Contents lists available at ScienceDirect

Heliyon



journal homepage: www.cell.com/heliyon

Research article

5²CelPress

Response of sweet potato cultivars to *Bacillus velezensis* T149-19 and *Bacillus safensis* T052-76 used as biofertilizers

Matheus Barbosa Bernardes^a, Isabella Dal'Rio^a, Marcia Reed Rodrigues Coelho^b, Lucy Seldin^{a,*}

^a Instituto de Microbiologia Paulo de Góes, Universidade Federal do Rio de Janeiro, Rio de Janeiro, RJ, Brazil ^b EMBRAPA-Agrobiologia, Seropédica, Rio de Janeiro, Brazil

ARTICLE INFO

Keywords: Sweet potato Bacillus safensis Bacillus velezensis Plant growth-promoting bacteria Rhizosphere bacterial community

ABSTRACT

The global market of sweet potato (Ipomoea batatas (L.) Lam.) is continuously growing and, consequently, demands greater productivity from the agricultural sector. The use of biofertilizers facilitates plant growth by making essential nutrients available to crops or providing resistance against different abiotic and biotic factors. The strains Bacillus safensis T052-76 and Bacillus velezensis T149-19 have previously been inoculated in the sweet potato cultivar Ourinho, showing positive effects on plant shoot growth and inhibiting the phytopathogen Plenodomus destruens. To elucidate the effects of these strains on sweet potato growth, four different cultivars of sweet potato were selected: Capivara, IAPAR 69, Rosinha de Verdan and Roxa. The plants were grown in pots in a greenhouse and inoculated with the combined strains according to a randomized block design. A control (without the inoculation of both strains) was also used. A slight positive effect of the inoculation of the two Bacillus strains was observed on the aerial parts of some of the cultivars. An increase in the fresh weight of the sweet potatoes of the inoculated plants was obtained, varying from 2.7 to 11.4 %. The number of sweet potatoes obtained from the inoculated cultivars IAPAR 69 and Roxa increased 15.2 % and 16.7 %, respectively. The rhizosphere soil of each cultivar was further sampled for DNA extraction, and the 16S rRNA gene metabarcoding technique was used to determine how the introduction of these Bacillus strains influenced the rhizosphere bacterial community. The bacterial communities of the four different cultivars were dominated by Actinobacteria, Proteobacteria and Firmicutes. Nonmetric multidimensional scaling (NMDS) revealed that the rhizosphere bacterial communities of plants inoculated with Bacillus strains were more similar to each other than to the bacterial communities of uninoculated plants. This study highlights the contribution of these Bacillus strains to the promotion of sweet potato growth.

1. Introduction

The sweet potato (*Ipomoea batatas* (L.) Lam., Convolvulaceae) is the seventh most important food crop in the world and is considered a superfood due to its nutritional properties [1]. Sweet potatoes contain bioactive compounds such as (poly)phenols,

E-mail address: lseldin@micro.ufrj.br (L. Seldin).

https://doi.org/10.1016/j.heliyon.2024.e34377

Received 19 December 2023; Received in revised form 5 July 2024; Accepted 9 July 2024

Available online 9 July 2024

^{*} Corresponding author. Laboratório de Genética Microbiana, Departamento de Microbiologia Geral, Instituto de Microbiologia Paulo de Góes, Universidade Federal do Rio de Janeiro, Centro de Ciências da Saúde, Bloco I, Ilha do Fundão, CEP 21941, Rio de Janeiro, Brazil.

^{2405-8440/© 2024} The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

terpenoids, tannins, saponins, glycosides, alkaloids and phytosterols [2]. These compounds are also responsible for the different colors of existing tuberous roots, which vary among white, cream, yellow, purple and intermediate shades [3]. Yellow and orange tuberous roots boast high carotenoid content, purple roots contain anthocyanins, and white roots are abundant in phenolic acids. These compounds are antioxidants, and their consumption is associated with a lower risk of diabetes, cardiovascular diseases, cognitive problems and cancer [2,4]. Moreover, sweet potato tuberous roots have a high energy value, are rich in low-glycemic carbohydrates and dietary fiber, and contain significant amounts of potassium (K), vitamin A (retinol) and other nutrients, especially vitamins from the B complex [5].

Sweet potatoes are cultivated worldwide, with cultivar selection driven by factors such as carotenoid content and productivity. In Brazil, the cultivars Capivara, IAPAR 69, Rosinha de Verdan, and Roxa are widely produced, each presenting different morphological traits and pigmentation characteristics. For example, the Rosinha de Verdan cultivar is extensively grown, especially in the state of Rio de Janeiro, despite its white flesh and low carotenoid content. In contrast, the IAPAR 69 cultivar is notable for its high carotenoid content and robust productivity. The Roxa cultivar, known for its purple pigmentation, and the Capivara cultivar, with its yellow flesh, are highly resilient to various climate conditions. These diverse cultivars ensure successful sweet potato cultivation across many regions and provide a variety of options to the consumer [6].

Sweet potatoes are also a raw material for various food and industrial applications and are used as ornamental plants [7]. In addition, sweet potatoes are used as a food source in livestock farming in several countries around the world [8]. Sweet potato starch can also be used to produce bioplastics and biofuels, expanding renewable sources for industry [9–11]. Therefore, there is growing interest in improving the yield, quality and standardization of sweet potatoes and their derived products [2,3].

