

Epiphytic bacteria from *Tacinga inamoena* (K. Schum.) N.P. Taylor & Stuppy improve plant growth in cucumber seedlings

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Abstract

Under stress conditions, the phyllosphere of host plants harbors microorganisms with potential for the development of agricultural bioinputs. In this study, the potential of *Brevibacillus* sp. UPT4 and *Pantoea* sp. SPM1, two epiphytic strains from *Tacinga inamoena* isolated from the Caatinga biome, was assessed through in vitro assays and a greenhouse experiment. The experiment was conducted in a randomized block design with four treatments (individual strains, bacterial consortium, and control) and five replicates. Biometric parameters (shoot and root length, stem diameter, root volume, and biomass allocation to shoot and root) were measured and analyzed by the Scott-Knott test at a probability level of 5%, as well as Redundancy Analysis (RDA). The strains exhibited auxin production, nitrogen fixation, and tolerance to abiotic stresses, showing significant increases ($p < 0.05$) in shoot and root parameters (13.58% to 194.86%) compared to the control. RDA indicated that most of the variability observed in the parameters was associated with auxin production and stress tolerance. These findings highlight the potential of epiphytic bacteria isolated from the Caatinga biome as promising tools to address challenges posed by climate change.

Introduction

The rapid growth of the global population poses significant challenges to food security, with projections estimating approximately 10 billion inhabitants by 2050. It is anticipated that population expansion, combined with changes in consumption patterns and increased per capita income, will raise global food demand by around 44% (OECD-FAO 2024; Sands et al. 2023). Concurrently, economic and territorial conflicts, together with the escalating climate crisis, exacerbate global food insecurity (Safi et al. 2024; Marson and Sacconel 2023).

In Brazil, vegetable production plays a strategic role in food security. Within this context, cucumber (*Cucumis sativus* L.) stands out due to its high domestic demand and market acceptance, despite its pronounced susceptibility to phytopathogens and adverse environmental conditions. This susceptibility often leads to the intensive use of chemical pesticides and fertilizers to ensure crop productivity (Mallick 2022). However, the indiscriminate application of these inputs negatively affects soil and water quality, generates toxic residues in the environment, and disrupts the composition and dynamics of microbial communities associated with crops (Kaur and Sharma 2022).

In this scenario, biofertilizers based on plant growth-promoting bacteria (PGPB) emerge as promising tools for developing ecologically sustainable agriculture in the face of climate change. These microorganisms act through multiple mechanisms, including phytohormone production, biological nitrogen fixation (BNF), nutrient solubilization, and induction of systemic resistance (ISR), thereby supporting crop development under stress conditions (Srivastava and Joshih 2021; Bahloul 2021; Shahwayr et al. 2023; Alzate Zuluaga et al. 2024).

Plants naturally exposed and adapted to conditions of water scarcity and high solar radiation, such as Cactaceae species, may harbor in their phyllosphere microbial communities resilient to environmental

adversities (Liu et al. 2023; Flores-Nuñez et al. 2024). Studies have demonstrated the potential of these microorganisms to promote the growth of various agricultural crops, integrating innovative approaches for the development of new agricultural technologies (Devarajan et al. 2021; Sharath et al. 2021; Agbodiato and Babalola 2024; Khosravi et al. 2024).

Thus, to contribute to the development of efficient biostimulants and foster sustainable agricultural practices, this study aimed to evaluate the effects of phyllosphere bacteria from *Tacinga inamoena* (K. Schum.) N.P. Taylor & Stuppy on the vegetative growth of cucumber seedlings.

Materials and methods

Microorganisms

Brevibacillus sp. UPT4 and *Pantoea* sp. SPM1 were isolated from the surface of *T. inamoena* cladodes and deposited in the microbial collection of the Laboratory of Microbial Ecology and Biotechnology of the Semi-Arid Region, State University of Bahia (LEBIMS – UNEB), Paulo Afonso, Bahia state, Brazil.

