CSIRO PUBLISHING

SPECIAL ISSUE | RESEARCH PAPER
https://doi.org/10.1071/CP21438

CROP & PASTURE SCIENCE

Exploring plant growth-promoting *Streptomyces* spp. for yield and nutrition traits in pearl millet hybrids

Vadlamudi Srinivas[A], Nimmala Naresh[A], Sambangi Pratyusha[A], Sravani Ankati[A], Mahalingam Govindaraj[A,*] and Subramaniam Gopalakrishnan[A,*]

For full list of author affiliations and declarations see end of paper

***Correspondence to:**
Subramaniam Gopalakrishnan
International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502324, Telangana, India
Email: s.gopalakrishnan@cgiar.org and
Mahalingam Govindaraj
International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502324, Telangana, India
Email: m.govindaraj@cgiar.org

Handling Editor:
Shahid Hussain

Received: 23 June 2021
Accepted: 27 September 2021
Published: 14 February 2022

Cite this:
Srinivas V *et al.* (2022)
Crop & Pasture Science
doi:10.1071/CP21438

ABSTRACT

The present study aimed to demonstrate the use of two strains of *Streptomyces albus* (CAI-24 and KAI-27) and one strain of *S. griseus* (MMA-32) for plant growth-promotion (PGP) and improving pearl millet yield and nutrient content under greenhouse and field conditions. Two hybrids, a low-Fe (PA-9444; non-biofortified hybrid) and high-Fe (ICMH-1201; biofortified hybrid), treated with selected *Streptomyces* strains, significantly enhanced a range of traits including grain yield in the glasshouse (13–23%) and field (9–12%) over the control. In the greenhouse experiments an enhanced stover and grain nutrient concentrations were observed in ICMH-1201 (Fe 53% and 40%; Zn 15% and 10%; Ca 11% and 29%) over the control, while such nutrition augmentations were not found in PA-9444. The field harvested stover and grain nutrient concentrations were also increased over the control in both hybrids. A higher stover nutrient concentration was found in ICMH-1201 while PA-9444 had an increase in grain nutrient concentration indicating the significance of these *Streptomyces* strains' PGP role in the non-biofortified hybrid. Based on this study, strains KAI-27 and MMA-32 significantly improved shoot weight, root weight and grain yield while CAI-24 and MMA-32 improved nutrient concentrations including Fe contents (up to 49%) in grain as well as in stover. Further, the stover samples of pearl millet contained a higher Fe concentration (150–200%) compared to grain samples. This study confirms that the selected *Streptomyces* strains have the potential for enhancing PGP and stover and grain nutrient concentrations in pearl millet and can complement the existing conventional biofortification strategies.

Keywords: beneficial bacteria, biofortification, iron, nutrition, pearl millet, PGP, PGP microbes, *Streptomyces*.

Introduction

Pearl millet is one of the most important foods and forage crops, largely cultivated in sub-Saharan Africa (approximately 16 million ha) and Asia (approximately 10 million ha). India stands as one of the largest producers of pearl millet with 7 m ha area and 8.6 m t production with an average productivity of 1243 kg ha^{-1} (Directorate of Millets Development 2020). Pearl millet is historically consumed by low and middle-income groups of the population, where a higher magnitude of malnutrition was reported. Malnutrition is mainly affecting children; therefore, it's become one of the world's leading causes of child mortality, also accounting for over 45% of deaths in children under the age of 5 years (WHO 2020).

Biofortification of staple food crops with specific micronutrients has emerged as a potent solution to fight against malnutrition, especially in developing countries, where the populations are economically impaired to afford fruits, vegetables, legumes, fish and other food products to meet their daily essential nutritional requirements. Biofortification complements, but differs from, food fortification by improving nutrients of food crops at genesis, besides its complementation. The HaversetPlus-supported global biofortification programs delivered nutri-dense hybrids largely through conventional breeding. As a result, many biofortified food crops are in the market such as orange, sweet potatoes, maize, cassava, squash, iron (Fe) enriched beans, lentils, pearl millet, zinc (Zn) enriched rice, wheat, lentil, sorghum and cowpea (Wakeel *et al.* 2018). In future, biofortification by genetic modification using modern biotechnology may improve the breeding efficiency for long-term sustainability. These hybrids are developed by conventional breeding methods, which took a long developmental time (≤8–10 years). Agronomic approaches are short-term alternatives to address malnutrition through optimised crop nutrition. In this context, apart from fertigation, selective microbial applications can help in achieving biofortification for targeting micronutrients. Although the native beneficial microflora supports crop fitness to a nominal level, application of plant growth-promoting (PGP) microbes as biofertilisers certainly enhance the crop growth to achieve its genetic potential yields and even act as phytopathogen fighters for plant protection (Nosheen *et al.* 2021). Numerous beneficial soil microbes are reported including bacteria, fungi, cyanobacteria, actinomycetes and mycorrhiza (Gopalakrishnan *et al.* 2020*a*, 2021; Yadav *et al.* 2020*a*, 2020*b*).

Currently, PGP microbes' uses are demonstrated for biofortification of specific micronutrient(s) with their ability to solubilise the integral soil micronutrient and convert them to easily bioavailable forms for plant uptake (Prasanna *et al.* 2016). Different mechanisms are involved in these PGP microbes for micronutrient enhancement from soil, where micronutrient accessibility is limited by various soil factors, moisture, nutrients, physico-chemical interactions and microbial activity (Kumar *et al.* 2016). A recent study reported beneficial microbes such as *Acinetobacter*, *Bacillus*, *Burkholderia*, *Enterobacter* and *Pseudomonas* for micronutrient enhancement in agriculturally important crops including rice, wheat, chickpea, pigeonpea and soybean (Kaur *et al.* 2020). Apart from the above-mentioned beneficial microflora, *Streptomyces* are widely reported for their usefulness in crop production and protection and in soil health management (Gopalakrishnan *et al.* 2011*a*, 2011*b*). Impact of *Streptomyces* inoculation on crop plants is well divulged for bio-fertilisation, bio-stimulation and bio-protection applications in agriculture. *Streptomyces* are Gram-positive, aerobic, filamentous, and spore-forming bacteria, which can survive as both saprophytes and endophytes by colonising the rhizosphere and/or rhizoplane of the plant roots (Saleem *et al.* 2016; Vijayabharathi *et al.* 2018; Gopalakrishnan *et al.* 2020*b*). *Streptomyces* release the free phosphate from soil rock phosphate by acidification and secrete organic acids like malic acid and gluconic acid (Hamdali *et al.* 2008). Also, they are reported to increase the number of branches and later roots, shoot length, and nutrient levels like Fe, Mn and P in wheat (Jog *et al.* 2014). Even the mineral supply to plants was promoted by *Streptomyces* by synthesising siderophores and siderophore uptake systems (Sadeghi *et al.* 2012). Apart from bio-fertilisation capability, *Streptomyces* are also reported as bio-stimulants of plant growth by the production of plant growth promoters such as indole acetic acid (IAA). PGP *Streptomyces* are also reported to be micronutrient fortifiers (mainly Fe and Zn) in the harvested grains of chickpea and pigeonpea (Sathya *et al.* 2016). However, such reports of microbial effect for pearl millet grain nutrient enrichment have not been investigated.

