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Microbial inoculants supporting sorghum (*Sorghum bicolor*) under low water and nitrogen supplies in the Brazilian drylands

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ABSTRACT

This study investigated the interactive effects of nitrogen (N) fertilization and water supply across distinct microbial treatments in sorghum (*Sorghum bicolor*). A factorial experiment was conducted under field conditions with different microbial strains, nitrogen application rates (20 and 140 kg N ha^{-1}), and two water availability levels (45 % and 100 % evapotranspiration, ET$_{C}$). Results indicate that N fertilization, irrigation level, and microbial inoculation significantly influenced aboveground biomass production and the efficiency of N fertilization under the different levels of nitrogen fertilization, water supply, and microbial inoculation tested, highlighting those inoculants with *Bacillus* spp. ESA 13 and ESA 402, *Rhizobium* sp. ESA 15, *Agrobacterium* sp. ESA 441, and *Herbaspirillum seropedicae* BR 11417. Triple interaction also influenced potassium (K) uptake, while water supply and microbial inoculation influenced the extraction of N, calcium, Cu, and Zn from the soil. The plant height, stem diameter, and leaf area index were influenced by different bacteria and water supply when Pelomonas sp. ESA 424, *Azospirillum baldaniorum* BR 11005^{T}, and the yeast *Meyerozyma* sp. ESA 37 stood out in two (out of three) parameters under the most detrimental condition (45 % ET$_{C}$ and 20 kg N ha^{-1}). These findings suggest the potential of the bacteria and yeasts tested to undergo further field assays using inoculants with more than one strain, each with complementary mechanisms, to enhance crop resilience and productivity in semiarid regions.

1. Introduction

Understanding the interplay between water and nitrogen availability, under different microbial inoculation scenarios, is essential for developing sustainable agricultural practices, particularly in semiarid and arid regions worldwide (Ben Gaied et al., 2024). These lands face significant challenges due to erratic rainfall, poor soil fertility and physical characteristics (e.g. depth and porosity), and high temperatures, which collectively constrain plant performance and productivity (Jain et al., 2024). Given that water deficit and nitrogen scarcity often co-occur in these environments, our experimental design explicitly integrates both stress factors to assess their combined impact on sorghum performance and the mitigating potential of microbial inoculants. These climatic constraints are likely to intensify with the projected rise in global mean temperature due to ongoing climate change, increasing the urgency to develop adaptation strategies for dryland agriculture. (Angelotti et al., 2011, 2025).

Sorghum (*Sorghum bicolor* L. Moench), a drought-tolerant Poaceae, has emerged as a strategic dryland crop due to its adaptability and potential for biomass production under water-limited conditions (Morales

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et al., 2024). However, optimizing its performance requires a deeper understanding of the synergistic effects of environmental and management factors, such as the interactive effects of drought stress and N availability, both molarity (e.g., N concentration in soil solution) and total availability (Swift et al., 2019). To achieve this level of understanding, experiments with different levels of irrigation and fertilization are essential. While previous studies have investigated microbial inoculants under single stress conditions (either drought or nutrient limitation), few have addressed their role in mitigating the combined impact of water and nitrogen deficits in sorghum. This dual-stress scenario remains unexplored mainly, representing a critical gap in the literature that our study aims to address.

Nitrogen (N) is a critical macronutrient for plant performance, influencing plant growth (including the number of stalks and tillers, plant height, stem diameter, and leaf area index), chlorophyll content, and, ultimately, yield (Galindo et al., 2024; Osman, 2013). In drylands, the availability of N is often limited not only by its inherent scarcity in soils but also by the effects of water stress [N amount (moles) vs. N concentration in soil solution (molarity)], which alters its uptake efficiency and plant physiology (Gava et al., 2022; Swift et al., 2019). Nitrogen molarity, or the concentration of N in the soil solution, becomes particularly relevant under drought conditions, as reduced water availability limits nutrient solubility and, consequently, plant uptake of N and other essential elements (Bghbani-Arani and Poureisa, 2024; Molina et al., 2024).

Applying microbial inoculants with selected and efficient microbes has become a sustainable agricultural practice worldwide, offering a biological solution to enhance the uptake of key nutrients such as nitrogen, as well as to improve stress resilience in annual crops (de Souza et al., 2015; Díaz-Rodríguez et al., 2025; Laishram et al., 2025). Beneficial microbes, such as efficient bacteria and yeast, can improve plant performance, chlorophyll profile, nutrient uptake, and mitigate the adverse effects of drought by influencing root architecture and water-use efficiency (Beura et al., 2020; Kavamura et al., 2013a). Furthermore, the inoculant application in dryland agriculture can benefit the host plant indirectly by the modulation of root microbiome leveraging more beneficial micro-organisms that promote plant growth, stress tolerance, and nutrient availability (Behera et al., 2024; Chakraborty et al., 2024). In this sense, microbial inoculants represent a sustainable and environmentally friendly alternative—or complement—to synthetic fertilizers and irrigation inputs, reducing chemical dependency and enhancing soil health, while maintaining productivity under water- and nutrient-limited conditions.

The interaction between drought stress and microbial inoculation is particularly intriguing, as both factors influence root biomass, morphology, and physiological activity, thereby affecting their capacity to acquire nutrients (Toor et al., 2024). Under drought conditions, root exudates and microbial activity are altered, influencing the rhizosphere dynamics and the efficiency of inoculated microbes (Kavamura et al., 2013b; Kruthika et al., 2024; Liao et al., 2025). Investigating these interactions in sorghum under controlled nitrogen availability presents an opportunity to identify management practices that optimize the cooperative relationships among soil microorganisms, plant nutrient uptake, and soil nutrient cycling, thereby overcoming water- and nitrogen-induced limitations (Li et al., 2022).

This study aimed to assess the combined effects of microbial inoculants and varying water and nitrogen levels on physiological performance, nutrient use efficiency, and yield components of sorghum in Brazilian drylands. By adopting an integrative approach, we provided actionable insights into sustainable crop management practices for resource-constrained environments. We hypothesized that different microbial inoculants in field-grown sorghum could mitigate the harmful effects of low water and nitrogen availability, as well as elevated nitrogen concentration in the soil solution (high N molarity), on the host plant. To achieve this goal, we adopted a novel integrative approach by inoculating plant growth-promoting microbes (PGPM) under combined drought stress and limited nitrogen availability. PGPM are known to enhance plant growth and stress tolerance through multiple biochemical mechanisms; their use as a synergistic biostimulant strategy has not been extensively explored in arid and semiarid environments. By simultaneously targeting soil fertility and plant physiological resilience, this dual amendment strategy addresses a critical gap in sustainable crop management, particularly in resource-limited agricultural systems where water scarcity and nutrient deficits often co-occur.

2. Material and methods

2.1. Experimental site, sorghum genotype, and microbial inoculants

The field experiment was carried out in the Bebedouro Experimental Station, a facility belonging to the Brazilian Agricultural Research Corporation, Tropical Semiarid Research Center (Embrapa Semiárido) in Petrolina, Pernambuco State, Northeastern Brazil (latitude = − 9.3941, longitude = − 40.5097, 365.5 m.a.s.l). The field experiment was conducted from July to October 2022. The climate in the experimental area is BSh type, characterized by irregular and low annual precipitation, high evaporation rates, and marked seasonality with a dry season lasting 7–11 months. During the field experiment, we registered the accumulated precipitation and mean air temperature of 26.5 mm and 27.8 °C, respectively.