The adoption of practices and technologies that are economically viable, preserve the environment and increase food production and quality is well regarded as necessary. The use of biofertilizers—a product, process or technology that contains microorganisms that act favorably in the development of plants—is increasingly common in the agricultural sector. They improve plant development by increasing the availability of nutrients and absorption by roots, by controlling agricultural pests and diseases, or by modulating plant growth hormones (phytohormones) [12]. In addition, the use of biofertilizers reduces the production costs associated with chemical inputs such as fertilizers and pesticides.

Bacillus strains used as biofertilizers have been demonstrated to act both for plant growth and for pest and disease control [13,14] in different plants, such as cotton, lettuce, maize, tomato crops, and others [15–19]. Different *Bacillus* strains have been demonstrated to improve soil nutrient availability by improving the nitrogen supply, solubilizing phosphate and potassium, and producing side-rophores to chelate Fe3+. They can also secrete hormones and volatile organic compounds (VOCs), which contribute to plant cell growth and root development and further improve nutrient uptake by plants. The resistance of plants to biotic stresses can be improved by the presence of *Bacillus* strains, as *Bacillus* strains can directly produce substances such as cyclic lipopeptides, polyketides, and volatile organic compounds (VOCs) against pathogens and/or induce system resistance in plants. Finally, they can lead to different physicochemical and genetic changes in plants, inducing tolerance to abiotic stresses, such as salinity and drought. These plant growth-promoting mechanisms were extensively reviewed in various strains, particularly in *Bacillus thuringiensis* [20] and *Bacillus anyloliquefaciens* [21].

Mateus et al. [22] observed that the sweet potato cultivar Ourinho, when inoculated with the strains *Bacillus velezensis* T149-19 and *Bacillus safensis* T052-76, showed better growth and greater resistance to foot rot disease caused by the fungus *Plenodomus destruens*. In addition, sweet potato plants inoculated with these bacterial strains had greater heights, greater numbers of leaves and greater occurrence of lateral stem shoots, demonstrating their potential as plant growth-promoting bacteria (PGPB). However, the effects reported were observed only in a single cultivar, in the aerial part of the plant, and the number of sweet potatoes obtained from the inoculated plants has not been evaluated. Therefore, the present study aims to shed light on (i) whether the effects reported on the Ourinho cultivar extend to other sweet potato cultivars, both in the aerial part and in the sweet potatoes produced, and (ii) the potential for using the two strains as PGPB for these cultivars. In addition, the influence of the inoculation of the two strains on the bacterial community present in the rhizosphere of these four selected sweet potato cultivars was observed through 16S rRNA (*rrs*) gene metabarcoding.

2. Materials and methods

2.1. Site description and experimental design

The greenhouse experiment was carried out at Embrapa Agrobiologia, Seropédica, RJ, between May and November 2021 and lasted 133 days. A randomized block design (RBL) was used: 96 pots were divided into 12 blocks (with 8 pots each) with four treatments and their respective controls (8 factors—4 treatments and 4 controls). The distribution (order) of the treatments and controls between the pots in each block was determined using Sisvar v. 5.6 software [23] (Table S1).

Flexible 14-liter Nutriplan pots were used, filled with a layer of approximately 5 cm of expanded clay at the bottom and 12 kg of a mixture of sieved soil with 20 % sand. In addition, each pot was enriched with 1 g of single superphosphate (SSP) and 200 mg of potassium chloride. The soil used to fill the pots was collected from the Terraço Experimental Field in Seropédica, RJ (S 22° 45′ 01." W 043° 39′ 58.8″). The results of the soil analysis in accordance with the Laboratory Manual: Soil, Water, Animal Nutrition and Food [24] are presented in Table S2.

The sweet potato cultivars selected for the study—Capivara, IAPAR 69, Rosinha de Verdan and Roxa—were collected from the field of Fazendinha Agroecológica km 47 in Seropédica, RJ. Their characteristics are presented in Fig. 1 (A-E, aerial part and tuberous roots of sweet potato cultivars). A total of 12 cuttings were randomly selected for each treatment and control and transplanted into their

respective pots. A hole approximately 10 cm deep was drilled in each pot before planting. Irrigation with filtered and dechlorinated water was maintained once a day throughout the experimental period.

2.2. Bacterial strains used as biofertilizers

The two strains *Bacillus velezensis* T149-19 and *Bacillus safensis* T052-76 were previously isolated from sweet potato [25,26] and were maintained in Trypticase Soy Broth (TSB; Difco) supplemented with 20 % glycerol at -80 °C.

To prepare the inoculum, the two strains were grown individually in 20 mL of TSB for 24 h at 32 °C under agitation (preinoculum). Subsequently, the two strains were grown in 1 L of TSB medium (1 % inoculum) under the same conditions. The CFU/ml of each strain was determined, and the cultures were diluted to 10^8 CFU/ml. On the 29th day after transplanting the sweet potato cuttings, the treatment plots were inoculated with 120 ml of the mixture (1 % per kg of soil) in the area of the soil around the plants, with approximately 10^7 CFU/ml of each of the bacterial strains. In the control plots, 120 ml of sterile distilled water was added.



Fig. 1. Morphological characteristics of the sweet potato cultivars used in this study. The aerial parts of the sweet potato cultivars Capivara (A), IAPAR 69 (B), Rosinha de Verdan (C) and Roxa (D) have similar characteristics, with the exception of the Capivara cultivar (A), whose leaves are flattened. The tuberous roots of sweet potato cultivars are shown in (E). From left to right: Capivara, IAPAR 69, Rosinha de Verdan and Roxa. The Capivara cultivar has a slightly pink skin with white flesh; IAPAR 69, known as "Cenoura", has orange skin and flesh; Rosinha de Verdan has deep pink skin and yellow flesh; and Roxa has both purple skin and flesh.



