



Potential of growth-promoting bacteria in maize (*Zea mays* L.) varies according to soil moisture

Victor Lucas Vieira Prudêncio Araújo^{a,*}, Giselle Gomes Monteiro Fracetto^{b,**}, Antonio Marcos Miranda Silva^a, Arthur Prudencio de Araujo Pereira^c, Caio Cesar Gomes Freitas^a, Felipe Martins do Rêgo Barros^a, Maiele Cintra Santana^a, Henrique Petry Feiler^d, Filipe Pereira Matteoli^a, Felipe José Cury Fracetto^b, Elke Jurandy Bran Nogueira Cardoso^a

^a Universidade de São Paulo, Escola Superior de Agricultura “Luiz de Queiroz”, Departamento de Ciência do Solo, Piracicaba, São Paulo, 13400-970, Brazil

^b Universidade Federal Rural de Pernambuco, Departamento de Agronomia, Recife, Pernambuco, 52171-900, Brazil

^c Universidade Federal do Ceará, Centro de Ciências Agrárias, Departamento de Ciências do Solo, Fortaleza, Ceará, 60355-636, Brazil

^d Purdue University, Department of Agronomy, West Lafayette, IN 47906, United States

ARTICLE INFO

Keywords:

Water deficit
Bacterial inoculation
Microbial inoculants
Maize cultivation
Biotechnological

ABSTRACT

Climate change has caused irregularities in water distribution, which affect the soil drying-wetting cycle and the development of economically important agricultural crops. Therefore, the use of plant growth-promoting bacteria (PGPB) emerges as an efficient strategy to mitigate negative impacts on crop yield. We hypothesized that the use of PGPB (in consortium or not) had potential to promote maize (*Zea mays* L.) growth under a soil moisture gradient in both non-sterile and sterile soils. Thirty PGPB strains were characterized for direct plant growth-promotion and drought tolerance induction mechanisms and were used in two independent experiments. Four soil water contents were used to simulate a severe drought (30% of field capacity [FC]), moderate drought (50% of FC), no drought (80% of FC) and, finally, a water gradient comprising the three mentioned soil water contents (80%, 50%, and 30% of FC). Two bacteria strains (BS28–7 *Arthrobacter* sp. and BS43 *Streptomyces albobiflavus*), in addition to three consortia (BC2, BC4 and BCV) stood out in maize growth performance in experiment 1 and were used in experiment 2. Overall, under moderate drought, inoculation with BS43 surpassed the control treatment in root dry mass and nutrient uptake. Considering the water gradient treatment (80–50–30% of FC), the greatest total biomass was found in the uninoculated treatment when compared to BS28–7, BC2, and BCV. The greatest development of *Z. mays* L. was only observed under constant water stress conditions in the presence of PGPB. This is the first report that demonstrated the negative effect of individual inoculation of *Arthrobacter* sp. and the consortium of this strain with *Streptomyces albobiflavus* on the growth of *Z. mays* L. based on a soil moisture gradient; however, future studies are needed for further validation.

1. Introduction

Drought is an abiotic factor that can harm plant development (Abou-Elwafa and Shehzad, 2021). Soil moisture deficit has a negative impact on physiological and biochemical processes in plants (i.e., accumulation of reactive oxygen species (ROS), lipid peroxidation, photosynthetic activity, etc.), reducing crop yield (Ojuederie et al., 2019). Climate change, due to anthropogenic degradation, is expected to intensify drought events in the 21st century (Chiang et al., 2021), mainly in tropical semi-arid regions (Cook et al., 2018). In the

agriculture sector, a loss of USD 37 billion was observed from 2008 to 2018 due to the negative effects of drought on crop yield (FAO, 2021). Therefore, isolation, characterization, and identification of microorganisms that promote plant tolerance to drought is an environmentally friendly alternative to sustain crop productivity (Ma et al., 2020). This approach is a bio-strategy to develop cutting-edge projects to address global issues (climate change, food security, and environmental degradation) (FAO, 2021).

Variation in the hydrological cycle caused by increases in evapotranspiration and greater frequency and intensity of rainfall, affecting

* Correspondence to: Soil Microbiology Laboratory, Luiz de Queiroz College of Agriculture, 13400-970, São Paulo, Brazil.

** Correspondence to: Microbiology and Biochemistry Soil Laboratory, Universidade Federal Rural de Pernambuco, 52171-900 Recife, Brazil.

E-mail addresses: victorlucas395@usp.br (V.L.V.P. Araújo), giselle.fracetto@ufrpe.br (G.G.M. Fracetto).

the drying-wetting (DW) cycle of soils is a known effect on climate change (Llopart et al., 2020; Morillas et al., 2015). DW cycles are important because they promote variations in soil physical, chemical, and biological properties. Frequent DW cycles can increase extracellular microbial enzyme activity, reduce microbial biomass, and change soil microbial community diversity and richness (Huang et al., 2021), affecting competitiveness of plant growth promoting microorganisms inoculated into the soil. However, soils with a history of droughts may contain bacteria adapted to moisture fluctuations, which take advantage of empty microhabitats and of the increase of substrate availability resulting from necromass after a DW event (Meisner et al., 2021). In the Brazilian Caatinga biome, where variable spatio-temporal rainfall patterns occur, soil microorganisms are adapted to environmentally stressful conditions, mainly induced by high temperatures and severe droughts (Leal et al., 2005; Santos et al., 2012). This adaptability has great biotechnological potential for agricultural crops, due to the characteristics of the microorganisms to thrive in severe climatic conditions (Fernandes-Júnior et al., 2015; Reis Antunes et al., 2019).

Plant growth promoting bacteria (PGPB) have mechanisms that benefit agricultural crops, such as the capacity of fixing nitrogen (N), producing indole-3-acetic acid (IAA), and solubilizing phosphate (Bonatelli et al., 2021; Cohen et al., 2015; Nascimento et al., 2021; Pathak et al., 2017). In addition, some mechanisms promote plant-systemic induced tolerance including the activity of the enzyme ACC deaminase (Glick, 2014), biofilm formation (Timmusk et al., 2014), production of exopolysaccharides (Rolli et al., 2015), and osmotic adjustment (Sarma and Saikia, 2014). Moreover, studies have reported the potential of these bacteria to alleviate effects of water deficit in different crops (Dubey et al., 2019; Jochum et al., 2019a; Lin et al., 2019).

Maize crop is affected by climatic changes, and water deficit is one of the major causes of instability in its production (Cao et al., 2019; Grote et al., 2021), promoting high financial losses (Zhao et al., 2017; Webber et al., 2018; Bucheli et al., 2021). Maize accounts for 41% of worldwide cereal production and is processed into products for animal feed, human consumption, and other industrial purposes (Erenstein et al., 2022). In Brazil, maize is the second most important crop, covering 22 M ha of cultivated area, responsible for 125 million tons produced (Conab, 2022). Currently, sustainable strategies have been used to minimize the negative impacts of water deficit, such as plant breeding, reduction of fertilizer input, and use of microbial inoculation (Rattis et al., 2021; Prasanna et al., 2021; Santos et al., 2021).

Recently, PGPB from semiarid temporary ponds were isolated, characterized, and identified, concluding that these bacteria could promote maize growth when inoculated individually or in consortia, under water stress conditions (Araújo et al., 2020). Currently, efforts are made to assess the potential of PGPB grown in an autochthonous microbial community on high-demanding crops, such as maize. Thus, high plant yield based on sustainable land use systems supports the intensive use of PGPB to replace synthetic inputs and prevent the worsening of climate change. Studies have investigated an improvement in the combination of soil-plant-PGPB (Efthimiadou et al., 2020; Trivedi et al., 2020), as an efficient inoculation of PGPB is associated with the complex interaction network of this system (Armada et al., 2018; Hu et al., 2018; Kong et al., 2019). Therefore, it is imperative to connect scientific knowledge of the rhizosphere microbial ecology of crops with studies aimed at bioprospecting of native microorganism (Santos et al., 2020).

The use of a consortium of PGPB shows greater efficiency to promote plant growth when compared to single strains under water stress (Asghari et al., 2020; Baas et al., 2016; Timm et al., 2016). These consortia may be formed because PGPB amplifies the functions of different growth promotion mechanisms through greater exploration of soil and plant niches (Saikia et al., 2018; Timm et al., 2016; Weidner et al., 2015). We hypothesized that efficient PGPB (single and co-inoculated) could promote the growth of *Z. mays* L. in a soil moisture gradient and in different constant water conditions in sterile and non-sterile soil.

Thus, the aim was to evaluate the efficiency of individual and consortium inoculation of PGPB to promote maize growth submitted to different water and soil conditions.

2. Material and methods

2.1. Study site and sampling strategy

The isolates were obtained from the PGPB collection of the Soil Microbiology and Biochemistry Laboratory of the Federal Rural University of Pernambuco, Brazil (UFRPE). The isolates were previously obtained from a tropical temporary pond in Parnamirim municipality, Pernambuco State, Brazil (8°17'05.2" S; 39°54'12.6" W) (Fig. S1). The climate is semi-arid (Köppen-Geiger climate classification: BSh) with 431.8 mm of annual precipitation and hyperxerophilous is the predominant vegetation in the Caatinga biome (Cruz, 2005). Sampling was performed in rhizosphere soil (RS) and bulk soil (BS) of *Mimosa bimu-cronata* (Fig. S1) in triplicate at 0–0.2 m depth. More details of the isolation procedure and selection of bacteria to integrate the PGPB bank were described in Araújo et al. (2020).

2.2. Selection and physiological characterization of isolates

Thirty PGPB isolates were selected: i-17 from RS; ii-8 from BS; iii-4 endospore-forming from rhizosphere soil (ERS) and one from bulk soil (EBS). The isolates were characterized in terms of direct and indirect mechanisms of growth promotion (Araújo et al., 2020) (Table S1).

Overall, isolates characterization was composed by the production of indole-3-acetic acid (IAA) and exopolysaccharide (EPS), biological nitrogen fixation (BNF) performance, phosphate solubilization capacity, biofilm formation (BIO), 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase synthesis, and water activity (A_w) (Araújo et al., 2020).

2.3. Experiment 1: Growth promotion of *Zea mays* L. under 80% field capacity

The experiment comprised 37 treatments with thirty isolates (Table S1), five bacterial consortia (BC) (Table 1), two controls without any inoculation, one of them conducted with complete fertilization (CH) and the other with 80% nitrogen restriction (NRC) under greenhouse conditions and in a completely randomized design. Fertilization was based on the application of nutrient solution (Hoagland and Arnon, 1950) and bacterial consortia had strains that showed the best

Table 1
In vitro features of the consortia of plant growth-promoting bacteria.