The soil type of the experimental area was categorized as an Ultisol, which was analyzed to characterize the soil chemical properties. A composite sample was assembled by collecting 25 spots randomly within the experimental site in the 0–0.2 and 0.2–0.4 m soil layers. Electrical conductivity was measured in a 1:5 soil-to-water suspension with an electrical conductivity meter. Soil pH was measured in a 1:2.5 soil-to-water suspension (Black et al., 1965). Phosphorus (P), exchangeable potassium (K^+), and exchangeable sodium (Na^+) were extracted using Mehlich-1 solution and determined via colorimetry and flame photometry, respectively (Page et al., 1982). Exchangeable calcium (Ca^{2+}) and magnesium (Mg^{2+}) were extracted using 1 mol L-1 KCl and quantified following the procedures described by Teixeira et al. (2017). Exchangeable aluminum (Al^{3+}) was measured from KCl extracts, while potential acidity ($H^+ + Al^{3+}$) was determined using calcium acetate (1 mol L-1 at pH 7.0) and titrated with 0.025 mol L-1 NaOH (Nascimento et al., 2021). Total nitrogen (N) content was quantified using the Kjeldahl method with steam distillation (Black et al., 1965). Soil organic carbon (C) was determined by wet oxidation with potassium dichromate (Teixeira et al., 2017). The sum of bases was estimated using the following equation: SB (cmolc dm-3) = $Na^+ + K^+ + Ca^{2+} + Mg^{2+\cdot}$ For CEC, we used the following equation: CEC (cmolc dm-3) = $SB^+(H^+ + Al^{3+})$. Soil micronutrients (Cu, Fe, Mn, and Zn) were estimated as proposed by Tedesco et al. (1995). The initial chemical properties before the experiment are presented in Table 1.

All plots received basal fertilization 90 kg ha^{-1} of P_2O_5 (using single superphosphate), 20 kg ha^{-1} of K_2O (using potassium chloride), 30 kg ha^{-1} of Mg (magnesium sulfate), 2 kg ha^{-1} of Cu and Zn (using copper sulfate and zinc sulfate, respectively), and 1 kg ha^{-1} of B (using boric acid) (Cavalcanti, 1998).

The sorghum genotype BRS 716 was used in this field experiment. This is a multipurpose genotype selected for its high biomass production and adaptation to the Brazilian semiarid region, producing relatively high biomass even under water limitations (Guimarães et al., 2022; Silva et al., 2024).

For the microbial inoculation, we tested the following strains: *Bacillus* sp. ESA 13, *Rhizobium* sp. ESA 15 (Fernandes-Júnior et al., 2015), *Chryseobacterium* sp. ESA 29 (Leite et al., 2017), *Rhizobium* sp. ESA 116 (Cavalcanti et al., 2020), *Bacillus* sp. ESA 402 (Antunes et al., 2019), *Pelomonas* sp. ESA 424 (da Silva et al., 2023) *Agrobacterium* sp. ESA 441 (Silva, 2017), *Bacillus* sp. ESA 600, *Paenibacillus* sp. ESA 601 (Nascimento et al., 2021), *Bacillus* sp. ESA 674 (Bomfim et al., 2020), *Azospirillum baldaniorum* BR 11005^T (Ferreira et al., 2020), *Azospirillum*

Table 1

Initial chemical properties of Ultisol at the Bebedouro experimental station (Petrolina, Pernambuco, Brazil) before the field experiment set up.

Soil properties	Soil depth (m)	
	0–0.2	0.2–0.4
Electrical conductivity (mS cm^{-1})	0.68	0.62
Soil pH (H_2O)	7.00	7.10
C (g kg^{-1})	7.30	4.10
N (g kg^{-1})	1.20	not determined
P (mg dm^{-3})	1.64	0.78
K^+ (cmol$_c$ dm^{-3})	0.73	0.75
Na^+ (cmol$_c$ dm^{-3})	0.22	0.24
Ca^{2+} (cmol$_c$ dm^{-3})	3.60	2.30
Mg^{2+} (cmol$_c$ dm^{-3})	1.80	1.10
Al^{3+} (cmol$_c$ dm^{-3})	0.00	0.00
H^++Al^{3+} (cmol$_c$ dm^{-3})	0.00	0.00
Sum of bases (cmol$_c$ dm^{-3})	6.40	4.40
C.E.C. (cmol$_c$ dm^{-3})	6.40	4.40
Base saturation (%)	100.0	100.0
Cu (mg dm^{-3})	0.64	0.76
Fe (mg dm^{-3})	61.47	45.47
Mn (mg dm^{-3})	60.89	29.79
Zn (mg dm^{-3})	6.57	3.17

brasiliense Ab-V5 (Hungria et al., 2010), *Herbaspirillum seropedicae* BR 11417 (J. I. Baldani et al., 1986). In addition to the 13 bacteria mentioned above, we tested two yeast strains, *Meyerozyma* spp. ESA 37 and ESA 45 (Targino et al., 2022). More information on each strain tested is available in Table 2.

The bacterial strains grew in LB and yeasts in malt-extract media for 3 days under constant stirring (150 rpm) at 25 ± 2 °C for inoculant preparation. The microbial broth was centrifuged at 6000 *g* at 10 °C, and the pellets were resuspended in 1 x PBS. The procedure was repeated twice, and the optical density was adjusted to 0.6 at 600 nm in a spectrophotometer (Multiskan GO, Thermo Scientific, USA). After preparation, the inoculants were transported to the field within 2 h and applied to seeds immediately to ensure microbial viability, which was confirmed by plate counts indicating $>10^8$ colony-forming units (CFU) mL^{-1} before inoculation. The inoculation was conducted by immersing 100 g of sorghum seeds in 200 mL of microbial culture for 30 min (Bomfim et al., 2020). To improve the inoculant adhering to the seeds, 10 g of sucrose was added to 100 mL of inoculant. The seeds were dried in the shade (around 1 h) and sown in the field. The non-inoculated control was immersed in 1 x PBS and submitted to the same procedure.

2.2. Experimental design

We investigated the interaction of sixteen inoculation treatments (15 microbial strains plus a non-inoculated control), two levels of N fertilization (20 and 140 kg N ha^{-1}), and two irrigation levels, corresponding to 45 % and 100 % of the crop evapotranspiration (ETc)—the estimated amount of water lost by the crop through evaporation and transpiration under standard growing conditions. The field experiment was conducted using a split-split-plot randomized complete block design with three factors (a three-way factorial ANOVA): 16 inoculation treatments, two irrigation levels, and two nitrogen fertilization levels, arranged across three blocks. Irrigation constituted the main plots, nitrogen fertilization the subplots, and microbial inoculation the sub-subplots. Each plot measured 8.0 m^2 and simulated a plant density of 100,000 plants ha ^{1}.

For the N fertilization, 20 kg ha^{-1} of N-urea was applied in each subplot. For the treatments involving 140 kg ha^{-1} of N, an additional two topdress applications of 60 kg N ha^{-1} each were applied at 20 and 40 days after germination. A drip irrigation system was installed with emitters spaced 30 cm apart, delivering a flow rate of 1.8 L h^{-1}. One drip line was used for every two rows of plants, ensuring efficient water distribution throughout the area. The experimental field had a history of watermelon and onion cultivation over the previous two years before the experiment was established.

2.3. Plant growth, relative chlorophyll contents, aboveground biomass production, plant nutrient contents, and nutrient extraction

To assess the relative leaf chlorophyll *a* and *b* content, a ClorofiLOG (Falker, Porto Alegre, Brazil) device was used. The measurements were performed in ten plants per plot, during the period when the plants had developed their fifth photosynthetic leaf (counted from the apex downward) at 45 days after emergence. At 90 days after emergence, the number of stalks and tillers (number plant^{-1}), plant height (m plant^{-1}), and stem diameter (cm plant^{-1}) were measured. The stalks and tillers were counted, and the stem diameter was measured with a digital pachymeter. The plant height was measured with a ruled tape from top to bottom (with a ladder). Aboveground biomass and leaf area were assessed for each plot 95 days after emergence. For the biomass, the plants were dried in the open air (in the sun) for 5 days before being oven-dried at 65 °C until constant weight. The dried biomass was weighed, subsampled, and ground for analysis of macro- and micronutrients. Samples were processed using a Willey-type knife mill, and the contents of N, P, K, Ca, Mg, S, Na, Cu, Zn, Fe, Mn, and B in the plant were determined according to Tedesco et al. (1995). Thus, nutrient

Table 2

Microbial strains, taxonomic classification, isolation (original) host, and culture collections where the microorganisms are deposited for each inoculum used in the present study.

