#### **ORIGINAL ARTICLE**

# Plant growth promotion of crops using phosphate solubilizing bacterial strains derived from insects

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#### Abstract

The aim of this study was to investigate insect derived bacteria for the ability to dissolve insoluble soil phosphate to release soluble phosphorus compounds, available to plants. Bacterial isolates were obtained from Diabrotica virgifera, Hermetia illucens, Oulema melanopus, and Ostrinia nubilalis. An in vitro evaluation of phosphate solubilization ability on Pikovskaya's medium was done and the phosphate solubilizing index (PSI) was calculated for each isolate. Bacteria were tested in a greenhouse experiment on seeds of oats, wheat, triticale, barley and soybeans. After incubation, the weight and length of their aerial plant parts were measured. The highest increase in the weight of aerial parts was recorded for oats after using strain Om046 for inoculation (88.98%), then, wheat (Dv097, 31.43%), soybean (strain 96, 53.79%), and triticale (bacterial consortium, 36.9%). Bacteria used were identified as Lactococcus lactis (strains Om030 and Om046), Acinetobacter sp. (Dv123), Lactococcus garvieae (Dv097) and Rothia kristinae (strains 90 and 96). We showed that a successful application of insect derived bacteria for phosphate solubilization in soil, to promote plant growth, is possible. Innovative agriculture requires constant improvements in increasing crop growth. Thus, new sources of bacterial strains effectively promoting plant growth, are needed. We described a new source of plant growth-promoting bacteria that can be used in agriculture.

Keywords: beneficial bacteria, insect derived bacteria, phosphorus solubilization

## Introduction

Phosphorus, along with nitrogen, is the most important nutrient for plants and is essential for plant growth (Rodriguez *et al.* 1999; Alam *et al.* 2002; Chen *et al.* 2006; Hameeda *et al.* 2008; Lambers 2022). It influences a variety of key metabolic processes in plants, including cell division and development, energy transport, signal transmission, and macromolecular biosynthesis. It is also essential for photosynthesis, respiration (Khan *et al.* 2014), formation of flowers, seeds, stalks, and stem strength (Khan *et al.* 2009). Phosphorus mitigates cold stress and strengthens the disease resistance of some plants. A phosphorus deficiency

significantly decreases a plant's viability, making it more susceptible to unfavorable conditions (Karpagam and Nagalakshmi 2014). Phosphorus is crucial for plant growth and productivity, as it is involved in various physiological, biochemical, and metabolomic processes such as photosynthesis, respiration, energy generation, and nucleic acid synthesis (Chen *et al.* 2023). It plays a crucial role in plant growth by facilitating energy transfer, photosynthesis, nutrient movement, and genetic transfer (Baroowa *et al.* 2022). As a macronutrient, phosphorus is essential for plant growth and plays a crucial role in improving the productive performance

of crops (Silva et al. 2023). Its crucial role exhibits itself in promoting the growth of plant roots, by aiding in the utilization of sugar and starch, supporting photosynthesis, and facilitating nucleus formation and cell division (Gurmu 2023). Understanding phosphorus uptake and utilization by plants is crucial for determining final crop yield. A holistic understanding of phosphorus dynamics from soil to plant is necessary for optimizing phosphorus management and improving phosphorus-use efficiency. This includes reducing the consumption of chemical phosphorus fertilizer, maximizing the exploitation of the biological potential of root/rhizosphere processes for efficient mobilization and acquisition of soil phosphorus by plants, as well as recycling phosphorus from manure and waste (Shen et al. 2011)

Despite its crucial role, phosphorus availability is a major limiting factor in agriculture. To provide plants with an optimal amount of phosphorus, mineral fertilizers are commonly used. However, it is estimated that only about 20% of the phosphorus fertilizer used for plant cultivation is accessible to plants (Gupta *et al.* 2014; Roberts and Johnston 2015; Bautista-Cruz *et al.* 2019). This inefficiency necessitates finding environmentally friendly and economically beneficial alternatives.

The problem of phosphate solubility is complex. Both inorganic and organic forms of phosphorus are assimilable by plants however, the organic form is much less assimilable. Furthermore, if linked to humic acids (humo-phosphates), phosphorus is much more assimilable, while in the soil it tends to bind with Ca, Fe, Mg and other elements, becoming insoluble.