Consortia	Isolates	Strains	Mechanisms
BC1	ERS16–2; ERS18; BS43–1; RS59–6; RS85	<i>Bacillus</i> sp.; <i>Micrococcus</i> sp.; <i>Streptomyces</i> sp.; <i>Bacillus</i> sp.; <i>Bacillus</i> sp.	ARA; ACC; IAA; P-CA; EPS; BIO
BC2	ERS16–2; ERS18; BS43–1; RS59–6	<i>Bacillus</i> sp.; <i>Micrococcus</i> sp.; <i>Streptomyces</i> sp.; <i>Bacillus</i> sp.	ARA; ACC; IAA; P-CA; EPS
BC3	ERS16–2; ERS18; BS43–1	<i>Bacillus</i> sp.; <i>Micrococcus</i> sp.; <i>Streptomyces</i> sp.	ARA; ACC; IAA; P-CA
BC4	ERS16–2; ERS18	<i>Bacillus</i> sp.; <i>Micrococcus</i> sp.	ARA; ACC; IAA
BC5	ERS16–2; ERS18; RS85	<i>Bacillus</i> sp.; <i>Bacillus</i> sp.; <i>Bacillus</i> sp.	ARA; ACC; EPS; BIO
BC2 ^(*)	EBS4; ERS16–2; ERS18; BS43–1	<i>Staphylococcus</i> sp.; <i>Bacillus</i> sp.; <i>Micrococcus</i> sp.; <i>Streptomyces</i> sp.	ARA; ACC; IAA; P-CA; A_w
BCV	BS28–7; BS43	<i>Arthrobacter</i> sp.; <i>Streptomyces albobiflavus</i>	IAA; P-CA; ACC

GenBank access number: EBS4 (NR156818.1); ERS16-2 (NR.152692.1); ERS18 (NR.116578.1); BS28-7 (MW.487809); BS43 (NR.044151.1); BS43-1 (NR.116578.1); RS59-6 (NR.152692.1); RS85 (NR.074540.1); (*)BC2, Araújo et al. (2020); ARA: acetylene reduction assay; IAA: Indole-3 acetic acid production; IS P-CA: Calcium phosphate solubilization index; BIO: biofilm formation; EPS: exopolysaccharides production.

Seeds of *Z. mays* L. (cultivar AG 1051) were inoculated with 1 mL of inoculum and reinoculated 14 days after planting. Inoculations were performed in a liquid medium King B for 24 h (108 UFC.mL⁻¹ (DO550 = 0.1)). After that, seeds were germinated in a sterile substrate of sand and vermiculite in liter pots at 80% of the field capacity (FC) throughout the experiment (Dourado et al., 2019). The evaluation was performed 50 days after planting. The total leaf area (TLA), shoot dry mass (SDM), and root dry mass (RDM) were determined after drying in a forced air oven at 60 °C for 72 h. Total biomass (TB) was obtained from the sum of SDM and RDM. TLA was obtained according to Sangoi et al. (2007).

The isolates with the best performance in the attributes evaluated in experiment 1 and that showed the highest residual contribution in the multivariate analysis (Table S2 and S3) were identified by 16 S rRNA gene sequencing. Bacterial genomic DNA was extracted by the bead-beating method and universal bacterial primers were used 27 F (5-AGAGTTTGACCTGGCTCAG-3) and 1492 R (5-GGTTACCTTGTTAC-GACTT-3) (Lane, 1991). The amplification reaction and conditions were described in Araujo et al. (2020). PCR products were sent to Macrogen Laboratory (South Korea) facility for purification and sequencing. Similar sequences were obtained from GenBank (NCBI database).

The experiment was performed under a day/night cycle of 13/11 h, at 28 °C and relative humidity of 50%, using pots with 7 kg of soil in completely randomized blocks with five replicates per treatment in a double factorial (6×4) scheme, totaling 24 treatments and thus 120 experimental units (Fig. 1A). The first factor was bacterial inoculation or not, corresponding to two single bacteria isolates (BS28-7, BS43), three bacterial consortia (BC) (BC2, BC4, and BCV) and an uninoculated control (C). While the second factor was soil water content: 30% of soil field capacity (FC) (simulating a severe drought), 50% of FC (simulating a moderate drought), 80% of FC (simulating no drought), and water range 80–50–30%.

For the treatment of the water range, a wetting/drying cycle of soil was simulated, in which the pots with 80% of FC were allowed to dry to 30% of FC then rehydrated to 80% of FC and allowed to dry to 30% FC. We used the multivariate approach based on the contribution of residuals combining results from [Araújo et al. \(2020\)](#) to find the most preeminent bacterial inoculum to use in experiment 2. Briefly, these authors tested the same treatments under water stress, highlighting the BS43 treatment at 30% field capacity and the BS28–7 treatment under 80% field capacity ([Fig. S4](#), [Tables S4](#), and [S5](#)).

The soil was classified as Oxisol with a kandic horizon according to WRB (Food and Agriculture Organization-FAO) (FAO, 2014). The soil was collected in the experimental site of the Luiz de Queiroz College of Agriculture (ESALQ-USP), in the municipality of Piracicaba, São Paulo State, Brazil (22°42'14.836"S; 47°38'11.695"W) and characterized according to Raji et al. (2001) (Table 2). The experimental site has been cultivated with soybeans and maize for the last 10 years. For the pot experiment, limestone and fertilizers were applied according to the

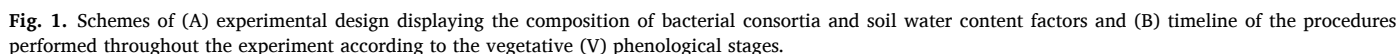


Table 2

Physical-chemical characteristics of the soil used for the plant growth promotion experiment in soil under different field capacity.

Textural class	pH	Ca ²⁺	Mg ²⁺	K ⁺	Al ³⁺	H ⁺ +Al ³⁺	SB	CEC	V	m	OM	P
					mmol _c dm ⁻³				%	%	g.dm ⁻³	mg.dm ⁻³
Clay	5.01	38.3	13.3	5.64	< 0.1	30.4	57.2	87.6	65	0	20.7	22

SB: sum of bases; CEC: cation exchange capacity; V: base saturation; m: aluminium saturation; OM: organic matter.

maize nutritional requirements (Raj et al., 1997).

Maize seeds (AG 1051) were superficially sterilized and inoculated by immersion for 2 h in an inoculum containing 10⁸ CFU.mL⁻¹ (OD₅₅₀ = 0.1) in a sterile saline solution (0.85% NaCl) of each strain and/or consortium. The control treatment contained mixing seeds in sterilized saline solution. Subsequently, five inoculated seeds were sown per pot. Thinning was performed after 14 days of germination, leaving two plants per pot and starting the induction of different water management. The pots were irrigated as described in experiment 1. Overall, moderate drought (50% of FC) was reached on the 19th day after planting (DAP), while severe drought (30% of FC) occurred on the 24th DAP when treatments with water range (80–50–30%) had rehydration to 80% of FC, leaving them to dry at 30% of FC at the end of the experiment. Harvest was performed at 35 DAP for all treatments (Fig. 1B).

TLA was determined using LI-COR (LI-3100 C), while SDM, RDM, and TB were determined as described in experiment 1. Nutrient contents (N, P, K, Ca, Mg, and S) were determined according to Embrapa (2009).

2.6. Statistical analyses

The data were initially submitted to normality using the Shapiro-Wilk test and to homoscedasticity of variance using the Bartlett test. Subsequently, differences in the analysis of variance (ANOVA) were evaluated using Dunnett's (experiment 1) and Duncan's tests ($p < 0.05$) (experiment 2). Next, we integrated the results of the principal component analysis (PCA) and Spearman correlations, using the FactoMineR, Factoextra and corplot statistical packages, respectively. For that, the data were log transformed ($C + 1$) to meet the r multivariate normality and the total biomass was removed from the dataset to avoid multicollinearity (Ramette, 2007). Statistical analyses were performed using the software R Core Team (2017) version 3.6 and all results were expressed as the means followed by standard deviation.

3. Results

3.1. Experiment 1: Growth promotion of *Zea mays* L. in sterile substrate under 80% field capacity

Total leaf area (TLA), shoot dry mass (SDM), root dry mass (RDM), and total biomass (TB) did not show significant differences ($p > 0.05$) in treatments inoculated with EBS4, ERS13–3, BS24, BS28–7, BS28–10, BS38, BS43–1, BS46–1, RS48, RS52, RS66–3, RS67–1, RS70, and BC5 comparing to control treatment. Furthermore, the BC1, BC3, BC4, and BC5 consortium treatments did not differ in terms of RDM and TB when compared to the CH control ($p > 0.05$). In addition, the CH control treatment outperformed ($p < 0.05$) the control that received 80% nitrogen restriction (NRC) in TLA, SDM, and TB (Table 3).

According to principal components analysis (PCA), the first two components explained 94% of the data variation and RDM and SDM showed positive correlations with each other (Fig. 2, Table S2 and S3). Overall, 11 treatments (i.e., ERS16–2, BS24, BS43–1, BS46–1, RS4, RS52, RS54, RS70, BC1, BC3, and BC5) correlated positively with TLA. However, the other 11 treatments (i.e., EBS4, ERS13–3, BS28–7, BS28–10, BS38, BS43, RS66–2, RS66–3, RS67–1, BC4, and CH) correlated positively with RDM and SDM, mainly the BS28–7 treatment (Fig. 2, Table S2).

Based on the spearman correlation, TLA, SDM, and RDM negatively correlated with BIO mechanism ($r = -0.35$, $p < 0.05$, $r = -0.39$,

Table 3Inoculation effect of plant growth-promoting bacteria isolated from rhizosphere and bulk soil of *Mimosa bimucronata* from a temporary pond in the Semiárid of Brazil on the agronomic parameters evaluated in *Zea mays* L. in sterile substrate under 80% field capacity.