Brevibacillus sp. UPT4 was isolated in Serra do Umbuzeiro (Latitude: – 9.58103091088262; Longitude: – 38.2047843933105), Paulo Afonso, Bahia state, Brazil. *Pantoea* sp. SPM1 was isolated in Environmental Protection Area Serra Branca (Latitude: – 9.945193254158575; Longitude: – 38.57322551035467), located in the municipality of Jeremoabo, Bahia state, Brazil.

Evaluation of plant growth-promoting potential and tolerance to abiotic stresses

Indole-3-acetic acid (IAA) production

Bacterial cultures ($OD_{600nm} = 0.3$) were inoculated into tryptic soy broth (TSB) supplemented with L-tryptophan (5 mM) and incubated under constant agitation (150 rpm) at $28 \pm 2^\circ C$ for 72 h. Cultures were centrifuged at 10,000 rpm for 10 min, and the cell-free supernatant was transferred to tubes containing Salkowski reagent (2% $FeCl_3$ in 35% $HClO_4$) (1:1), following Gordon and Weber (1951). The mixture was incubated in the dark for 30 min, and IAA concentration was determined spectrophotometrically at 530 nm, using a standard curve of IAA.

Asymbiotic nitrogen fixation

Bacterial cultures ($OD_{600nm} = 0.3$) were inoculated into tubes containing semi-solid nitrogen-free Burk's medium (Wilson and Knight 1952) with the following composition ($g\ L^{-1}$): glucose (10), agar (1.8), K_2HPO_4 (0.52), KH_2PO_4 (0.41), $CaCl_2$ (0.2), $MgSO_4 \cdot 7H_2O$ (0.1), Na_2SO_4 (0.05), $FeSO_4 \cdot 7H_2O$ (0.005), and $Na_2MoO_4 \cdot 2H_2O$ (0.0025), pH adjusted to 7.0. Tubes were incubated at $28 \pm 2^\circ C$ for 7 days, and the formation of a sub-surface pellicle indicated asymbiotic nitrogen fixation capacity.

Phosphorus (P) and potassium (K) solubilization

Bacterial colonies were streaked onto Pikovskaya's agar (TM Media®) and Aleksandrow agar (TM Media®) plates for the determination of phosphorus and potassium solubilization capacity, respectively. Plates were incubated at $28 \pm 2^\circ\text{C}$ for 15 days, and solubilization activity was evidenced by halo formation around the bacterial colonies.

Growth under reduced water activity (A_w)

Strains were streaked onto tryptic soy agar (TSA) supplemented with different concentrations of sorbitol (285, 405, 520, and 780 g L^{-1}), corresponding to water activity (A_w) values of 0.957, 0.919, 0.897, and 0.807, respectively (Hallworth et al. 1998). Plates were incubated at $28 \pm 2^\circ\text{C}$ for 48 h, and tolerance to water stress was determined based on bacterial growth at each A_w level.

Salt tolerance

Strains were streaked onto TSA supplemented with NaCl at concentrations of 0, 2, 4, 6, 8, and 10%. Plates were incubated at $28 \pm 2^\circ\text{C}$ for 48 h, and salt tolerance was evaluated based on bacterial growth at each concentration.

Evaluation of plant growth promotion in cucumber

Experimental design

The experiment was conducted in a greenhouse covered with polyethylene film and sidewalls protected with 30% shade cloth, under natural photoperiod, with average temperatures of $36 \pm 2^\circ\text{C}$ (day) and $24 \pm 2^\circ\text{C}$ (night), at the State University of Bahia (UNEB), Campus VIII, Paulo Afonso, Bahia, Brazil, in December 2024.

Cucumber seeds were surface-sterilized with 70% ethanol (1 min), 1% NaOCl (3 min), and rinsed three times with sterile distilled water. Seeds were then microbiolized by immersion in bacterial inoculum adjusted to $\text{OD}_{600\text{nm}} = 1.0$ with xanthan gum (0.1%) as an adhesive agent. The control treatment consisted of seeds immersed only in 0.1% xanthan gum solution.

