Plant Soil
DOI 10.1007/s11104-017-3199-8

REGULAR ARTICLE

Plant growth promoting rhizobacteria are more effective under drought: a meta-analysis

Rachel L. Rubin · **Kees Jan van Groenigen** ·
Bruce A. Hungate

Received: 18 August 2016 / Accepted: 31 January 2017

Abstract

Background and aims Plant growth promoting rhizobacteria (PGPR) have been shown to reduce abiotic stress on plants, but these effects have not been quantitatively synthesized. We evaluated the degree to which plant growth promoting rhizobacteria (PGPR) improve plant performance with and without drought stress.

Methods We used meta-analysis to summarize 52 published articles on the effects of PGPR on root mass, shoot mass and yield under well-watered and drought conditions. We also asked whether fertilization treatments, experimental conditions, inoculum taxonomic complexity, plant functional group, or inoculum delivery method introduce variation in the effect size of PGPR.

Results Across all treatments, plants were highly responsive to PGPR; under well-watered conditions, root mass increased by 35%, shoot mass increased by 28%, and reproductive yield increased by 19%. Under drought conditions, the effect was even higher: root mass increased by 43%, shoot mass increased by 45%, and reproductive yield increased by 40%. The effect of PGPR was significantly larger under drought for shoot mass ($p < 0.05$) and reproductive yield ($p < 0.05$), but not for root mass. PGPR responsiveness also varied according to plant functional group, with C_3 grass shoot production responding the least strongly to PGPR.

Conclusions We demonstrate that PGPR are highly effective for improving plant growth, with a greater effect under drought for above ground traits. While previously known for their bio-control abilities, we show that PGPR may also contribute to drought amelioration and water conservation.

Keywords Drought · PGPR · Biofertilizer · Plant productivity · Agriculture · Irrigation · Meta-analysis

Responsible Editor: Hans Lambers.

Electronic supplementary material The online version of this article (doi:10.1007/s11104-017-3199-8) contains supplementary material, which is available to authorized users.

R. L. Rubin · B. A. Hungate
Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011, USA

R. L. Rubin (✉) · B. A. Hungate
Center for Ecosystem Science and Society, Flagstaff, AZ 86011, USA
e-mail: rlr276@nau.edu

K. J. van Groenigen
Geography, University of Exeter, Exeter, EX4 4RJ, UK

Introduction

By 2050, the world's population will exceed 9.1 billion (Carvalho 2006), and food demand is expected to more than double (Green et al. 2005). Although the Green Revolution has vastly increased food production over the past 50 years, drought and salinization threaten more than 50% of earth's arable lands. In 2003, a continental wide drought reduced Europe's gross primary productivity by 30% (Ciais et al. 2005), and a severe drought in 2012 reduced US maize yields by 25% (Rosenzweig et al. 2014). In addition to causing plant mortality, drought increases demand for irrigation, which already comprises 70% of global water consumption (Shiklomanov and Rodda 2003), and is expected to rise 10% by 2050 due to climate change alone (Wada et al. 2013). Thus, it will not be possible to combat drought by simply increasing irrigation infrastructure.

To address this growing socioeconomic and ecological crisis, efforts have been devoted to understanding mutualisms in agricultural ecosystems (Wall and Moore 1999; Kiers et al. 2002). This approach was motivated by the stress gradient hypothesis, which posits that inter-specific interactions shift from competitive to facilitative under increasing abiotic stress (Bertness and Callaway 1994). Originally describing interspecific facilitation among salt marsh grasses, the stress gradient hypothesis has also been observed in mutualistic assemblages. For example, positive interactions between mussels and cordgrass increased under drought conditions (Angelini et al. 2016), mutualisms among ants, trees, and scale insects intensified along a precipitation gradient (Pringle et al. 2013), and arbuscular mycorrhizal inoculation increased stomatal conductance more under drought conditions than under well-watered conditions (Augé et al. 2015).

Plant growth promoting rhizobacteria (PGPR) directly associate with plant roots and can exist within root tissue (as endophytes), on the surface of plant roots (the rhizoplane), or within the zone of soil specifically influenced by the root system (the rhizosphere). Characterized by their plant-growth promoting properties, PGPR are a diverse group of bacteria that produce a wide range of enzymes and metabolites, influence nutrient acquisition, modulate hormone levels, and ameliorate the negative impacts of biotic and abiotic stressors (Kloepper 1992; Rudrappa et al. 2008; Hartmann et al. 2009; Lugtenberg and Kamilova 2009; Beneduzi et al. 2012; Ahemad and Kibret 2014; Ngumbi and Kloepper 2016). The term "PGPR" was first introduced in the late 1970's, when it was shown that fluorescent *Pseudomonas* strains improved potato yields by up to 500% by producing iron chelating siderophores, depriving native bacterial pathogens of iron (Kloepper et al. 1980a, b). Later, it was shown that PGPR activate several stress response genes, suggesting that biotic and abiotic plant defenses may be co-regulated (Timmusk and Wagner 1999).

PGPR are varied in their chemical and physical mechanisms of plant growth promotion under drought. For example, *Bacillus licheniformus* can produce ACC deaminase, which degrades ethylene, a plant hormone that is responsible for reduced root and shoot growth under drought (Lim and Kim 2013). Additionally, PGPR can physically make soils more drought adapted through the production of an extracellular matrix containing oligo- and polysaccharides that increase water retention capacity (Naseem and Bano 2014; Timmusk et al. 2014). The use of PGPR for drought amelioration is a burgeoning field, and two recent review papers (Ngumbi and Kloepper 2016; Vurukonda et al. 2016) extensively review the drought tolerance and drought avoidance mechanisms discovered thus far, including enhanced root architecture, osmotic adjustment, and antioxidant metabolism.

As a potential management tool to increase plant growth, PGPR have several practical advantages: 1) they are widespread, found on all 7 continents (Sahai 1999; Berríos et al. 2013), 2) they are not phylogenetically constrained, and occur within at least 5 phyla (Egamberdieva et al. 2015) and 24 genera (Barriuso et al. 2008; Babalola 2010), 3) they can be dried and stored, with a shelf life of up to 8 months (Nakkeeran et al. 2005), and 4) most exhibit low host-specificity — many plants will maintain symbioses with introduced PGPR, even when the bacterium has been isolated from a distantly related host plant (Bashan 1988; Antoun et al. 1998; Marasco et al. 2013; Timmusk et al. 2014). Today, 60–75% of cotton, peanut, soybean, corn, vegetables, and small grain crops are treated with *Bacillus subtilis* as a seed coating, seedling dip or rhizosphere injection to control soil borne pathogens including *Fusarium* and *Rhizoctonia* (Nakkeeran et al. 2005).

Although the positive effects of fungal symbionts under drought stress are summarized in several meta-analyses (Kivlin et al. 2013; Jayne and Quigley 2014; Augé et al. 2015), there is only one existing quantitative analysis on PGPR. Veresoglou and Menexes (2010) evaluated wheat-*Azospirillum* interactions and determined that inoculation increased seed yield by 9% and shoot mass by 18%. However, their conclusions were limited to only one type of PGPR and one crop species, and abiotic stress was not evaluated. Building upon this framework, we synthesized all drought-PGPR studies, encompassing a diversity of bacterial and plant taxa. We asked the following questions:

1) To what degree does PGPR inoculation improve root mass, shoot mass and yield?
2) Does drought stress influence the magnitude of this benefit?

3) Which moderators influence variation in plant response to PGPR inoculation?

Materials and methods

Literature search & data extraction

We conducted an exhaustive search of published literature using *ISI Web of Science* and *Google Scholar* to locate PGPR and drought literature. A preliminary screening revealed that shoot mass, root mass, and reproductive yield were the most commonly reported performance metrics. Using the search terms "*PGPR and drought*" and "*rhizobacteria and drought*", we conducted a search on both databases on September 20, 2015, yielding 370 titles from Web of Science and 1375 titles from Google Scholar published between 1985 and 2015. After screening titles for relevancy and filtering duplicates, we reviewed the remaining 314 papers by reading the abstracts, and if necessary, the full paper. These 314 papers were reduced to 52 final papers based on the following criteria: 1) studies must have been written in English; 2) studies must have measured shoot mass, root mass or reproductive yield; 3) studies must have imposed a full factorial drought × PGPR inoculation design; and 4) studies must have imposed drought treatments through irrigation deficit. Studies that manipulated salinity or added polyethylene glycol (PEG) were excluded, due to confounding issues with plant nutrient uptake (Burnett et al. 2005). All PGPR taxa were included in this meta-analysis, including nodule-forming *Rhizobium*.

For root mass and shoot mass, we extracted data from dry mass when available in order to control for potential differences in plant water content due to PGPR. If fresh mass was reported but dry mass was not reported, we extracted data for fresh mass. For yield, we extracted seed mass when available, but if seed mass was not reported, we extracted values for grain count. The level of drought stress was described differently in each paper, with metrics ranging from volumetric water content, number of days without water, to the degree of evaporation, making it impossible to quantify drought severity across citations. Thus, when citations employed multiple drought levels, we extracted data from the most extreme drought treatment available.

