

Isolation and characterization of a plant growth promoting bacterium *Burkholderia cenocepacia* CE2

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Abstract

The search for efficient plant growth-promoting rhizobacteria (PGPR) has become increasingly important in the pursuit of sustainable agricultural practices. In this study, a novel bacterial strain, *Burkholderia cenocepacia* CE2, was isolated from the rhizospheric soil of a healthy crop field and characterized for its potential plant growth-promoting attributes. The isolate was identified based on morphological characteristics, biochemical profiling, and 16S rRNA gene sequencing, which confirmed its identity as *B. cenocepacia*. The strain exhibited multiple PGP traits including phosphate solubilization and indole-3-acetic acid (IAA) production, all of which are critical for enhancing plant nutrient uptake, root development, and stress tolerance. In addition to its growth-promoting capabilities, *B. cenocepacia* CE2 showed significant antagonistic activity against common soil-borne phytopathogens, indicating its biocontrol potential. Pot experiments further validated its effectiveness, showing enhanced seed germination, root and shoot elongation, and overall plant vigor in treated plants compared to controls. These findings suggest that the strain not only supports plant growth but also plays a protective role in the rhizosphere. This study contributes to the growing body of knowledge on beneficial rhizobacteria and highlights *B. cenocepacia* CE2 as a promising bioinoculant candidate for sustainable crop production.

Keywords: *B. cenocepacia*, Indole-3-acetic acid, *V. mungo*, Phosphate solubilization, Phylogeny tree.

INTRODUCTION

Agricultural productivity is continuously challenged by a variety of biotic and abiotic stresses, including nutrient deficiencies, soil salinity, drought, and pathogen infestations. To address these challenges sustainably, there is an increasing focus on harnessing beneficial soil microorganisms

known as plant growth-promoting rhizobacteria (PGPR). These microbes are known to colonize plant roots and promote plant growth directly by enhancing nutrient availability or indirectly through disease suppression (Vessey, 2003). Among the many genera identified as PGPR, *Burkholderia* species have gained considerable attention due to their metabolic versatility and ecological adaptability (Compant et al., 2008). The genus *Burkholderia* encompasses a diverse group of Gram-negative, rod-shaped bacteria that are widely distributed in soil, water, and plant-associated environments. While some species within this genus are known for their pathogenicity in humans and plants, others exhibit beneficial traits, particularly in plant–microbe interactions (Coenye and Vandamme, 2003). One such species, *Burkholderia cenocepacia*, has traditionally been studied as an opportunistic pathogen in cystic fibrosis patients. However, recent studies have indicated that certain environmental strains of *B. cenocepacia* possess remarkable plant growth-promoting capabilities, including phosphate solubilization, nitrogen fixation, siderophore production, and the synthesis of phytohormones such as indole-3-acetic acid (IAA) (Mitter et al., 2013; Dias et al., 2019).

The dualistic nature of *B. cenocepacia* as both a potential pathogen and a beneficial PGPR necessitates a thorough evaluation of individual isolates to determine their suitability for agricultural applications. In this context, strain-specific characterization becomes crucial for identifying isolates that lack pathogenic determinants while retaining desirable agronomic traits. Such evaluations often include phenotypic, biochemical, and molecular analyses, along with functional assays that assess a strain's ability to promote plant growth under controlled conditions (Suárez-Moreno et al., 2012). Furthermore, the ecological niche and source of isolation significantly influence the functional traits exhibited by these bacteria. Isolates obtained from rhizospheric soils, particularly those from nutrient-poor or stressed environments, are more likely to exhibit plant growth-promoting features as adaptive responses to resource limitations (Glick, 2012). The mechanisms through which PGPR like *B. cenocepacia* enhance plant growth are multifaceted. Direct mechanisms include nitrogen fixation, solubilization of inorganic phosphate, and production of growth-promoting substances such as gibberellins and cytokinins. Indirectly, these bacteria contribute to plant health by producing siderophores that chelate iron, making it unavailable to plant pathogens, and by synthesizing antimicrobial compounds that inhibit pathogenic fungi and bacteria (Lugtenberg and Kamilova, 2009). Some strains are also capable of producing 1-aminocyclopropane-1-carboxylate (ACC) deaminase, an enzyme that

lowers plant ethylene levels under stress conditions, thereby improving root elongation and stress tolerance (Glick et al., 2007). Given the increasing global emphasis on sustainable agriculture and the reduction of chemical fertilizer inputs, the identification and application of effective PGPR such as *B. cenocepacia* are of paramount importance. However, concerns about the pathogenic potential of this species have limited its use in commercial bioinoculants. This calls for the development of rigorous screening protocols to ensure biosafety while exploiting its beneficial traits. Whole-genome sequencing and comparative genomics are emerging as valuable tools in this regard, enabling the identification of pathogenicity islands, antibiotic resistance genes, and plant-beneficial gene clusters (Chain et al., 2006). Such approaches can facilitate the development of safe and effective microbial inoculants based on non-pathogenic *Burkholderia* strains.

