

Article

Phosphate-Solubilizing Bacteria from Different Genera, Host Plants, and Climates: Influence of Soil pH on Plant Growth and Biochemistry

Jacinta Santos ¹ , Paulo Cardoso ^{1,2} , Ricardo Rocha ^{1,2} , Ricardo Pinto ^{1,2} , Tiago Lopes ^{1,2,*} , Carla Patinha ³ , Rosa Guilherme ^{4,5} , António Ferreira ^{5,6}  and Etelvina Figueira ^{1,2,*} 

- ¹ Department of Biology, University of Aveiro, 3810-193 Aveiro, Portugal; jacinta.santos@ua.pt (J.S.); pjcardoso@ua.pt (P.C.); ricardorocha16@ua.pt (R.R.); rl.pinto@ua.pt (R.P.)
- ² Centre for Environmental and Marine Studies (CESAM), University of Aveiro, 3810-193 Aveiro, Portugal
- ³ GEOBIOTEC—Department of Geosciences, University of Aveiro, Santiago University Campus, 3810-193 Aveiro, Portugal; cpatinha@ua.pt
- ⁴ Comissão de Coordenação e Desenvolvimento Regional do Centro, Polo de Inovação de Coimbra, Quinta de N. Senhora do Loreto, 3020-201 Coimbra, Portugal; rosa.guilherme@ccdr.pt
- ⁵ Research Centre for Natural Resources Environment and Society (CERNAS), Polytechnic Institute of Coimbra, Bencanta, 3045-601 Coimbra, Portugal; aferreira@esac.pt
- ⁶ Polytechnic University of Coimbra, Rua da Misericórdia, Lagar dos Cortiços, S. Martinho do Bispo, 3045-093 Coimbra, Portugal
- * Correspondence: tslopes@ua.pt (T.L.); efigueira@ua.pt (E.F.)

Abstract

Phosphorus (P) is an essential element for plant growth, yet it is only available to plants in the form of orthophosphate. In most soils, P occurs predominantly in insoluble forms, such as calcium phosphates in alkaline soils and aluminum/iron phosphates in acidic soils, limiting plant uptake. Fertilization is commonly used to overcome this limitation; however, large fractions of applied P rapidly become unavailable. Phosphorus-solubilizing bacteria (PSB) are a sustainable alternative to enhance P availability. This study evaluated the P-solubilization capacity of bacterial strains belonging to different genera isolated from different host plants, soil types, and climates (mainland Portugal, Cape Verde, and Angola). Following initial screening, the most efficient strains were tested under greenhouse conditions in soils with pH 7 and 8. Strains exhibited diverse solubilization capacities, with highly efficient PSB (phosphate solubilization index ≥ 2) accounting for 5% of the total isolates, predominantly originating from the Namib Desert (Angola) and Southern Portugal, and mainly belonging to the genera *Pseudomonas*, *Flavobacterium*, *Enterobacter*, *Chryseobacterium* and *Pantoea*. At pH 7, most PSB promoted maize growth, with strain C11 increasing plant P content around 2-fold compared to the control. At pH 8, fewer strains were effective, but strains F and C11 enhanced shoot weight and M shoot length by 28%, 27%, and 10%, respectively. These findings highlight the potential of selected PSB strains as next-generation bioinoculants for sustainable agriculture. However, strain selection must consider geography, crop type, and management practices to ensure consistent efficacy, thereby supporting the broader application of PSB as a precision tool for improving food security.

Keywords: phosphate-solubilizing bacteria; climate; host plant; sustainable agriculture; nutrients; oxidative stress; biochemical changes



Academic Editor: Nick B. Comerford

Received: 22 August 2025

Revised: 6 October 2025

Accepted: 11 October 2025

Published: 16 October 2025

Citation: Santos, J.; Cardoso, P.; Rocha, R.; Pinto, R.; Lopes, T.; Patinha, C.; Guilherme, R.; Ferreira, A.; Figueira, E. Phosphate-Solubilizing Bacteria from Different Genera, Host Plants, and Climates: Influence of Soil pH on Plant Growth and Biochemistry. *Land* **2025**, *14*, 2065. <https://doi.org/10.3390/land14102065>

Copyright: © 2025 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

One of the most effective strategies for adaptation and evolutionary success is the establishment of interactions with microorganisms and plants, enabling more efficient nutrient acquisition and colonization of new habitats. These interactions are being explored for biotechnological purposes to create new and more sustainable agricultural production methodologies. The bioinoculant market currently exceeds USD 5.48 billion and is projected to reach USD 9.52 billion by 2034 [1], highlighting the increasingly widespread use of bioinoculants. However, the vast majority of bioinoculants are “broad-spectrum” in terms of crops and geographic use and have strict application conditions; consequently, the results of their application are highly variable [2].

Phosphorus (P) is one of the nutrients that most limit plant growth. Phosphorus is an essential macronutrient for plants, being part of important biomolecules [3,4]. Plants take up phosphate in the form of orthophosphate [3,5]. However, P availability is often limited to plants due to the formation of complexes with minerals and clays in the soil, which are strongly influenced by soil pH. At pH values higher than 7, P tends to complex with Ca [6,7]. On the other hand, a decrease in pH favors P binding to aluminum (Al) and iron (Fe) [7]. The low availability of P in soils increases the energy expenditure of plants to take up P [8], frequently leading to P deficiency in plants. pH not only affects the availability of phosphate in the soil but also directly impacts plant growth. Low pH directly impacts nutrient uptake by bonding macronutrients to Al or Fe ions, which will lead, in the latter, to root growth inhibition and changes in cell structure [9,10]. Also, high pH affects firstly root development and structure due to the disruption of the acidic environment of the cell [11]. In addition, the lack of a negative charge disrupts plant metabolic homeostasis and leads to the generation of reactive oxygen species, compromising the optimal functioning of proteins and resulting in oxidative damage [12,13].

A common response of plants to P deficiency is the enhancement of their interaction with phosphate-solubilizing bacteria (PSB). *Pseudomonas*, *Bacillus*, *Rhizobium*, and *Enterobacter* are the main bacterial genera that solubilize P. PSB can release bound P, making phosphate available for plant use [14–16]. In addition to solubilizing P, PSB may also induce osmolyte production and antioxidant enzyme activity [17–20], produce phytohormones, or synthesize siderophores [19–21]. In addition, PSB can effectively reduce the pH of alkaline soil by producing organic acids, such as gluconic acid and citric acid. These acids release protons (H⁺) into the soil, which helps chelate metals increasing phosphate availability to plants [5]. All these functions contribute to plant growth and resilience under environmental constraints.

PSB are important for decreasing the dependency on chemical fertilizers while enhancing sustainable agriculture and soil fertility. However, several aspects of bacterial P solubilization and its impact on plant growth need to be clarified. PSB are widely distributed in soils [22–24], but soil microbial communities do not always include highly efficient PSB [3,21,25]. Their solubilizing capabilities are influenced by several factors, such as climate, soil properties, ecological conditions, other microorganisms, metabolites, host plants, vegetation, agricultural practices, and land use [23,26–28]. Strategies for the isolation of plant growth-promoting bacteria (PGPB), including PSB, from dry sites have been performed [29,30]. The majority of existing studies on PSB have been conducted within a single climatic zone, such as agricultural soils in China [31], Morocco [32], and India [33], as well as urban and forest soils [34–36]. In contrast, relatively few studies have examined PSB in arid or high-salinity environments, such as the Namib Desert [30,37] and Cape Verde Salt Island [17,18]. Comprehensive comparisons of plant growth-promoting traits across bacteria isolated from different rainfall and temperature regimes, soil types, and plant hosts remain limited. Consequently, further research is needed to elucidate

how these environmental factors influence the effectiveness and adaptability of PSB. Such endeavors necessitate comprehensive geographical screenings of PSB strains that maintain phosphate solubilization across different climates and soil types and can provide soluble phosphorus for different crops.

This study aimed to isolate PSB from different ecosystems to identify strains capable of efficiently solubilizing P in different climates and conditions, thus supporting sustainable agriculture at a global level. To accomplish this goal, PSB were isolated from different plant hosts growing in distinct regions in continental Portugal with different climatic conditions and soil occupations, as well as from regions experiencing high salinity (Sal Island, Cape Verde) and drought (Huíla and Namib Desert, Angola). Based on the high number of strains screened, we assessed the relationship between P solubilization and abiotic (land use, soil pH, and climate) and biotic (bacterial genera and host plant species) factors. Moreover, the efficiency of PSB strains on plant fitness (biomass, length, nutrient status, and biochemistry) was evaluated. This information will allow the integration of PSB as inoculants in precision agriculture and the development of decision support tools using artificial intelligence/machine learning to recommend PSB application across different crops and agro-climatic regions.

2. Materials and Methods

2.1. Bacterial Strains

The bacterial strains used in this study were collected from several regions with contrasting environmental conditions. In mainland Portugal, strains originated from Murtosa, Vale de Cambra, Alvito, and Aljustrel [38]; Vila do Conde, Mogadouro, Ílhavo, Beja, and Elvas [38,39]; and Vagos [40]. Additional isolates were obtained from Sal Island, Cape Verde [17,18], as well as from arid environments in Huíla and the Namib Desert, Angola [30]. Detailed strain information is provided in the Supplementary Material (Supplementary Table S1).

2.2. Phosphate-Solubilizing Capacity

Phosphate solubilization was determined according to the method described by Pikovskaya [41] and Nautiyal [42], with some modifications. The bacterial strains were inoculated on Pikovskaya medium, in which tricalcium phosphate ($\text{Ca}_3(\text{PO}_4)_2$) was replaced with calcium hydroxyphosphate ($\text{Ca}_5(\text{OH})(\text{PO}_4)_3$), and incubated for 10 days at 26 °C. Hydroxyphosphate is the dominant form of phosphorus in calcareous, alkaline soils [43], such as those from Angola and southern Portugal. Thus, the ability of bacteria to solubilize complexed phosphorus in soils is identified more closely with reality, improving the ecological relevance of the determination of phosphate-solubilizing capacity.

The ability to solubilize phosphate was detected as a clear halo around the colony. The phosphate solubilization index (PSI) was calculated following the equation of Benbrik et al. [44]: $\text{PSI} = \text{halo zone diameter (including the colony)} / \text{colony diameter}$. In this study, the solubilization ability of bacterial strains was classified based on [45] with some modifications: $\text{PSI} < 1.5$, low; $1.5 \leq \text{PSI} < 2$, medium; and $\text{PSI} \geq 2$, high.

2.3. Greenhouse Experiment

PSB's ability to promote plant growth was determined in a greenhouse experiment with soils of different pH (7 and 8), where soils were homogenized in H_2O for 72 h and pH was measured. The initial available phosphorus content of the soils was determined. The results show that the initial available phosphorus in the pH 7 soil was 0.58 mg/g, and in the pH 8 soil, it was 0.32 mg/g. Bacterial strains with a higher ability to solubilize P (C11 = *Enterobacter*; C20 = Unknown; D8 = *Pseudomonas*; F = *Acinetobacter*; H = *Enterobacter*;

M = *Rhizobium*; O4 = *Herbaspirillum*; Q4 = *Lysobacter*; V4 = *Stenotrophomonas*) were used. Bacterial inoculum was grown in yeast mannitol broth (YMB) overnight at 26 °C in an orbital shaker [46]. A commercial product containing phosphate-solubilizing bacteria belonging to the *Pseudomonas* genus was used as a positive control. *Zea mays* seeds (LG, variety LG31250) were kindly offered by Comissão de Coordenação e Desenvolvimento Regional do Centro, I.P. (CCDR Centro, I.P.). The seeds were then hydrated overnight. Seed inoculation was performed by submerging the seeds in YMB medium, with a final concentration of 10^8 cells/mL determined by measuring culture turbidity at 600 nm and calibrated with a standard curve, followed by coating with diatomite. Non-inoculated seeds were submerged in a non-inoculated liquid medium, sterilized synchronously with the YMB medium containing the inoculum to avoid the impact of differences in aseptic operation on the results, and were coated with diatomite. Three seeds were sown in containers with 2 L of soil (pH 7 and 8, respectively). For each soil pH, the experiment included 11 conditions (nine bacterial strains, a non-inoculated negative control, and a positive control). Each inoculated condition was replicated 5-fold, while for the negative control, 10 replicates were used, with a total of 120 containers. The containers were randomly distributed in a greenhouse with natural illumination between 29 September and 28 October 2022 at the Polo de Inovação de Coimbra (40.230708, −8.443932). The maize plants were watered weekly with 100 mL of tap water. At the end of the experiment, plants were collected, and shoots and roots were separated and washed first with tap water and then with deionized water to remove substrate particles. Shoot and root lengths and fresh weights were determined. Leaf samples were taken for immediate photosynthetic pigments determination or stored (−80 °C) for subsequent biochemical analysis.

2.4. Plant Macronutrients

The concentrations of calcium (Ca), iron (Fe), potassium (K), magnesium (Mg), sodium (Na), phosphorus (P), and zinc (Zn) were analyzed in the shoots using inductively coupled plasma mass spectrometry (ICP-MS) (Agilent 7700x) after acid digestion [47]. Dried and homogenized tissue (200 mg) was mixed with 3 mL of 65% HNO₃ (v/v) and 1 mL of 30% H₂O₂ (v/v) in DigiPrep tubes. After reacting overnight (14–16 h), the solutions were heated on a digestion block (DigiPrep, SCP Science, Montreal, QC, Canada). The heating program included heating from room temperature to 50 °C and maintaining this temperature for 15 min. The temperature was then increased from 50 °C to 85 °C over 15 min. When the temperature stabilized at 85 °C, it was maintained for 15 min until the end of the cycle. The heating program was repeated twice. The digests were evaporated until dry at 50 °C, and 25 mL of 1% HNO₃ was added. The solutions were centrifuged for 20 min at 3500 rpm (Heraeus Multifuge 16, Hanau, Germany) and analyzed using ICP-MS. A rigorous quality control procedure was performed during these analyses, which included the analysis of the blanks, triplicate samples, and certified reference materials ERM-CD200 SEAWEED and synthetic CRM. The recovery rates of key elements (P, Fe, and Zn) were 90–110%, meeting the requirements of ICP-MS analysis, and the precision and bias errors of the chemical analysis were less than 10%. Element concentrations were calculated in µg/g DW. For each sample, carbon and nitrogen quantifications were performed using a LECO CN 828 dry combustion analyzer (LECO Corp., St. Joseph, MI, USA). The accuracy of the analysis was evaluated using certified reference materials (EDTA and LECO soil LCRM) [48].

