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Stage-dependent effect of multifunctional rhizobacteria in cowpea: Early seedling performance does not consistently predict growth and yield under pot conditions

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Abstract

Plant growth-promoting rhizobacteria (PGPR) are often screened using short-duration early seedling assays, but the extent to which early seedling performance corresponds to later crop performance remains uncertain. This study investigated the stage-dependent efficacy of multifunctional rhizobacteria in cowpea *Vigna unguiculata* (L.) Walp., by comparing responses from seedling establishment through vegetative growth, flowering, biomass accumulation and yield. Five isolates-*Bacillus subtilis* JE9, *Bacillus megaterium* JE7, *Priestia aryabhattai* DS2, *Enterobacter mori* BE2 and *Ochrobactrum pseudintermedium* G1-were selected based on multiple plant growth-promoting and biocontrol traits. Following seed biopriming, their effects on early seedling performance were assessed and the three selected isolates (JE9, JE7 and DS2) were subsequently evaluated individually and as a consortium under pot conditions. *Priestia aryabhattai* DS2 showed strong early seedling performance, with a significantly higher shoot fresh weight (1340 mg seedling^{-1}) and root fresh weight (370 mg seedling^{-1}) compared to other isolates and had a seedling vigour index of 4361. However, the relative responses varied across traits and between the seedling assay and the subsequent pot experiment. Under pot conditions, *B. subtilis* JE9 showed the strongest overall performance across subsequent developmental stages indicated by enhanced vegetative growth, biomass accumulation, flowering and yield, increasing yield by 55.4 % over the uninoculated control. The consortium improved several growth and yield attributes but did not consistently outperform the individual isolates. These findings demonstrate that rhizobacterial efficacy is developmentally dynamic and that among the three isolates selected for the pot experiment, early seedling performance did not consistently correspond to subsequent vegetative growth and yield. A stage-wise screening strategy may therefore provide a more reliable basis for selecting effective microbial inoculants for crop improvement.

Keywords: bioinoculant; cowpea; developmental stages; multifunctional rhizobacteria; seed biopriming; stage-dependent efficacy

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1. Introduction

Cowpea (*Vigna unguiculata* (L.) Walp.) is an important grain legume widely cultivated in tropical and subtropical regions and contributes substantially to food and nutritional security, particularly because of its high-quality dietary protein. In addition to its nutritional value, cowpea contributes to sustainable agricultural production through biological nitrogen fixation and its adaptability to relatively low-input production systems (1). However, cowpea productivity is constrained by several biotic and abiotic stresses, including drought, salinity, nutrient limitations and soil-borne pathogens (2). These constraints can affect different phases of crop development, from seed germination and seedling establishment to vegetative and reproductive growth, ultimately reducing yield (3, 4).

Plant growth-promoting rhizobacteria (PGPR) have emerged as promising biological inputs for improving crop establishment, growth and productivity. Depending on the strain and plant–microbe context, rhizobacteria may promote plant performance through diverse mechanisms, including nutrient solubilisation and mobilisation, phytohormone production or modulation, siderophore-mediated iron acquisition and suppression of phytopathogens (5–7). The multifunctional nature of these bacteria makes them attractive candidates for development as bioinoculants because a single strain may potentially provide several complementary benefits to the host

plant (8). However, the presence of multiple plant growth-promoting or biocontrol traits in an isolate does not necessarily translate to consistent beneficial effects throughout the crop growth cycle. The expression of these traits and their contribution to plant performance may depend on the physiological status of the host, environmental conditions and the ability of the bacterium to establish and remain functional in the root-associated environment (9, 10).

Successful establishment and persistence in the root-associated environment are important determinants of rhizobacterial performance. Biofilm formation is one trait that may contribute to these processes by promoting bacterial attachment and aggregation through the production of an extracellular matrix, thereby facilitating microbial persistence and interactions with plant roots (11, 12). Biofilm-associated rhizobacteria have been reported to improve plant growth, nutrient acquisition and productivity in different crops (13–15). However, these functional attributes should not be interpreted as direct predictors of plant performance across all developmental stages. Even bacteria possessing strong plant growth-promoting, biocontrol or biofilm-forming characteristics may differ in their effectiveness as the plant progresses from early establishment to vegetative and reproductive development. Accordingly, biofilm formation was included among the functional traits used for the initial screening of the cowpea-associated rhizobacterial isolates evaluated in the present study.

Plant–microbe interactions are dynamic and may change with plant developmental stage. Changes in plant physiology, root development, nutrient demand and the root-associated environment during crop development can influence bacterial establishment and the expression or effectiveness of beneficial microbial functions. Consequently, a rhizobacterial isolate that produces a strong response during seed germination or early seedling growth may not necessarily remain the most effective treatment during later vegetative growth, flowering or pod development (16, 17). This distinction is particularly important for the selection of microbial inoculants because short-duration seedling assays are frequently used as preliminary screening approaches for identifying promising PGPR. Although such assays are useful for rapidly identifying strains with early plant growth-promoting potential, strong seedling vigour may not necessarily translate into superior biomass accumulation, reproductive development or final yield (18, 19).

Despite the increasing interest in multifunctional rhizobacteria, the relationship between early seedling responses and subsequent agronomic performance in cowpea remains insufficiently understood. In particular, there is a need to determine whether isolates that perform well during early seedling establishment retain their superiority throughout plant development under pot conditions (20). A comparative evaluation of bacterial treatments at different developmental stages can provide a stronger basis for identifying effective bioinoculant candidates than relying on short-term seedling responses alone. Furthermore, combining compatible bacterial isolates into consortia may provide complementary functions and potentially broaden their beneficial effects (21). However, compatibility observed under *in vitro* conditions does not necessarily result in additive or synergistic effects in planta. Therefore, the performance of the consortium should be evaluated directly against individual strains.

The present study evaluated selected biofilm-forming multifunctional rhizobacteria previously isolated from cowpea for their effects on seed germination and early seedling development. The performance of selected isolates, both individually and as a bacterial consortium, was subsequently assessed under pot conditions. This study focused on vegetative growth, flowering, biomass accumulation, pod production and yield. Particular emphasis was placed on determining whether the isolates exhibiting superior performance during early seedling establishment also remained superior during subsequent stages of crop development. By comparing bacterial responses across developmental stages, the study aimed to evaluate the consistency of rhizobacterial performance and determine whether early seedling responses could correspond to subsequent growth and yield in cowpea. We hypothesised that rhizobacterial effects would vary with plant developmental stage and that the isolate with the strongest overall early seedling performance would not necessarily produce the greatest growth and yield under pot conditions. We further examined whether combining selected compatible isolates would promote plant growth more than individual inoculants.

2. Materials and Methods

Selection of bacterial isolates

Cowpea-associated rhizobacterial isolates were initially screened in vitro for multiple plant growth-promoting and biocontrol traits to identify multifunctional candidates for subsequent plant-based evaluations. The screening included exopolysaccharide (EPS) production, biofilm formation, phytohormone production, phosphate solubilisation, siderophore production and antagonistic activity against major fungal pathogens of cowpea. The individual trait responses were evaluated collectively to identify isolates exhibiting a broad spectrum of beneficial characteristics. Genomic DNA was extracted from the selected isolates and its quality was assessed by agarose gel electrophoresis and UV spectrophotometry. The 16S rRNA gene was amplified using universal primers (16S-RS-F: 5'CAGGCCTAACACATGCAAGTC3' and 16S-RSR: 5'GGGCGGWGTGTACAAGGC3') and sequenced

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using the BigDye Terminator v3.1 Cycle Sequencing Kit. The sequences were analysed using Sequence Scanner Software and BioEdit and bacterial identification was performed by comparing the sequences with reference sequences in the NCBI database using BLASTn. Based on their overall multifunctional profiles, five isolates were selected for evaluation: *Bacillus subtilis* JE9, *Bacillus megaterium* JE7, *Priestia aryabhattai* DS2, *Enterobacter mori* BE2 and *Ochrobactrum pseudintermedium* G1 were selected for plant-based evaluation (Table 1). The five shortlisted isolates and their consortium were subsequently used for seed biopriming to evaluate their effects on early seedling establishment. The resulting plant-response data were analysed comparatively and subjected to ranking analysis, to identify isolates showing the most consistent and pronounced effects on plant growth. The isolates with higher values were assigned better ranks; the arithmetic mean of the eight ranks was then calculated for each isolate and a lower mean rank indicated stronger aggregate performance. Based on this second-stage evaluation, three isolates viz., *B. subtilis* JE9, *B. megaterium* JE7 and *P. aryabhattai* DS2, were selected and used along with their consortium for further evaluation under pot conditions. Plants from hydroprimed seeds and those without any priming served as controls in the pot experiment. Thus, isolate selection involved two sequential stages: (i) selection of five multifunctional isolates from the initial collection based on their in vitro functional profiles and multivariate analysis and (ii) selection of three isolates from these five based on their performance in planta. This experimental approach enabled comparison of rhizobacterial performance between the early seedling stage and subsequent vegetative and reproductive stages of cowpea.