This study aims to isolate and characterize a novel strain of *Burkholderia cenocepacia* from the rhizosphere of healthy agricultural plants. The isolate will be evaluated for various plant growth-promoting attributes, including phosphate solubilization, IAA production, siderophore secretion, and antifungal activity. In addition, molecular identification through 16S rRNA gene sequencing and phenotypic characterization will be performed to confirm species-level classification and assess its biosafety. The findings are expected to contribute to the growing body of knowledge on the beneficial applications of *B. cenocepacia* in sustainable agriculture and to offer insights into the strain-specific traits that underpin its interaction with host plants.

MATERIAL AND METHODS

Isolation of plant growth bacteria from *Barleria prionitis* roots

To identify plant development bacteria from plant roots, five-week-old *Barleria prionitis* plants were gathered from an agricultural field in Guntur, Andhra Pradesh. The plant roots were mixed and rinsed with tap water to remove the surface-attached soil, followed by 5 rinses with dd-H₂O over 30 minutes. A sterilised pestle and mortar was used to grind approximately 5 g of roots in 2 mL of dd-H₂O. The root mixture was diluted and plated in a phosphate growth medium (1% glucose, 0.5% Ca₃(PO₄)₂, 0.5% MgCl₂, 0.01% (NH₄)₂SO₄, 0.0.5% MgSO₄ · 7H₂O, 0.02% KCl, 1.5% agar) (Nautiyal, 1999), where growth is associated with the capacity to use inorganic phosphate in the form of Ca₃(PO₄)₂ as a sole phosphate source. Plates were incubated at 28°C for 7 days. Phosphate solubilising bacteria were recognized by halos around the colony, and their

capacity was confirmed by transferring isolated colonies to medium. The solubilisation index is computed by dividing the diameter of the dissolution halo by the colony diameter.

Computational analysis of bacterial Phylogenetic

The 16S rRNA and recA genes of this strain were identified by searching the full genome at the NCBI (www.ncbi.nlm.nih.gov/). The 16S rRNA gene was aligned with the NCBI nucleotide database using Blastn. This alignment shows 99.93% identity with several strains of *Burkholderia cenocepacia*, as well as strong identity matches (>99.5%) with additional *Burkholderia* species. Searching BioProjects at the NCBI yielded whole genomes of additional *Burkholderia* strains. The recA genes were extracted from the genomes using the "align two or more sequences" feature in the NCBI's Blastn suite. The recA phylogeny was inferred by the Neighbor-Joining technique using the EMBL-EBI Phylogeny tool, followed by alignment by Clustal Omega at <https://www.ebi.ac.uk/Tools/msa/clustalo/>. (Madeira et al., 2019) used the default parameters.

Production Assay Indo-3-acetic acid

The colorimetric approach was used to determine the production of Indo-3-acetic acid and its intermediates, as described by Weselowski et al. (2016) and adapted from Glickmann and Dessaux (1995). To initiate IAA production, 20 μ L of bacterial culture (OD₆₀₀=0.5) was added to 3 mL of liquid medium, either with or without 500 mg/L L-Tryptophan as a precursor. After 42 hours of incubation at 28 °C and 150 rpm, the culture was centrifuged at 5500 \times g for 10 minutes. 1 mL of the supernatant was mixed with 4 mL of Salkowski's reagent. The reaction yields a proportionate amount of tris-(indole-3-acetic) iron (III) complex, which is pink in colour and can be measured at 535 nm.

***Vigna mungo* growth promotion experiments**

B. cenocepacia CE2 was cultured in LB Broth at 28 °C for 24 hours. Bacterial cells were recovered by centrifugation and rinsed with sterile saline solution (0.85% NaCl). The cell pellet was resuspended in 0.85% NaCl at an OD₆₀₀ of 1.0. *V. mungo* were steeped in the bacterial suspension or sterile 0.85% NaCl for 30 minutes before being sown into soil-filled pots. Following seed germination, 2 g of Ca₃(PO₄)₂ was added to the soil's surface as inorganic phosphate. *V. mungo* plants were grown for 6 weeks in a greenhouse with 55.6% relative humidity, 315 μ mol of parabolic aluminized reflector light, and an ambient temperature of 26.75 °C. Following harvest, chlorophyll content, shoot length, and moist weight were immediately

determined. The Chlorophyll Meter SPAD-502 (Konica Minolta Inc., Tokyo, Japan) was used to quantify the amount of chlorophyll in single-photon avalanche diode (SPAD) devices. Dry weight was measured after two days of drying at 65 °C. For each maize growth measurement, the means from the three biological replicates were compared using Tukey's HSD post-test after a standard weighted-means two-way ANOVA for independent samples (with *B. cenosepacia* CE2 and phosphate as the two factors) using the tool available at vassarstats.net (Lowry, 1998).