2.5. Physiological and Biochemical Parameters

2.5.1. Photosynthetic Pigments

For chlorophyll and carotenoid quantification, 100 mg of fresh shoots were homogenized in 1.5 mL of cold 80% acetone using a mortar and pestle, as described by Cruz

et al. [18]. The homogenate was centrifuged at $10,000\times g$ for 20 min at 4°C . Supernatants (300 μL) were pipetted into a 96-well microplate, and 300 μL of acetone was used as a blank. Absorbance was measured at 470, 646, and 663 nm for chlorophylls a and b and carotenoids. To calculate the photosynthetic pigments, the equations proposed by Wellburn and Lichtenthaler [49] were used, and values are expressed in $\mu\text{g/g FW}$:

$$\text{Chlorophyll } a = 12.21 \times A_{663} - 2.81 \times A_{646}$$

$$\text{Chlorophyll } b = 20.13 \times A_{646} - 5.03 \times A_{663}$$

$$\text{Carotenoids} = [(1000 \times A_{470} - 3.27 \times \text{Chlorophyll } a) - (104 \times \text{Chlorophyll } b)]/229$$

2.5.2. Anthocyanins

The protocol described by Zhao et al. [50] was followed to quantify the amount of anthocyanins. Frozen shoots (0.1 g) previously milled in N_2 were added to 1 mL of methanol/HCl (99:1 *v/v*) and incubated for 24 h at 20°C in the dark. The supernatant was then centrifuged for 5 min at $13,000\times g$, and 300 μL was collected for spectrophotometric (Thermo Scientific, Waltham, MA, USA) quantification at 530, 620, and 650 nm. The anthocyanin content is expressed as $\mu\text{g/g FW}$ and was calculated using the following formula:

$$\text{Anthocyanins} = 46,200 \times [(A_{530} - A_{620}) - 0.1 \times (A_{650} - A_{620})]$$

2.5.3. Antioxidant Enzyme Activity, Metabolic Activity, Carbohydrates, and Oxidative Damage

Frozen shoots (0.1 g) previously milled in N_2 were homogenized with a mortar and pestle in 1 mL potassium phosphate buffer (50 mM K_2HPO_4 and 50 mM KH_2PO_4 , 1 mM ethylenediaminetetraacetic acid disodium salt dihydrate (EDTA), 1% (*v/v*) Triton X-100, 1 mM dithiothreitol (DTT), pH 7.0) and centrifuged $3000\times g$ for 10 min at 4°C for electron transport system (ETS) activity determination. The homogenates were centrifuged at $10,000\times g$ for 10 min at 4°C to determine the protein content (Prot), protein carboxylation (PC), superoxide dismutase (SOD), and catalase (CAT) activity, and the pellet was used to determine lipid peroxidation (LPO).

ETS activity was evaluated based on the method described by King and Packard [51], using the modifications described by Owens and King [52]. Samples were mixed with BSS buffer (130 mM Tris-HCl, 0.3% Triton X-100, pH 8.5), NAD(P)H (1.7 mM NADH and 250 μM NADPH), and the reaction was initiated by the addition of 8 mM p-iodonitrotetrazolium (INT). The absorbance was measured at 490 nm for 10 min at 25 s intervals. The extinction coefficient of formazan ($\epsilon = 15,900 \text{ M}^{-1} \text{ cm}^{-1}$) was used, and the results are expressed in $\mu\text{mol/min/g fresh weight (FW)}$.

SOD activity was evaluated using the method described by Beauchamp and Fridovich [53]. Samples were mixed with reaction buffer (50 mM Tris-HCl, pH 8.0, 0.1 mM diethylenetriaminepentaacetic acid (DTPA), 0.1 mM hypoxanthine, 68.4 μM nitroblue tetrazolium (NBT)) and xanthine oxidase (51.6 mU/mL) and incubated for 20 min at room temperature with orbital rotation. The absorbance was measured at 640 nm, and the results are expressed in U/g FW, where U (one unit of enzymatic activity) corresponds to a 50% reduction in NBT.

CAT activity was evaluated using the methodology described by Johansson and Borg [54]. Samples were mixed with reaction buffer (50 mM K_2HPO_4 and 50 mM KH_2PO_4 , pH 7.0), methanol, and hydrogen peroxide (35.28 mM). After 20 min of incubation at room temperature, potassium hydroxide (10 M) and purpald (34.2 mM) were added, followed by incubation for 10 min at room temperature. Potassium periodate (65.2 mM) was then added,

and after incubation for 5 min, the absorbance was measured at 540 nm. Formaldehyde standards (0–40 μM) were used, and the results are expressed as mU/g FW.

Protein content was evaluated based on the methodology described by Robinson and Hogden [55]. The samples were mixed with the biuret reaction solution and incubated in the dark for 10 min at room temperature. Absorbance was measured at 540 nm, and bovine serum albumin (BSA) was used as a standard (0–40 mg/mL). The results are expressed as mg/g FW.

PC levels were determined using the methodology described by Mesquita et al. [56]. Samples were mixed with 2,4-dinitrophenylhydrazine (DNPH) (10 mM) and incubated for 10 min at room temperature. Sodium hydroxide (6 M) was added, the reaction was incubated for 10 min, and the absorbance was measured at 450 nm. The extinction coefficient of DNPH ($\epsilon = 22,308 \text{ M}^{-1} \text{ cm}^{-1}$) was used for calculations, and the results are expressed in $\mu\text{mol/g FW}$.

LPO levels were evaluated using the methodology described by Buege and Aust [57]. Samples were mixed with 0.5% 2-thiobarbituric acid (TBA) and 20% trichloroacetic acid (TCA) and incubated for 25 min at 96 °C. The reaction was terminated by placing the samples on ice, centrifuged at $12,000 \times g$ for 10 min, and the supernatant was collected. Absorbance was measured at 532 nm, the extinction coefficient of malondialdehyde (MDA) ($1.56 \times 10^5 \text{ M/cm}$) was used for calculations, and the results are expressed in nmol/g FW.

For sugar and starch content determination, frozen shoots (0.2 g) previously milled in N_2 were homogenized with a mortar and pestle in deionized water (1:2 w/v). Samples were centrifuged at $10,000 \times g$ for 4 min, and the supernatant was collected to determine soluble sugars. The pellet was washed twice with deionized water and centrifuged ($10,000 \times g$ for 4 min). The washed pellet was resuspended in sulfuric acid (2.5 mM), incubated at 95 °C for 1 h, and centrifuged at $10,000 \times g$ for 10 min. Sugar and starch contents were determined using the methodology described by DuBois et al. [58]. The absorbance was measured at 492 nm, and glucose standards (0–20 mg/mL) were used. The results are expressed in mg/g FW.

2.6. Statistical Analysis

The results were analyzed using R 64-bit version 4.3.1 (R Foundation for Statistical Computing, Vienna, Austria). The pairwise Wilcoxon test was performed using the “rstatix” package, “Pipe-Friendly Framework for Basic Statistical Tests,” with p -values < 0.05 considered significant. The results are expressed as mean $\pm$ standard deviation (SD) with $n \geq 5$. The graphs were created using the packages “ggplot2” (version 3.4.4), “Create Elegant Data Visualizations Using the Grammar of Graphics”, and “ggpubr” (version 0.6.0), “ggplot2’ Based Publication Ready Plots”. The functions of `fviz_pca` of the “factoextra” package, “Extract and Visualize the Results of Multivariate Data Analyses”, were used to generate principal component analysis (PCA) plots. The hierarchical clustering heatmap was generated using Metaboanalyst version 6.0 [59]. The data were normalized by auto-scaling.

3. Results

3.1. Ability of Strains to Solubilize Phosphate

3.1.1. Prospecting of PSB Across Distinct Climate Zones

The isolation of bacteria in the different regions included in this study allowed us to obtain a total of 342 strains with different capacities to solubilize P. In total, 36% did not have the capacity to solubilize P, 43% had a low capacity, 16% had a medium ability, and 5% had a high capacity, indicating that the ability to solubilize P is a common characteristic among bacteria, but superior capability is rare (detailed information about the ability of each strain to solubilize P is available in Supplementary Table S1).

Bacteria isolated in northern Portugal (regions 1–4 in Figure 1A) and Elvas (region 5), with climates varying from inferior hyperhumid to inferior dry (ombrotype) and inferior mesotemperate to inferior thermomediterranean (thermotype), showed poor solubilization capacity, with all or most strains being unable or having low capacity to solubilize P. Only Ílhavo, Murtosa, and Vagos (region 4) included PSB with high PSI capacity. In Aljustrel and Beja (region 6), with an inferior dry and superior thermomediterranean climate, a few strains did not show the capacity to solubilize P, with the majority (69%) showing low capacity. A higher proportion of bacteria with medium or high capacity to solubilize P was observed in region 6 in continental Portugal. In Sal Island (region 7), with an inferior infratropical and ultrahyperarid climate, the proportion of non-solubilizing bacteria is low (17%). Approximately half have low capacity, 28% have medium capacity, and no strain shows high capacity to solubilize P. In Angola (regions 8 and 9), with hyperarid to dry and inferior to superior mesotropical climates, the proportion of PSB unable to solubilize P was identical to that in most of the other regions, but the proportion of bacteria with medium or high capacity was higher, especially in region 8.

3.1.2. Soil Use and Solubilization Ability

The soil use influenced the percentage of bacteria able to solubilize P. In agricultural soils, approximately half of the strains (56%) showed the capacity to solubilize P, whereas in natural soils, the proportion of PSB increased, with nearly two-thirds (73%) being able to solubilize this nutrient (Figure 1B). Among the solubilizing strains, the solubilization level also varied, with strains from natural soils presenting a higher PSI than those from agricultural soils. In both soil uses, strains with a high capacity to solubilize P were found.

3.1.3. Host Plant and Bacterial Ability to Solubilize P

The plant species influenced the level of solubilization. The number of strains obtained from each plant species also contributed to this differentiation (Figure 1C). There are strains from plant species with only one level of P solubility, such as *Lathyrus clymenum* L., *Pisum sativum* L., *Vicia benghalensis* L., and *Vicia sativa* subsp. *sativa* L. with a low PSI, *Medicago littoralis* Rohde ex Loisel. with a medium PSI, and *Ornithopus pinnatus* (Mill.) Druce with a high PSI; most of which had one strain. From other plants, strains with two levels of solubility were observed: *Lotus corniculatus* L., *Melilotus indicus* (L.) All., *Ornithopus compressus* L., *Ornithopus sativus* subsp. *sativus* Brot., *Scorpiurus vermiculatus* L., and *Vicia lutea* L. with a null and low PSI, and *Amaranthus viridis* L., *Medicago lupulina* L., and *Trifolium repens* L. with a low and medium PSI; from these plants, two to five strains were isolated. The strains from five plants displayed three levels of solubilization: for *Faidherbia albida* (Delile) A. Chev., *Glycine max* (L.) Merr., *Tetraena stapfii* (Schinz) Beier & Thulin, and *Vicia cordata* Hoppe, a null, low, and medium PSI, and for *Medicago* sp., a low, medium, and high PSI; more than ten strains were isolated from these plant species, except for *V. cordata*, from which four were isolated. In four plant species, the strains displayed the four levels of P solubilization: *Phaseolus vulgaris* L., *Stipagrostis* sp., *Tetraena simplex* (L.) Beier & Thulin, and *Zea mays* L. together accounted for 70% of the strains studied.

3.1.4. Solubilization per Bacterial Genus

The bacterial genera at each P solubilization level are shown in Figure 2. The number of different genera at each P solubilization level was 28 in the null, 29 in the low, 23 in the medium, and 5 in the high PSI, reflecting the total number of strains (122, 147, 55, and 18, respectively). There are genera represented by one strain and therefore only appear at one PSI level. Genera with a higher number of strains were common to three or four PSI levels. Three genera (*Pseudomonas*, *Flavobacterium*, and *Enterobacter*) were the most abundant at the four PSI levels. *Pantoea* was also present at all four PSI levels. *Bacillus*

exhibited low solubilization capacity, with most strains having null or low PSI, a few strains having medium PSI, and no strains having high PSI. *Rhizobium* also showed a low capacity to solubilize P (null or low levels). The *Chryseobacterium* genus only occurred at a high PSI.