The experimental design was a completely randomized block design with four treatments and five replicates, totaling 20 experimental units. Treatments included: (T1) uninoculated control, (T2) co-inoculation of *Pantoea* sp. SPM1 and *Brevibacillus* sp. UPT4, (T3) inoculation with *Pantoea* sp. SPM1, and (T4) inoculation with *Brevibacillus* sp. UPT4. Seeds were sown in pots containing 2 kg of soil with the following chemical characteristics: pH 7.91; 89.5 mg/dm^3 P (Mehlich-1); 0.64 cmolc/dm^3 K⁺; 9.99 cmolc/dm^3 calcium (Ca^{2+}); and electrical conductivity of 1.00 dS/m. Plants were irrigated daily to

maintain adequate soil water content, which was monitored by daily weighing of the pots in the late afternoon, considering both plant fresh mass and soil mass.

Evaluations were performed 25 days after emergence (DAE). Shoots were cut at the cotyledonary node, separating roots and shoots. Stem diameter was measured in millimeters using a digital caliper. Shoot length (SL) and root length (RL) were measured with a graduated ruler. Root volume (RV) was determined by water displacement in a graduated cylinder. Shoots and roots were placed in paper bags and oven-dried at $60 \pm 2^\circ\text{C}$ until constant weight, which was used to determine shoot biomass allocation (SBA) and root biomass allocation (RBA).

Statistical analysis

Data were subjected to analysis of variance (ANOVA) using the F-test ($p < 0.05$). When significant differences were detected, means were compared using the Scott-Knott test at the 5% probability level. Relationships between in vitro assay parameters and cucumber growth experiment variables were assessed by Redundancy Analysis (RDA) based on Pearson's correlation matrix. Statistical analyses were performed in RStudio software (v. 4.3.3) (R Core Team 2024).

Results

Functional profile of *Brevibacillus* sp. UPT4 and *Pantoea* sp. SPM1 indicates potential for plant growth promotion and tolerance to abiotic stresses

Both strains exhibited multiple traits associated with plant growth promotion and tolerance to abiotic stresses (Table 1). *Brevibacillus* sp. UPT4 and *Pantoea* sp. SPM1 demonstrated the ability to produce indole-3-acetic acid (IAA), with concentrations of 58.93 and 53.19 $\mu\text{g/mL}$, respectively. Similarly, both strains displayed the capacity for symbiotic nitrogen fixation.

Regarding the solubilization of mineral nutrients, only *Pantoea* sp. SPM1 exhibited potassium-solubilizing ability, whereas neither strain demonstrated phosphorus-solubilizing capacity. With respect to growth under abiotic stress conditions, both strains were able to grow under low water availability as well as under saline stress. *Pantoea* sp. SPM1 sustained growth at NaCl concentrations of up to 8%, while *Brevibacillus* sp. UPT4 tolerated up to 4% NaCl.

Table 1

Functional traits associated with plant growth promotion and tolerance to abiotic stresses exhibited by *Brevibacillus* sp. UPT4 and *Pantoea* sp. SPM1.

STRAIN	IAA	ANF	K	P	Aw	NaCl
<i>Pantoea</i> sp. SPM1	53.19	+	+	-	0.957	8%
<i>Brevibacillus</i> sp. UPT4	58.93	+	-	-	0.957	4%
Notes: IAA = Indole-3-acetic acid production ($\mu\text{g/mL}$); ANF = Asymbiotic nitrogen fixation; K = Potassium solubilization; P = Phosphorus solubilization; Aw = Growth under reduced water activity; NaCl = Salinity tolerance.						

Epiphytic strains from *T. inamoena* modulate growth, root architecture, and biomass allocation in cucumber seedlings

The experiment demonstrated a significant effect ($p < 0.05$) of strain inoculation on cucumber growth. For shoot length (SL), distinct responses were observed among the treatments (Fig. 1a), with the bacterial consortium (Fig. 1b) and *Brevibacillus* sp. UPT4 (Fig. 1c) standing out, promoting increases of 38.52% and 56.59%, respectively, compared to the control treatment (Fig. 2a). Similarly, for stem diameter (SD), co-inoculation and inoculation with *Brevibacillus* sp. UPT4 resulted in values 13.58% and 20.20% higher, respectively, than the uninoculated treatment (Fig. 2b). Inoculation with *Pantoea* sp. SPM1 (T3) did not differ statistically from the control.