The present study aimed to evaluate two strains of *Streptomyces albus* (CAI-24 and KAI-27) and one strain of *S. griseus* (MMA-32), for improved crop growth, yield and nutritional traits in pearl millet hybrids in both greenhouse and field conditions. Use of these strains was demonstrated previously for PGP and enhanced mineral nutrients in rice (Gopalakrishnan *et al.* 2012, 2013*a*, 2013*b*), sorghum (Gopalakrishnan *et al.* 2013*a*), pigeonpea (Gopalakrishnan *et al.* 2016*b*) and chickpea (Gopalakrishnan *et al.* 2015*a*, 2015*b*, 2015*c*; Sathya *et al.* 2016). The novelty of this study is to exploit the potential for PGP *Streptomyces* spp. to complement the existing conventional biofortification strategies for enhancing yield and nutrition traits in grains and stover of pearl millet hybrids.

Materials and methods

Streptomyces strains and pearl millet hybrids

Two *Streptomyces albus* strains (CAI-24 and KAI-27 with WGS GenBank accession numbers: JAANOE010000000 and JAANNU000000000, respectively) and a *Streptomyces griseus* strain (MMA-32 with WGS GenBank accession number: JAANNS000000000) (Subramaniam *et al.* 2020) demonstrated previously for PGP and biofortification of mineral nutrients in rice (Gopalakrishnan *et al.* 2012, 2013*a*, 2013*b*), sorghum (Gopalakrishnan *et al.* 2013*a*), pigeonpea (Gopalakrishnan *et al.* 2016*b*) and chickpea (Gopalakrishnan *et al.* 2015*a*, 2015*b*, 2015*c*; Sathya *et al.* 2016) were used in this study. Pearl millet hybrids with different Fe acquisition capabilities, one with low Fe contents Pro-Agro 9444 (hereafter referred to as PA-9444) and another with high Fe contents ICRISAT Millet Hybrid 1201 (hereafter referred to as ICMH-1201) were acquired from pearl millet breeding, ICRISAT, Patancheru, India.

Evaluation of *Streptomyces* strains for plant growth, yield and nutrition traits

Greenhouse experiment

A total of four treatments, including three test strains CAI-24, KAI-27 and MMA-32 and one control inoculate only with water, were made and evaluated on two hybrids of pearl millet (PA-9444 and ICMH-1201) with six replications. The trial was conducted in a completely randomised design (CRD). A pot mixture, comprising red soil and farmyard manure in 3:1 ratio, was used to fill 8-inch plastic pots (for taking observation of plants at 40 days after sowing; DAS) and 10-inch plastic pots (for taking observations of plants at harvesting). Seeds of both the pearl millet hybrids were surface sterilised with 2.5% sodium hypochlorite solution in water for 3 min and rinsed several times with sterilised distilled water. The surface sterilised seeds were soaked in an actively grown test *Streptomyces* spore suspension (at 10^7 colony forming units (CFU) mL^{-1}) for 45 min, whereas sterile water treated seeds served as the control. At the end of soaking, three treated seeds were sown immediately in each pot and thinned to one plant per pot after germination. Booster doses (5 mL) of the test strains were applied on both 8-inch and 10-inch plastic pots by the soil drench method at 15 day intervals. At 40 DAS, 8-inch pots were dismantled and PGP traits such as plant height (cm $plant^{-1}$), leaf area (measured with a leaf area meter, LI-3100C LI-COR, USA), shoot dry weight, (g $plant^{-1}$) root volume and root length (cm $plant^{-1}$) were recorded. At harvest, 10-inch pots were dismantled and PGP traits such as plant height (cm $plant^{-1}$), shoot, root and panicle dry weight (g $plant^{-1}$) and grain yield (g $plant^{-1}$) were recorded.

Field experiment

The three test *Streptomyces* strains, CAI-24, KAI-27 and MMA-32 assessed in the greenhouse, were also evaluated for their PGP potential on pearl millet under field conditions at ICRISAT, Patancheru (17°30′N; 78°16′E; altitude 549 m) during 2016–2017. In the cropping season, a maximum temperature ranging from 28.2 to 37.8°C and a minimum temperature ranging from 11.1 to 17.6°C were recorded. Soils at the experimental site are classified as red soils having 90.47% non-soluble material, 3.61% iron, 2.92% aluminium, 1.01% organic matter, 0.7% magnesium, 0.56% lime, 0.3% carbon dioxide, 0.24% potash, 0.12% soda, 0.09% phosphorus and 0.08% nitrogen. A total of four treatments, including three test strains such as CAI-24, KAI-27 and MMA-32 and one control, were made. The experiment was carried out with three replications in 4 m plots with a spacing of 75 cm between the rows and 15 cm between the plants in a Randomised Complete Block design (RCBD). A basal dose of 100 kg ha^{-1} of DAP (Di-ammonium phosphate which carries 18% N and 46% P) was applied once at the field preparation and a 100 kg ha^{-1} of urea (which carries 46% N) was applied once as side-dressing after the thinning. Seeds of pearl millet hybrids PA-9444 and ICMH-1201 were treated with test *Streptomyces* strains (coated with a peat formulation of test *Streptomyces* strains using 2% carboxymethyl cellulose (CMC) and air dried in shade) and sown at a distance of 10 cm between plants and at 3 cm depth. Booster doses of *Streptomyces* strains were applied (at 10^7 CFU mL^{-1}) by the soil drenching method once in every 15 days up to the flowering stage. Control plots were applied only with water without any test *Streptomyces*.

All the agronomic practices including weeding and irrigation were carried out as and when required. At 40 DAS, plant height (cm $plant^{-1}$), leaf area (measured with a leaf area meter), shoot dry weight (g $plant^{-1}$), root volume and root length (with EPSON TWAIN Pro window in Adobe Photoshop and winRHIZO Pro software (Regent Instruments)) were recorded. The crop was harvested manually at physiological maturity and the growth and yield parameters such as plant height (cm $plant^{-1}$), shoot, root and panicle dry weight (g $plant^{-1}$) and grain yield (t ha^{-1}) were recorded. At harvest, 5–6 panicles with self-seed sets that shared above 80% of mature seeds in each plot were harvested and sun dried for 15 days.

Grain and stover nutrition analysis

After harvest of both greenhouse and field grown pearl millet, grain samples of every replication were made into ground samples. All the grain and stover samples were analysed for mineral nutrient densities of iron (Fe), zinc (Zn), calcium (Ca) and magnesium (Mg). Grain and stover samples of both greenhouse and field experiments were ground in a titanium-coated mill (SuperMill 1500, Newport Scientific Europe Ltd.). The samples were analysed in an Inductively Coupled Plasma-Mass Spectrometer (ICP-MS; Agilent 7500c, Agilent Technologies) for the elements Fe, Zn, Ca and Mg and expressed in ppm.