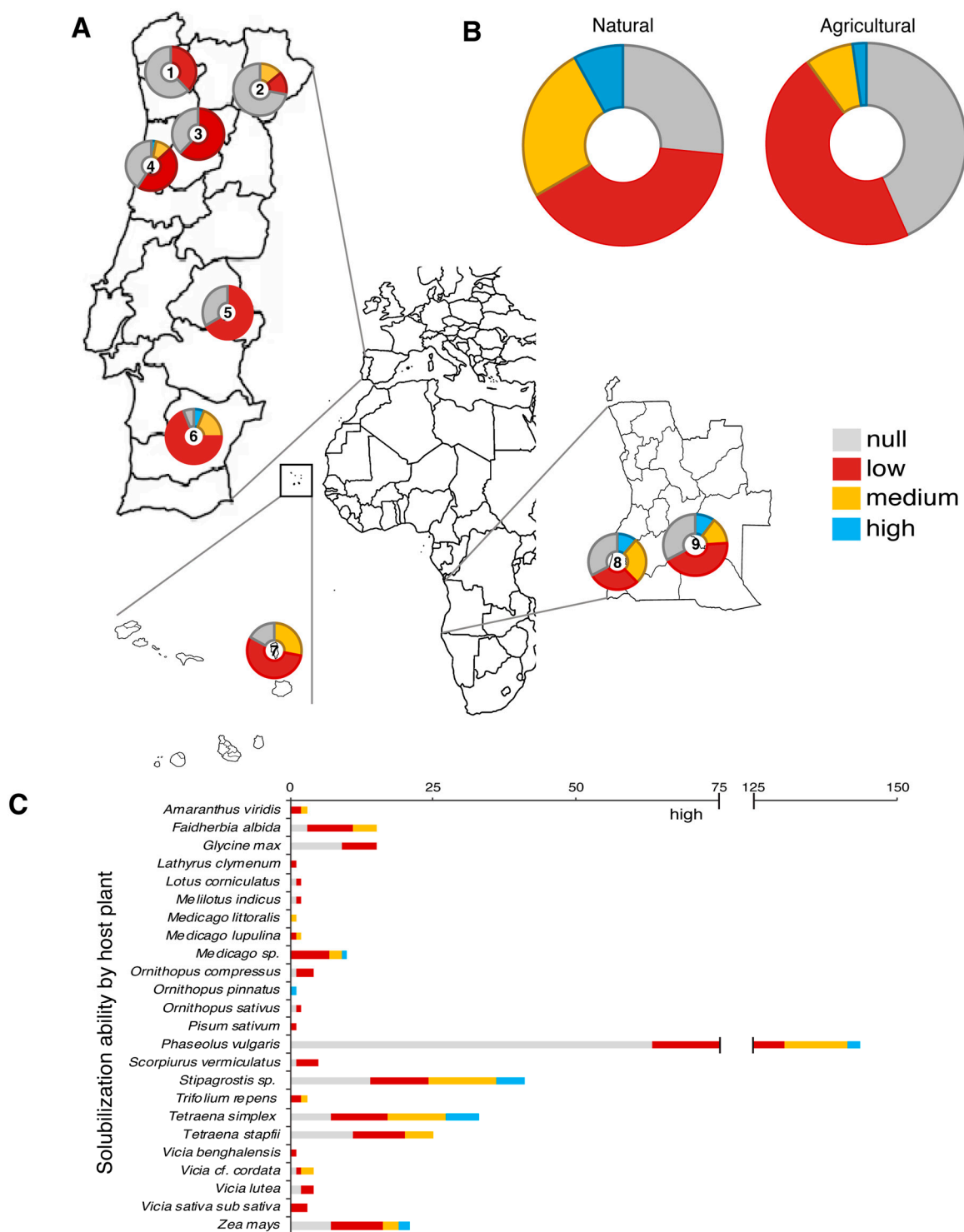


Figure 1. Distribution and characterization of the phosphate solubilization index (PSI) among bacterial strains. (A) Geographic distribution of sampled regions across Portugal (1—Vila do Conde, 2—Mogadouro, 3—Vale de Cambra, 4—Ílhavo, Murtosa and Vagos, 5—Elvas, 6—Aljustrel and Beja), Cape Verde (7—Sal island) and Angola (8—Namib Desert, 9—Huila), according their PSI (grey—null; red—low; yellow—medium; blue—high); (B) proportion of PSI classes in isolates obtained from natural and agricultural soils (grey—null; red—low; yellow—medium; blue—high); (C) PSI of strains across different plant hosts.

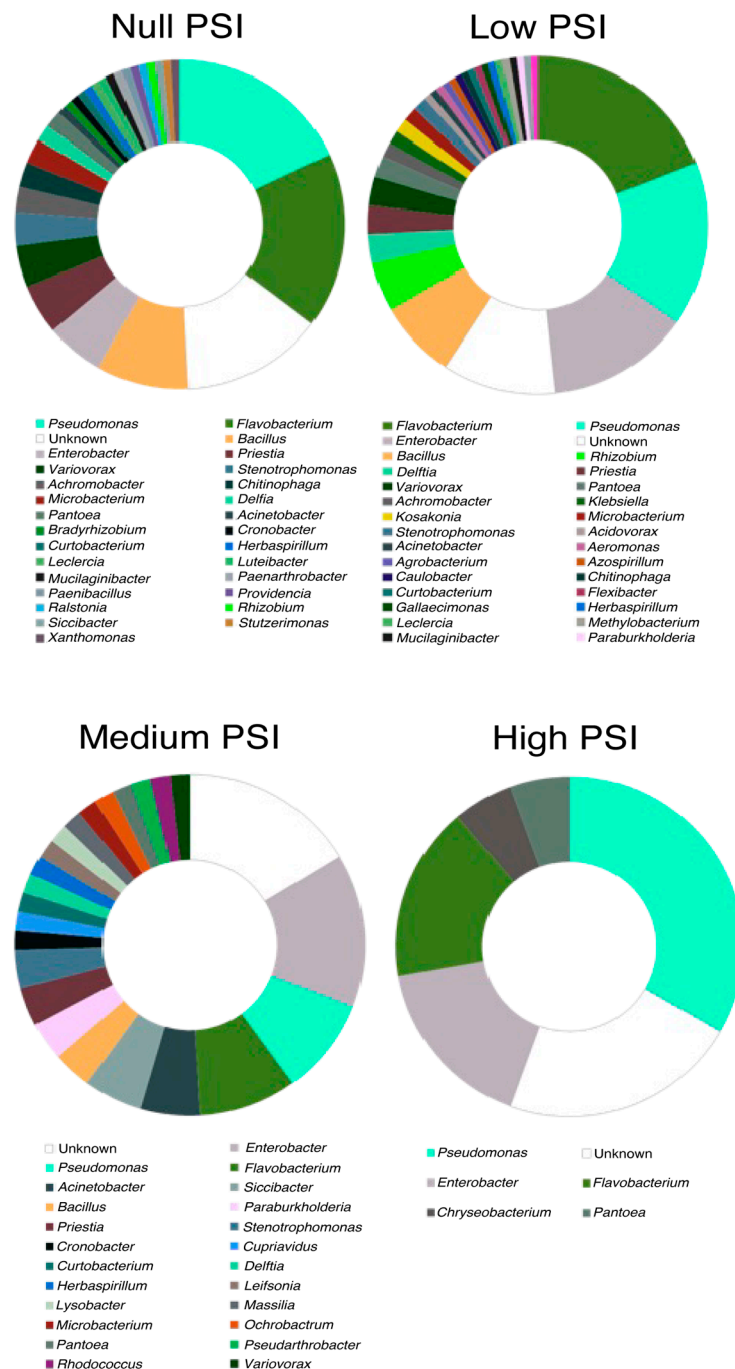


Figure 2. Taxonomic composition at the genus level of bacteria across PSI categories.

3.2. Influence of PSB on Maize Plants at Two pH Levels

As soil pH is a key factor in the availability of P to plants, this study evaluated the influence of PSB on the growth, biochemistry, and nutrition of maize plants grown at two pH levels (7 and 8).

3.2.1. Growth and Biochemistry

The pH influenced shoot and root growth (Figure 3A). The shoot length was significantly higher at pH 7 than at pH 8 for both inoculated and non-inoculated plants. Plants inoculated with the M strain were the exception, with shoot length not significantly different between the two pH values. At each pH, inoculation had no significant influence on shoot length for most conditions, but strain M at pH 8 increased significantly compared

to non-inoculated plants. Shoot weight was also significantly higher at pH 7 than at pH 8. Inoculation with Q4, O4, F, M, and C20 strains significantly affected plant growth at pH 7, and F, M, and C11 at pH 8. The roots of plants grown at pH 8 were longer than those grown at pH 7, but significant differences were only observed for the positive control and for inoculation with the C11 and C20 strains. No significant differences were observed among the inoculation conditions for any pH. Root weight was higher at pH 7 than at pH 8, with significant differences observed in plants inoculated with Q4, H, and M conditions. At pH 7, no significant differences among the inoculation conditions were detected, but at pH 8, four strains (Q4, H, M, and C20) induced higher weights than non-inoculated plants.

Shoot pigments were not influenced by pH (Figure 3A), as no significant differences were noted in non-inoculated plants between pH 7 and pH 8. However, plants inoculated with the M strain had higher chlorophyll (*a* and *b*) content at pH 7 than at pH 8. At each pH, significant increases in chlorophyll *a* were observed for the H strain at pH 7 and the O4 strain at pH 8. Inoculation with H significantly increased chlorophyll *b* at pH 7 and pH 8, and two strains (V4 and O4) and the positive control significantly increased this photosynthetic pigment. Inoculation also influenced the carotenoid content of the shoots. At pH 7, the M and D8 strains and at pH 8, the Q4, V4, F, M, C11, and C20 strains increased carotenoid content significantly compared to non-inoculated controls. Inoculation also influenced anthocyanin levels in the shoots, with a higher content at pH 8 than at pH 7. At pH 7, V4 significantly decreased anthocyanin levels, and at pH 8, three strains (H, F, and C11) significantly increased anthocyanin levels compared to the non-inoculated controls.

Both bacterial inoculation and pH influenced the antioxidant enzyme activity and oxidative damage (Figure 3A). Catalase (CAT) was influenced by pH, as non-inoculated plants (negative control) had significantly higher CAT activity at pH 8 than at pH 7. Differences between pH 7 and 8 were also detected in the inoculated plants (O4, H, and C11). Inoculation also induced significant changes at each pH. At pH 7, the F, C11, C20, and D8 strains and the positive control significantly induced CAT activity compared to the non-inoculated control. At pH 8, only C11 induced a significant increase in CAT activity. Superoxide dismutase (SOD) was also influenced by pH, as non-inoculated plants had significantly higher SOD activity at pH 8 than at pH 7. Differences between pH 7 and pH 8 were only detected in plants inoculated with the H strain. No differences among the inoculation conditions were observed at pH 7. At pH 8, Q4, M, and C11 induced a significant decrease in SOD activity compared to non-inoculated plants.

Damage to proteins (PC) was higher at pH 8 in non-inoculated and most inoculated plants (M and C20 being the exceptions) compared to pH 7. At pH 7, inoculation with most strains increased PC, but H and D8 maintained PC levels similar to those of the non-inoculated control. At pH 8, three strains (H, F, and C11) induced a significant increase in PC levels compared to the control. Damage to membranes (LPO) was influenced by pH, as non-inoculated plants had significantly higher LPO at pH 8 than at pH 7. Differences between pH 7 and pH 8 were also detected in the inoculated plants (Q4, H, F, and positive control). At pH 7, the Q4, H, and F strains decreased LPO compared to the non-inoculated control. At pH 8, six strains (Q4, V4, O4, C11, C20, and D8) decreased LPO relative to the control.

The protein concentration of non-inoculated plants was not affected by pH. However, some differences between pH 7 and pH 8 were detected in the M and C11 inoculated plants. At pH 7, M, C11, C20, and the positive control significantly increased protein levels compared to the non-inoculated control. At pH 8, no differences were detected among the inoculation conditions.

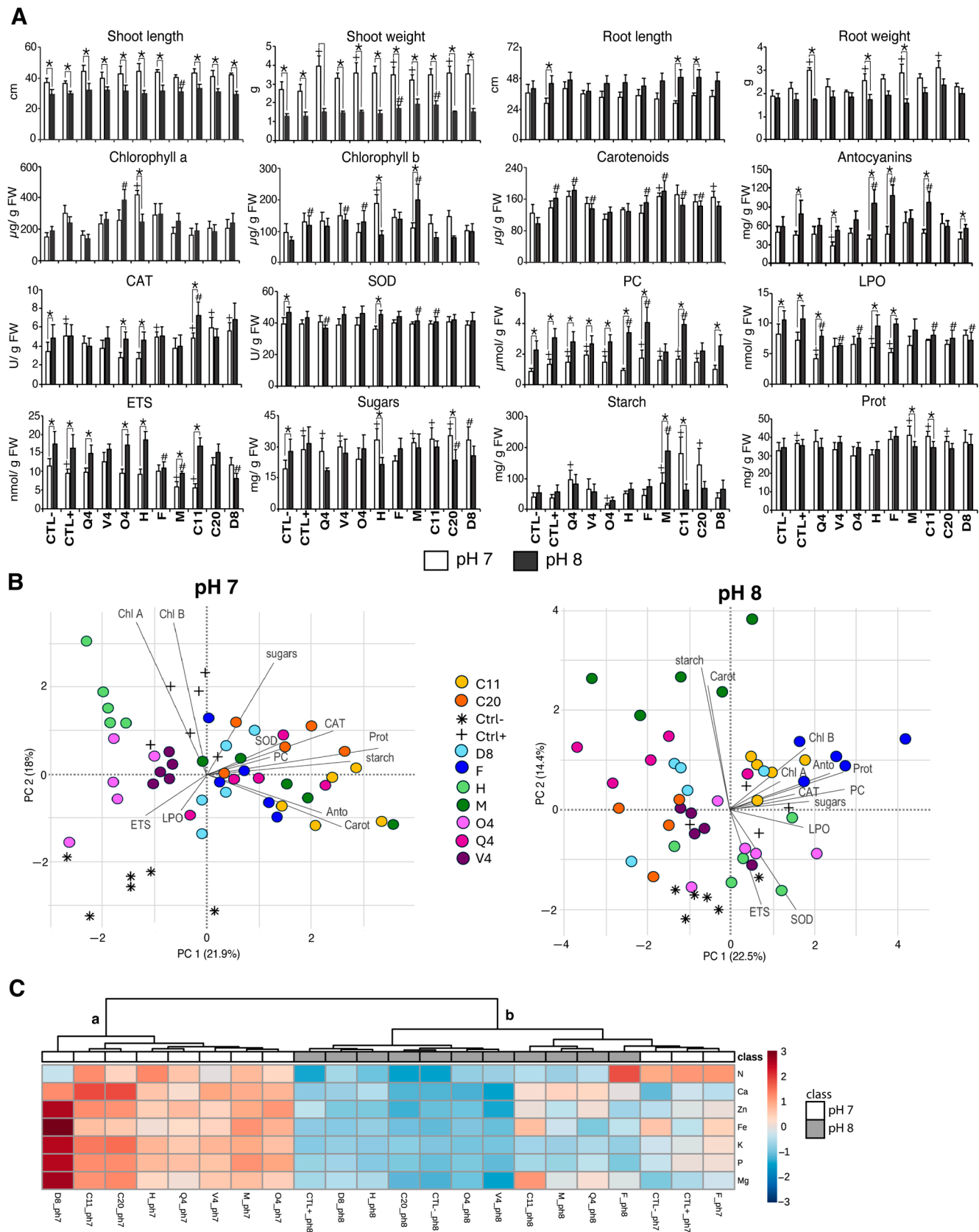


Figure 3. The influence of PSB inoculation on the growth, biochemistry, and nutrient level of *Zea mays* (maize) plants under two pH (7 and 8) and inoculation conditions (no inoculation—CTL—, and inoculation—CTL+).