To provide plants with phosphorus, in an amount optimal for their growth, mineral fertilizers are commonly used. However, it is estimated that only about 20% of the phosphorus fertilizer used for plant cultivation is accessible to plants (Gupta *et al.* 2014; Roberts and Johnston 2015; Bautista-Cruz *et al.* 2019). Moreover, phosphorus occurs in soil in both organic and inorganic forms, of which the organic form is much less assimilable by plants and constitutes the majority of phosphorus reservoirs (Zaidi *et al.* 2009). As a result, phosphorus deficiency in plants is a frequent phenomenon (Karpagam and Nagalakshmi 2014). Therefore environmentally friendly and economically beneficial alternatives for synthetic phosphorus are desired.

Organic phosphorus is derived from the breakdown of plant and animal residues. It is then converted into inorganic forms of phosphorus, which are easily assimilable by plants. A significant portion of organic phosphorus is mineralized in soil due to rhizosphere--associated bacteria that use a group of enzymes responsible for phosphorus hydrolysis – phosphatases (Rodríguez and Fraga 1999; Gupta *et al.* 2014). They catalyze the process of transforming organic phosphorus into inorganic forms (HPO<sub>4</sub>. and  $H_2PO_4$ .), which are absorbed through the roots (He *et al.* 2004; Hussain *et al.* 2013).

Different phosphatase activities related to phosphate solubilizing bacteria (PSB) have been observed in various types of soil (Tarafdar and Jungk 1987; Ponmurugan and Gopi 2006; Jorquera et al. 2008; Teng et al. 2019; Bautista-Cruz et al. 2019). Phosphatase activity is higher in the rhizosphere, and the main source of this activity is of microbial origin (Rodríguez and Fraga 1999; Gupta et al. 2014). The highest abundance of all soil bacteria, including PSB, is found in the rhizosphere, the sphere adherent to plant roots, where biochemical and physicochemical conditions are determined by the plant. Chemical substances secreted by plant roots, mainly sugars and organic acids, determine the selection of bacterial species utilizing the root exudates as their carbon source (Oteino et al. 2015). The concentration of bacteria in the rhizosphere is up to a thousand times higher than in the soil not affected by plant root exudations (Lugtenberg and Kamilova 2009). Also, the activity of rhizosphere bacteria is higher than in other parts of the soil (Jorquera et al. 2008). Plant growth promoting bacteria, including PSB, colonize plant organs. Moreover, roots, stems, leaves, flowers, fruits or seeds are characterized by distinct bacterial communities, which may be the result of chemical preferences or the ability of bacterial strains to colonize different parts of plants (Compant et al. 2010). To facilitate plant growth, bacteria must effectively inhabit various plant-related environments such as the rhizosphere, epidermis, and internal tissues, engaging with the host plant through biochemical and physiological traits like motility, attachment, degradation of plant polymers, and evasion of plant defenses (Afzal et al. 2019). Key activities like motility and polysaccharide production are vital for the successful colonization of the rhizosphere by endophytic bacteria such as Alcaligenes faecalis and Azospirillum brasilense (Santoyo et al. 2016). Additionally, functions like dissolving inorganic phosphates and synthesizing protease, lipase, and chitinase enzymes support rhizosphere colonization (Krawczyk et al. 2016). Phosphate dissolution, for example, is a trait that enhances tomato plant growth, as demonstrated by the utilization of phosphate-dissolving bacteria like Paenibacillus polymyxa and Bacillus megaterium var. phosphaticum, which yielded results comparable to those of costly fertilizers(Abou El-Yazeid and Abou-Aly 2011).