We extracted mean values and variances (standard deviation, standard error) for shoot biomass, root biomass, and reproductive yield from all combinations of drought, well-watered, inoculated and non-inoculated treatments directly from tables, when provided. For figures, we extracted data using Image J 1.5 (Abramoff et al. 2004). We assigned yield measurements to biologically relevant categories. For example, for studies on lettuce and asparagus, "aboveground yield" was classified as shoot mass. For repeated measures studies, we extracted data from the final time-point. Citations and observations that applied amino acids or growth promoting hormones were excluded, as were co-inoculations with mycorrhizal fungi, in the interest of examining the sole impacts of PGPR.

When provided, measures of variance were extracted directly. For studies that included a variance but did not specify the variance measure, we conservatively assumed it to be standard error. We imputed missing variances using the average coefficient of variation (cv value) for inoculated and control plants (Wiebe et al. 2006; van Groenigen et al. 2011) (Supplementary Data File 1). Imputing the variance allowed us to include 279 out of 448 total observations, and enabled us to construct meta-regression models, which are necessarily weighted on the inverse of the variance (Koricheva et al. 2013).

We also recorded categorical metadata on experimental conditions (greenhouse vs. field), soil fertilization treatments (unfertilized, organic fertilizer, or inorganic fertilizer), inoculation method (seed, seedling, or soil), inoculant taxa richness (single taxon or multiple taxa), and plant functional group (forb, legume, shrub, C_3 grass, and C_4 grass) to evaluate them as moderators. Unfertilized studies were differentiated into two groups: unfertilized soil that had either been left intact, or steam sterilized to kill indigenous soil microbes. Inoculum delivery method was differentiated by soil applications (either topically applied or injected), seedling dips, or seed coatings.

Overview

This meta-analysis was based on 52 papers published in 44 unique journals, with lead authors from 18 countries. These papers yielded a total of 448 total observations, where each observation includes a treatment (inoculated) and control comparison. Some of these observations had independent controls, and some had shared controls (see Sensitivity Analysis, below). There were 140 observations from 27 papers on root mass, 162 observations from 31 papers on shoot mass, and 146 observations from 26 papers on reproductive yield. The primary plant species used in this analysis were *Zea mays* (maize)*,* (27%), *Triticum aestivum* (common wheat) (12%), *Helianthus annuus* (common sunflower) (10%), and *Lactuca sativa* (lettuce) (8%). The primary bacterial genera used were *Pseudomonas* (35%), *Azospirillum* (35%), *Azotobacter* (13%) and *Bacillus* (8%). The majority of the observations in this meta-analysis were conducted in the greenhouse: 2/3 of the papers contained at least one greenhouse manipulation, whereas only 1/3 of the papers contained at least one field manipulation. Greenhouse studies typically applied additional manipulations in addition to PGPR and drought (e.g. different plant cultivars or PGPR types); thus, greenhouse studies comprised 3/4 of the total observations in this meta-analysis (Supplementary Data File 1). However, the majority of "yield" papers (70%) were conducted in the field rather than the greenhouse.

Analysis

To estimate the overall effect of PGPR on root mass, shoot mass, and yield under well-watered and drought conditions, we used the log response ratio as the metric of effect size: $\mathrm{LnR} = \ln (V_i/V_c)$, where V_i is the treatment (inoculated) mean and V_c is the control (non-inoculated) mean (Hedges et al. 1999). The response ratio is useful when different units are reported across studies (grams/pot vs. kg/ha for example), and the log transformation is needed to maintain symmetry within the analysis (Borenstein et al. 2009). Furthermore, it can easily be transformed to percent change using the formula: $\%\Delta = 100^* (\exp.(\mathrm{LnR}) - 1)$. We calculated associated pooled variances using the "escalc" function in the metafor package in R (Viechtbauer 2010).

Before building meta-analysis models, we conducted a heterogeneity test to determine whether a fixed effects approach or a random/mixed effects approach was appropriate. Heterogeneity (Q) on the full dataset was highly significant ($Q = 8874.6$, $df = 447$, $p < 0.0001$), indicating that a random/mixed effects approach was warranted. All subsequent meta-analyses were performed as multivariate random or mixed-effects meta-analysis models using the "rma.mv" function in metafor (Viechtbauer 2010) and weighted using the inverse of the variance in effect size (Hedges et al. 1999). This approach enabled us to simultaneously account for observation-level (σ^2_{obs}) and citation-level ($\sigma^2_{citation}$) variation by treating them as random effects. To calculate the estimated effect of PGPR under drought and watered conditions, we extracted parameter estimates and 95% confidence intervals from multivariate mixed-effects meta-regression models performed on six subsets of data (root mass, watered; root mass, drought; shoot mass, watered; shoot mass, drought; yield, watered; yield, drought).

To evaluate whether the beneficial effects of PGPR are greater under drought conditions, we used two different approaches: 1) We used the effect sizes as described above and evaluated "drought" as a fixed effects covariate in a mixed effects model for each dataset for root mass, shoot mass and yield; and 2) Utilizing the full factorial design of each study, we calculated a second effect size: $R_{diff} = \ln (V_{di}/V_{dc}) - \ln (V_{ci}/V_{cc})$, where V_{di} is the value under drought and PGPR inoculation, V_{dc} is the value under drought and no PGPR, V_{ci} is the value under well-watered conditions with PGPR inoculation, and V_{cc} is the value under well-watered conditions and no PGPR (Lajeunesse 2011; Koricheva et al. 2013). This composite effect size shows the average additional gain from PGPR inoculation when the plant is grown under drought conditions, at the study level. We calculated the associated variance as the sum of the pooled variances for the effect sizes of PGPR under drought and control conditions, $\sigma^2(R_{diff}) = \sigma^2 \ln (V_{di}/V_{dc}) + \sigma^2 \ln (V_{ci}/V_{cc})$.

Moderators

We evaluated the following moderators that might introduce variation in plant response to PGPR: fertilization treatments, inoculum complexity, growth conditions, plant functional group, and inoculum delivery method. First, we filtered moderators that had a minimum number of 12 observations, to ensure that moderators contained at least three papers. Next, we used several methods to evaluate moderators that introduce variation in plant response to PGPR. To construct forest plots, we plotted parameter estimates and 95% confidence intervals for individual random effects multivariate meta-regression models (rma.mv function in metafor) conducted on subsets of data for each available moderator that met minimum sample size requirements. Next, to determine which moderators influence significant variation in the effect size, we performed five additional mixed effects multivariate regression models (one for each moderator category), on the root mass, shoot mass, and yield datasets, with each moderator as a fixed-effects covariate and observations and citations as random effects. Forest plots were constructed using the "ggplot2" package (Wickham 2009) in R Statistical Software (Version 3.2.2, R Core Team 2015). Last, we used the glmulti package (Calcagno 2013) to evaluate the most parsimonious set of parameters that can help to explain root mass, shoot mass, and yield responses to PGPR (Supplementary Table 3).

Sensitivity analyses

We considered two potential sources of non-independence within this meta-analysis. The first source is when multiple observations come from the same citation, which we accounted for as a random effect in our random effects and mixed effects meta-analysis models. The second source of non-independence comes from shared controls within papers. For example, Bano et al. (2013) compared the effectiveness of seed inoculation vs. soil inoculation with a shared, inoculated control, Barnawal et al. (2013) examined the effects of two different bacterial species (*Bacillus subtilis, Ensifer meliloti*) against one shared, uninoculated control, and Tittabutr et al. (2013) evaluated whether inoculum diversity influenced plant performance by inoculating with *Bradyrhizobium* sp. alone, and with *Enterobacter* sp. We compared the overall effect sizes under drought and watered conditions due to shared controls (see Supplementary Table 1); none of our conclusions were affected.

Differential assessment of merit at any stage of the process of preparing a manuscript can result in suppression of non-significant findings (the "file-drawer effect") (Koricheva et al. 2013). We tested for publication bias by visually inspecting a funnel plot. We also tested for asymmetry using a trim-and-fill analysis in metafor and estimated that there were zero studies missing from the left side of the plot. Lastly, we calculated a fail-safe number, which asks how many observations (N_{obs}) averaging an effect size of zero would need to exist to negate the significance of our observed effects of PGPR (Koricheva et al. 2013). We calculated Rosenberg's fail-safe N and determined that 113,317 studies with null results for root mass, 137,680 studies with null results for shoot mass, and 11,060 studies with null results for reproductive yield would have to be added to the given set of observed outcomes to reduce the combined significance level of $p = 0.05$.