Isolates	TLA (cm ²)	SDM (g)	RDM (g)	TB (g)
CH	3032.88 ± 1110.37	2.98 ± 1.49	1.64 ± 0.77	4.63 ± 2.10
NRC	1316.13 * ± 122.87	1.51 *	0.79 ± 0.02	2.30 *
		± 0.14		± 0.13
EBS4	1803.11 ± 211.30	2.02 ± 0.46	1.31 ± 0.16	3.34 ± 0.62
ERS13–3	1701.91 ± 504.57	1.66 ± 0.53	1.50 ± 0.41	3.16 ± 0.89
ERS13–9	658.98 * ± 479.32	1.31 *	0.55 *	1.86 *
		± 0.01	± 0.05	± 0.05
ERS16–2	1460.35 * ± 807.16	1.60 ± 0.48	0.92 ± 0.58	2.52 ± 0.58
ERS18	1466.89 *	1.32 *	1.02 ± 0.69	2.34 ± 0.69
	± 1056.70	± 0.01		
BS24	1985.60 ± 417.57	1.87 ± 0.89	1.23 ± 0.73	3.09 ± 1.62
BS24–1	1386.40 * ± 421.70	1.55 ± 0.26	1.05 ± 0.22	2.60 ± 0.17
BS28–7	1921.90 ± 502.69	2.35 ± 0.37	1.72 ± 0.49	4.07 ± 0.78
BS28–10	1957.38 ± 409.17	2.30 ± 0.66	1.56 ± 0.42	3.86 ± 0.76
BS38	2112.55 ± 796.51	2.02 ± 0.24	1.50 ± 0.48	3.52 ± 0.70
BS43	1521.64 * ± 747.71	1.60 ± 0.84	1.09 ± 0.58	2.68 ± 1.42
BS43–1	1710.40 ± 585.55	1.55 ± 0.65	0.87 ± 0.42	2.42 ± 1.07
BS46–1	1804.65 ± 36.01	1.61 ± 0.22	0.82 ± 0.28	2.42 ± 0.46
RS48	1782.18 ± 145.87	1.92 ± 0.40	1.16 ± 0.16	3.08 ± 0.46
RS52	2077.20 ± 374.39	2.06 ± 0.83	1.14 ± 0.39	3.20 ± 1.21
RS54	1597.15 * ± 33.99	1.52 *	1.10 ± 0.12	2.62 ± 0.28
		± 0.24		
RS59	878.38 * ± 594.32	0.98 *	0.64 ± 0.30	1.61 *
		± 0.50		± 0.79
RS59–3	1396.10 * ± 209.69	1.47 *	1.19 ± 0.64	2.65 ± 1.27
		± 0.62		
RS59–6	1054.65 * ± 549.13	1.14 *	0.61 ± 0.42	1.75 *
		± 0.54		± 0.96
RS64	982.61 * ± 489.56	0.79 *	0.54 *	1.33 *
		± 0.53	± 0.22	± 0.75
RS66–1	1510.05 * ± 875.05	1.49 *	0.80 ± 0.49	2.29 *
		± 0.99		± 1.46
RS66–2	1593.10 * ± 266.86	2.06 ± 0.09	1.48 ± 0.21	3.54 ± 0.13
RS66–3	1753.09 ± 258.08	1.78 ± 0.05	1.40 ± 0.15	3.18 ± 0.11
RS67–1	1764.08 ± 490.30	1.68 ± 0.31	1.21 ± 0.17	2.89 ± 0.47
RS70	2267.45 ± 187.79	1.87 ± 0.07	1.21 ± 0.24	3.08 ± 0.17
RS76–1	1736.21 ± 898.49	1.44 *	0.84 ± 0.39	2.27 *
		± 0.49		± 0.85
RS79–1	990.24 * ± 245.77	1.01 *	0.52 *	1.53 *
		± 0.37	± 0.18	± 0.53
RS82	1442.10 * ± 620.47	1.41 *	0.90 ± 0.54	2.32 *
		± 1.07		± 1.61
RS84	1388.49 * ± 202.12	1.42 *	1.11 ± 0.51	2.53 ± 1.18
		± 0.68		
RS85	826.74 * ± 162.32	0.76 *	0.65 ± 0.35	1.41 *
		± 0.41		± 0.76
BC1	1665.23 * ± 137.54	1.75 ± 0.25	1.05 ± 0.30	2.80 ± 0.42
BC2	1291.70 * ± 815.52	1.10 *	1.10 ± 0.59	2.20 *
		± 0.57		± 1.16
BC3	1568.18 * ± 59.38	1.49 *	1.21 ± 0.17	2.69 ± 0.36
		± 0.29		
BC4	1551.12 * ± 45.57	1.56 ± 0.05	1.34 ± 0.16	2.90 ± 0.11
BC5	1788.60 ± 533.52	1.63 ± 0.48	0.92 ± 0.12	2.55 ± 0.58

CH: uninoculated control that received complete synthetic chemical fertilization; NRC: uninoculated control that received 80% nitrogen restriction; TLA: total leaf area; SDM: shoot dry mass; RDM: root dry mass. TB: total biomass; BC: bacterial consortia (see Table 1 for more information on consortia composition). Significant values when compared to CH are found with * and when compared to NRC are found in bold according to Dunnett's test ($p < 0.05$). Standard deviation are shown ($n = 3$).

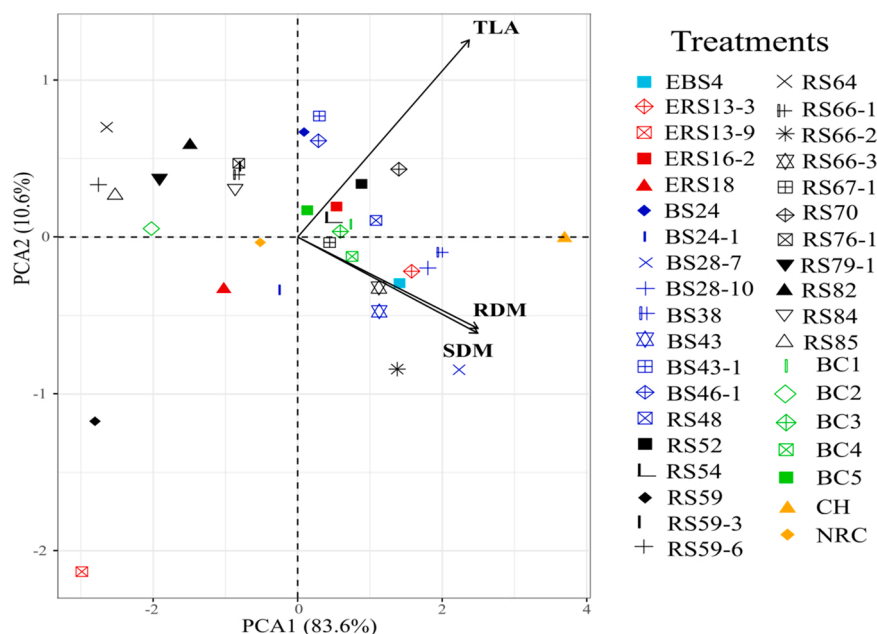


Fig. 2. Principal Component Analysis considering all treatments and parameters *in vivo* evaluated in *Zea mays* L. without water stress in sterile substrate. TLA: total leaf area; SDM: shoot dry mass; RDM: root dry mass.

$p < 0.05$, $r = -0.29$, $p < 0.05$, respectively). The IAA negatively correlated with the P-Ca ($r = -0.5$, $p < 0.05$). In addition, TLA, SMD and RDM correlated positively with each other (Fig. S3).

According to the molecular analysis, BS28-7 strain was identified as *Arthrobacter* sp. (84% similarity and 94% query coverage: access number 149802.1). Sequence data were submitted to GenBank under accession number MW487809. Strain BS43 was identified as *Streptomyces albobiflavus*, access: NR044151.1 by Araújo et al. (2020).

3.2. Experiment 2: Growth promotion of *Zea mays* L. in soil under different field capacities

Fig. S5 presents an overview of the experiment at 34 days after planting. Differences in TLA were found only in treatments inoculated under severe and no drought when compared to the control treatment (Fig. 3B and D), with BCV treatment showed significance (Fig. 4B and D). In the water range treatment, BS28-7, BS43, and BC4 surpassed the BCV consortium in TLA (Fig. 4A).

Differences in SDM, RDM, and TB were found only in the water range treatment and moderate stress treatment ($p < 0.05$) (Figs. 5A and 5C). In the water range treatment, C treatment showed higher ($p < 0.05$) TB values when compared to BS28-7, BC2, and BCV inoculated treatments. Under moderate drought, BS43 treatment increased ($p < 0.05$) RDM when compared to BS28-7, BC2, BCV, and C treatments. Under water range and severe drought, no differences were found between BS28-7 and BCV treatments for SDM, RDM, and TB (Fig. 5A and B).

According to the PCA, the first two components explained 85% (water range), 78% (severe drought), 74% (moderate drought), and 77% (no drought) of data variability (Fig. 6, Tables S6 and S7). In water range, C treatment correlated positively with SDM, RDM, N, P, and K (Fig. 6A) and presented the highest residuals multivariate contribution in the first two components (Table S6A). Under severe drought, BCV treatment correlated positively with SDM, TLA, N, and Ca (Fig. 6B). Likewise, under moderate drought, BS43 correlated positively with TLA, RDM, N, and P (Fig. 6C) and presented the highest residuals multivariate contribution (Table S6C). In addition, BS43 showed the highest N and P contents under moderate drought (Table S8C). Under no drought, BC2, BCV, and BS28-7 correlated positively with TLA, SDM, RDM, N, and Ca (Fig. 6D), with BC2 showing the highest N and S contents (Table S8D).

Overall, treatments with higher TB values correlated positively with the N content. The main differences in P and S contents were observed under severe drought in BS28-7, BS43, BC2, BCV, and C treatments (Table S8).

Based on the Spearman correlation in the water range (Fig. S6A), SDM and RDM correlated positively with the N content ($r = 0.71$, $p < 0.01$, $r = 1$, $p < 0.001$, respectively). However, the P content correlated positively with RDM ($r = 0.6$, $p < 0.05$) and negatively correlated with TLA ($r = -0.43$, $p < 0.01$). Under severe drought (Fig. S6B), TLA and SDM correlated positively with N and Ca, while RDM correlated positively with the P, Mg, and S contents. Under moderate drought (Fig. S6C), TLA and SDM correlated positively with the N content ($r = 0.89$, $p < 0.001$, $r = 0.03$, $p < 0.05$, respectively), while RDM correlated positively with the S content ($r = 0.94$, $p < 0.001$). Under no drought (Fig. S6D), SDM and RDM correlated positively with the N and Ca contents and negatively with the Mg content.

4. Discussion

In this investigation, native PGPB screened from harsh environments showed potential to promote maize growth under soil water stress. Overall, in the presence of PGPB, maize grew better under constant soil water moisture than under varying soil moisture, thus partially confirming our initial hypothesis. In other words, the soil drying-wetting cycle affected negatively the PGPB potential, individually or in consortium. The interest in evaluating the applicability of PGPB in different soil water conditions is imperative because maize is one of the most economically and nutritionally important cereal crops worldwide (Efthimiadou et al., 2020; Erenstein et al., 2022).