Plant growth-promoting bacteria (PGPB) are primarily isolated from the rhizosphere, yet they also exist in other environments indirectly linked to plants, such as the rhizosphere or plant surface, where they can be transmitted between plants by insects (Przemieniecki *et al.* 2020) or in the insect's body (Krawczyk *et al.* 2022). Relationships between bacteria and insects

encompass both commensalism and mutualism (Araujo 2004), with the insect gut providing an optimal setting for bacterial conjugation and gene transfer (Dillon and Dillon 2004). Various insect gut bacteria are closely associated with the rhizosphere, phyllosphere, and soil bacteria (Indiragandhi et al. 2007), and certain insect gut bacteria, like those isolated from Plutella xylostella larvae, exhibit plant growth-promoting characteristics such as nitrogen fixation and the production of salicylic and indole-3-acetic acids (Indiragandhi et al. 2008). The intestines of insects could serve as a potential habitat for the discovery of plant growthpromoting (PGP) bacteria, which have the potential to enhance plant growth and mineral uptake. For instance, bacteria were extracted from the intestines of Plutella xylostella larvae, yielding three strains: Acinetobacter sp., Pseudomonas sp., and Serratia sp. These bacteria exhibited responses to phosphorus and zinc depletion and were found to influence various solubilization reactions, such as chelation or the conversion of insoluble to soluble phosphorus, which could impact soybean growth in phosphorus-deficient soil (Indiragandhi et al. 2008).

Understanding the interactions between insect and plant microbiota is emerging, with implications for modifying plant defenses against foliar insects, shaping plant-associated microbial communities, and influencing multi-trophic interactions (Gadhave and Holloway 2015). The role of rhizobacteria in controlling pest insects in agriculture has also been delineated (Erica 2015). The use of certain strains of PSB may contribute to the reduction of the amount of mineral phosphorous fertilizers used in crops. By facilitating plants with phosphorus uptake, the yield of crops such as oats, barley, soybeans, mustard, or corn can increase up to 20%. Studies on the influence of PSB on cereals and other economically important plants have shown that these microorganisms are capable of improving plant condition (Egamberdiyeva et al. 1996; Afzal and Bano 2008; Hameeda et al. 2008; Hussain et al. 2013; Schoebitz et al. 2013; Bakhshandeh et al. 2015; Suleman et al. 2018; You et al. 2020; Mei et al. 2021; Song et al. 2022a, b; Ait-Ouakrim et al. 2023a, b). PSB are able to solubilize phosphorus from its insoluble forms (Chen et al. 2006; Zaidi et al. 2009; Sharma et al. 2011; Kirui et al. 2022). The most frequently described bacterial taxa exhibiting the phosphate solubilization ability are representatives of the following genera: Achromobacter, Agrobacterium, Arthrobacter, Bacillus, Burkholderia, Enterobacter, Erwinia, Flavobacterium, Micrococcus, Pantoea, Pseudomonas, Ralstonia, Rhizobium, Rhodococcus and Serratia (Rodríguez and Fraga 1999; Chen et al. 2006; Afzal and Bano 2008; Hameeda et al. 2008; Karpagam and Nagalakshmi 2014; Oteino et al. 2015; Bautista-Cruz et al. 2019). Bacteria solubilize

phosphorus by releasing low molecular weight organic acids, where the hydroxyl and carboxyl groups chelate the cations attached to the phosphate, transforming it into soluble forms (Bhattacharya 2019; Vazquez *et al.* 2000; Alam *et al.* 2002).

Considering the arguments above, plant growth--promoting bacteria, including PSB, can serve as an alternative to mineral fertilizers, which are generally harmful to the environment and are overused (Savci 2012). PSB are considered promising bio-fertilizers that can increase the availability of phosphorus to plants (Afzal and Bano 2008; Zaidi et al. 2009; Tang et al. 2018). Therefore, new sources of PSB are desired. We turned our attention to insects, an integral part of plant-bacteria-insect relationships, which are extensively studied (Maheshwari 2013; Krawczyk et al. 2021; Wielkopolan et al. 2021). Insects constitute the most diverse and numerous group of animals inhabiting a wide variety of ecological niches. Their vast diversity enables them, e.g., to metabolize nutrients from various sources. It is known that insect intestines harbor large numbers of bacteria, which contribute to the remarkable adaptability of insects supported by their associated microorganisms (Feldhaar 2011). PGP bacteria have been successfully isolated from cornworm (Diabrotica virgifera) (Prischmann et al. 2008), moth (Spodoptera litura) (Rajashekhar and Kalia 2017), or termite (Microcerotermes diversus) (Pourramezan et al. 2012). Keeping in mind the above arguments we concluded that it is highly probable that multi-host insect pests of plants like D. virgifera, O. melanopus and O. nubilalis harbor PSB bacteria, especially since the diet of insects often does not provide them with enough nutrients. However, the presence of symbiotic microorganisms can replenish these deficiencies (Feldhaar 2011). Similarly, H. illucens, as an insect which breeds mainly on plant debris might also contain phosphate solubilizing bacteria, like other tested insects whose diet is based mainly on plants which do not always meet nutrient needs. Thus, they must have their own mechanism to metabolize the organic phosphorous compounds, which might be of bacterial origin. To assess the potential of bacterial strains for phosphate metabolism we used Pikovskaya medium to determine the ability of bacteria to solubilize phosphates (Sanchez-Gonzalez et al. 2023) and we calculated the PSI to assess the potency of phosphate-solubilizing bacteria (Ait-Ouakrim et al. 2023a).