Results

Effects of PGPR under drought and watered conditions

Overall, PGPR stimulated plant growth, increasing root mass, shoot mass and reproductive yield by an overall average of 35% (CI 27.7–43.8%). Although the mean effect of PGPR was consistently higher for root mass, shoot mass, and reproductive yield under drought conditions, the difference was significant for shoot mass and reproductive yield only (Fig. 1). Notably, shoot mass increased by an average of 45% under drought conditions, whereas it only increased by 28% under well-watered conditions. At the study level, we observed the same overall trend: PGPR were 6% (CI–5.4–19.7%) more effective under drought for root mass, 12% (CI 1.8–23.0%) more effective under drought for shoot mass, and 9% (CI 0.6–18.3%) more effective under drought for reproductive yield; however, the effect was not significantly greater for root mass, because the CI overlapped zero (Fig. 2).

Other moderators

For root mass, the only moderator that influenced plant response to PGPR was fertilization treatments (Fig. 3a, $p < 0.001$), with organic fertilizer increasing the benefits of PGPR, and unfertilized soil decreasing the benefits of PGPR.

For shoot mass, inoculum containing two or more PGPR taxa was more effective than inoculum containing only one PGPR taxon (Fig. 4b, $p = 0.03$). Furthermore, C_3 grasses responded less strongly PGPR than forbs, legumes, and C_4 grasses (Fig. 4d, $p = 0.006$). Last, inoculum delivery method also significantly influenced the effect of PGPR on shoot mass (Fig. 4e, $p = 0.003$), with seed coatings having a greater effect than soil applications.

For reproductive yield, greenhouse-reared plants responded more strongly to PGPR than field-reared plants (Fig. 5c, $p = 0.04$).

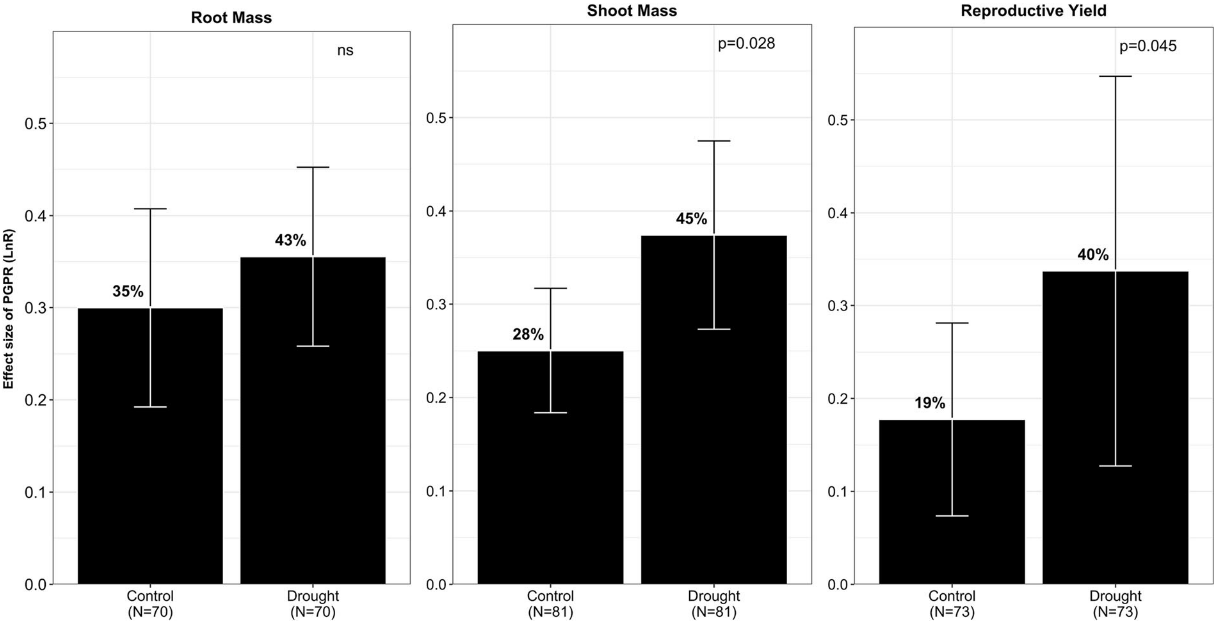


Fig. 1 Mean effect sizes (LnR) of PGPR on root biomass, shoot biomass and reproductive yield under well-watered and drought conditions. Graph reflects parameter estimates from random-effects multivariate meta-regression models conducted on subsets of data and error bars reflect 95% CI. *P* values were extracted from an additional mixed-effects multivariate meta-regression model with "drought" as a fixed effect moderator. For ease of interpretation, graphs were annotated with back-transformed effect sizes (reported as a percent change under PGPR inoculation). The effect of PGPR was significantly greater under drought for shoot mass and reproductive yield, but not root mass

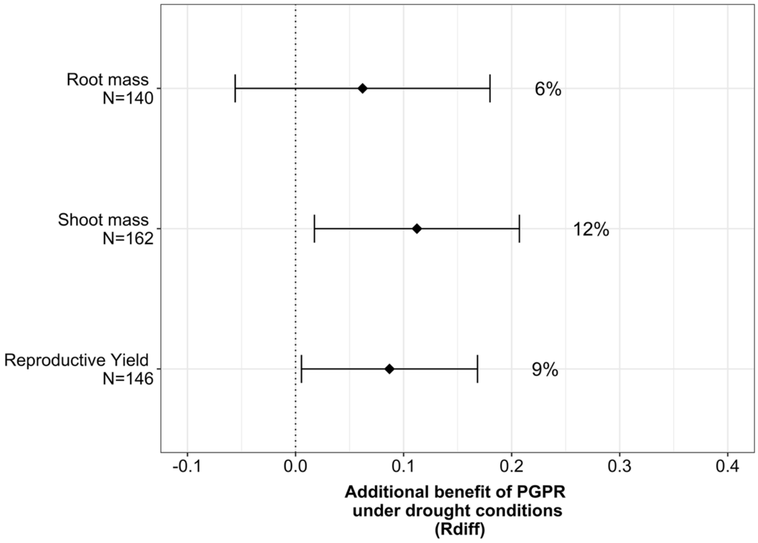
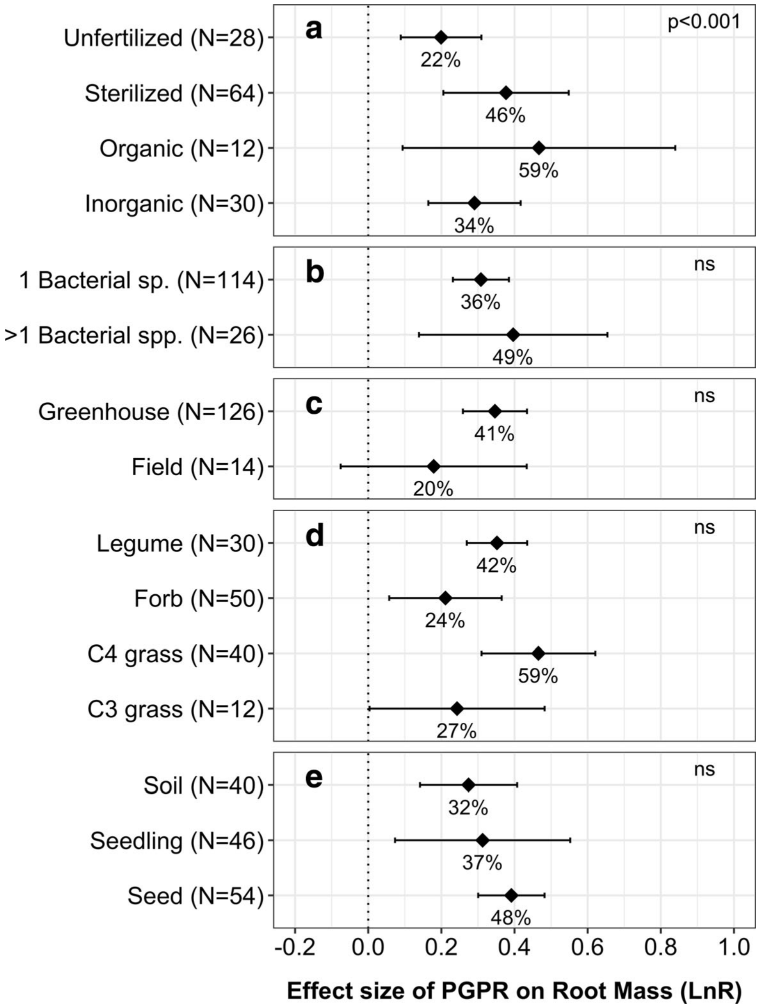


Fig. 2 This graph reflects the difference in effect size, R_{diff} for the effect of PGPR on root mass, shoot mass and reproductive yield under drought conditions and the effect of PGPR on root mass, shoot mass and reproductive yield under well-watered conditions. When error bars do not overlap zero, there is a consistent additional gain of PGPR under drought conditions compared to watered conditions at the study level. These results corroborate the results found in the mixed-effects meta-regressions shown in Fig. 1; the effects of PGPR were greater under drought for shoot mass and reproductive yield but not for root mass. Graph reflects parameter estimates from random-effects multivariate meta-regression models conducted on each dataset and error bars reflect 95% CI

Fig. 3 Effect sizes of PGPR on root mass grouped by moderators: **a** fertilization treatments; **b** inoculum complexity; **c** growth conditions; **d** plant functional group; **e** inoculation method. *P* values for each moderator panel reflect a mixed-effects multivariate regression model (one for each moderator category) within the root mass dataset. Substantial variation in the effects of PGPR on root mass was explained by fertilization treatments



Discussion

Agricultural intensification has been responsible for dramatic increases in crop yields over the past 50 years (Evenson and Gollin 2003). However, continued intensification is unsustainable under climate change and associated drought, which threatens both irrigated and rain-fed agricultural systems (Kijne et al. 2003). This meta-analysis indicates that PGPR can substantially improve plant performance, with a greater effect under drought for shoot mass and reproductive yield. These results have implications for the commercialization of PGPR, as drought conditions are expected to become more frequent and severe (Wang 2005; Dai 2013).

