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Environmental Technology & Innovation

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Plant growth promoting bacteria improve growth and phytostabilization potential of *Zea mays* under chromium and drought stress by altering photosynthetic and antioxidant responses

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ARTICLE INFO

Article history:

Received 30 September 2021

Received in revised form 10 November 2021

Accepted 19 November 2021

Available online 3 December 2021

Keywords:

Chromium

Drought

Plant growth promoting bacteria

Bio-inoculant

Photosynthesis

Phytostabilization

ABSTRACT

Drought in heavy metal polluted arid and semiarid regions severely inhibits the plant growth and phytoremediation potential by affecting photosynthesis, antioxidant defense mechanism, and other biochemical processes. In the present study, we explored the role of plant growth-promoting bacteria (PGPB) on *Zea mays* growth and phytoremediation efficiency in Chromium (Cr) contaminated soils under drought stress by assessing plant stress tolerance, photosynthetic gas exchange activities, chlorophyll fluorescence, and Cr accumulation. Two efficient Cr and drought resistant PGPB with the potential to reduce Cr(VI) to Cr(III) and produce plant growth-promoting metabolites even under Cr, drought, or Cr+drought stress conditions were isolated and identified as *Providencia* sp. (TCR05) and *Proteus mirabilis* (TCR20). In pot experiments, the inoculation of TCR05 and TCR20 increased the plant growth, pigments, protein, phenolics, and relative water content and decreased the lipid peroxidation, proline, and superoxide dismutase activity under Cr, drought, or Cr+drought conditions. Irrespective of stress treatment, TCR05 and TCR20 also improved plant photosynthetic efficiency by increasing the CO₂ assimilation rate, stomatal conductance to water vapor, transpiration rate, maximum quantum efficiency of PSII, actual quantum efficiency of PSII, electron transport rate, photochemical quenching, reducing the internal CO₂ concentration and non-photochemical quenching. Besides, the PGPB decreased the translocation of Cr through immobilization of Cr in root. These results denoted that strains TCR05 and TCR20 could be a capable bio-inoculant for improving plant growth and phytostabilization practices in Cr contaminated sites even under water-limited conditions.

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1. Introduction

Phytoremediation is an eco-friendly and cost effective technology which involves the use of plants and their associated microbes to extract, immobilize or detoxify heavy metals from soil. Although some plants have shown the potential to tolerate and accumulate high concentrations of heavy metals, drought in heavy metal polluted arid and semi-arid regions causes severe damages to plants which limits the plant growth, establishment and phytoremediation efficiency by altering series of physiological, biochemical, and molecular processes (Liu et al., 2019; Silambarasan et al., 2019a). Indeed, drought and/or metal stress reduce the photosynthetic efficiency of the plants by affecting the pigment concentration, ultra-structures of photosystems, electron transport systems, and gas exchange mechanism (Wu et al., 2020; Xu et al., 2020). The restriction in stomatal regulation (stomatal closure and conductance) due to drought or metal stress reduces the CO₂ availability to chloroplasts, eventually inhibits photosynthetic rate and increase the vulnerability of photosystem (PS I and PS II) (Brilli et al., 2019; Murata et al., 2012; Win et al., 2018). Further, drought or metal stress drastically affects the energy conversion rate by hampering the efficacy of photosynthetic electron transport that leads to photoinhibition (Wu et al., 2020; Xu et al., 2020). In addition, drought and metal stress affect the antioxidant defense mechanism and induce oxidative damages in plants by producing reactive oxygen species (ROS) that cause damages to lipids, membrane permeability, and nucleic acids (Rajkumar et al., 2017; Sarker and Oba, 2018). Therefore, an efficient strategy is currently required in order to improve the plant health and establishment for efficient phytoremediation in drought-prone arid and semi-arid regions. In this context, an emerging and preferred approach to combat multiple stresses (heavy metal and drought) and to promote the plant growth, tolerance and phytoremediation is utilization of multiple stress-tolerant plant growth-promoting bacteria (MST-PGPB) (Rajkumar et al., 2013; Silambarasan et al., 2019a). Such MST-PGPB improve plant health and photosynthetic efficiency by regulating the stomatal conductance, gas exchange, electron transport, water use efficiency, and maintaining the integrity of the photosystem through producing several plant growth-promoting (PGP) molecules including indole-3-acetic acid (IAA), 1-aminocyclopropane-1-carboxylate deaminase (ACCD), and siderophores (Ouledali et al., 2019; Win et al., 2018). Besides, these MST-PGPB reduce the stress-mediated effect through activating antioxidant enzymes including superoxide dismutase (SOD), catalase (CAT), and phenolic compound which detoxifies the stress-induced ROS production in plants (Gupta et al., 2018).

Recent studies have reported that the inoculation of PGPB could enhance the growth, photosynthetic efficiency, stress tolerance, and phytoremediation ability of the plants in metal contaminated soils (de-Lima et al., 2019; Liu et al., 2019; Wu et al., 2020). However, so far no study has been focused on how MST-PGPB influence the plant growth, gas exchange, chlorophyll (chl) fluorescence, and phytoremediation efficiency in chromium (Cr) contaminated soils under drought stress condition. Thus, the specific objective of the study was: (i) to isolate, identify and characterize MST-PGPB, (ii) to assess the MST-PGPB interaction on harnessing plant growth, biochemical parameters (chl, proline, lipid peroxidation, phenolics, and antioxidants), (iii) to assess the role of MST-PGPB in improving photosynthetic gas exchange activities, chl fluorescence, and phytoremediation ability of plant, in presence and absence of Cr, drought, or Cr+drought stress conditions. To assess the above objectives, we have used *Zea mays* (maize) as a model plant due to its rapid growth and high susceptibility to drought (de-Lima et al., 2019) and heavy metal (Aliu et al., 2013) stress.

2. Materials and methods

2.1. Bacterial strains

MST-PGPB strains TCR05 and TCR20 were isolated from rhizosphere of *Z. mays* grown in Cr contaminated soils (26.24 ± 3.6 mg kg⁻¹) at Tiruchirappalli, India and identified as *Providencia* sp. (accession number No. MH718832.1) and *Proteus mirabilis* (accession number No. MH718824.1), respectively (Ma et al., 2013). MST-PGPB strains showed high resistance to Cr (up to 250 mg L⁻¹) and drought stress (up to 15% w/v PEG-6000) as well as the potential to reduce Cr(VI) to Cr(III). Moreover, both strains were able to produce IAA and siderophores under Cr, drought or Cr+drought stress condition, while synthesise of ACCD was detected only in TCR20 (Table 1).