(caption on next page)

Fig. 2. Comparison between uninoculated and inoculated plants at intervals of days in terms of (A) the number of healthy leaves, (B) lateral branches, (C) main branch length and (D) circumference of the sweet potato cultivars Capivara, IAPAR 69, Rosinha de Verdan and Roxa. The presence of * represents a significant difference (one-way ANOVA test: $p \le 0.05$; n = 12 replicates for each treatment) between the uninoculated and inoculated plants.

2.3. Evaluation of the growth of the sweet potato cultivars

After inoculation with the two *Bacillus* strains, nine periodic measurements (up to 133 days) were taken to assess the growth of the aerial parts of the sweet potato cultivars. The length of the main branch was measured from the base of the stalk to the apical bud. The circumference of the stem was measured around the area close to the collar. The number of healthy leaves and lateral branches was determined visually.

At the end of the experimental period in the greenhouse, the roots were removed, washed and left to dry for 24 h at room temperature. After this period, the number of sweet potatoes produced by each plant was counted manually, and the sweet potatoes produced were weighed fresh (fresh mass). Total yields were also calculated, i.e., the sum of the total produced in the 12 pots by each cultivar (inoculated and uninoculated).

2.4. Total DNA isolation from the rhizosphere soil of sweet potato cultivars

Before washing the roots, the rhizosphere soil (adhering to the sweet potatoes) was collected (5 \times) for each cultivar (as described in [25]) randomly between the blocks, with the treatment and its respective control always being collected in the same block. The samples were kept at -20 °C before total community DNA extraction.

DNA was extracted from the rhizosphere using the DNeasy 96 PowerSoil Pro QIAcube HT Kit (Qiagen®, Hilden, Germany) following the manufacturer's instructions. Its integrity was checked using agarose gel electrophoresis (0.8 %) for 1:30 h at 90 V. Subsequently, the DNA obtained was quantified using a NanoDropTM spectrophotometer (Thermo Fisher ScientificTM, MA, USA). The total DNA extracted was sent to Novogene (Sacramento, CA, USA) and sequenced on an Illumina NovaSeq 6000 platform, as recommended by the manufacturer. The primers used to amplify the V5–V7 hypervariable region of the *rrs* gene (which encodes 16S rRNA) were 799 F (AACMGGATTAGATACCCKG) and 1193 R (ACGTCATCCCCACCTTCC).

2.4.1. Rhizosphere bacteriome analyses through 16S rRNA gene metabarcoding

The sequences obtained (40 samples) were analyzed using Mothur v.1.48.0 software [27]. The direct and reverse sequences were paired in contigs and ambiguities, and homopolymers (\geq 8) and sequences of inconsistent sizes were removed. Virtual PCR was performed on the Silva v.138 database [28] with the 799 F and 1193 R primers before alignment. An error removal step was performed using the pre.cluster command to remove chimeric sequences. The sequences were classified based on the Ribosomal Database Project (RDP) with a bootstrap value of 80 % [29], and possible contaminants, such as mitochondrial DNA, chloroplasts, Archaea, Eukarya and sequences not assigned to any domain, were removed. Similar sequences were classified into operational taxonomic units (OTUs) using the "cluster.split" command (cutoff = 3 %). Finally, the Chao1, Shannon and Simpson indices, the number of OTUs and the relative bacterial abundance (%) at the phylum and genus levels were exported from Mothur v.1.48.0 software for subsequent statistical analyses.

2.5. Statistical analyses

The data collected during and at the end of the experimental period in the greenhouse as well as the data from the bioinformatics analyses were submitted to Past v.4.08 software [30] to apply the Shapiro–Wilk normality and Levene homoscedasticity tests. ANOVA (parametric) and the Kruskal–Wallis (nonparametric) test were then applied. For the similarity analysis, which was carried out using nonmetric multidimensional scaling (NMDS) based on the Bray–Curtis dissimilarity index, the data were subjected to PERMANOVA. A heatmap of the relative abundance of taxa was generated with the package pheatmap [31] in R Studio v4.3.2 [32].

3. Results

3.1. Effects of biofertilization on the growth of the four cultivars

During the greenhouse experiment, plants inoculated with *B. velezensis* T149-19 and *B. safensis* T052-76 were compared to uninoculated plants considering their number of healthy leaves, lateral branches, and main branch length and circumference (Fig. 2 A-D). The number of healthy leaves was quite similar between inoculated and uninoculated plants of the four cultivars (Fig. 2 A). An increasing trend in the number of lateral branches was observed for all inoculated cultivars, mainly from the beginning to the middle of the experiment (Fig. 2 B). Considering the main branches of the inoculated sweet potato cultivars, we observed an increase in the circumference of Capivara and in both the length and circumference of Roxa. Nevertheless, not all measurements were statistically significant (Fig. 2 C, D).

The total yield (sum of the values produced by the 12 plants) of the fresh weight and number of sweet potatoes resulting from the different cultivars at the end of the experiment was further considered (Table 1). All sweet potato cultivars responded positively to an

increase in fresh weight, with enhancements varying between 2.7 % (IAPAR 69) and 11.4 % (Capivara). Furthermore, the number of sweet potatoes obtained from the inoculated cultivars IAPAR 69 and Roxa increased by 15.2 % and 16.7 %, respectively (Table 1).