Across treatments, the effects of PGPR were of a similar order of magnitude as arbuscular mycorrhizal fungi, which have been shown to improve yields between 30% under drought stress (Jayne and Quigley 2014) and 52% under salt stress (Chandrasekaran et al. 2014). As plant mutualists, PGPR and AM fungi coevolved with their plant hosts and each other (Revillini et al. 2016). Thus, mutualisms may be enhanced through interactions among PGPR and AM fungi; for example, *Bacillus megaterium* increased mycorrhizal root colonization from 40% to 70% in drought-stressed clover roots (Ortiz et al. 2015), AM fungi may act as a vehicle to spread PGPR to neighboring rhizospheres (Bianciotto and Bonfante 2002), and phosphorus solubilizing PGPR could enhance P foraging efficiency of extraradical hyphae (Toro et al. 1997; Bianciotto and Bonfante 2002). However, interactions between PGPR and AM fungi may also be antagonistic or commensal under certain conditions (Wu et al. 2005), and there is no

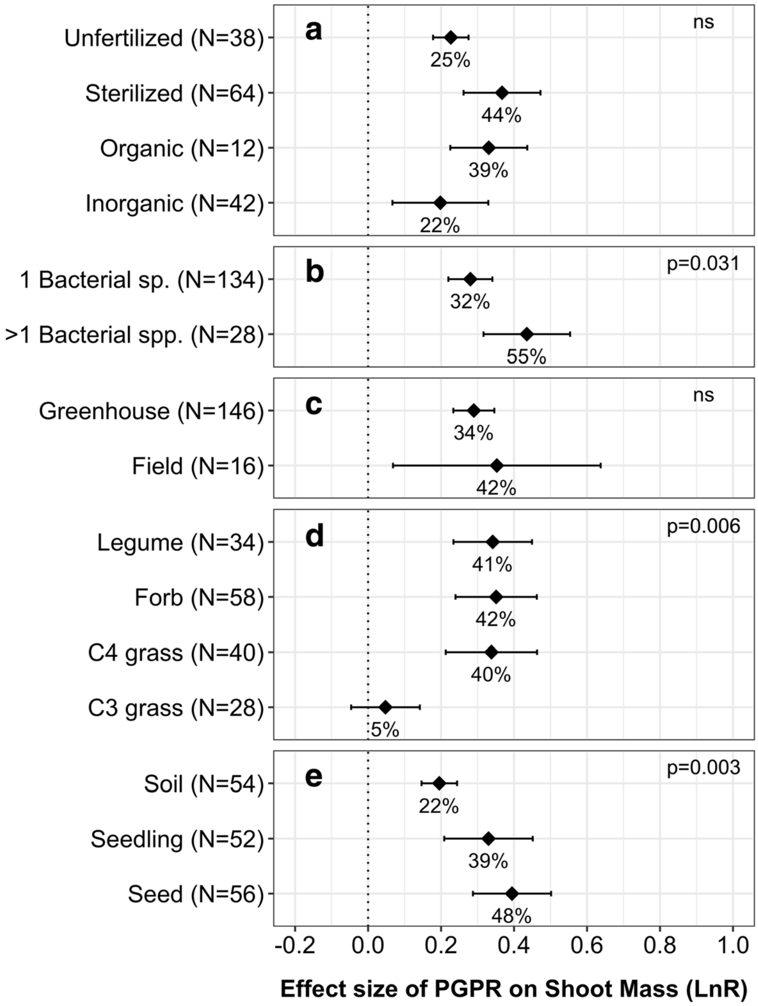


Fig. 4 Effect sizes of PGPR on shoot mass grouped by moderators: **a** fertilization treatments; **b** inoculum complexity; **c** growth conditions; **d** plant functional group; **e** inoculation method. *P* values for each moderator panel reflect an additional mixed effects multivariate regression model (one for each moderator category) within the root mass dataset. Substantial variation in the effects of PGPR on shoot mass was explained by inoculum complexity, plant functional group and inoculation method

general consensus of the expected additional gain in plant growth under AM-PGPR co-inoculations.

Our findings for the effects of PGPR on seed yield (15%) of C_3 grasses were slightly higher than the effects of *Azospirillum* inoculation on wheat yield, also a C_3 grass (9%) (Veresoglou and Menexes (2010). However, for shoot mass, our estimate of 5% was slightly lower than their estimate of 18%. Although we did not find a consistent pattern for plant functional group responses to PGPR across the three metrics of root mass, shoot mass, and yield, C_4 grasses on average responded more strongly to PGPR. This finding has also been observed in empirical and meta-analytical studies of AM fungi, with greater increases in plant growth for C_4 grasses than C_3 grasses (Hetrick et al. 1988, 1990; Wilson and Harnett 1997, 1998; Hoeksema et al. 2010; others). These data suggest that PGPR formulations would be a worthwhile pursuit for C_4 grasses such as corn, but may exhibit less potential within C_3 grasses such as wheat and rice.

Under artificial selection for high yield varieties, plant-soil mutualisms may be compromised (Dasilva et al. 1977; Kiers et al. 2002; Kiers et al. 2007; Pérez-Jaramillo et al. 2016). For example, modern wheat cultivars show reduced dependency on mycorrhizae compared to cultivars released before 1950 (Hetrick et al. 1993), and soybean artificial selection has been shown to impair host plant defense against ineffective rhizobia (Kiers et al. 2007). While modern cultivars may have lost some of the traits necessary to recruit host-specific root microbiota (Pérez-Jaramillo et al. 2016), our study demonstrates that high-yield varieties consistently benefit from inoculation with PGPR. To maximize these benefits, we suggest that plant breeders also

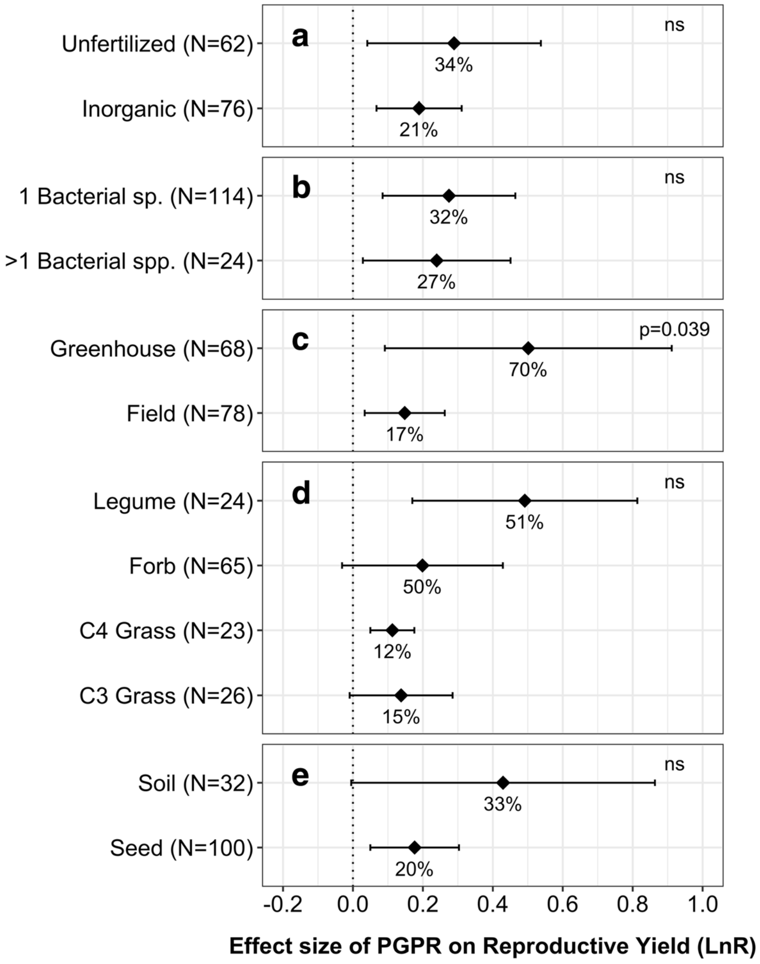


Fig. 5 Effect sizes of PGPR on reproductive yield grouped by moderators: **a** fertilization treatments; **b** inoculum complexity; **c** growth conditions; **d** plant functional group; **e** inoculation method. *P* values for each moderator panel reflect a mixed effects multivariate regression model (one for each moderator category) within the yield dataset. Substantial variation in the effects of PGPR on reproductive yield was explained by growth conditions (greenhouse vs. field)

select for the ability to maintain symbioses, which appears to be a heritable trait (Kiers et al. 2002).

