al., 2012), they were uncorrelated in our subset ($r = -0.09$, $p = 0.64$; Appendix S1: Figure S1), allowing us to statistically partition the effects of each bacterial trait on plant traits. Additionally, we prepared four sterile control inocula (Appendix S2). Prior to inoculation, each bacterial strain was grown in R2B medium (BD Difco, Sparks, Maryland, USA). Cells were then washed three times in PBS. High densities of each strain were applied (i.e., strains were applied when all cultures were turbid), but cell densities were not standardized across inocula (see "*Caveats*" below). For details on strains and inoculum preparation, see Appendix S2.

Greenhouse experiment

We sterilized and filled 656 ml Deepots (Stuewe and Sons, Tangent, Oregon, USA) with a sterile base soil composed of a 1:1 mixture of sand and our standard greenhouse mix (field soil mixed with organic material) that was twice steam sterilized (6 hours at 77°C with a 24 hour rest between sterilizations), and we planted a single scarified and imbibed *Chamaecrista* seed (Prairie Moon Nursery, Winona, Minnesota, USA) into each pot. We then inoculated each bacterial strain onto 10 spatially randomized pots by pipetting 1 ml of inoculum onto the thin layer of soil directly covering the seed. To aid in bacterial establishment, we reinoculated all pots 12 days after the initial inoculation (when most plants were at the three-leaf stage) by pipetting 1 ml of inoculum onto soil at the base of the plant.

We kept all plants wellwatered for the first two weeks to promote plant establishment, at which point we began imposing drought stress on half of the replicates of each microbial inoculum treatment ($n = 5$ per strain). We watered all plants in the drought treatment only when they began showing signs of stress (i.e., wilting, 250 ml every ~10 days), whereas we kept plants in the well-watered treatment well-watered throughout (250 ml approximately every 5 days). We fertilized all plants with 250 ml of 1% 20:20:20 NPK fertilizer 7 and 10 weeks after planting.

Plant measurements

We measured six plant traits that commonly respond to drought: early growth, leaf chlorophyll concentration, SLA, timing of reproduction, size at reproduction, and final biomass. Four weeks after planting, we counted the number of fully expanded leaves as an estimate of early growth, and measured leaf chlorophyll concentration as an indicator of plant nitrogen status (SPAD 502; Spectrum Technologies, Inc., Plainfield, Illinois, USA). Ten weeks after planting, we estimated SLA (leaf area/leaf dry weight) on the fifth fully expanded leaf on the main stem (or the nearest healthy leaf if the fifth was damaged) by measuring the area of each leaf on a leaf area meter (LI-3100C, LI-COR Biosciences, Lincoln, Nebraska, USA), then drying (60°C for 14 days) and weighing. We recorded flowering date and the number of fully expanded leaves at the time of first flower as an estimate of plant size at reproduction. After all plants had flowered (10.5 weeks), we separated, dried (for at least 2 weeks at 60°C), and weighed all shoot and root biomass.

Statistical analyses

To test whether bacterial biofilm production and optimum water potential predicted plant responses to soil moisture, we fit phylogenetic generalized least squares (PGLS) models in R (*nlme* package v3.1-150; Martins & Hansen, 1997; Pinheiro et al., 2018; R Core Team, 2020). These models control for phylogenetic nonindependence of the bacterial strains, but they cannot account for variation among individuals inoculated with a given strain or microsite differences in the greenhouse (i.e., strain and greenhouse block cannot be included as random or fixed effects). To statistically control for microsite differences in the greenhouse, we created a detrended dataset by first regressing greenhouse block onto each plant trait, then adding each plant's residual trait value to the global mean to return traits to their original scale. Then, because the unit of replication is the bacterial strain, we conducted our analyses on strain means within each watering treatment (Huang et al., 2018). Strains did not differ in variance for any plant traits except time of reproduction and final biomass, which were not significantly predicted by bacterial traits (see *Results*; Bartlett's K^2: all $p > 0.3$ except time of reproduction $p = 0.047$, and final biomass $p = 0.002$), suggesting that this was a reasonable approach. We constructed a phylogenetic tree using the 16S rRNA gene sequences of our strains generated by Lennon et al. (2012). We aligned these sequences (MUSCLE v3.8.31; Edgar, 2004) and generated a maximum likelihood tree with 100 bootstrap replicates (RAxML v8.2.12; Stamatakis, 2014) using the General Time Reversible (GTR) model of nucleotide substitution with a gamma distributed substitution rate. We then built the correlation structure of our tree that would be expected if the traits evolve under Brownian motion (*ape* package v5.4-1; Paradis & Schliep, 2019) and fit PGLS models assuming this correlation structure.