Strain	Taxonomic classification	Original host	Origin(culture collection)[a]	Reference
ESA 13	*Bacillus* sp.	*Tripogonella spicata*	CMISA	Fernandes-Júnior et al. (2015)
ESA 15	*Rhizobium* sp.	*Tripogonella spicata*	CMISA	Fernandes-Júnior et al. (2015)
ESA 29	*Chryseobacterium* sp.	*Vigna unguiculata*	CMISA	Leite et al. (2017)
ESA 37	*Meyerozyma* sp.	*Zea mays*	CMISA	Targino et al. (2022)
ESA 45	*Meyerozyma* sp.	*Zea mays*	CMISA	Targino et al. (2022)
ESA 116	*Rhizobium* sp.	*Zea mays*	CMISA	Cavalcanti et al. (2020)
ESA 402	*Bacillus* sp.	*Sorghum bicolor*	CMISA	Antunes et al. (2019)
ESA 424	*Pelomonas* sp.	*Vigna unguiculata*	CMISA	da Silva et al. (2023)
ESA 441	*Agrobacterium* sp.	*Pennisetum glaucum*	CMISA	Silva (2017)
ESA 600	*Bacillus* sp.	*Zea mays*	CMISA	Nascimento et al. (2021)
ESA 601	*Paenibacillus* sp.	*Zea mays*	CMISA	Nascimento et al. (2021)
ESA 674	*Bacillus* sp.	*Zea mays*	CMISA	Bomfim et al. (2020)
Ab-V5	*Azospirillum brasilense*	*Zea mays*	CRB-CNPSo	Hungria et al. (2010)
BR 11005^T	*Azospirillum baldaniorum*	*Triticum aestivum*	CRB-JD	Ferreira et al. (2020)
BR 11417	*Herbaspirillum seropedicae*	*Triticum aestivum*	CRB-JD	Baldani et al. (1986)

[a] CMISA = Culture Collection of Microorganisms with Agricultural Interest of Embrapa Semiárido. Embrapa Semiárido, Petrolina, Pernambuco, Brazil; CRB-CNPSo = Biological Resources Center of Embrapa Soja, Embrapa Soja, Londrina, Paraná, Brazil; CRB-JD = Johanna Döbereiner Biological Resources Center. Embrapa Agrobiologia, Seropédica, Rio de Janeiro, Brazil.

extraction was calculated by multiplying the nutrient contents by the aboveground biomass produced, with the results expressed in kg ha^{-1} for macronutrients and g ha^{-1} for micronutrients and sodium. The nitrogen use efficiency (NYE) was calculated as the ratio of total aboveground biomass production (kg ha^{-1}) to the amount of nitrogen fertilizer applied (kg N ha^{-1}), representing the biomass produced per kilogram of applied nitrogen, following the methodology described by Moll et al. (1982).

2.4. Statistical analysis

All statistical analyses were conducted in the R environment v. 4.3.2 using the RStudio interface v. 2023.12.1 + 402 (R Core Team, 2023). We assessed the dataset for normal distribution of the errors and homoscedasticity using the Shapiro-Wilk and Bartlett tests, respectively. To meet these assumptions, all data were log-transformed using the *vegan::decostand* function from the *vegan* R-package (Oksanen et al., 2017). A three-way ANOVA was conducted to analyze plant growth, chlorophyll content, aboveground biomass production, and nutrient extraction across microbial strains, N fertilization, and water supply treatments. Two-way or one-way ANOVA was applied when one or two factors showed no significant effects (See details about the ANOVA outputs in Supplementary Table S1). ANOVAs were performed using the *ssp.plot::agricolae* function in the *agricolae* R-package, with Scott-Knott's mean range test ($p < 0.05$) as the post-hoc analysis (Mendiburu, 2015). Pearson correlation analysis summarized variable relationships and informed predictive models built using the stepwise correction and *corrplot::ggcorr* function in the R-package *corrplot* (Wei et al., 2017).

3. Results

3.1. Microbial inoculation, water supply, and N fertilization influence the aboveground biomass production and N use efficiency of Sorghum bicolor

Significant differences ($p < 0.05$) in aboveground biomass production were observed due to the triple interaction among N fertilization, water supply, and inoculation treatments (Table 3 and Supplementary Table S1). Considering the irrigation with 100 % ET_C, the inoculation of 15 microbial strains increased biomass production when fertilized with 140 kg N ha^{-1}, compared with the non-inoculated control. The yield increase ranged from 4.55 % to 39.32 % when bacterial strains *Azospirillum brasilense* Ab-V5 and *Bacillus* sp. ESA 13 were inoculated, respectively. Under 100 % ETc with only 20 kg N ha^{-1}, yields exceeded 42 Mg ha^{-1}. Using 11 inoculants (out of 15 assessed) resulted in higher sorghum biomass production than the non-inoculated control, with an increase of 8.09–36.55 % in dry mass compared to the non-inoculated control, when the bacteria *Herbaspirillum seropedicae* BR 11417 and *Paenibacillus* sp. ESA 674 were used, respectively. At the same time, the water supply treatment, the inoculation of *Rhizobium* sp. ESA 15, *Bacillus* spp. ESA 402/ESA 674, and *Pelomonas* sp. ESA 424 resulted in the same biomass production in both N fertilization treatments.

Table 3
Sorghum BRS 716 aboveground biomass production (Mg ha^{-1}) and N-fertilizer yield efficiency (Mg plant kg N^{-1}) (mean ± standard deviation) influenced by the triple interaction among the Inoculation, water supply, and N fertilization treatments.