inoculation with a commercial strain—CTL+, and inoculation with different strains from our laboratory (C11, C20, D8, F, H, M, O4, Q4, and V4)). **(A)** Shoot and root growth (weight and length), pigment content (chlorophyll *a*, chlorophyll *b*, carotenoids, anthocyanins), antioxidant enzyme activity (catalase—CAT and superoxide dismutase—SOD), oxidative damage (protein carbonylation—PC and lipid peroxidation—LPO), metabolic activity (electron transport system activity—ETS, protein content—Prot, sugars and starch content) at pH 7 (white bars) and pH 8 (black bars). Values are means of five replicates + SD, with asterisk (*) indicating significant differences between pH, plus (+) among pH 7 and cardinal (#) among pH 8. **(B)** Principal coordinate analysis (PCA) based on the tested conditions and biochemical markers measured in shoots under pH 7 (**left**) and pH 8 (**right**). Pearson correlation vectors are superimposed as supplementary variables, namely, biochemical data ($r > 0.7$): Chl *a*—chlorophyll *a* content; Chl *b*—chlorophyll *b* content; Carot = carotenoids content; Anto = anthocyanins content; ETS—electron transport system activity; SOD—superoxide dismutase activity; CAT—catalase activity; LPO—lipid peroxidation levels; PC—protein carbonylation content; Sugars—sugars content; Starch—starch content; prot = protein content. **(C)** Heatmap of the elemental nutrients (calcium—Ca, iron—Fe, potassium—K, nitrogen—N, magnesium—Mg, phosphorus—P, and zinc—Zn) in shoots under different inoculation conditions, where the class represents the soil pH (7—white; 8—grey), with two clusters presented (**a** and **b**). Three replicates were performed for each condition. The scale represents z-scores, where red and blue represent higher and lower concentrations, respectively.

The electron transport system (ETS) activity was higher in non-inoculated plants grown at pH 8 than at pH 7. Differences between pH 7 and pH 8 were also detected in the inoculated plants (Q4, O4, H M, C11, and positive control). At each pH, inoculation also induced significant changes. At pH 7, M, C11, and the positive control induced significantly lower ETS activity than the non-inoculated control. At pH 8, the F, M, and D8 strains induced a significant decrease in ETS activity.

Sugar concentration was significantly different between pH 8 and pH 7 for non-inoculated plants. Differences between the two pH values were also detected in plants inoculated with the H and C20 strains. At pH 7, only the O4 and F strains did not significantly increase the soluble sugar levels. At pH 8, three strains (Q4, H, and C20) decreased the soluble sugar content relative to the control. The main factor influencing starch content was bacterial inoculation. Differences between pH 7 and pH 8 were detected only in plants inoculated with the M and C11 strains. At pH 7, four strains (Q4, M, C11, and C20) increased, and one (O4) decreased starch levels compared to the non-inoculated control. At pH 8, only the C11 strain significantly increased the insoluble sugar content relative to the control.

3.2.2. Principal Components Analysis

A principal components analysis (Figure 3B) was carried out for each pH. At pH 7, inoculation conditions imposed variation in the biochemical responses of shoots. PC1 explained 21.9% of total variation and allowed the separation of C11, C20, Q4, F, and M strains (positive side) from both negative and positive controls and H, O4, V4 strains (negative side). The biochemical parameters with higher correlation with the positive side are CAT, PROT, Starch, Anto, and Carot. The ETS was highly correlated with the negative side. PC2 (18% of variation) separated H and the positive control on the positive side, the negative control on the negative side, and most inoculated conditions near the origin of axis 2. The parameters with higher correlation with the positive side are Chl *a*, *b*, and Sugars. LPO was the parameter most correlated with the negative side. Vectors superimposed related chlorophyll content with H and the positive control, the ETS and LPO with the negative control, and antioxidant enzyme activity, carotenoids, anthocyanins, protein, and starch with C11, C20, Q4, F, and M strains. At pH 8, inoculation conditions also imposed variation in the biochemical responses of shoots. PC1 explained 22.5% of total variation and

allowed the separation of M, Q4, C20, D8, V4, and the negative control on the axis negative side, H and O4 near the axis origin, and C11, F, and the positive control on the positive side. The parameters more correlated with the positive side are Prot and PC. PC2 (14.4% of variation) separated M on the far positive side, H and O4 and the negative control on the negative side, and the remaining conditions near the origin of axis 2. The parameters that were more correlated with the positive side were Starch and Carot, and the ETS and LPO with the negative side.

Vectors superimposed related starch and carotenoid content with M strain inoculation, the ETS and SOD with H, O4, and the negative control, and antioxidant enzyme activity, chlorophylls, anthocyanins, protein, damage, and soluble sugars with F and C11 strains.

3.2.3. Nutrients

The heatmap (Figure 3C) represents the element levels in maize shoots under different inoculation conditions and soil pH. Two main clusters (a and b) were formed. Cluster (a) mostly comprised inoculated conditions at pH 7. Cluster (b) mostly included pH 8 conditions, uninoculated plants growing at pH 7 (pH 7 control), and replicates of F-inoculated plants at pH 7. In cluster (a), the shoots contained higher levels of all nutrients. In cluster (b), the nutrient levels were generally lower, but higher differences among conditions could be observed, with some showing higher levels of nitrogen (control pH 7 and inoculation with F at pH 7).

4. Discussion

Previous studies on phosphate-solubilizing bacteria (PSB) have primarily focused on isolates from temperate regions, particularly agricultural soils, with limited attention given to arid or high salinity environments. Additionally, few studies have considered host plant identity or examined the effects of pH on biochemical responses in plants. Our study addresses these shortcomings by conducting cross-regional screenings of PSB from temperate (Portugal), saline (Sal Island, Cape Verde), and drought-prone (Namib Desert and Huíla, Angola) environments. The combination of these screenings with multi-host isolation and functional assays under different soil pH conditions can further elucidate the mechanisms of phosphate solubilization. This integrative approach explores how environmental and host factors shape PSB activity and identifies strains capable of promoting plant growth in challenging agro-climatic contexts.

4.1. Influence of Soil Type and Land Use on PSB Functional Capacity

Soils with low available P tend to have a higher number of PSB with high solubilization capacities [34,60]. Consequently, agricultural soils, often enriched with fertilizers, are expected to contain PSB with lower solubilizing efficiency than natural unfertilized soils. Consistent with this expectation, our results show a lower solubilizing capacity of bacteria isolated from agricultural soils than from natural soils. Despite the lower general capacity to solubilize P, our study also shows that high solubilizing PSB remained in agricultural soils, which might be expected to decline due to high available P levels. This may be due to a significant portion of the applied P fertilizers forming insoluble complexes with calcium (in alkaline soils) or iron and aluminum (in acidic soils). PSBs remain relevant because they convert insoluble P forms into plant-available phosphates, even in soils with high P levels [61]. In addition to solubilizing phosphorus, PSB also exhibit other PGP traits, such as phytohormone production, siderophore synthesis, and the solubilization of other nutrients [17,18,40,62]. Other studies have also reported the high capacity of bacteria from agricultural soils to solubilize P [44,63–65]. Thus, agricultural soils maintain microbial

communities with different levels of P solubilization and can be used as resources to obtain isolates with high solubilization performance.

Temperature and moisture are limiting factors for bacterial growth and soil function. In mainland Portugal, most strains in region 2 did not have the capacity to solubilize P, but some strains displayed medium capacity. This region is located in the northeast of the country, and bacterial communities are exposed to a wide range of temperatures (low in winter and high in summer); therefore, these bacteria must be able to solubilize P over a wide range of temperatures, influencing the solubilization capacity of bacteria. Liu et al. [66] reported that the higher ability of bacteria to solubilize P is within the 18–28 °C interval, and Lima et al. [67] showed that high temperature negatively influences the ability of bacteria to solubilize P. During summer, the maximum temperatures in most of the territory in mainland Portugal frequently exceed 30 °C for several days, and P solubilization during these periods may be compromised. Ait-Ouakrim et al. [68] reported that bacteria able to tolerate temperatures between 28 and 50 °C, mainly have a medium PSI, and under high temperatures, P solubilization decreased.

Most regions in Portugal, especially region 6, are subjected not only to high temperatures during summer but also to severe/extreme drought, requiring that bacteria experiencing these conditions are able to solubilize P under extremely stressful conditions. Ghorehshizadeh et al. [69] reported bacteria with medium-to-high ability to solubilize P from areas subjected to high temperature and drought, but the percentage of bacteria able to solubilize P was low (18%). The results of our study show a high range of ability to solubilize P, but contrary to the results reported by Ghorehshizadeh et al. [69], most (94%) bacteria in hot, dry climates showed the capacity to solubilize P. According to Janati et al. [27], approximately 31% of the isolates lost the ability to solubilize P under high temperatures and low humidity, but some of the isolates that retained the ability to solubilize P displayed high solubilization levels. The ability of PSB to solubilize P can be maintained or increased under osmotic stress [70,71], showing that even under drought conditions, these bacteria can continue to provide soluble P to the ecosystem.

According to Ameen et al. [72] and Janati et al. [27], in addition to temperature and rainfall, other limiting factors, such as salinity, may influence the ability to solubilize P. Different studies have reported the isolation of highly phosphorus-solubilizing salt-tolerant PSB from the root system of salt-stressed plants, such as wheat (89 in [73]), soybean (76 in [73]), *Tamarix ramosissima* (90 in [73]), and *Salicornia fruticosa* [65]. In our study, strains from Sal Island were also halotolerant [18], but our study shows that most strains were low-to-medium P solubilizers; however, under salinity, the ability of most strains to solubilize P was enhanced compared to non-saline conditions [13].

Our results also show that a higher percentage (approximately 10%) of PSB isolated in Angola exhibited high solubilizing capacity, and a lower percentage of a null PSI. High solubilization ability has also been reported in Africa by Ndung'u-Magiroy et al. [74] and Rfaki et al. [75]. In Angolan regions with high alkalinity [30], a high percentage of PSB with high P-solubilizing capacity was observed. Since in alkaline soils, P forms complexes with Ca, most P is unavailable for uptake, and P deficiency becomes common. The presence of PSB with a strong solubilization capacity can be an important factor for the survival of microorganisms and plant growth in environments with severely restricted P availability.

Our study evidences that bacteria isolated from most plant species displayed no or low capacity to solubilize P. However, some degree of variation was observed. Strains of *T. simplex* and *Stipagrostis* sp. (Namib Desert) and *Z. mays*, *O. pinnatus*, and *Medicago* sp. (Portugal) exhibited a higher P-solubilizing ability than bacteria isolated from other plant species. Nabati et al. [76] reported that certain plant species can have a higher influence on the abundance and activity of PSB in the soil than others by creating a favorable envi-

ronment for PSB proliferation. Plants recruit bacteria from their surroundings, a process mediated by root exudates. These include sugars, amino acids, organic acids, enzymes, growth factors, vitamins, flavonoids, fatty acids, sterols, volatile organic compounds, and other molecules [77]. These chemotactic influences can encourage, limit, or inhibit microbial activity and proliferation, tuning the rhizomicrobiome from a reservoir of microorganisms present in the soil, which will help plants to uptake nutrients, induce resistance to diseases, and tolerance to abiotic factors [78–81]. This implies that hosts influence their symbiont selection. Exudates, such as exopolysaccharides, can correlate positively with the ability to solubilize P by providing a stable environment for the release of organic acids and maximizing solubilization [79,82]. The nutritional needs of plants can also contribute to this selection process. Dastogeer et al. [83] and Collavino et al. [84] reported that in plant species with high P demands, such as *Phaseolus vulgaris* and *Z. mays* [85], a high proportion of rhizobacteria can solubilize P. In our study, most of the strains obtained from *P. vulgaris* were unable to solubilize P or had a low ability to solubilize P; however, the strains with the highest PSI were isolated from *P. vulgaris*. *Z. mays* was described as one of the cereals with the most diverse niche of PSB genera [28,86]. Our study corroborates this statement, as 21 strains from 7 genera were obtained from maize roots, and different levels of solubilization, including high solubilizers, were observed. These species, being crops or cover crops, can help build a biologically active soil system that improves phosphorus availability naturally, increases plant growth and crop productivity, boosts the effectiveness of cover crops and crop rotation, and increases soil microbial diversity and health while reducing the dependence on chemical fertilizers and supporting sustainable and regenerative agriculture.

The literature reports a genetic influence on the bacterial ability to solubilize P, with *Bacillus* and *Pseudomonas* being the two most tested genera as PSB in inoculants [87]. *Burkholderia*, *Pantoea*, *Serratia*, and *Enterobacter* are also frequently used as single-species inocula. Other genera considered for inoculation tests include *Sinorhizobium*, *Klebsiella*, *Microbacterium* and *Acinetobacter* [87]. The genera *Bacillus*, *Paraburkholderia* and *Rhizobium* are represented in our study but mainly at lower PSI levels. In the literature, *Pseudomonas*, *Enterobacter* and *Pantoea* are well represented as effective solubilizers [28,87–89]. In our study, these three genera also included strains with high solubilization ability, in addition to *Flavobacterium* and *Chryseobacterium*. The genus *Chryseobacterium* is uncommon [28] and rarely reported as PSB [90]. This genus belongs to the order *Flavobacteriales* and the family *Weeksellaceae*. It is a Gram-negative, non-spore-forming, rod-shaped bacterium that is often found in soil, water, and sometimes in clinical settings. This genus is known for its yellow-pigmented colonies due to the production of flexirubin-type pigments. It can act as an opportunistic pathogen in humans and animals [91,92]. When isolated from plants, it has growth-promoting capabilities [91], growing between 2 and 42 °C (optimum at 25–30 °C), at pH 5.0–8.0 (optimum at 7.0), with a NaCl tolerance of 0–2% (optimum at 0%), and has acid and alkaline phosphatase activities [91,92]. Its ability as a high P solubilizer has already been reported by Jiang et al. [93].