Preparation of bacterial inoculum and seed biopriming

The selected bacterial isolates were grown individually in nutrient broth for 24 hr at 28 ± 2 °C under shaking conditions (120 rpm). The cultures were adjusted to an optical density (OD) of approximately 0.6 at 600 nm to obtain a standardised bacterial suspension. The viable bacterial population (in CFU mL^{-1}) corresponding to the standardised OD was determined by serial dilution and plate counting. For seed biopriming, each standardised culture was diluted with sterile distilled water to obtain a desired working inoculum concentration of approximately 10^6 CFU mL^{-1}. For individual bacterial treatments, each isolate was prepared separately at this concentration. For the seedling assay, the five-isolate consortium comprising JE9, JE7, DS2, BE2 and G1 was prepared by mixing equal volumes of the respective individual bacterial suspensions, each adjusted to 10^6 CFU mL^{-1}. For the subsequent pot experiment, the three-isolate consortium comprised of JE9, JE7 and DS2 in equal proportions. Thus, the resulting five-isolate consortium had a final total bacterial concentration of approximately 10^6 CFU mL^{-1}. Similarly, for the pot experiment, the three-isolate consortium comprising JE9, JE7 and DS2 was prepared by mixing equal volumes of the respective individual suspensions, each adjusted to 10^6 CFU mL^{-1}, resulting in a final total concentration of approximately 10^6 CFU mL^{-1}. The freshly prepared individual and consortium inocula were used for seed biopriming and subsequent experiments.

Cowpea seeds were surface sterilised under aseptic conditions and subsequently immersed in the respective bacterial suspensions for 4 hr, then dried at 28 ± 2 °C for 1 hr and stored at room temperature till sowing. Seeds of uniform shape and size were used and surface sterilisation was carried out by immersing in 4 % sodium hypochlorite solution for 3 min and the seeds were subsequently washed five times with sterile distilled water to remove residual disinfectant. The last wash was plated on nutrient agar medium to check for sterility. Following biopriming, the seeds were removed aseptically and used for the respective seedling or pot experiments. For the early seedling growth study, seeds hydroprimed with sterile distilled water for the same duration served as the control, whereas the pot experiment included both hydroprimed and non-primed seeds as controls. The primed seeds were sown within 24 hr.

Evaluation of seed germination and seedling growth

A roll-towel assay was conducted to evaluate the effects of bacterial inoculation on seed germination and early seedling development of cowpea. Seeds of cowpea (*Vigna unguiculata* (L.) Walp.) cv. Anaswara obtained from the Instructional Farm, Vellayani, were used for the experiment. The selected bacterial isolates were grown individually for 24 hr and standardised to an optical density (OD_{600}) of 0.6 as mentioned earlier.

For each bacterial treatment, seeds were bioprimed by immersing them in the respective bacterial suspension for 4 hr under aseptic conditions. The experiment was conducted with 3 independent replications (n = 3), with 30 seeds per replication. The 30 seeds were treated as subsamples within the biological replication and replication-level responses were used for statistical analysis. Following biopriming, the treated seeds were placed on sterile, moistened germination paper at approximately 1 cm intervals, with 10 seeds arranged per roll. The papers were rolled carefully and maintained in an upright position in sterile beakers containing sterile distilled water. The rolls were incubated at 28 °C under controlled conditions and germination and seedling growth were assessed after 10 days.

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Table 1. Functional characteristics of cowpea rhizosphere bacterial isolates selected for plant evaluation

Bacterial isolatez	EPS (g L^{-1})	Biofilm formation (OD_{595})	IAA production (µg mL^{-1})	Gibberellic acid production (µg mL^{-1})	Phosphate Solubilisation Index	Siderophore Producing Index	Antagonism against fungal pathogens [a]
Enterobacter mori BE2	0.69 ± 0.01	1.51 ± 0.05	17.02 ± 0.42	49.71 ± 5.27	2.34 ± 0.13	2.71 ± 0.06	Negative
Priestia aryabhattai DS2	0.76 ± 0.01	1.88 ± 0.04	112.82 ± 6.22	106.68 ± 2.47	6.63 ± 0.06	2.64 ± 0.07	Negative
Ochrobactrum pseudintermedium G1	0.75 ± 0.01	1.61 ± 0.06	118.87 ± 4.53	78.88 ± 2.37	1.00 ± 0.00	2.56 ± 0.08	Negative
Bacillus megaterium JE7	1.06 ± 0.02	1.59 ± 0.03	133.77 ± 2.58	101.39 ± 4.06	5.93 ± 0.21	2.65 ± 0.09	Negative
Bacillus subtilis JE9	1.21 ± 0.01	1.75 ± 0.03	111.53 ± 8.32	86.68 ± 11.64	3.57 ± 0.06	5.07 ± 0.31	Positive

EPS: exopolysaccharide; OD_{595}: optical density measured at 595 nm; IAA: indole-3-acetic acid. Values are mean ± standard error. Superscript *a* indicates antagonistic activity against the fungal pathogens *Fusarium oxysporum*, *Phytophthora* sp., *Colletotrichum gloeosporioides*, *Sclerotium rolfsii*, *Rhizoctonia solani*.

Germination per cent was calculated based on the proportion of seeds that produced normal seedlings. Seedling growth was evaluated by measuring shoot length and root length. Shoot and root fresh weights were recorded separately, after which the respective tissues were dried to constant weight for determination of shoot and root dry weights. Seedling vigour index was calculated based on germination per cent and total seedling length using the given formula.

Seedling vigour index (I) = Germination (%) x (Shoot length (cm) + Root length (cm))

The parameters recorded were germination percentage, shoot length, root length, seedling vigour index, shoot fresh weight, root fresh weight, shoot dry weight and root dry weight (22, 23). This assay was used to assess the effects of the selected rhizobacteria during the early stage of plant establishment and to determine whether early seedling responses differed among bacterial isolates.

Evaluation of rhizobacterial performance across subsequent crop development under pot conditions

The five bacterial isolates were ranked independently for each of the eight seedling parameters, with higher values considered more desirable. An overall mean rank was calculated across the eight parameters for each isolate. The three isolates with the lowest mean rank values were selected for subsequent pot evaluation. The selected bacterial isolates were further evaluated under pot conditions to determine whether their effects observed during early seedling development were maintained throughout subsequent vegetative and reproductive stages of cowpea. The treatments comprised individual inoculation with *B. subtilis* JE9, *B. megaterium* JE7 and *P. aryabhattai* DS2; a three-isolate consortium comprising DS2 + JE7 + JE9; hydropriming; and an uninoculated control. The experiment consisted of 6 treatments with four independent replications (n = 4) per treatment, with 10 pots per replication. Each pot contained one plant. The 240 pots were randomly distributed throughout the experimental area according to a completely randomised design (CRD) generated prior to the experiment, with 40 pots allocated to each treatment (Supplementary Table 1). The replication was considered the independent statistical unit and replicate-level means were used for statistical analysis. The pot experiment enabled comparison of the performance of individual isolates and their consortium during later stages of crop development following the initial seed-biopriming treatment.

The pot experiment was conducted in the open land area near the Department of Agricultural Microbiology, College of Agriculture, Vellayani, Thiruvananthapuram, Kerala from March to June 2026, during the pre-monsoon season, with the ambient temperature, relative humidity and natural photoperiod/light conditions recorded throughout the experimental period (Supplementary Fig. 1 and 2). The soil represents the southern lateritic soils (AEU-8) and belongs to the Vellayani series. The soil was sandy clay loam and acidic in reaction. Before establishing the experiment, the soil was analysed for pH, electrical conductivity (EC), organic carbon and available N, P_2O_5 and K_2O using standard procedures. The initial soil properties were: pH 5.73, EC 0.168 dS m^{-1}, organic carbon 1.24 %, available N 121.02 kg ha^{-1}, available P_2O_5 39.14 kg ha^{-1} and available K_2O 235.57 kg ha^{-1}.

For initial seedling establishment, the bioprimed seeds were sown in a substrate consisting of vermiculite, perlite, sand, vermicompost and coir pith in a 1: 1: 1: 1: 0.25 (v/v) ratio. Following establishment, uniform seedlings were transplanted into pots containing sand, cow dung and soil mixed at a 1 : 1 : 1 ratio. The experiment was conducted in 10-inch diameter pots, each containing approximately 7 kg of soil. Nutrient application was based on the Kerala Agricultural University Package of Practices

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Recommendations (24) for cowpea, corresponding to 20: 30: 10 kg N: P_2O_5: K_2O ha^{-1}, together with FYM at 20 t ha^{-1} and lime at 250 kg ha^{-1}. Half of the recommended N and the full recommended quantities of P_2O_5 and K_2O were applied basally and the remaining half of N was applied 15–20 days after transplanting. The recommended dose of fertilisers was applied uniformly to the treatments. A bacterial suspension of 10 mL (with approximately 10^6 CFU mL^{-1}) was subsequently applied to the rhizosphere at monthly intervals as per treatment. The same inoculation procedure and inoculum concentration were maintained across bacterial treatments to ensure comparability among treatments.

The present study monitored plant growth and developmental responses throughout the crop cycle. Plant height, number of leaves and number of branches measured at 30 and 60 days were analysed using repeated-measures analysis of variance (ANOVA), with treatment as the between-subject factor and sampling time as the within-subject factor. The treatment × time interaction was also tested. Flowering days were recorded to assess reproductive transition. Yield performance was evaluated based on the number of pods and pod weight recorded across three successive harvests. At the end of the experiment, plants were carefully uprooted and evaluated for biomass-related parameters i.e., shoot and root fresh weight and dry weight.

The pot experiment evaluation was therefore designed to determine whether the isolate showing superior performance during early seedling establishment also maintained its effectiveness during vegetative growth, flowering, biomass accumulation and yield formation. This stage-wise comparison provided the basis for assessing the stage-dependent efficacy of the selected rhizobacteria and determining whether early seedling performance could serve as a reliable indicator of performance throughout the cowpea crop cycle.

Statistical analysis

Seedling-growth traits and single-time-point pot experiment traits were analysed using one-way ANOVA, with treatment as the fixed factor. When the overall treatment effect was statistically significant, pairwise comparisons among treatment means were performed using Tukey's honestly significant difference (HSD) at $\alpha = 0.05$.