Water supply	45 % ET_C		100 % ET_C	
N fertilization	20 kg ha^{-1}	140 kg ha^{-1}	20 kg ha^{-1}	140 kg ha^{-1}
Inoculation treatment	Aboveground biomass production (Mg ha^{-1})			
ESA 13	35.3 ± 2.08 bAβ	44.0 ± 3.61 aAβ	42.5 ± 5.03 bCγ	61.3 ± 3.21 aAγ
ESA 15	37.2 ± 3.40 aAβ	39.4 ± 3.29 aBβ	43.9 ± 3.48 aCγ	48.0 ± 2.54 aDγ
ESA 29	36.8 ± 3.88 aAβ	37.0 ± 3.01 aBβ	48.8 ± 3.55 bAγ	58.7 ± 4.04 aAγ
ESA 37	34.3 ± 5.13 aAβ	35.6 ± 6.04 aCβ	47.0 ± 2.36 bBγ	59.0 ± 2.21 aAγ
ESA 45	32.2 ± 2.54 bBβ	38.3 ± 3.21 aBβ	43.3 ± 4.04 bCγ	56.1 ± 5.00 aBγ
ESA 116	30.0 ± 3.11 bBβ	39.4 ± 2.50 aBβ	36.7 ± 1.54 bDγ	51.2 ± 1.57 aCγ
ESA 402	36.3 ± 5.69 aAβ	40.3 ± 4.04 aAγ	46.9 ± 2.70 aBγ	42.5 ± 5.94 aEγ
ESA 441	36.7 ± 3.51 aAβ	40.0 ± 4.36 aAβ	44.3 ± 2.52 bBγ	54.7 ± 2.52 aBγ
ESA 424	31.0 ± 2.81 aBβ	34.1 ± 5.24 aCβ	40.4 ± 6.35 aCγ	44.3 ± 5.86 aEγ
ESA 600	26.4 ± 4.04 aCβ	29.7 ± 2.52 aDβ	46.5 ± 2.20 bBγ	53.3 ± 2.08 aBγ
ESA 601	25.8 ± 3.46 bCβ	32.2 ± 1.80 aCβ	37.6 ± 1.60 bDγ	53.6 ± 2.25 aBγ
ESA 674	31.0 ± 2.01 aBβ	33.8 ± 2.88 aCβ	52.3 ± 1.53 aAγ	56.2 ± 3.33 aBγ
Ab-V5	29.1 ± 2.01 bBβ	37.0 ± 2.65 aBβ	33.7 ± 2.05 bEγ	46.0 ± 1.01 aDγ
BR 11005^T	32.6 ± 1.50 aBβ	35.6 ± 1.52 aCβ	37.9 ± 2.01 bDγ	49.5 ± 2.40 aCγ
BR 11417	34.8 ± 2.31 aAβ	39.7 ± 2.05 aBβ	41.4 ± 1.94 bCγ	49.3 ± 2.08 aCγ
Control	31.5 ± 2.18 aBβ	35.5 ± 1.01 aCβ	38.3 ± 1.53 bDγ	44.0 ± 2.73 aEγ
Inoculation treatment	N-fertilizer yield efficiency (Mg plant kg N^{-1})			
ESA 13	1.77 ± 0.10 aAβ	0.31 ± 0.03 bAβ	2.13 ± 0.25 aDγ	0.43 ± 0.02 bAγ
ESA 15	1.86 ± 0.17 aAβ	0.28 ± 0.02 bAγ	2.20 ± 0.17 aCγ	0.34 ± 0.01 bAγ
ESA 29	1.84 ± 0.19 aAβ	0.26 ± 0.02 bAβ	2.44 ± 0.18 aBγ	0.42 ± 0.03 bAγ
ESA 37	1.72 ± 0.26 aBβ	0.25 ± 0.04 bAβ	2.35 ± 0.12 aBγ	0.42 ± 0.02 bAγ
ESA 45	1.61 ± 0.13 aCβ	0.27 ± 0.02 bAβ	2.17 ± 0.20 aCγ	0.40 ± 0.04 bAγ
ESA 116	1.50 ± 0.16 aCβ	0.28 ± 0.02 bAγ	1.84 ± 0.08 aEγ	0.37 ± 0.01 bAγ
ESA 402	1.82 ± 0.29 aAβ	0.29 ± 0.03 bAγ	2.35 ± 0.14 aBγ	0.30 ± 0.04 bBγ
ESA 441	1.84 ± 0.18 aAβ	0.29 ± 0.03 bAγ	2.22 ± 0.13 aCγ	0.39 ± 0.02 bAγ
ESA 424	1.55 ± 0.14 aCβ	0.24 ± 0.04 bAγ	2.02 ± 0.32 aDγ	0.31 ± 0.04 bBγ
ESA 600	1.32 ± 0.20 aEβ	0.21 ± 0.02 bAβ	2.33 ± 0.11 aBγ	0.38 ± 0.02 bAγ
ESA 601	1.29 ± 0.17 aEβ	0.23 ± 0.01 bAβ	1.88 ± 0.08 aEγ	0.38 ± 0.01 bAγ
ESA 674	1.55 ± 0.10 aCβ	0.24 ± 0.02 bAβ	2.62 ± 0.08 aAγ	0.40 ± 0.02 bAγ
Ab-V5	1.46 ± 0.10 aDγ	0.26 ± 0.02 bAγ	1.69 ± 0.10 aFγ	0.33 ± 0.01 bAγ
BR 11005^T	1.63 ± 0.08 aBβ	0.25 ± 0.01 bAγ	1.90 ± 0.10 aEγ	0.35 ± 0.02 bAγ
BR 11417	1.74 ± 0.12 aAβ	0.28 ± 0.02 bAγ	2.07 ± 0.10 aDγ	0.35 ± 0.02 bAγ
Control	1.58 ± 0.11 aCβ	0.25 ± 0.07 bAγ	1.92 ± 0.08 aEγ	0.31 ± 0.02 bBγ

At the lowest water supply treatment (45 % ET_C), when 140 kg N ha^{-1} was applied, the inoculation of eight bacteria and a yeast strain led to a higher biomass production, with increasing ranging from 4.23 (*Azospirillum brasilense* Ab-V5 and *Chryseobacterium* sp. ESA 29) to 23.94 % (*Bacillus* sp. ESA 13) compared to the non-inoculated control. In the worst experimental scenario, with lower water and N supply, seven inoculants demonstrated higher biomass production compared to the non-inoculated control, increasing sorghum biomass from 8.89 % (*Meyerozyma* sp. ESA 37) to 18.10 % (*Rhizobium* sp. ESA 15). With 45 % ET_C, the inoculation of 10 microorganisms and the non-inoculated control treatment showed the same biomass production for both N fertilization treatments. Comparing the different water supplies with the same N fertilization treatment, all 16 treatments assessed showed higher aboveground biomass production when irrigated with 100 % ET_C. The same result was observed when 140 kg N ha^{-1} was applied, except for

Lowercase letters represent significant differences of N fertilization treatments (within the same inoculation and water supply treatments combination), Greek letters represent significant differences of water supply treatments (within the same inoculation and N fertilization treatments combination), while capital letters represent significant differences of inoculantion treatments (within the same water supply and N fertilization treatments combination) within the same inoculation and N fertilization treatmentsby Scott-Knott's mean range test ($p <$ 0.05).

the treatment with *Bacillus* sp. ESA 402 inoculation with no differences between 45 and 100 % ET_C.

The N-fertilizer yield efficiency (NYE) indicated that at 20 kg N ha^{-1}, sorghum plants produced more biomass per unit of N applied than at 140 kg N ha^{-1}, under both irrigation conditions. With 20 kg N ha^{-1} and 45 % ET_C, the inoculation of eight microbes demonstrated higher NYE than the non-inoculated control, particularly *Bacillus* sp. ESA 13 and ESA 402, *Rhizobium* sp. ESA 15, *Agrobacterium* sp. ESA 441, and *Herbaspirillum seropedicae* BR 11417 achieved an average of 232 kg of sorghum biomass per kg of N fertilizer applied compared to the non-inoculated control. When considering irrigation with 100 % ET_C, 13 out of 15 tested inoculants improved N fertilization efficiency, especially the inoculant with *Bacillus* sp. ESA 674 produced 700 kg more sorghum biomass per kg of N as fertilizer compared to the non-inoculated plants under the same experimental conditions.

3.2. *Effects of microbial inoculation, nitrogen, and water on nutrient extraction: significant interactions for K, N, Ca, Cu, and Zn, and minimal effects on P, Mg, S, Fe, Mn, and Na*

Triple interaction was significant ($p < 0.001$) for the sorghum K extraction (Table 4). At 45 % ET_C, when 20 kg N ha^{-1} was applied, the inoculation of five bacterial strains increased the total K extraction compared to the control, resulting in a 74.83 % increment when the inoculant contained *Rhizobium* sp. ESA 116 was applied. Considering the 140 kg N ha^{-1} application, three inoculants stood out compared to the non-inoculated control treatment, highlighting the effectiveness of inoculating with *Agrobacterium* sp. ESA 441 induced a 71.65 % higher K extraction compared to the control without microbial inoculation. Comparing the two N fertilization levels at 45 % ETC, the inoculation of four bacteria and the non-inoculated control showed the same extraction rates at both N levels. Surprisingly, the inoculation of *Bacillus* spp. ESA 13 and ESA 600, *Chryseobacterium* sp. ESA 29, and *Rhizobium* sp. ESA 116 induced higher K extraction (with the same K fertilization for the whole experiment) with lower N fertilization (20 kg N ha^{-1}).

With 100 % ET_C and application of 20 kg N ha^{-1}, the inoculation of 10 bacteria and one yeast increased the K extraction compared to the non-inoculated control. *Bacillus* sp. ESA 674 showed an outstanding performance, increasing the sorghum K extraction by 79.76 % when compared to the non-inoculated control. Within the 140 kg N ha^{-1} six bacteria and one yeast increased the sorghum K extraction, highlighting *Pelomonas* sp. ESA 424 more than doubled the sorghum K extraction in this combination, achieving 116.90 % more than the control without inoculation. Only the treatment inoculated with *Herbaspirillum seropedicae* BR 11417 showed no differences between the K extraction levels when both N fertilization treatments were compared at 100 % ET_C.

Table 4

Sorghum BRS 716 potassium extraction (kg ha^{-1}) (mean ± standard deviation) influenced by the triple interaction among the inoculation, water supply, and N fertilization treatments.