Given the limitations of synthetic fertilizers and the potential of PSB, new sources of these beneficial bacteria are desired. Insects, with their diverse microbiota, present a promising yet underexplored source of PSB. Insect gut bacteria have shown plant growthpromoting traits, such as nitrogen fixation and phosphate solubilization (Indiragandhi *et al.* 2008). This study aimed to explore the potential of insect-derived bacteria as a new source of PSB and their implications for agriculture.

Considering the above, insect derived bacteria may potentially be new sources of PSB. The objectives of this study were:

(1) To test a wide range of bacteria isolated from the following insects: the western corn rootworm (*Diabrotica virgifera* family Chrysomelidae), cereal leaf beetle (*Oulema melanopus* family Chrysomelidae), European corn borer (*Ostrinia nubilalis* family Pyralidae) and black soldier fly (*Hermetia illucens* family Stratiomyidae), for the ability to solubilize phosphorus on Pikovskaya medium and to determine their PSI;

(2) To demonstrate the plant growth-promoting effect of insect-derived PSB bacteria on economically important plants – including oat (Avena sativa L.), wheat (Triticum aestivum L.), triticale (×Triticosecale), soybean (Glycine max L.) and barley (Hordeum vulgare L.) under greenhouse conditions;

(3) To assess the phosphatase activity of rhizosphere soil inoculated with the tested PSB, to verify if the plant growth promoting effect is a consequence of the PSB activity.

By addressing these objectives, this study aimed to highlight the potential of insect-derived PSB as a sustainable alternative to chemical fertilizers, contributing to enhanced agricultural productivity and environmental sustainability. To our knowledge this is the first report of the application of insect-derived PSB to enhance growth of crops.

### **Materials and Methods**

#### **Insect specimens**

The insect samples used in the experiment were specimens of the western corn rootworm (Diabrotica virgifera family Chrysomelidae), cereal leaf beetle (Oulema melanopus family Chrysomelidae), European corn borer (Ostrinia nubilalis family Pyralidae) and black solider fly (Hermetia illucens family Stratiomyidae). Imago specimens of D. virgifera, O. melanopus, and O. nubilalis were captured in corn fields in southeastern Poland. Larval specimens of H. illucens were sourced from in-house cultivation and fed on corn debris. All insect specimens were supplied by the Department of Entomology and Animal Agrophages of the Institute of Plant Protection - National Research Institute, Poznań, Poland. Each of the insect samples consisted of five individuals of a given species. In the case of D. virgifera, O. melanopus and O. nubilalis the

imago were used, while for *H. illucens*, the larval stage was used, as this stage is foraging.

#### **Bacterial strains**

Bacterial isolates were obtained from the imago or the larvae of tested insects. Insect individuals, regardless of the developmental stage, were euthanized and subjected to surface sterilization by placing them in 70% ethanol (3 min), followed by triple washing with sterile distilled water (SDW) to remove the ethanol residues. To confirm the effectiveness of the sterilization process, a 100 µl aliquot from the final wash was plated on tryptic soy agar medium (TSA, Sigma Aldrich Co. Ltd.) and incubated to assess bacterial growth. Next, 20 insect individuals per sample were placed in a mortar and ground with the addition of 5 ml of sterile physiological saline (0.9% NaCl). The resulting homogenous suspension was diluted in a decimal series and the aliquots of 100 µl were taken from the dilutions of 10<sup>-4</sup> to 10<sup>-7</sup> cfu ml<sup>-1</sup>, plated on tryptic soy agar medium (TSA, Sigma Aldrich Co. ltd.) spread with a glass rod, and incubated for 72 hours on TSA medium at 27°C. After incubation, the grown colonies were submitted to a series of purification streaks until a pure culture of each grown morphotype was obtained. The purity of each tested colony was verified on the basis of colony morphology using Gram staining under a light microscope.