Statistical analysis

The data collected from two experiments (glasshouse and field) were subjected to statistical analysis through ANOVA (Genstat 20. ver.) to examine the efficiency of the selected three test *Streptomyces* strains on pearl millet growth and yield parameters along with biofortification efficiency. *Post hoc* analysis for significant differences between means was performed through Tukey's HSD test for multiple comparisons by setting the *P* value to 0.05 (Tukey 1977).

Results

Greenhouse experiment

In greenhouse conditions, both the pearl millet hybrids, PA-9444 and ICMH-1201, recorded significant increases in agronomic and yield traits in plants treated with each of the three test *Streptomyces* strains (CAI-24, KAI-27 and MMA-32) over the control. At 40 DAS, in PA-9444 and ICMH-1201 hybrids, all the three strains significantly enhanced the plant height (up to 8.8% and 11.9%, respectively), leaf area (up to 12.9% and 11.1%, respectively), shoot dry weight (up to 5.3% and 3.2%, respectively), root dry weight (up to 17.5% and 8.5%, respectively), root length (up to 11% and 6%, respectively) and root volume (up to 15.5% and 9.4%, respectively) over the control. At harvest, in PA-9444 and ICMH-1201 hybrids, all the three strains significantly enhanced the plant height (up to 5.3% and 4.3%, respectively), shoot dry weight (up to 13.2% and 9.8%, respectively), root dry weight (up to 33.4% and 31.4%, respectively), panicle weight (up to 16.7% and 9.1%, respectively) and grain yield (up to 22.8% and 13%, respectively) over the control (Tables 1 and 2). Among the three tested *Streptomyces* strains, KAI-27 and MMA-32 exhibited good PGP potential in both the pearl millet hybrids.

The harvested grains and the stover of the pearl millet hybrids were evaluated for their micronutrient contents. The hybrids, PA-9444 and ICMH-1201, treated with the selected strains enhanced the grain mineral contents of Fe (up to 49% and 40%, respectively), Zn (up to 13% and 10%, respectively), Ca (up to 2.4% and 29%, respectively) and Mg (up to 19% and 13%, respectively) over the control. The hybrids, PA-9444 and ICMH-1201, treated with the selected strains also enhanced the stover mineral contents of Fe (up to 62% and 54%, respectively), Zn (up to 10% and 15%, respectively), Ca (up to 17% and 11%, respectively) and Mg (up to 11% and 6%, respectively) over the control (Tables 3 and 4). Among the nutritional traits studied, only Fe was found to be significantly enhanced in both the hybrids by all the test strains, with PA-9444 being highest (49% in grain and 62% in stover). The highest Fe content was recorded in CAI-24 treatment, with a maximum of 258 and 237 ppm in grain and 256 and 253 ppm in stover in PA-9444 and ICMH-1201, respectively.

Field experiment

In field conditions, the pearl millet hybrids treated with the three test *Streptomyces* strains (CAI-24, KAI-27 and MMA-32) also significantly enhanced the PGP traits. At 40 DAS, in PA-9444 and ICMH-1201 hybrids, all the three strains significantly enhanced the plant height (up to 6% and

Table 1. Comparison of the three test *Streptomyces* strains on their PGP traits in two pearl millet hybrids (PA-9444 and ICMH-1201) under greenhouse conditions at 40 days after sowing.

Strains	Plant height (cm)		Leaf area (cm^{-2} plant^{-1})		Shoot weight (g plant^{-1})		Root weight (g plant^{-1})		Root length (cm^{-2} plant^{-1})		Root volume (plant^{-1})	
	9444	1201	9444	1201	9444	1201	9444	1201	9444	1201	9444	1201
CAI-24	143^{a}	155^{b}	1418^{a}	1524^{a}	10.54^{a}	10.98^{a}	5.06^{a}	5.84^{a}	11 779^{a}	14 180^{a}	32.7^{ab}	34.4^{a}
KAI-27	153^{a}	139^{ab}	1383^{a}	1690^{ab}	10.90^{a}	11.01^{a}	4.92^{a}	6.04^{a}	11 464^{a}	13 576^{a}	30.5^{a}	35.0^{a}
MMA-32	141^{a}	147^{ab}	1577^{ab}	1534^{a}	11.01^{a}	10.90^{a}	5.87^{a}	6.22^{a}	12 679^{a}	13 702^{a}	35.8^{b}	36.8^{a}
Control	139^{a}	136^{a}	1373^{a}	1503^{a}	10.43^{a}	10.66^{a}	4.84^{a}	5.69^{a}	11 298^{a}	13 331^{a}	30.2^{a}	33.3^{a}
Mean	144	144	1438	1563	10.72	10.89	5.17	5.94	11 805	13 697	32.3	34.9
s.e.+	5.8	3.7	42.8	52.6	0.44	0.35	0.23	0.14	309.4	585.6	0.90	1.98
s.d.	12.0	14.02	99.29	99.42	0.58	0.47	0.53	0.33	760.59	1291.0	2.66	4.11
CV%	7.0	4.4	5.2	5.8	7.2	5.6	7.8	4.3	4.5	7.4	4.9	9.8
THSD	28.01	19.0	14.37	14.39	2.32	1.84	1.212	0.75	110.07	186.80	4.70	10.28

Means having the same letter within a column do not differ significantly using Tukey's test at $P = 0.05$.
THSD, Tukey's honestly significant difference; s.e., standard error; CV, coefficients of variation; s.d., standard deviation.

Table 2. Comparison of the three test *Streptomyces* strains on their yield performance traits in two pearl millet hybrids (PA-9444 and ICMH-1201) under greenhouse conditions at harvest.

Strains	Plant height (cm)		Shoot weight (g plant^{-1})		Root weight (g plant^{-1})		Panicle weight (g plant^{-1})		Grain yield (g plant^{-1})	
	9444	1201	9444	1201	9444	1201	9444	1201	9444	1201
CAI-24	190^{a}	195^{a}	29.66^{ab}	34.96^{a}	7.20^{a}	8.27^{a}	29.78^{a}	51.10^{a}	22.47^{a}	22.93^{a}
KAI-27	196^{a}	196^{a}	29.87^{ab}	33.13^{a}	7.24^{a}	6.73^{a}	48.58^{a}	54.50^{a}	24.35^{a}	20.58^{a}
MMA-32	200^{a}	189^{a}	31.07^{b}	36.18^{a}	8.14^{a}	9.33^{a}	35.48^{a}	60.50^{a}	20.62^{a}	23.61^{a}
Control	189^{a}	188^{a}	26.96^{a}	32.65^{a}	5.42^{a}	6.40^{a}	40.38^{a}	55.00^{a}	18.80^{a}	20.54^{a}
Mean	194	192	29.39	34.23	7.00	7.68	38.58	55.30	21.56	21.92
s.e.+	5.7	7.3	0.62	1.41	1.34	0.96	4.20	3.15	2.92	1.82
s.d.	8.7	20.1	1.8	2.0	2.0	1.7	8.8	6.2	4.1	3.1
CV%	5.1	6.6	3.7	5.1	33.8	21.8	18.8	9.9	13.5	14.5
THSD	28.7	25.1	3.229	4.21	0.35	0.32	1.29	0.92	0.63	0.49

Means having the same letter within column do not differ significantly using Tukey's test at $P = 0.05$.
THSD, Tukey's honestly significant difference; s.e., standard error; CV, coefficients of variation; s.d., standard deviation.