Climate change projections indicate increases in irregularities of rainfall patterns and drought traits (e.g., intensity, frequency, and duration) worldwide, compromising crop growth and yield (Llopert et al., 2020; Grote et al., 2021). Nowadays, mitigating the effect of drought to ensure food security is considered one of the main issues for global agriculture (FAO, 2021; Krishnamurthy et al., 2022). Thus, the use of PGPB emerges as an eco-friendly strategy (Trivedi et al., 2020; Kumawat et al., 2022; Khatoon et al., 2022) due to the positive effects on plant growth (Ali and Khan, 2021; Ali and Xie, 2020; Kavamura et al., 2013). According to Mendes et al. (2013), the manipulation of beneficial

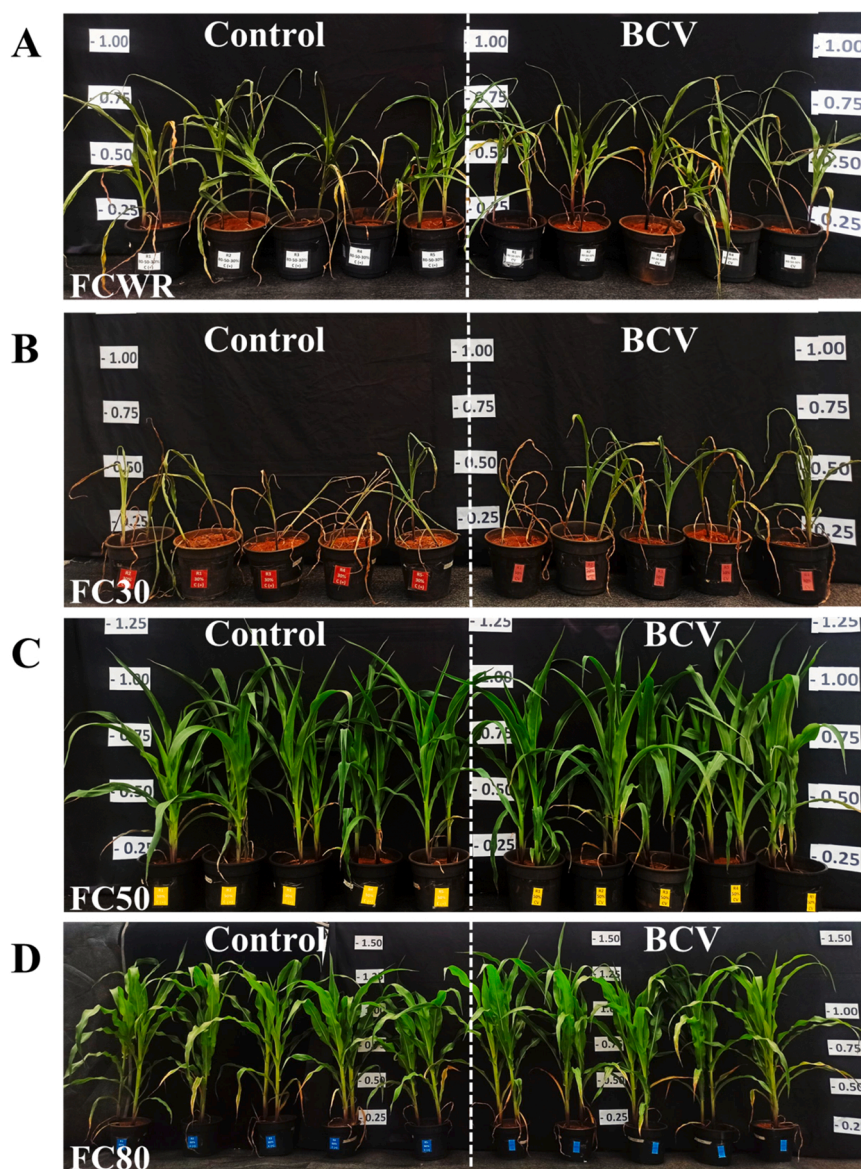


Fig. 3. Effect of bacterial inoculation in *Zea mays* L. growth promotion in soil at A) water range (FCWR), B) 30% (FC30) and C) 50% (FC50) and D) 80% (FC80) field capacity. Control – control without inoculation; BCV – plants inoculated with the consortia BCV.

plant-microbe interactions can contribute to diverse applications ranging from sustainable increases in agricultural production to mitigating climate change effects.

Previously, we investigated a bacteria screening from temporary pond soils in tropical semiarid Northeast Brazil to determine morpho-physiological and molecular characterization and evaluate the potential of screened bacteria in growth of maize under water stress, using sterile soil (Araújo et al., 2020). Particularly, we explored the potential of PGPB considering a range of soil moisture and non-sterile soil. In this investigation, 14 inoculated treatments under N fertilizer restriction did not differ in growth parameters (*i.e.*, TLA, SDM, RDM, and TB) when compared to the uninoculated control treatment that received full synthetic chemical fertilization. The results were more pronounced when strain BS28–7 was inoculated, which increased TB of maize by 56% compared to the uninoculated control with or without N fertilizer restriction.

Strain BS28–7 was identified as *Arthrobacter* sp. and belongs to the phylum Actinobacteria. Bacteria of the phylum Actinobacteria are widely observed in harsh environments (Chauhan et al., 2018; Rego

et al., 2019; Zhang et al., 2016), which can be attributed to their ecological breadth and metabolic versatility (Romaniuk et al., 2018; Yao et al., 2015). These traits confer resistance to various abiotic stresses, such as drought (Chukwuneme et al., 2020), salinity (Khan et al., 2021), cold (Mukhia et al., 2021), chromium (Arshad and Ahmed, 2017), and iron (Sharma et al., 2016). Gianese et al. (2002) attributed the high resistance of *Arthrobacter* sp. to adverse conditions due to the presence of flexible proteins, which cause a reduction of amounts of acidic residues (fewer salt-bridges) as well as the R/K ratio observed (R- arginine and K- lysine). Mukhia et al. (2021) reinforce these findings by describing specific heat-adapted proteins in the genome of *Arthrobacter* sp. These investigations shed light on the relevance of studying the biotechnological potential of *Arthrobacter* sp. under different soil water contents and soil temperatures, mainly in the context of the increasing effects of climate change.

Several studies have demonstrated the capacity of *Arthrobacter* sp. to increase plant growth and nutrient availability through IAA production, siderophores, and inorganic phosphate solubilization (Fernández-González et al., 2017; Safdarian et al., 2019; Sharma et al., 2016;

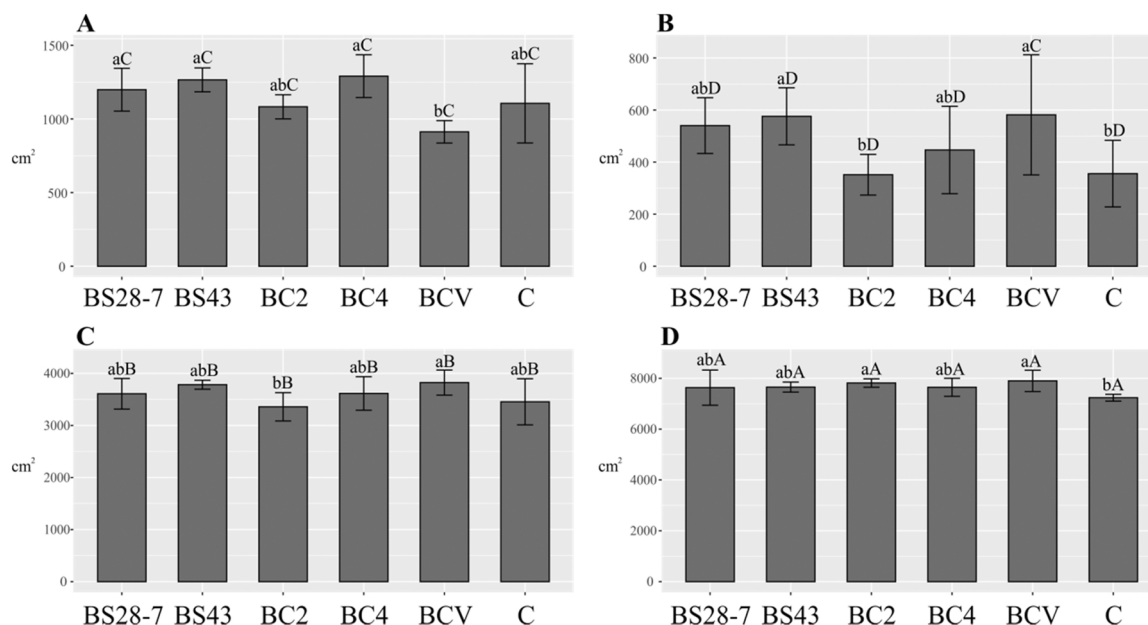


Fig. 4. Inoculation effect of plant growth-promoting bacteria on total leaf area evaluated in *Zea mays* L. in soil at A) water range, B) severe drought, C) moderate drought and D) no drought. Uppercase letters compare differences of treatments between different field capacities, while lowercase letters compare differences between treatments in the same water condition by Duncan's test ($p < 0.05$). Mean values are followed by standard deviation ($n = 5$).

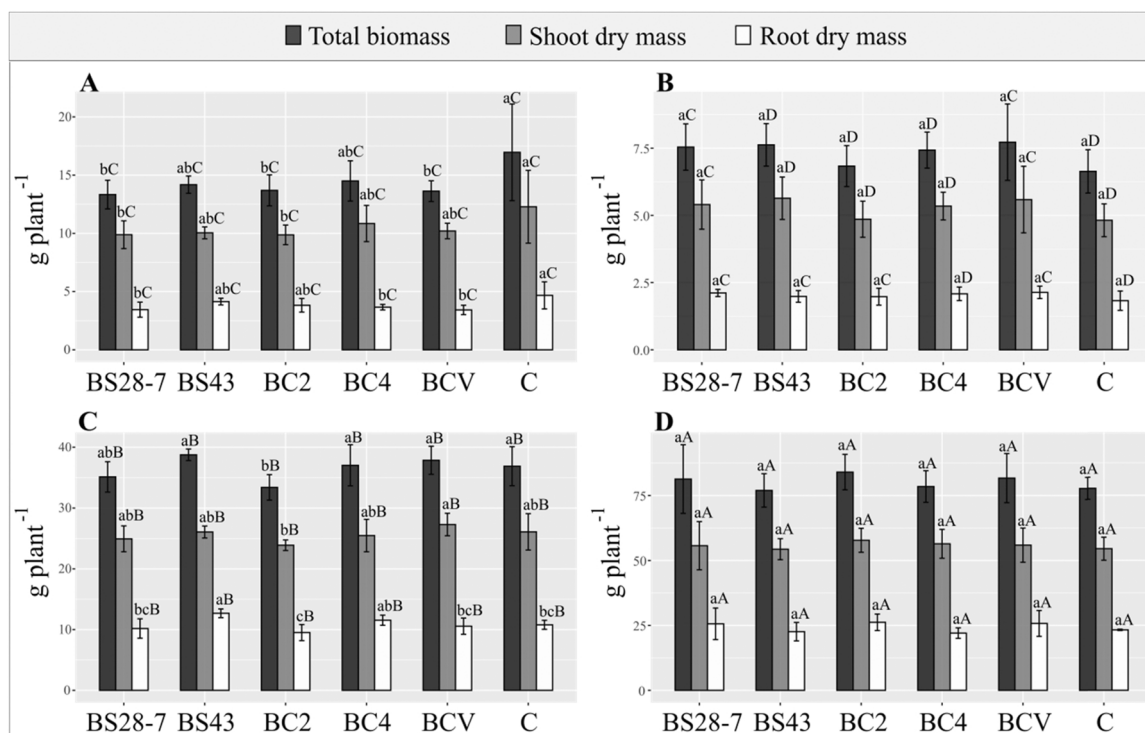


Fig. 5. Inoculation effect of plant growth-promoting bacteria on the total biomass, shoot dry mass and root dry mass evaluated in *Zea mays* L. in soil at A) water range, B) severe drought, C) moderate drought and D) no drought. Uppercase letters compare differences of treatments between different field capacities, while lowercase letters compare differences between treatments in the same water condition by Duncan's test ($p < 0.05$). Mean values are followed by standard deviation ($n = 5$).