Result and Discussion

Identification of bacterial species

Bacteria from *B. prionitis* roots were plated on solid media, and growth was linked to the ability to consume inorganic phosphate in the form of $\text{Ca}_3(\text{PO}_4)_2$ (Nautiyal, 1999). One of the 15 bacterial colonies that formed on the plates produced distinct dissolution halos, indicating $\text{Ca}_3(\text{PO}_4)_2$ solubilisation via dramatic acidity of the colony's surroundings. Among the 15 isolates, strain CE2 created the greatest halo, and it was transplanted to additional plates to validate the result (Fig. 1). To identify this isolate, the 16S rRNA gene was matched with the NCBI nucleotide database using Blastn. This alignment shows 99.84% identity with several strains of *Burkholderia cenosepacia*, as well as strong identity matches (>99.5%) with additional *Burkholderia* species. This research shows that strain CE2 is a member of the *Burkholderia cepacia* complex (Vandamme and Dawyndt, 2011), which encompasses at least 20 species. While rRNAs can be used to differentiate some species of the *Burkholderia cepacia* complex, they cannot distinguish between *Burkholderia seminalis*, *Burkholderia cepacia*, *B. cenosepacia*, *Burkholderia contaminans*, *Burkholderia lata*, *Burkholderia pyrrocinia*, and *Burkholderia stabilis* (Fig. 3 &4).

The *recA* gene sequence analysis can help distinguish these species (Vandamme and Dawyndt, 2011). A phylogenetic tree was then constructed based on the *recA* sequences, confirming strain CE2 as *B. cenosepacia* (Fig. 2).



Figure.1 Phosphate solubilisation test of *B. cenocepacia* CE2 was grown on plates for 7 days.