In the pot experiment, plant height, number of branches and number of leaves recorded at 30 and 60 days after sowing (DAS) were analysed using repeated-measures ANOVA, with treatment as the between-subject factor and sampling time as the within-subject factor; the treatment × sampling time interaction was also evaluated. Tukey-adjusted pairwise comparisons of estimated marginal means were used to compare treatments within each sampling time. With only two sampling times, the sphericity condition is not a separate estimable concern; residual diagnostics were used to assess model fit.

The independent experimental unit was the replication-level mean, with three independent replications for the seedling assay (30 seeds per replication) and four independent replications (10 pots per replicate set) per treatment for the pot experiment. Seeds and pots within each replication were treated as subsamples where applicable. The assumptions of the fitted models were assessed using appropriate residual diagnostics. The statistical significance threshold was set at $p < 0.05$. For each analysis, the F statistic, degrees of freedom and p - value were reported. All statistical analyses, including one-way ANOVA and repeated-measures ANOVA, were performed using RAISINS 2.0.0 software (25) with the appropriate analysis procedures selected according to the experimental design. Heat maps were generated from Z-score-standardised data to visualise the relative multifunctional profiles of the bacterial isolates and the growth and yield responses of cowpea following bacterial biopriming.

3. Results

Multifunctional characteristics of selected rhizobacteria

The selected isolates exhibited distinct multifunctional profiles when the measured plant growth-promoting traits were standardised as Z-scores (Fig. 1). *Bacillus subtilis* JE9 showed the highest standardised scores for EPS and siderophore production and a positive standardised score for biofilm formation. *Priestia aryabhattai* DS2 showed the highest standardised biofilm-associated score and relatively high scores for gibberellic acid production and phosphate solubilisation, whereas *B. megaterium* JE7 showed comparatively high Z-scores for IAA production and phosphate solubilisation. In contrast, *E. mori* BE2 exhibited predominantly negative standardised scores across the measured functional traits. The results indicate substantial differences in the relative functional profiles of the selected isolates and provided the basis for their subsequent evaluation in plant assays.

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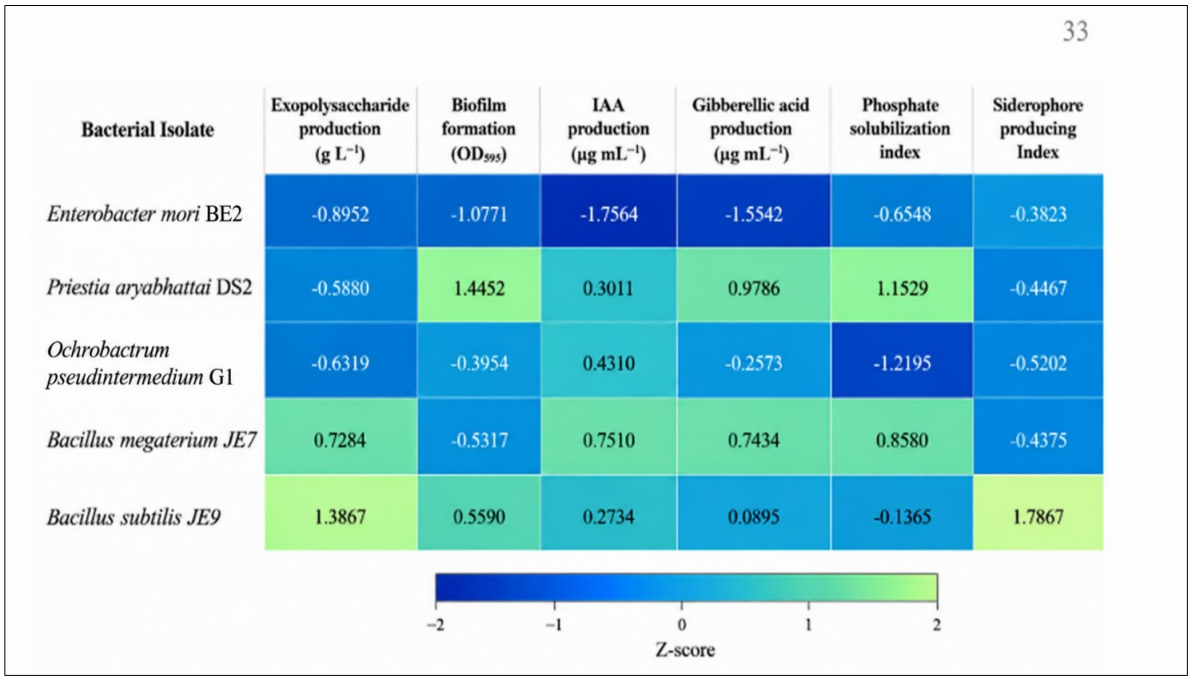


Fig. 1. Z-score standardised multifunctional profile of selected rhizobacterial isolates. Positive and negative Z-scores indicate above- and below-average performance, respectively, for each functional trait. *Bacillus subtilis* JE9 showed the strongest EPS and siderophore profiles, *Priestia aryabhattai* DS2 showed strong biofilm formation, gibberellic acid production and phosphate solubilisation, while *Bacillus megaterium* JE7 showed relatively high IAA production and phosphate-solubilising activity.

Rhizobacterial effects on early seedling establishment and growth

Among the isolates evaluated in roll towel assay, *P. aryabhattai* DS2 exhibited strong performance for several seedling growth traits (Fig. 2) and biomass parameters. Seeds treated with DS2 recorded significantly longer shoots (19.88 cm) and roots (29.00 cm) compared to hydropriming, it was on par with *B. megaterium* JE7. The seedling vigour index of *P. aryabhattai* DS2 (4361.00) was statistically comparable to that of *B. subtilis* JE9 (4496.67) (Table 2). *Priestia aryabhattai* DS2 also recorded significantly higher fresh weight of shoot (1340 mg seedling^{-1}) and root (370 mg seedling^{-1}) and dry weights of shoot (77.50 mg seedling^{-1}) and root (52.50 mg seedling^{-1}) compared to other treatments ($p < 0.05$). In contrast, *B. subtilis* JE9-treated seeds recorded the maximum germination percentage (94.67 %) and seedling vigour index (4496.67), whereas *B. megaterium* JE7 promoted root elongation, recording the highest root length (30.50 cm).

These results revealed that the isolates exhibited distinct growth-promoting profiles. *Priestia aryabhattai* DS2 showed strong performance for several growth and biomass parameters, *B. subtilis* JE9 enhanced germination and seedling vigour and *B. megaterium* JE7 promoted root development. Based on these the isolates were ranked across the measured seedling parameters and DS2, JE7 and JE9 were selected for pot evaluation, individually and as a consortium, to determine whether early seedling responses predicted rhizobacterial performance during subsequent vegetative and reproductive stages of cowpea development.

Stage-dependent effects of rhizobacterial isolate on vegetative growth under pot conditions

Inoculation with growth-promoting rhizobacteria influenced cowpea vegetative growth under pot conditions, with differences among treatments observed in plant height, branching and leaf production (Table 3). Among the isolates evaluated, *B. subtilis* JE9 showed the strongest overall vegetative growth response and it was statistically on par with *B. megaterium* JE7 (Fig. 3).

Plant height increased from 30 to 60 DAS across all treatments. On comparing the treatment effects, *B. subtilis* JE9-treated plants recorded the maximum height 87.50 cm which was on par with *B. megaterium* JE7-treated plants (83.11 cm). All treatments showed significantly higher plants compared to control plants (59.88 cm) (Fig. 4, Table 3). Notably, *P. aryabhattai* DS2, which exhibited strong performance for several parameters during the early seedling assay, did not show the strongest overall vegetative growth under pot conditions. Instead, *B. subtilis* JE9, which exhibited a different pattern of responses during the seedling assay, recorded the highest plant height across the assessment period. This divergence indicates that performance across individual seedling traits did not necessarily result in subsequent vegetative performance, supporting the stage-dependent nature of rhizobacterial effects observed in the present study.

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Table 2. Effect of seed biopriming with rhizobacteria on germination and early seedling growth of cowpea (*Vigna unguiculata* (L.) Walp.) var Anaswara

Treatment	Germination (%)	Shoot length (cm)	Root length (cm)	Seedling vigour index	Shoot fresh weight (mg)	Root fresh weight (mg)	Shoot dry weight (mg)	Root dry weight (mg)
Enterobacter mori BE2	79.00 ± 1.41^{cd}	15.25 ± 0.96^{e}	12.50 ± 1.73^{d}	2291.00 ± 41.01^{f}	475.00 ± 31.09^{d}	157.50 ± 5.00^{f}	25.00 ± 5.77^{e}	12.50 ± 5.00^{cd}
Priestia aryabhattai DS2	89.00 ± 1.41^{ab}	19.88 ± 0.48^{a}	29.00 ± 0.71^{ab}	4361.00 ± 69.30^{ab}	1340.00 ± 87.56^{a}	370.00 ± 0.00^{a}	77.50 ± 5.00^{a}	52.50 ± 5.00^{a}
Ochrobactrum pseudintermedium G1	91.00 ± 1.41^{a}	16.00 ± 0.58^{de}	27.38 ± 0.75^{b}	3867.50 ± 60.10^{c}	1022.50 ± 75.00^{c}	272.50 ± 5.00^{e}	55.00 ± 5.77^{bc}	22.50 ± 5.00^{c}
Bacillus megaterium JE7	83.67 ± 0.47^{bc}	18.75 ± 0.29^{ab}	30.50 ± 0.71^{a}	4183.33 ± 23.57^{b}	1165.00 ± 12.91^{b}	340.00 ± 0.00^{b}	67.50 ± 9.57^{ab}	42.50 ± 5.00^{ab}
Bacillus subtilis JE9	94.67 ± 1.89^{a}	17.75 ± 0.50^{bc}	30.12 ± 0.25^{a}	4496.67 ± 89.57^{a}	1155.00 ± 30.00^{b}	310.00 ± 0.00^{d}	32.50 ± 5.00^{de}	35.00 ± 5.77^{b}
Consortium	75.33 ± 1.89^{d}	18.38 ± 0.25^{b}	29.25 ± 0.29^{ab}	3578.33 ± 89.57^{d}	1225.00 ± 12.91^{b}	325.00 ± 5.77^{c}	65.00 ± 5.77^{ab}	37.50 ± 5.00^{b}
Hydropriming	81.67 ± 2.36^{cd}	16.88 ± 0.75^{cd}	20.88 ± 0.48^{c}	3000.83 ± 57.75^{e}	1157.50 ± 9.57^{b}	267.50 ± 5.00^{e}	45.00 ± 5.77^{cd}	10.00 ± 0.00^{d}
HSD (α= 0.05)	6.51	1.36	1.93	259.63	108.46	9.04	14.41	10.93
SE(m)	1.16	0.3	0.42	46.32	23.59	1.97	3.13	2.38
CV (%)	1.93	3.36	3.27	1.78	4.38	1.35	11.94	15.67