2.2. Effects of inoculation of MST-PGPB on *Z. mays* growth and biochemical parameters under Cr and drought stress

2.2.1. Plant growth experiment

A greenhouse trail was performed to assess the effect of MST-PGPB inoculation on *Z. mays* growth, biochemical and gaseous parameters under Cr and drought stress. The soil used in this study was comprised with total organic matter 1.8%, potassium 180 mg kg⁻¹, Cr 2.43 mg kg⁻¹, pH 7.2, electrical conductivity 220 mS m⁻¹. The soil was sterilized (autoclaved at 121 °C; 30 min; five consecutive days) and artificially contaminated with an aqueous solution of sterile K₂Cr₂O₇ to attain a final concentration of 50 mg kg⁻¹ of Cr. The experiment was conducted under different conditions (Control, Cr, drought, and Cr+drought) with three bacterial treatments (uninoculated, TCR05, and TCR20). Uniform sized disease free seeds of *Z. mays* were surface sterilized with 70% ethanol (2 min), 2% sodium hypochlorite (2 min), washed with sterile distilled water (3–4 times) and subjected for green house trail (Silambarasan et al., 2019b). For bacterial inoculation, disinfected seeds were soaked in TCR05 and TCR20 suspension (cfu 10⁶) for 2 h whereas, seeds soaked in sterile distilled water were considered as uninoculated treatment. The bacterial treated and untreated seeds were seeded in pots and maintained in a growth chamber at 36/24 ± 1 °C (day/night) with 16 h photoperiod. Initially, the pots were watered regularly and soil moisture was maintained at 100% of field capacity. For drought stress treatment, the plants (15 d after emergence) were subjected to grow under water limited condition by maintaining the soil moisture at 50% of field capacity.

Table 1
Cr reduction and PGP traits of MST-PGPB under different stress conditions.

Bacterial strains	Treatments	Cr reduction (%)	IAA production ($\mu\text{g mL}^{-1}$)	Siderophores			ACCD ($\mu\text{M } \alpha\text{-KB mg}^{-1} \text{ protein h}^{-1}$)
				Units (%)	Catechol type	Hydroxamate type	
TCR05	Control	ND	$29.68 \pm 0.26^{\text{b}}$	$63.78 \pm 2.65^{\text{a}}$	+	+	–
	Cr	97.12 ± 1.38	$16.76 \pm 0.39^{\text{d}}$	$43.69 \pm 3.41^{\text{c}}$	+	+	–
	Drought	ND	$23.16 \pm 1.93^{\text{c}}$	$53.58 \pm 2.71^{\text{b}}$	+	+	–
	Cr+drought	90.67 ± 1.73	$14.24 \pm 0.87^{\text{d}}$	$48.66 \pm 1.92^{\text{bc}}$	+	+	–
TCR20	Control	ND	$35.43 \pm 0.12^{\text{a}}$	$42.15 \pm 2.55^{\text{c}}$	+	+	$16.12 \pm 0.65^{\text{a}}$
	Cr	98.05 ± 1.13	$26.71 \pm 0.48^{\text{bc}}$	$26.22 \pm 1.24^{\text{de}}$	+	+	$6.89 \pm 0.22^{\text{c}}$
	Drought	ND	$29.69 \pm 1.44^{\text{b}}$	$28.29 \pm 2.42^{\text{d}}$	+	+	$10.39 \pm 1.02^{\text{b}}$
	Cr+drought	83.44 ± 2.88	$25.95 \pm 1.37^{\text{c}}$	$21.16 \pm 1.0^{\text{e}}$	+	+	$4.48 \pm 1.21^{\text{d}}$

Note: Cr - 50 mg Cr L⁻¹, [iiij] Drought - 15% w/v PEG 6000. Values are means \pm standard deviations of three replicates. Values indexed with the same letter are not significantly different between treatments according to the HSD Tukey test at $p < 0.05$. ND, not detected; ACCD, 1-aminocyclopropane-1-carboxylatedeaminease; KB, ketobutyrate. '+' Positive for PGP activity, '-' negative for PGP activity.

2.2.2. Measurement of growth and stress-related parameters in *Z. mays*

The plants were harvested after 40 d for determining the biomass (fresh and dry biomass), and other biochemical parameters such as relative water content (RWC) (Barrs and Weatherley, 1962), pigments (Ni et al., 2009), total soluble protein (Bradford, 1976), malondialdehyde (MDA) (Heath and Packer, 1968), proline (Bates et al., 1973), total phenolics (Barka et al., 2006) and SOD activity (Dhindsa and Matowe, 1981) in the leaves of *Z. mays*.

2.2.3. Assessment of gas exchange and chlorophyll fluorescence indexes

The gas exchange and chl fluorescence parameters were measured through portable open-flow gas exchange system (LI-6400XT, LI-COR, Lincoln, NE, USA) integrated with a fluorescence chamber head (LI-6400-40, LI-COR Inc.). To determine the gas exchange parameter of the leaf, the following conditions were adapted; 1200 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ photosynthetic photon flux density (PPFD), 400 $\mu\text{mol mol}^{-1}$ reference CO₂ content, 25 °C leaf temperature, and ambient relative humidity. The photosynthetic physiological indicators such as CO₂ assimilation rate (A), stomatal conductance (g_s), transpiration rate (E), and internal CO₂ concentrations (C_i) were recorded on the first fully developed *Z. mays* leaf (fourth leaf from the apex) of each treatment. The apparent water use efficiency (WUE) of leaf was estimated from CO₂ assimilation and transpiration rate as $WUE = A/E$ (Ribeiro et al., 2009). The chl fluorescence parameters were recorded simultaneously on the same leaf of *Z. mays*. In dark-adapted state, minimal fluorescence yield (F_0) and maximal fluorescence yield (F_m) were recorded with a weak modulated measuring beam (0.03 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) and a saturating light pulse (800-ms; 8000 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, 0.8 s), respectively. Whereas, in light-adapted state, maximal fluorescence (F'_m) and steady-state fluorescence (F_s) were recorded with illumination of saturating pulse of white light (800-ms, 8000 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, 0.8 s). Further, minimal fluorescence (F'_0) was evaluated by ensuring turned off actinic light and providing a far-red pulse (2 $\mu\text{mol m}^{-2} \text{ s}^{-1}$). From the above saturation pulse inputs, the chl fluorescence parameters were calculated by the software operating in LI-6400-40. The fluorescence parameters including maximum quantum efficiency of PSII [$\Phi_{\text{PSII}} = 1 - (F_0/F_m)$] (Schreiber et al., 1995), actual quantum efficiency of PSII [$\Phi_{\text{PSII}} = (F_m - F')/F'_m$] (Genty et al., 1989), photochemical quenching [$q_p = (F'_m - F_s)/(F'_m - F'_0)$] (Bilger and Bjorkman, 1990), non-photochemical quenching [$\text{NPQ} = (F_m - F'_m)/F'_m$] (Walters and Horton, 1991), and electron transport rate [$\text{ETR} = \Phi_{\text{PSII}} \times \text{PPFD} \times 0.87 \times 0.5$] (Krall and Edwards, 1992) were analyzed in this study.