Flavobacterium is generally reported to have low PSI ability [27,94]. However, in our study, strains of this genus displayed all levels of P solubilization, including the highest level. The occurrence of *Flavobacterium* strains with high P-solubilizing capacities may be linked to the environment from which they were isolated, the Namib Desert, which has extremely dry, alkaline, and hot conditions. In particular, the alkaline conditions of this region favor P complexation, and the presence of high solubilizing PSB can be a valuable resource in such environments.

In our study, *Bacillus* appeared as a genus with limited ability to solubilize P (a null to medium PSI), which does not support the findings of other studies, which indicated

that *Bacillus* has a high solubilization capacity [28,69,88,95]. However, Zutter et al. [87] reported that other genera outperformed the more commonly reported *Bacillus*. These authors attributed the wider use of *Bacillus* to ease of storage and longer shelf life due to its sporulation abilities. *Paraburkholderia* and *Rhizobium* are also genera that include PSB strains with high solubilization ability [27,87,96,97]. In our study, these two genera displayed null-to-low (*Rhizobium*) or low-to-medium (*Paraburkholderia*) PSI values. However, Kirui et al. [89] and Ben Zineb et al. [98] only reported the existence of *Paraburkholderia* with a medium PSI.

Based on our results, *Enterobacter* and *Pseudomonas* genera included high P-solubilizing strains, which might be linked to the high number of strains. This indicates that they may be keystone taxa in interactions with plant roots [83]. *Enterobacter* releases acids and enzymes that solubilize phosphorus [14,79,99]. *Pseudomonas* are known to produce organic acids, such as gluconic acid, which chelates calcium ions and releases soluble phosphate, and to synthesize siderophores that release iron and P from P-Fe complexes [69,100,101].

Phosphorus bioavailability is often low because of its high propensity to form complexes, leading to frequent P deficiencies in plants. The application of PSB as a sustainable complement to chemical fertilizers is gaining increasing attention. However, the efficiency of PSB inoculation is strongly influenced by the physicochemical properties of the soil, particularly pH, as well as other abiotic factors that influence PSB survival and functioning, such as salinity, drought, and temperature of the region where PSB inoculation will be applied, as the effectiveness of PSB is largely dependent on these factors.

4.2. Influence of PSB on Maize Plant Development at Two pH Levels

The growth, biochemical status, and nutrient levels of plants inoculated with effective PSB at two pH levels allowed us to evaluate the efficiency of this methodology for promoting crop productivity under different conditions.

Alkaline soil decreased maize growth, confirming the preference of maize for slightly acidic to neutral soils [102]. In alkaline soils, the solubility and uptake of essential nutrients are lower, leading to deficiencies and thus reducing plant growth [8]. Studies [102,103] have shown that both shoot and root growth (height and fresh weight) can be impaired by alkaline conditions. In our study, root growth was not affected by high pH, indicating that the effect of alkalinity on root elongation described by Yang et al. [104] was not observed. However, strong shoot inhibition was observed. The availability and absorption of different nutrients are not equally affected by high pH, with elements such as Fe and Mn being highly affected [105]. Fe and Mn play important roles in the photosynthetic process (oxygen-evolving complex, Fe-S clusters, and heme groups in photosystem I, cytochrome b6f, and ferredoxin) and antioxidant enzyme activity (CAT and SOD). Their scarcity can affect the normal functioning of photosynthesis and antioxidant responses, resulting in lower biomass production and oxidative stress. Our results show that nutrient levels in non-inoculated plants did not vary significantly with the pH. However, the antioxidant enzyme response (SOD and CAT activity) increased at pH 8, suggesting the overproduction of reactive oxygen species (ROS). Liu et al. [103] and Yang et al. [104] also reported induction of oxidative stress in plants exposed to alkaline stress. In our study, the induction of the enzymatic response was unable to prevent membrane (lipid peroxidation) and protein (protein carbonylation) damage. Chlorophyll *b* and carotenoid levels decreased at pH 8, implying that the membrane protection afforded by these molecules with antioxidant properties was lower at pH 8 than at pH 7 and did not contribute to decreased lipid peroxidation. Increased lipid peroxidation destabilizes membranes and interferes with membrane processes, such as photosynthesis, resulting in lower photosynthetic efficiency

and reduced production of photosynthates, which are resources that plants use to function and grow, resulting in reduced growth.

Our results show that inoculation with most PSB strains increased shoot and root weights at pH 7 and induced root elongation at pH 8, but only three strains significantly increased shoot weight at pH 8. Faced with nutritional deficiencies, plants tend to increase the length of the root system as a mechanism to increase nutrient absorption [106]. In our study, the root length was not significantly changed by pH in non-inoculated plants, but at pH 8, roots of inoculated plants were generally longer than at pH 7, indicating the attempt of plants to overcome the difficulty of nutrient uptake in alkaline soil.

Nutrient analysis also shows that P levels in plants improved with PSB inoculation at pH 7, except for one strain (F). However, at pH 8, no strain increased the P concentration in plants, indicating a decrease in the P-solubilization ability of all strains at pH 8. Our results contrast with those of Zutter et al. [87], who described higher PSB effectiveness in alkaline soils for P uptake and shoot biomass. The differences may be due to the strain species (high phosphate-solubilizing strains in this study are mainly *Enterobacter* and *Pseudomonas*, while Zutter et al. [87] used *Burkholderia*), and the initial available phosphorus in soil (12 mg/kg at pH 8 in our study) is lower than that in Zutter et al. [87] (25 mg/kg). Under low available phosphorus, PSB must consume more energy to solubilize phosphorus, resulting in limited effects under alkaline conditions.

An important result of our study is that at pH 7, PSB not only increased the absorption of P but also of other nutrients, increasing the overall nutritional status of the plants. Most mechanisms that increase P solubilization are nonspecific and may also increase the solubility of other nutrients in the soil [107]. One such mechanism is soil acidification through proton release or the production of organic acids that mobilize different nutrients (iron, zinc, potassium, and calcium) [107]. Many PSB also produce plant growth-promoting hormones. These factors stimulate overall plant growth, indirectly increasing nutrient demand and uptake efficiency. Indeed, our study shows higher nutritional levels and growth in plants inoculated with most PSB.

The increased growth may also be due to the biochemical changes induced by PSB in the plants. These changes varied with the strain and pH. Our study shows that at pH 7, non-inoculated plants exhibited high levels of metabolic activity and membrane damage. Some strains (O4, V4, and D8) induced few changes. However, other strains influenced plant biochemistry; the positive control and strain H induced chlorophylls and lowered protein carbonylation. These changes may boost photosynthesis and reduce the need for the degradation of misfolded and damaged proteins, which must be replaced by new ones to maintain metabolism. Other authors have also observed increased chlorophyll content in plants inoculated with *Bacillus* sp., *Pantoea* sp., and *Pseudomonas* sp. [108,109] at neutral pH. The remaining strains (C11, C20, F, M, and Q4) had a higher influence on plant biochemistry, increasing starch and protein levels, antioxidant enzyme activity, carotenoids, and protein carbonylation. These strains increased protein content to compensate for the lower activity of proteins with a higher level of carbonylation [110], which originated from oxidative stress that antioxidant enzymes could not quench. Other studies have also described an increase in lipid peroxidation by plant growth-promoting bacteria [17,111]; this induction can be important as lipid peroxidation plays an important role in signal transduction and phytohormone production [112]. Differentiated responses induced by different PSB strains on plant biochemistry have been reported by other authors [18,113,114] and can be explained by the release of different signaling molecules that can change plant gene expression and protein profile, regulate metabolic activity, or promote growth [115–117]. In our study, the different strategies induced were successful, as the inoculated plants showed higher growth, demonstrating a more efficient use of resources.

At pH 8, most PSB did not affect or even increase the damage caused by alkaline pH to proteins, but they reduced the membrane damage. Pinto et al. [118] observed that inoculation with *Pantoea* sp. induced changes in the lipid profile of maize plants subjected to heat stress, which reduced lipid peroxidation and increased plant thermotolerance. A similar mechanism may be induced by PSB to mitigate the oxidative impact of alkaline stress on the membranes. The three strains that induced higher growth at pH 8 (F, M, and C11) presented either lower protein carbonylation and metabolic activity and higher energy reserves (M) or higher levels of anthocyanins and chlorophylls. Lower damage to proteins increases their catalytic efficiency and half-life, reducing the energy costs required to maintain metabolism and leaving more resources for growth [110]. Anthocyanins have been linked to antioxidant defense and reduction in oxidative damage [119], metal detoxification and ion homeostasis by chelating metal ions (e.g., Al^{3+} , Fe^{3+} , and Ca^{2+}) [120], sequestering excess ions in vacuoles and reducing toxicity [121], and photoprotection by absorbing excess light and protecting chloroplasts from photooxidative damage under various stresses, including nutrient deficiency [121]. Analysis of our results shows that the first two mechanisms were unlikely to be responsible for the increased growth at pH 8, since plants with higher anthocyanin levels also exhibited higher levels of protein carbonylation and lipid peroxidation. Metal ion chelation also did not appear to be the reason, since plants at pH 8 had lower metal ion levels. However, plants with higher anthocyanin levels also had higher starch levels, indicating protection of the photosynthetic process, resulting in more high-energy compounds available to support growth.

This study identifies specific phosphate-solubilizing bacterial (PSB) strains that exhibited high P-solubilization capacity and significantly enhanced maize plant growth and biochemical status. Strains such as C11, F, and M consistently demonstrated superior phosphate solubilization in vitro and, when applied to plants, improved nutrient uptake, antioxidant enzyme activity, and energy reserve accumulation. Their effectiveness is influenced by both the host plant and the climate of origin. Strains isolated from maize (*Zea mays*) and other high-P-demand plants, as well as from regions with arid, alkaline, or high-temperature conditions, tend to display higher solubilization capacity and stress resilience. These strains were particularly effective at pH 7, promoting shoot and root growth, enhancing starch and protein contents, and mitigating oxidative stress. Their dual ability to efficiently solubilize phosphorus and positively modulate plant metabolism, combined with their adaptability to diverse environmental conditions, highlights their potential as keystone inoculants for sustainable agriculture. Targeting such high-performance, climate- and host-adapted PSB strains offers a promising strategy to increase nutrient availability, optimize plant physiological responses, and reduce dependence on chemical fertilizers in different soils and cropping systems.

5. Conclusions

The results of this study endorse the ubiquity of P-solubilizing bacteria. However, the solubilization capacity varied with bacterial genus and was influenced by factors such as soil use, climate, and host plants. Bacteria isolated from water-restricted and hot regions (Angola and southern Portugal) emerged as the best sources for obtaining highly efficient PSB. *Flavobacterium* and *Chryseobacterium* emerged as genera with highly efficient PSB and can be added to the list of bacterial genera with high phosphate-solubilizing capacity. Both crops (*Z. mays*, *P. vulgaris*) and wild plants (*T. simplex*, *Stipagrostis* sp., *O. pinnatus*, and *Medicago* sp.) were identified as suitable hosts for bioprospecting highly efficient PSB. The ability of PSB to improve the growth and nutritional status of maize plants was influenced by pH. The strategies used to influence plant biochemistry and promote plant growth differed among the PSB strains and showed higher efficacy under neutral than alkaline

conditions, with a few strains maintaining the ability to promote plant growth under alkaline conditions. This study opens up good prospects for designing a new generation of PSB inoculants that are highly efficient in different environments. However, a thorough selection should be made so that the application of PSB matches the climate, crops, and soil pH, considering these variables to obtain effective results. This will allow the general use of PSB as a sustainable agricultural practice to improve crop yield and food security.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/land14102065/s1>, Table S1: Overview of bacterial strains selected for this study. Each entry includes strain designation, bacterial genus, and accession number, together with information on the host species, collection site, geographical coordinates, and country of origin. Environmental context is described by soil use and bioclimatic classification. Phosphate Solubilization Index (PSI) values and levels are provided to indicate the capacity of phosphate solubilization for each strain.

Author Contributions: Conceptualization, J.S. and E.F.; methodology, J.S., E.F. and T.L.; software, J.S. and E.F.; validation, J.S. and E.F.; formal analysis, J.S. and T.L.; investigation, J.S., R.R. and R.P.; resources, R.G., E.F. and C.P.; data curation, J.S., E.F. and C.P.; writing—original draft preparation, J.S., T.L., E.F. and P.C.; writing—review and editing, T.L., E.F. and P.C.; visualization, T.L.; supervision, E.F. and R.G.; funding acquisition, R.G., E.F., A.F., P.C. and C.P. All authors have read and agreed to the published version of the manuscript.

Funding: We acknowledge financial support from UID Centro de Estudos do Ambiente e Mar (CESAM) + LA/P/0094/2020, and from PRR—Plano de Recuperação e Resiliência e pelos Fundos Europeus NextGenerationEU (PRR-C05-i03-I-000032). Paulo Cardoso acknowledges funding from national funds (OE) through the Portuguese Foundation for Science and Technology (FCT) (2023.06755.CEECIND). Ricardo Pinto is grateful for a PhD scholarship provided by FCT (SFRH/BD/132332/2017). Ricardo Rocha is grateful for a PhD scholarship provided by FCT (<https://doi.org/10.54499/2023.04964.BDANA>). Tiago Lopes is grateful for a PhD scholarship provided by FCT (<https://doi.org/10.54499/2023.01311.BD>).

