Native and commercial microbial inoculants show equal effects on plant growth in dryland ecosystems

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Abstract

There are a wide variety of microbial inoculant types available to restoration practitioners, but little information as to which performs best under field conditions in dryland ecosystems. We used a meta-analysis of 62 dryland studies to provide the first quantitative comparison of native vs commercial, diverse vs single species, and fungal vs bacterial microbial inoculants. We found that while microbial inoculation increases plant growth compared to uninoculated counterparts, contrary to our expectations, the magnitude of effect was statistically similar for all the inoculant pairs. Our results suggest that land managers should use inoculant types that are readily available and easy to handle rather than complicated and expensive inoculants that combine multiple taxa of local origin microbes.

Introduction

Microbial inoculants can allow land managers to increase plant growth while avoiding the negative impact of fertilizer application (Soozandehfar et al., 2023). The use of microbial inoculants is now well established in mesic agricultural settings (Fox, 2015; Timmusk et al., 2017; Waltz 2017), and there is growing interest in using microbial inoculation to assist with the restoration of degraded dryland ecosystems (Kaushal and Wani, 2016; Zhu et al., 2014). However, systematic studies examining the effect of microbial inoculants on plant growth at the field scale in drylands are lacking (Hart et al., 2017). In this study, we conduct a meta-analysis of dryland ecosystems to quantify the effect of microbial inoculation on plant growth and increase understanding of which types of inoculants are most effective.

Our first hypothesis is that plants inoculated with microorganisms in drylands will have higher growth than uninoculated plants. Microorganisms are thought to facilitate plant growth by increasing access to water and nutrients (Canbolat et al., 2006; Lai et al., 2008), and may also produce phytohormones that stimulate plant growth (Jaral et al., 2012; van der Heijden et al., 2008; Ruzi and Aroca, 2015 van der Putten et al., 2016). For example, biomass production in tomatoes was doubled when inoculated with microorganisms (Almaghrabi et al., 2013). Also, inoculating wheat with microorganisms increased the shoot and root biomass by increasing phosphorus uptake from the soil (Karimzadeh et al., 2021). However, the efficacy of microbial inoculation in field situations varies substantially (Hart et al., 2018; Ryan et al., 2018; O'Callaghan, 2016), and it is unclear whether microbial inoculation is likely to be effective in drylands. High temperatures can reduce microbial activity (Fang, 2022), so benefits may be reduced in dryland ecosystems with challenging environmental conditions. Conversely, there is some suggestion that microbial inoculation is more likely to be successful in drylands due to organisms shifting to facilitative strategies in high-stress environments (Bertness and Callaway, 1994). For instance, inoculating with microorganisms increased seedling emergence (Dadzie et al., 2022) and biomass production (Shirmohammadi et al., 2020) in drylands suggesting a facilitation effect of microbial inoculation on plant growth.

Our second hypothesis is that inoculation with native microorganisms yields greater growth than inoculation with commercial microorganisms. The dominant theory is that because native microorganisms have co-evolved with native plants and are adapted to local conditions, they will result in greater plant growth than commercial inoculants (Dadzie et al., 2022; Emam, 2016; Koziol et al., 2022; Middleton et al., 2015). Some studies have supported the hypothesis that native microorganisms enhance plant growth better than exotic microorganisms (Koziol et al., 2022; Chaudhary et al., 2020). However, the massive development of bio-fertilizers in ecological domains (Timmusk et al., 2017; Islam et al., 2021) compels a systematic evaluation of the magnitude of effect between native and commercial inoculants under dryland field conditions. This information will help ecologists and restoration managers to select appropriate inoculants within their economic means.

Our third hypothesis is that bulk inoculation of different microbial species will affect plant growth more than inoculation of single microbial species. One of the most prominent theories in ecology is the idea that increasing biodiversity leads to increased resource use efficiency and functional redundancy, whereas the loss of an organism will cause a reduction in ecosystem function (Bender et al., 2016; Philippot et al., 2013; Wagg et al., 2014). This idea has readily been adopted from plant ecology into microbial ecology with little testing, despite studies showing that microbial activities and trends do not follow patterns of macroecological theories (Fierer et al., 2011; Hendershot et al., 2017). Some studies show a greater effect of biodiverse microbial inoculants than single taxon inoculants (Bradáčová et al., 2019; Devi et al., 2022; Jain et al., 2015; Lally et al., 2017). Other studies have shown a similar magnitude of effect from single-strain microbial inoculation as from multi-species microbial inoculations (Bhatia et al., 1998; Onwuchekwa et al., 2014; Shirmohammadi et al., 2020). Here, we provide a systematic evaluation of the effect of single-strain and multiple-strain microbial effect on plant growth in drylands.