2.2.4. Measurements of Cr accumulation

The accumulation of Cr in *Z. mays* tissues (shoot and root) was estimated using Inductively Coupled Plasma Mass Spectrometry (ICP-MS, X-serous II, Thermo, US) (Estefan et al., 2013). Further, the Cr translocation factor (TF) was estimated as detailed by Cui et al. (2007).

2.3. Statistical analysis

The experiments were performed in triplicates ($n = 3$) and results were presented as mean \pm standard deviation (SD). The statistical differences among the treatments were determined and compared through analysis of variance (ANOVA) by Tukey's HSD tests ($p < 0.05$) using statistical package (SPSS 20.0).

3. Results

3.1. Effects of inoculation of MST-PGPB on *Z. mays* biomass

In pot experiment, the uninoculated *Z. mays* grown under Cr, drought, or Cr+drought stress displayed a significant decrease in plant fresh and dry biomass. However, the maximum decrease in plant fresh and dry biomass by 60 and 57%,

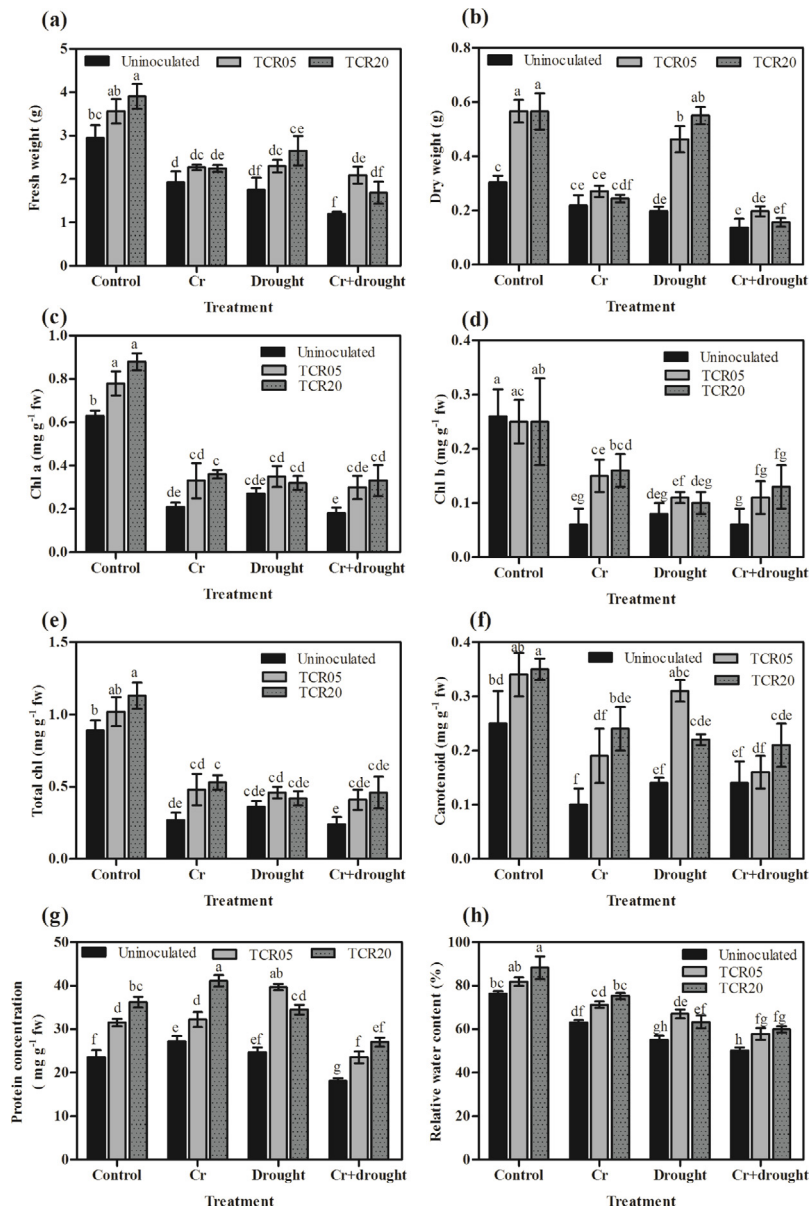


Fig. 1. Inoculation effect of TCR05 and TCR20 on (a) fresh weight, (b) dry weight, (c) chl a, (d) chl b, (e) total chl, (f) carotenoid content, (g) protein concentration, and (h) relative water content of *Z. mays* under Cr, drought, and Cr+drought stress. Bars represent standard deviations of three replicates. Bars indexed with the same letter are not significantly different between treatments according to the HSD Tukey test at $p < 0.05$. Fresh weight (fw).

respectively was found under Cr+drought stress as compared with control (Fig. 2a and b). Whereas, the inoculation of MST-PGPB increased the plant biomass by diminishing the negative effects of Cr and drought. Under Cr+drought stress, strain TCR05 increased the fresh and dry biomass by 76 and 46%, respectively, compared to corresponding uninoculated plants. Similarly, strain TCR20 increased the fresh and dry biomass by 41 and 14%, respectively (Fig. 1a and b).