# Assessing bacterial ability to solubilize phosphates and solubilizing index

The ability of bacteria to solubilize phosphorus from its insoluble forms was tested using Pikovskaya medium (glucose 10 g, yeast extract 0.5 g, ammonium sulphate  $(NH_4)_2SO_4 0.5$  g, magnesium sulphate MgSO<sub>4</sub> × 7H<sub>2</sub>O 0.1 g, calcium phosphate  $Ca_3(PO_4)_2$  5 g, sodium chloride NaCl 0.2 g, potassium chloride KCl 0.2 g, manganese sulphate  $MnSO_4 \times H_2O$  0.002 g, iron sulphate  $FeSO_4 \times 7H_2O 0.002$  g, 15 g agar; pH 7.0) (Sharma *et al.* 2011). A 24-hour, pure culture of each insect derived isolate was spot inoculated on Pikovskaya medium in eight replicates. After 7 days of incubation at 27°C, the appearance of a halo zone around the grown bacterial colony was recorded as a positive result. The size of the halo zones was measured, along with the diameter of bacterial colony. Based on the obtained results, for each isolate, the value of the PSI was calculated using the formula presented below, where z is a diameter of the halo, c is a diameter of the bacterial colony (Alam et al. 2002). The average of eight repetitions was calculated:

$$PSI = \frac{c+z}{c}$$

Twenty isolates with the highest PSI value were selected for further tests including growth rate and the ability to maintain phosphate solubilization after glycerol preservation at -80°C, as indicators of potential bacterial usefulness in practice. The growth rate of 15 chosen isolates was measured after 24 h of incubation on TSA medium at 25°C, using visual assessment with a three grade scale (good, average, poor) in comparison to the fast-growing *Pantoea agglomerans* strain, commonly occurring in soil, water and plants. The ability of phosphate solubilization after glycerol preservation at -80°C was measured the same way with PVK medium, as described previously. Based on these results the isolates were chosen for the greenhouse experiment.

# Assessment of the influence of phosphate solubilizing bacteria on plant growth

#### **Plant inoculation**

The greenhouse experiment was designed to assess the influence of the six selected bacterial isolates on the growth of the following plants: wheat (*Triticum aesti-vum* L.), triticale (×*Triticosecale*), oats (*Avena sativa* L.), barley (*Hordeum vulgare* L.) and soy (*Glycine max* L.). The soil used in the research came from agricultural wasteland, belonging to a fawn soil, constituting 80% of the soil in Poland (Ochric humus level. Typical sequence of genetic levels in the profile: O-A-Et-Bt-C) (Kabała *et al.* 2019).

Wheat, triticale, oats, barley and soy seeds were surface sterilized by soaking in 10% sodium hypochlorite solution for 10 minutes. Then the seeds were rinsed three times in sterile distilled water. Surface sterilized seeds were placed in suspensions of 24-hour bacterial cultures, for each isolate individually and for the consortium comprising the six selected isolates. The concentration of each suspension was adjusted to 10<sup>7</sup> cfu ml<sup>-1</sup>. After soaking in bacterial suspension, the seeds were allowed to dry. Five dried seeds were sown per pot containing agricultural wasteland soil.

#### Greenhouse experimental design

Isolates Om030, Om046 and Dv097 were tested on oats, wheat and triticale plants, isolates 90, 96 and Dv123 were tested on soybean and barley plants. Three treatments were analyzed: each isolate separately, consortium of all tested isolates and control (seeds treated with sterile distilled water). For measurements, 10 plants were taken randomly from each combination. Pots were placed in a greenhouse cabin (conditions: temp. 20–23°C day, 16–18°C night, humidity approx. 60–65%, lighting 16/8). No fertilizers were applied during plant development. Three replications (3 pots with 5 plants each; pot diameter – 25.5 cm, height – 20 cm, base width – 19.8 cm, capacity 7.5 l) were used for each variable tested: single bacterial isolate, consortium and control (seeds placed in sterile distilled water, without the addition of bacteria). After the plants had grown (oats BBCH-scale 22, wheat BBCH-scale 22, triticale BBCH-scale 61, barley BBCH-scale 71, soy BBCH--scale 70), growth (leaf length) was measured and the above-ground parts were weighed. The root length was not measured since in cereals it has no economic value.