For root length (RL), all inoculated treatments showed higher means than the control; however, only *Brevibacillus* sp. UPT4 exhibited a significant increase of 43.40% (Fig. 3a). All inoculated treatments increased the root volume (RV) of cucumber seedlings compared to the control, with increments ranging from 92.86% to 117.86% (Fig. 3b).

For shoot biomass allocation (SBA), all inoculated treatments showed lower mean values compared to the control (Fig. 4a). Conversely, inoculation resulted in a higher percentage of biomass allocation to the roots (RBA) compared to the control (Fig. 4b). *Pantoea* sp. SPM1 exhibited the greatest increase (194.86%), followed by the microbial consortium (141.94%) and *Brevibacillus* sp. UPT4 (110.69%).

Redundancy analysis (RDA) enabled the correlation of the functional profile of the strains with the evaluated phytometric parameters, explaining 83.3% and 16.7% of the variance along the first (RDA1) and second (RDA2) axes, respectively (Fig. 4). The results revealed that the greatest variability in RV, SD, RL, and SL was associated with the ability of the strains to produce indole-3-acetic acid (IAA). Moreover, asymbiotic nitrogen fixation capacity exhibited a positive correlation with root biomass allocation values, whereas SBA displayed distinct distribution patterns compared to the other parameters.

Discussion

Arid and semi-arid regions are often characterized by stress conditions such as high temperatures, low relative air humidity, and reduced water availability. These factors modulate plant microbiome interactions, favoring the presence of microorganisms capable of assisting in nutrient uptake and stress responses, thereby promoting plant development (Yang et al. 2023; López-Hernández et al. 2020). Phyllosphere microorganisms are exposed to extreme climatic fluctuations, which compel them to develop biochemical and physiological strategies that ensure their adaptability to hostile conditions.

The formulation of inoculants based on microorganisms from the phyllosphere of semi-arid regions represents a promising biotechnological tool. Studies have shown that the genetic repertoire of epiphytic bacteria from cacti in such regions includes various mechanisms associated with phytohormone synthesis, nitrogen fixation, and stress tolerance (López-Hernández et al. 2020). Similarly, Li et al. (2023) emphasizes that epiphytic bacteria from desert plants possess specialized functional capabilities, serving as sources of metabolites and mechanisms applicable to agriculture.

A specialized functional profile was identified in the present study, as both strains exhibited tolerance to abiotic stresses, including high salinity and low water activity. These findings are consistent with reports of phyllosphere microorganisms adapted to harsh environments, such as those associated with *Tillandsia landbeckii* Phil. in the Atacama Desert (Hakobyan et al. 2023) and phyto bacteria associated with rice cultivars (Devarajan et al. 2020). The results of this study indicate that strains isolated from *T. inamoena* possess potential for agricultural application, particularly in cropping systems subjected to environmental stresses.

The high IAA production observed suggests that the strains have potential for plant growth promotion (Table 1). The adverse conditions of the semi-arid climate exert selective pressure on the phyllosphere microbiota, triggering osmotic stress and inducing the expression of genes related to IAA production (Etesami and Glick 2024). As a result, tryptophan present in foliar exudates is assimilated by epiphytic communities, which secrete the phytohormone and stimulate plant development (Saleem and Paul 2015), as verified in this study.

Mechanisms associated with mineral nutrient availability were also identified. Potassium solubilization, observed in *Pantoea* sp. SPM1, represents an important trait in plant growth promotion, enhancing photosynthesis and activating key enzymes (Pandey and Saharan 2025). In addition, the asymbiotic nitrogen fixation observed in both strains may integrate into the set of nutritional mechanisms available to cropping systems. The assimilation of atmospheric nitrogen in the phyllosphere, as reported for *Methylobacterium symbioticum*, may serve as an alternative in environments with low nutrient availability, while also reducing the need for chemical fertilizers (Valente et al. 2024).