Table 3. Effect of the three test *Streptomyces* strains on grain mineral contents (on dry weight basis) in two pearl millet hybrids (PA-9444 and ICMH-1201) under greenhouse conditions at harvest.

Strains	Fe (mg kg^{-1})		Zn (mg kg^{-1})		Ca (mg kg^{-1})		Mg (mg kg^{-1})	
	9444	1201	9444	1201	9444	1201	9444	1201
CAI-24	258^{a}	237^{ab}	30.7^{ab}	41.6^{b}	212^{a}	243^{ab}	1281a^{b}	1353^{a}
KAI-27	125^{a}	300^{b}	28.8^{a}	44.4^{ab}	190^{a}	309^{a}	1149^{a}	1503^{bc}
MMA-32	132^{a}	227^{ab}	33.7^{b}	41.0^{ab}	207^{a}	229^{ab}	1281^{ab}	1560^{c}
Control	132^{a}	180^{a}	29.5^{ab}	40.0^{a}	207^{a}	221^{a}	1371^{b}	1368^{ab}
Mean	162	236	30.7	41.8	204	250	1271	1446
s.e.+	27.4	21.2	0.88	0.75	6.51	17.1	36.7	28.5
s.d.	66.1	57.0	2.1	1.9	12.0	43.4	96.8	97.5
CV%	29.4	15.5	5.0	3.1	5.5	11.9	5.0	3.4
THSD	9.56	8.24	4.59	3.89	1.75	6.27	14.01	14.11

Means having the same letter within column do not differ significantly using Tukey's test at $P = 0.05$.
THSD, Tukey's honestly significant difference; s.e., standard error; CV, coefficients of variation; s.d., standard deviation.

Table 4. Effect of the three test *Streptomyces* strains on stover mineral contents (on dry weight basis) in two pearl millet hybrids (PA-9444 and ICMH-1201) under greenhouse conditions at harvest.

Strains	Fe (mg kg^{-1})		Zn (mg kg^{-1})		Ca (mg kg^{-1})		Mg (mg kg^{-1})	
	9444	1201	9444	1201	9444	1201	9444	1201
CAI-24	256^{b}	253^{b}	28.2^{b}	17.5^{a}	9667^{a}	8578^{b}	4102^{a}	4229^{ab}
KAI-27	118^{a}	151^{ab}	23.4^{a}	20.4^{a}	7716^{a}	7936^{ab}	3647^{a}	4108^{ab}
MMA-32	171^{ab}	154^{ab}	28.0^{b}	18.1^{ab}	8716^{a}	7765^{a}	3985^{a}	4301^{b}
Control	97^{a}	118^{a}	25.5^{ab}	17.4^{a}	8025^{a}	7673^{a}	3636^{a}	4032^{a}
Mean	161	169	26.3	18.3	8531	7988	3843	4168
s.e.+	25.8	31.3	0.72	0.57	655.5	153.6	105.5	45.0
s.d.	69.1	59.8	2.3	1.4	1358.9	437.3	254.8	153.3
CV%	27.9	22.7	4.8	5.5	13.3	3.3	4.8	1.9
THSD	10.00	8.65	3.78	3.0	196.60	63.28	36.87	22.18

Means having the same letter within column do not differ significantly using Tukey's test at $P = 0.05$;
THSD, Tukey's honestly significant difference; s.e., standard error; CV, coefficients of variation; s.d., standard deviation.

12%, respectively), leaf area (up to 19% and 17%, respectively), shoot dry weight (up to 21% and 19%, respectively) and root weight (up to 18% and 17%, respectively) over the control. At harvest, in PA-9444 and ICMH-1201 hybrids, all the three selected *Streptomyces* strains enhanced the plant height (up to 5% and 5%, respectively), panicle number (up to 4% and 6%, respectively), panicle weight (up to 9% and 14%, respectively), stover yield (up to 19% and 20%, respectively) and grain yield (up to 12% and 9%, respectively) over the control (Tables 5 and 6). As observed in the greenhouse conditions, here also KAI-27 and MMA-32 showed good PGP potential in both the pearl millet hybrids.

The harvested grains and the stover of the pearl millet hybrids treated with the three test *Streptomyces* strains also enhanced micronutrients (Fe, Zn, Ca and Mg). The hybrids, PA-9444 and ICMH-1201, treated with the selected strains enhanced the grain mineral contents of Fe (up to 37% and 14%, respectively), Zn (up to 16% and 5%, respectively), Ca (up to 25% and 45%, respectively) and Mg (up to 28% and 12%, respectively) and the stover mineral contents of Fe (up to 18% and 15%, respectively), Zn (up to 36% and 15%, respectively), Ca (up to 13% and 21%, respectively) and Mg (up to 16% and 29%, respectively) over the control (Tables 7 and 8). Among the three test strains, only CAI-24 significantly enhanced the Fe, Zn, Ca and Mg contents in both the grain and stover samples of both pearl millet hybrids. CAI-24 recorded the highest Fe contents, 90 and 108 ppm in grains and 165 and 164 ppm in stover, in PA-9444 and ICMH-1201, respectively.

Discussion

Streptomyces and their secondary metabolites are widely reported to have PGP and biocontrol abilities against many

Table 5. Comparison of the three test *Streptomyces* strains on their PGP traits in two pearl millet hybrids (PA-9444 and ICMH-1201) under field conditions at 40 days after sowing.

Strains	Plant height (cm)		Leaf area (cm^{-2} $plant^{-1}$)		Shoot weight (g $plant^{-1}$)		Root weight (g $plant^{-1}$)	
	9444	1201	9444	1201	9444	1201	9444	1201
CAI-24	164[a]	173[b]	1895[a]	1886[a]	38.56[a]	43.60[a]	6.79[a]	6.92[ab]
KAI-27	167[a]	184[c]	1865[a]	2242[b]	41.00[ab]	51.60[b]	7.62[b]	7.33[b]
MMA-32	168[a]	173[b]	2248[b]	1990[a]	47.49[b]	42.52[a]	7.87[b]	6.47[ab]
Control	157[a]	162[a]	1832[a]	1856[a]	37.61[a]	41.54[a]	6.44[a]	6.10[a]
Mean	164	173	1960	1994	41.16	44.81	7.18	6.71
s.e.+	3.9	1.34	54.5	27.0	1.11	0.82	0.09	0.15
s.d.	5.5	7.9	171.3	153.5	4.0	4.1	0.6	0.5
CV%	3.4	1.1	2.8	1.9	3.8	2.6	2.0	3.3
THSD	23.25	7.94	38.80	34.80	6.57	4.85	0.58	0.93

Means having the same letter within column do not differ significantly using Tukey's test at $P = 0.05$.
THSD, Tukey's honestly significant difference; s.e., standard error; CV, coefficients of variation; s.d., standard deviation.