Sreevidya et al., 2016; Upadhyay et al., 2012; Vanissa et al., 2020). In our investigation, *Arthrobacter* sp. (BS28-7) showed multiple plant growth promotion mechanisms (IAA, EPS, ACC, and Aw), highlighting one of the greatest production of IAA ($114.67 \mu\text{g}\cdot\text{mL}^{-1}$), synthesizing 10-fold more IAA than *Streptomyces albobiflavus* (BS43) (Table S1), the most important phytohormone that regulates plant growth (Ali and

Khan, 2021; Glick et al., 2007). These mechanisms may have contributed to the positive correlation observed between *Arthrobacter* sp. (BS28-7) with RDM and SDM (Fig. 3). As we observed a negative correlation of agronomic parameters with the formation of biofilm, we argue that other mechanisms may be acting under adequate soil water conditions to promote the maize growth.

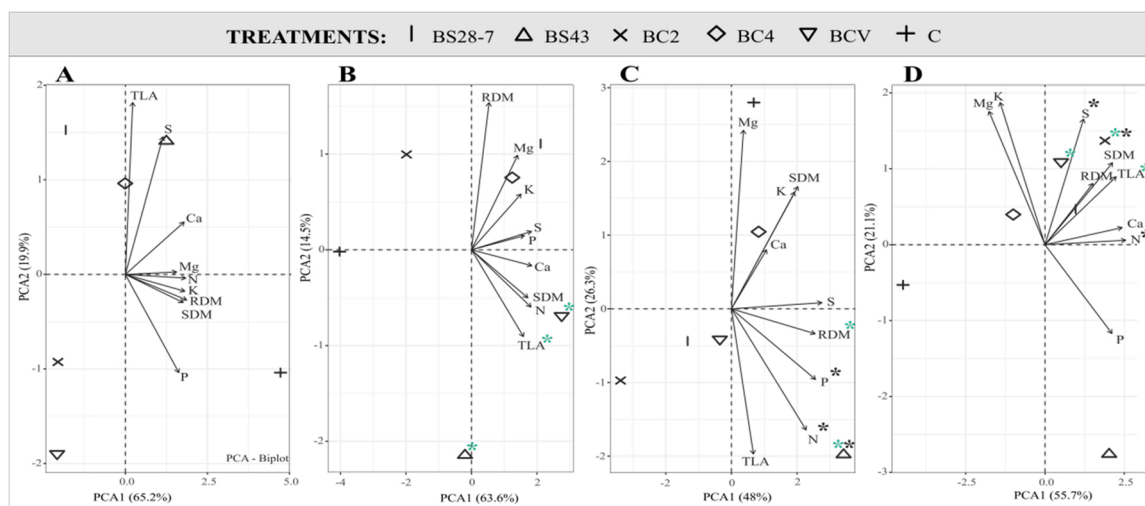


Fig. 6. Principal Component Analysis for the treatments, total nutrient and parameters *in vivo* evaluated in *Zea mays* L. at A) water range, B) severe drought, C) moderate drought and D) no drought. TLA: total leaf area; SDM: dry mass of the stem; RDM: dry root mass. Significant values when compared to Control (C) treatment for nutritional contents are found with * and when compared to agronomic parameters fx1 in bold according to Duncan's test ($p < 0.05$).

Soil microbiome is directly affected by climate change (Jansson and Hofmockel, 2020; Schimel and Schaeffer, 2012). Xie et al. (2021) found that drought and drastic changes in soil moisture significantly influenced the rhizospheric microbial community, increasing the relative abundance of dominant phyla, such as Actinobacteria and Firmicutes. Strains of these phyla are related drought resistance (Araújo et al., 2020; Kavamura et al., 2013); therefore, efforts should be made to answer how the promising PGPB belonging to these phyla can contribute to mitigating the negative effects of drought or drying-wetting cycles on crops. Here, we addressed this subject, when we evaluated the individual and consortium response of PGPB belonging to these phyla against the native soil community (non-sterile soil), expecting that the diversity of a microbial inoculum would result in synergistic processes, expanding available plant-associated niches (Weidner et al., 2015; Barbosa et al., 2021). This synergism would induce greater tolerance to soil water stress and maintain plant development during adequate water conditions (Ali and Khan, 2021; Saikia et al., 2018).

Previous studies have shown that the combination of *Arthrobacter* spp. with other PGPB promoted the growth of maize, wheat, alfalfa (Bazhanov et al., 2017; Kumar et al., 2014, 2015; Hone et al., 2021), and mitigated the effects of salinity stress on soybean and increased plant growth (Khan et al., 2021). Here, we demonstrated that inoculation of *Arthrobacter* sp. and *Streptomyces albobiflavus* (BCV) under constant water moisture (severe, moderate, and no drought) did not differ from the individual inoculation of these strains. However, under severe and no drought, BCV inoculation showed significance in TLA of maize (Fig. 6) when compared to the uninoculated control, positively correlating with TLA, SDM, N, and Ca. We highlight these correlations as it is widely accepted that PGPB-mediated benefits may be the result of direct effects, such as the release of essential nutrients to plants (Trivedi et al., 2020).

Plants overcome drought events by allocating energy to the roots to recruit key microbes, such as PGPB (Barnawal et al., 2019). Under moderate water stress conditions, our study demonstrated that inoculation of BS43 increased RDM and the N and P contents of *Z. mays* L. when compared to the other treatments and corroborating the positive correlations found. This increase may be a result of IAA production and ACC deaminase enzyme activity, which contributed to development of the root system, ensuring the absorption of water and nutrients (Ali and Khan, 2021; Cherif et al., 2015; Khan et al., 2020; Ullah et al., 2019). Partially corroborating to our results, Chukwuneme et al. (2020) found that inoculation of *Streptomyces pseudovenezuelae* in maize under moderate drought resulted in greater development of the root system than the uninoculated treatment, whereas inoculation of this strain in

consortium with *Arthrobacter arilaitensis* resulted in greater gains.

In the water range (drying-wetting cycle of soil), there was a negative interaction between *Arthrobacter* sp. (BS28-7) and *Streptomyces albobiflavus* (BS43) based on maize growth. We argue that this negative effect may be associated to changes in soil moisture, which directly affect the plant-associated microbiome (Baetz and Martinoia, 2014; Santos-Medellín et al., 2017; Xu et al., 2018), resulting in undesirable effects, such as elimination of key taxa. Studies assert that the effects of drought significantly affect the composition and diversity of rhizosphere microbiome (Xu et al., 2018; Jochum et al., 2019b), increasing specific phyla represented by potentially drought-tolerant strains (Naylor et al., 2017; Hone et al., 2021). Xie et al. (2021) demonstrated under severe drought that the growth of Actinobacteria and Firmicutes decreased rapidly after soil rehydration. However, more studies are needed to assess the effects of these PGPB (individual or in consortium) considering the variation of soil moisture on the soil-plant-microbiome.

Our finding suggests that plant-PGPB interactions under variations in soil moisture may act as modulator, generating a reorganization of the indigenous microbial community, and affecting the potential of PGPB (individual or in consortium) to promote maize growth. As key microorganisms have a regulatory effect on the network of soil-plant microbial interactions, their removal results in significant losses of host-microbiome interactions (Trivedi et al., 2020). Therefore, further investigations should expand the knowledge of keystone species that comprise the central soil-plant microbiome, which may have deleterious effects on plant growth.

In general, inoculation of PGPB under constant soil water conditions resulted in beneficial effects on the development of *Z. mays* L., mainly under soil water stress. Particularly, we reject our initial hypothesis, as inoculation of PGPB in a soil moisture gradient would mitigate the effect of drought on *Z. mays*. Thus, we provide crucial insights into the impacts of drying-wetting cycles of soil on the potential of PGPB to attenuate soil water stress and promote growth of *Z. mays* L.

5. Conclusions

We demonstrated that *Streptomyces albobiflavus* promoted growth of *Z. mays* especially under moderate drought (50% of soil field capacity), as it promoted root system growth and increased the nutritional contents of N and P in the plant. The consortium between *Arthrobacter* sp. and *Streptomyces albobiflavus* under severe and no drought resulted in an increase of TLA of *Z. mays* and correlated positively with TLA, SDM, N, and Ca.

This is the first report on the negative effect of individual inoculation of *Arthrobacter* sp. or in consortium with *Streptomyces albobiflavus* on growth of *Z. mays* in soil under drying-wetting cycles. Further investigations are needed to understand if the inoculation of these PGPB during variations in soil moisture influences the native microbial community, in addition to verifying the specificity of these PGPBs in other maize cultivars.

CRediT authorship contribution statement

Victor Lucas Vieira Prudêncio Araújo: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Visualization, Writing – original draft, Writing – review & editing. **Giselle Gomes Monteiro Fracetto:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Writing – original draft, Visualization, Supervision, Project administration, Funding acquisition. **Antonio Marcos Miranda Silva:** Conceptualization, Formal analysis, Investigation, Data Curation, Writing – original draft. Funding acquisition. **Arthur Prudencio de Araujo Pereira:** Conceptualization, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing. **Caio Cesar Gomes Freitas:** Methodology, Formal analysis, Writing – original draft. **Felipe Martins do Rêgo Barros:** Conceptualization, Formal analysis, Writing – original draft. **Maiele Cintra Santana:** Methodology, Formal analysis, Writing – original draft. **Henrique Petry Feiler:** Conceptualization, Methodology, Writing – original draft. **Filipe Pereira Matteoli:** Conceptualization, Formal analysis, Methodology, Writing – original draft. **Felipe José Cury Fracetto:** Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft. **Elke Jurandy Bran Nogueira Cardoso:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Writing – original draft, Visualization, Supervision, Project administration, Funding acquisition.

Data Availability

No data was used for the research described in the article.

Acknowledgments

We thank Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, Project No: 2016/18944–3, 2018/20553–8, 2019/13436–8, 2019/27682–0) for financial support in this investigation. The author and G.G.M.F. (306252/2021–0) thank Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Brazil) for the fellowship provided. We appreciate Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES, Brazil) - Finance Code 001. We are also grateful to Fernando Baldesin and Denise Mescolotti for their collaboration as technicians.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.micres.2023.127352](https://doi.org/10.1016/j.micres.2023.127352).