3.2. Effects of MST-PGPB on leaf photosynthetic pigments

The photosynthetic pigments (chl a, chl b, and total chl) and carotenoid content of uninoculated plants were reduced significantly upon Cr, drought, or Cr+drought stress treatment (Fig. 1c-f). The maximum reduction of chl a (71%), chl b (77%), and total chl (73%) were found in uninoculated plants grown under Cr+drought stress.

On contrary, maximum reduction of carotenoid content (60%) was detected in plants grown under Cr stress. However, MST-PGPB inoculation increased the photosynthetic pigments irrespective of stress treatment. Interestingly, the beneficial

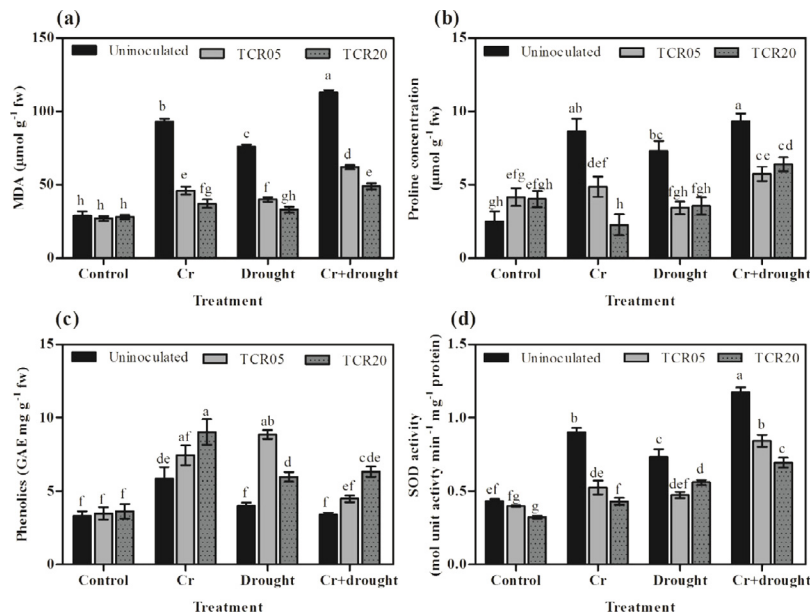


Fig. 2. Inoculation effect of TCR05 and TCR20 on (a) MDA content, (b) proline, (c) phenolics, and (d) SOD activity of *Z. mays* under Cr, drought, and Cr+drought stress. Bars represent standard deviations of three replicates. Statistical notation is the same as in Fig. 1. Gallic acid equivalent (GAE).

activity was most apparent in Cr+drought stress condition; for instance, TCR20 increased the chl a, chl b, total chl and carotenoid content by 83, 117, 92, and 50%, respectively, under Cr+drought stress condition compared to respective uninoculated plants. Similarly, TCR05 increased by 67, 84, 71, and 14%, respectively (Fig. 1c–f).

3.3. Effects of MST-PGPB on leaf protein and RWC

A slight increase in protein content was observed in uninoculated plants grown under Cr and drought stress. On contrary, the combined stress (Cr+drought) reduced the protein content of the uninoculated plants. Nevertheless, the inoculation of MST-PGPB significantly increased the protein content of *Z. mays* compared to uninoculated plants, irrespective of stress condition (Fig. 1g). Similarly, inoculation with MST-PGPB increased the leaf RWC of the plant. While, the uninoculated plants displayed a reduction in RWC by 17, 28, and 34% under Cr, drought, and Cr+drought stress conditions, respectively, compared to the uninoculated control plant (Fig. 1h).

3.4. Effects of MST-PGPB on MDA, proline, and antioxidants

The leaf MDA and proline content were remarkably increased in uninoculated plants grown under Cr, drought, and Cr+drought stress conditions. However, the inoculation with MST-PGPB decreased the leaf MDA and proline content under different stress compared to the respective uninoculated plants. The maximum decrease of MDA and proline content by 60 and 73%, respectively, was observed in TCR20 inoculated plants grown under Cr stress (Fig. 2a and b); while, TCR05 reduced by 50 and 44%, respectively, under the same stress condition. In contrast, inoculation of MST-PGPB slightly increased the proline content in non-stressed plants, though the increase was not significant.

The phenolic content and SOD activity of the uninoculated plants under different stress conditions were increased compared to uninoculated control plants (Fig. 2c and d). A further increase in phenolic content was observed in the plants inoculated with MST-PGPB. Under Cr+drought stress, TCR05 and TCR20 increased the phenolic content by 32 and 86%, respectively, compared to uninoculated control plants (Fig. 2c). In contrast to the trends observed in phenolic content, the inoculation of MST-PGPB decreased the SOD activity, irrespective of stress condition. The maximum decrease in SOD activity by 41 and 52% were found in TCR05 and TCR20 inoculated plants, respectively, grown under Cr stress. On the other hand, they decreased the SOD activity by 28 and 41%, respectively under Cr+drought stress (Fig. 2d).

3.5. Effects of MST-PGPB on gaseous exchange indexes

The inoculation effect of MST-PGPB on photosynthetic capacity of *Z. mays* under Cr, drought, or Cr+drought stress was measured by gas exchange analysis. The uninoculated plants grown under various stress showed a decrease in *A*, *E*, *WUE*, and *g_s* values compared to the non-stressed uninoculated plants (Fig. 3a–d). The maximum reduction of *A*, *E*, *WUE*, and