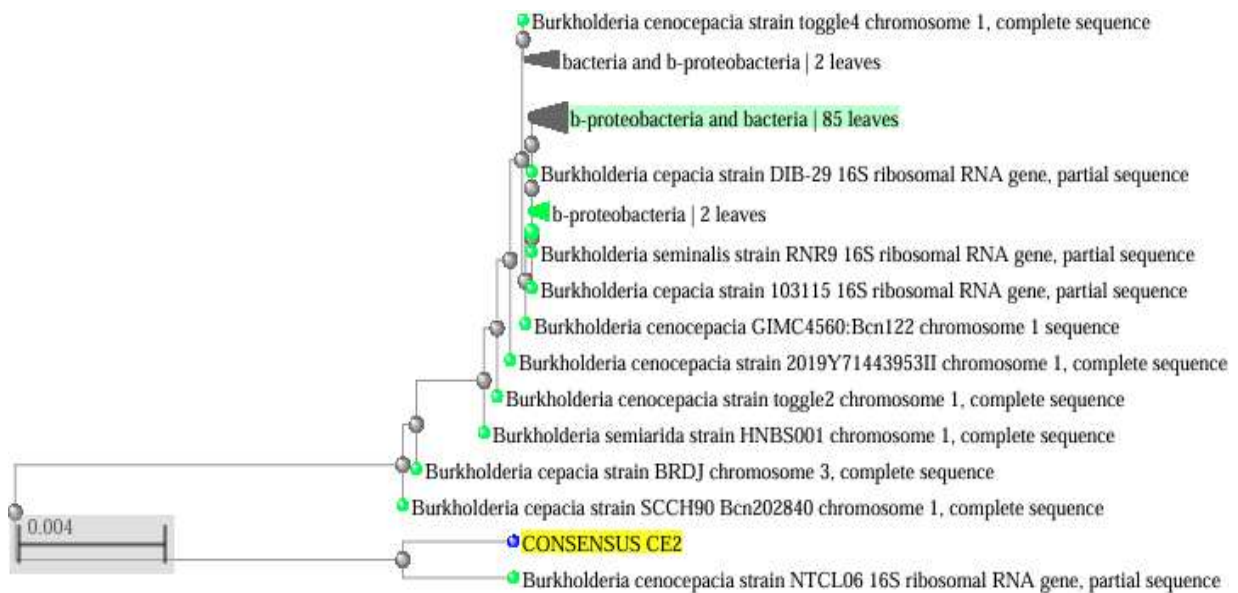


Figure 2: BLAST phylogeny tree

Description	Scientific Name	Max Score	Total Score	Query Cover	E value	Per Ident	Acc. Len	Accession
Burkholderia cenocepacia strain NTCL06 16S ribosomal RNA gene, partial sequence	Burkholderia cenocepacia	2460	2460	98%	0.0	99.20%	1513	PQ119837.1
Burkholderia sp. strain 52LG 16S ribosomal RNA gene, partial sequence	Burkholderia sp.	2242	2242	90%	0.0	94.84%	1399	MF765318.1
Burkholderia cenocepacia H111 chromosome 3, complete genome	Burkholderia cenocepacia H111	2242	2242	91%	0.0	94.60%	1039263	HG938372.1
Burkholderia cenocepacia strain 2019Y71443953II chromosome 1, complete sequence	Burkholderia cenocepacia	2242	8944	91%	0.0	94.60%	3511327	CP090676.1
Burkholderia sp. strain INS81.3 16S ribosomal RNA gene, partial sequence	Burkholderia sp.	2242	2242	90%	0.0	94.84%	1415	OR053877.1
Burkholderia seminalis strain KMR31 16S ribosomal RNA gene, partial sequence	Burkholderia seminalis	2242	2242	90%	0.0	94.84%	1412	OM758186.1
Burkholderia seminalis strain AGR 16S ribosomal RNA gene, partial sequence	Burkholderia seminalis	2242	2242	90%	0.0	94.84%	1469	MH748603.1
Burkholderia cepacia strain Baghdad cov.3 16S ribosomal RNA gene, partial sequence	Burkholderia cepacia	2242	2242	90%	0.0	94.84%	1399	OK103927.1
Burkholderia cepacia strain 3-1 16S ribosomal RNA gene, partial sequence	Burkholderia cepacia	2242	2242	90%	0.0	94.84%	1496	MN398146.1
Burkholderia seminalis strain CC-DD2w 16S ribosomal RNA gene, partial sequence	Burkholderia seminalis	2242	2242	90%	0.0	94.84%	1531	JN89363.1
Burkholderia cenocepacia H111 chromosome 1, complete genome	Burkholderia cenocepacia H111	2242	8912	91%	0.0	94.84%	3572953	HG938370.1
Burkholderia cenocepacia H111 chromosome 2, complete genome	Burkholderia cenocepacia H111	2242	2242	91%	0.0	94.60%	3102677	HG938371.2
Burkholderia cenocepacia strain 2009Ycf95III chromosome 1, complete sequence	Burkholderia cenocepacia	2242	8938	91%	0.0	94.84%	3511529	CP090760.1
Burkholderia cenocepacia strain 2008Ycf657 chromosome 1, complete sequence	Burkholderia cenocepacia	2242	8938	91%	0.0	94.84%	3511584	CP090763.1
Burkholderia cepacia strain KMR28 16S ribosomal RNA gene, partial sequence	Burkholderia cepacia	2242	2242	90%	0.0	94.84%	1417	OM758185.1
Burkholderia cepacia 16S ribosomal RNA gene, partial sequence	Burkholderia cepacia	2242	2242	90%	0.0	94.84%	1416	OL469786.1