Although neither strain exhibited phosphorus solubilization capacity, this result did not compromise the plant growth gains observed. On the contrary, it suggests that other mechanisms, such as IAA production and nitrogen fixation, were more decisive, as observed on RDA. This finding reinforces that the potential of PGPB is not necessarily linked to the presence of all classical mechanisms, but rather to the functional effectiveness of those most relevant under specific environmental and physiological

conditions. In this context, it is essential to consider the identification and selection of elite microorganisms, i.e., strains that, even with a limited set of traits, display high agronomic efficiency and functional plasticity across different cropping systems.

In cucumber assays, significant increases in shoot growth were observed in treatments inoculated with the microbial consortium and with *Brevibacillus* sp. UPT4, particularly in SL and SD. These results suggest a possible synergistic action between IAA production and nitrogen fixation, promoting greater structural development and biomass allocation. Similar findings were reported in tomato and pepper seedlings inoculated with *Brevibacillus brevis* FJAT-0809-GLX, which showed significant increases in growth parameters after 14 days of cultivation (Che et al. 2018).

The root system showed superior development in inoculated plants compared to the control. Increases in root architecture are strongly associated with IAA synthesis, which directly influences root growth. A more robust root system enhances water and nutrient uptake, thereby increasing crop resilience under conditions of water and nutrient limitation (Dias et al. 2020). In studies with maize (Maulina et al. 2023) and cotton (Nehra et al. 2018), inoculation with *Brevibacillus* spp. also resulted in significant gains in root length and biomass, reinforcing the ecological and functional plasticity of these microorganisms, even when originating from the phyllosphere.

The effects observed with the microbial consortium may indicate advantages over single-strain formulations, as the combination of different microorganisms can broaden the spectrum of benefits to crops (Mir et al. 2019). Studies with common bean (Verma et al., 2018), millet (Kushwaha et al. 2020), and pearl millet (Kaur et al. 2023) have shown that microbial consortia improve growth, biomass, and chlorophyll content.

The present study also revealed differences in shoot and root biomass allocation. Inoculated plants displayed greater root biomass allocation compared to the control, consistent with findings by Awasthi et al. (2024) in *Bacopa monnieri* (L.) Wettst inoculated with *Pantoea* sp. MTP17. In this study, the higher root allocation rate observed with *Pantoea* sp. SPM1 may be related to its high IAA production and potassium solubilization, traits that favor biomass accumulation in roots.

RDA confirmed the association between the responses obtained in vitro and the phenotypic performance in vivo, suggesting that the functional traits of the strains were decisive for the differences among treatments. The contrasting distribution of SBA and RBA likely reflects distinct biomass allocation strategies induced by each strain. The dissociation of SBA from the other variables in the RDA suggests the occurrence of an adaptive trade-off. In this strategy, the plant reduces biomass allocation to the shoot and prioritizes root growth, ensuring greater efficiency in water and nutrient acquisition under stress conditions, albeit at the expense of immediate shoot growth (Chieb and Gachomo 2023; Grover et al. 2021; Bektas et al. 2023)

The positive correlation between symbiotic nitrogen fixation and root variables reinforces the role of these bacteria in plant nutrition, while the association between IAA and RL, SL, and SD highlights the

direct contribution of the phytohormone to cucumber growth under the tested conditions, identifying the inoculated treatments with the greatest agronomic potential. Nevertheless, as this study was conducted at an early stage under controlled conditions, further field trials are necessary to validate these effects and confirm strain efficiency across different environments and cropping systems.

Conclusion

These results highlight the potential of the phyllosphere of native semi-arid plants as a source for the development of new technologies aimed at sustainable agriculture. The integration of epiphytic microorganisms represents a promising tool to address the challenges posed by population growth and climate change. *Brevibacillus* sp. UPT4 exhibited the greatest improvements in cucumber vegetative development, promoting increases in shoot and root system length, thereby enhancing plant efficiency and resilience, particularly under water and salt stress conditions.

Declarations

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Competing Interests

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

Author Contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Ellie José Pereira and Vinícius de Souza. The first draft of the manuscript was written by Ellie José Pereira and Vinícius de Souza, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data Availability

The authors confirm that the data supporting the findings of this study are available within the article.

Ethics approval and consent to participate

Not applicable.