3.2. Bacterial communities associated with the rhizosphere of the four sweet potato cultivars

Sequencing of the 16S rRNA (*rrs*) gene from the DNA of the 40 rhizosphere soil samples obtained at the end of the greenhouse experiment (133 days) generated a total of 7,342,015 sequences. After classifying these sequences into OTUS, 2,070,790 sequences remained, resulting in approximately 412,810 sequences per cultivar, of which 206,405 were from the treatment group (5 samples of plants inoculated with *B. velezensis* T149-19 and *B. safensis* T052-76) and 206,405 from the control group (5 samples of uninoculated plants). From these sequences, the richness (Chao1), diversity (Shannon) and dominance (Simpson) indices were calculated, as well as the relative abundance of bacterial taxa (Fig. S1).

Analyses of the different cultivar sequences showed no significant difference between inoculated and uninoculated plants in terms of richness (Chao1), diversity (Shannon) or bacterial dominance (Simpson), with the exception of between inoculated and uninoculated Capivara plants, where a decrease in diversity (Shannon) was observed in the inoculated plants (Fig. S1). Although the difference was not statistically significant, the inoculated plants had greater median bacterial diversity in Rosinha de Verdan and lower median bacterial diversity in Rosa. Additionally, a lower median bacterial dominance was observed in IAPAR 69 and Rosinha de Verdan, while a greater median bacterial dominance was observed in Capivara and Roxa, compared to the uninoculated plants (Fig. S1).

Concerning the relative bacterial abundance, in all the cultivars (inoculated and uninoculated), 79.86 % of the sequences were classified at the phylum level. The top 10 most abundant phyla (>0.05 % relative abundance) and classified genera (>0.33 % relative abundance) are shown in Fig. 3 (A, B). The bacterial community of the four different cultivars was dominated by the phyla Actinobacteria, Proteobacteria and Firmicutes, and no significant differences were detected among the four cultivars or treatments (uninoculated and inoculated). At the genus level, 37,83 % of the sequences were classified, and the top 10 genera classified, from most abundant to least abundant, were *Bacillus, Streptomyces, Pseudolabrys, Solirubrobacter, Bradyrhizobium, Mycobacterium, Paenibacillus, Sphingomonas, Micromonospora* and *Pedomicrobium* (Fig. 3 B).

Using nonmetric multidimensional scaling (NMDS) based on the Bray–Curtis dissimilarity index, the bacterial community of each cultivar from both inoculated and uninoculated plants was compared (Fig. 4 A-D and 5 A, B). The bacterial communities of the inoculated cultivars Rosinha de Verdan and Roxa were significantly different from those of the uninoculated plants (PERMANOVA test, $p \le 0.05$ - Fig. 4 C, D). Additionally, the structures of the bacterial communities of the inoculated cultivars were more similar to each other (Fig. 5 A, B). The bacterial community structure of the Capivara cultivar differed significantly (PERMANOVA test, $p \le 0.05$) from the bacterial community structure of the Rosinha de Verdan and Roxa cultivars among the inoculated cultivars; however, these two latter cultivars did not differ from each other (Fig. 5 B). In addition, the bacterial community structures of the IAPAR 69 and Roxa cultivars differed from each other (PERMANOVA test, $p \le 0.05$; Fig. 5 B).

4. Discussion

The increasing interest in sweet potato worldwide is mainly due to its association with healthy eating and living. It fulfills the basic requirements for human food needs and is a key vegetable crop for reducing poverty and increasing global food security [33,34]. Chemical fertilizers and pesticides are still widely used to control pests and diseases in sweet potato, although their continued use is a threat to soil, plants and human beings. Therefore, investment in sustainable technologies, such as the use of microorganisms to promote plant growth and as biological control agents, is essential for the development of agriculture in the future [35–39]. To contribute to the advancement of knowledge in this area, the present study evaluated the effects of *Bacillus safensis* T052-76 and *Bacillus velezensis* T149-19 on the growth promotion of four sweet potato cultivars—Capivara, IAPAR 69, Rosinha de Verdan and Roxa—as well as the influence of these *Bacillus* strains on the bacterial communities present in their rhizospheres.

During the greenhouse experiment, the inoculation of the sweet potato cultivars studied here with the strains T052–76 and T149-19 had a positive effect to some extent on the four features evaluated. Similarly, in previous studies by our group, positive effects on the growth of the aerial part of the sweet potato cultivar Ourinho were observed after inoculation with strains T149–19 and T052-76 [22].

Table 1

Total yield (sum of the values produced by the 12 plants) of the fresh weight and number of sweet potatoes resulting from the different cultivars at the end of the experiment.

Sweet potato cultivars		fresh weight of the sweet potatoes (g)	% of increase *	Number of sweet potatoes	% of increase *
Capivara	С	1,439.1	11.4	67	-
	I	1,602.6		63	
IAPAR 69	С	1,580.4	2.7	79	15.2
	I	1,622.8		91	
Rosinha de Verdan	С	1,774.5	5.5	55	-
	I	1,871.5		49	
Roxa	С	721.6	3.1	60	16.7
	I	743.7		70	

C – control; I – sweet potato cultivars inoculated with *Bacillus velezensis* T149-19 and *Bacillus safensis* T052-76. (*) Percentage increase when the results obtained after inoculation are compared to those obtained without inoculation (control). (–) no increase observed.