Figure 3: BLAST analysis of consensus sequence CE2

Description	Score	E value	Accession
Burkholderia cenocepacia [b:proteobacteria]	Next	Previous	First
Burkholderia cenocepacia strain NTCL06 16S ribosomal RNA gene, partial sequence	2460	0.0	PQ119837
Burkholderia cenocepacia strain 2019Y71443953III chromosome 1, complete sequence	2242	0.0	CP090676
Burkholderia cenocepacia strain 2009Ycf95III chromosome 1, complete sequence	2242	0.0	CP090760
Burkholderia cenocepacia strain 2008Ycf657 chromosome 1, complete sequence	2242	0.0	CP090763
Burkholderia cenocepacia strain toggle3 chromosome 1, complete sequence	2242	0.0	CP073702
Burkholderia cenocepacia strain toggle2 chromosome 1, complete sequence	2242	0.0	CP073673
Burkholderia cenocepacia strain BKP_SB54 16S ribosomal RNA gene, partial sequence	2237	0.0	MW383910
Burkholderia cenocepacia strain MSMB384WGS chromosome 2, complete sequence	2237	0.0	CP013452
Burkholderia cenocepacia strain BKP_NB47 16S ribosomal RNA gene, partial sequence	2237	0.0	MW383626
Burkholderia cenocepacia strain K5R-2 chromosome 3, complete sequence	2237	0.0	CP053302
Burkholderia cenocepacia strain toggle3 chromosome 2, complete sequence	2237	0.0	CP073704
Burkholderia cenocepacia strain MNR-239 16S ribosomal RNA gene, partial sequence	2237	0.0	KY810685
Burkholderia cenocepacia strain 842 chromosome 1, complete sequence	2237	0.0	CP015033
Burkholderia cenocepacia strain BKP_NB44 16S ribosomal RNA gene, partial sequence	2237	0.0	MW383623
Burkholderia cenocepacia strain VC12308 chromosome 2, complete sequence	2237	0.0	CP019672
Burkholderia cenocepacia strain TY921 chromosome 3, complete sequence	2237	0.0	CP155789
Burkholderia cenocepacia GIMC4560 Bcn122 chromosome 1, sequence	2237	0.0	CP020599
Burkholderia cenocepacia strain BKP_CB42 16S ribosomal RNA gene, partial sequence	2237	0.0	MW383754

Figure 4: Organism identification by BLAST for consensus sequence CE2

Plant growth promoting traits

B. cenocepacia CE2 was tested for its capacity to solubilise and use inorganic phosphates in the form of tricalcium phosphate. After one week of incubation on a solid medium containing $\text{Ca}_3(\text{PO}_4)_2$ as the only phosphate source, a clear and visible dissolution halo with a mean diameter of 1.8 cm (n=3) formed around the colony (Fig. 1), with a solubilisation index of 2.0. The dissolving halo suggests that *B. cenocepacia* CE2 excretes organic acids or enzymes into the surrounding medium, solubilising $\text{Ca}_3(\text{PO}_4)_2$, which is white in its unaltered state. *B. cenocepacia* CE2 also dissolved phosphate (mean halo diameter 3.1 cm, n=3; see Fig. 1).

Because of its phosphate solubilising ability, *B. cenocepacia* CE2 may help provide insight into the natural phosphorous cycle and may be used as an alternative to, or in addition to, synthetic phosphorous fertiliser for better plant growth while reducing agricultural environmental impacts, though potential limitations due to pathogenicity must be considered. In nature, CE2 may help plants develop by solubilising potassium. Another significant strategy to enhance plant growth and development is to synthesise the phytohormone IAA (Kim et al., 2011). After 42 hours of incubation with tryptophan, *B. cenocepacia* CE2 produced an average of $27.2 \pm 1.25 \mu\text{g/mL}$ of IAA. In comparison, using the same technique, the plant-beneficial *Paenibacillus polymyxa* CR1 produced an average of $62.8 \pm 3.4 \mu\text{g} \cdot \text{mL}^{-1}$ of IAA (Weselowski et al., 2016). It is difficult to establish fair comparisons to other studies because IAA production is affected by incubation duration and other environmental conditions (e.g. temperature, media components). For example, de Pereira et al. (2012) reported that production varied from 1.36 to $19.42 \mu\text{g mL}^{-1}$ after 72 h incubation for strains of the genus *Bacillus*, while Maheshwari et al. (2019) reported 4.40-110 $\mu\text{g mL}^{-1}$ after 5 days of incubation for 58 strains of endophytic bacteria isolated from pea and chickpea.

***V. mungo* plant growth promotion in greenhouse conditions**

An experiment using *V. mungo* was undertaken in greenhouse soil to test *B. cenocepacia* CE2's ability to enhance plant development via phosphate solubilisation. The combination of *B. cenocepacia* CE2 and inorganic phosphate [$\text{Ca}_3(\text{PO}_4)_2$] considerably increased various maize plant development metrics when compared to *B. cenocepacia* CE2 alone, $\text{Ca}_3(\text{PO}_4)_2$ alone, or no treatment (Fig. 3). After 6 weeks of growth, the combination of *B. cenocepacia* CE2 and $\text{Ca}_3(\text{PO}_4)_2$ resulted in an 83% increase in chlorophyll content, a 65% increase in whole-plant wet weight, a 61% increase in whole-plant dry weight, a 77% increase in root wet weight, and a 95% increase in root dry weight over $\text{Ca}_3(\text{PO}_4)_2$ alone. The 11% increase in shoot length was not