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Figures



Figure 1

Cucumber seedlings inoculated with epiphytic bacterial isolated from the Caatinga biome. (a) Comparison between treatments. (b) Cucumber inoculated with bacterial consortium, and (c) cucumber inoculated with *Brevibacillus* sp. UPT4.

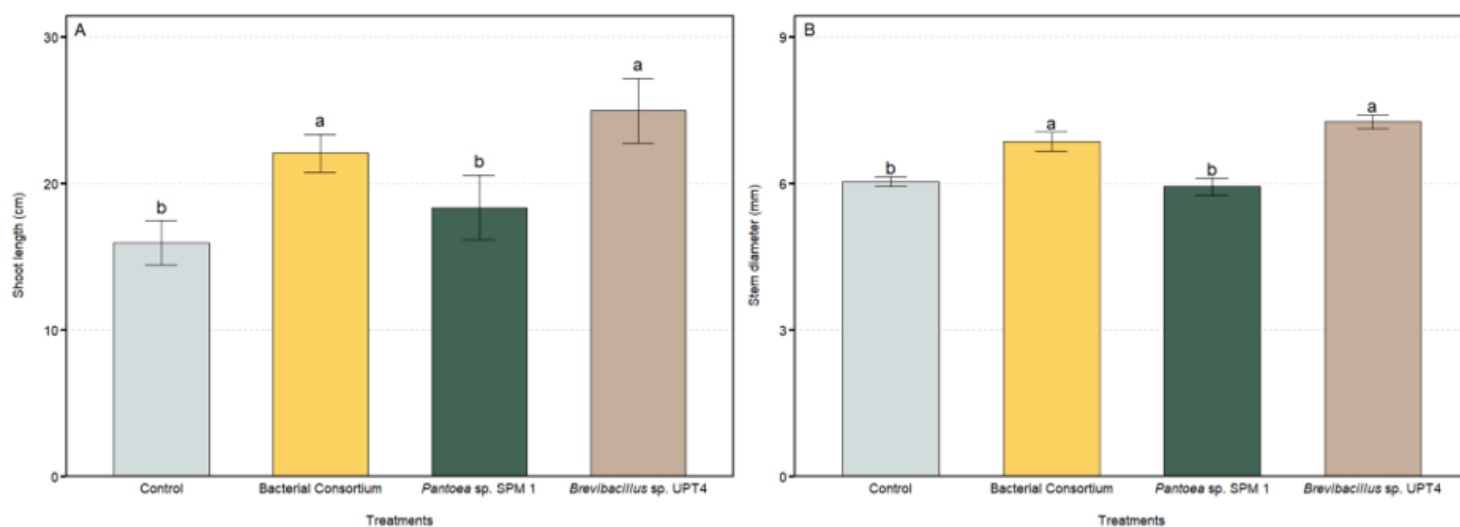


Figure 2

Effect of epiphytic bacterial from *T. inamoena* (a) shoot length (SL) and (b) stem diameter (SD) of cucumber seedlings.