Water supply	45 % ET_C		100 % ET_C	
N fertilization	20 kg ha^{-1}	140 kg ha^{-1}	20 kg ha^{-1}	140 kg ha^{-1}
Inoculation treatment	Plant K extraction (kg ha^{-1})			
ESA 13	575 ± 32.9 aBγ	520 ± 21.3 bCβ	488 ± 25.2 bAβ	684 ± 53.8 aCγ
ESA 15	368 ± 5.60 aCβ	320 ± 6.9 aDβ	541 ± 26.4 bAγ	709 ± 11.1 aBγ
ESA 29	696 ± 20.70 aAγ	535 ± 29.7 bCβ	448 ± 6.8 bBβ	633 ± 26.5 aCγ
ESA 37	343 ± 31.90 bCβ	441 ± 12.3 aCβ	402 ± 15.2 bBγ	582 ± 17.8 aCγ
ESA 45	362 ± 30.5 bCγ	541 ± 16.2 aBγ	272 ± 16.8 bCβ	498 ± 7.6 aDβ
ESA 116	764 ± 6.9 aAγ	520 ± 27.0 bCγ	409 ± 20.3 bBβ	512 ± 21.4 aDγ
ESA 402	417 ± 13.8 bCγ	488 ± 38.6 aCβ	359 ± 19.0 bCβ	558 ± 12.8 aDγ
ESA 424	572 ± 41.4 aDγ	528 ± 27.5 aCβ	534 ± 11.9 bAγ	939 ± 21.4 aAγ
ESA 441	518 ± 22.2 bBγ	781 ± 13.3 aAγ	214 ± 6.7 bDβ	438 ± 9.8 aDβ
ESA 600	475 ± 18.4 aBγ	421 ± 14.5 bCβ	372 ± 12.9 bBβ	572 ± 37.3 aDγ
ESA 601	309 ± 7.6 aDβ	323 ± 9.3 aDβ	385 ± 21.9 bBγ	641 ± 35.7 aCγ
ESA 674	453 ± 35.9 aCβ	490 ± 29.0 aCγ	604 ± 30.5 aAγ	468 ± 11.8 bDγ
Ab-V5	373 ± 23.6 bCβ	564 ± 31.8 aBβ	479 ± 32.4 bBγ	806 ± 16.9 aBγ
BR 11005^T	398 ± 11.2 bCγ	463 ± 25.5 aCβ	386 ± 12.2 bBγ	487 ± 22.4 aDγ
BR 11417	247 ± 4.1 bDβ	326 ± 12.2 aDβ	344 ± 11.8 aCγ	386 ± 13.1 aDγ
Control	437 ± 19.0 aCγ	455 ± 13.8 aCγ	336 ± 9.3 bCβ	433 ± 29.3 aDγ

Lowercase letters represent significant differences of N fertilization treatments (within the same inoculation and water supply treatments combination), Greek letters represent significant differences of water supply treatments (within the same inoculation and N fertilization treatments combination), while capital letters represent significant differences of inoculantion treatments (within the same water supply and N fertilization treatments combination) within the same inoculation and N fertilization treatmentsby Scott-Knott's mean range test ($p <$ 05).

One-way ANOVA with N fertilization as sole treatment increased significantly ($p < 0.05$) the N extraction from 312 ± 10.5 to 362 ± 9.9 kg N ha^{-1} (15.75 %) when 20 and 140 kg N ha^{-1} were used. For Ca, Cu, and Zn, one-way ANOVA also attributed the increase in nutrient extraction to the same range of increment rates (17.78 %, 14.67 %, and 16.58 %, respectively). The two-way ANOVA revealed a significant interaction between microbial strains and drought stress, influencing the plant extraction of N ($p < 0.01$), Ca ($p < 0.001$), Cu ($p < 0.05$), and Zn ($p < 0.001$, Table 5). For N extraction, sorghum nitrogen extraction at 45 % ET_C, was favored by the inoculation of *Agrobacterium* sp. ESA 441, *Bacillus* sp. ESA 402, *Herbaspirillum seropedicae* BR 11417, and *Rhizobium* sp. ESA 15 is increasing by 13.60, 10.20, 9.63, and 3.12 % more N extraction than the non-inoculated control (average = 353 kg N ha^{-1}). Considering both irrigation levels, the inoculation of the yeast *Meyerozyma* sp. ESA 37 showed no difference between the water supply treatments. At 100 % ET_C, seven inoculation treatments resulted in more N extraction than the control, highlighting the effectiveness of *Bacillus* sp. ESA 402 and ESA 674, *Rhizobium* sp. ESA 15, and *Azospirillum baldaniorum* BR 11005^T, increasing the total N extraction by, respectively, 24.93, 23.27, 14.68, and 14.13 %, when compared with the non-inoculated control (average = 361 kg N ha^{-1}).

Calcium extraction was positively influenced by the inoculation of two bacteria at 45 % ET_C and four microbes (three bacteria and one yeast) at 100 % ET_C, with the bacterial strain *Bacillus* sp. ESA 13 stood out, being ranked in the highest Scott-Knott stratum ($p < 0.05$) for calcium extraction in both irrigation levels. For copper, ten microbial inoculants induced higher accumulation than the treatment without microorganisms at 45 % ET_C level, while with 100 % ET_C, ten inoculants provided more Cu extraction than the treatment without inoculation. The bacterial strain *Herbaspiriullum seropedicae* BR 11417 stood out, achieving the highest level of Scott-Knott stratum ($p < 0.05$) in both water supply situations for this micronutrient extraction. However, for zinc, at 45 % ET_C, the inoculation of the different microbes did not

Table 5

Sorghum BRS 716 nitrogen, calcium (kg ha^{-1}), copper, and zinc extraction (g ha^{-1}) (mean ± standard deviation) influenced by the double interaction between water supply and inoculation treatments.

Inoculation treatments	Water supply							
	45 % ET$_C$	100 % ET$_C$	45 % ET$_C$	100 % ET$_C$	45 % ET$_C$	100 % ET$_C$	45 % ET$_C$	100 % ET$_C$
	N (kg ha^{-1})		Ca (kg ha^{-1})		Cu (g ha^{-1})		Zn (g ha^{-1})	
ESA 13	290 ± 63.4 bC	371 ± 85.6 aB	138 ± 29.8 bA	178 ± 23.2 aA	269 ± 17.3 bE	386 ± 23.3 aE	2332 ± 46.6 bA	3552 ± 77.7 aA
ESA 15	364 ± 70.9 bA	414 ± 10.1 aA	111 ± 25.4 bB	134 ± 24.0 aC	399 ± 16.1 bA	471 ± 17.6 aB	2259 ± 32.9 bA	2778 ± 30.7 aB
ESA 29	269 ± 10.6 bD	407 ± 80.6 aB	101 ± 22.9 bB	193 ± 29.4 aA	388 ± 19.3 bA	419 ± 25.2 aD	2216 ± 58.3 bA	3650 ± 87.3 aA
ESA 37	321 ± 49.5 aB	317 ± 89.5 aD	86 ± 15.8 bC	142 ± 42.2 aC	347 ± 14.7 bB	457 ± 24.7 aC	2060 ± 39.4 bA	3029 ± 55.1 aB
ESA 45	308 ± 91.9 aC	251 ± 12.4 bE	104 ± 25.0 bB	153 ± 39.4 aB	374 ± 17.6 aB	384 ± 21.8 aE	2181 ± 45.4 bA	2921 ± 59.8 aB
ESA 116	309 ± 50.0 bC	367 ± 88.4 aC	95 ± 12.8 aB	104 ± 35.9 aD	357 ± 12.3 aB	302 ± 17.7 bF	2153 ± 60.6 aA	2322 ± 44.1 aC
ESA 402	389 ± 44.6 bA	451 ± 94.2 aA	143 ± 26.4 aA	124 ± 31.2 bD	323 ± 17.3 bC	348 ± 27.4 aE	2432 ± 52.5 aA	2351 ± 22.4 aC
ESA 424	258 ± 44.2 bD	339 ± 68.9 aC	102 ± 16.0 bB	123 ± 27.2 aD	274 ± 18.7 aE	291 ± 18.3 aG	2018 ± 34.2 aA	2433 ± 11.9 aC
ESA 441	401 ± 12.2 aA	412 ± 16.0 aA	114 ± 21.9 bB	136 ± 29.8 aC	355 ± 21.5 bB	522 ± 78.9 aA	2416 ± 42.8 bA	3114 ± 40.1 aB
ESA 600	256 ± 45.0 bD	342 ± 16.4 aC	98 ± 10.5 bC	142 ± 31.1 aC	240 ± 14.5 bF	514 ± 17.5 aA	1669 ± 24.6 bB	2944 ± 52.3 aB
ESA 601	235 ± 55.4 bE	333 ± 12.1 aC	104 ± 16.5 bB	127 ± 35.8 aD	234 ± 13.7 bF	457 ± 17.0 aC	1813 ± 41.6 bB	2581 ± 62.2 aC
ESA 674	225 ± 70.4 bE	445 ± 98.9 aA	102 ± 10.9 bB	152 ± 24.4 aB	320 ± 15.4 bC	417 ± 23.3 aD	2210 ± 23.8 bA	3427 ± 39.8 aA
Ab-V5	281 ± 20.8 bC	333 ± 91.5 aC	113 ± 29.7 aB	118 ± 39.1 aD	292 ± 10.8 aD	236 ± 17.3 bG	2018 ± 39.1 bA	2686 ± 74.3 aB
BR 11005^T	288 ± 52.5 bC	412 ± 11.8 aA	102 ± 19.4 bB	122 ± 23.o aD	365 ± 81.6 aB	357 ± 16.8 aF	1832 ± 41.5 bB	2713 ± 40.3 aB
BR 11417	387 ± 14.9 aA	287 ± 84.9 bE	102 ± 14.7 bB	134 ± 20.6 aC	407 ± 14.9 bA	491 ± 17.0 aA	2268 ± 30.1 aA	2652 ± 41.7 aB
Control	353 ± 89.8 aB	361 ± 74.8 aC	110 ± 21.9 bB	134 ± 29.2 aC	286 ± 14.8 aE	294 ± 17.5 aG	2017 ± 45.6 aA	2524 ± 49.2 aC