#### Bacterial phosphatase activity in the rhizosphere soil

One gram of rhizosphere soil was taken from each pot and placed in falcon tubes, 5 cm<sup>3</sup> of Modified Universal Buffer (MUB) together with p-nitrophenylphosphate were added, and then incubated for 1 hour at 37°C. After incubation, the reaction was stopped by adding 1 cm<sup>3</sup> of 0.5 M calcium chloride (CaCl<sub>2</sub>) and 4 cm<sup>3</sup> of 0.5 M NaOH (Bielinska 2005; Tabatabai and Bremner 1969). Two milliliters of the supernatant of each sample were centrifuged (10 000 g × 2 min.). Next, 100 µl of supernatant was measured with a spectrophotometer at 400 nm. Measurements were made in triplicate, and results were given as an arithmetic mean of three repetitions (Table S1).

#### **Determination of phosphatase activity**

Phosphatase activity, expressed as mg of released p-nitrophenol per 1 kg of soil for 1 hour, was calculated based on the standard curve, expressing the relationship between a measurement reading and the corresponding measured quantity value. The standard curve was made by preparing dilutions of the solution containing, respectively: 0, 1, 2, 3, 4 and 5 mg of p-nitrophenol in 5 cm<sup>3</sup> of water, and then proceeded as with soil samples after incubation (Table S2, Fig. S1).

#### **Statistical analysis**

The variables in each group were described by the arithmetic mean  $\pm$  standard deviation. The normality of the distribution was tested with the Shapiro-Wilk test. The groups were compared using ANOVA for independent variables and Dunnett's multiple comparison test. Data distribution significantly different from the normal distribution were compared using the Kruskal-Wallis test and Dunn's multiple comparison test. The significance level was 0.05. The calculations were carried out in the Statistica 12.0 program.

#### **Bacterial identification**

The six isolates with the highest values of the PSI were subjected to biochemical and molecular identification.

The biochemical identification involved the use of the BIOLOG® Gen III System (database v. 2.8) (BIOLOG®, Hayward, USA) according to the manufacturer's instructions. Molecular identification was based on the analysis of partial sequences of the 16S rRNA gene. The bacterial isolates were grown on tryptic soy agar (TSA) medium (Sigma Aldrich, Saint Louis, Missouri, USA) for 24 hours. After incubation single colonies were picked and resuspended in 100 µl of sterile distilled water. The bacterial solution was incubated at 96°C for 10 minutes, then cooled and centrifuged (10 000 g  $\times$  10 min.). One microliter of the supernatant was used as the template in PCR reaction preformed using GoTaq® Green Master Mix (Sigma Aldrich, Saint Louis, Missouri, USA) and a pair of primers 16SA1 (5'-AGAGTTTGATCMTGGCTCAG-3') and 16SB1 (5'-TACGGYTACCTTGTTACGACTT-3'). The expected product size was ~1500bp. (Kikuchi et al. 2002; Matsuura et al. 2014) (Table 2). The PCR reaction profile was as follows:  $95^{\circ}C - 2 \text{ min.}$ ,  $32 \times (94^{\circ}C - 45 \text{ sec.})$ , 62°C - 45 sec., 72°C - 1 min. 30 sec.), 72°C - 5 min. Obtained nucleotide sequences were aligned using BioEdit software (v7.2) to obtain consensus sequences. Each consensus sequence was made from two sequencing reads. Next, the consensus sequences were identified using BLAST (https://blast.ncbi.nlm. nih.gov), with the flagged option "Sequences from type material", to retrieve the match with type strains only, for a more rigorous taxonomic assignment. In addition, the sequences were checked using RDP Classifier (http://rdp.cme.msu.edu/classifier/classifier. jsp), which assigns the taxonomy through the naive Bayesian approach (Wang et al. 2007). The analyzed

#### Table 1. Bacterial strains identification

sequences were deposited in the GenBank database (https://www.ncbi.nlm.nih.gov).