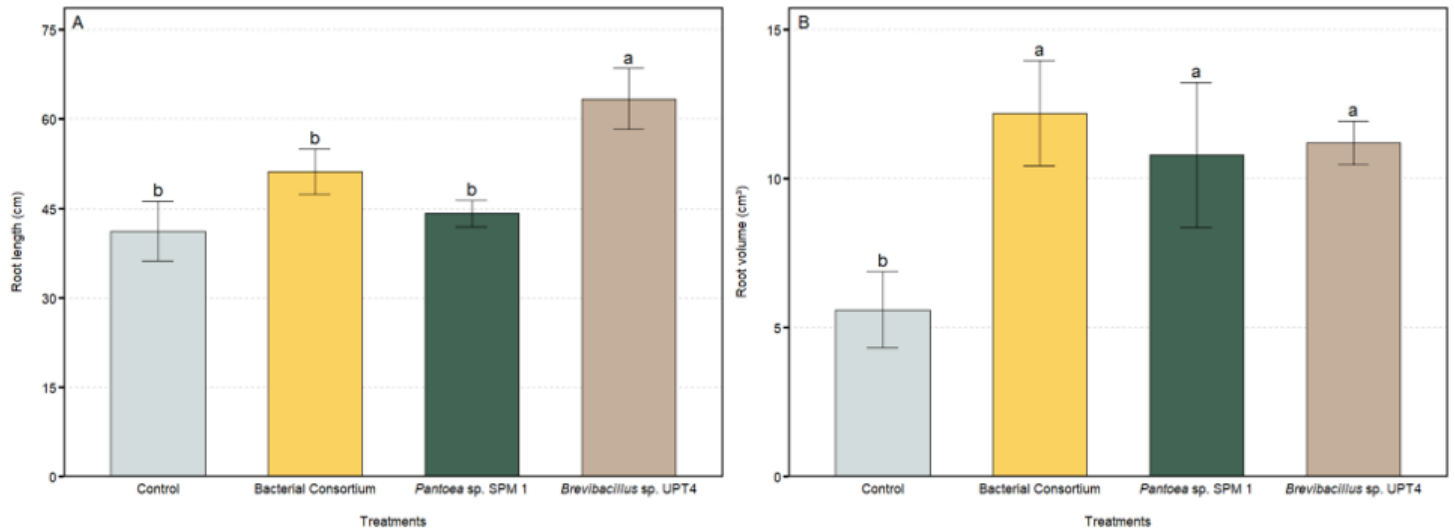


Figure 3

Influence of inoculated treatments on (a) root length (RL) and (b) root volume (RV) of cucumber seedlings.

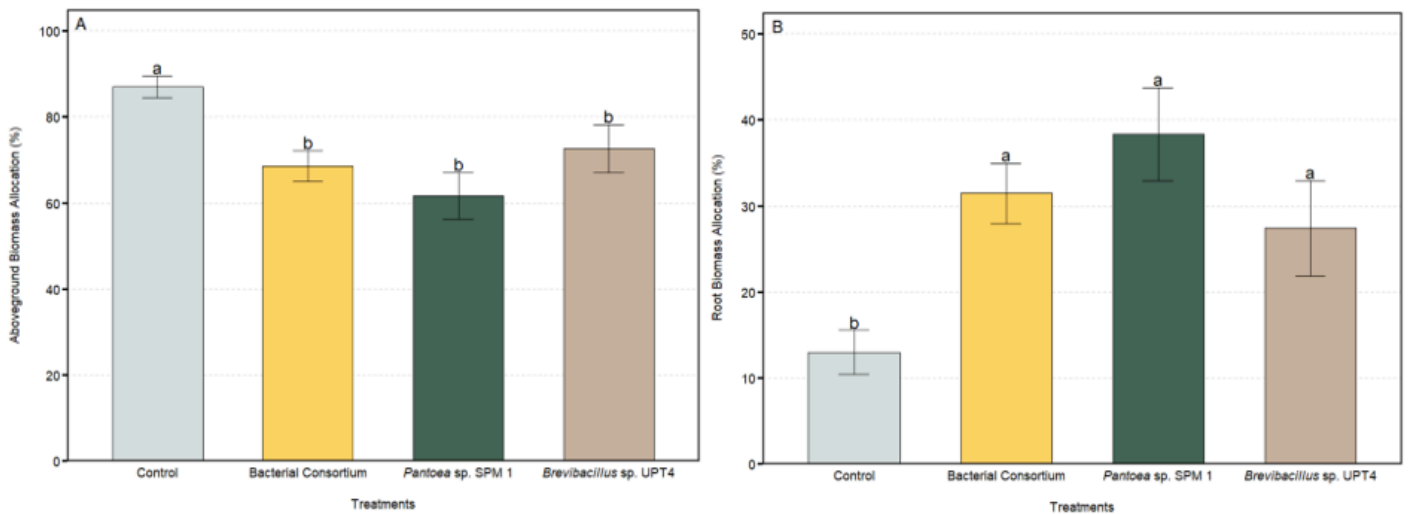


Figure 4

Biomass allocation in cucumber seedlings inoculated with epiphytic bacteria from *T. inamoena*: percentage of (a) shoot biomass allocation (SBA) and (b) root biomass allocation (RBA).