Data Availability Statement: The dataset is available on request from the authors.

Conflicts of Interest: The authors declare that they have no conflicts of interest.

References

1. Market Research Future. Microbial Inoculant Market Size, Share, Growth | Report, 2034, September 2025. Available online: <https://www.marketresearchfuture.com/reports/microbial-inoculant-market-34924> (accessed on 8 August 2025).
2. O’Callaghan, M.; Ballard, R.A.; Wright, D. Soil Microbial Inoculants for Sustainable Agriculture: Limitations and Opportunities. *Soil Use Manag.* **2022**, *38*, 1340–1369. [\[CrossRef\]](#)
3. Bargaz, A.; Elhaissofi, W.; Khourchi, S.; Benmrid, B.; Borden, K.A.; Rchiad, Z. Benefits of Phosphate Solubilizing Bacteria on Belowground Crop Performance for Improved Crop Acquisition of Phosphorus. *Microbiol. Res.* **2021**, *252*, 126842. [\[CrossRef\]](#)
4. Bechtaoui, N.; Rabiou, M.K.; Raklami, A.; Oufdou, K.; Hafidi, M.; Jemo, M. Phosphate-Dependent Regulation of Growth and Stresses Management in Plants. *Front. Plant Sci.* **2021**, *12*, 679916. [\[CrossRef\]](#) [\[PubMed\]](#)
5. Kalayu, G. Phosphate Solubilizing Microorganisms: Promising Approach as Biofertilizers. *Int. J. Agron.* **2019**, *2019*, 4917256. [\[CrossRef\]](#)
6. Jones, D.L.; Oburger, E. Solubilization of Phosphorus by Soil Microorganisms. In *Phosphorus in Action: Biological Processes in Soil Phosphorus Cycling*; Bünemann, E., Oberson, A., Frossard, E., Eds.; Springer: Berlin/Heidelberg, Germany, 2011; pp. 169–198, ISBN 978-3-642-15271-9.
7. Penn, C.J.; Camberato, J.J. A Critical Review on Soil Chemical Processes That Control How Soil pH Affects Phosphorus Availability to Plants. *Agriculture* **2019**, *9*, 120. [\[CrossRef\]](#)
8. Vance, C.P.; Uhde-Stone, C.; Allan, D.L. Phosphorus Acquisition and Use: Critical Adaptations by Plants for Securing a Non-renewable Resource. *New Phytol.* **2003**, *157*, 423–447. [\[CrossRef\]](#)
9. Bojórquez-Quintal, E.; Escalante-Magaña, C.; Echevarría-Machado, I.; Martínez-Estévez, M. Aluminum, a Friend or Foe of Higher Plants in Acid Soils. *Front. Plant Sci.* **2017**, *8*, 1767. [\[CrossRef\]](#) [\[PubMed\]](#)

10. Kaur, C.; Selvakumar, G.; Ganeshamurthy, A.N. Acid Tolerant Microbial Inoculants: A Requisite for Successful Crop Production in Acidic Soils. In *Phyto and Rhizo Remediation*; Arora, N.K., Kumar, N., Eds.; Springer: Singapore, 2019; pp. 235–247, ISBN 978-981-329-664-0.
11. Yang, C.; Shi, D.; Wang, D. Comparative Effects of Salt and Alkali Stresses on Growth, Osmotic Adjustment and Ionic Balance of an Alkali-Resistant Halophyte *Suaeda glauca* (Bge.). *Plant Growth Regul.* **2008**, *56*, 179–190. [\[CrossRef\]](#)
12. Soliman, W.S.; Fujimori, M.; Tase, K.; Sugiyama, S. Oxidative Stress and Physiological Damage under Prolonged Heat Stress in C3 Grass *Lolium perenne*. *Grassl. Sci.* **2011**, *57*, 101–106. [\[CrossRef\]](#)
13. Soliman, W.S.; Fujimori, M.; Tase, K.; Sugiyama, S. Heat Tolerance and Suppression of Oxidative Stress: Comparative Analysis of 25 Cultivars of the C3 Grass *Lolium perenne*. *Environ. Exp. Bot.* **2012**, *78*, 10–17. [\[CrossRef\]](#)
14. Rawat, P.; Das, S.; Shankhdhar, D.; Shankhdhar, S.C. Phosphate-Solubilizing Microorganisms: Mechanism and Their Role in Phosphate Solubilization and Uptake. *J. Soil Sci. Plant Nutr.* **2021**, *21*, 49–68. [\[CrossRef\]](#)
15. da Silva, L.I.; Pereira, M.C.; de Carvalho, A.M.X.; Buttrós, V.H.; Pasqual, M.; Dória, J. Phosphorus-Solubilizing Microorganisms: A Key to Sustainable Agriculture. *Agriculture* **2023**, *13*, 462. [\[CrossRef\]](#)
16. Wang, X.; Fan, J.; Xing, Y.; Xu, G.; Wang, H.; Deng, J.; Wang, Y.; Zhang, F.; Li, P.; Li, Z. Chapter Three—The Effects of Mulch and Nitrogen Fertilizer on the Soil Environment of Crop Plants. In *Advances in Agronomy*; Sparks, D.L., Ed.; Academic Press: San Diego, CA, USA, 2019; Volume 153, pp. 121–173.
17. Cruz, C.; Cardoso, P.; Santos, J.; Matos, D.; Figueira, E. Bioprospecting Soil Bacteria from Arid Zones to Increase Plant Tolerance to Drought: Growth and Biochemical Status of Maize Inoculated with Plant Growth-Promoting Bacteria Isolated from Sal Island, Cape Verde. *Plants* **2022**, *11*, 2912. [\[CrossRef\]](#) [\[PubMed\]](#)
18. Cruz, C.; Cardoso, P.; Santos, J.; Matos, D.; Sá, C.; Figueira, E. Application of Plant Growth-Promoting Bacteria from Cape Verde to Increase Maize Tolerance to Salinity. *Antioxidants* **2023**, *12*, 488. [\[CrossRef\]](#)
19. Oleńska, E.; Małek, W.; Wójcik, M.; Swiecicka, I.; Thijs, S.; Vangronsveld, J. Beneficial Features of Plant Growth-Promoting Rhizobacteria for Improving Plant Growth and Health in Challenging Conditions: A Methodical Review. *Sci. Total Environ.* **2020**, *743*, 140682. [\[CrossRef\]](#)
20. Parray, J.A.; Jan, S.; Kamili, A.N.; Qadri, R.A.; Egamberdieva, D.; Ahmad, P. Current Perspectives on Plant Growth-Promoting Rhizobacteria. *J. Plant Growth Regul.* **2016**, *35*, 877–902. [\[CrossRef\]](#)
21. Vejan, P.; Abdullah, R.; Khadiran, T.; Ismail, S.; Nasrulhaq Boyce, A. Role of Plant Growth Promoting Rhizobacteria in Agricultural Sustainability—A Review. *Molecules* **2016**, *21*, 573. [\[CrossRef\]](#)
22. Djuuna, I.A.F.; Prabawardani, S.; Massora, M. Population Distribution of Phosphate-Solubilizing Microorganisms in Agricultural Soil. *Microbes Environ.* **2022**, *37*, ME21041. [\[CrossRef\]](#)
23. Pan, L.; Cai, B. Phosphate-Solubilizing Bacteria: Advances in Their Physiology, Molecular Mechanisms and Microbial Community Effects. *Microorganisms* **2023**, *11*, 2904. [\[CrossRef\]](#)
24. Sharma, S.B.; Sayyed, R.Z.; Trivedi, M.H.; Gobi, T.A. Phosphate Solubilizing Microbes: Sustainable Approach for Managing Phosphorus Deficiency in Agricultural Soils. *SpringerPlus* **2013**, *2*, 587. [\[CrossRef\]](#)
25. Amy, C.; Avice, J.-C.; Laval, K.; Bressan, M. Are Native Phosphate-Solubilizing Bacteria a Relevant Alternative to Mineral Fertilizations for Crops? Part II: PSB Inoculation Enables a Halving of P Input and Improves the Microbial Community in the Rapeseed Rhizosphere. *Rhizosphere* **2022**, *21*, 100480. [\[CrossRef\]](#)
26. Alori, E.T.; Glick, B.R.; Babalola, O.O. Microbial Phosphorus Solubilization and Its Potential for Use in Sustainable Agriculture. *Front. Microbiol.* **2017**, *8*, 971. [\[CrossRef\]](#) [\[PubMed\]](#)
27. Janati, W.; Bouabid, R.; Mikou, K.; Ghadraoui, L.E.; Errachidi, F. Phosphate Solubilizing Bacteria from Soils with Varying Environmental Conditions: Occurrence and Function. *PLoS ONE* **2023**, *18*, e0289127. [\[CrossRef\]](#) [\[PubMed\]](#)
28. Kour, D.; Rana, K.L.; Kaur, T.; Yadav, N.; Yadav, A.N.; Kumar, M.; Kumar, V.; Dhaliwal, H.S.; Saxena, A.K. Biodiversity, Current Developments and Potential Biotechnological Applications of Phosphorus-Solubilizing and -Mobilizing Microbes: A Review. *Pedosphere* **2021**, *31*, 43–75. [\[CrossRef\]](#)
29. Zhang, Q.; White, J.F. Bioprospecting Desert Plants for Endophytic and Biostimulant Microbes: A Strategy for Enhancing Agricultural Production in a Hotter, Drier Future. *Biology* **2021**, *10*, 961. [\[CrossRef\]](#)
30. Lopes, T.; Santos, J.; Matos, D.; Sá, C.; Pina, D.; Pinto, R.; Cardoso, P.; Figueira, E. Soil Bacteria from the Namib Desert: Insights into Plant Growth Promotion and Osmotolerance in a Hyper-Arid Environment. *Land* **2024**, *13*, 1678. [\[CrossRef\]](#)
31. Liu, H.; Wu, X.-Q.; Ren, J.-H.; Ye, J.-R. Isolation and Identification of Phosphobacteria in Poplar Rhizosphere from Different Regions of China. *Pedosphere* **2011**, *21*, 90–97. [\[CrossRef\]](#)
32. Janati, W.; Mikou, K.; El Ghadraoui, L.; Errachidi, F. Isolation and Characterization of Phosphate Solubilizing Bacteria Naturally Colonizing Legumes Rhizosphere in Morocco. *Front. Microbiol.* **2022**, *13*, 958300. [\[CrossRef\]](#)
33. Gandhi, A.; Muralidharan, G.; Sudhakar, E. Isolation and Identification of Elite Phosphate Solubilizing Bacteria from Soil under Paddy Cultivation. *Int. Lett. Nat. Sci.* **2014**, *11*, 62–68. [\[CrossRef\]](#)