Table 6. Comparison of the three test *Streptomyces* strains on their yield performance traits in two pearl millet hybrids (PA-9444 and ICMH-1201) under field conditions at harvest.

Strains	Plant height (cm)		Panicle number (m^{-2})		Panicle weight (t ha^{-1})		Stover yield (t ha^{-1})		Grain yield (t ha^{-1})	
	9444	1201	9444	1201	9444	1201	9444	1201	9444	1201
CAI-24	177[b]	184[ab]	23.5[b]	15.5[a]	5.43[a]	4.77[b]	5.17[b]	3.70[a]	3.96[b]	3.51[ab]
KAI-27	177[b]	187[b]	22.0[a]	14.5[a]	5.52[a]	5.06[b]	4.92[b]	4.44[b]	4.01[b]	3.70[b]
MMA-32	177[b]	184[ab]	23.5[b]	15.5[a]	5.37[a]	4.71[ab]	4.98[b]	4.02[ab]	4.03[b]	3.61[ab]
Control	169[a]	178[a]	22.5[ab]	14.5[a]	5.00[a]	4.33[a]	4.20[a]	3.55[a]	3.54[a]	3.38[a]
Mean	175	183	22.9	15.0	5.33	4.72	4.81	3.92	3.88	3.55
s.e.+	0.96	0.90	0.20	0.40	0.082	0.058	0.068	0.084	0.053	0.036
s.d.	3.41	3.30	0.78	0.71	0.22	0.27	0.38	0.35	0.21	0.14
CV%	1.0	0.9	1.5	4.7	2.7	2.1	2.5	3.7	2.4	1.8
THSD	6.01	5.64	1.27	2.54	0.51	0.36	0.42	0.52	0.33	0.22

Means having the same letter within column do not differ significantly using Tukey's test at $P = 0.05$.
THSD, Tukey's honestly significant difference; s.e., = standard error; CV, coefficients of variation; s.d., standard deviation.

insect pests and pathogens of agriculturally important crop plants (Khamna *et al.* 2010; Gopalakrishnan *et al.* 2020*a*, 2021; Ankati *et al.* 2021). However, the biofortification capabilities of *Streptomyces* in food crops are negligible and still need to be explored. Thus, in the present study, *S. albus* strains (CAI-24 and KAI-27) and *S. griseus* strain (MMA-32) were evaluated for their plant growth-promotion traits in pearl millet. All the *Streptomyces* strains (CAI-24, KAI-27 and MMA-32) significantly influenced the pearl millet growth characteristics in greenhouse and field conditions in relation to plant height (5–12%), leaf area (17–19%), shoot dry weight (19–21%), root dry weight (17–18%), root length (6–11%), root volume (9–15%), panicle weight (9–14%) and grain yield (9–12%) compared to the control plants. Superior root length is always more advantageous to plant growth, assisting with higher absorption of water, nutrients and vitamins from the deeper zones of the soil. This was already reported for various PGP bacteria including *Streptomyces*. The selected test strains previously demonstrated similar trait enhancement in rice, sorghum, pigeonpea and chickpea (Gopalakrishnan *et al.* 2012, 2013*a*, 2013*b*, 2015*a*, 2015*b*, 2015*c*, 2016*b*). Microbiomes do this by producing growth-promoting hormones such as IAA and adjusting the root morphology for nutrient and water absorption, thereby promoting root cell differentiation and root elongation (Sousa *et al.* 2008; Khamna *et al.* 2009). Likewise, in this study, pearl millet root length was significantly increased by *Streptomyces* treatments, up to a maximum of 11% in the hybrids PA-9444 by MMA-32. PA-9444 is widely adapted dual-purpose

Table 7. Effect of the three test *Streptomyces* strains on grain mineral contents (on dry weight basis) in two pearl millet hybrids (PA-9444 and ICMH-1201) under field conditions at harvest.

Strains	Fe (mg kg^{-1})		Zn (mg kg^{-1})		Ca (mg kg^{-1})		Mg (mg kg^{-1})	
	9444	1201	9444	1201	9444	1201	9444	1201
CAI-24	90^{a}	108^{a}	35.9^{a}	36.8^{a}	153^{a}	190^{a}	1876^{b}	1486^{a}
KAI-27	61^{a}	100^{a}	31.2^{a}	37.1^{a}	166^{a}	115^{a}	1416^{a}	1313^{a}
MMA-32	58^{a}	89^{a}	32.0^{a}	35.7^{a}	151^{a}	132^{a}	1474^{a}	1369^{a}
Control	56^{a}	93^{a}	30.0^{a}	35.3^{a}	125^{a}	106^{a}	1355^{a}	1309^{a}
Mean	66	97	32.3	36.2	149	136	1530	1369
s.e.+	8.63	6.48	3.65	1.77	13.93	41.5	85.2	50.0
s.d.	18.6	9.8	4.4	1.9	22.6	50.3	226.8	84.3
CV%	18.4	9.4	16.0	6.9	13.3	43.3	7.9	5.2
THSD	4.22	2.23	1.04	0.51	51.20	11.40	51.45	19.12

Means having the same letter within column do not differ significantly using Tukey's test at $P = 0.05$.
THSD = Tukey's honestly significant difference; s.e., = standard error; CV, coefficients of variation; s.d., standard deviation.

Table 8. Effect of the three test *Streptomyces* strains on stover mineral contents (on dry weight basis) in two pearl millet hybrids (PA-9444 and ICMH-1201) under field conditions at harvest.