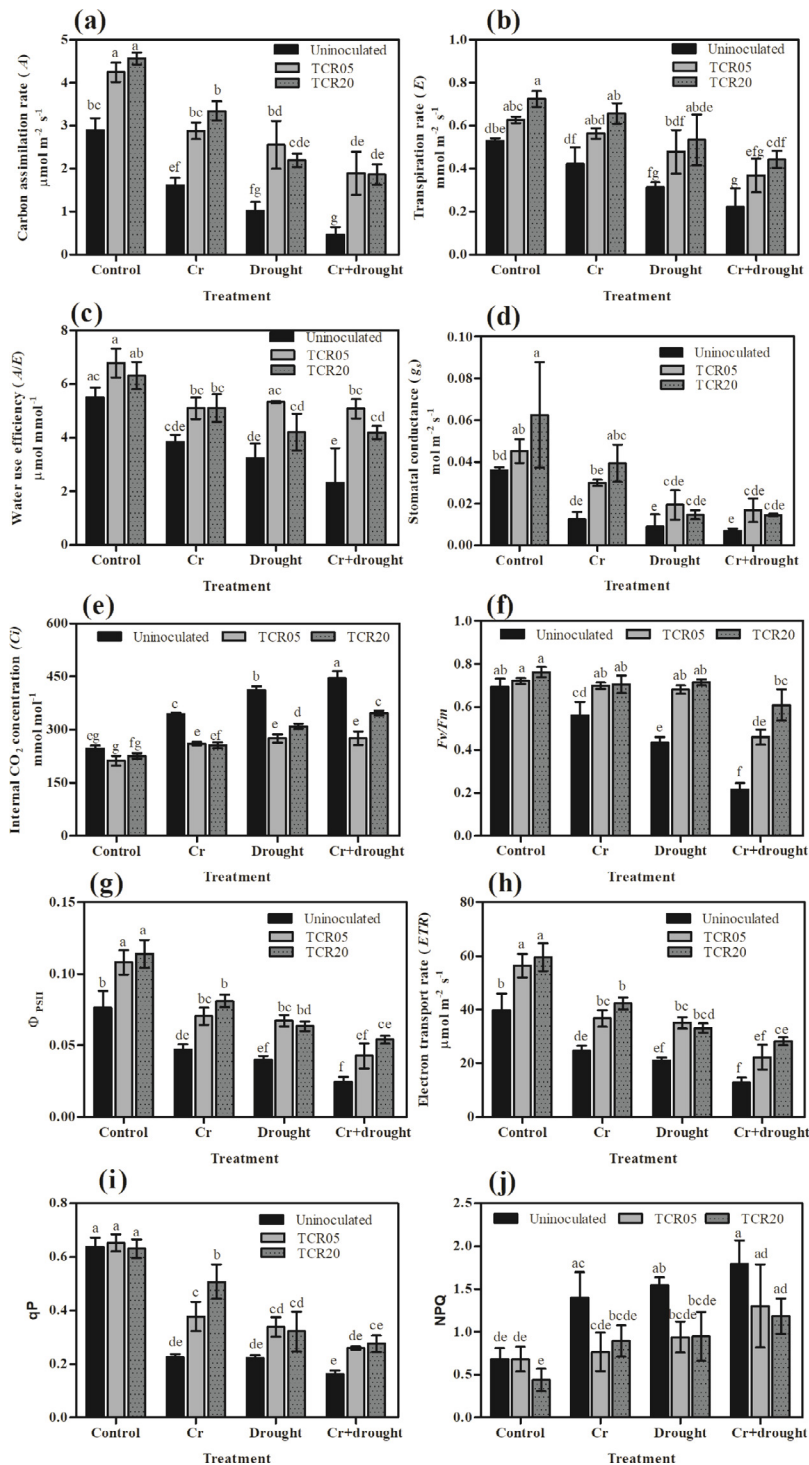


Fig. 3. Inoculation effect of TCR05 and TCR20 on (a) carbon assimilation rate, (b) transpiration rate, (c) water use efficiency, (d) stomatal conductance, (e) internal CO_2 concentration, (f) maximum quantum efficiency of PSII [F_v/F_m], (g) actual quantum efficiency of PSII [Φ_{PSII}], (h) electron transport rate, (i) photochemical quenching [q_p], and (j) non-photochemical quenching [NPQ] of *Z. mays* under Cr, drought, and Cr+drought stress. Bars represent standard deviations of three replicates. Statistical notation is the same as in Fig. 1.

g_s by 84, 58, 58, and 80%, respectively, were found in the uninoculated plants grown under Cr+drought stress. However, the inoculation of MST-PGPB increased the A , E , WUE , and g_s parameters compared to uninoculated plants grown under

respective treatments. For instance, TCR05 increased the values of A , E , WUE , and g_s under Cr+drought stress by 309, 68, 120, and 129%, respectively, compared to uninoculated plants. Similarly, TCR20 increased A , E , WUE , and g_s by 304, 100, 81, and 100%, respectively (Fig. 3a–d). In contrast, a significant increase was observed in C_i values of uninoculated plants under Cr, drought, or Cr+drought stress. While, *Z. mays* inoculated with MST-PGPB showed a decrease in the C_i , irrespective of stress condition. For instance, TCR05 and TCR20 decreased the C_i value under Cr+drought stress by 38 and 22%, respectively (Fig. 3e).

3.6. Effects of MST-PGPB on chlorophyll fluorescence indexes

The chl fluorescence parameters were analyzed to explore the effects of MST-PGPB on photochemical responses, behavior, and performance of PSI and PSII in *Z. mays* under Cr and drought stress conditions. These exposures considerably reduced the maximum quantum efficiency of PSII (F_v/F_m) of the plant. However, the stress-induced reduction was higher in uninoculated plants grown under Cr+drought (68%) followed by drought (37%) and Cr stress (19%) conditions. Similarly, Cr, drought, and Cr+drought stress significantly reduced the actual quantum efficiency of PSII (Φ_{PSII}), electron transport rate (ETR), and photochemical quenching (q_p) of uninoculated plants (Fig. 3f–i). However, MST-PGPB increased the performance of PSI and PSII by increasing F_v/F_m , Φ_{PSII} , ETR, and q_p under Cr, drought, or Cr+drought stress condition. Under Cr+drought stress, the maximum increases of F_v/F_m , Φ_{PSII} , ETR, and q_p were found in TCR20 inoculated plants, where the increase was 177, 125, 121, and 75%, respectively. While, plants inoculated with TCR05 increased the F_v/F_m , Φ_{PSII} , ETR, and q_p by 109, 75, 75, and 63%, respectively (Fig. 3f–i).

On the other hand, a remarkable upsurge in NPQ was found in uninoculated plants grown under Cr, drought, and Cr+drought stress conditions; however, these effects were statistically non-significant among treatments. Nevertheless, the inoculation of MST-PGPB reduced the NPQ of the plants grown under various stress conditions. Notably, the reduction of NPQ under Cr+drought stress was 28 and 33% in plants inoculated with TCR05 and TCR20, respectively, compared to the uninoculated plants (Fig. 3j).