34. Amri, M.; Rjeibi, M.R.; Gatrouni, M.; Mateus, D.M.R.; Asses, N.; Pinho, H.J.O.; Abbes, C. Isolation, Identification, and Characterization of Phosphate-Solubilizing Bacteria from Tunisian Soils. *Microorganisms* **2023**, *11*, 783. [\[CrossRef\]](#)
35. Hayat, W.; Aman, H.; Irshad, U.; Azeem, M.; Iqbal, A.; Nazir, R. Analysis of Ecological Attributes of Bacterial Phosphorus Solubilizers, Native to Pine Forests of Lower Himalaya. *Appl. Soil Ecol.* **2017**, *112*, 51–59. [\[CrossRef\]](#)
36. Anzum, N.; Khan, F.I.; Hossain, M.Z.; Islam, M.N.; Saha, M.L. Isolation and Identification of Pigment Producing Bacteria from the Ratargul Swamp Forest Soil. *Dhaka Univ. J. Biol. Sci.* **2022**, *31*, 1–8. [\[CrossRef\]](#)
37. Vikram, S.; Guerrero, L.D.; Makhalanyane, T.P.; Le, P.T.; Seely, M.; Cowan, D.A. Metagenomic Analysis Provides Insights into Functional Capacity in a Hyperarid Desert Soil Niche Community. *Environ. Microbiol.* **2016**, *18*, 1875–1888. [\[CrossRef\]](#) [\[PubMed\]](#)
38. Cardoso, P.; Alves, A.; Silveira, P.; Sá, C.; Fidalgo, C.; Freitas, R.; Figueira, E. Bacteria from Nodules of Wild Legume Species: Phylogenetic Diversity, Plant Growth Promotion Abilities and Osmotolerance. *Sci. Total Environ.* **2018**, *645*, 1094–1102. [\[CrossRef\]](#)
39. Figueira, E.M.D.A.P. Aspectos da Tolerância Salina em *Pisum sativum* L.: Influência da Nutrição Azotada. Ph.D. Thesis, Universidade de Aveiro, Aveiro, Portugal, 2000.
40. Rocha, R.; Lopes, T.; Fidalgo, C.; Alves, A.; Cardoso, P.; Figueira, E. Bacteria Associated with the Roots of Common Bean (*Phaseolus vulgaris* L.) at Different Development Stages: Diversity and Plant Growth Promotion. *Microorganisms* **2023**, *11*, 57. [\[CrossRef\]](#)
41. Pikovskaya, R. Mobilization of Phosphorus in Soil in Connection with Vital Activity of Some Microbial Species. *Mikrobiologiya* **1948**, *287*, 77–84.
42. Nautiyal, C.S. An Efficient Microbiological Growth Medium for Screening Phosphate Solubilizing Microorganisms. *FEMS Microbiol. Lett.* **1999**, *170*, 265–270. [\[CrossRef\]](#)
43. Hazrah, K.S.; Antao, S.M. Apatite, $\text{Ca}_{10}(\text{PO}_4)_6(\text{OH}, \text{F}, \text{Cl})_2$: Structural Variations, Natural Solid Solutions, Intergrowths, and Zoning. *Minerals* **2022**, *12*, 527. [\[CrossRef\]](#)
44. Benbrik, B.; Elabed, A.; El Modafar, C.; Douira, A.; Amir, S.; Filali-Maltouf, A.; El Abed, S.; El Gachtouli, N.; Mohammed, I.; Koraichi, S.I. Reusing Phosphate Sludge Enriched by Phosphate Solubilizing Bacteria as Biofertilizer: Growth Promotion of *Zea mays*. *Biocatal. Agric. Biotechnol.* **2020**, *30*, 101825. [\[CrossRef\]](#)
45. Baig, K.S.; Arshad, M.; Zahir, Z.; Cheema, M.A. Comparative Efficacy of Qualitative and Quantitative Methods for Rock Phosphate Solubilization with Phosphate Solubilizing Rhizobacteria. *Soil Environ.* **2010**, *29*, 82–86.
46. Somasegaran, P.; Hoben, H.J. *Handbook for Rhizobia: Methods in Legume-Rhizobium Technology*; Springer Science & Business Media: New York, NY, USA, 2012; ISBN 978-1-4613-8375-8.
47. Costa, C.; Reis, A.P.; Ferreira da Silva, E.; Rocha, F.; Patinha, C.; Dias, A.C.; Sequeira, C.; Terroso, D. Assessing the Control Exerted by Soil Mineralogy in the Fixation of Potentially Harmful Elements in the Urban Soils of Lisbon, Portugal. *Environ. Earth Sci.* **2012**, *65*, 1133–1145. [\[CrossRef\]](#)
48. Wright, A.F.; Bailey, J.S. Organic Carbon, Total Carbon, and Total Nitrogen Determinations in Soils of Variable Calcium Carbonate Contents Using a Leco CN-2000 Dry Combustion Analyzer. *Commun. Soil Sci. Plant Anal.* **2001**, *32*, 3243–3258. [\[CrossRef\]](#)
49. Wellburn, A.R.; Lichtenthaler, H. Formulae and Program to Determine Total Carotenoids and Chlorophylls A and B of Leaf Extracts in Different Solvents. In *Advances in Photosynthesis Research: Proceedings of the VIth International Congress on Photosynthesis, Brussels, Belgium, 1–6 August 1983, Volume 2*; Sybesma, C., Ed.; Springer: Dordrecht, The Netherlands, 1984; pp. 9–12, ISBN 978-94-017-6368-4.
50. Zhao, J.; Xie, X.; Shen, X.; Wang, Y. Effect of Sunlight-Exposure on Antioxidants and Antioxidant Enzyme Activities in ‘d’Anjou’ Pear in Relation to Superficial Scald Development. *Food Chem.* **2016**, *210*, 18–25. [\[CrossRef\]](#) [\[PubMed\]](#)
51. King, F.D.; Packard, T.T. Respiration and the Activity of the Respiratory Electron Transport System in Marine Zooplankton. *Limnol. Oceanogr.* **1975**, *20*, 849–854. [\[CrossRef\]](#)
52. Owens, T.G.; King, F.D. The Measurement of Respiratory Electron-Transport-System Activity in Marine Zooplankton. *Mar. Biol.* **1975**, *30*, 27–36. [\[CrossRef\]](#)
53. Beauchamp, C.; Fridovich, I. Superoxide Dismutase: Improved Assays and an Assay Applicable to Acrylamide Gels. *Anal. Biochem.* **1971**, *44*, 276–287. [\[CrossRef\]](#)
54. Johansson, L.H.; Borg, L.A. A Spectrophotometric Method for Determination of Catalase Activity in Small Tissue Samples. *Anal. Biochem.* **1988**, *174*, 331–336. [\[CrossRef\]](#)
55. Robinson, H.W.; Hogden, C.G. The biuret reaction in the determination of serum proteins: 1. A study of the conditions necessary for the production of a stable color which bears a quantitative relationship to the protein concentration. *J. Biol. Chem.* **1940**, *135*, 707–725. [\[CrossRef\]](#)
56. Mesquita, C.S.; Oliveira, R.; Bento, F.; Geraldo, D.; Rodrigues, J.V.; Marcos, J.C. Simplified 2,4-Dinitrophenylhydrazine Spectrophotometric Assay for Quantification of Carbonyls in Oxidized Proteins. *Anal. Biochem.* **2014**, *458*, 69–71. [\[CrossRef\]](#)
57. Buege, J.A.; Aust, S.D. Microsomal Lipid Peroxidation. *Methods Enzymol.* **1978**, *52*, 302–310. [\[CrossRef\]](#)
58. DuBois, M.; Gilles, K.A.; Hamilton, J.K.; Rebers, P.A.; Smith, F. Colorimetric Method for Determination of Sugars and Related Substances. *Anal. Chem.* **1956**, *28*, 350–356. [\[CrossRef\]](#)

59. Pang, Z.; Lu, Y.; Zhou, G.; Hui, F.; Xu, L.; Viau, C.; Spigelman, A.F.; MacDonald, P.E.; Wishart, D.S.; Li, S.; et al. MetaboAnalyst 6.0: Towards a Unified Platform for Metabolomics Data Processing, Analysis and Interpretation. *Nucleic Acids Res.* **2024**, *52*, W398–W406. [\[CrossRef\]](#)
60. Liu, F.-P.; Liu, H.-Q.; Zhou, H.-L.; Dong, Z.-G.; Bai, X.-H.; Bai, P.; Qiao, J.-J. Isolation and Characterization of Phosphate-Solubilizing Bacteria from Betel Nut (*Areca catechu*) and Their Effects on Plant Growth and Phosphorus Mobilization in Tropical Soils. *Biol. Fertil. Soils* **2014**, *50*, 927–937. [\[CrossRef\]](#)
61. Xie, J.; Yan, Z.; Wang, G.; Xue, W.; Li, C.; Chen, X.; Chen, D. A Bacterium Isolated from Soil in a Karst Rocky Desertification Region Has Efficient Phosphate-Solubilizing and Plant Growth-Promoting Ability. *Front. Microbiol.* **2021**, *11*, 625450. [\[CrossRef\]](#) [\[PubMed\]](#)
62. Kour, D.; Rana, K.L.; Yadav, A.N.; Yadav, N.; Kumar, V.; Kumar, A.; Sayyed, R.Z.; Hesham, A.E.-L.; Dhaliwal, H.S.; Saxena, A.K. Drought-Tolerant Phosphorus-Solubilizing Microbes: Biodiversity and Biotechnological Applications for Alleviation of Drought Stress in Plants. In *Plant Growth Promoting Rhizobacteria for Sustainable Stress Management: Volume 1: Rhizobacteria in Abiotic Stress Management*; Sayyed, R.Z., Arora, N.K., Reddy, M.S., Eds.; Springer: Singapore, 2019; pp. 255–308, ISBN 9789811365362.
63. Aliyat, F.Z.; Maldani, M.; El Guilli, M.; Nassiri, L.; Ibijbijen, J. Phosphate-Solubilizing Bacteria Isolated from Phosphate Solid Sludge and Their Ability to Solubilize Three Inorganic Phosphate Forms: Calcium, Iron, and Aluminum Phosphates. *Microorganisms* **2022**, *10*, 980. [\[CrossRef\]](#)
64. Liu, Z.; Li, Y.C.; Zhang, S.; Fu, Y.; Fan, X.; Patel, J.S.; Zhang, M. Characterization of Phosphate-Solubilizing Bacteria Isolated from Calcareous Soils. *Appl. Soil Ecol.* **2015**, *96*, 217–224. [\[CrossRef\]](#)
65. Teles, E.A.P.; Xavier, J.F.; Arcênio, F.S.; Amaya, R.L.; Gonçalves, J.V.S.; Rouws, L.F.M.; Zonta, E.; Coelho, I.S. Characterization and Evaluation of Potential Halotolerant Phosphate Solubilizing Bacteria from *Salicornia fruticosa* Rhizosphere. *Front. Plant Sci.* **2024**, *14*, 1324056. [\[CrossRef\]](#) [\[PubMed\]](#)
66. Liu, F.; Qian, J.; Zhu, Y.; Wang, P.; Hu, J.; Lu, B.; He, Y.; Tang, S.; Shen, J.; Liu, Y.; et al. Phosphate Solubilizing Microorganisms Increase Soil Phosphorus Availability: A Review. *Geomicrobiol. J.* **2024**, *41*, 1–16. [\[CrossRef\]](#)
67. de Lima, J.D.; Monteiro, P.H.R.; Rivadavea, W.R.; Barbosa, M.; Cordeiro, R.D.; Garboggini, F.F.; Auer, C.G.; da Silva, G.J. Potential of Endophytic Bacteria from *Acacia mearnsii*: Phosphate Solubilization, Indole Acetic Acid Production, and Application in Wheat. *Appl. Soil Ecol.* **2024**, *196*, 105315. [\[CrossRef\]](#)
68. Ait-Ouakrim, E.H.; Chakhchar, A.; El Modafar, C.; Douira, A.; Amir, S.; Ibensouda-Koraichi, S.; Belkadi, B.; Filali-Maltouf, A. Valorization of Moroccan Phosphate Sludge Through Isolation and Characterization of Phosphate Solubilizing Bacteria and Assessment of Their Growth Promotion Effect on *Phaseolus vulgaris*. *Waste Biomass Valorization* **2023**, *14*, 2673–2690. [\[CrossRef\]](#)
69. Ghorehshizadeh, S.; Calvo-Peña, C.; Ruiz-Muñoz, M.; Otero-Suárez, R.; Coque, J.J.R.; Cobos, R. *Pseudomonas taetrolens* ULE-PH5 and *Pseudomonas* Sp. ULE-PH6 Isolated from the Hop Rhizosphere Increase Phosphate Assimilation by the Plant. *Plants* **2024**, *13*, 402. [\[CrossRef\]](#)
70. Kour, D.; Rana, K.L.; Sheikh, I.; Kumar, V.; Yadav, A.N.; Dhaliwal, H.S.; Saxena, A.K. Alleviation of Drought Stress and Plant Growth Promotion by *Pseudomonas libanensis* EU-LWNA-33, a Drought-Adaptive Phosphorus-Solubilizing Bacterium. *Proc. Natl. Acad. Sci. India Sect. B Biol. Sci.* **2020**, *90*, 785–795. [\[CrossRef\]](#)
71. Bouremani, N.; Cherif-Silini, H.; Silini, A.; Rabhi, N.E.H.; Bouket, A.C.; Belbahri, L.; Bouremani, N.; Cherif-Silini, H.; Silini, A.; Rabhi, N.E.H.; et al. Osmotolerant Plant Growth Promoting Bacteria Mitigate Adverse Effects of Drought Stress on Wheat Growth. *AIMS Microbiol.* **2024**, *10*, 507–541. [\[CrossRef\]](#)
72. Ameen, F.; AlYahya, S.A.; AlNadhari, S.; Alasmari, H.; Alhoshani, F.; Wainwright, M. Phosphate Solubilizing Bacteria and Fungi in Desert Soils: Species, Limitations and Mechanisms. *Arch. Agron. Soil Sci.* **2019**, *65*, 1446–1459. [\[CrossRef\]](#)
73. Dey, G.; Banerjee, P.; Sharma, R.K.; Maity, J.P.; Etesami, H.; Shaw, A.K.; Huang, Y.-H.; Huang, H.-B.; Chen, C.-Y. Management of Phosphorus in Salinity-Stressed Agriculture for Sustainable Crop Production by Salt-Tolerant Phosphate-Solubilizing Bacteria—A Review. *Agronomy* **2021**, *11*, 1552. [\[CrossRef\]](#)
74. Ndung'u-Magiroi, K.W.; Herrmann, L.; Okalebo, J.R.; Othieno, C.O.; Pypers, P.; Lesueur, D. Occurrence and Genetic Diversity of Phosphate-Solubilizing Bacteria in Soils of Differing Chemical Characteristics in Kenya. *Ann. Microbiol.* **2012**, *62*, 897–904. [\[CrossRef\]](#)
75. Rfaki, A.; Zennouhi, O.; Aliyat, F.Z.; Nassiri, L.; Ibijbijen, J. Isolation, Selection and Characterization of Root-Associated Rock Phosphate Solubilizing Bacteria in Moroccan Wheat (*Triticum aestivum* L.). *Geomicrobiol. J.* **2020**, *37*, 230–241. [\[CrossRef\]](#)
76. Nabati, J.; Nezami, A.; Yousefi, A.; Oskoueian, E.; Oskoueian, A.; Ahmadi-Lahijani, M.J. Biofertilizers Containing Plant Growth Promoting Rhizobacteria Enhance Nutrient Uptake and Improve the Growth and Yield of Chickpea Plants in an Arid Environment. *Sci. Rep.* **2025**, *15*, 8331. [\[CrossRef\]](#)
77. Wankhade, A.; Wilkinson, E.; Britt, D.W.; Kaundal, A. A Review of Plant–Microbe Interactions in the Rhizosphere and the Role of Root Exudates in Microbiome Engineering. *Appl. Sci.* **2025**, *15*, 7127. [\[CrossRef\]](#)
78. Pantigoso, H.A.; Newberger, D.; Vivanco, J.M. The rhizosphere microbiome: Plant–microbial interactions for resource acquisition. *J. Appl. Microbiol.* **2022**, *133*, 2864–2876. [\[CrossRef\]](#)