A) PHYLA RELATIVE ABUNDANCE







Fig. 3. Heatmap of the relative abundance of phyla (A) and genera (B) in the bacterial community of the four different sweet potato cultivars inoculated with *Bacillus velezensis* T149-19 and *Bacillus safensis* T052-7 in comparison to uninoculated plants.

At the end of our experiment, increases were also observed in the fresh mass of sweet potatoes (in all cultivars) and in the number of resulting sweet potatoes in Roxa and in IAPAR 69. These positive results related to productivity show that strains T149–19 and T052-76 have beneficial effects, once again reinforcing the potential of the bacterial strains studied as plant growth-promoting strains for different sweet potato cultivars.

In the literature, several plant growth-promoting characteristics (both direct and indirect) have been attributed to different strains of *B. safensis* [40] and *B. velezensis* [41]. Shi et al. [42] reported an increase in the diameter and height of *Prunus davidiana*, along with soil enrichment with N, P, K and organic matter following the inoculation of strains belonging to these species. Similarly, Mosela et al. [43] demonstrated an increase in the biomass of aerial parts and roots, as well as in the P content of maize. In studies with rice, Khan et al. [44] and Wang et al. [45] reported an increase in germination percentage, seedling growth, photosynthetic pigment contents, plant height, and fresh and dry weights. Similarly, Azzem et al. [46] demonstrated that *Bacillus safensis* PM22 has great potential for promoting the growth of maize plants under salinity stress through the induction of photosynthesis, the deposition of soluble solutes, the production of nonenzymatic and enzymatic antioxidants, the production of osmoprotectants, and the reduction of oxidative stress markers. *Bacillus safensis* VRKK2 improved the growth of cowpea through several plant growth-promoting traits, such as IAA production, phosphate solubilization, HCN production, ammonia production, nitrogen fixation and siderophore production [47]. *Bacillus velezensis* FZB42 can stimulate plant growth and produce different types of biologically active secondary metabolites that suppress plant pathogenic microflora [48]. As several *Bacillus* species have been reclassified as *B. velezensis*, based on recent phylogenetic analysis, different plant growth-promoting mechanisms that have been extensively reviewed in *Bacillus amyloliquefaciens* [21] could also be attributed to the strain used here.

The abovementioned reports, combined with the results presented here, emphasize the biofertilization potential of the strains T149–19 and T052-76 under controlled greenhouse conditions. Further studies are essential to elucidate the metabolic mechanisms and key modulating factors responsible for plant growth promotion induced by the inoculation of these strains. Moreover, field trials are imperative to evaluate the strains' performance under diverse agricultural conditions and with other crops, thus contributing for



Fig. 4. Nonmetric multidimensional scaling (NMDS) generated in a 3D graph based on the Bray–Curtis dissimilarity index between uninoculated and inoculated sweet potato cultivars: (A) Capivara, (B) IAPAR69, (C) Rosinha de Verdan and (D) Roxa. Differences were considered significant when $p \le 0.05$ (PERMANOVA test; n = 5 for each treatment).



Fig. 5. Nonmetric multidimensional scaling (NMDS) generated in a 3D graph based on the Bray–Curtis dissimilarity index between (A) uninoculated and (B) inoculated sweet potato cultivars. The letters (a, b and c) indicate similarities and significant differences (PERMANOVA test, $p \le 0.05$; n = 5 for each treatment) between the structures of the bacterial communities of the cultivars.

the development of a biofertilizer.

The influence of the inoculation of the two *Bacillus* strains on the bacterial community present in the rhizosphere of the four sweet potato cultivars was analyzed after 16S rRNA (*rrs*) gene metabarcoding. Alpha-diversity analyses revealed that the strains did not significantly alter the composition, richness or dominance of the bacterial communities present in the rhizosphere of the four cultivars. Similarly, Mateus et al. [22] reported that inoculation of strains T149–19 and T052-76 into the sweet potato cultivar Ourinho did not significantly alter the local bacterial community (for 180 days). However, in this study, an increase in bacterial diversity (Shannon) was observed in Rosinha de Verdan, while a decrease was observed in Roxa and Capivara, all of which were inoculated with *Bacillus* strains. This suggests that the inoculated strains somewhat affect the bacterial diversity of the rhizosphere depending on the cultivar studied. Wang et al. [45] observed that both the individual inoculation of *Bacillus velezensis* FH-1 and its coinoculation with *Brevundimonas diminuta* NYM3 in rice led to an increase in the diversity (Shannon), similar to that observed here in the Rosinha de Verdan cultivar.

When the different phyla and genera associated with the rhizosphere of the four cultivars were compared, it was observed that the same bacterial taxa were recruited, although they were found in different relative abundances, especially considering the lowabundance taxa. It is plausible that the effects (both on plant growth and the composition of the bacterial community) observed after inoculation with the *Bacillus* strains may vary due to genotypic and phenotypic variations between the cultivars. Marques et al. [25] showed that both the age and genotype of three sweet potato cultivars significantly influenced the structure of the rhizosphere bacterial community. Furthermore, the same sweet potato cultivars showed different recruitment of members of the bacterial communities (phosphate mineralizers and nitrogen fixers) in their rhizospheres [49]. Some bacterial taxa that occur in low abundance are still of great importance because they are increasingly being recognized as drivers of key functions for the ecosystem [50].

Finally, beta diversity analyses revealed that the bacterial communities of the inoculated cultivars Rosinha de Verdan and Roxa were significantly different from those of the uninoculated plants. Greater similarity was also observed between the structures of the bacterial communities of the four cultivars that were inoculated with the *Bacillus* strains, corroborating previous results that demonstrated the influence of inoculating these strains on the bacterial community in the rhizospheres of sweet potato cultivars [22]. However, the differences observed depending on the cultivar analyzed should be considered relevant in selecting potential cultivars to be grown in the field. Further studies are also necessary to correlate the changes in bacterial communities observed in this study with the increase in productivity.