We analyzed each plant response variable separately in models that included bacterial biofilm production, bacterial optimum water potential, watering treatment (drought or well-watered), and all interactions as fixed effects. We *ln*-transformed optimum water potential because water potential is a nonlinear function of volumetric water content such that small reductions in water content in dry soils are associated with large reductions in water potential (Bilskie and Campbell Scientific, 2001). To do this we multiplied all values by −1 to make them positive (water potentials are always negative), took the natural logarithm of the positive value, then multiplied again by −1 to return values to their original order. We standardized both bacterial traits to a mean of zero and a variance of one to make coefficients comparable and to

prevent the generation of spurious correlations between each trait and their interaction, which can happen when predictors are expressed on different scales (Aiken et al., 1991). We assessed statistical significance using Type III ANOVA (*car* package v3.1-10; Fox & Weisberg, 2019).

Because we could not include within-strain variation in our PGLS models, we conducted additional analyses that accounted for within-strain variation, but that did not control for phylogenetic non-independence. We fit linear mixed models (*lme4* package in R; Bates et al., 2015) using the original non-detrended data that included bacterial biofilm production, bacterial optimum water potential, watering treatment, and all interactions as fixed effects, and included strain and greenhouse block as random effects.

RESULTS

Bacterial traits predicted the magnitude of plant responses to soil moisture. Bacteria with low optimum water potentials (dry-adapted bacteria) reduced the negative effects of drought on plant early growth and size at reproduction, whereas bacteria with high optimum water potentials (wet-adapted bacteria) increased the benefits plants received from growing in well-watered conditions (drought × optimum, early growth: $\chi^2_{1,20} = 8.3$, $p < 0.01$; size at reproduction: $\chi^2_{1,20} = 7.6$, $p < 0.01$; Figure 1a,c; Appendix S1: Table S2). As a result, drought reduced predicted plant early growth by 44% and size at reproduction by 49% when pots were inoculated with microbes with the highest optimum water potential, compared with only 33% and 30%, respectively, when inoculated with microbes with the lowest optimum water potential. Additionally, plants inoculated with bacteria with low optimum water potentials showed smaller reductions in SLA in response to drought than plants inoculated with bacteria with high optimum water potentials (drought × optimum: $\chi^2_{1,20} = 4.3$, $p = 0.04$; Figure 1e, Appendix S1: Table S2). Mixed models that included strain variation but excluded phylogeny showed similar effects for plant early growth, but resulted in nonsignificant effects for size at reproduction and SLA (drought × optimum, early growth: $\chi^2_{1,20} = 4.1$, $p = 0.04$; size at reproduction: $\chi^2_{1,20} = 2.4$, $p = 0.12$; SLA: $\chi^2_{1,20} = 0.05$, $p = 0.82$; Appendix S1: Table S3).

Bacteria that produce large amounts of biofilm also mitigated the negative effects of drought on plants. Drought reduced predicted plant early growth by 42% and size at reproduction by 45% when pots were inoculated with microbes with the lowest biofilm production, compared to only 33% and 31%, respectively, when inoculated with microbes with the highest biofilm production (drought × biofilm, early growth: $\chi^2_{1,20} = 6.2$, $p = 0.01$; size at reproduction: $\chi^2_{1,20} = 4.4$, $p = 0.04$; Figure 1b,d; Appendix S1: Table S2). Bacterial biofilm production also influenced plant chlorophyll responses to soil moisture (drought × biofilm: $\chi^2_{1,20} = 30.1$, $p < 0.001$; Figure 1f). Specifically, well-watered plants had lower chlorophyll concentrations (drought: $\chi^2_{1,20} = 243$, $p < 0.001$), especially when inoculated with high biofilm-producing bacteria. This occurred because high biofilm-producing bacteria reduced chlorophyll in well-watered conditions (biofilm: $\chi^2_{1,10} = 7.8$, $p < 0.01$), whereas biofilm did not affect chlorophyll under drought ($\chi^2_{1,10} = 0.03$, $p = 0.86$). Note, however, that well-watered plants had more chlorophyll on a per plant basis (estimated as chlorophyll concentration per leaf × leaf number) than drought-stressed plants because they were larger (drought: $p < 0.001$; Figure 1a; Appendix S1: Figure S3). Mixed models that included strain variation, but excluded phylogeny, did not reveal any effects of biofilm production on plant traits (all $p > 0.16$; Appendix S1: Table S3).