Furthermore, PGPR that evolved under stressful abiotic conditions could be leveraged in commercial PGPR formulations. For example, several bacterial strains isolated from dry environments have been shown to produce indole acetic acid and increase leaf proline content (Marulanda et al. 2009). Furthermore, bacteria isolated from a south (African) facing, high stress slope in Evolution Canyon, Israel, were more likely to solubilize phosphorus, form biofilms, and produce ACC deaminase than bacteria isolated from the lower stress, north (European) facing slope (Timmusk et al. 2011). Thus, screening bacteria that occur under natural drought conditions may yield optimal candidates for agricultural drought applications.

Management techniques that accompanied plant domestication, including fertilization, pesticide application and tilling can also influence plant-microbe mutualisms (Thomson et al. 1986; Treseder 2004). For example, long term (8 year) N and P addition selected for less mutualistic AM fungi in prairie grasses (Johnson 1993), and 22 years of N addition caused the evolution of less-cooperative rhizobia in several clover varieties (Weese et al. 2015). Furthermore, PGPR propagation in maize roots was inhibited when soil ammonium nitrate concentration exceeded 200 mg kg (Wu et al. 2005). We found that fertilization influenced root mass response to PGPR, with the greatest response under organic fertilization. One possibility is that organic fertilizers typically have a higher C content and a lower nutrient content that is designed to be “slow release”, providing resources and conditions that favor PGPR growth. However, there was no generalizable trend across the three metrics of root mass, shoot mass and reproductive yield. With harvest yield as the primary goal, we suggest that PGPR application may be compatible with moderate fertilizer use. Prior research has shown that select strains of N-fixing and P solubilizing PGPR allow for a 25%–50% reduction in NPK fertilizer application rates (Adesemoye et al. 2009; Kumar et al. 2009) without sacrificing yield. Thus, "bio-fertilizer" PGPR effectiveness may be limited by key fertilization application thresholds (Treseder and Allen 2002; Shukla et al. 2012); future research should address whether these thresholds are affected by drought.

Our finding that reproductive yield was significantly higher in the greenhouse is consistent with the notion that greenhouse conditions can magnify treatment effects (Hester and Harrison 2005), and suggests that the effect sizes we observed may be smaller under conditions typical of agricultural operations. We urge caution in evaluating these results because the majority of the papers included in this study were greenhouse studies, and most agricultural operations occur in the field. Within our meta-analysis, the subset of studies that measured reproductive yield in the field are the most similar to genuine agricultural systems, because plants are harvested at reproductive maturity and because field soil contains indigenous bacterial flora. It is also important to note that the way that drought is applied in the greenhouse (continuous drought), can differ from the way drought is typically experienced in the field (cyclic drought). In general, PGPR effects are likely context dependent, and the large confidence intervals for both greenhouse and field studies may reflect differences in site conditions and the ways that drought and PGPR treatments were applied.

Prior research has shown that the root microbiome has the greatest effect on plants during the early stages of development (Bell et al. 2015). Our finding that seed coatings resulted in the largest increase in shoot mass is likely due to an increased concentration of PGPR around the germinating plant, facilitating recruitment and assimilation of PGPR into the root microbiome. We recommend the use of seed coatings to maximize PGPR effectiveness; however, further research on the effects of different carriers (e.g. talc or guar gum) on inoculum viability and performance (Nakkeeran et al. 2005; Malusà et al. 2012) is still needed.

Agricultural soils often exhibit reduced microbial community complexity compared to natural systems (Levine et al. 2011; Hartmann et al. 2015). In severe cases of soil degradation, growers may choose to inoculate using multi-taxon blends, as a "consortium" (Naseem and Bano 2014). We did not find any differences in effectiveness between single taxon and multiple taxa inoculations; however, studies applied three taxa at most, so we were unable to fully explore the effects of microbial diversity on agricultural productivity. A significant hurdle remains in addressing whether commercial PGPR, indigenous PGPR, dark septate endophytes and AM fungi can coexist in the rhizosphere or whether they undergo competitive exclusion (Requena et al. 1997; Barea et al. 2002; Kiers et al. 2002; Waag et al. 2011). Further research should address the longevity of inoculants applied in the field, as well as interactions with indigenous flora.

Overall, this study demonstrates that PGPR can substantially enhance plant growth, with shoot mass increasing the most from PGPR. PGPR also increased shoot mass and yield by a greater magnitude under drought than under well-watered conditions. Our findings suggest that PGPR can be used in situations other than biological control, the feature that PGPR are best known for. Furthermore, arid regions of the developing world may benefit the most from PGPR because these regions are characterized by rapid population growth and are also the most vulnerable to climate change (Schmidhuber and Tubiello 2007). Lastly, improved understanding of "mycorrhizosphere" interactions (Barea et al. 2002) is imperative in order to preserve crop yield stability under an increasingly unstable climate.

Acknowledgements We would like to acknowledge Dr. George Koch, Molly Shuman-Goodier, Brianna Finley and Elaine Pegoraro for assistance in reviewing this manuscript. Dr. Liza Holeski and Dr. Nathan Nieto provided conceptual feedback during the formulation of this study. We would also like to acknowledge three anonymous reviewers for their helpful critiques and suggestions. Funding to support Rachel Rubin was provided by NSF Dimensions of Biodiversity award no. 1241094, the ARCS Phoenix AZ Chapter, and the Soil Science Society of America (SSSA) Francis and Evelyn Clark Soil Biology Scholarship.

References

References marked with an asterisk were included in the meta-analysis

Abramoff MD, Magalhães PJ, Ram SJ (2004) Image processing with image J. Biophoton Int 11:36–42

Adesemoye AO, Torbert HA, Kloepper JW (2009) Plant growth-promoting rhizobacteria allow reduced application rates of chemical fertilizers. Microb Ecol 58:921–929

Ahemad M, Kibret M (2014) Mechanisms and applications of plant growth promoting rhizobacteria: current perspective. King Saud Univ Sci 26:1–20

Angelini C, Griffin JN, van de Koppel J, Lamers LPM, Smolders AJP, Derksen-Hooijberg M, van der Heide T, Silliman BR (2016) A keystone mutualism underpins resilience of a coastal ecosystem to drought. Nat Commun 7:12473

Antoun H, Cj B, Goussard N, Chabot R, Lalande R (1998) Potential of rhizobium and Bradyrhizobium species as plant growth promoting rhizobacteria on non-legumes: effect on radishes (*Raphanus sativus* L.). Plant Soil 204:57–67

*Arvin P, Vafabakhsh J, Mazaheri D, Noormohamadi G, Azizi M (2012) Plant growth promoting rhizobacteria (PGPR) on yield, yield components and seed oil content of different cultivars and species of brassica oilseed rape. Ann Biol Res 9:4444–4451

*Arzanesh MH, Alikhani HA, Khavazi K, Rahimian HA, Miransari M (2011) Wheat (*Triticum aestivum* L.) growth enhancement by Azospirillum sp. under drought stress. World J Microb Biotechnol 27:197–205

Augé RM, Toler HD, Saxton AM (2015) Arbuscular mycorrhizal symbiosis alters stomatal conductance of host plants more under drought than under amply watered conditions: a meta-analysis. Mycorrhiza 25:13–24

Babalola OO (2010) Beneficial bacteria of agricultural importance. Biotechnol Lett 32:1559–1570

*Bano Q, Ilyas N, Bano A, Zafar N, Akram A, Hassan F (2013) Effect of Azospirillum inoculation on maize (*Zea mays* L.) under drought stress. Pakistan J Bot 45:13–20

Barea JM, Pozo MJ, Azcón R, Azcón-Aguilar C (2002) Microbial co-operation in the rhizosphere. J Exp Bot 56:1761–1778

*Barman P, Singh SJ, Patel VB, Nain L, Pandey A (2015) Cleopatra mandarin (*Citrus reshni* Hort. Ex tan.) modulate physiological mechanisms to tolerate drought stress due to arbuscular mycorrhizal fungi and mycorrhizal helper bacteria. African J Microbiol Res 9:1236–1246

*Barnawal D, Maji D, Bharti N, Chanotiya CS, Kalra A (2013) ACC deaminase-containing *Bacillus subtilis* reduces stress ethylene-induced damage and improves mycorrhizal colonization and rhizobial nodulation in *Trigonella foenum-graecum* under drought stress. J Plant Growth Regul 32: 809–822

Barriuso J, Solano BR, Lucas JA, Lobo AP, García-Villaraco A, Mañero FJG (2008) Ecology, genetic diversity and screening strategies of plant growth promoting rhizobacteria (PGPR). In: Ahmad I, Pichtel J, Hayat S (eds) Plantbacteria interactions: strategies and techniques to promote plant growth. Wiley-VCH Verlag GmbH & Co. KGaA, Weinheim, pp 1–17