5. Conclusion

The strains *Bacillus velezensis* T149-19 and *Bacillus safensis* T052-7 promoted growth not only of the Ourinho cultivar but also of four other sweet potato cultivars (Capivara, IAPAR 69, Rosinha de Verdan, and Roxa), which are typically cultivated in different countries under different types of soil and climatic conditions. The observed increase in the total yield of the fresh weight and number of sweet potatoes resulting from the different cultivars at the end of the experiment is encouraging for further field studies. Additionally, the rhizosphere bacterial community was only slightly influenced by the cultivar studied when inoculated with the two *Bacillus* strains.

Availability of data and materials

Data associated with the study have not been deposited into a publicly available repository. The data are available from the corresponding author upon reasonable request.

Funding

This study was supported by grants from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES, financial code 001) and Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ).

CRediT authorship contribution statement

Matheus Barbosa Bernardes: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis. Isabella Dal'Rio: Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Formal analysis. Marcia Reed Rodrigues Coelho: Writing – review & editing, Supervision, Resources, Methodology, Investigation, Conceptualization. Lucy Seldin: Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

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

Acknowledgments

We would like to express our gratitude to the members of Embrapa Agrobiologia for their help with the establishment and maintenance of the experiment in the greenhouse.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.heliyon.2024.e34377.

References

- M. Mohammed, Postharvest Handling and Quality Management of Sweet Potato (Ipomoea Batatas (L.) Lam), FAO, Rome, Italy, 2022. Retrieved from, https:// www.fao.org/publications/card/en/c/CC0034EN.
- [2] E.P. Laveriano-Santos, A. López-Yerena, C. Jaime-Rodríguez, J. González-Coria, R.M. Lamuela-Raventós, A. Vallverdú-Queralt, J. Romanyà, M. Pérez, Sweet potato is not simply an abundant food crop: a comprehensive review of its phytochemical constituents, biological activities, and the effects of processing, Antioxidants 11 (2022) 1648.
- [3] S.K. Campos, L. Pilon, R.A.C. Melo, Mudanças recentes no padrão de consumo da batata-doce no Brasil: perspectivas para o mercado nacional, in: Proceedings of the Congresso da Sociedade Brasileira de Economia, Administração e Sociologia rural, Brasília, DF, Brazil, 6, 2021.
- [4] M.K. Alam, A comprehensive review of sweet potato (Ipomoea batatas [L.] Lam): revisiting the associated health benefits, Trends Food Sci. Technol. 115 (2021) 512–529.
- [5] C. Sánchez, M. Santos, P. Vasilenko, Batata-doce branca, roxa ou alaranjada? Avaliação qualitativa e nutricional, Rev. Vida Rural 1847 (2019) 30-32.
- [6] M. Jesus, J.G. Guerra, J.A. Espindola, S. Pacheco, R.G. Borguini, R.L.O. Godoy, Carotenoid content of three varieties of sweet potato (*Ipomoea batatas* L.) grown under organic and conventional production systems, in: Proceedings of the VI Congresso Latino-americano de Agroecologia; X Congresso Brasileiro de Agroecologia; V Seminário de Agroecologia do Distrito Federal e Entorno, Brasília, DF, Brazil, 2017.
- [7] G. Padmaja, J.T. Sheriff, M.S. Sajeev, Food uses and nutritional benefits of sweet potato, Fruit, Veg. Cereal Sci. Biotechnol. 6 (1) (2012) 115–123.
- [8] S. Murigan, S.K. Paramasivam, M. Nedunchezhizyan, Sweet potato as animal feed and fodder, Fruit, Veg. Cereal Sci. Biotechnol. 6 (1) (2012) 106-114.
- [9] C. Lareo, M.D. Ferrari, Sweet potato as a bioenergy crop for fuel ethanol production: perspectives and challenges, in: R.C. Ray, S. Ramachandran (Eds.), Bioethanol Production from Food Crops, Elsevier, Amsterdam, 2019, pp. 115–147.
- [10] R. Lyu, S. Ahmed, W. Fan, J. Yang, X. Wu, W. Zhou, P. Zhang, L. Yuan, H. Wang, Engineering properties of sweet potato starch for industrial applications by biotechnological techniques including genome editing, Int. J. Mol. Sci. 22 (17) (2021) 9533.
- [11] C. Tang, Y. Lu, B. Jiang, J. Chen, X. Mo, Y. Yang, Z. Wang, Energy, economic, and environmental assessment of sweet potato production on plantations of various sizes in South China, Agronomy 12 (6) (2022) 1290.
- [12] B. Aloo, B. Makumba, E. Mbega, The potential of Bacilli rhizobacteria for sustainable crop production and environmental sustainability, Microbiol. Res. 219 (2019) 26–39.