statistically significant ($p > 0.05$) (Fig. 5). There were no significant differences found between adding *B. cenocepacia* CE2 alone, $\text{Ca}_3(\text{PO}_4)_2$ alone, or no therapy. The fact that *V.mungo* growth improves with the addition of both *B. cenocepacia* CE2 and insoluble phosphate, but not with either alone, leads to the conclusion that the observed growth enhancement is caused by inorganic phosphate solubilisation. The lack of better development from *B. cenocepacia* CE2 alone could imply low inorganic phosphate levels in the soil. It also contradicts the finding that IAA production should boost plant growth; nevertheless, production in vitro does not always reflect IAA levels in the soil environment. Although IAA synthesis does not appear to promote growth in CE2-associated plants, more research into *B. cenocepacia* CE2 may be beneficial due to its other plant-benefiting properties. In 1999, Rodríguez and Fraga discovered a strain of *Burkholderia cepacia* that did not produce IAA but did significantly solubilise mineral phosphate. This strain improved crop output in field tests and is now utilised as a commercial biofertilizer in Cuba. Despite the lack of benefit from *B. cenocepacia* CE2, we cannot rule out the possibility of other growth-promoting mechanisms that are situation-specific, such as improved protection against pests or diseases that were not present in this study. Further research is needed to investigate other growth promoting mechanisms of *B. cenocepacia* CE2, as well as its competitiveness in the natural environment and soil/field conditions.