Values are expressed as mean ± standard error (SE) of three replications. HSD: honestly significant difference; SE(m): standard error of the mean; CV: coefficient of variation. Seedling vigour index was calculated as germination percentage × total seedling length (cm). Data were analysed using one-way analysis of variance (ANOVA), followed by Tukey's HSD test for mean separation at $p \leq 0.05$. Means sharing at least one common superscript letter within a column are not significantly different at the 5% probability level.

Table 3. Effects of bacterial inoculation and assessment days on vegetative growth of cowpea (*Vigna unguiculata*) var Anaswara under repeated-measures two-way analysis of variance (ANOVA)

Factor / Treatment × Day	Plant height (cm)	No. of branches	No. of leaves
Main effect: Treatment			
T1 (*Bacillus subtilis* JE9)	87.50 ± 4.63^{a}	8.50 ± 0.93^{a}	49.62 ± 6.44^{a}
T2 (*Bacillus megaterium* JE7)	83.11 ± 5.18^{a}	8.25 ± 1.04^{ab}	46.12 ± 6.03^{a}
T3 (*Priestia aryabhattai* DS2)	74.57 ± 6.50^{b}	6.62 ± 0.52^{cd}	38.86 ± 3.54^{b}
T4 (DS2 + JE7 + JE9)	73.25 ± 3.88^{b}	7.38 ± 0.92^{bc}	48.25 ± 6.32^{a}
T5 (Hydropriming)	65.62 ± 3.50^{bc}	6.00 ± 0.76^{de}	30.00 ± 6.39^{c}
Absolute control	59.88 ± 5.14^{c}	5.38 ± 1.30^{e}	30.38 ± 4.37^{c}
F (5, 18)	31.04**	33.61**	54.61**
p-value	<0.001	<0.001	<0.001
MSE	27.98	0.37	11.51
Generalised η^2	0.89	0.83	0.91
Main effect: Day			
30 days	71.42 ± 10.58^{b}	6.38 ± 1.31^{b}	36.00 ± 8.15^{b}
60 days	76.92 ± 10.27^{a}	7.67 ± 1.31^{a}	44.88 ± 9.33^{a}
F (1, 18)	189.24**	58.84**	169.08**

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p-value	<0.001	<0.001	<0.001
MSE	2.06	0.34	5.59
Generalised η²	0.43	0.61	0.75
Interaction: Treatment × Day			
Bacillus subtilis JE9 × 30 D	85.00 ± 4.08	7.75 ± 0.50	44.00 ± 2.45[a]
Bacillus subtilis JE9 × 60 D	90.00 ± 4.08	9.25 ± 0.50	55.25 ± 2.50[a]
Bacillus megaterium JE7 × 30 D	80.00 ± 5.00	7.50 ± 0.58	41.00 ± 3.16[ab]
Bacillus megaterium JE7 × 60 D	87.00 ± 1.41	9.00 ± 0.82	51.25 ± 2.22[a]
Priestia aryabhattai DS2 × 30 D	70.00 ± 5.00	6.50 ± 0.58	36.00 ± 2.71[b]
Priestia aryabhattai DS2 × 60 D	78.00 ± 5.60	6.75 ± 0.50	40.50 ± 2.89[b]
Consortium (DS2 + JE7 + JE9) × 30 D	70.75 ± 3.30	6.75 ± 0.50	43.25 ± 2.99[a]
Consortium (DS2 + JE7 + JE9) × 60 D	75.75 ± 2.75	8.00 ± 0.82	53.25 ± 4.19[a]
Hydropriming × 30 D	63.50 ± 3.11	5.50 ± 0.58	24.50 ± 1.91[c]
Hydropriming × 60 D	67.75 ± 2.63	6.50 ± 0.58	35.50 ± 3.32[b]
Absolute control × 30 D	56.75 ± 5.38	4.25 ± 0.50	27.25 ± 2.50[c]
Absolute control × 60 D	63.00 ± 2.58	6.50 ± 0.58	33.50 ± 3.51[b]
F (5, 18)	1.54[Ns]	2.56[Ns]	2.82*
p-value	0.23	0.06	0.05
Generalised η²	0.03	0.25	0.20

Values are mean ± standard deviation. Within each main-effect section (Treatment and Day), means followed by the same superscript letter are not significantly different according to the post-hoc multiple-comparison test. The treatment and day main effects were significant at the 1 % level for all three growth parameters, whereas the treatment × day interaction was significant at the 5 % level for no. of leaves and it was non-significant for plant height and no. of branches. JE9, JE7 and DS2 denote the respective treatments; T1 = JE9, T2 = JE7, T3 = DS2, T4 = DS2 + JE7 + JE9, T5 = hydropriming. MSE = mean square error; η² = generalised eta squared (effect size); NS: non-significant; **: significant at $p < 0.01$. Data are from the repeated-measures two-way ANOVA of cowpea growth.

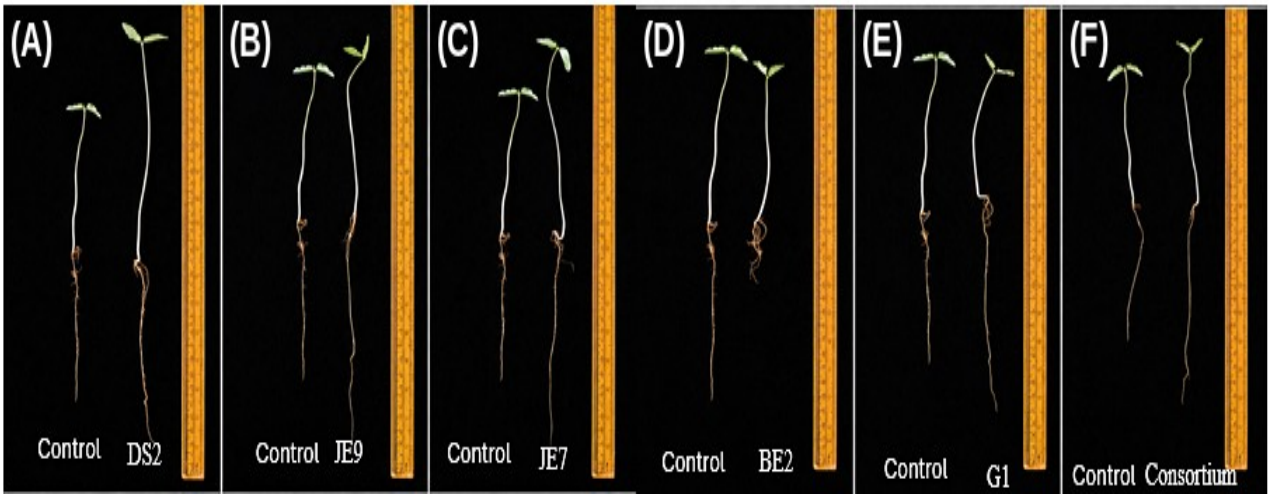


Fig. 2. Effect of rhizobacterial isolates on cowpea seedling growth in the roll-towel assay. (A) *Priestia aryabhattai* DS2; (B) *Bacillus subtilis* JE9; (C) *Bacillus megaterium* JE7; (D) *Enterobacter mori* BE2; (E) *Ochrobactrum pseudintermedium* G1; (F) consortium, each compared with the respective control.