Our final objective was to test the hypothesis that inoculation with fungi will yield greater plant growth than inoculation with bacteria in dryland ecosystems. Bacteria and fungi are the most widely used microbial organisms for inoculation studies. Both taxa have been found to enhance plant growth when inoculated with plants (Coleine et al., 2022; Zhang et al., 2019). Some previous work suggests that inoculation with fungi will have greater effects on plant growth due to their ability to ameliorate stress (Porter et al., 2020) and ability to thrive in soils with a high carbon: nitrogen ratio (Güsewell and Gessner, 2009). On the other hand, the quick turnover of bacteria can cause them to perform better than fungi (Hasheem et al., 2016). By understanding the differences in the effect of fungal and bacterial inoculants on dryland soils, we can inform future dryland restoration projects to direct their limited resources more effectively.

Material and Methods

We conducted a systematic literature search following the general PRISMA EcoEvo guidelines (O'Dea et al. 2021) to find a representative sample of all published literature testing the impact of microbial inoculation on plant growth in dryland ecosystems. We searched Scopus and ISI Web of Science databases using UNSW Sydney's institution subscriptions for all studies published before 1st April, 2022 using the search terms: (inocula*) AND (”plant growth” OR ”plant biomass” OR ”plant development”) AND (”dryland*” OR ”arid land*” OR ”semi-arid land*”) AND (“restor*” OR “remediat*” OR “rehabilita*”). Our search resulted in 923 publications for Web of Science and 850 for Scopus. The total number of publications was reduced to 1235 after 538 duplicates were removed (Table S1). We additionally included one study from the author, Dadzie et al. (2022).

We selected studies based on five main eligibility criteria. First, we only considered peer-reviewed primary studies, thus excluding books, review papers, and theses. Second, the study must have been conducted in a dryland ecosystem. We defined drylands as areas with annual precipitation under 600 mm where potential evapotranspiration was greater than the annual precipitation. When studies did not provide climate information, we used location information to obtain approximate climate information within the study duration via cross-checking with historical WorldClim data (version 2.1, 30 seconds resolution ~ 1 km square grid; Fick and Hijmans, 2017). Third, only field studies were considered. Studies that were conducted in pots (mesocosms) and left in the field were not included since the pots provided a microclimatic condition.

Fourth, studies must have compared microbially inoculated and non-inoculated plants. We defined microbial inoculation as bacteria and fungi that are purposefully added to plants to improve their growth. Finally, studies must have reported above-ground biomass as a metric for plant growth and development. Studies that reported plant growth with other metrics were not included. For studies that reported plant growth in consecutive years, only the last year of the growing season was considered since we were interested in the overall effect of microbial inoculation on plant growth.

To increase the comparability of our estimates, we ensured that the conditions applied to each treatment were equally applied to the control in each study. For example, when studies reported on the application of fertilizer to the field before planting seeds, we ensured that the controls were given similar fertilizer treatment else they were excluded. In studies that reported both fertilizer application and microbial inoculations as individual treatments, we selected controls that were unfertilized and uninoculated, whereas only treatments that were unfertilized but inoculated with microbial were considered for the response measure. Where there was a crop rotation, we only included data from the first rotation season since subsequent rotations were not receiving direct inoculation and were confounded with plough-back remnant crops.

Data extraction and effect size estimation

From each study, we extracted the mean above-ground biomass with its associated measure of dispersion (i.e. standard deviations or standard errors) for control and inoculated plants, the number of replicates per treatment, the duration of plant growth, the environmental condition of the site, the type of inoculated microorganism (i.e. bacteria or fungi), the composition of the inoculated microorganisms (i.e. individual or in a consortium), and the source of microbial inoculum (i.e. native, foreign or commercial inoculant). Native microbial inoculants were defined as microbes that were isolated from soils within the local study area. Foreign microbes were those obtained from the same country but in a different study area. Commercial microbes were those obtained from commercial companies. Commercial microorganisms were separated from foreign microbes in that the former often has additional plant growth-associated components in addition to the microbial communities. Therefore, in the analysis comparing effects between commercial and native inoculation inoculants, foreign microbial communities were excluded.