References

- Abou-Elwafa, S.F., Shehzad, T., 2021. Genetic diversity, GWAS and prediction for drought and terminal heat stress tolerance in bread wheat (*Triticum aestivum* L.). Genet. Resour. Crop Evol. 68, 711–728. <https://doi.org/10.1007/s10722-020-01018-y>.
- Ali, S., Khan, N., 2021. Delineation of mechanistic approaches employed by plant growth promoting microorganisms for improving drought stress tolerance in plants. Microbiol. Res. 249, 126771 <https://doi.org/10.1016/j.micres.2021.126771>.
- Ali, S., Xie, L., 2020. Plant growth promoting and stress mitigating abilities of soil born microorganisms. Recent Pat. Food, Nutr. Agric. 11, 96–104. <https://doi.org/10.2174/2212798410666190515115548>.
- Araújo, V.L.V.P., Lira Junior, M.A., Souza Júnior, V.S. de, de Araújo Filho, J.C., Cury Fracetto, F.J., Andreote, F.D., de Araújo Pereira, A.P., Mendes Júnior, J.P., Rêgo Barros, F.M. do, Monteiro Fracetto, G.G., 2020. Bacteria from tropical semiarid

- temporary ponds promote maize growth under hydric stress. Microbiol. Res. 240, 126564 <https://doi.org/10.1016/j.micres.2020.126564>.
- Armada, E., Leite, M.F., Medina, A., Azcón, R., Kuramae, E.E., 2018. Native bacteria promote plant growth under drought stress condition without impacting the rhizomicrobiome. Fiy092 FEMS Microb. Ecol. 94. <https://doi.org/10.1093/femsec/fiy092>.
- Arshad, Q., Ahmed, A., 2017. Chromium-resistant PGPB: growth stimulatory impact on *Vigna radiata* L. under chromium stress. Rom. Biotechnol. Lett. 22, 12988.
- Asghari, B., Khademian, R., Sedaghati, B., 2020. Plant growth promoting rhizobacteria (PGPR) confer drought resistance and stimulate biosynthesis of secondary metabolites in pennyroyal (*Mentha pulegium* L.) under water shortage condition. Sci. Hortic. 263, 109132 <https://doi.org/10.1016/j.scienta.2019.109132>.
- Baas, P., Bell, C., Mancini, L.M., Lee, M.N., Conant, R.T., Wallenstein, M.D., 2016. Phosphorus mobilizing consortium Mammoth P™ enhances plant growth. PeerJ 4, e2121. <https://doi.org/10.7717/peerj.2121>.
- Baetz, U., Martinoia, E., 2014. Root exudates: the hidden part of plant defense. Trends Plant Sci. 19, 90–98. <https://doi.org/10.1016/j.tplants.2013.11.006>.
- Barbosa, J.Z., Hungria, M., da Silva Sena, J.V., Poggere, G., dos Reis, A.R., Corrêa, R.S., 2021. Meta-analysis reveals benefits of co-inoculation of soybean with *Azospirillum brasilense* and *Bradyrhizobium* spp. in Brazil. Appl. Soil Ecol. 163, 103913 <https://doi.org/10.1016/j.apsoil.2021.103913>.
- Barnawal, D., Singh, R., Singh, R.P., 2019. Role of plant growth promoting rhizobacteria in drought tolerance: regulating growth hormones and osmolytes. In: Singh, A.K., Kumar, A., Singh, P.K. (Eds.), PGPR Amelioration in Sustainable Agriculture. Woodhead Publishing.
- Bazhanov, D.P., Yang, K., Li, H., Li, C., Li, J., Chen, X., Yang, H., 2017. Colonization of plant roots and enhanced atrazine degradation by a strain of *Arthrobacter ureafaciens*. Appl. Microb. Biotechnol. 101, 6809–6820. <https://doi.org/10.1007/s00253-017-8405-3>.
- Bonatelli, M.L., Lacerda-Júnior, G.V., dos Reis Junior, F.B., Fernandes-Júnior, P.I., Melo, I.S., Quecine, M.C., 2021. Beneficial plant-associated microorganisms from semiarid regions and seasonally dry environments: a review. Front. Microbiol. 11, 3331. <https://doi.org/10.3389/fmicb.2020.553223>.
- Bucheli, J., Dalhaus, T., Finger, R., 2021. The optimal drought index for designing weather index insurance. Eur. Rev. Agric. Econ. 48 (3), 573–597. <https://doi.org/10.1093/erae/ebaa014>.
- Cao, L.R., Lu, X.M., Zhang, P.Y., Wang, G.R., Wei, L., Wang, T.C., 2019. Systematic analysis of differentially expressed maize ZmZIP genes between drought and rewetting transcriptome reveals bZIP family members involved in abiotic stress responses. Int. J. Mol. Sci. 20, 4013. <https://doi.org/10.3390/ijms20174103>.
- Chauhan, A., Pathak, A., Jaswal, R., Edwards III, B., Chappell, D., Ball, C., Garcia-Sillas, R., Stothard, P., Seaman, J., 2018. Physiological and comparative genomic analysis of *Arthrobacter* sp. SRS-W-1-2016 provides insights on niche adaptation for survival in uraniferous soils. Genes 9, 31. <https://doi.org/10.3390/genes9010031>.
- Cherif, H., Marasco, R., Rolli, E., Ferjani, R., Fusi, M., Soussi, A., Mapelli, F., Blilou, I., Borin, S., Boudabous, A., Cherif, A., Daffonchio, D., Ouzari, H., 2015. Oasis desert farming selects environment-specific date palm root endophytic communities and cultivable bacteria that promote resistance to drought. Environ. Microbiol. 7, 668–678. <https://doi.org/10.1111/1758-2229.12304>.
- Chiang, F., Mazdiyasi, O., AghaKouchak, A., 2021. Evidence of anthropogenic impacts on global drought frequency, duration, and intensity. Nat. Commun. 12, 2754. <https://doi.org/10.1038/s41467-021-22314-w>.
- Chukwuneme, C.F., Babalola, O.O., Kutu, F.R., Ojuederie, O.B., 2020. Characterization of actinomycetes isolates for plant growth promoting traits and their effects on drought tolerance in maize. J. Plant Inter. 15, 93–105. <https://doi.org/10.1080/17429145.2020.1752833>.
- Cohen, A.C., Bottini, R., Pontin, M., Berli, F.J., Moreno, D., Boccanlandro, H., Travaglia, C.N., Piccoli, P.N., 2015. *Azospirillum brasilense* ameliorates the response of *Arabidopsis thaliana* to drought mainly via enhancement of ABA levels. Physiol. Plant. 153, 79–90. <https://doi.org/10.1111/ppi.12221>.
- Conab-Brazilian National Food Supply Agency (Companhia Nacional do Abastecimento), 2022. Acompanhamento da Safra Brasileira. Boletim da Safra de Grãos.
- Cook, B.I., Mankin, J.S., Anchukaitis, K.J., 2018. Climate change and drought: from past to future. Curr. Clim. Chang. Rep. 4, 164–179. <https://doi.org/10.1007/s40641-018-0093-2>.
- Cruz, R., 2005. Geologia e recursos minerais da Folha Parnamirim, estado de Pernambuco: texto explicativo. Recife Cia. De. Pesqui. De. Recur. Miner., CPRM 146.
- Dourado, P.R.M., Souza, E.R., Lins, C.M.T., Melo, H.F., Santos, H.R.B., Monteiro, D.R., Paulino, M.K.S.S., Leal, L.Y.C., 2019. Osmotic adjustment in cowpea plants: Interference of methods for estimating osmotic potential at full turgor. Plant Physiol. Biochem. 145, 114–119. <https://doi.org/10.1016/j.plaphy.2019.10.020>.
- Dubey, A., Kumar, A., Abd Allah, E.F., Hashem, A., Khan, M.L., 2019. Growing more with less: Breeding and developing drought resilient soybean to improve food security. Ecol. Indic. 105, 425–437. <https://doi.org/10.1016/j.ecolind.2018.03.003>.
- Efthimiadou, A., Katsenios, N., Chanioti, S., Giannoglou, M., Djordjevic, N., Katsaros, G., 2020. Effect of foliar and soil application of plant growth promoting bacteria on growth, physiology, yield and seed quality of maize under Mediterranean conditions. Sci. Rep. 10, 21060 <https://doi.org/10.1038/s41598-020-78034-6>.
- Embrapa (2009). Manual de Análises Químicas de Solos, Plantas e Fertilizantes, 2° ed. Brasília, Embrapa Informação Tecnológica, 627 p.
- Erenstein, O., Jaleta, M., Sonder, K., Mottaleb, K., Prasanna, B.M., 2022. Global maize production, consumption and trade: trends and R&D implications. Food Secur. 14, 1295–1319. <https://doi.org/10.1007/s12571-022-01288-7>.