79. Cheng, Y.; Narayanan, M.; Shi, X.; Chen, X.; Li, Z.; Ma, Y. Phosphate-Solubilizing Bacteria: Their Agroecological Function and Optimistic Application for Enhancing Agro-Productivity. *Sci. Total Environ.* **2023**, *901*, 166468. [\[CrossRef\]](#)
80. Pantigoso, H.A.; Manter, D.K.; Fonte, S.J.; Vivanco, J.M. Root Exudate-Derived Compounds Stimulate the Phosphorus Solubilizing Ability of Bacteria. *Sci. Rep.* **2023**, *13*, 4050. [\[CrossRef\]](#) [\[PubMed\]](#)
81. Yahya, M.; Islam, E.U.; Rasul, M.; Farooq, I.; Mahreen, N.; Tawab, A.; Irfan, M.; Rajput, L.; Amin, I.; Yasmin, S. Differential Root Exudation and Architecture for Improved Growth of Wheat Mediated by Phosphate Solubilizing Bacteria. *Front. Microbiol.* **2021**, *12*, 744094. [\[CrossRef\]](#) [\[PubMed\]](#)
82. Vives-Peris, V.; de Ollas, C.; Gómez-Cadenas, A.; Pérez-Clemente, R.M. Root Exudates: From Plant to Rhizosphere and Beyond. *Plant Cell Rep.* **2020**, *39*, 3–17. [\[CrossRef\]](#) [\[PubMed\]](#)
83. Dastogeer, K.M.G.; Tumpa, F.H.; Sultana, A.; Akter, M.A.; Chakraborty, A. Plant Microbiome—an Account of the Factors That Shape Community Composition and Diversity. *Curr. Plant Biol.* **2020**, *23*, 100161. [\[CrossRef\]](#)
84. Collavino, M.M.; Sansberro, P.A.; Mroginski, L.A.; Aguilar, O.M. Comparison of in Vitro Solubilization Activity of Diverse Phosphate-Solubilizing Bacteria Native to Acid Soil and Their Ability to Promote *Phaseolus vulgaris* Growth. *Biol. Fertil. Soils* **2010**, *46*, 727–738. [\[CrossRef\]](#)
85. Wang, Z.; Zhang, H.; Liu, L.; Li, S.; Xie, J.; Xue, X.; Jiang, Y. Screening of Phosphate-Solubilizing Bacteria and Their Abilities of Phosphorus Solubilization and Wheat Growth Promotion. *BMC Microbiol.* **2022**, *22*, 296. [\[CrossRef\]](#)
86. Kour, D.; Yadav, A.N. First Report on Novel Psychrotrophic Phosphorus-Solubilizing *Ochrobactrum thiophenivorans* EU-KL94 from Keylong Region in Great Himalayas and Their Role in Plant Growth Promotion of Oats (*Avena sativa* L.). *Curr. Microbiol.* **2023**, *80*, 227. [\[CrossRef\]](#)
87. De Zutter, N.; Ameye, M.; Bekaert, B.; Verwaeren, J.; De Gelder, L.; Audenaert, K. Uncovering New Insights and Misconceptions on the Effectiveness of Phosphate Solubilizing Rhizobacteria in Plants: A Meta-Analysis. *Front. Plant Sci.* **2022**, *13*, 858804. [\[CrossRef\]](#)
88. Ducouso-Détrez, A.; Lahrach, Z.; Fontaine, J.; Lounès-Hadj Sahraoui, A.; Hijri, M. Cultural Techniques Capture Diverse Phosphate-Solubilizing Bacteria in Rock Phosphate-Enriched Habitats. *Front. Microbiol.* **2024**, *15*, 1280848. [\[CrossRef\]](#)
89. Kirui, C.K.; Njeru, E.M.; Runo, S. Diversity and Phosphate Solubilization Efficiency of Phosphate Solubilizing Bacteria Isolated from Semi-Arid Agroecosystems of Eastern Kenya. *Microbiol. Insights* **2022**, *15*, 11786361221088991. [\[CrossRef\]](#) [\[PubMed\]](#)
90. da Silva, A.V.; de Oliveira, A.J.; Tanabe, I.S.B.; Silva, J.V.; da Silva Barros, T.W.; da Silva, M.K.; França, P.H.B.; Leite, J.; Putzke, J.; Montone, R.; et al. Antarctic Lichens as a Source of Phosphate-Solubilizing Bacteria. *Extremophiles* **2021**, *25*, 181–191. [\[CrossRef\]](#)
91. Chhetri, G.; Kim, J.; Kim, I.; Kang, M.; Seo, T. *Chryseobacterium caseinilyticum* Sp. Nov., a Casein Hydrolyzing Bacterium Isolated from Rice Plant and Emended Description of *Chryseobacterium piscicola*. *Int. J. Syst. Evol. Microbiol.* **2021**, *71*, 004854. [\[CrossRef\]](#) [\[PubMed\]](#)
92. Zhang, Z.; Yang, L.-L.; Li, C.-J.; Jiang, X.-W.; Zhi, X.-Y. *Chryseobacterium paridis* Sp. Nov., an Endophytic Bacterial Species Isolated from the Root of *Paris polyphylla* Smith Var. *Yunnanensis*. *Arch. Microbiol.* **2021**, *203*, 4777–4783. [\[CrossRef\]](#)
93. Jiang, H.; Wang, T.; Chi, X.; Wang, M.; Chen, N.; Chen, M.; Pan, L.; Qi, P. Isolation and Characterization of Halotolerant Phosphate Solubilizing Bacteria Naturally Colonizing the Peanut Rhizosphere in Salt-Affected Soil. *Geomicrobiol. J.* **2020**, *37*, 110–118. [\[CrossRef\]](#)
94. Özdoğan, D.K.; Akçelik, N.; Akçelik, M. Genetic Diversity and Characterization of Plant Growth-Promoting Effects of Bacteria Isolated from Rhizospheric Soils. *Curr. Microbiol.* **2022**, *79*, 132. [\[CrossRef\]](#)
95. Mažylytė, R.; Kaziūnienė, J.; Orola, L.; Valkovska, V.; Lastauskienė, E.; Gegeckas, A. Phosphate Solubilizing Microorganism *Bacillus* Sp. MVY-004 and Its Significance for Biomineral Fertilizers' Development in Agrobiotechnology. *Biology* **2022**, *11*, 254. [\[CrossRef\]](#)
96. Nascimento, E.; Klepa, M.S.; Olchanheski, L.R.; de Alencar Almeida, M.; Chicora, K.; Prestes, L.; Rodrigues, E.P.; Hungria, M.; da Silva Batista, J.S. Phenotypic and Genomic Characterization of Phosphate-Solubilizing Rhizobia Isolated from Native *Mimosa* and *Desmodium* in Brazil. *Braz. J. Microbiol.* **2024**, *55*, 3321–3334. [\[CrossRef\]](#)
97. Solanki, A.C.; Gurjar, N.S.; Sharma, S. Co-Inoculation of Non-Symbiotic Bacteria *Bacillus* and *Paraburkholderia* Can Improve the Soybean Yield, Nutrient Uptake, and Soil Parameters. *Mol. Biotechnol.* **2025**, *67*, 3041–3053. [\[CrossRef\]](#)
98. Ben Zineb, A.; Trabelsi, D.; Ayachi, I.; Barhoumi, F.; Aroca, R.; Mhamdi, R. Inoculation with Elite Strains of Phosphate-Solubilizing Bacteria Enhances the Effectiveness of Fertilization with Rock Phosphates. *Geomicrobiol. J.* **2020**, *37*, 22–30. [\[CrossRef\]](#)
99. Kumar, C.; Wagh, J.; Archana, G.; Naresh Kumar, G. Sucrose Dependent Mineral Phosphate Solubilization in *Enterobacter asburiae* PSI3 by Heterologous Overexpression of Periplasmic Invertases. *World J. Microbiol. Biotechnol.* **2016**, *32*, 194. [\[CrossRef\]](#)
100. Emami-Karvani, Z.; Chitsaz-Esfahani, Z. Phosphorus Solubilization: Mechanisms, Recent Advancement and Future Challenge. In *Soil Microbiomes for Sustainable Agriculture: Functional Annotation*; Yadav, A.N., Ed.; Springer International Publishing: Cham, Switzerland, 2021; pp. 85–131, ISBN 978-3-030-73507-4.
101. Timofeeva, A.M.; Galyamova, M.R.; Sedykh, S.E. Plant Growth-Promoting Soil Bacteria: Nitrogen Fixation, Phosphate Solubilization, Siderophore Production, and Other Biological Activities. *Plants* **2023**, *12*, 4074. [\[CrossRef\]](#) [\[PubMed\]](#)

102. Mandić, V.; Krnjaja, V.; Simić, A.; Petričević, M.; Gogić, M.; Brankov, M.; Stanojković, A. Effect of pH on Germination and Seedling Growth of Maize. *Biotechnol. Anim. Husb.* **2023**, *39*, 195–203. [CrossRef]
103. Liu, D.; Ma, Y.; Rui, M.; Lv, X.; Chen, R.; Chen, X.; Wang, Y. Is High pH the Key Factor of Alkali Stress on Plant Growth and Physiology? A Case Study with Wheat (*Triticum aestivum* L.) Seedlings. *Agronomy* **2022**, *12*, 1820. [CrossRef]
104. Yang, S.; Xu, Y.; Tang, Z.; Jin, S.; Yang, S. The Impact of Alkaline Stress on Plant Growth and Its Alkaline Resistance Mechanisms. *Int. J. Mol. Sci.* **2024**, *25*, 13719. [CrossRef]
105. Li, J.; Yang, Y. How Do Plants Maintain pH and Ion Homeostasis under Saline-Alkali Stress? *Front. Plant Sci.* **2023**, *14*, 1217193. [CrossRef]
106. Taiz, L.; Zeiger, E.; Møller, I.M.; Murphy, A.S. *Plant Physiology and Development*; Sinauer Associates, Incorporated, Publishers: Sunderland, MA, USA, 2015; ISBN 978-1-60535-353-1.
107. Zhu, Y.; Xing, Y.; Li, Y.; Jia, J.; Ying, Y.; Shi, W. The Role of Phosphate-Solubilizing Microbial Interactions in Phosphorus Activation and Utilization in Plant–Soil Systems: A Review. *Plants* **2024**, *13*, 2686. [CrossRef]
108. Azizi, A.; Bagnazari, M.; Mohammadi, M. Seaweed and Phosphate-Solubilizing Bacteria Biofertilizers Ameliorate Physiochemical Traits and Essential Oil Content of *Calendula officinalis* L. under Drought Stress. *Sci. Hortic.* **2024**, *328*, 112653. [CrossRef]
109. Shi, Z.; Pan, F.; Kong, X.; Lang, J.; Ye, M.; Wu, Q.; Wang, G.; Han, L.; Zhou, N. Effects of Inoculation with Phosphate Solubilizing Bacteria on the Physiology, Biochemistry, and Expression of Genes Related to the Protective Enzyme System of *Fritillaria taipaiensis* P. Y. Li. *Phyton Int. J. Exp. Bot.* **2024**, *93*, 247–260. [CrossRef]
110. Fangué-Yapseu, G.Y.; Tola, A.J.; Missihoun, T.D. Proteome-Wide Analysis of Hydrogen Peroxide-Induced Protein Carbonylation in *Arabidopsis thaliana*. *Front. Plant Sci.* **2022**, *13*, 1049681. [CrossRef]
111. Lastochkina, O.V.; Garipova, S.R.; Pusenkova, L.I.; Garshina, D.Y.; Baymiev, A.K.; Koryakov, I.S. Effect of Endophytic Bacteria *Bacillus subtilis* on Seedling Growth and Root Lignification of *Pisum sativum* L. under Normal and Sodium Chloride Salt Conditions. *Russ. J. Plant Physiol.* **2023**, *70*, 97. [CrossRef]
112. Labudda, M. Lipid Peroxidation as a Biochemical Marker for Oxidative Stress during Drought. In *An Effective Tool for Plant Breeding*; E-Wydaw: Poznan, Poland, 2013; pp. 1–12. Available online: <http://www.e-wydawnictwo.eu/document/documentpreview/3342> (accessed on 8 August 2025).
113. Lopes, T.; Costa, P.; Cardoso, P.; e Silva, J.A.; Figueira, E. Inducing Drought Resilience in Maize Through Encapsulated Bacteria: Physiological and Biochemical Adaptations. *Plants* **2025**, *14*, 812. [CrossRef] [PubMed]
114. Lopes, T.; Cruz, C.; Cardoso, P.; Pinto, R.; Marques, P.A.A.P.; Figueira, E. A Multifactorial Approach to Untangle Graphene Oxide (GO) Nanosheets Effects on Plants: Plant Growth-Promoting Bacteria Inoculation, Bacterial Survival, and Drought. *Nanomaterials* **2021**, *11*, 771. [CrossRef] [PubMed]
115. Thilakarathne, A.S.; Liu, F.; Zou, Z. Plant Signaling Hormones and Transcription Factors: Key Regulators of Plant Responses to Growth, Development, and Stress. *Plants* **2025**, *14*, 1070. [CrossRef]
116. Alberts, B.; Johnson, A.; Lewis, J.; Raff, M.; Roberts, K.; Walter, P. Signaling in Plants. In *Molecular Biology of the Cell*, 4th ed.; Garland Science: New York, NY, USA, 2002.
117. Das, S.; Shil, S.; Rime, J.; Alice, A.K.; Yumkhaibam, T.; Mounika, V.; Singh, A.P.; Kundu, M.; Lalmangaihzuai, H.; Hazarika, T.K.; et al. Phytohormonal Signaling in Plant Resilience: Advances and Strategies for Enhancing Abiotic Stress Tolerance. *Plant Growth Regul.* **2025**, *105*, 329–360. [CrossRef]
118. Pinto, R.; Cardoso, P.; Carneiro, B.; Pinto, G.; Bedia, C.; Figueira, E. Maize Crops Under Rising Temperatures: Bacterial Influence on Biochemical and Lipidomic Changes Induced by Heat. *Plants* **2025**, *14*, 2593. [CrossRef]
119. Jiang, T.; He, Y.; Wu, Z.; Cui, Y.; Wang, X.; Huang, H.; Fan, Y.; Han, M.; Wang, J.; Wang, S.; et al. Enhancing Stimulation of Cyaniding, GhLDOX3 Activates Reactive Oxygen Species to Regulate Tolerance of Alkalinity Negatively in Cotton. *Ecotoxicol. Environ. Saf.* **2023**, *267*, 115655. [CrossRef]
120. Li, Y. Effects of Different Metal Ions on the Stability of Anthocyanins as Indicators. *IOP Conf. Ser. Earth Environ. Sci.* **2019**, *300*, 52015. [CrossRef]
121. Landi, M.; Tattini, M.; Gould, K.S. Multiple Functional Roles of Anthocyanins in Plant-Environment Interactions. *Environ. Exp. Bot.* **2015**, *119*, 4–17. [CrossRef]

Disclaimer/Publisher’s Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.