Lowercase letters represent significant differences of water supply, while capital letters represent significant differences of inoculation treatment by Scott-Knott's mean range test ($p < 05$).

increase the level of soil extraction. Otherwise, at 100 % ET$_C$ the inoculation of 11 strains improved the micronutrient extraction from the soil. For boron extraction, two-way ANOVA revealed a significant interaction between microbial strains and N fertilization treatments ($p < 0.05$, Supplementary Table S2). When 20 kg N ha^{-1} was applied, the inoculation of *Bacillus* spp. ESA 13 and ESA 674, in addition to *Paenibacillus* sp. ESA 601 favored soil micronutrient extraction. However, at 140 kg N ha^{-1} application, all 15 microbial inoculation treatments increased the B uptake compared to the non-inoculated control. *Bacillus* sp. ESA 13 was the only one to achieve the highest Skott-Knott stratum ($p < 0.05$) in both N fertilization treatments.

No influences of microbial inoculation were observed for Phosphorus ($p = 0.81$), Magnesium ($p = 0.39$), Sulfur ($p = 0.27$), Iron ($p = 0.14$), and Manganese ($p = 0.15$). Two-way ANOVA revealed a significant interaction between N fertilization and water supply treatments (Supplementary Table S3). Overall, the highest values for these traits were observed under the combination of 100 % ETC and 140 kg N ha^{-1}, enhancing the plant extraction of P, Mg, S, Fe, Mn, and Na by 30.90 %, 24.34 %, 25.29 %, 17.94 %, 23.34 %, and 16.35 %, respectively, comparing to the combination of 45 % ET$_C$ and 20 kg N ha^{-1}.

3.3. *Two sources of variation influenced growth parameters and chlorophyll content*

The two-way ANOVA showed a significant interaction between nitrogen fertilization and water availability, affecting the number of stalks ($p < 0.001$), tillers ($p < 0.05$), and chlorophyll *b* content ($p < 0.01$, Supplementary Table S4). The highest values for these traits were observed under the combination of 100 % ET$_C$ and 140 kg N ha^{-1}. Overall, this interaction enhanced the number of stalks, tillers, and chlorophyll *b* content by 23.38 %, 25.57 %, and 26.78 %, respectively, compared to the lower water supply and N fertilization.

Significant disparities in plant height ($p < 0.01$), stem diameter ($p < 0.01$), and leaf area ($p < 0.01$) were noticed due to the interaction between the water supply and the inoculation treatments, with no discernible effects attributable to N fertilization (Supplementary Table S5). Sorghum plants inoculated with five bacteria and two yeasts were, on average, taller than the other inoculation and control treatments at 100 % ET$_C$. At 45 % ET$_C$, the best performance was observed in sorghum plants inoculated with six bacteria and one yeast. The inoculants containing the yeast *Meyerozyma* sp. ESA 37 and the bacterium *Bacillus* sp. ESA 647 excelled in both water supply treatments, showing no differences between the two water level supplies.

Applying 13 inoculants (out of 15 tested) resulted in plants with thicker diameters compared to the non-inoculated control treatment at 100 % ET$_C$. At 45 ET$_C$, the same result was achieved when seven different microbes were applied. Plants inoculated with 10 different microbes showed no differences in stem diameter between the irrigation treatments. The leaf area index was positively influenced by the inoculation of three bacteria at 45 % ET$_C$, whereas no inoculation effects were observed at the highest water supply level ($p < 0.05$). *Pelomonas* sp. ESA 424 and *Azospirillum baldaniorum* BR 11005^T inoculation induced the same stem diameter in both water supply treatments. The two-way ANOVA revealed a significant interaction ($p < 0.001$) between N fertilization and microbial inoculation treatment on Chlorophyll *a*, without influence on the irrigation level (Supplementary Table S6). Plants inoculated with the yeast *Meyerozyma* sp. ESA 45 and the bacterium *Pelomonas* sp. ESA 424 showed no differences between the N fertilization levels. Surprisingly, the inoculation of *Azospirillum baldaniorum* BR 11005^T induced the sorghum leaves with increased Chlorophyll *a* index when 20 kg N ha^{-1} was applied, compared to the higher N fertilization rate.

3.4. *Univariate relationships among plant growth, chlorophyll content, and plant nutrient extraction parameters*

Pearson's correlation analysis revealed associations among plant growth parameters, aboveground biomass production, and soil nutrient extraction. Overall, all studied parameters showed positive correlations ($p < 0.001$), except for plant height and stem diameter ($p < 0.001$), leaf area index and stem diameter ($p < 0.01$), plant Ca extraction and stem diameter ($p < 0.001$), and plant Na extraction and plant Ca extraction ($p < 0.01$) (Fig. 1).

4. Discussion

The microbes selected for the present study have been shown as plant growth promoters for different crops like sorghum (Antunes et al., 2019; da Silva et al., 2018), maize (Bomfim et al., 2020; Cavalcanti et al., 2020; Nascimento et al., 2021; Targino et al., 2022), cowpeas (da Silva et al., 2023), and rice (*Oryza sativa*) (J. I. Baldani et al., 1986; Fernandes-Júnior et al., 2015) and forage species (Hungria et al., 2016; Santos et al., 2021; Gomes et al., 2023). The bacterial strains ESA 116, ESA 600, and ESA 601 have been proven effective as maize growth promoters