- FAO, 2014. World reference base for soil resources 2014: International soil classification system for naming soils and creating legends for soil maps. World Soil Resources Report No 106. FAO, Rome.
- Fernandes-Júnior, P.I., Aidar, S.D.T., Morgante, C.V., Gava, C.A.T., Zilli, J.É., Souza, L.S. B.D., Marinho, R.C.N., Nóbrega, R.S.A., Brasil, M.S., Seido, S.L., Martins, L.M.V., 2015. The resurrection plant *Triposon spicatus* (Poaceae) harbors a diversity of plant growth promoting bacteria in northeastern Brazilian Caatinga. *Rev. Bras. Cienc. Solo* 39, 993–1002. <https://doi.org/10.1590/01000683rbc20140646>.
- Fernández-González, A.J., Martínez-Hidalgo, P., Cobo-Díaz, J.F., Villadas, P.J., Martínez-Molina, E., Toro, N., Tringe, S.G., Fernández-López, M., 2017. The rhizosphere microbiome of burned holm-oak: potential role of the genus *Arthrobacter* in the recovery of burned soils. *Sci. Rep.* 7, 1–12. <https://doi.org/10.1038/s41598-017-06112-3>.
- FAO, 2021. *The impact of disasters and crises on agriculture and food security: 2021*. Rome. <https://doi.org/10.4060/cb3673en>.
- Gianese, G., Bossa, F., Pascarella, S., 2002. Comparative structural analysis of psychrophilic and meso-and thermophilic enzymes. *Protein Struct. Funct. Bioinform.* 47, 236–249. <https://doi.org/10.1002/prot.10084>.
- Glick, B.R., 2014. Bacteria with ACC deaminase can promote plant growth and help to feed the world. *Microbiol. Res.* 169, 30–39. <https://doi.org/10.1016/j.micres.2013.07.001>.
- Glick, B.R., Todorovic, B., Czarny, J., Cheng, Z., Duan, J., McConkey, B., 2007. Promotion of plant growth by bacterial ACC deaminase. *Plant Sci.* 26, 227–242. <https://doi.org/10.1080/07352680701572966>.
- Grote, U., Fasse, A., Nguyen, T.T., Erenstein, O., 2021. Food security and the dynamics of wheat and maize value chains in Africa and Asia. *Front. Sustain. Food Syst.* 4, 617009. <https://doi.org/10.3389/fsufs.2020.617009>.
- Hoagland, D.R., Arnon, D.I., 1950. The water-culture method for growing plants without soil. *Calif. Agric.* 347.
- Hone, H., Mann, R., Yang, G., Kaur, J., Tannenbaum, I., Li, T., Spangenberg, G., Sawbridge, T., 2021. Profiling, isolation and characterisation of beneficial microbes from the seed microbiomes of drought tolerant wheat. *Sci. Rep.* 11, 11916. <https://doi.org/10.1038/s41598-021-91351-8>.
- Hu, L., Robert, C.A.M., Cadot, S., Zhang, X., Ye, M., Li, B., Manzo, D., Chervet, N., Steinger, T., Van der Heijden, M.G.A., Schlaeppli, K., Erb, M., 2018. Root exudate metabolites drive plant-soil feedbacks on growth and defense by shaping the rhizosphere microbiota. *Nat. Commun.* 9, 2738. <https://doi.org/10.1038/s41467-018-05122-7>.
- Huang, Y., Ren, W., Liu, H., Wang, H., Xu, Y., Han, Y., Teng, Y., 2021. Contrasting impacts of drying-rewetting cycles on the dissipation of di-(2-ethylhexyl) phthalate in two typical agricultural soils. *Sci. Total Environ.* 792, 148433. <https://doi.org/10.1016/j.scitotenv.2021.148433>.
- Jansson, J.K., Hofmockel, K.S., 2020. Soil microbiomes and climate change. *Nat. Rev. Microbiol.* 18, 35–46. <https://doi.org/10.1038/s41579-019-0265-7>.
- Jochum, M.D., McWilliams, K.L., Borrego, E.J., Kolomiet, M.V., Niu, G., Pierson, E.A., Jo, Y.K., 2019a. Bioprospecting plant growth-promoting rhizobacteria that mitigate drought stress in grasses. *Front. Microbiol.* 10, 2106. <https://doi.org/10.3389/fmicb.2019.02106/BIBTEX>.
- Jochum, M.D., McWilliams, K.L., Pierson, E.A., Jo, Y.K., 2019b. Host-mediated microbiome engineering (HME) of drought tolerance in the wheat rhizosphere. *PLoS One* 14 (12), e0225933. <https://doi.org/10.1371/journal.pone.0225933>.
- Kavamura, V.N., Santos, S.N., Silva, J.L., Parma, M.M., Ávila, L.A., Visconti, A., Zucchi, T.D., Taketani, R.G., Andreote, F.D., Melo, I.S., 2013. Screening of Brazilian cacti rhizobacteria for plant growth promotion under drought. *Microbiol. Res.* 168, 183–191. <https://doi.org/10.1016/j.micres.2012.12.002>.
- Khan, M.A., Sahile, A.A., Jan, R., Asaf, S., Hamayun, M., Imran, M., Adhikari, A., Kang, S. M., Kim, K.M., Lee, J.J., 2021. Halotolerant bacteria mitigate the effects of salinity stress on soybean growth by regulating secondary metabolites and molecular responses. *BMC Plant Biol.* 21, 1–15. <https://doi.org/10.1186/s12870-021-02937-3>.
- Khan, N., Ali, S., Tariq, H., Latif, S., Yasmin, H., Mehmood, A., Shahid, M.A., 2020. Water conservation and plant survival strategies of rhizobacteria under drought stress. *Agron* 10, 1683. <https://doi.org/10.3390/agronomy10111683>.
- Khatoun, Z., Huang, S., Farooq, M.A., Santoyo, G., Rafique, M., Javed, S., Gul, B., 2022. Role of plant growth-promoting bacteria (PGPB) in abiotic stress management. In: Santoyo, G., Kumar, A., Aamir, M., Uthandi, S. (Eds.), *Mitigation of Plant Abiotic Stress by Microorganisms*. Academic Press, Massachusetts, pp. 257–272. <https://doi.org/10.1016/B978-0-323-90568-8.00012-2>.
- Kong, Z., Wu, Z., Glick, B.R., He, S., Huang, C., Wu, L., 2019. Co-occurrence patterns of microbial communities affected by inoculants of plant growth-promoting bacteria during phytoremediation of heavy metal-contaminated soils. *Ecotox. Environ. Safe* 183, 109504. <https://doi.org/10.1016/j.ecoenv.2019.109504>.
- Krishnamurthy, R.P.K., Fisher, J.B., Choularton, R.J., Kareiva, P.M., 2022. Anticipating drought-related food security changes. *Nat. Sustain.* 5, 956–964. <https://doi.org/10.1038/s41893-022-00962-0>.
- Kumar, A., Maurya, B.R., Raghuwanshi, R., 2014. Isolation and characterization of PGPR and their effect on growth, yield and nutrient content in wheat (*Triticum aestivum* L.). *Biocatal. Agric. Biotechnol.* 3, 121–128. <https://doi.org/10.1016/j.bcab.2014.08.003>.
- Kumar, A., Maurya, B.R., Raghuwanshi, R., 2015. Characterization of bacterial strains and their impact on plant growth promotion and yield of wheat and microbial populations of soil. *Afr. J. Agric. Res.* 10, 1367–1375. <https://doi.org/10.5897/AJAR2014.8894>.
- Kumawat, K.C., Razdan, N., Saharan, K., 2022. Rhizospheric microbiome: bio-based emerging strategies for sustainable agriculture development and future perspectives. *Microbiol. Res.* 254, 126901. <https://doi.org/10.1016/j.micres.2021.126901>.
- Lane, D.J., 1991. 16S/23S rRNA sequencing. In: Stackebrandt, E., Goodfellow, M. (Eds.), *Nucleic Acid Techniques in Bacterial Systematics*. John Wiley and Sons, West Sussex.
- Leal, I.R., Da Silva, J.M.C., Tabarelli, M., Lacher Jr, T.E., 2005. Changing the course of biodiversity conservation in the Caatinga of northeastern Brazil. *Biol. Conserv.* 19, 701–706. <https://doi.org/10.1016/j.biolcon.2005.07.003>.
- Lin, Y., Watts, D.B., Kloepper, J.W., Feng, Y., Torbert, H.A., 2019. Influence of Plant Growth-Promoting Rhizobacteria on Corn Growth under Drought. *Stress* 51, 250–264. <https://doi.org/10.1080/00103624.2019.1705329>.
- Llopart, M., Reboita, M.S., Rocha, R.P., 2020. Assessment of multi-model climate projections of water resources over South America CORDEX domain. *Clim. Dyn.* 54, 99–116. <https://doi.org/10.1007/s00382-019-04990-z>.
- Ma, Y., Dias, M.C., Freitas, H., 2020. Drought and salinity stress responses and microbe-induced tolerance in plants. *Front. Plant Sci.* 11. <https://doi.org/10.3389/fpls.2020.591911>.
- Meisner, A., Snoek, B.L., Nesme, J., Dent, E., Jacquiod, S., Classen, A.T., Priemé, A., 2021. Soil microbial legacies differ following drying-rewetting and freezing-thawing cycles. *ISME J.* 15, 1207–1221. <https://doi.org/10.1038/s41396-020-00844-3>.
- Mendes, R., Garbeva, P., Raaijmakers, J.M., 2013. The rhizosphere microbiome: significance of plant beneficial, plant pathogenic, and human pathogenic microorganisms. *FEMS Microbiol. Rev.* 37, 634–663. <https://doi.org/10.1111/1574-6976.12028>.
- Morillas, L., Durán, J., Rodríguez, A., Roales, J., Gallardo, A., Lovett, G.M., Groffman, P. M., 2015. Nitrogen supply modulates the effect of changes in drying-rewetting frequency on soil C and N cycling and greenhouse gas exchange. *Glob. Chang. Biol.* 21, 3854–3863. <https://doi.org/10.1111/gcb.12956>.
- Mukhia, S., Khatri, A., Acharya, V., Kumar, R., 2021. Comparative genomics and molecular adaptational analysis of *Arthrobacter* from Sikkim Himalaya provided insights into its survivability under multiple high-altitude stress. *Genomics* 113, 151–158. <https://doi.org/10.1016/j.ygeno.2020.12.001>.
- Nascimento, R.D.C., Cavalcanti, M.I.P., Correia, A.D.J., Escobar, I.E.C., Freitas, A.D.S., Nobrega, R.S.A., Fernandes-Júnior, P.I., 2021. Maize-associated bacteria from the Brazilian semiarid region boost plant growth and grain yield. *Symbiosis* 83, 347–359. <https://doi.org/10.1007/s13199-021-00755-7>.
- Naylor, D., DeGraaf, S., Purdom, E., Coleman-Derr, D., 2017. Drought and host selection influence bacterial community dynamics in the grass root microbiome. *ISME J.* 11, 2691–2704. <https://doi.org/10.1038/ismej.2017.118>.
- Ojuederie, O.B., Olanrewaju, O.S., Babalola, O.O., 2019. Plant growth promoting rhizobacterial mitigation of drought stress in crop plants: Implications for sustainable agriculture. *Agronomy* 9, 712. <https://doi.org/10.3390/agronomy9110712>.
- Pathak, D.V., Kumar, M., Rani, K., 2017. Biofertilizer Application in Horticultural Crops. In: Panpatte, D., Jhala, Y., Vyas, R., Shelat, H. (Eds.), *Microorganisms for Green Revolution*. Microorgan. Sustainab, 6. Springer, Singapore, pp. 215–227. https://doi.org/10.1007/978-981-10-6241-4_11.
- Prasad, A.A., Babu, S., 2017. Compatibility of Azospirillum brasilense and Pseudomonas fluorescens in growth promotion of groundnut (Arachis hypogaea L.). *Acad. Bras. Cienc.* 89, 1027–1040. <https://doi.org/10.1590/0001-3765201720160617>.
- Prasanna, B.M., Cairns, J.E., Zaidi, P.H., Beyene, Y., Makumbi, D., Gowda, M., Magorokosho, C., Zaman-Allah, M., Olsen, M., Das, A., Worku, M., Gethi, J., Vivek, B.S., Nair, S.K., Rashid, Z., Vinayan, M.T., Issa, A.B., San Vicente, F., Dhlwiyato, T., Zhang, X., 2021. Beat the stress: Breeding for climate resilience in maize for the tropical rainfed environments. *Theor. Appl. Genet.* 134, 1729–1752. <https://doi.org/10.1007/s00122-021-03773-7>.
- R Core Team, 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing Vienna, Austria. <https://www.r-project.org/>.
- Raij, B.Van., Cantarella, H., Quaggio, J.A., Furlani, A., 1997. *Recomendação de adubação e calagem para o Estado de São Paulo*. 2 ed. Campinas, Instituto Agrônomo/Fundação IAC.
- Raij, B.Van., Andrade, J.C., Cantarella, H., Quaggio, J.A., 2001. *Análise química para avaliação da fertilidade de solos tropicais*. Campinas. Inst. Agrônôm. 285.
- Ramette, A., 2007. Multivariate analyses in microbial ecology. *FEMS Microbiol. Ecol.* 62, 142–160. <https://doi.org/10.1111/j.1574-6941.2007.00375.x>.
- Rattis, L., Brando, P.M., Macedo, M.N., Spera, S.A., Castanho, A.D.A., Marques, E.Q., Costa, N.Q., Silverio, D.V., Coe, M.T., 2021. Climatic limit for agriculture in Brazil. *Nat. Clim. Change* 11, 1098–1104. <https://doi.org/10.1038/s41558-021-01214-3>.
- Rego, A., Raio, F., Martins, T.P., Ribeiro, H., Sousa, A.G., Sêneca, J., Baptista, M.S., Lee, C.K., Cary, S.C., Ramos, V., Carvalho, M.F., Leão, P.N., Magalhães, C., 2019. Actinobacteria and cyanobacteria diversity in terrestrial antarctic microenvironments evaluated by culture-dependent and independent methods. *Front. Microbiol.* 10, 1018. <https://doi.org/10.3389/fmicb.2019.01018>.
- Reis Antunes, G., Santana, S.R.A., Escobar, I.E.C., Silva Brasil, M., de Araújo, G.G.L., Voltolini, T.V., Fernandes-Júnior, P.I., 2019. Associative diazotrophic bacteria from forage grasses in the Brazilian semi-arid region are effective plant growth promoters. *Crop Pasture*. Sci 70, 899–907. <https://doi.org/10.1071/CP19076>.
- Rolli, E., Marasco, R., Vigani, G., Ettoumi, B., Mapelli, F., Deangelis, M.L., Gandolfi, C., Casati, E., Previtali, F., Gerbino, R., Cei, F.P., Borin, S., Sorlini, C., Zocchi, G., Daffonchio, D., 2015. Improved plant resistance to drought is promoted by the root-associated microbiome as a water stress-dependent trait. *Environ. Microbiol.* 17, 316–331. <https://doi.org/10.1111/1462-2920.12439>.
- Romaniuk, K., Golec, P., Dziewit, L., 2018. Insight into the diversity and possible role of plasmids in the adaptation of psychrotolerant and metalotolerant *Arthrobacter* spp. to extreme Antarctic environments. *Front. Microbiol.* 9, 3144. <https://doi.org/10.3389/fmicb.2018.03144>.
- Safarian, M., Askari, H., Shariati, J.V., Nematzadeh, G., 2019. Transcriptional responses of wheat roots inoculated with *Arthrobacter nitroguajacolicus* to salt stress. *Sci. Rep.* 9, 1–12. <https://doi.org/10.1038/s41598-018-38398-2>.
- Saikia, J., Sarma, R.K., Dhandia, R., Yadav, A., Bharali, R., Gupta, V.K., Saikia, R., 2018. Alleviation of drought stress in pulse crops with ACC deaminase producing