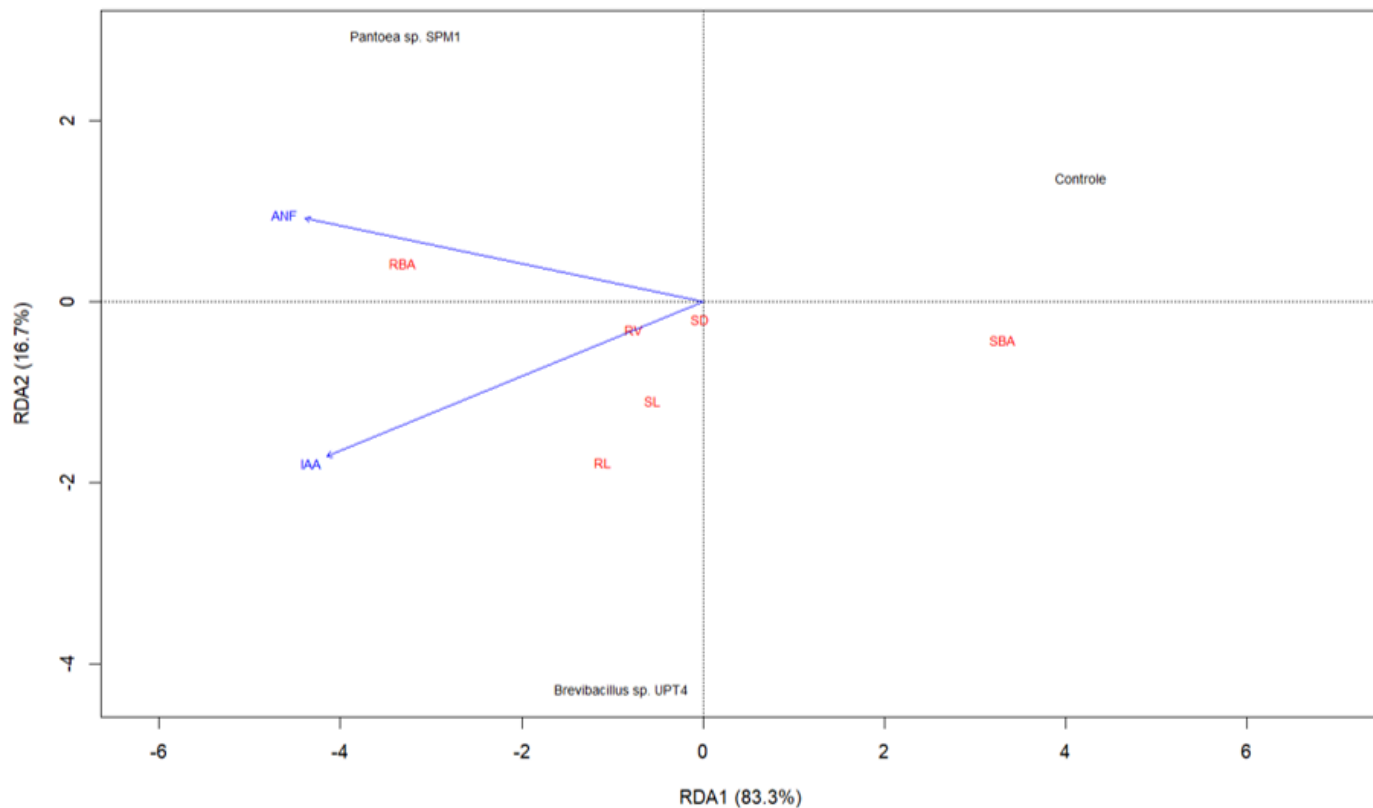


Figure 5

Principal component analysis (PCA) showing the correlation between the observed functional traits and the results obtained in the cucumber experiment.

Notes: IAA = Indole-3-acetic acid production; ANF = Asymbiotic nitrogen fixation; K = Potassium solubilization; P = Phosphorus solubilization; Aw = Growth under reduced water activity; NaCl = Salinity tolerance; SL= Shoot length; SD= Stem diameter; RL= Root length; RV= Root volume; ABA= Aboveground biomass allocation; RBA= Root biomass allocation.