Strains	Fe (mg kg^{-1})		Zn (mg kg^{-1})		Ca (mg kg^{-1})		Mg (mg kg^{-1})	
	9444	1201	9444	1201	9444	1201	9444	1201
CAI-24	165^{a}	164^{a}	17.8^{a}	14.5^{a}	5392^{b}	6112^{a}	3742^{a}	3949^{a}
KAI-27	135^{a}	151^{a}	22.7^{a}	11.3^{a}	5027^{b}	4794^{a}	3250^{a}	3101^{a}
MMA-32	153^{a}	143^{a}	21.9^{a}	12.0^{a}	5143^{b}	5173^{a}	3132^{a}	3430^{a}
Control	134^{a}	140^{a}	14.6^{a}	10.7^{a}	4704^{a}	4816^{a}	3146^{a}	2800^{a}
Mean	147	149	19.2	12.1	5067	5224	3318	3320
s.e.+	10.58	27.5	2.51	1.91	350.3	533.6	199.7	403.9
s.d.	16.1	37.1	4.5	2.3	396.0	706.6	365.5	580.7
CV%	10.2	26.2	18.4	22.4	9.8	14.4	8.5	17.2
THSD	3.66	8.41	1.05	0.59	89.81	160.26	82.90	131.71

Means having the same letter within column do not differ significantly using Tukey's test at $P = 0.05$.
THSD, Tukey's honestly significant difference; s.e., standard error; CV, coefficients of variation; s.d., standard deviation.

hybrid, can withstand heat and moisture stress and is known for its drought tolerance compared to ICMH-1201, hence, root traits are highly responsive in PA-9444 (Yadav and Rai 2013). Perhaps, this could be one of the reasons for the enhanced yield and shoot and root biomass observed in the *Streptomyces* treated plants, in contrast to the control. This is possible through mechanisms related to PGP bacteria including secretion of PGP hormones such as IAA, chelation of iron by producing siderophores, phosphorus solubilising acids and enzymes and antagonistic metabolites towards phytopathogens (Panhwar *et al.* 2012; Sreevidya *et al.* 2016). The selected *Streptomyces* strains (CAI-24, KAI-27 and MMA-32) were earlier reported to produce hydrolytic hormones and enzymes such as IAA, siderophores, lipase, cellulase, protease, β-1,3-glucanase, chitinase and hydrocyanic acid (Gopalakrishnan *et al.* 2011*a*, 2011*b*). Hence, one of these mechanisms could be the reason for the selected *Streptomyces* strain's growth promotion abilities in pearl millet.

Besides producing siderophores and solubilising phosphate, *Streptomyces* are acknowledged for secreting enzymes including amylase, chitinase, cellulase, invertase, lipase, keratinase, peroxidase, pectinase, protease, phytase and xylanase, which supports the conversion of complex soil nutrients into accessible mineral forms (Jog *et al.* 2016). However, their impact on grain and fodder nutrient profiles of crops is less known on different crops. Therefore, we looked for the micronutrient (Fe, Zn, Ca and Mg) levels in pearl millet grain and stover that are the two most useful plant parts for food and fodder. In the present study, all the three tested *Streptomyces* strains enriched micronutrients irrespective of hybrids studied (low Fe PA-9444 and high Fe ICMH-1201) in both greenhouse and field conditions in comparison with the control. However, the extent of nutrient concentration change varied with respect to the hybrids used and *Streptomyces* strain applied. Among the three tested strains, *Streptomyces* strain CAI-24 significantly enhanced Fe contents in both the grain and stover in both the hybrids over the control, in both the greenhouse as well as field trials. Among the four nutritional traits studied, more Fe was found in the grains of hybrid ICMH-1201 (20–63% higher) compared to PA-9444. Further, stover samples contained more Fe (150–200%) compared to grain samples. Thus, the selected *Streptomyces* stains, CAI-24, KAI-27 and MMA-32, complement the Fe contents (up to 49%) of the ICMH-1201, which is already a high Fe containing hybrid. Up to 150–200% more Zn was found in grain samples compared to stover samples of both the hybrids. Ca was found at concentrations of up to 40–50 times higher in stover samples over grain samples while Mg was also found at concentrations of up to 2–2.5 times higher in stover samples over grain samples of both the hybrids. This increase in mineral densities of grains and stover of *Streptomyces* treated plants, would be due to their mineral mobilising potentials *via* secretion of siderophores, which was earlier confirmed through our *in vitro* biochemical and gene level studies (Sathya *et al.* 2016). In the current study, although all the tested strains enhanced micronutrient contents in both grain and stover, there are variations in the specific micronutrient enriched and growth parameter enhanced. This might be due to the habituation potentials of the applied strains with the already existing microflora in the rhizosphere; its capability to ease the soil bound minerals and their expression levels.

The current study revealed that stover samples of pearl millet contained more Fe (150–200%) compared to grain samples. Recent research on microbial biofortification demonstrated that many bacteria including *Streptomyces* spp. enhanced plant growth along with micronutrient concentrations in various crops. *Bacillus pichinotyi* reported increased Fe levels by 70% in kernels and 147% in stems over the un-inoculated wheat plants (Yasin *et al.* 2015). An enhancement of wheat Fe levels by 67% and 47% was reported in low and high Fe accumulating wheat genotypes, respectively, by *Arthrobacter sulfonivorans* DS-68 and *Enterococcus hirae* DS-163 (Singh *et al.* 2018). Microbial biofortification capabilities with *Providencia* sp. and its various combinations was reported to enhance the Fe, Zn, Cu, and Mn concentrations ranging from 13 to 16% in rice (Rana *et al.* 2015). Seven bacterial strains, namely, *Pseudomonas plecoglossicida* SRI-156, *Brevibacterium antiquum* SRI-158, *Bacillus altitudinis*, SRI-178, *Enterobacter ludwigii* SRI-211, *E. ludwigii* SRI-229, *Acinetobacter tandoii* SRI-305 and *Pseudomonas monteilii* SRI-360 significantly enhanced the mineral density in the grains of chickpea and pigeonpea (Gopalakrishnan *et al.* 2016*a*). *Streptomyces* strains were also reported to enhance micronutrition contents including Fe (10–38%), Zn (13–30%), Ca (14–26%), Cu (11–54%), Mn (18–35%) and Mg (14–21%) in the harvested grains of chickpea (Sathya *et al.* 2016). The higher level of Fe in some cases might be due to possible unavoidable contamination during sampling (grain and stover), however, the level of Fe in these two hybrids are well studied and reported (Govindaraj *et al.* 2019, 2020). In contrast, other nutrients are not influenced by dust contamination. Hence, it is good to monitor sample contamination using index elements such as aluminium and titanium, which are largely present in dust/atmosphere.

It is concluded that the tested *Streptomyces* strains improved PGP traits and enhanced yield of the selected hybrids of pearl millet under both greenhouse and field conditions. Of the three *Streptomyces* strains studied in the current investigation, KAI-27 and MMA-32 were found superior to CAI-24 in terms of their effects on root and shoot development and crop productivity whereas CAI-24 was found superior in nutritional traits, especially on Fe, over KAI-27 and MMA-32 under both greenhouse and field conditions. Hence, application of all the three strains of *Streptomyces* as consortia will help to enhance the pearl millet crop yield and its nutritional contents. Further, this was the first study that suggests the use of *Streptomyces* inoculum as a complimentary tool for supporting existing biofortification strategies in order to enrich the essential nutrients of popular low mineral density cultivars. The results of this study merit further investigation on the genotype (G) × strain (S) interactions with the environment ($G \times S \times E$) for large-scale applications. Further experimental evidence is required to determine the mechanisms behind the mineral transfer from soil to seed and the effectiveness of these *Streptomyces* strains under different field conditions.