3.7. Effects of MST-PGPB on Cr accumulation

The accumulation of Cr in shoot and root of *Z. mays* under Cr and Cr+drought stress conditions are presented in Fig. 4a. Irrespective of MST-PGPB inoculation, *Z. mays* grown under Cr+drought stress showed reduced Cr accumulation in tissues compared with those grown under Cr stress alone. However, inoculation with MST-PGPB resulted in an increase in Cr accumulation in root tissues of plants grown under Cr and Cr+drought stress conditions. For instance, TCR05 increased Cr accumulation in root by 124 and 93% under Cr and Cr+drought stress, respectively, compared with the corresponding uninoculated plants. Similarly, TCR20 increased Cr accumulation in root by 89 and 140%, respectively. Nevertheless, the inoculation of MST-PGPB decreased Cr accumulation in shoot under Cr and Cr+drought stress. For instance, TCR20 reduced Cr accumulation in shoot of plants exposed to Cr and Cr+drought by 61 and 51%, respectively (Fig. 4a). TF of Cr in *Z. mays* was also determined under Cr and Cr+drought stress conditions. Irrespective of MST-PGPB inoculation, drought did not influence TF of Cr in plants. However, plants inoculated with MST-PGPB showed reduced TF of Cr compared to respective uninoculated plants. For instance, TCR20 decreased the TF in plants under Cr and Cr+drought conditions by 78 and 79%, respectively; similarly, TCR05 reduced the TF by 67 and 47%, respectively (Fig. 4b).

4. Discussion

The abiotic stress tolerant PGPB improve the plant growth and survival under individual and combined stress through establishing beneficial interaction with host plants (Manoj et al., 2020; Rajkumar et al., 2017). Although, the potential of such PGPB to produce PGP metabolites and reduce Cr(VI) to Cr(III) has been previously reported (Wani et al., 2018), the present investigation is the first report exploring the potential of Cr reducing MST-PGPB in the alleviation of combined stress effects of Cr and drought on *Z. mays* growth and photosynthetic attributes.

The pot experiments reveal that both MST-PGPB TCR05 and TCR20 are efficient in protecting *Z. mays* from growth inhibition caused by individual (Cr or drought) and combined stress (Cr+drought), as strongly supported by the plant biomass data. Cr and drought stress can hamper plant growth and pigment content by interrupting cell elongation, water flow, mineral uptake, chl biosynthesis, etc., (Kosova et al., 2018; Sarker and Oba, 2018). Further, the combined stress conditions (Cr+drought) exacerbated the negative effects resulted in reduced plant growth as compared to the plants grown under individual stress environment. Recently, Ma et al. (2017) observed a maximum decrease in growth and pigment content of *Trifolium arvense* under combined (drought+multimetal) stress conditions. In our study, regardless of the stress condition, the biomass and chl content of *Z. mays* were enhanced by the inoculation of MST-PGPB. These could be attributed to the potential of MST-PGPB on the production of siderophores, IAA, ACCD and reduction of Cr(VI) to Cr(III) even under Cr, drought, or Cr+drought stress condition (Table 1). It is known that siderophores produced by PGPB increase the chl content and thereby improve plant health under abiotic stress conditions. Zhang et al. (2009) reported the role of siderophores towards iron and chl contents in plants and found *Bacillus subtilis* GB03 producing siderophores improve *Arabidopsis* growth. Further, the siderophores produced by GB03 chelates Fe^{3+} and consequently increased the iron levels, chl content and photosynthetic efficiency of *Arabidopsis*. Similarly, increased plant growth was also reported in

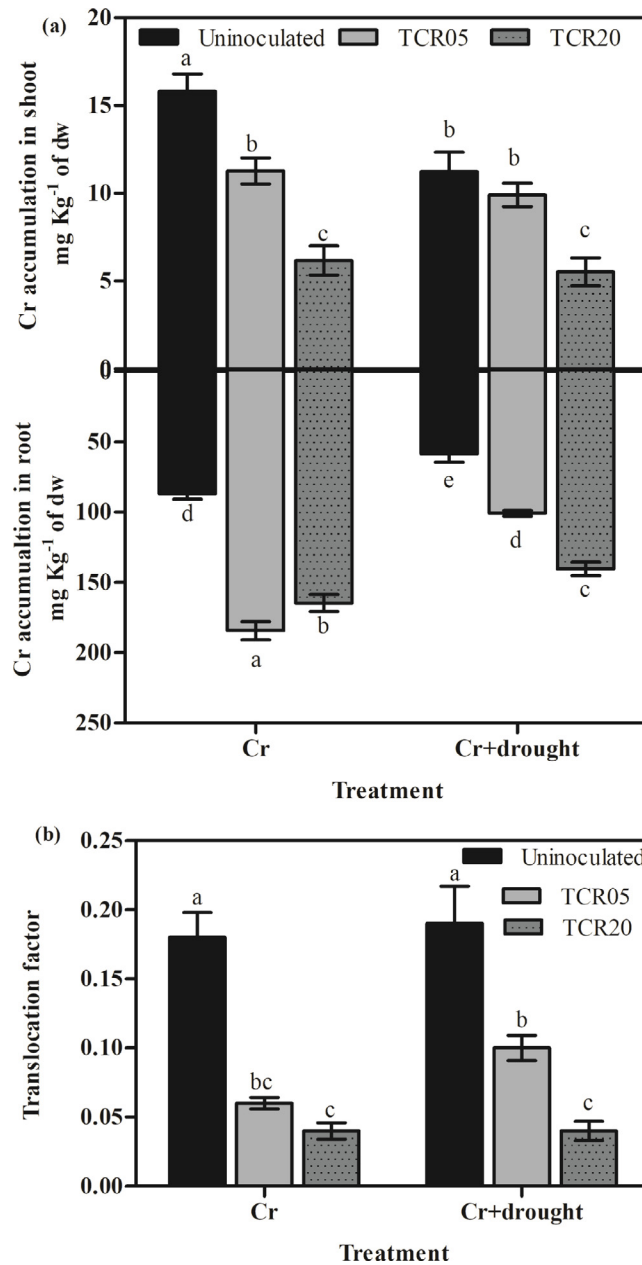


Fig. 4. Inoculation effect of TCR05 and TCR20 on (a) Cr accumulation and (b) translocation factor of *Z. mays* under Cr, drought, and Cr+drought stress. Bars represent standard deviations of three replicates. Statistical notation is the same as in Fig. 1. Dry weight (dw).