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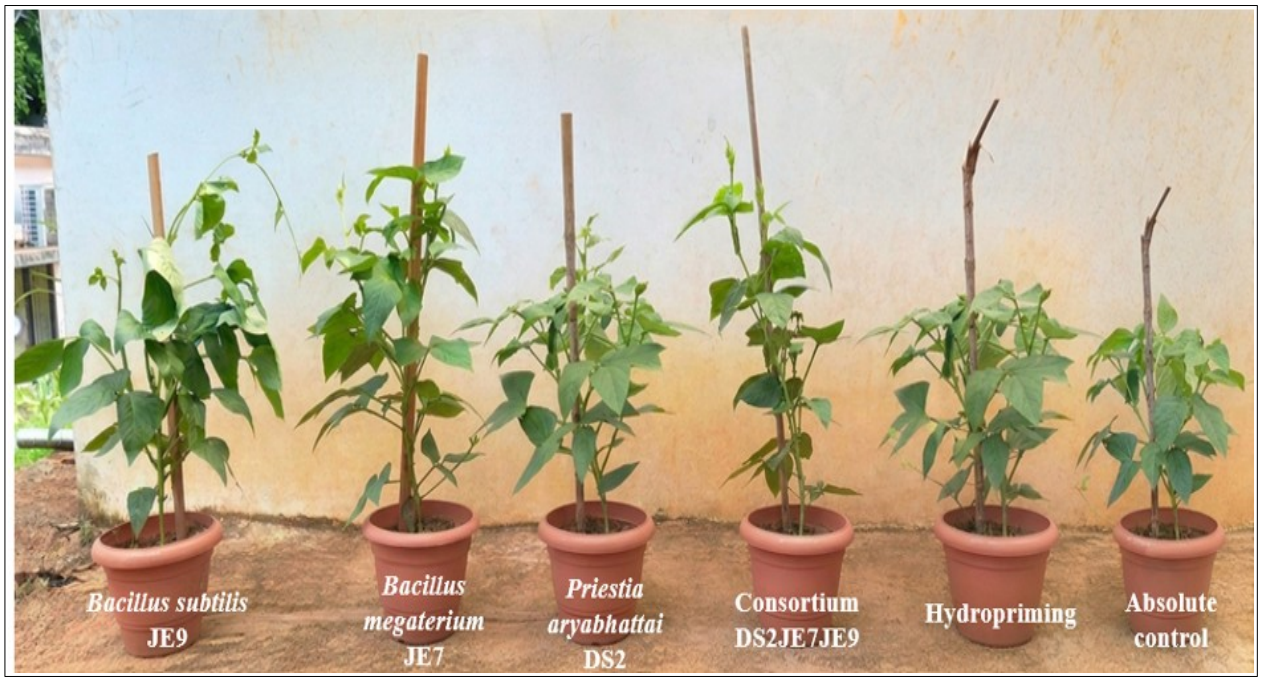


Fig. 3. Comparative growth performance of cowpea plants (*Vigna unguiculata*) var Anaswara at 30 days after sowing following inoculation with individual multifunctional rhizosphere bacterial isolates and their consortium.

Rhizobacterial effects on branching and leaf development

Rhizobacterial treatments influenced the development of primary branches and leaves during plant growth under pot conditions. Bacterial treatments influenced branch development at both assessment times. *Bacillus subtilis* JE9 recorded 7.75 and 9.25 branches plant^{-1} at 30 and 60 DAS, respectively, while *B. megaterium* JE7 recorded 7.50 and 9.00 branches plant^{-1}. The consortium recorded 6.75 and 8.00 branches plant^{-1}, whereas *P. aryabhattai* DS2 recorded 6.50 and 6.75 branches plant^{-1}. Hydropriming recorded 5.50 and 6.50 branches plant^{-1}, while the absolute control recorded 4.25 and 6.50 branches plant^{-1} at 30 and 60 DAS, respectively (Table 3). A similar treatment pattern was observed for leaf production.

Bacillus subtilis JE9 recorded 44.00 and 55.25 leaves plant^{-1} at 30 and 60 DAS, respectively, followed by *B. megaterium* JE7 which recorded 39.60 and 51.25 leaves plant^{-1}. The consortium recorded 43.25 and 53.25 leaves plant^{-1}, whereas DS2 recorded 36.67 and 40.50 leaves plant^{-1}. Hydropriming and the absolute control recorded lower leaf numbers, with 24.50 and 35.50 leaves plant^{-1} and 27.25 and 33.50 leaves plant^{-1}, respectively (Table 3). The interaction effect was found to be significant in the case of the number of leaves. The plants with *B. subtilis* JE9, *B. megaterium* JE7 and consortium (DS2 + JE7 + JE9) treatment showed a significantly higher number of leaves compared to *P. aryabhattai* DS2, hydropriming and absolute control

The consistently higher branching and leaf production observed in cowpea plants treated with *B. subtilis* JE9 further indicated its stronger performance during the vegetative phase. Notably, this response contrasted with the early seedling assay, in which *P. aryabhattai* DS2 exhibited strong performance for several seedling growth and biomass parameters, while JE9 recorded the highest germination per cent and seedling vigour index. These contrasting responses further support the observation that rhizobacterial performance can vary with the developmental stage of the host plant.

Rhizobacterial effects on flowering time

Rhizobacterial treatments also influenced the onset of flowering in cowpea. *Bacillus subtilis* JE9 (31.75 days after sowing) and *B. megaterium* JE7 (34.00 days) primed plants showed early flowering, which was significantly earlier compared to other treatments. Plants treated with *P. aryabhattai* DS2 reached flowering at 37.00 days, whereas flowering occurred at 39.00 and 40.25 days in the hydroprimed and uninoculated control treatments, respectively.

Compared with the uninoculated control, *B. subtilis* JE9 treatment advanced flowering by approximately 8.5 days. The earlier flowering of *B. subtilis* JE9-treated plants, together with their superior vegetative growth, indicated that *B. subtilis* JE9 maintained stronger performance during the transition from vegetative to reproductive development.

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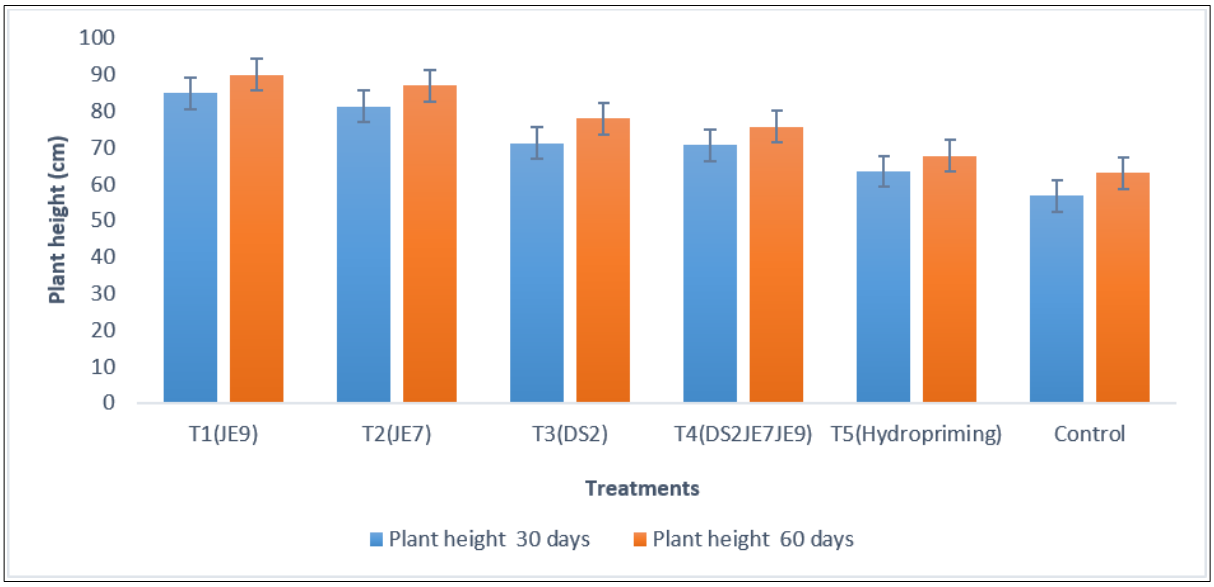


Fig. 4. Effect of seed biopriming with the rhizosphere bacterial isolates on plant height at 30 and 60 days after sowing.

Rhizobacterial effects on pod production and yield

The differences among rhizobacterial treatments became particularly evident during pod production and yield formation. *Bacillus subtilis* JE9 produced the highest number of pods (24.25 pods plant^{-1}), followed by *B. megaterium* JE7 (22.75 pods plant^{-1}) (Table 4). *Priestia aryabhattai* DS2 and the three-isolate consortium each produced 19.00 pods plant^{-1}, whereas the uninoculated control produced 17.25 pods plant^{-1}.

A similar treatment pattern was observed for yield. *Bacillus subtilis* JE9 recorded the highest cumulative pod yield (80.57 g plant^{-1}), followed by *B. megaterium* JE7 (67.88 g plant^{-1}), the three-isolate consortium (63.31 g plant^{-1}) and DS2 (56.03 g plant^{-1}). The uninoculated control recorded a cumulative yield of 51.85 g plant^{-1}. Thus, JE9 resulted in a 55.4 % higher yield than the uninoculated control (Table 4).

The superior pod production and yield recorded with *B. subtilis* JE9, together with its greater vegetative growth and earlier flowering, indicated that its strong performance extended from vegetative development into the reproductive phase. In contrast, *P. aryabhattai* DS2, which exhibited strong performance for several early seedling growth and biomass parameters, did not maintain the same level of performance during later crop development. These results provide further evidence that early seedling responses alone were not necessarily predictive of subsequent yield performance under the pot conditions tested.

Rhizobacterial effects on plant biomass accumulation

Rhizobacterial inoculation also influenced biomass accumulation at the end of the pot experiment. Among the treatments, *B. subtilis* JE9 recorded the maximum shoot fresh weight (193.75 g plant^{-1}) and root fresh weight (35.75 g plant^{-1}). *Bacillus megaterium* JE7 recorded corresponding shoot and root fresh weights of 157.50 and 31.00 g plant^{-1}, respectively, while the three-isolate consortium recorded 131.25 and 27.50 g plant^{-1}, respectively. The uninoculated control recorded comparatively lower shoot and root fresh weights of 116.00 and 21.25 g plant^{-1}, respectively (Table 4).

The greater biomass accumulation observed in *B. subtilis* JE9-treated plants was consistent with their superior vegetative growth and reproductive performance, indicating that the effectiveness of *B. subtilis* JE9 extended across multiple stages of crop development. However, these observations were interpreted in relation to the statistical comparisons among treatments rather than solely on the basis of numerical differences.