Bashan Y (1988) Nonspecific responses in plant growth, yield and root colonization of non cereal crop plants to inoculation with *Azospirillum brasilense*. Can J Bot 67:1317–1324

*Belimov AA, Dodd IC, Hontzeas N, Theobals JC, Safranova VI, Davies WJ (2009) Rhizosphere bacteria containing 1-aminocyclopropane-1-carboxylate deaminase increase yield of plants grown in drying soil via both local and systemic hormone signaling. New Phytol 181:413–423

*Belimov AA, Dodd IC, Safronova VI, Shaposhnikov AI, Azaroza TS, Makarova NM, Davies WJ, Tikhonovich IA (2015) Rhizobacteria that produce auxins and contain 1-amino-cyclopropane-1-carboxylic acid deaminase decrease amino acid concentrations in the rhizosphere and improve growth and yield of well-watered and water-limited potato (*Solanum tuberosum*). Ann Appl Biol 167:11–25

Bell TH, Cloutier-Hurteau B, Al-Otaibi F, Turmel M, Yergeau E, Courchesne F, St-Arnaud M (2015) Early rhizosphere microbiome composition is related to the growth and Zn uptake of willows introduced to a former landfill. Environ Microbiol 17:3025–3038

Beneduzi A, Ambrosini A, Passaglia LMP (2012) Plant growth-promoting rhizobacteria (PGPR): their potential as antagonists and biocontrol agents. Genet Mol Biol 35:1044–1051

Berríos G, Cabrera G, Gidekel M, Gutiérrez-Moraga A (2013) Characterization of a novel Antarctic plant growth-promoting bacterial strain and its interaction with Antarctic hair grass (*Deschampsia Antarctica* Desv). Polar Biol 36:349–362

Bertness MD, Callaway R (1994) Positive interactions in communities. Trends Ecol Evol 9:191–193

Bianciotto V, Bonfante P (2002) Arbuscular mycorrhizal fungi: a specialised niche for rhizospheric and endocellular bacteria 81:365–371

Borenstein M, Hedges LV, Higgins J, Rothstein H (2009) Introduction to meta-analysis. Wiley, Hoboken, NJ

*Bresson J, Varoquaux F, Bontpart T, Touraine B, Vile D (2013) The PGPR strain Phyllobacterium brassicacearum STM196 induces a reproductive delay and physiological changes that result in improved drought tolerance in Arabidopsis. New Phytol 200:558–569

Burnett S, van Iersel M, Thomas P (2005) PEG alters morphology and nutrient composition of hydroponic impatiens. Hortic Sci 40:1768–1722

Calcagno V (2013) glmulti: Model selection and multimodel inference made easy. R package version 1.0.7. http://CRAN.R-project.org/package=glmulti

Carvalho FP (2006) Agriculture, pesticides, food security and food safety. Environ Sci Pol 9:685–692

Chandrasekaran M, Boughattas S, Hu S, Oh SH, Sa T (2014) A meta-analysis of arbuscular mycorrhizal effects on plants grown under salt stress. Mycorrhiza 24:611–625

*Chaudhry V, Bhatia A, Bharti SK, Mishra SK, Chauhan PS, Mishra A, Sidhu OP, Nautiyal CS (2015) Metabolite profiling reveals abiotic stress tolerance in Tn5 mutant of *Pseudomonas putida*. PLoS One 10:e0113487

Ciais P, Reichstein M, Viovy N, Granier A, Ogée J, Allard V, Aubinet M, Buchmann N, Bernhofer C, Carrara A, Chevallier F, De Noblet N, Friend AD, Friedlingstein P, Grünwald T, Heinesch B, Keronen P, Knohl A, Krinner G, Loustau D, Manca G, Matteucci G, Miglietta F, Ourcival JM, Papale D, Pilegaard K, Rambal S, Seufert G, Soussana JF, Sanz MJ, Schulze ED, Vesala T, Valentini R (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437:529–533

*Cohen AC, Travaglia CN, Piccoli PN (2009) Participation of abscisic acid and gibberellins produced by endophytic *Azospirillum* in the alleviation of drought effects in maize. Botany 87:455–462

*Cohen AC, Bottini R, Pontin M, Berli F, Moreno D, Boccanlandro H, Travaglia CN, Piccoli PN (2015) *Azospirillum brasilense* ameliorates the response of *Arabidopsis thaliana* to drought mainly via enhancement of ABA levels. Physiol Plant 153:79–90

*Creus CM, Sueldo RJ, Barassi CA (2004) Water relations and yield in *Azospirillum*- inoculated wheat exposed to drought in the field. Can J Bot 82:273–281

*Dadrasan M, Chaichi MR, Pourbabae AA, Yazdani D, Keshavarz-Afshar R (2015) Deficit irrigation and biological fertilizer influence on yield and trigonelline production of fenugreek. Ind Crop Prod 77:156–162

Dai A (2013) Increasing drought under global warming in observations and models. Nat Clim Chang 3:52–58

Dasilva EJ, Henriksson LE, Udris M (1977) Growth responses of mycorrhizal *Boletus* and *Rhizopogon* species to pesticides. Trans Br Mycol Soc 68:434–437

*Dastgiri L, Daneshian J, Rahmani HA, Sayfzadeh S (2013) Effect of PGPRs on agronomic characteristics of sunflower under different humidity regimes. Intl J Agron Plant Prod 4:2901–2905

*del Mar Alguacil M, Kohler J, Caravaca F, Roldán A (2009) Differential effects of *Pseudomonas mendocina* and *Glomus intraradices* on lettuce plants physiological response and aquaporin PIP2 gene expression under elevated atmospheric CO_2 and drought. Microb Ecol 58:942–951

Egamberdieva D, Shrivastava M, Varma A (2015) Plant-growth-promoting rhizobacteria (PGPR) and medicinal plants. Springer, New York

Evenson RE, Gollin D (2003) Assessing the impact of the green revolution, 1960 to 2000. Science 300:758–762

Fan X, Hu H, Huang F, Li Y, Palta J (2015) Soil inoculation with *Burkholderia sp*. LD-11 has positive effect on water-use efficiency in inbred lines of maize. Plant Soil 390:337–349

*Fard MD, Habibi D, Fard FD (2011) Effect of plant growth promoting rhizobacteria and foliar application of amino acids and silicic acid on antioxidant enzyme activity of wheat under drought stress. Chem Eng 23:80–85

*Figueiredo MVB, Burity HA, Martínez CR, Chanway CP (2008) Alleviation of drought stress in the common bean (*Phaseolus vulgaris* L.) by co-inoculation with *Paenibacillus polymyxa* and *Rhizobium tropici*. Appl Soil Ecol 40:182–188

*Gachomo EW, Kefela T, Houngnandan P, Baba-Moussa L, Kotchoni SO (2014) Bradyrhizobium japonicum IRAT FA3 increases biomass, yield and drought tolerance in plants. J Biosci (Z Naturforsch) 1:12–23

*Ghorbanpour M, Hatami M, Khavazi K (2013) Role of plant growth promoting rhizobacteria on antioxidant enzyme activities and tropane alkaloids production of *Hyoscyamus niger* under water deficit stress. Turk J Biol 37:350–360

Green RE, Cornell SJ, Scharlemann JPW, Balmford A (2005) Farming and the fate of wild nature. Science 307:550–555

*Habibi D (2014) The effects of plant growth-stimulating bacteria and foliar application of silicic acid and amino acids on biochemical markers in barley under drought stress. MAGNT Research Report 2:217–224

Hartmann AM, Schmid MD, van Tuinen D, Berg G (2009) Plant-driven selection of microbes. Plant Soil 321:235–257

Hartmann M, Frey B, Mayer J, Mäder P, Widmer F (2015) Distinct soil microbial diversity under long-term organic and conventional farming. ISME J 9:1177–1194

Hedges LV, Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental ecology. Ecology 80:1150–1156

Hester RE, Harrison RM (2005) Sustainability in agriculture. RSC Publishing, Cambridge, UK

Hetrick BAD, Gerscheksje K, Wilson GT (1988) Mycorrhizal dependence and growth habit of warm-season and cool-season tallgrass prairie plants. Can J Bot 66:1376–1380

Hetrick BAD, Wilson GWT, Todd TC (1990) Differential responses of C3 and C4 grasses to mycorrhizal symbiosis, phosphorus fertilization and soil microoganisms. Can J Bot 68:461–467

Hetrick BAD, Wilson GWT, Cox TS (1993) Mycorrhizal dependence of modern wheat cultivars and ancestors: a synthesis. Can J Bot 71:512–518

Hoeksema JD, Chaudhary VB, Gehring CA, Johnson NC, Karst J, Koide RT, Pringle A, Zabinski C, Bever JD, Moore JC, Wilson GWT, Klironomos JN, Umnamhowar J (2010) A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. Ecol Lett 13:394–407