ACCD producing PGPB that was inoculated in heavy metal stressed *Helianthus annuus* (Kumar et al., 2021) and in drought stressed maize (Danish et al., 2020). ACCD has vital role in amelioration of metal and drought stress by lowering plant ethylene levels via catalyzing the conversion of ACC to ammonia and α -ketobutyrate (Rajkumar et al., 2017). In addition, PGPB can improve root elongation and cell proliferation by producing IAA, resulting in greater root surface for water and nutrient uptake (Manoj et al., 2020).

PGPB can improve plant stress tolerance, biomass production, and also the protein content especially under abiotic stress conditions through altering plant RWC, enzymatic and non-enzymatic antioxidants etc (Manoj et al., 2020; Rajkumar et al., 2017). In our study, Cr+drought caused a drastic decrease in the protein content of *Z. mays*. This is possibly due to altered protein metabolism and homeostasis caused by excess toxicity of abiotic stress (Kosova et al., 2018). However, the inoculation of MST-PGPB significantly increased plant protein content under Cr+drought stress over the uninoculated plants, indicating that PGPB was able to maintain the physiological status of plants to cope with stress

conditions (Arefian et al., 2019; Kosova et al., 2018). Our studies were in agreement with Singh et al. (2018) who found that *Enterobacter ludwigii* when inoculated to metal exposed *Triticum aestivum* resulted in the higher protein content. The increased protein content under Cr and drought stress caused by MST-PGPB indicates that the bacteria helped plants to diminish the stress effect of Cr and drought. As demonstrated by Singh et al. (2018) in *T. aestivum*, the increase of plant protein under heavy metal stress following PGPB inoculation might be associated to the enhanced plant RWC. In our study Cr, drought, and Cr+drought stress conditions caused a drastic decrease in the RWC of uninoculated plants. This may be attributed to the loss in turgor and hydraulic conductance due to toxicity exerted by concomitant metal and drought stress and subsequently decreasing the plant growth (De Silva et al., 2012; Tatrai et al., 2016). However, inoculation of MST-PGPB increased the RWC under various stress conditions (Fig. 1h), suggesting the PGPB could influence the stomatal functioning and maintain water potential to prevent the water loss. Previously, Ma et al. (2017) also noticed increased RWC in *P. azotoformans* inoculated plants subjected to metal+drought stress and indicated this was due to improved hydraulic conductance and decreased negative effects of abiotic stresses. Similarly, Pattnaik et al. (2020), Silambarasan et al. (2019b) and Woo et al. (2020) also suggested that the inoculation of PGPB improve the plant RWC by increasing root growth through various PGP metabolites including siderophores production, ACCD activity, phosphate solubilization and IAA synthesis.

MDA content, a result of ROS mediated lipid peroxidation, is used as biomarker of membrane damage caused by various abiotic stresses. In our study, *Z. mays* inoculated with MST-PGPB showed lower MDA levels under Cr, drought, and Cr+drought stress. This might be due to the ability of MST-PGPB to protect plants from oxidative damages by reducing Cr(VI) toxicity (Cr reduction), regulating the levels of secondary metabolites (proline and phenolics), and antioxidant activities in *Z. mays*. This finding is corroborated with the results of *Curtobacterium herbarum* inoculated *Lactuca sativa* that exhibited reduced MDA level under aluminium (Al) and drought stress conditions due to Al bioaccumulation and activity of enzymatical antioxidants (Silambarasan et al., 2019b). In addition, an increase in the accumulation of proline, and phenolics in plants as an internal detoxification mechanism has also been reported in PGPB inoculated plants under heavy metal and drought stress conditions (Sarker and Oba, 2018; Gill and Tuteja, 2010). In the present work, increased accumulation of total phenolics following TCR05 and TCR20 inoculation (Fig. 2c), illustrated that PGPB attenuates the toxic effects of Cr and drought by regulating the biosynthesis of phenolic compounds (Li et al., 2015). The low molecular weight antioxidants such as phenols can act as a redox buffer, which donates electrons and hydrogen atoms to scavenge ROS-mediated free radicals and influence the plant growth and establishment (Gill and Tuteja, 2010; Li et al., 2015). Furthermore, increased accumulation of proline and activity of SOD minimize the adverse effects of stress by regulating membrane stability, osmotic adjustment, and ROS scavenging mechanisms (Rajkumar et al., 2017). However, in this study, a reduction in proline and SOD activity was recorded in the inoculated plants under stress conditions (Fig. 2b–c). These results are correlated with decreased MDA content in MST-PGPB inoculated plants (Fig. 2a), resulting in improved plant growth, suggesting an active role of inoculated PGPB in Cr and drought stress tolerance. Previously, Islam et al. (2016) observed similar results in PGPB inoculated maize plant exposed to Cr stress and reported that *P. mirabilis* decreased the metal toxicity and oxidative stress, which resulted in decreased proline accumulation and SOD activity.

Since PSII is highly sensitive to abiotic stresses like drought and heavy metals, the measurement of photosynthetic and chl fluorescence parameters can be used as an indicator of stress level in plants (Win et al., 2018). In this study, the concomitant decrease in A , E , WUE , and g_s and increase in C_i observed in uninoculated plants under different stress conditions (Fig. 3a–e) suggest that the abiotic stress negatively influence the stomatal regulation [reduced CO_2 diffusion and transpiration (E)] by reducing g_s , thus decreasing WUE and carbon assimilation rate (A) (Brilli et al., 2019; Liu et al., 2019; Win et al., 2018). Previous studies have also confirmed that abiotic stress increases C_i by decreasing CO_2 assimilation through altering RubisCO activity and reducing mesophyll conductance, and other non-stomatal factors (Bermúdez-Cardona et al., 2015; Brilli et al., 2019). However, in the present study an increase in gaseous parameters (A , E , WUE , and g_s , except C_i) (Fig. 3a–e) as the results of PGPB inoculation was observed, indicate that both TCR05 and TCR20 were efficient in regulating stomatal functions and decreasing the structural damages of photosynthetic apparatus through inducing plant osmolyte accumulation including abscisic acid, IAA, etc., (Brilli et al., 2019; Ouledali et al., 2019). Recently, Liu et al. (2019) noticed an increased gas exchange parameters in *Acinetobacter calcoaceticus* inoculated *Sambucus williamsii* under drought condition and reported this effect was due to reduction in stress mediated damages of photosynthetic organs and improved stomatal functioning of the leaves. Furthermore, the uninoculated plants exposed to Cr, drought, or Cr+drought conditions exhibited a marked decrease in fluorescence parameters as the results of decreased quantum efficiency of PSII (i.e., F_v/F_m and Φ_{PSII}) (Fig. 3f–g). In general, the maximum quantum efficiency of PSII (F_v/F_m) has been considered as a key stress indicator of photosynthetic performance. The reduction in the quantum efficiency of PSII under stress condition might be associated with photoinhibition as the results of alterations in the integrity and functionality of the PSII reaction centers, resulting in decreased Φ_{PSII} and thus the lower values of F_v/F_m (Murata et al., 2012; Xiao et al., 2019). Moreover, impairment of PSII reaction center affects the photosynthetic electron transport activity and decreases the photochemical efficiency, leading greater dissipation of excess light energy as heat through non-photochemical pathways (Xu et al., 2020). In this study, the uninoculated plants exposed to individual or combined stress had the least values of q_p and higher value of NPQ, which are consistent with the earlier observations (Wu et al., 2020; Xu et al., 2020) suggested that this might be associated with lower ETR. However, the strains TCR05 and TCR20 markedly increased the fluorescence parameter (i.e. increased F_v/F_m , Φ_{PSII} , ETR, and q_p ; decreased NPQ) in *Z. mays* under stress conditions (Fig. 3f–j), indicate that PGPB inoculation protected PSII reaction center and improved the photosynthetic electron transport by reducing the