Ranking-based comparison of treatment performance across developmental stages

The stage-wise relative ranking analysis was used to describe changes in relative numerical ordering of treatments across developmental stages (Fig. 5), indicating stage-dependent variation in rhizobacterial efficacy. The ranking analysis does not constitute a test of statistical significance and was not used to infer significant differences among treatments. *Bacillus subtilis* JE9 ranked first for germination and became the highest-ranked treatment for growth at 30 and 60 DAS and for yield, although it ranked second for harvest biomass. *Priestia aryabhattai* DS2 ranked first for early seedling growth but declined to third rank from 30 DAS through yield and harvest biomass. *Bacillus megaterium* JE7 showed comparatively stable intermediate performance, ranking second for early seedling growth, vegetative growth and yield and first for harvest biomass. Hydropriming remained among the lowest-ranked treatments from early seedling growth through harvest. Overall, the rank shifts demonstrate that treatment performance was not uniform across developmental stages.

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Table 4. Effect of selected rhizobacterial isolates on flowering, biomass and yield of cowpea under pot conditions

Treatments	Days to flowering	No. of pods (per plant)	Yield (g/plant)	Fresh weight (g/plant)		Dry weight (g/plant)	
				Shoot	Root	Shoot	Root
Bacillus subtilis JE9	31.75 ± 2.06^{e}	24.25 ± 0.50^{a}	80.57 ± 2.09^{a}	193.75 ± 7.50^{a}	35.75 ± 0.96^{a}	40.00 ± 2.94^{a}	10.25 ± 0.96^{a}
Bacillus megaterium JE7	34.00 ± 1.63^{de}	22.75 ± 0.96^{b}	67.88 ± 4.50^{b}	157.50 ± 6.45^{b}	31.00 ± 1.15^{b}	31.75 ± 2.22^{b}	6.50 ± 0.58^{b}
Priestia aryabhattai DS2	37.00 ± 0.82^{bc}	19.00 ± 0.82^{c}	56.03 ± 2.32^{d}	122.50 ± 2.89^{d}	22.50 ± 2.89^{d}	24.75 ± 0.96	5.25 ± 0.50^{c}
Consortium (DS2 + JE7 + JE9)	34.75 ± 0.96^{cd}	19.00 ± 1.15^{c}	63.31 ± 1.02^{c}	131.25 ± 4.79^{c}	27.50 ± 2.89^{b}	27.25 ± 2.22^{c}	5.50 ± 0.58^{c}
Hydropriming	39.00 ± 0.82^{ab}	18.00 ± 0.82^{cd}	53.75 ± 3.30^{de}	117.25 ± 3.20^{d}	22.50 ± 2.89^{d}	23.00 ± 0.82^{de}	4.75 ± 0.50^{c}
Absolute control	40.25 ± 2.63^{a}	17.25 ± 0.96^{d}	51.85 ± 3.42^{e}	116.00 ± 4.55^{d}	21.25 ± 2.50^{d}	21.00 ± 0.82^{e}	4.50 ± 0.58^{c}
HSD (α = 0.05)	3.68	2.00	5.84	11.61	5.31	3.55	1.38
SE(m)	0.82	0.44	1.34	2.58	1.18	0.93	0.32
CV (%)	4.5	4.4	4.8	3.7	8.8	6.65	10.36

Values are mean ± SE. Means followed by different superscript letters are significantly different according to Tukey's honestly significant difference (HSD) ($p < 0.05$). Six treatments were evaluated with 4 replications in each treatment.

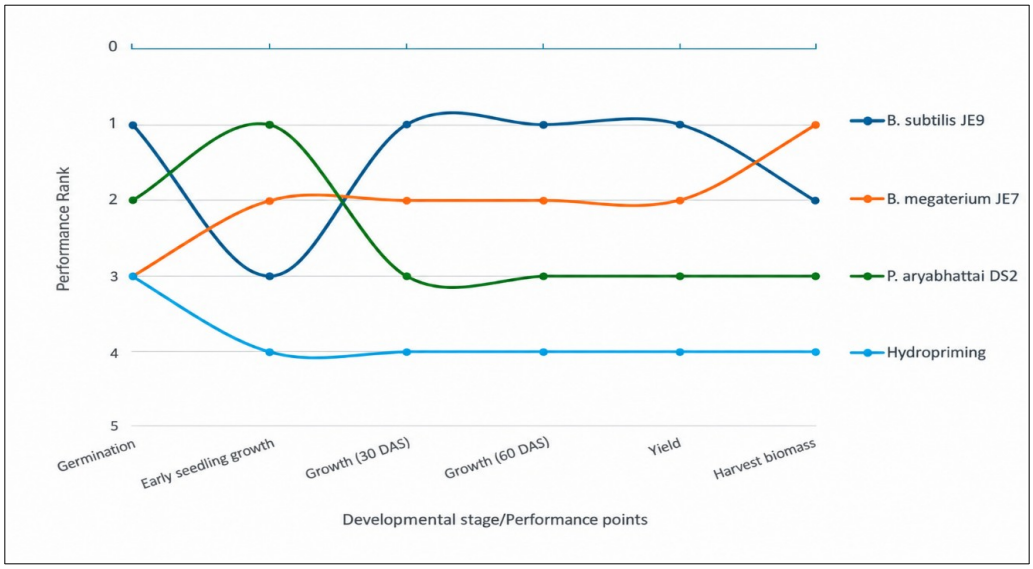


Fig. 5. Ranking based comparison of **s**tage-dependent shifts in the relative performance of rhizobacterial isolates in cowpea. The ranking includes *Bacillus subtilis* JE9, *Bacillus megaterium* JE7, *Priestia aryabhattai* DS2 and hydropriming; the three-isolate consortium and uninoculated absolute control are excluded. Rank 1 denotes the largest mean for the stated endpoint and rank 4 the smallest. The bump chart illustrates changes in isolate ranking from germination and early seedling growth through vegetative development, yield and harvest biomass, highlighting the stage-dependent nature of rhizobacterial efficacy. Rankings are descriptive and do not represent statistical significance testing; treatment differences should be interpreted using the corresponding ANOVA and post-hoc results reported in Tables 2–4.

Comparative performance of individual isolates and the three-isolate consortium

The three-isolate consortium comprising *P. aryabhattai* DS2, *B. megaterium* JE7 and *B. subtilis* JE9 improved several growth and yield parameters compared with the uninoculated control. However, *B. subtilis* JE9 recorded higher numerical values for plant height, branching and leaf production than the consortium at both 30 and 60 days after sowing and produced higher pod number and yield under pot conditions (Tables 3 and 4). The consortium did not provide an apparent overall advantage over *B. subtilis* JE9 under the conditions tested.

Thus, under the pot conditions evaluated, combining the three isolates did not result in a greater overall plant response than the best-performing individual isolate, *B. subtilis* JE9. This finding suggests that combining multiple beneficial bacterial strains does not necessarily result in enhanced plant performance under the conditions tested. Although compatibility among the selected isolates had been established during earlier screening, the present results indicate that in vitro compatibility alone may not be sufficient to predict superior consortium performance under pot conditions.

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4. Discussion

Stage-dependent performance of rhizobacteria in cowpea

A major finding of the present study was that the relative effectiveness of the rhizobacterial isolates varied across stages of cowpea development. Although different isolates showed superior performance for individual traits during the early seedling assay, *B. subtilis* JE9 emerged as the most effective treatment during subsequent vegetative and reproductive development under pot conditions. Notably, *B. subtilis* JE9 recorded the highest values for plant height, number of branches and number of leaves at both 30 and 60 DAS, with values increasing from 85.00 to 90.00 cm for plant height, from 7.75 to 9.25 branches plant^{-1} and from 44.00 to 55.25 leaves plant^{-1}, respectively (Table 3). This contrasting performance is particularly relevant to PGPR screening because superiority for individual traits during early seedling establishment cannot necessarily be extrapolated to subsequent performance throughout the crop cycle.

The isolate *P. aryabhattai* DS2 showed strong performance for several shoot, root and biomass parameters in the roll-towel assay (Table 2). Its pronounced effects on early seedling growth may have contributed to improved seedling establishment. The multifunctional screening conducted before the plant experiments provides possible functional explanations for this response. *Priestia aryabhattai* DS2 showed high gibberellic acid production and phosphate-solubilising ability (Table 1), which are potential functional attributes associated with plant growth promotion (26). However, these associations should be interpreted cautiously because the present study did not directly establish causal relationships between individual bacterial traits and seedling growth.

Interestingly, the early advantages observed for individual seedling traits were not consistently maintained during subsequent plant development. Under pot conditions, *B. subtilis* JE9 consistently recorded superior vegetative growth, earlier flowering, greater pod production, biomass accumulation and yield compared with the other bacterial treatments (Tables 3 and 4). Although cowpea plants raised from isolate *B. subtilis* JE9-treated seeds recorded the maximum germination per cent and seedling vigour index in the early assay, those treated with *P. aryabhattai* DS2 showed strong performance for several seedling growth and biomass parameters, while cowpea plants from *B. megaterium* JE7 treatment recorded the maximum root length. Thus, the isolate showing the strongest response for a particular early seedling trait was not necessarily the one showing the strongest overall performance during subsequent crop development. This observation highlights an important limitation of relying exclusively on short-duration seedling assays for PGPR selection. Seedling assays remain valuable for rapid screening, but their predictive value for later crop performance should be validated through longer-duration experiments extending into vegetative growth, reproductive development and yield formation (27).