References

Ankati S, Srinivas V, Pratyusha S, Gopalakrishnan S (2021) *Streptomyces* consortia-mediated plant defense against *Fusarium* wilt and plant growth-promotion in chickpea. *Microbial Pathogenesis* **157**, 104961. doi:10.1016/j.micpath.2021.104961

Directorate of Millets Development (2020) 'Department of Agriculture, Co-operation & Farmers' Welfare Ministry of Agriculture and Farmers' Welfare, Government of India'. (Directorate of Millets Development)

Gopalakrishnan S, Pande S, Sharma M, Humayun P, Kiran BK, Sandeep D, Vidya MS, Deepthi K, Rupela O (2011*a*) Evaluation of actinomycete isolates obtained from herbal vermicompost for biological control of *Fusarium* wilt of chickpea. *Crop Protection* **30**, 1070–1078. doi:10.1016/j.cropro.2011.03.006

Gopalakrishnan S, Kiran BK, Humayun P, Vidya MS, Deepthi K, Jacob S, Vadlamudi S, Alekhya G, Rupela O (2011*b*) Biocontrol of charcoal-rot of sorghum by actinomycetes isolated from herbal vermicompost. *African Journal of Biotechnology* **10**, 18142–18152. doi:10.5897/AJB11.2710

Gopalakrishnan S, Humayun P, Vadlamudi S, Vijayabharathi R, Bhimineni RK, Rupela O (2012) Plant growth-promoting traits of *Streptomyces* with biocontrol potential isolated from herbal vermicompost. *Biocontrol Science and Technology* **22**, 1199–1210. doi:10.1080/09583157.2012.719151

Gopalakrishnan S, Srinivas V, Vidya MS, Rathore A (2013*a*) Plant growth-promoting activities of *Streptomyces* spp. in sorghum and rice. *SpringerPlus* **2**, 574. doi:10.1186/2193-1801-2-574

Gopalakrishnan S, Vadlamudi S, Apparla S, Bandikinda P, Vijayabharathi R, Bhimineni RK, Rupela O (2013*b*) Evaluation of *Streptomyces* spp. for their plant growth-promoting traits in rice. *Canadian Journal of Microbiology* **59**, 534–539. doi:10.1139/cjm-2013-0287

Gopalakrishnan S, Srinivas V, Alekhya G, Prakash B, Kudapa H, Rathore A, Varshney RK (2015*a*) The extent of grain yield and plant growth enhancement by plant growth-promoting broad-spectrum *Streptomyces* sp. in chickpea. *SpringerPlus* **4**(31), 31. doi:10.1186/s40064-015-0811-3

Gopalakrishnan S, Vadlamudi S, Alekhya G, Prakash B, Kudapa H, Varshney RK (2015*b*) Evaluation of broad-spectrum *Streptomyces* sp. for plant growth promotion traits in chickpea (*Cicer arietinum* L.). *The Philippine Agricultural Scientist* **98**, 270–278.

Gopalakrishnan S, Srinivas V, Alekhya G, Prakash B, Kudapa H, Varshney RK (2015*c*) Evaluation of *Streptomyces* sp. obtained from herbal vermicompost for broad spectrum of plant growth-promoting activities in chickpea. *Organic Agriculture* **5**, 123–133. doi:10.1007/s13165-015-0099-1

Gopalakrishnan S, Vadlamudi S, Samineni S, Sameer Kumar CV (2016*a*) Plant growth-promotion and biofortification of chickpea and pigeonpea through inoculation of biocontrol potential bacteria, isolated from organic soils. *SpringerPlus* **5**, 1882. doi:10.1186/s40064-016-3590-6

Gopalakrishnan S, Srinivas V, Sameer Kumar CV (2016*b*) Plant growth-promotion traits of *Streptomyces* sp. in pigeonpea. *Legume Perspectives* **11**, 43–44. Available at http://ils.nsseme.com/assets/LegumPerspect11.pdf

Gopalakrishnan S, Sharma R, Srinivas V, Naresh N, Mishra SP, Ankati S, Pratyusha S, Govindaraj M, Gonzalez SV, Nervik S, Simic N (2020*a*) Identification and characterization of a *Streptomyces albus* strain and its secondary metabolite organophosphate against charcoal rot of sorghum. *Plants* **9**, 1727. doi:10.3390/plants9121727

Gopalakrishnan S, Srinivas V, Prasanna SL (2020*b*) *Streptomyces*. In 'Beneficial microbes in agro-ecology: bacteria and fungi'. (Eds N Amaresan, K Annapurna, A Sankaranarayanan, M Senthil Kumar, K Kumar) pp. 55–71. (Academic Press Inc.) doi:10.1016/B978-0-12-823414-3.00005-8

Gopalakrishnan S, Srinivas V, Naresh N, Pratyusha S, Ankati S, Madhuprakash J, Govindaraj M, Sharma R (2021) Deciphering the antagonistic effect of *Streptomyces* spp. and host-plant resistance induction against charcoal rot of sorghum. *Planta* **253**, 57. doi:10.1007/s00425-021-03577-5

Govindaraj M, Rai KN, Cherian B, Pfeiffer WH, Kanatti A, Shivade H (2019) Breeding biofortified pearl millet varieties and hybrids to enhance millet markets for human nutrition. *Agriculture* **9**(5), 106. doi:10.3390/agriculture9050106

Govindaraj M, Yadav OP, Rajpurohit BS, Kanatti A, Rai KN, Dwivedi SL (2020) Genetic variability, diversity and interrelationship for twelve grain minerals in 122 commercial pearl millet cultivars in India. *Agricultural Research* **9** (4), 516–525. doi:10.1007/s40003-020-00470-7

Hamdali H, Bouizgarne B, Hafidi M, Lebrihi A, Virolle MJ, Ouhdouch Y (2008) Screening for rock phosphate solubilizing actinomycetes from moroccan phosphate mines. *Applied Soil Ecology* **38**, 12–19. doi:10.1016/j.apsoil.2007.08.007

Jog R, Pandya M, Nareshkumar G, Rajkumar S (2014) Mechanism of phosphate solubilization and antifungal activity of *Streptomyces* spp. isolated from wheat roots and rhizosphere and their application in improving plant growth. *Microbiology* **160**, 778–788. doi:10.1099/mic.0.074146-0

Jog R, Nareshkumar G, Rajkumar S (2016) Enhancing soil health and plant growth promotion by actinomycetes. In 'Plant growth promoting actinobacteria'. (Eds S Gopalakrishnan, A Sathya, R Vijayabharathi) pp. 33–45. (Springer: Singapore) doi:10.1007/978-981-10-0707-1_3

Kaur T, Rana KL, Kour D, Sheikha I, Yadav N, Kumar V, Yadav AN, Dhaliwal HS, Saxena AK (2020) Microbe-mediated biofortification for micronutrients: present status and future challenges. In 'New and future developments in microbial biotechnology and bioengineering'. (Eds AA Rastegari, AN Yadav, N Yadav) pp. 1–17. (Elsevier Inc.) doi:10.1016/B978-0-12-820528-0.00002-8