toxicity exerted by Cr and drought. This observation is in good agreement with the pigment (Fig. 1c–f) content of *Z. mays* suggesting that there was a significant relationship between PGPB mediated increase in chl contents and photosynthetic characteristics of plants. Both MST-PGPB with various PGP traits and Cr reduction potential were not only able to improve the plant growth but also ameliorate the deleterious effect of Cr and drought stress by regulating the antioxidant activities, RWC and secondary metabolites accumulation in plants. As a result, the increase in photosynthetic pigment content improved biochemical rate of CO₂ fixation, which have a pivotal role in increasing the net photosynthesis and growth rate of plants under abiotic stress (Taj and Challabathula, 2021).

The role of PGPB is noteworthy in improving heavy metal phytoremediation under drought stress conditions since the PGPB greatly influence metal bioavailability and its uptake by plants through several mechanisms including metal reduction and oxidation, methylation, formation of insoluble complexes, chelation through siderophores, bioaccumulation and intracellular sequestration (Manoj et al., 2020; Rajkumar et al., 2017). In our study, the exposure of uninoculated plants to drought stress led to a significant decrease in the accumulation of Cr in both shoot and root tissues and these might be due to low solubility of metal and inhibition of root growth under water-limited condition (Silambarasan et al., 2019b). Interestingly, MST-PGPB further reduced Cr accumulation in plant shoots, although they upsurge the root Cr uptake, irrespective of drought stress condition, suggesting that PGPB immobilized Cr in plant roots and suppressed the translocation probably through Cr(VI) reduction mechanism (Tirry et al., 2018). Previously, Wani et al. (2018) and Tirry et al. (2018) also observed decreased Cr content in shoot tissues of soybean and alfalfa and demonstrated this effect was due to PGPB-associated immobilization of Cr in roots. Moreover, the role of PGPB in controlling Cr translocation from root to shoot in our study was further evidenced by the lower TF indicating that both TCR05 and TCR20 are suitable for improving phytostabilization process in Cr contaminated soils even under drought stress conditions.

5. Conclusion

In this study, the exposure of Cr, drought and Cr+drought stress negatively affected the plant growth and physiological behavior. Interestingly, the inoculation of MST-PGPB compensated the negative effects of Cr, drought and Cr+drought stress on plant health by increasing RWC and phenolics content and decreasing MDA, proline and SOD activity. The altered level of such metabolites due MST-PGPB could potentially increase the performance of *Z. mays* under Cr, drought and Cr+drought conditions and showed higher plant biomass, pigments and protein contents. Further, MST-PGPB improved the photosynthetic efficiency including gaseous and fluorescence parameters of *Z. mays* under both stressed and non-stressed conditions. Besides, both MST-PGPB reduced Cr accumulation in shoot by reducing Cr translocation from root to shoot, although they improved Cr content in root. The effective role played by PGPB on plant growth, stress tolerance, gaseous parameters, fluorescence parameters, and Cr accumulation due to their PGP traits and Cr(VI) reduction provides new knowledge which may pave the way to utilize such MST-PGPB with non-edible perennial plants for effective and permanent phytostabilization in Cr contaminated arid and semiarid regions. Further experiments including the analysis of transcriptional variations in PGPB inoculated *Z. mays* under Cr and drought stress are under progress to explore the molecular mechanisms involved in the microbial mediated alleviation of Cr and drought stress in plants.

CRedit authorship contribution statement

R. Vishnupradeep: Isolation and screening of bacteria, pot experiment, and ICP-MS were carried out, The paper and supporting information of the original draft. **L. Benedict Bruno:** Conceptualized, Isolation and screening of bacteria, pot experiment, and ICP-MS were carried out, Photosynthetic parameter was carried out, The paper and supporting information of the original draft. **Zarin Taj:** Photosynthetic parameter was carried. **Chinnannan Karthik:** Writing - review and editing. **Dinakar Challabathula:** Photosynthetic parameter was carried out. **Tripti:** Writing - review and editing. **Adarsh Kumar:** Writing - review and editing. **Helena Freitas:** The paper and supporting information of the original draft. **Mani Rajkumar:** Conceptualized, Isolation and screening of bacteria, pot experiment, and ICP-MS were planned, The paper and supporting information of the original draft.

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.

Acknowledgments

L.B.B thankful to the Science and Engineering Research Board (SERB), India for providing National Post-Doctoral Fellowship (Grant No. PDF/2017/001074). A.K., T, and M.R. are grateful for the “Department of Science and Technology (DST), India (Project No. INT/RUS/RFB/363) and Russian Foundation for Basic Research, Russia (Project No. 19-516-45006) bilateral research grant”. A.K. acknowledge the work support by Russian Science Foundation (Project No. 21-76-00011). Many thanks to Benedict Analin from the Department of Life Sciences, Central University of Tamil Nadu for helping to analyze photosynthetic parameters in the laboratory. The manuscript was written through the contributions of all authors.

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