Data Analysis

To estimate the overall effect of microbial inoculants on above-ground biomass, we used the natural log response ratio as our effect size, calculated as $\mathrm{lnRR} = \ln(\mathrm{V_i}/\mathrm{V_c})$ (Hedges et al., 1999), where $\mathrm{V_i}$ is the mean of the treatments (inoculated) and $\mathrm{V_c}$ is the mean of the control (uninoculated). Thus, the lnRR is positive when the magnitude of the above-ground plant biomass of inoculated plants is greater than the biomass of uninoculated plants, and vice versa. Statistical significance was determined when 95% confidence intervals did not overlap with zero.

We used hierarchical meta-analytic models using the *rma.mv*function from the *metafor* package (Viechtbauer, 2010; version 3.0.2) to test for the mean effect of microbial inoculation on plant growth. Study type, site, and species were found to be non-independent so we included them as random variables in the analyses.

We performed a meta-analytic model to determine the overall mean effect of inoculation on plant growth, using an intercept-only model with random effects for study type, site, and species. We then performed meta-regressions using the moderators; microbial source (either native or commercial), microbial type (either bacteria or fungi), and microbial composition (single or multiple inoculants) in separate models to test our hypotheses. All statistical analyses were conducted in R version 4.2.1 (2022). Statistical significance was determined when 95% confidence intervals did not overlap with zero. We reported back-transformed effect sizes converted to the percentage scale to facilitate interpretation (a percentage increase in plant growth in inoculated plants versus non-inoculated plants). We also reported 95% prediction intervals (PI), which represent 95% of the expected values from future empirical studies, and also to put the result in perspective to climate-specific comparisons (Moles, 2018). Plots were created with the *orchaRd* package (Nakagawa et al., 2021) supported under the*ggplot2* package (Wickham 2016).

Publication bias implies that statistically significant findings are more likely to be published than non-statistically significant findings. We assessed publication bias in our dataset by using hierarchical meta-regressions using standard error or sampling variance as moderators in our models (Nakagawa et al., 2022) and assessed it using Egger's regression test (Figure Appendix 2). We also assessed the robustness of our findings by performing sensitivity analysis (leave one out analysis), where each study from the 62 studies was iteratively removed, and the resulting data were fitted in an intercept-only meta-analytic model.

We obtained a total of 172 effect sizes comparing inoculated from uninoculated plants from 62 studies across the globe (Figure S1). Ninety-four of the effect sizes were from restoration studies, 63 from agriculture, and 15 from phytoremediation studies. The most commonly used genus of fungi in plant inoculation was *Rhizophagus* spp. (N=34) while *Pseudomonas* spp. (N=20) was the most abundant genus of bacteria used in plant inoculation.

We found no strong evidence for publication bias nor an association between plant responses to inoculation and either standard error (slope = -0.48, CI = -0.78 - 1.11, N = 172). Our results were also robust to the iterative removal of one study at a time. Across all models, the inoculated increased plant biomass by 43.76% (CI = 29.69% - 58.8%), which is consistent with the overall effect previously reported (43.3%, CI = 29.69% - 58%, Figure 1A).

Results

Overall plant growth was increased by an average of 43.3% when inoculated with microorganisms (p = 0.0001, CI = 29.69% - 58%, Figure 1A). Most studies reported positive effects of microbial inoculation on plant growth (N = 158, 92%), with only 13 of the 172 observations (7.5 %) reporting negative effects of microbial inoculation and a single record finding no statistically significant effect of inoculation on plant growth.

Native microbial inoculants increased plant growth on average by 53% (CI = 31% - 80%, replicates (N) = 78) while commercial inoculants increased plant growth by 40% (CI = 9% - 78%, replicates (N) = 23). However, we found no statistically significant difference between the two types of inoculants (p = 0.57, CI = -0.18 – 0.37, Figure 1B).

Single microbial inoculants increased plant biomass by an average of 39% (CI = 24% - 55%, replicates (N) = 108) while multiple strain inoculants (biodiverse microbes) increased plant biomass by 49% (CI = 32% - 68%, N = 64). This difference was not statistically significant (p = 0.27, CI = -16.71% – 5.12%, Figure 1C).

Fungal inoculation increased plant biomass by 39% (CI = 28% - 61%, N = 88) while bacteria inoculation increased plant biomass by 43% (CI = 23% - 58%, N = 77). We found no statistically significant difference between the effect of bacteria and the effect of fungi on plant growth (p = 0.69, CI = -15.6% - 11%, Figure 1D).