The stage-wise ranking analysis further illustrates this temporal shift in rhizobacterial efficacy (Fig. 5). *Priestia aryabhattai* DS2, which ranked first for the composite early seedling growth response, declined to third position from 30 DAS through yield formation. In contrast, *B. subtilis* JE9, despite not being the top-ranked treatment for all individual early seedling traits, occupied the leading position during vegetative growth and yield formation. *Bacillus megaterium* JE7 showed comparatively greater stability across developmental stages, while hydropriming remained among the lowest-performing treatments after the seedling stage. These rank shifts provide additional evidence that the relative effectiveness of rhizobacterial inoculants can change as the host plant progresses through different developmental phases. Thus, early seedling performance may identify promising candidates for further evaluation, but sustained performance across vegetative and reproductive stages appears more relevant for selecting inoculants with agronomic potential.

The stage-dependent changes in rhizobacterial efficacy may reflect the dynamic nature of the plant–microbe interaction throughout crop development. As cowpea progresses from seedling establishment to vegetative and reproductive growth, changes in root architecture, exudation patterns, nutrient demand and the surrounding microbial community can alter the ecological conditions governing bacterial establishment and activity. An isolate that provides a strong early response through hormone production or nutrient mobilisation may therefore not retain the same advantage as the root-associated environment becomes more complex. In the present study, the strong early performance of *P. aryabhattai* DS2 coincided with relatively high gibberellic acid production and phosphate-solubilising activity, whereas *B. subtilis* JE9 showed a comparatively strong EPS- and siderophore-associated profile. These contrasting functional profiles provide plausible explanations for the observed shift in relative performance, with *P. aryabhattai* DS2 showing strong early seedling promotion but *B. subtilis* JE9 maintaining superior vegetative and reproductive performance under pot conditions. In particular, traits associated with rhizosphere persistence, such as EPS production and biofilm formation, may become increasingly relevant during prolonged plant development, although this was not directly tested in the present study. Thus, the observed stage-dependent efficacy likely reflects an interaction between bacterial functional traits and the changing physiological and ecological environment of the developing cowpea plant rather than the effect of any single plant growth-promoting trait.

The shift in relative performance may reflect differences in the ability of individual isolates to establish and function under the changing biological and physicochemical conditions associated with plant

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development. As the plant grows, changes in root architecture, root exudation, nutrient demand and rhizosphere conditions may alter the ecological opportunities available to individual bacterial strains (28). However, because bacterial colonisation and rhizosphere population dynamics were not measured in the present study, these mechanisms remain hypotheses requiring further investigation.

Bacillus subtilis JE9 maintained superior performance during vegetative development

The superior performance of *B. subtilis* JE9 became particularly evident during the vegetative phase. Plants derived from *B. subtilis* JE9-bioprimed seeds recorded the highest plant height, number of primary branches and number of leaves among the bacterial treatments at both 30 and 60 DAS (Table 3). These responses indicate that the advantage of *B. subtilis* JE9 was not restricted to a single growth parameter but was expressed across several components of vegetative development.

The earlier functional screening provides a plausible basis for this response. Isolate JE9 exhibited the highest exopolysaccharide (EPS) production (1.21 g L^{-1}), strong biofilm formation and high siderophore production (Table 1). The EPS production and biofilm formation may facilitate bacterial attachment and persistence in the root-associated environment, potentially supporting sustained plant–microbe interactions (29). Nevertheless, the present study did not quantify root colonisation or bacterial persistence in the rhizosphere. Therefore, enhanced colonisation cannot be claimed as the mechanism underlying the superior performance of *B. subtilis* JE9 under the pot conditions tested. Rather, its biofilm- and EPS-associated characteristics represent plausible functional attributes that warrant direct investigation.

The sustained response of *B. subtilis* JE9 during vegetative growth is particularly relevant when considered alongside the seedling results. Although different isolates showed superiority for different seedling traits, JE9 recorded the highest germination percentage (94.67 %) and seedling vigour index (4496.67), whereas *P. aryabhattai* DS2 showed strong performance for several shoot, root and biomass parameters and *B. megaterium* JE7 recorded the highest root length (Table 2). *B. subtilis* JE9 subsequently showed the strongest overall performance during vegetative development under pot conditions. This suggests that the expression of PGPR efficacy may be temporally dynamic, with different isolates providing greater benefits for particular traits at different stages of plant development. Consequently, selection of microbial inoculants should consider not only the magnitude of individual early responses but also the consistency of beneficial effects across the crop cycle.

Effects on flowering, pod formation and yield

The differences among isolates became even more agronomically relevant during reproductive development. *Bacillus subtilis* JE9-treated plants flowered at 31.75 DAS, approximately 8.5 days earlier than the uninoculated control, which flowered at 40.25 days (Table 4). Earlier flowering was accompanied by a higher number of pods and greater yield, with JE9 producing 24.25 pods $plant^{-1}$ and 80.57 g $plant^{-1}$, compared with 17.25 pods $plant^{-1}$ and 51.85 g $plant^{-1}$, respectively, in the uninoculated control. The resulting 55.4 % increase in yield represents an important agronomic response observed in the study.

The relationship between earlier flowering and higher yield is biologically relevant because reproductive transition represents a critical stage at which improved vegetative development may translate into agronomic benefits. However, the present study demonstrates an association rather than causation. Earlier flowering alone cannot be assumed to account for the increase in yield, since *B. substilis* JE9 also produced greater plant height, branching, leaf production and biomass. The higher yield therefore appears to have occurred in the context of an overall improvement in plant growth and development.

Bacillus megaterium JE7 also showed relatively strong performance during the pot experiment, particularly for vegetative growth and yield, whereas *P. aryabhattai* DS2, despite showing strong performance for several early seedling traits, produced a lower yield than *B. substilis* JE9 and *B. megaterium* JE7. The different responses among isolates reinforce the conclusion that performance for individual traits at one developmental stage does not necessarily predict overall effectiveness at later stages (30). This observation is particularly important for microbial inoculant development because the ultimate agronomic objective is sustained improvement in crop productivity rather than transient enhancement of seedling growth.

The earlier screening also revealed differences in bacterial phytohormone production, with *B. megaterium* JE7 showing high indole-3-acetic acid (IAA) production and *P. aryabhattai* DS2 showing high gibberellic acid (GA) production. These characteristics may contribute to differences in plant developmental responses, but direct causal relationships cannot be established from the present data. Future experiments incorporating bacterial metabolite quantification in the rhizosphere and plant hormonal measurements would be required to establish such relationships.

Multifunctionality and the superior pot performance of *Bacillus subtilis* JE9

Among the isolates evaluated, *B. subtilis* JE9 demonstrated the most consistent performance across the major parameters measured under pot conditions. Its superior performance extended across plant height, branching, leaf production, flowering, pod production, yield and biomass. This consistency is noteworthy because the initial functional screening identified *B. subtilis* JE9 as possessing several potentially beneficial plant growth-promoting and biocontrol-related traits.

Bacillus subtilis JE9 recorded the highest EPS production (1.21 g L^{-1}) and the highest siderophore production index (5.07) among the selected isolates and exhibited antagonistic activity against all five fungal

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pathogens tested (Table 1). Its antagonistic activity against *Fusarium oxysporum*, *Phytophthora* sp., *Colletotrichum gloeosporioides*, *Sclerotium rolfsii* and *Rhizoctonia solani* was confirmed during in vitro screening. Thus, *B. subtilis* JE9 possessed a combination of plant growth-promoting, EPS- and biofilm-associated characteristics, together with *in vitro* antagonistic activity against multiple fungal pathogens.

The standardised multifunctional profile further revealed marked differences among the selected rhizobacteria (Fig. 1). *Bacillus subtilis* JE9 showed the strongest EPS and siderophore-associated profiles, together with comparatively positive biofilm formation, whereas *P. aryabhattai* DS2 was characterised by strong biofilm formation, gibberellic acid production and phosphate-solubilising activity. *Bacillus megaterium* JE7 showed relatively high IAA production and phosphate-solubilising activity but comparatively weaker biofilm and siderophore profiles. These contrasting functional configurations suggest that the isolates differed not simply in the number of plant growth-promoting traits, but in the combination and relative strength of those traits. Notably, the isolate with strong early seedling responses (*P. aryabhatta* DS2) did not subsequently show the highest vegetative growth or yield, whereas *B. subtilis* JE9, characterised by a comparatively strong EPS-, biofilm- and siderophore-associated profile, maintained superior performance under pot conditions. Thus, multifunctionality at the in vitro level may provide a useful basis for candidate selection, but the relative contribution of individual traits to plant performance is likely to depend on developmental stage and the plant-associated environment. Because bacterial colonisation, persistence and in planta expression of these traits were not measured in the present study, these functional associations should be regarded as plausible explanations rather than demonstrated mechanisms.

The concurrence of these functional traits with superior performance under pot conditions supports the potential value of a multifunctional screening strategy for identifying promising rhizobacterial candidates. Nevertheless, multifunctionality should not be interpreted as evidence that each individual trait contributed directly to the observed growth and yield responses. The pot experiment did not include pathogen-challenge treatments and therefore the contribution of *B. subtilis* JE9's antagonistic activity to its growth and yield advantage could not be separated from its other plant growth-promoting characteristics. Moreover, root colonisation, bacterial persistence and the expression of these functional traits in planta were not quantified.

An important implication is that the strongest candidate for further development should not necessarily be the isolate with the highest value for any single in vitro trait (31). Rather, the present results suggest that a combination of functional characteristics, together with consistent plant performance across developmental stages, may provide a more meaningful basis for selecting bioinoculant candidates (32). However, validation under pathogen pressure and across different environmental conditions would be necessary before drawing conclusions regarding the broader biocontrol potential of *B. subtilis* JE9.