Khamna S, Yokota A, Lumyoung S (2009) Actinomycetes isolated from medicinal plant rhizosphere soils: diversity and screening of antifungal compounds, indole-3-acetic acid and siderophore production. *World Journal of Microbiology and Biotechnology* **25**, 649–655. doi:10.1007/s11274-008-9933-x

Khamna S, Yokota A, Peberdy JF, Lumyong S (2010) Indole-3-acetic acid production by *Streptomyces* sp. isolated from some Thai medicinal plant rhizosphere soils. *EurAsian Journal of BioSciences* **4**, 23–32. doi:10.5053/ejobios.2010.4.0.4

Kumar A, Choudhary AK, Pooniya V, Suri VK, Singh U (2016) Soil factors associated with micronutrient acquisition in crops-biofortification perspective. In 'Biofortification of food crops'. (Eds U Singh, CS Praharaj, SS Singh, NP Singh) pp. 159–176. (Springer India) doi:10.1007/978-81-322-2716-8_13

Nosheen S, Ajmal I, Song Y (2021) Microbes as biofertilizers, a potential approach for sustainable crop production. *Sustainability* **13**, 1868. doi:10.3390/su13041868

Panhwar QA, Othman R, Rahman ZA, Meon S, Ismail MR (2012) Isolation and characterization of phosphate-solubilizing bacteria from aerobic rice. *African Journal of Biotechnology* **11**, 2711–2719. doi:10.5897/AJB10.2218

Prasanna R, Nain L, Rana A, Shivay YS (2016) Biofortification with microorganisms: present status and future challenges. In 'Biofortification of food crops'. (Eds U Singh, CS Praharaj, SS Singh, NP Singh) pp. 249–262. doi:10.1007/978-81-322-2716-8_19

Rana A, Kabi SR, Verma S, Adak A, Pal M, Shivay YS, Prasanna R, Nain L (2015) Prospecting plant growth promoting bacteria and cyanobacteria as options for enrichment of macro and micronutrients in grains in rice–wheat cropping sequence. *Cogent Food & Agriculture* **1**, 1037379. doi:10.1080/23311932.2015.1037379

Sadeghi A, Karimi E, Dahaji PA, Javid MG, Dalvand Y, Askari H (2012) Plant growth promoting activity of an auxin and siderophore producing isolate of Streptomyces under saline soil conditions. *World Journal of Microbiology and Biotechnology* **28**, 1503–1509. doi:10.1007/s11274-011-0952-7

Saleem M, Law AD, Moe LA (2016) Nicotiana roots recruit rare rhizosphere taxa as major root-inhabiting microbes. *Microbial Ecology* **71**, 469–472. doi:10.1007/s00248-015-0672-x

Sathya A, Vijayabharathi R, Srinivas V, Gopalakrishnan S (2016) Plant growth-promoting actinobacteria on chickpea seed mineral density: an upcoming complementary tool for sustainable biofortification strategy. *3 Biotech* **6**, 138. doi:10.1007/s13205-016-0458-y

Singh D, Geat N, Rajawat MVS, Prasanna R, Kar A, Singh AM, Saxena AK (2018) Prospecting endophytes from different Fe or Zn accumulating wheat genotypes for their influence as inoculants on plant growth, yield, and micronutrient content. *Annals of Microbiology* **68** (12), 815–833. doi:10.1007/s13213-018-1388-1

Sousa CS, Soares ACF, Garrido MS (2008) Characterization of Streptomyces with potential to promote plant growth and biocontrol. *Scientia Agricola* **65**, 50–55. doi:10.1590/S0103-90162008000100007

Sreevidya M, Gopalakrishnan S, Kudapa H, Varshney RK (2016) Exploring plant growth-promotion actinomycetes from vermicompost and rhizosphere soil for yield enhancement in chickpea. *Brazilian Journal of Microbiology* **47**, 85–95. doi:10.1016/j.bjm.2015.11.030

Subramaniam G, Thakur V, Saxena RK, Vadlamudi S, Purohit S, Kumar V, Rathore A, Chitikineni A, Varshney RK (2020) Complete genome sequence of sixteen plant growth promoting Streptomyces strains. *Scientific Reports* **10**, 10294. doi:10.1038/s41598-020-67153-9

Tukey JW (1977) 'Exploratory data analysis', (Addison-Weeley Publishing Company: Reading, MA, CA)

Vijayabharathi R, Gopalakrishnan S, Sathya A, Srinivas V, Sharma M (2018) Deciphering the tri-dimensional effect of endophytic *Streptomyces* sp. on chickpea for plant growth promotion, helper effect with Mesorhizobium ciceri and host-plant resistance induction against *Botrytis cinerea*. *Microbial Pathogenesis* **122**, 98–107. doi:10.1016/j.micpath.2018.06.019

Wakeel A, Farooq M, Bashir K, Ozturk L (2018) Micronutrient malnutrition and biofortification: recent advances and future perspectives. In 'Plant micronutrient use efficiency'. (Eds MA Hossain, T Kamiya, DJ Burritt, L-SP Tran, T Fujiwara) pp. 225–243. (Academic Press: London, UK) doi:10.1016/B978-0-12-812104-7.00017-4

WHO (2020) Children: reducing mortality. Available at https://www.who.int/en/news-room/fact-sheets/detail/children-reducing-mortality. [Accessed 8 September 2020]

Yadav OP, Rai KN (2013) Genetic improvement of pearl millet in India. *Agricultural Research* **2**, 275–292. doi:10.1007/s40003-013-0089-z

Yadav AN, Rastegari AA, Yadav N, Kour D (Eds) (2020*a*) 'Advances in plant microbiome and sustainable agriculture: functional annotation and future challenges'. Vol. 2. (Springer: Singapore) doi:10.1007/978-981-15-3204-7

Yadav AN, Singh J, Rastegari AA, Yadav N (Eds) (2020*b*) 'Plant microbiomes for sustainable agriculture', (Springer International Publishing: Cham, Switzerland)

Yasin M, El-Mehdawi AF, Anwar A, Pilon-Smits EAH, Faisal M (2015) Microbial enhanced selenium and iron biofortification of wheat (*Triticum aestivum* L.) - applications in phytoremediation and biofortification. *International Journal of Phytoremediation* **17**, 341–347. doi:10.1080/15226514.2014.922920

Data availability. The data that support this study will be shared upon reasonable request to the corresponding author.

Conflicts of interest. The authors declare no conflicts of interest.

Declaration of funding. This work has been undertaken as part of the CGIAR Research Program on Grain Legumes and Dry Land Cereals and HarvestPlus program of the CGIAR.

Acknowledgements. We thank PVS Prasad for his significant contribution in the laboratory, greenhouse and field studies.

Author affiliation

[A]International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502324, Telangana, India.