Discussion

Our study confirms that even in harsh dryland soils, microbial inoculation improves plant growth (Fig 1). The results suggest a mutualistic relationship between microorganisms and plants, where the plants benefit from an increase in growth as has been found in mesic systems (Hoeksema et al., 2010; Nuenkamp et al., 2019; Rubin et al., 2017; Schutz et al., 2018). The magnitude of the effect seen in drylands (a 43% increase in plant growth with inoculation) is similar to the study of Rubin et al. (2017), who found that the effect of microbial inoculation on plant growth under drought conditions is higher than under well-watered conditions. Thus, our findings are consistent with the stress-facilitation hypothesis of community interactions which suggests that environmental stress increases facilitative interactions between organisms (Bertness and Callaway 1994; Hammerlund and Harcombe 2019).

We did not find evidence to support the hypothesis that inoculation with native microbes is more effective than commercially available inoculants. Our results suggest that any advantage native microbes have as a result of being adapted to the abiotic conditions of the site might be counterbalanced by the fact that commercial inoculants have presumably been developed to contain highly effective strains (Tsoi et al., 2019). The lack of difference between native and commercial inoculants (Fig 1) presents an opportunity for more effective dryland restoration programs. Currently, commercial inoculants are more expensive than native microorganisms (Kaminski et al., 2019), but have a much lower barrier to entry compared to developing native inoculants (Bell et al., 2019). Our results suggest that restoration practitioners who have low technical knowledge of microbial isolation and culturing can simply use readily available commercial inoculants.

Our hypothesis that inoculating biodiverse microorganisms will show a stronger effect on plant growth than inoculating a single microbial inoculum was not supported (Figure 1C). This observation is contrary to the idea that increasing biodiversity enhances ecosystem function through complementary and synergistic associations between individuals (Wagg et al., 2014). However, there is evidence that microorganisms' effects on ecosystem functionality are more strongly correlated with microbial functional diversity than with species richness (Kitz et al., 2015; Nielsen et al., 2011; Zhou et al., 2020). That is, increasing species richness without concern for functional diversity might not provide extra benefits to plant growth (Bender et al., 2016).

Our results show no clear benefit to the added expense and complexity of including more diverse species in the inoculant (Fig 1). That is, single-species inoculum provides a cost-effective and simple approach to improving plant growth in dryland ecosystems. Maybe instead of developing complex inoculants, we should be focusing our efforts on identifying groups of inoculants that perform similar functions first. By understanding individual functional groups of inoculants that produce similar effects, we can avoid redundant diversity and create more effective inoculant combinations with known results.

We found no evidence to support our hypothesis that the magnitude of the effect from fungal inoculation is stronger than that of bacteria inoculation. This result is contrary to the previous studies of Porter et al. (2020) and Morris et al. (2007), who found that fungi had a greater effect on plant growth than bacteria. However, there is evidence that greenhouse studies maximise fungal effects on plant growth leading to an overestimation of results when compared to field studies (Hart et al., 2018; Rubin et al., 2017). This example highlights how caution must be exercised when interpreting glasshouse studies in the context of microbial influence on plant growth, especially within environments that differ greatly from typical greenhouse climates.

Conclusion

Our work shows that microbial inoculation strongly increases plant growth in drylands, and that different types of microbial inoculants have broadly similar effects. Our work will help restoration practitioners and also agriculturalists select affordable and effective inoculants to enhance plant growth in drylands.

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Conflict of Interest

Authors had no conflicts of interest.

Data Availability

Data and codes will be stored publicly at Open Science Framework upon acceptance of this manuscript.

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Figure 1: Effect size of microbial inoculation on plant growth in drylands. Panel A demonstrates the overall effect of all microbial inoculants on plant growth while Panel B compares the effect sizes between native and commercial inoculants on plant growth. Panel C compares the effect sizes between inoculating a single microbial strain and inoculating multiple microbial strains. Panel D compares the effect sizes of inoculating with fungi and inoculating with bacteria on plant growth in dryland systems. The thicker horizontal line next to the meta-analytic mean shows the confidence interval at 95 % while the thinner horizontal line shows the 95 % prediction intervals (where you expect individual effect sizes to be within this range). The letter K represents the number of observations used for the analysis while the number in parenthesis represents the

total number of studies from which the data was collected. An effect size of zero means there is no treatment effect compared to the control while an effect size less or greater than zero means there is a negative or positive effect on plant growth respectively.