The effect of each bacterial trait on plant SLA and chlorophyll responses to soil moisture depended on the other bacterial trait (PGLS analyses: drought × optimum × biofilm, SLA: $\chi^2_{1,20} = 17.75$, $p < 0.001$; chlorophyll: $\chi^2_{1,20} = 18.76$, 17.75, $p < 0.001$; Appendix S1: Figure S4). However, these results should be interpreted cautiously because our data are not evenly distributed across the response surface (Albert et al., 2010), and these interactions were not statistically significant in the mixed models.

Drought stress reduced plant final biomass by 36% (drought: $\chi^2_{1,20} = 76.5$, $p < 0.001$), and accelerated plant flowering by 4.5 days (drought: $\chi^2_{1,20} = 9.1$, $p < 0.01$), but these plant traits were not affected by bacterial traits (Appendix S1: Figure S5).

DISCUSSION

We showed that self-beneficial bacterial traits under drought (low optimum water potential and high biofilm production) also benefited plants under drought, while self-beneficial bacterial traits in well-watered soils (high optimum water potential and low biofilm production) also benefited plants in well-watered soils. This resulted in drought-stressed plants more closely resembling the well-watered phenotype when grown with bacteria with drought-ameliorating traits (Figure 1a–d,f). These findings indicate that byproduct benefits can contribute to microbial rescue, and illustrate how theory on the evolution of cooperation can explain fitness correlations between diffusely interacting pairs of species.

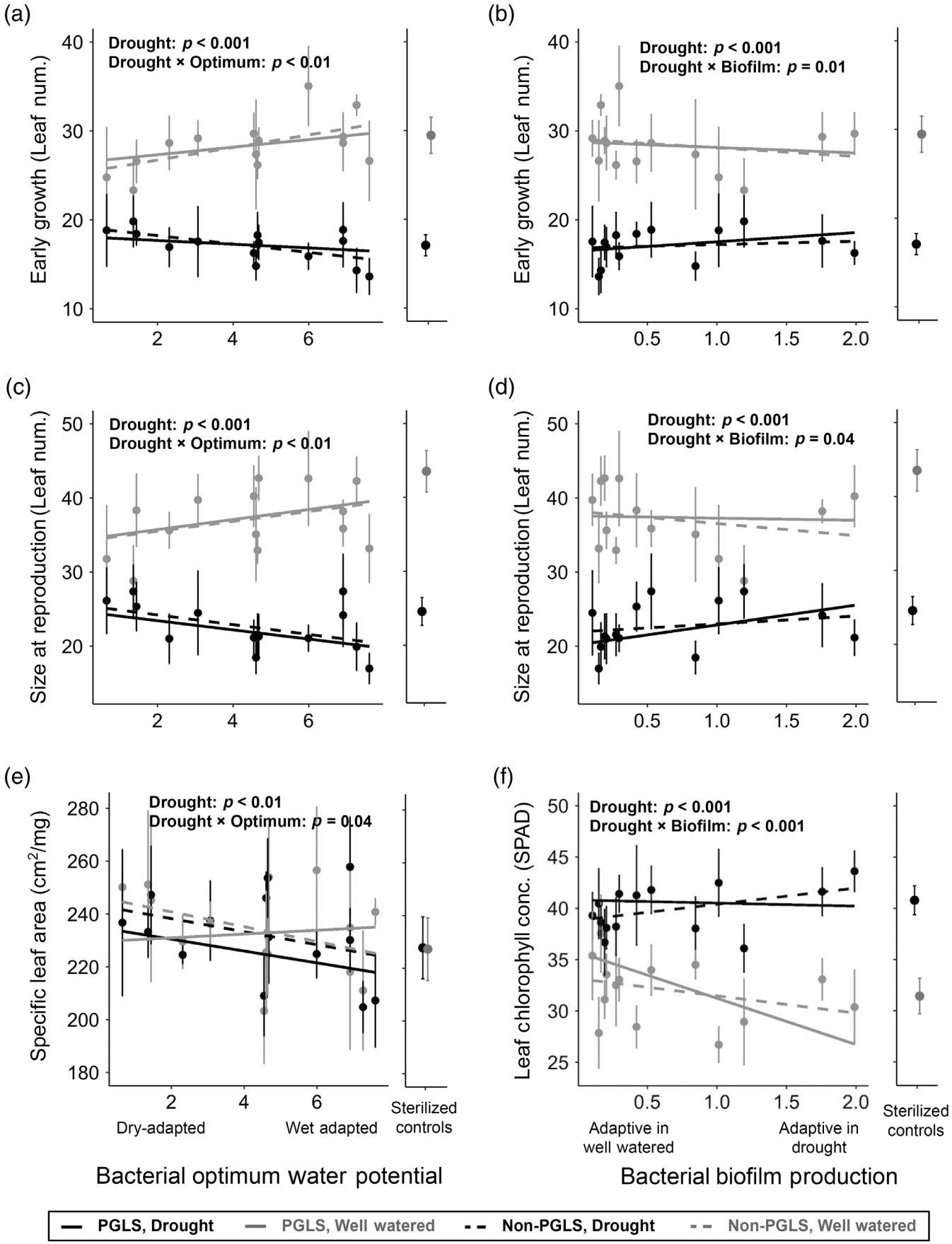

FIGURE 1 Legend on next page.