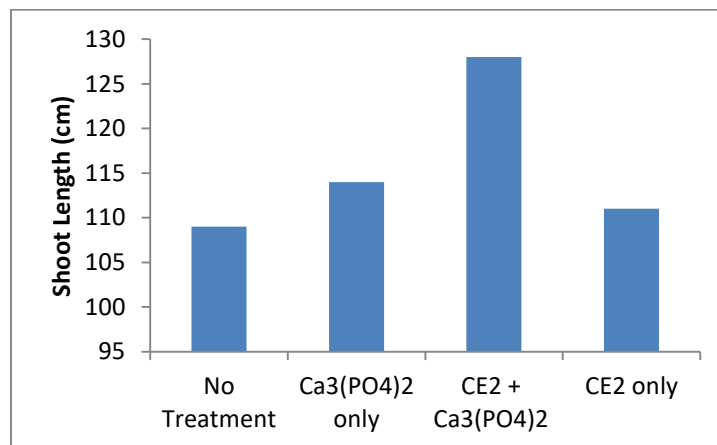


Figure 5: Shoot length of *V.mungo*

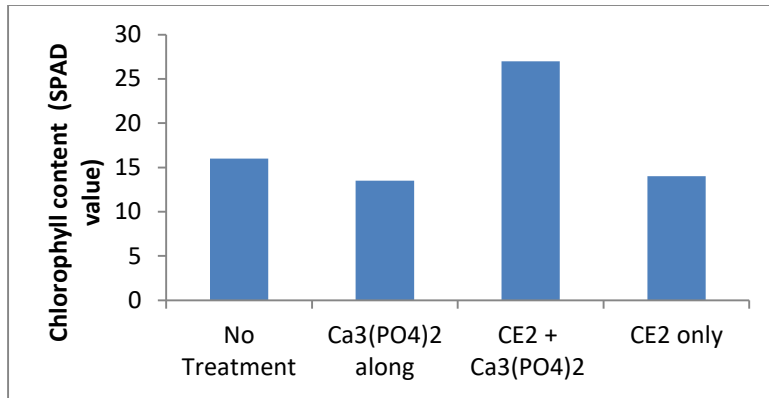


Figure 6: Chlorophyll content of *V.mungo*

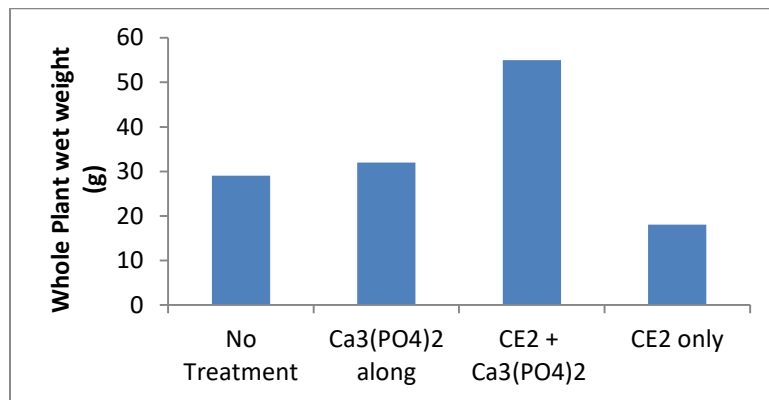


Figure 7: Whole plant wet of *V.mungo*

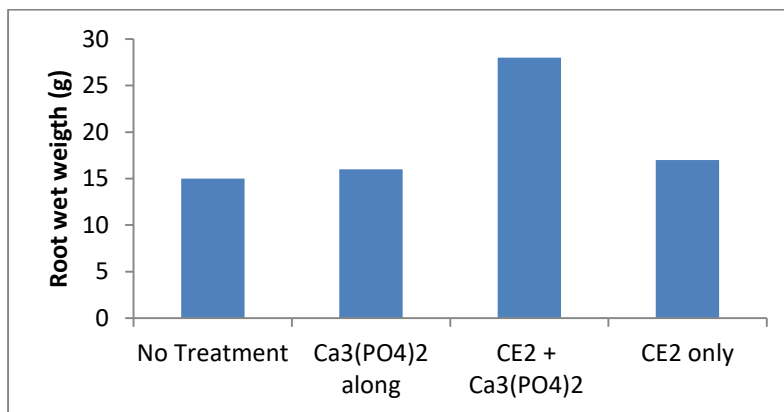


Figure 8: Root wet Weight of *V.mungo*.

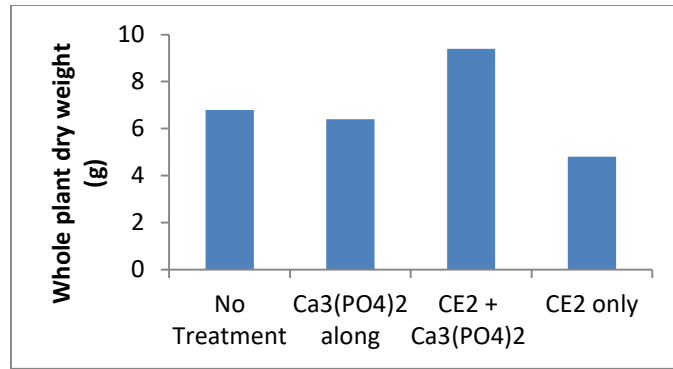


Figure 9: Whole plant Dry weight of *V.mungo*.

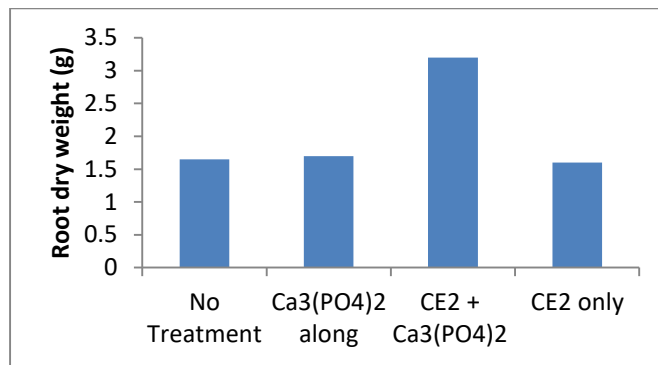


Figure 10: Root Dry Weight of *V.mungo*



Figure 5. The combination of *B. cenocepacia* CE2 and $Ca_3(PO_4)_2$ improves growth of *V. mungo*

Conclusion

The present study successfully isolated and characterized a promising plant growth-promoting rhizobacterium (PGPR), *Burkholderia cenocepacia* CE2, from the rhizospheric soil. Detailed biochemical, morphological, and molecular analyses confirmed the identity of the strain, which demonstrated multiple plant growth-promoting (PGP) traits such as phosphate solubilization, siderophore production, and indole-3-acetic acid (IAA) synthesis activity. These functional attributes highlight the strain's potential role in enhancing nutrient availability and mitigating plant stress under unfavorable conditions. Additionally, the strain exhibited significant antagonistic activity against phytopathogens, suggesting its biocontrol potential. The results from in vitro assays indicate that *B. cenocepacia* CE2 not only promotes root and shoot growth in test plants but also contributes to improved seed germination and vigor. The dual ability of the strain to promote growth and suppress pathogens makes it a promising candidate for development as a bioinoculant in sustainable agriculture. However, considering that some strains of *B. cenocepacia* are opportunistic pathogens in immunocompromised humans, further genomic and safety evaluations are essential before field-scale applications. Overall, this study contributes valuable insights into the utilization of beneficial Burkholderia strains in agriculture and lays the groundwork for future studies focused on field performance and biosafety assessment of *B. cenocepacia* CE2.