Jayne B, Quigley M (2014) Influence of arbuscular mycorrhiza on growth and reproductive response of plants under water deficit: a meta-analysis. Mycorrhiza 24:109–119

*Joe MM, Kathikeyan B, Chauhan PS, Shagol C, Islam MR, Deiveekasundaram M, Sa T (2012) Survival of *Azospirillum brasilense* flocculated cells in alginate and its inoculation effect on growth and yield of maize under water deficit conditions. Eur J Soil Biol 50:198–206

Johnson NC (1993) Can fertilization of soil select less mutualistic mycorrhizae? Ecol Appl 3:749–757

*Khan N, Mishra A, Chauhan PS, Nautiyal CS (2011) Induction of *Paenibacillus lentimorbus* biofilm by sodium alginate and CaCl2 alleviates drought stress in chickpea. Ann Appl Biol 159:372–386

*Kheybari M, Daneshian J, Rahmani HA, Seyfzadeh S, Khiavi M (2013a) Response of sunflower head charachteristics to PGPR and amino acid application under water stress conditions. Intl J Agron Plant Prod 4:1760–1765

*Kheybari M, Daneshian J, Taei A, Hadi AR, Seyfzadeh S (2013b) Effect of PGPR and amino acid application on sunflower yield under different water deficit conditions. Int J Agric Res 3:467–471

Kiers ET, West SA, Denison RF (2002) Mediating mutualisms: farm management practices and evolutionary changes in symbiont co-operation. J Appl Ecol 39:745–754

Kiers ET, Hutton MG, Denison RF (2007) Human selection and the relaxation of legume defences against ineffective rhizobia. Proc Biol Sci 274:3119–3126

Kijne JW, Barker R, Molden DJ (2003) Water productivity in agriculture: limits and opportunities for improvement. CABI, IWMI, Wallingford, UK

Kivlin SN, Emery AM, Rudgers JA (2013) Fungal symbionts alter plant responses to global change. Am J Bot 100:1445–1457

Kloepper JK (1992) Plant growth-promoting rhizobacteria as biological control agents. In: Soil microbial ecology: applications in agricultural and environmental management. Ed. F B Metting. Taylor & Francis, Abingdon, pp 255–274

Kloepper JW, Schroth MN, Miller TD (1980a) Effects of rhizosphere colonization by plant growth-promoting rhizobacteria on potato plant development and yield. Ecol Epidemio 70: 1078–1082

Kloepper JW, Schroth MN, Miller TD (1980b) Enhanced growth by siderophores produced by plant growth-promoting rhizobacteria. Nature 286:885–886

*Kohler J, Hernández A, Caravaca F, Roldán A (2008) Plant-growth-promoting rhizobacteria and arbuscular mycorrhizal fungi modify alleviation biochemical mechanisms in water-stressed plants. Funct Plant Biol 35:141–151

*Kohler J, Caravaca F, Roldán A (2009) Effect of drought on the stability of rhizosphere soil aggregates of *Lactuva sativa* grown in a degraded soil inoculated with PGPR and AM fungi. Soil Biol Biochem 42:429–434

*Kohler J, Knapp BA, Waldhuber S, Caravaca F, Roldán A, Insam H (2010) Effects of elevated CO2, water stress, and inoculation with *Glomus intraradices* or *Pseudomonas mendocina* on lettuce dry matter and rhizosphere microbial and functional diversity under growth chamber conditions. J Soils Sediments 10:1585–1597

Koricheva J, Gurevitch J, Mengersen K (2013) The handbook of meta-analysis in ecology and evolution. Princeton University Press, Princeton

Kumar S, Pandey P, Maheshwari DK (2009) Reduction in dose of chemical fertilizers and growth enhancement of sesame (*Sesamum indicum L.*) with application of rhizospheric competent *Pseudomonas aeruginosa* LES4. Eur J Soil Biol 45: 334–340

*Kumar M, Mishra S, Dixit V, Agarwal L, Chauhan PS, Nautiyal S (2015) Synergistic effect of *Pseudomonas putida* and *Bacillus amyloliquefaciens* ameliorates drought stress in chickpea *(Cicer arietinum* L.). Plant Signal Behav 11: e1071004

Lajeunesse MJ (2011) On the meta-analysis of response ratios for studies with correlated and multi-group designs. Ecology 92: 2049–2055

Levine UY, Teal TK, Robertson GP, Schmidt TM (2011) Agriculture's impact on microbial diversity and associated fluxes of carbon dioxide and methane. ISME J 5:1683–1691

*Liddycoat SM, Greenberg BM, Wolyn DJ (2009) The effect of plant growth-promoting rhizobacteria on asparagus seedlings and germinating seeds subjected to water stress under greenhouse conditions. Can J Microbiol 55:388–394

Lim J, Kim S (2013) Induction of drought stress resistance by multi-functional PGPR *Bacillus licheniformis* K11 in Pepper. Plant Pathol J 29:201–208

*Liu F, Xing S, Ma H, Du Z, Ma B (2013) Cytokinin-producing, plant growth-promoting rhizobacteria that confer resistance to drought stress in *Platycladus orientalis* container seedlings. Appl Microbiol Biotechnol 97:9155–9164

Lugtenberg B, Kamilova F (2009) Plant-growth-promoting rhizobacteria. Annu Rev Microbiol 63:541–556

Malusà E, Sas-Paszt L, Ciesielska J (2012) Technologies for beneficial microorganisms inocula used as biofertilizers. Sci World J 2012 :12Article ID 491206

*Malusà E, Sala G, Chitarra W, Bardi L (2013) Improvement of response to low water availability in maize plants inoculated with selected rhizospheric microbial consortia under different irrigation regimes. J Environ Qual 12:13–21

Marasco R, Rolli E, Vigani G, Borin S, Sorlini C, Ouzari H, Zocchi G, Daffonchio D (2013) Are drought-resistance promoting bacteria cross-compatible with different plant models? Plant Signal Behav 8:e26741

Marulanda A, Barea JM, Azcón R (2009) Stimulation of plant growth and drought tolerance by native microorganisms (AM Fungi and Bacteria) from dry environments: mechanisms related to bacterial effectiveness. J Plant Growth Regul 28: 115–124

*Miri MR, Moghadam HRT, Ghooshchi F, Zahedi H (2012) Growth, seed yield and phosphorus uptake of wheat as influenced by *Azotobacter* and arbuscular mycorrhizal colonization under drought stress conditions. Res Crop 13:21–28

*Moslemi Z, Habibi D, Asgharzadeh A, Ardakani MR, Modommadi A, Mohammadi M (2011) Response of phytohormones and biochemical markets of maize to super absorbent polymer and plant growth promoting rhizobacteria under drought stress. American-Eurasian J Agric & Environ Sci 10:787–796

*Moslemi Z, Habibi D, Asgharzadeh A, Ardakani MR, Mohammadi A, Sakari A (2012) Effects of super absorbent polymer and plant growth promoting rhizobacteria on yield and yield components of maize under drought stress and normal conditions. Am J Agric Environ Sci 12:358–364

Nakkeeran S, Dilantha Fernando WG, Siddiqui ZA (2005) Plant growth promoting rhizobacteria formulations and its scope in commercialization for the management of pests and diseases. In: Siddiqui (ed) PGPR: biocontrol and biofertilization. Springer, Dordrecht, pp 257–296

*Naseem H, Bano A (2014) Role of plant growth-promoting rhizobacteria and their exopolysaccharide in drought tolerance of maize. J Plant Interact 9:689–701

*Naseri R, Moghadam A, Darabi F, Hatami A, Tahmasebei GRT (2013) The effect of deficit irrigation and *Azotobacter chroococcum* and *Azospirillum brasilense* on grain yield, yield components of maize (SC 704) as a second cropping in western Iran. Bull Env Pharmacol Life Sci 2:104–112

*Naveed M, Mitter B, Reichenauer TG, Wieczorek K, Sessitsch A (2014) Increased drought stress resilience of maize through endophytic colonization by *Burkholderia phytofirmans* PsJN and *Enterobacter sp*. FD17. Environ Exp Bot 97:30–39

Ngumbi E, Kloepper J (2016) Bacterial-mediated drought tolerance: current and future prospects. Appl Soil Ecol 105:109–125

*Omar MH, Zulkarami B, Ariffin N, Ismail MR, Saud HM, Amalina N, Habib SH, Kausar H (2014) Improved water use efficiency in rice under limited water environment through microbial inoculation. Intl J Food, Agric And Environ 12:149–154

Ortiz N, Armada E, Duque E, Roldán A, Azcón R (2015) Contribution of arbuscular myorrhizal fungi and/or bacteria to enhancing plant drought tolerance under natural soil conditions: effectiveness of autochtonous or allochthonous strains. J Plant Physiol 174:87–96

Pérez-Jaramillo JE, Mendes R, Raaijmakers JM (2016) Impact of plant domestication on rhizosphere microbiome assembly and functions. Plant Mol Biol 90:635–644