The predictive power of microbial traits

Our results highlight the potential importance of microbial traits in determining plant responses to the environment. In fact, additional comparisons with sterile inocula revealed that trait effects were stronger than the effects of live versus sterile inoculation, which did not predict any plant responses to soil moisture (Appendix S3). This suggests that studies manipulating live versus sterile inoculation may be missing important microbial effects on plants that are mediated by microbial traits.

Additionally, our results provide strong support for the utility of a predictive trait-based approach. Whereas ecological models are reasonably good at predicting how traits affect species responses to the environment (e.g., Chapin III, 1980; Grime, 1977; Litchman & Klausmeier, 2008), and to a lesser extent how traits affect other community members (e.g., Baxter et al., 2019), we have shown that microbial traits measured in a laboratory can predict not only the traits of other community members, but also how those community members respond to the environment.

We focused on microbial rescue in response to soil moisture, but there is no reason to expect this is a soil moisture-specific phenomenon. Similar patterns could emerge in any environment where adaptive microbial traits also benefit plants. For example, herbicide can select for microbes that degrade herbicide (El Fantroussi et al., 1999; Lancaster et al., 2010), which could benefit plants by removing herbicide from soils. Such plant benefit mediated by diffuse microbial communities may be widespread, but is rarely investigated.

Microbial traits predict plant soil moisture responses: Potential mechanisms

Byproduct benefits from microbial traits might promote beneficial plant responses to soil moisture by at least three non-mutually exclusive mechanisms: microbial trait expression could directly manipulate plant phenotype (e.g., production of phytohormones; Yang et al., 2009), modify the soil environment (e.g., alter soil water holding capacity; Lennon & Lehmkuhl, 2016; Martiny et al., 2015), or allow generally beneficial microbes to survive and maintain their beneficial function (e.g., help rhizobia survive and continue fixing nitrogen for plants). We did not attempt to differentiate among mechanisms in our study, but we speculate that biofilm production may have increased plant growth under drought by increasing soil water holding capacity. Increased survival of generally beneficial microbes seems less likely, as inoculation did not increase plant growth relative to uninoculated pots (Appendix S1: Figure S6), and although we cannot rule out plant hormone-mediated effects, we have no *a priori* reason to predict that bacterial phytohormone production would correlate with biofilm production.

The mechanism underlying the impact of microbes with low optimum water potentials on plant drought responses is less clear. These bacteria were not generally beneficial to plants, but it is unclear how other traits known to contribute to the soil moisture niche besides biofilm production, such as dormancy (Lennon & Jones, 2011), solute production (Schimel et al., 2007), and the ability to change intracellular stoichiometry (Fredrickson et al., 2008), would increase plant growth or SLA, or alter phytohormone production.

Two of our strains belong to genera with known plant growth-promoting properties: a *Burkholderia* species and a *Pseudomonas* species (Hayat et al., 2012). However, these strains did not drive microbial rescue in either watering treatment. Although these strains often increased plant growth relative to predicted growth for a given biofilm production or optimum water potential, particularly under drought, they almost always weakened microbial trait effects (Appendix S1: Figure S7). These findings support our conclusions that the traits of these microbes, and not their identities, drove microbial rescue in response to soil moisture.

Models controlling for phylogenetic non-independence detected stronger effects of bacterial biofilm production on

FIGURE 1 Bacterial optimum water potential ("Optimum") predicted plant responses to soil moisture in (a) early growth, (c) size at reproduction, and (e) specific leaf area, whereas bacterial biofilm production ("Biofilm") predicted plant responses to soil moisture in (b) early growth, (d) size at reproduction, and (f) chlorophyll concentration when phylogeny, but not within-strain variation, was accounted for (solid lines: fitted phylogenetic least squares [PGLS] regressions). In mixed models accounting for within-strain variation, but not phylogeny, only bacterial optimum water potential predicted plant responses in (a) early growth (dashed lines: fitted regressions that do not control for bacterial phylogeny). Biofilm production is reported as the relative absorbance generated from the biofilm assay (Lennon et al., 2012). High biofilm production is adaptive for bacteria in drought, whereas low biofilm production is adaptive in well-watered environments. Optimum water potential was *ln*-transformed as described in "*Methods*". Bacteria with low optimum water potentials have high growth rates in dry environments, whereas bacteria with high optimum water potentials have high growth rates in well-watered environments. Error bars are SE. Reported *p*-values are from PGLS models.