- rhizobacteria isolated from acidic soil of Northeast India. *Sci. Rep.* 8, 3560. <https://doi.org/10.1038/s41598-018-21921-w>.
- Sangoi, L., Schmitt, A., Zanin, C.G., 2007. Área foliar e rendimento de grãos de híbridos de milho em diferentes populações de plantas. *Rev. Bras. Milho Sorgo* 6, 263–271. <https://doi.org/10.18512/1980-6477/rbms.v6n03p25p>.
- Santos, R.M., Oliveira-Filho, A.T., Eisenlohr, P.V., Queiroz, L.P., Cardoso, D.B., Rodal, M. J., 2012. Identity and relationships of the Arboreal Caatinga among other floristic units of seasonally dry tropical forests (SDTFs) of north-eastern and Central Brazil. *Ecol. Evol.* 2, 409–428. <https://doi.org/10.1002/ece3.91>.
- Santos, R.M., Diaz, P.A.E., Lobo, L.L.B., Rigobelo, E.C., 2020. Use of plant growth-promoting rhizobacteria in maize and sugarcane: characteristics and applications. *Front. Sustain. Food Syst.* 4, 136. <https://doi.org/10.3389/fsufs.2020.00136>.
- Santos-Medellín, C., Edwards, J., Liechty, Z., Nguyen, B., Sundaresan, V., 2017. Drought stress results in a compartment-specific restructuring of the rice root-associated microbiomes. *MBio* 8, e00764–17. <https://doi.org/10.1128/mBio.00764-17>.
- Sarma, R.K., Saikia, R., 2014. Alleviation of drought stress in mung bean by strain *Pseudomonas aeruginosa* GGRJ21. *Plant Soil* 377, 111–126. <https://doi.org/10.1007/s11104-013-1981-9>.
- Schimel, J.P., Schaeffer, S.M., 2012. Microbial control over carbon cycling in soil. *Front. Microb.* 3, 348. <https://doi.org/10.3389/fmicb.2012.00348>.
- Sharma, M., Mishra, V., Rau, N., Sharma, R.S., 2016. Increased iron-stress resilience of maize through inoculation of siderophore-producing *Arthrobacter globiformis* from mine. *J. Basic Microbiol* 56, 719–735. <https://doi.org/10.1002/jobm.201500450>.
- Sreevidya, M., Gopalakrishnan, S., Kudapa, H., Varshney, R., 2016. Exploring plant growth-promotion actinomycetes from vermicompost and rhizosphere soil for yield enhancement in chickpea. *Braz. J. Microbiol.* 47, 85–95. <https://doi.org/10.1016/j.bjbm.2015.11.030>.
- Timm, C.M., Pelletier, D.A., Jawdy, S.S., Gunter, L.E., Henning, J.A., Engle, N., Aufrecht, J., Gee, E., Nookaew, I., Yang, Z., Lu, T.Y., Tschaplinski, T.J., Doktycz, M. J., Tuskan, G.A., Weston, D.J., 2016. Two poplar-associated bacterial isolates induce additive favorable responses in a constructed plant-microbiome system. *Front. Plant Sci.* 7, 497. <https://doi.org/10.3389/fpls.2016.00497>.
- Timmusk, S., Abd El-Daim, I.A., 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. <https://doi.org/10.1371/journal.pone.0096086>.
- Trivedi, P., Leach, J.E., Tringe, S.G., Sa, T., Singh, B.K., 2020. Plant-microbiome interactions: from community assembly to plant health. *Nat. Rev. Microbiol.* 18, 607–621. <https://doi.org/10.1038/s41579-020-0412-1>.
- Ullah, A., Nisar, M., Ali, H., Hazrat, A., Hayat, K., Keerio, A.A., Ihsan, M., Laiq, M., Ullah, S., Fahad, S., Khan, A., Khan, A.H., Akbar, A., Yang, X., 2019. Drought tolerance improvement in plants: an endophytic bacterial approach. *Appl. Microbiol. Biotechnol.* 103, 7385–7397. <https://doi.org/10.1007/s00253-019-10045-4>.
- Upadhyay, S.K., Singh, J.S., Saxena, A.K., Singh, D.P., 2012. Impact of PGPR inoculation on growth and antioxidant status of wheat under saline conditions. *Plant Biol.* 14, 605–611. <https://doi.org/10.1111/j.1438-8677.2011.00533.x>.
- Vanissa, T.T.G., Berger, B., Patz, S., Becker, M., Turečková, V., Novák, O., Tarkowská, D., Henri, F., Ruppel, S., 2020. The response of maize to inoculation with *Arthrobacter* sp. and *Bacillus* sp. in phosphorus-deficient, salinity-affected soil. *Microorganisms* 8, 1005. <https://doi.org/10.3390/microorganisms8071005>.
- Webber, H., Ewert, F., Olesen, J.E., Müller, C., Fronzek, S., Ruane, A.C., Bourgault, M., Martre, P., Ababaei, B., Bindi, M., Ferrise, R., Finger, R., Fodor, N., Gabaldón-Leal, C., Gaiser, T., Jabloun, M., Kersebaum, K.C., Lizaso, J.I., Lorite, I.J., Manceau, L., Moriondo, M., Nendel, C., Rodríguez, A., Ruiz-Ramos, M., Semenov, M. A., Siebert, S., Stella, T., Stratonovitch, P., Trombi, G., Wallach, D., 2018. Diverging importance of drought stress for maize and winter wheat in Europe. *Nat. Commun.* 9, 4249. <https://doi.org/10.1038/s41467-018-06525-2>.
- Weidner, S., Koller, R., Latz, E., Kowalchuk, G., Bonkowski, M., Scheu, S., Jousset, A., 2015. Bacterial diversity amplifies nutrient-based plant–soil feedbacks. *Funct. Ecol.* 29, 1341–1349. <https://doi.org/10.1111/1365-2435.12445>.
- Xie, J., Dawwam, G.E., Sehim, A.E., Li, X., Wu, J., Chen, S., Zhang, D., 2021. Drought stress triggers shifts in the root microbial community and alters functional categories in the microbial gene pool. *Front. Microbiol.* 12, 744897. <https://doi.org/10.3389/fmicb.2021.744897>.
- Xu, L., Naylor, D., Dong, Z., Simmons, T., Pierroz, G., Hixson, K.K., Kim, Y.M., Zink, R.M., Engbrecht, K.M., Wang, Y., Gao, C., DeGraaf, S., Madera, M.A., Sievert, J.A., Hollingsworth, J., Birdseye, D., Scheller, H.V., Huttmacher, R., Dahlberg, J., Jansson, C., Taylor, J.W., Lemaux, P.G., Coleman-Derr, D., 2018. Drought delays development of the sorghum root microbiome and enriches for monoderm bacteria. *PNAS* 115, E4284–E4293. <https://doi.org/10.1073/pnas.1717308115>.
- Yao, Y.X., Tang, H.Z., Su, F., Xu, P., 2015. Comparative genome analysis reveals the molecular basis of nicotine degradation and survival capacities of *Arthrobacter*. *Sci. Rep.* 5, 8642. <https://doi.org/10.1038/srep08642>.
- Zhang, B., Wu, X., Zhang, G., Li, S., Zhang, W., Chen, X., Sun, L., Zhang, B., Liu, G., Chen, T., 2016. The diversity and biogeography of the communities of Actinobacteria in the forelands of glaciers at a continental scale. *Environ. Res. Lett.* 11, 054012. <https://doi.org/10.1088/1748-9326/11/5/054012>.
- Zhao, C., Liu, S., Wang, X., Lobell, D.B., Huang, Y., Huang, M., Yao, Y., Bassu, S., Ciaia, P., Durand, J.L., Elliott, J., Ewert, F., Janssens, I.A., Li, T., Liu, Q., Martre, P., Müller, C., Peng, S., Peñuelas, J., Ruane, A.C., Wallch, D., Wang, T., Wu, D., Liu, Z., Zhu, Y., Zhu, Z., Asseng, S., 2017. Temperature increase reduces global yields of major crops in four independent estimates. *Proc. Natl. Acad. Sci.* 114 (35), 9326–9331. <https://doi.org/10.1073/pnas.170176211>.