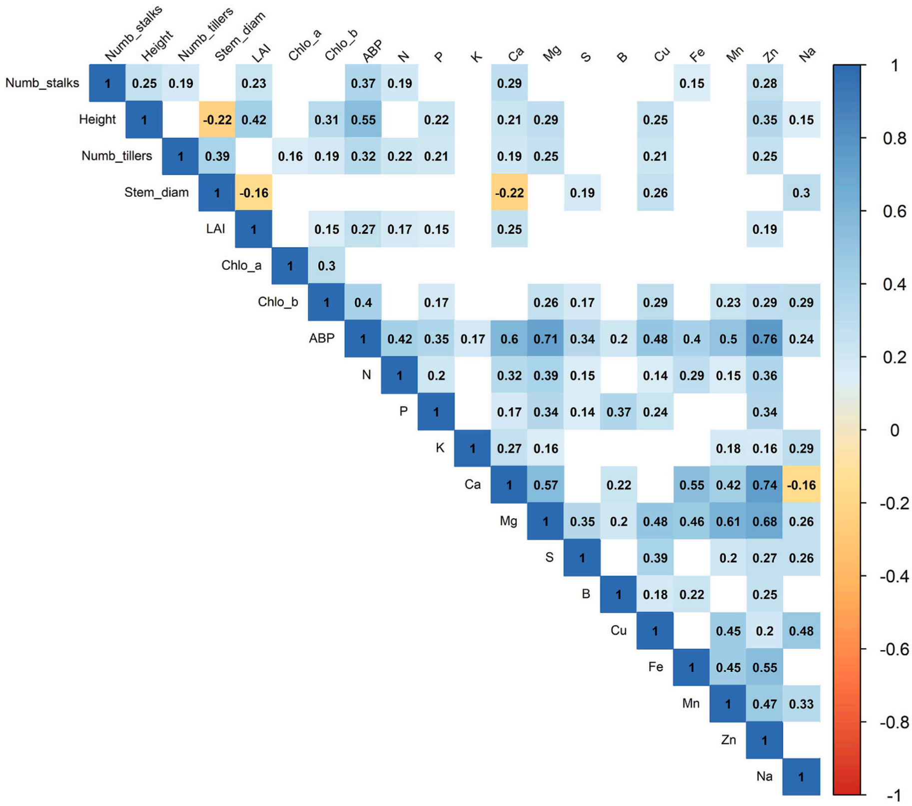

Fig. 1. Pearson's correlation among the plant growth parameters (Numb_stalks = number of stalks, unit plant^{-1}; Height = plant height, m; Numb_tillers = number of tillers, unit plant^{-1}; Stem_diam = stem diameter, cm; LAI = Leaf area index, m^2 plant^{-1}), chlorophyll contents (Chlo_a = chlorophyll *a*, Index ClorofiLog; and Chlo_b = chlorophyll *b*, Index ClorofiLog), ABP = aboveground biomass production (Mg ha^{-1}), and macro- (N, P, K, Ca, Mg, and S, kg ha^{-1}) and micronutrient (B, Fe, Cu, Mn, and Zn, g ha^{-1}) of *Sorghum bicolor* under microbial inoculation, drought stress, and N molarity. Blank cells indicate no significant correlation. Significant differences ($p < 0.05$) are presented.

under low-nitrogen but standard irrigation conditions in the Brazilian drylands (Cavalcanti et al., 2020; Nascimento et al., 2021). However, the current study is the first attempt to determine the agronomic performance of this bundle of strains under combined water and N levels supply. Some of the bacteria tested in the present study had been shown as stress-alleviating bacteria in different crops; for example, sorghum (ESA 402) (Santana et al., 2020) and sesame (*Sesamus indicus* - ESA 13, ESA 402, and ESA 441) (dos Santos et al., 2024; Lima et al., 2023).

The results on plant biomass accumulation corroborated the previous findings achieved in pots, indicating the performance of the above-mentioned bacteria on plant growth under low water and N supplies. Under low water and low N supply, other bacteria, such as ESA 29 and BR 11417, were also positive for biomass production. *Chryseobacterium* sp. ESA 29 is a nodule-endophytic strain isolated from cowpeas in Petrolina, Pernambuco, Brazil (Leite et al., 2017). This strain had promoted the cowpea growth under co-inoculation with *Bradyrhizobium* (da Silva et al., 2023). Since this bacterium was not isolated from grasses, its performance in sorghum under low N and restricted water availability indicated that this strain has high adaptation to different hosts and field conditions. Corroborating this hypothesis, we observed higher biomass production induced by the inoculation of ESA 29 under both low and high N fertilization conditions, with 100 % ETC, thereby broadening the field conditions under which ESA 29 can promote the growth of a non-original crop host. *Herbaspirillum seropedicae* BR 11417 has proven to be a growth promoter for sorghum (dos Santos et al., 2017) and maize (Alves et al., 2015) under a range of nitrogen fertilization conditions, with standard water supply. The results in the present study indicate that BR 11417 can also promote growth under low water availability, broadening the field conditions for the efficiency of this *Herbaspirillum seropedicae* strain.

Some bacteria, such as ESA 13, ESA 15, ESA 29, ESA 402, ESA 441, BR 11417 (under 45 % ET$_C$), and ESA 674 (under 100 % ET$_C$), reduced the need for N for each sorghum biomass unit produced, increasing the NYE under low N-fertilization. The ability of these bacteria to promote plant growth and improve root robustness and the ability to scavenge soils for nutrients could be an important player in this game, reducing the N fertilization needs for high biomass production (Araújo et al., 2015).

In addition to the aboveground biomass production, overall nutrient extraction was influenced by the inoculation of the microbes tested in the present study, among the bacteria that stood out for aboveground biomass production under the most detrimental experimental conditions (45 % ET$_C$, 20 kg N ha^{-1}), the strains ESA 13, ESA 29, and ESA 441 also induced higher K uptake, indicating the multifaceted nature of the growth promotion of these different inoculants. These bacterial strains were not assessed for K solubilization *in vitro*. However, they are P-solubilizing strains (da Silva et al., 2023; Fernandes-Júnior et al., 2015; Silva, 2017) despite no influence observed by microbial inoculation on P extraction. Inorganic P and K solubilization typically involves a linked mechanism, where the microbe produces organic acids (Nath et al., 2017; Roslan et al., 2020). In the present study, the mechanisms displayed by the bacterial strains likely differentially contributed to the amount of bioavailable K under our most detrimental experimental condition. Comparing the number of microorganisms that differed from the control when the irrigation reached 100 % ET$_C$, it is clear that water availability influenced the bacterial ability to induce plants to uptake K. However, the uncommon ability to cause these characteristics under low-water conditions is desirable for inoculants in dryland agriculture (O'Callaghan et al., 2022). No distinguishable patterns of sorghum K accumulation were observed when 0 or 224 kg N ha^{-1} was applied on a non-inoculated biomass sorghum in Missouri (USA) under a rainfed system (Maw et al., 2020), in agreement with the results observed in our lower irrigation level with no inoculation. Therefore, the differences observed when comparing the different N application rates and the inoculation treatments within the same irrigation level indicate a clear microbial role in plant K uptake in sorghum BRS 716.

In experiments on nitrogen fertilization and water supply, a previously overlooked aspect involves nitrogen concentration (molarity) and total nitrogen application (total number of moles). Swift et al. (2019) conducted an insightful study examining the effects of nitrogen molarity and total moles on growth and differential gene expression in rice. They found that gene expression was significantly affected at the highest nitrogen concentration, overshadowing the effects of a large amount of nitrogen applied (moles). Here, the inoculation of ESA 45, ESA 441, and Ab-V5 stood out cumulatively in terms of aboveground biomass and K extraction, reducing the potentially harmful effects of high N molarity on sorghum development, indicating homeostasis-inducing effects of these bacterial and yeast strains.

Surprisingly, N fertilization treatment only affected the sorghum's N exportation, with no interactions with the other factors. However, water availability and microbial inoculation interacted with each other. Sorghum is a crop that can scavenge soil N and obtain high amounts of soil N even under low N fertilization levels (Barros et al., 2020; Maw et al., 2020; Pannacci and Bartolini, 2018). This feature enables biomass sorghum to grow vigorously in marginal lands with insufficient N fertilization (Tang et al., 2018). N fertilization rates did not influence the extraction of Ca, Cu, and Zn, corroborating the results already shown by Maw et al. (2020) under rainfed conditions. However, different bacteria contributed to the differences observed in the four nutrient extraction rates. The experimental soil had 1.2 g kg^{-1} of N in the first 0.2 m layer, in other words, the soil N reservoir is around 3120 kg N ha^{-1}. Considering a potential mineralization and release of 2–4 % of soil N under irrigated conditions (Drinkwater and Snapp, 2007), a total release of 60–120 kg N ha^{-1} may have occurred, increasing the amount of N available to plants (Giongo et al., 2020). Since water availability is a critical factor for N mineralization, likely, more N was released when the irrigation applied was 100 % ET_C than 45 % ET_C. In this case, the irrigation rate also played a significant role in the N release in the soil, even more important than the application itself.