- [13] R. Borriss, Toward a new generation of commercial microbial disease control and plant growth promotion products, in: B. Lugtenberg (Ed.), Principles of Plant-Microbe Interactions: Microbes for Sustainable Agriculture, Springer, Switzerland, 2015, pp. 329–337.
- [14] F. Kamilova, Y. Okon, S. de Weert, K. Hora, Commercialization of microbes: manufacturing, inoculation, best practice for objective field testing, and
- registration, in: B. Lugtenberg (Ed.), Principles of Plant Microbe Interactions: Microbes for Sustainable Agriculture, Springer, Switzerland, 2015, pp. 319–327.
 B. Fan, L.C. Carvalhais, A. Becker, D. Fedosevenko, N. Von Wiren, R. Boriss, Transcriptomic profiling of *Bacillus amyloliquefaciens* FZB42 in response to maize root exudates. BMC Microbiol. 12 (2012) 116.
- [16] O.A. Almaghrabi, S.I. Massoud, T.S. Abdelmoneim, Influence of inoculation with plant growth promoting rhizobacteria (PGPR) on tomato plant growth and nematode reproduction under greenhouse conditions, Saudi J. Biol. Sci. 20 (1) (2013) 57–61.
- [17] T. Chaudhary, P. Shukla, Chapter 6 bioinoculants development for sustainable agriculture by innovative optimization processes: a future roadmap to
- commercialization, in: P. Shukla (Ed.), Progress in Biochemistry and Biotechnology, Microbial Bioprocesses, Academic Press, 2023, pp. 107–119.
 [18] S. Tan, Y. Dong, H. Liao, J. Hung, S. Song, Y. Xu, Q. Shaen, Antagonistic bacterium *Bacillus amyloliquefaciens* induces resistance and controls the bacterial wilt of tomato, Pest Manag. Sci. 69 (11) (2013) 245–1252.
- [19] T.S. Matsumura, I.C.P. Paz, A.M. Guimarães, M.E. Silva, A.P. Ott, V. Duarte, Effect of three formulations of Bacillus amyloliquefaciens ICBB200 on lettuce growth (Lactuca sativa L.) in five soil and climate conditions, Sci. Agrar. Parana. 15 (2) (2016) 146–152.
- [20] U. Azizoglu, Bacillus thuringiensis as a biofertilizer and biostimulator: a mini-review of the little-known plant growth-promoting properties of Bt, Curr. Microbiol. 76 (11) (2019) 1379–1385.
- [21] L. Luo, C. Zhao, E. Wang, A. Raza, C. Chunying Yin, Bacillus amyloliquefaciens as an excellent agent for biofertilizer and biocontrol in agriculture: an overview for its mechanisms, Microbiol. Res. 259 (2022) 127016.
- [22] J.R. Mateus, I. Dal'Rio, D. Jurelevicius, F.F. da Mota, J.M. Marques, R.T.J. Ramos, A.L. da Costa da Silva, P.R. Gagliardi, L. Seldin, Bacillus velezensis T149-19 and Bacillus safensis T052-76 as potential biocontrol agents against foot rot disease in sweet potato, Agriculture 11 (2021) 1046.
- [23] D.F. Ferreira, Sisvar: um sistema computacional de análise estatística, Cienc. E Agrotecnol 35 (6) (2011) 1039–1042.
- [24] A.R.A. Nogueira, G.B. Souza, Manual de Laboratórios: Solo, Água, Nutrição Vegetal, Nutrição Animal e Alimentos, in: São Carlos, Embrapa Pecuária Sudeste, 313p. 2005.
- [25] J.M. Marques, T.F. da Silva, R.E. Vollú, A.F. Blank, G.C. Ding, L. Seldin, K. Smalla, Plant age and genotype affect the bacterial community composition in the tuber rhizosphere of field-grown sweet potato plants, FEMS Microbiol. Ecol. 88 (2) (2014) 424–435.
- [26] J.M. Marques, T.F. da Silva, R.E. Vollú, J.R.M. De Lacerda, A.F. Blank, K. Smalla, L. Seldin, Bacterial endophytes of sweet potato tuberous roots affected by the plant genotype and growth stage, Appl. Soil Ecol. 96 (2015) 273–281.
- [27] P.D. Schloss, S.L. Westcott, T. Ryabin, J.R. Hall, M. Hartmann, E.B. Hollister, R.A. Lesniewski, B.B. Oakley, D.H. Parks, C.J. Robinson, J.W. Sahl, B. Stres, G. G. Thallinger, D.J. Van Horn, C.F. Weber, Introducing mothur: open-source, platform-independent, community-supported software for describing and comparing microbial communities, Appl. Environ. Microbiol. 75 (23) (2009) 7537–7541.
- [28] C. Quast, E. Pruesse, P. Yilmaz, J. Gerken, T. Schweer, P. Yarza, J. Peplies, F.O. Glöckner, The SILVA ribosomal RNA gene database project: improved data processing and web-based tools, Nucleic Acids Res. 41 (Database issue) (2013) D590–D596.
- [29] J.R. Cole, Q. Wang, E. Cardenas, J. Fish, B. Chai, R.J. Farris, A.S. Kulam-Syed-Mohideen, D.M. McGarrell, T. Marsh, G.M. Garrity, J.M. Tiedje, The Ribosomal Database Project: improved alignments and new tools for rRNA analysis, Nucleic Acids Res. 37 (Database issue) (2009) D141–D145.
- [30] O. Hammer, D.A.T. Harper, P.D. Ryan, Past: paleontological statistics software package for education and data analysis, Paleontol. Electron. 1 (2001) 9.
- [31] R. Kolde, M.R. Kolde, Package 'pheatmap', R packag. 1 (7) (2015) 790.
- [32] R Core Team, R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria, 2022. https://www.R-project. org/. (Accessed 2 July 2023).