REFERENCE

1. Chain, P. S. G., Deneff, V. J., Konstantinidis, K. T., Vergez, L. M., Agulló, L., Reyes, V. L., ... & Tiedje, J. M. (2006). *Burkholderia xenovorans* LB400 harbors a multi-replicon, 9.73-Mbp genome shaped for versatility. *Proceedings of the National Academy of Sciences*, 103(42), 15280–15287. <https://doi.org/10.1073/pnas.0606924103>
2. Coenye, T., & Vandamme, P. (2003). Diversity and significance of *Burkholderia* species occupying diverse ecological niches. *Environmental Microbiology*, 5(9), 719–729. <https://doi.org/10.1046/j.1462-2920.2003.00471.x>
3. Compant, S., Nowak, J., Coenye, T., Clément, C., & Barka, E. A. (2008). Diversity and occurrence of *Burkholderia* spp. in the natural environment. *FEMS Microbiology Reviews*, 32(4), 607–626. <https://doi.org/10.1111/j.1574-6976.2008.00113.x>

4. Dias, A. C. F., van Elsas, J. D., & Salles, J. F. (2019). *Burkholderia* species in the rhizosphere: Environmental and biological perspectives. *Applied Microbiology and Biotechnology*, 103(21–22), 8459–8470. <https://doi.org/10.1007/s00253-019-10129-7>
5. Glick, B. R. (2012). Plant growth-promoting bacteria: Mechanisms and applications. *Scientifica*, 2012, Article ID 963401. <https://doi.org/10.6064/2012/963401>
6. Glick, B. R., Cheng, Z., Czarny, J., & Duan, J. (2007). Promotion of plant growth by ACC deaminase-producing soil bacteria. *European Journal of Plant Pathology*, 119(3), 329–339. <https://doi.org/10.1007/s10658-007-9162-4>
7. Glickmann, E., Dessaux, Y., 1995. A critical examination of the specificity of the Salkowski reagent for indolic compounds produced by phytopathogenic bacteria. *Appl. Environ. Microbiol.* 61, 793–796.
8. Lugtenberg, B., & Kamilova, F. (2009). Plant-growth-promoting rhizobacteria. *Annual Review of Microbiology*, 63, 541–556. <https://doi.org/10.1146/annurev.micro.62.081307.162918>
9. Lowry, R., 1998. Vassarstats: Website for Statistical Computation. Retrieved 2019/10/16 from. <http://vassarstats.net/>.
10. Mitter, B., Petric, A., Shin, M. W., Chain, P. S. G., Hauberg-Lotte, L., Reinhold-Hurek, B., & Sessitsch, A. (2013). Comparative genome analysis of *Burkholderia phytofirmans* PsJN reveals a wide spectrum of endophytic lifestyles and plant growth promotion mechanisms. *BMC Genomics*, 14(1), 1–19. <https://doi.org/10.1186/1471-2164-14-585>
11. Madeira, F., Park, Y.M., Lee, J., Buso, N., Gur, T., Madhusoodanan, N., Basutkar, P., Tivey, A.R.N., Potter, S.C., Finn, R.D., Lopez, R., 2019. The EMBL-EBI search and sequence analysis tools APIs in 2019. *Nucleic Acids Res.* 47, W636–W641.
12. Nautiyal, C.S., 1999. An efficient microbiological growth medium for screening phosphate solubilizing microorganisms. *FEMS Microbiol. Lett.* 170, 265–270.
13. Patten, C. L., & Glick, B. R. (2002). Role of *Pseudomonas putida* indoleacetic acid in the development of the host plant root system. *Applied and Environmental Microbiology*, 68(8), 3795–3801. <https://doi.org/10.1128/AEM.68.8.3795-3801.2002>
14. Suárez-Moreno, Z. R., Caballero-Mellado, J., & Venturi, V. (2012). The *Burkholderia cepacia* complex encompasses some strains that are beneficial to plants and others that

- are lethal to humans: What determines the difference? *Microbial Biotechnology*, 5(2), 180–190. <https://doi.org/10.1111/j.1751-7915.2011.00269.x>
15. Vessey, J. K. (2003). Plant growth promoting rhizobacteria as biofertilizers. *Plant and Soil*, 255(2), 571–586. <https://doi.org/10.1023/A:1026037216893>
16. Vandamme, P., Dawyndt, P., 2011. Classification and identification of the *Burkholderiacepacia* complex: past, present and future. *Syst. Appl. Microbiol.* 34, 87–95.
17. Weselowski, B., Nathoo, N., Eastman, A.W., MacDonald, J., Yuan, Z.C., 2016. Isolation, identification and characterization of *Paenibacillus polymyxa* CR1 with potentials for biopesticide, biofertilization, biomass degradation and biofuel production. *BMC Microbiol.* 16, 244.