Individual strains versus the bacterial consortium

The three-isolate consortium comprising *P. aryabhatta* DS2, *B. megaterium* JE7 and *B. subtilis* JE9 improved several growth and yield parameters compared with the uninoculated control. However, the consortium did not consistently outperform the individual bacterial treatments. *Bacillus subtilis* JE9 alone recorded higher values for plant height, branching and leaf production, at both 30 and 60 DAS than the consortium, as well as higher pod number, yield and biomass under pot conditions (Tables 3 and 4). Thus, under the conditions tested, combining the three isolates did not provide an apparent additive or synergistic advantage over the best-performing individual strain (33).

This finding is important because the combination of individually beneficial bacteria does not necessarily result in enhanced plant performance (34). Even when bacterial strains are compatible in vitro, such compatibility should not be equated with synergistic activity in planta. Following introduction into the rhizosphere, bacterial strains may interact through competition for nutrients and colonisation sites, differences in growth rates, metabolite production or root-association ability (35). Consequently, the performance of a bacterial community may differ from that predicted from the characteristics of its individual members.

The present findings should not, however, be interpreted as evidence that the consortium approach is inherently ineffective. Only one three-isolate combination and one inoculation regime were evaluated in the pot experiment. Different strain ratios, inoculation densities, application timings or formulations could potentially produce different outcomes. In particular, the contrasting trait-specific responses observed during the seedling assay and the subsequent superior overall performance of *B. subtilis* JE9 under pot conditions raise the possibility that the timing or sequence of inoculation may influence consortium efficacy. This hypothesis warrants investigation through experiments comparing different strain ratios, inoculation schedules and formulations under both non-challenged and pathogen-challenged conditions.

Implications of stage-dependent performance for plant growth-promoting rhizobacteria screening and bioinoculant development

The findings have broader implications for the evaluation and development of microbial inoculants for cowpea. Conventional PGPR screening frequently relies on seed germination and early seedling assays to identify promising isolates. The present results demonstrate that such assays can identify bacteria with strong early plant growth-promoting effects, but that the relative performance of isolates may vary among traits and change during subsequent plant development. In the present study, *P. aryabhattai* DS2 showed strong

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performance for several early seedling growth and biomass parameters, *B. subtilis* JE9 recorded the highest germination percentage and seedling vigour index and *B. megaterium* JE7 recorded the maximum root length. During subsequent pot cultivation, however, *B. subtilis* JE9 exhibited the strongest overall performance across major vegetative and reproductive parameters and produced the highest yield (Fig. 6).

Accordingly, early seedling performance should be regarded as an initial screening criterion rather than a definitive predictor of crop-cycle performance. A more robust selection strategy should progressively evaluate promising isolates from seed germination and seedling establishment through vegetative growth, flowering, biomass accumulation and yield. Such stage-wise assessment may prevent potentially valuable isolates from being selected or rejected solely on the basis of an early response that does not persist, or does not translate into broader agronomic benefits, during longer-term crop development.

From an applied perspective, *B. subtilis* JE9 represents the most promising candidate among the isolates tested because its beneficial effects extended across multiple developmental stages and culminated in the highest yield under the pot conditions evaluated. Its approximately 55.4 % higher yield relative to the uninoculated control provides a strong basis for further evaluation. The contrasting response profiles of the isolates provide a graphical representation of the stage-dependent efficacy observed in the present study and support the conclusion that performance for individual seedling traits cannot necessarily be used to predict overall performance at later developmental stages.

However, the observed pot-stage performance should not yet be interpreted as evidence of field-level efficacy. The present experiment was conducted under open-field conditions using pots and performance under such conditions may still differ from that observed in agricultural field environments. Soil physicochemical properties, native microbial communities, climatic variability, water availability, plant density and crop-management practices can influence bacterial establishment and plant responses. Therefore, field validation across locations and seasons is required to determine the stability and reproducibility of the response of *B. subtilis* JE9 under practical agricultural conditions.

Further studies should investigate bacterial colonisation and persistence, dose optimisation, formulation and shelf life, compatibility with fertilisers and other agricultural inputs and performance under relevant abiotic and biotic stresses. Importantly, future experiments could examine sequential inoculation strategies, such as early application of *P. aryabhattai* DS2 followed by *B. subtilis* JE9, to determine whether the strong responses associated with *P. aryabhattai* DS2 during seedling establishment can be combined with the superior later-stage performance observed for *B. subtilis* JE9. Such approaches should be tested experimentally rather than assumed to provide an additive benefit.

Overall, the present study demonstrates that rhizobacterial efficacy in cowpea is developmentally dynamic and may vary among traits rather than remaining uniform throughout the crop cycle. The contrasting response profiles observed among *P. aryabhattai* DS2, *B. megaterium* JE7 and *B. subtilis* JE9 during seedling establishment, followed by the superior overall pot performance of JE9, provide evidence that an early seedling assay alone may not consistently correspond to subsequent crop performance. These findings support a comprehensive, stage-wise approach to PGPR selection and provide a practical framework for identifying bacterial inoculants with sustained agronomic potential.

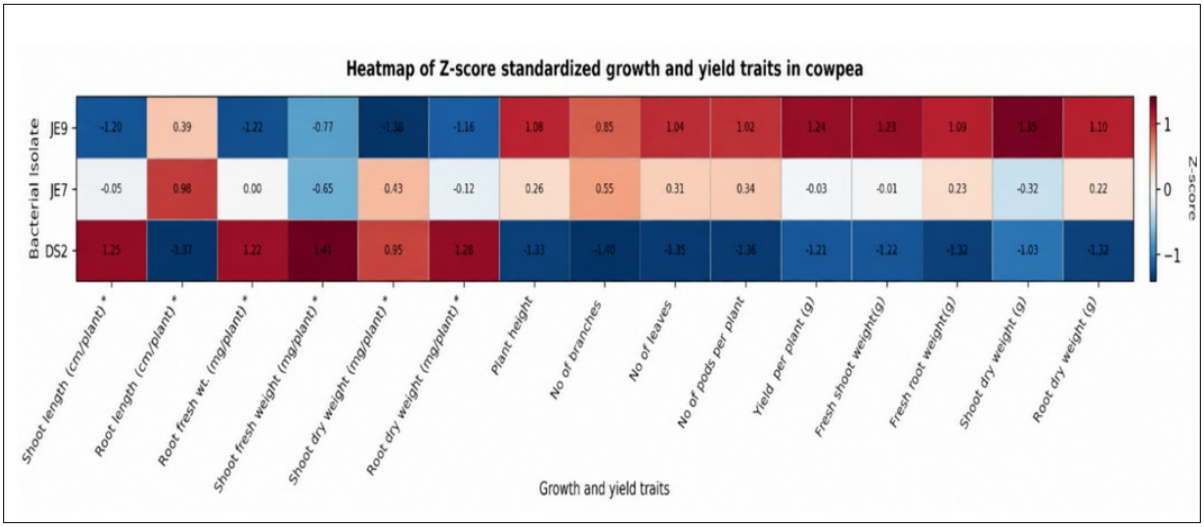


Fig. 6. Z-score standardised heatmap of selected growth and yield traits for JE9, JE7 and DS2, showing Z-scores ranging from −1.40 to +1.41. Asterisks indicate traits measured during the 10-day seedling assay; unmarked traits represent measurements obtained during the pot experiment. Z-scores were calculated across the three isolates only. Positive and negative values indicate performance above and below the three-isolate mean, respectively.

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5. Conclusion

This study demonstrates that multifunctional rhizobacteria can exhibit stage- and trait- dependent effects on cowpea growth and yield. In the seedling assay, *Priestia aryabhattai* DS2, exhibited strong performance across several shoot, root and biomass parameters. *Bacillus subtilis* JE9 recorded the highest germination percentage and seedling vigour index and *Bacillus megaterium* JE7 produced the longest root. However, the response varied across the developmental stage of the crop. Under pot conditions, *Bacillus subtilis* JE9 showed consistent overall performance across vegetative and reproductive stages, with enhanced plant growth, earlier flowering, increased pod production, biomass accumulation and the highest yield (80.57 g plant^{-1}), approximately 55.4 % higher yield than the uninoculated control.

These findings indicate that individual early seedling traits may not consistently correspond to subsequent crop performance, highlighting the importance of evaluating candidate plant growth-promoting rhizobacteria (PGPR) beyond early seedling growth and including vegetative development, flowering, biomass production and yield for the evaluation. The consortium consisting of *P. aryabhattai* DS2, *B. megaterium* JE7 and *B. subtilis* JE9 improved several growth and yield parameters relative to the uninoculated control but did not consistently outperform individual isolates, suggesting that combining promising strains does not necessarily produce additive or synergistic effects under the conditions tested. Among the isolates evaluated, *B. subtilis* JE9 showed the most consistent performance across developmental stages and represents a promising candidate for further evaluation as a cowpea bioinoculant. However, these findings were obtained from an open-field pot experiment and should not be extrapolated directly to field performance. Multi-location and multi-season field trials, together with studies on formulation, inoculum dose, bacterial persistence, compatibility with agricultural inputs and performance under variable soil and environmental conditions, are required to validate the agronomic potential and stability of *B. subtilis* JE9 before practical recommendations for farmer use can be made.

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Authors' contributions

NC contributed to conceptualisation, supervision, data analysis, visualisation, methodology and writing review and editing. TA contributed to methodology, investigation, formal analysis, data curation, visualisation and writing original draft preparation. SAR, VIS, RB and KNA contributed to methodology and writing review and editing, while VIS also contributed to investigation. All authors have read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest

Authors do not have any conflict of interests to declare.

Ethical issues

None

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used RAISINS software (Version: 2.0.0) for all data analysis and visualisation tasks. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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