Pringle EG, Akçay E, Raab TK, Dirzo R, Gordon DM (2013) Water stress strengthens mutualism among ants, trees, and scale insects. PLoS Biol 11:e1001705

R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria URL http://www.Rproject.org

Requena N, Jimenez I, Toro M, Barea JM (1997) Interactions between plant growth-promothing rhizobacteria (PGPR), arbuscular mycorrhizal fungi and *Rhizobium* spp. in the rhizosphere of *Anthyllis cytisoides,* a model legume for revegetation in Mediterranean semi-arid ecosystems. New Phytol 136:667–677

Revillini D, Gehring CA, Johnson NC (2016) The role of locally adapted mycorrhizas and rhizobacteria in plant–soil feedback systems. Funct Ecol 30:1086–1098

Rosenzweig C, Elliot J, Deryng D, Ruane AC, Müller C, Arneth A, Boote KJ, Folberth C, Glotter M, Khabarov N, Neumann K, Piontek F, Pugh TAM, Schmid E, Stehfest E, Yang H, Jones JW (2014) Assessing agricultural risks of climate change in the twenty-first century in a gridded crop model intercomparison. PNAS 111:3268–3273

Rudrappa T, Czymmek KJ, Pare PW, Bais HP (2008) Root-secreted malic acid recruits beneficial soil bacteria. Plant Physiol 148:1547–1556

*Ruíz-Sánchez M, Armada E, Muñoz Y, García de Salamone IE, Aroca R, Ruíz-Lozano JM, Azcón R (2011) *Azospirillum* and arbuscular mycorrhizal colonization enhance rice growth and physiological traits under well-watered and drought conditions. J Plant Physiol 168:1031–1037

*Sadeghipour O, Abbasi S (2012) Soybean response to drought and seed inoculation. World Appl Sci J 17:55–60

Sahai S (1999) Biotechnology capacity of less developed countries in the Asian Pacific Rim. AgBioforum 2:189–197

*Sakari A, Ardakani MR, Khavazi K, Paknejad F, Moslemi Z (2012) Effect of *Azospirillum lipoferum* and *Thiobacillus thioparus* on quantitative and qualitative characters of rapeseed (*Brassica napus* L.) under water deficit conditions. Middle East J Sci Res 11:819–827

*Sandhya V, Ali SKZ, Grover M, Reddy G, Venkateswarlu B (2009) Alleviation of drought stress effects in sunflower seedlings by the exopolysaccharides producing *Pseudomonas putida* strain GAP-P45. Biol Fertil Soils 46: 17–26

Schmidhuber J, Tubiello FN (2007) Global food security under climate change. PNAS 104:19703–19708

*Shafighi A, Pazoki A, Asli DE (2014) Alleviation of water stress in fenugreek (*Trigonella foenum-graecum* L.) using different PGPR application methods. Adv Environ Biol 8:275–280

Shiklomanov IA, Rodda JC (2003) World water resources at the beginning of the twenty-first century. Cambridge Univ Press, Cambridge, UK, International Hydrology Series

*Shintu PV, Jayaram KM (2015) Phosphate solubilising bacteria (*Bacillus polymyxa*) - an effective approach to mitigate drought in tomato (*Lycopersicon esculentum* mill.). Tropical Plant Research 2:17–22

Shukla A, Kumar A, Jha A, Rao DVKN (2012) Phosphorus threshold for arbuscular mycorrhizal colonization of crops and tree seedlings. Biol Fertil Soils 48:109–116

*Singh NB, Singh D, Singh A (2015) Biological seed priming mitigates the effects of water stress in sunflower seedlings. Physiol Mol Biol Plants 21:207–214

Thomson BD, Robson AD, Abbott LK (1986) Effects of phosphorus on the formation of mycorrhizas by *Gigaspora calospora* and *Glomus fasciculatum* in relation to root carbohydrates. New Phytol 103:751–765

Timmusk S, Wagner EG (1999) The plant-growth-promoting rhizobacterium *Paenibacillus polymyxa* induces changes in *Arabidopsis thaliana* gene expression: a possible connection between biotic and abiotic stress responses. Mol Plant-Microbe Interact 12:951–959

Timmusk S, Paalme V, Pavlicek T, Bergquist J, Vangala A, Danilas T, Nevo E (2011) Bacterial distribution in the rhizosphere of wild barley under contrasting microclimates. PLoS One 6:1–7

*Timmusk S, Abd El-Daim IA, Copolovici L, Tanilas T, Kännaste A, Behers L, Nevo E, Seisenbaeva G, Stenström E, Niinemets U (2014) Drought-tolerance of wheat improved by rhizosphere bacteria from harsh environments: enhanced biomass production and reduced emissions of stress volatiles. PLoS One 9:e96086

*Tittabutr P, Piromyou P, Longtonglang A, Noisa-Ngiam R, Boonkerd N, Teaumroong N (2013) Alleviation of the effect of environmental stresses using co-inoculation of mungbean by Bradyrhizobium and rhizobacteria containing stress-induced ACC deaminase enzyme. Soil Sci Plant Nutr 59:559–571

Toro M, Azcon R, Barea JM (1997) Improvement of arbuscular mycorrhiza development by inoculation of soil with phosphate-solubilizing rhizobacteria to improve rock phosphate bioavailability and nutrient cycling. Appl Environ Microbiol 63:4408–4412

Treseder KK (2004) A meta-analysis of mycorrhizal response to nitrogen, phosphorus and atmospheric CO_2 in field studies. New Phytol 164:347–355

Treseder KK, Allen MF (2002) Direct nitrogen and phosphorus limitation of arbuscular mycorrhizal fungi: a model and field test. New Phytol 155:507–515

van Groenigen KJ, Osenberg CW, Hungate BA (2011) Increased soil emissions of potent greenhouse gases under increased atmospheric CO_2. Nature 475:214–216

Veresoglou SD, Menexes G (2010) Impact of inoculation with *Azospirillum spp*. on growth properties and seed yield of wheat: a meta-analysis of studies in the ISI web of science from 1981 to 2008. Plant Soil 337:469–480

Viechtbauer W (2010) Conducting meta-analyses in R with the metafor package. J Stat Softw 36:1–48 URL: http://www.jstatsoft.org/v36/i03/

*Volkmar KM, Bremer E (1998) Effects of seed inoculation with a strain of *Pseudomonas fluorescens* on root growth and activity of wheat in well-watered and drought-stressed glass-fronted rhizotrons. Can J Plant Sci 78:545–551

Vurukonda SSK, Vardharajula S, Shrivastava AS (2016) Enhancement of drought stress tolerance in crops by plant growth promoting rhizobacteria. Microbiol Res 184:13–24

Waag CW, Jansa J, Schmid B, van der Heijden MGA (2011) Belowground biodiversity effects of plant symbionts supports aboveground productivity. Ecol Lett 14:1001–1009

Wada Y, Wisser D, Eisner S, Flörke M, Gerten D, Haddeland I, Hanasaki N, Masaki Y, Portmann FT, Stacke T, Tessler Z, Schewe J (2013) Multimodel projections and uncertainties of irrigation water demand under climate change. Geophys Res Lett 40:4626–4632

Wall DH, Moore JC (1999) Interactions underground: soil biodiversity, mutualism and ecosystem processes. Bioscience 49: 109–117

Wang GL (2005) Agricultural drought in a future climate: results from 15 global climate models participating in the IPCC 4th assessment. Clim Dyn 25:739–753

Weese DJ, Heath KD, Dentinger BTM, Lau JA (2015) Long-term nitrogen addition causes the evolution of less-cooperative mutualists. Evolution 69:631–642

Wickham H (2009) ggplot2: elegant graphics for data analysis. Springer-Verlag, New York

Wiebe N, Vandermeer B, Platt RW, Klassen TP, Moher D, Barrowman NJ (2006) A systematic review identified a lack of standardization in methods for handling missing variance data. J Clin Epidemiol 59:342–353

Wilson G, Harnett D (1997) Effects of mycorrhizae on plant growth and dynamics in experimental tall grass prairie microcosms. Am J Bot 84:478–482

Wilson GWT, Hartnett DC (1998) Interspecific variation in plant responses to mycorrhizal colonization in tallgrass prairie. Am J Bot 85:1732–1738

Wu SC, Cao ZH, Li ZG, Cheung KC, Wong MH (2005) Effects of biofertilizer containing N-fixer, P and K solubilizers and AM fungi on maize growth: a greenhouse trial. Geoderma 125: 155–166

*Yasmin H, Bano A, Samiullah (2013) Screening of PGPR isolates from semi-arid region and their implication to alleviate drought stress. Pak J Bot 45:51–58

*Yuwono T, Handayani D, Soedarsono J (2005) The role of osmotolerant rhizobacteria in rice growth under different drought conditions. Aust J Agric Res 56:715–721

*Zarmehri G, Moosavi SG, Zabihi HR, Seghateslami MJ (2013) The effect of plant growth promoting rhizobacteria (PGPR) and zinc fertilizer on forage yield of maize under water deficit stress conditions. TJEAS 23:3281–3290