- [33] Z. Sapakhova, N. Raissova, D. Daurov, K. Zhapar, A. Daurova, A. Zhigailov, K. Zhambakin, M. Shamekova, Sweet potato as a key crop for food security under the conditions of global climate change: a review, Plants 12 (2023) 2516.
- [34] D. Tedesco, B.R.A. Moreira, M.R.B. Júnior, M. Maeda, R.P. Silva, Sustainable management of sweet potatoes: a review on practices, strategies, and opportunities in nutrition-sensitive agriculture, energy security, and quality of life, Agric. Syst. 210 (2023) 103693.
- [35] M. Scagliota, F. Valentinuzzi, T. Mimmo, S. Cesca, C. Crecchio, Y. Pii, Bioinoculants as promising complement of chemical fertilizers for a more sustainable agricultural practice, Front. Sustain. Food Syst. 4 (2021) 1–12.
- [36] M. Singh, S. Bhasin, N. Madan, D.C. Suyal, R. Soni, D. Singh, Bioinoculants for agricultural sustainability, in: R. Soni, D.C. Suyal, P. Bhargava, R. Goel (Eds.), Microbiological Activity for Soil and Plant Health Management, Springer Nature, Singapore, 2021, pp. 629–641.
- [37] S. Maitra, M. Brestic, P. Bhadra, T. Shankar, S. Praharaj, J.B. Palai, M.M.R. Shah, V. Barek, P. Ondrisik, M. Skalický, A. Hossain, Bioinoculants-natural biological Resources for sustainable plant production, Microorganisms 10 (1) (2021) 51.
- [38] T. Chaudhary, P. Shukla, Bioinoculants development for sustainable agriculture by innovative optimization processes: a future roadmap to commercialization, in: P. Shukla (Ed.), Microbial Bioprocesses: Applications and Perspectives, Elsevier, Academic Press, 2023, pp. 107–119.
- [39] D. Shahwar, Z. Mushtaq, H. Mushtaq, A.A. Alqarawi, Y. Park, T.S. Alshahrani, S. Faizan, Role of microbial inoculants as bio fertilizers for improving crop productivity: a review, Heliyon 9 (2023) e16134.
- [40] A. Lateef, I.A. Adelere, E.B. Gueguim-Kana, The biology and potential biotechnological applications of *Bacillus safensis*, Biologia 70 (4) (2015) 411–419.
 [41] F.N. Alenezi, H.B. Slama, A.C. Bouket, H. Cherif-Silini, A. Silini, L. Luptakova, J.A. Nowakowska, T. Oszako, L. Belbahri, *Bacillus velezensis*: a treasure house of
- bioactive compounds of medicinal, biocontrol and environmental importance, Forests 12 (2021) 1714.
 [42] H. Shi, L. Lu, J. Ye, L. Shi, Effects of two *Bacillus velezensis* microbial inoculants on the growth and rhizosphere soil environment of *Prunus davidiana*, Int. J. Mol.
- [42] H. Shi, E. Li, J. Te, E. Shi, Elects of two Bachus vetezensis incrobial moculants on the growth and mizosphere son environment of Pranas davidana, int. J. Mol. Sci. 23 (21) (2022) 13639.
- [43] M. Mosela, G. Andrade, L.R. Massucato, et al., *Bacillus velezensis* strain Ag75 as a new multifunctional agent for biocontrol, phosphate solubilization and growth promotion in maize and soybean crops, Sci. Rep. 12 (2022) 15284.
- [44] M.H.U. Khan, J.Z.K. Khattak, M. Jamil, I. Malook, S.U. Khan, M. Jan, I. Din, S. Saud, M. Kamran, H. Alharby, S. Fahad, Bacillus safensis with plant-derived smoke stimulates rice growth under saline conditions, Environ. Sci. Pollut. Res. Int. 24 (30) (2017) 23850–23863.
- [45] J. Wang, S. Zhao, S. Xu, W. Zhao, X. Zhang, Y. Lei, H. Zhai, Z. Huang, Coinoculation of antagonistic Bacillus velezensis FH-1 and Brevundimonas diminuta NYM3 promotes rice growth by regulating the structure and nitrification function of rhizosphere microbiome, Front. Microbiol. 14 (2023) 1101773.
- [46] M.A. Azeem, F.H. Shah, A. Ullah, K. Ali, D.A. Jones, M.E.H. Khan, A. Ashraf, Biochemical characterization of halotolerant *Bacillus safensis* PM22 and its potential to enhance growth of maize under salinity stress, Plants 1 (13) (2022) 1721.
- [47] K. Kannan, V.R. Kannan, S. Rajendran, C. Sekar, R.A. Arokiaswamy, M. Arjunan, Behavioural pattern of Bacillus safensis VRKK2 a potential PGPR isolated from cowpea rhizosphere, J. Soil Ecol. Biol. 39 (2019) 1–14.
- [48] M.F. Rabbee, S. Ali, J. Choi, B.S. Hwang, S.C. Jeong, K-h. Baek, Bacillus velezensis: a valuable member of bioactive molecules within plant microbiomes, Molecules 24 (6) (2019) 1046.
- [49] J.M. Marques, J.R. Mateus, T.F. da Silva, C.R.A. Couto, A.F. Blank, L. Seldin, Nitrogen fixing and phosphate solubilizing bacterial communities in sweet potato rhizosphere show a genotype-dependent distribution, Diversity 11 (2019) 231.
- [50] S. Compant, A. Samad, H. Faist, A. Sessitsch, A review on the plant microbiome: ecology, functions, and emerging trends in microbial application, J. Adv. Res. 19 (2019) 29–37.