The amount of N exported by the plants under irrigation conditions exceeded the amount of N fertilized, as well as the generic estimations mentioned above. Several microbes that promoted N extraction in both irrigation conditions are diazotrophs, like BR 11417, BR 11005^T, ESA 13, ESA 402, ESA 674, and ESA 441 (Antunes et al., 2019; J. I. Baldani et al., 1986; V. L. D. Baldani et al., 1986; Bomfim et al., 2020; Fernandes-Júnior et al., 2015) and sorghum genotypes can be benefited by the biological nitrogen fixation (BNF) from its microsymbionts under field conditions (Barros et al., 2020; dos Santos et al., 2017). However, the contribution of BNF for sorghum BRS 716 was probably small in this field trial. Recent reports indicated that an underestimated trait crucial to the BNF in sorghum is the presence of aerial (brace) roots with slimy mucilage production (Venado et al., 2025; Wolf et al., 2023). Our field observations recorded the production of aerial roots on the first node above ground in BRS 716; however, no mucilage production was observed even after irrigation or short rainfall. In addition to BNF, the bacteria assessed in the present study exhibit several other plant growth-promoting traits, including calcium phosphate solubilization, siderophore production, auxin synthesis, and biofilm formation. These mechanisms typically induce root development, enhancing fertilizer and soil nutrient use efficiency, as the roots dig deeper to uptake nutrients (da Silva et al., 2022).

The observed interaction between N fertilization and microbial inoculation on chlorophyll *a* suggests that the physiological response of sorghum to microbial partners is influenced by nutrient availability (Lima et al., 2023). Chlorophyll *a* is the primary pigment involved in the light-harvesting complex, directly contributing to the efficiency of the photosynthetic apparatus (dos Santos et al., 2024). Higher chlorophyll *a* levels typically enhance the plant's capacity to capture light energy and facilitate electron transport, which can ultimately increase carbon assimilation. The robust response of *A. baldaniorum* BR 11005^T to the lower N fertilization rate (20 kg N ha-1) may indicate that this bacterium enhances nitrogen assimilation or modulates hormonal signaling in a way that promotes chlorophyll biosynthesis, thereby compensating for reduced external N inputs (Chakraborty et al., 2024). In contrast, the lack of chlorophyll *a* increase under higher N supply for this treatment could reflect a physiological ceiling for pigment accumulation or a shift in resource allocation away from the photosynthetic apparatus under luxury N conditions (Galindo et al., 2024). Such microbe–nutrient interactions highlight the potential of targeted bacterium use to sustain photosynthetic efficiency under reduced fertilizer inputs, contributing to both crop productivity and input-use efficiency.

Environmental conditions significantly impact bacterial performance and their abilities to promote plant growth (Chakraborty et al., 2024). For these reasons, bacterial growth promotion was influenced differentially by the different combinations tested in the present experiment. The microbial inoculants shifted the top positions when the Scott-Knott test ranked the averages for the plant developmental (plant height, stem diameter, and leaf area index) and nutrition (K, N, Ca, Mn, Zn, and B) variables, which were assessed. However, some bacteria like *Bacillus* sp. ESA 402 ranked in the top stratum in all the above-mentioned variables, mainly when the lowest water availability was tested. ESA 402 is a sorghum-borne bacterium that can improve plant growth even under drought conditions in pot experiments (Antunes et al., 2019; dos Santos et al., 2024; Lima et al., 2023; Santana et al., 2020), and is now validated as a field growth promoter bacterium under sub-optimal irrigation conditions.

Yeasts from arid and semiarid regions are often underestimated as plant growth-promoting microbes, and their bioprospection could reveal potential new inoculant strains (Raklami et al., 2024). Both yeasts in the present study stood out in different variables assessed, for example, aboveground biomass production with 45 % ET_C and 20 kg N ha^{-1}, plant height, stem diameter, and nutrient extraction. Both *Meyerozyma* spp. ESA 37 and ESA 45, which were assessed in the present study, were isolated from field-grown maize and exhibited several plant-growth-promoting mechanisms (Targino et al., 2022). The present study showed, for the first time, the ability of these yeasts to promote plant growth under field conditions with variable cropping strategies. Nevertheless, since the microbes of the present study acted positively for sorghum growth, yield, and nutrient uptake under different conditions, an approach to maximize each microbe's beneficial ability relies on the development of mixed inoculants containing multiple strains (Behera et al., 2024; Jing et al., 2024; Tharanath et al., 2024). Our findings support the development of a cross-kingdom inoculant with *Herbaspirillum seropedicae* BR 11417, *Bacillus* spp. ESA 402 and ESA 674, *Agrobacterium* sp. ESA 441, and *Mayerozyma* sp. ESA 37 or ESA 45 could produce a promising bio-input for sorghum production in dryland agriculture. Furthermore, microbiome investigations into the interactions between microbial inoculants and the soil community could provide crucial insights into the microbial roles in the sorghum rhizosphere, ultimately contributing to the sustainability of dryland agricultural business.

The results regarding the use of PGPR demonstrated in this study represent a significant advancement over conventional single-intervention practices in arid and semiarid land agriculture. Our findings indicate that the synergistic effects of these amendments not only improved crop biomass and physiological performance under drought stress but also enhanced plant nutrition, thereby contributing to both immediate yield benefits and long-term soil sustainability. This dual strategy aligns with the growing demand for climate-resilient and environmentally responsible agronomic solutions, providing a practical framework for optimizing plant productivity while reducing reliance on synthetic fertilizers. This work is among the first studies to demonstrate the potential of microbial inoculants under concurrent nitrogen and water stress in sorghum, as supported by physiological, nutritional, and yield indicators. By clearly demonstrating the complementary mechanisms of microbes, our findings provide a foundation for refining integrated biostimulant approaches in future research and field applications.

5. Conclusion

The results of the present study highlight the significant influence of microbial inoculation on sorghum yield, growth, and nutritional variables under different N and water availabilities in a dryland field. Those optimal (100 % ET_C and 100 kg N ha^{-1}) and most detrimental (45 % ET_C and 20 kg N ha^{-1}) conditions influenced sorghum growth differentially under the presence of different microbes, improving sorghum development at this extreme situation and those in between. These results contribute to global sustainability efforts by supporting climate-resilient, resource-efficient farming practices aligning with SDG 2 (Zero Hunger) and SDG 13 (Climate Action). This work's main strength lies in its integrated use of microbial biostimulants with precise N and water management, coupled with a comprehensive evaluation of plant responses. The findings provide field-applicable insights for sustainable crop production under drought stress and N-limited conditions. Although this study represents a single growing season, future long-term assessments are necessary to evaluate the persistence of microbial benefits, their influence on soil microbiome dynamics, and the sustainability of inoculant effects across successive cropping cycles. Additionally, future research should explore using multiple strains of inoculants, applying microbes that promoted different sorghum agronomic and developmental aspects in the present study, to further integrate microbial-based bioinputs into sustainable cropping systems in semiarid environments.

CRediT authorship contribution statement

Amon Rafael de Macedo: Visualization, Investigation, Data curation. **Welson Lima Simões:** Supervision, Resources, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization. **Tancredo Augusto Feitosa de Souza:** Writing – original draft, Visualization, Software, Formal analysis, Data curation. **Angela Liriel Pereira Umbelino:** Investigation, Data curation. **Italla Mikelly Barbosa:** Investigation, Data curation. **Bruno de Oliveira Dias:** Supervision, Resources. **Paula Rose de Almeida Ribeiro:** Validation, Supervision, Investigation, Data curation. **Jucicléia Soares da Silva:** Validation, Supervision, Investigation, Data curation. **Anderson Ramos Oliveira:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Alessandra Monteiro Salviano:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Paulo Ivan Fernandes-Júnior:** Writing – original draft, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Generative AI use statement

During the preparation of this paper the authors used "Grammarly" in order to double check language mistakes. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the paper's content.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jaridenv.2025.105502.

Data availability

Data will be made available on request.

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