plant soil moisture responses relative to models that excluded phylogeny. This difference was driven by phylogeny explaining variation in plant traits in environment-specific ways (Appendix S1: Figure S8, Tables S2 and S4). For example, Actinobacteria generally promoted plant growth in dry soil regardless of biofilm production, but inhibited plant growth in wet soil. When these clade differences were accounted for, patterns of biofilms affecting plant growth emerged. By contrast, the relationship between bacterial optimum water potential and plant responses was repeated across the bacterial phylogenetic tree, so controlling for phylogeny had little effect on the qualitative patterns we observed (Appendix S1: Figure S9). However, models accounting for within-strain variation (but not phylogeny) typically failed to detect the effects of optimum water potential on plant responses (Appendix S1: Tables S3 and S4), which is perhaps unsurprising given that strain variation introduces error into models. These weaker effects might suggest that optimum water potential had a relatively weak effect on plant responses or could simply be a symptom of low within-strain replication.

Potential mechanisms of microbe-mediated plant benefit

For microbial traits to benefit plants, one might expect that microbial traits would shift plant traits in an adaptive manner. Thicker leaves (low SLA) are putatively adaptive under drought (Ackerly, 2004), and we found that plants produced thicker leaves under drought. However, the magnitude of the effect was greatest when grown with microbes with high, not low, optimum water potentials. Rather than altering the expression of plant traits in an adaptive manner, perhaps the protective benefits of these microbes simply reduced the need for plants to plastically produce thicker leaves in response to drought. Indeed, microbes with low optimum water potentials generally caused drought-stressed plants to resemble well-watered plants, suggesting a protective effect (Figure 1a–d,f).

Caveats

We tested for byproduct benefits using a simple system of single strain inoculations on a single plant species. By inoculating high densities of each strain into sterile soils, we created ideal conditions for these strains to establish. We did this to better isolate the effects of microbial traits, but it is unclear whether these effects will scale up to more complex communities found in nature. Microbial communities certainly vary in biofilm production and other traits that may benefit plants under drought (e.g., Berard et al., 2015), but microbial trait expression is complex and could be strongly affected by other community members (Classen et al., 2015). In fact, a small pilot study involving these same strains did not find consistent effects of simple communities comprised of high versus low biofilm-producing strains on plant drought responses (Appendix S4: Figure S1). In general, the extent to which byproduct benefits promote microbial rescue will likely depend on community context, which microbial traits are under the strongest selection, and the extent to which these traits provide a byproduct benefit to plants.

We also did not control for cell density in this experiment. However, it is unlikely that dosage effects drove our results because the effects of bacterial traits were environment specific. Dosage effects would need to increase a plant trait in one environment while decreasing the trait in the opposite environment, and we see no mechanism by which this could occur.

Finally, while our experimental design explicitly tested byproduct benefits, modes of classic cooperation (e.g., partner choice and partner fidelity feedbacks) could contribute alongside byproduct benefits. Quantifying the relative importance of byproduct benefits, classic modes of cooperation, and other drivers of plant stress responses (e.g., phenotypic plasticity or adaptive evolution) could be a fruitful area for future research.

Implications and Conclusions

If microbial traits commonly influence plant responses to the abiotic environment, and if our results scale up to diverse microbial communities, then microbial rescue driven by byproduct benefits could be common. Because microbial traits can respond rapidly to environmental change, sometimes within a single week (e.g., Mackelprang et al., 2011), microbial traits could promote plant population persistence under a range of short-term events like seasonal drought, as well as facilitate plant persistence under longer term global changes (Hawkes et al., 2020; Petipas et al., 2021). Ultimately, our results show that byproduct benefits are a feasible mechanism that could promote commonly observed, but previously challenging to explain, patterns of microbial rescue in both plants and animals.

AUTHOR CONTRIBUTIONS

Lana G. Bolin, Jennifer A. Lau, and Jay T. Lennon designed the study, and Lana G. Bolin performed the research and analyzed the data. Lana G. Bolin wrote the first draft of the manuscript, and Jennifer A. Lau and Jay T. Lennon contributed substantially to the revisions.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Bolin et al., 2022a) are available in Dryad at https://doi.org/10.5061/dryad.612jm6455. Code (Bolin et al., 2022b) is available in Zenodo at https://doi.org/10.5281/zenodo.7076153.

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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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