### Results

#### **Bacterial strains identification**

Results of identification are given in Table 1. In the case of discrepancies of the molecular and biochemical identifications, the final identification was based on the molecular data, due to a significantly larger database of NCBI than the BIOLOG Gen III system. The identification of strains obtained with using RDP Classifier (http://rdp.cme.msu.edu/classifier/classifier.jsp), which assigns the taxonomy through the naive Bayesian approach, gave the following results with the confidence threshold of 95%: Strain Dv123 – *Acinetobacter* sp., strain Dv097 – *Lactococcus* sp., strain Om030 – *Lactococcus* sp., strain Om046 – *Lactococcus* sp., strain 90 – *Rothia* sp., strain 96 – *Rothia* sp.

# The solubilization of phosphorus on Pikovskaya medium

Out of the 171 tested strains, only 20 were not able to solubilize phosphates on Pikovskaya medium (Fig. 1). The values of PSI are presented in a supplement (Table S1).

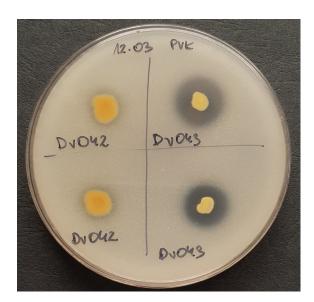
For the greenhouse experiments the bacterial isolate with the highest PSI value, fast growing and wellenduring the glycerol preservation at  $-80^{\circ}$ C, were selected and used (Table 2).

				NC	BIOLOG <sup>®</sup> results		
Isolate	isolate`s biological source	identification based on 16S rRNA sequence (~1.5 kbp)	accession number assigned by GenBank	query covery	Percen-tage of identity	accession	identification
Dv123	Diabrotica virgifera	Acinetobacter guillouiae	OP891014	100%	99.44%	NR_117626.1	Acinetobacter sp.
Dv097	Diabrotica virgifera	Lactococcus garvieae	OM536191	90%	90.73%	LC145570.1	Lactococcus garvieae
Om030	Oulema melanopus	Lactococcus lactis	OM538405	100%	97.14%	CP065737	Lactococcus sp.
Om046	Oulema melanopus	Lactococcus lactis	OM570559	99%	98.31%	NR_113960.1	Enterococcus casseliflavus
90	Oulema melanopus	Rothia kristinae	OM491326	98%	95.33%	CP065738.1	Rothia sp.
96	Oulema melanopus	Rothia kristinae	OM491517	98%	99.30%	CP065738.1	<i>Rothia</i> sp.

**Table 2.** Isolates' growth rate measured after 24 h of incubation (TSA medium. 25°C) based on visual assessment with 3 grade scale in comparison to fast growing *Pantoea agglomerans* strain; the ability of phosphate solubilization after glycerol preservation in  $-80^{\circ}$ C. Selected isolates used in greenhouse experiments are bolded

No.	lsolate	PSI value	PSI value after glycerol preservation in –80°C	Growth rate
1	Dv123	5	2.77	3*
2	Om001	5	3.29	1
3	Om031	4.75	4.2	2
4	Om030	4.66	4.5	3
5	Om046	4.66	4.3	3
6	Om038	4.44	2.54	2
7	Dv097	4.33	4.04	3
8	Om015	4.33	2.42	2
9	Om029	4.33	3.07	2
10	Dv012	4.12	3.1	2
11	Dv125	4.12	3.6	2
12	Om009	4	2.74	3
13	Om013	4	2.52	3
14	Dv117	3.9	2.5	2
15	Dv135a	3.88	2.42	2
16	Om035	3.88	2.0	2
17	Dv058	3.87	3.1	2
18	90	3.8	3.8	3
19	96	3.8	3.8	3
20	Om045	3.77	2.81	2

\*visual assessment with 3 grade scale. where 3 – good. 2 – average. 1 – poor



**Fig. 1.** Example of phosphate solubilization on Pikovskaya's medium. On the right: halo around bacterial colony of the Dv043 isolate, able to solubilize phosphorus. On the left: isolate Dv042 with no halo and with no ability to solubilize phosphorus

#### Influence of phosphate solubilizing bacteria (PSB) on plant growth

#### **Plant height**

There was no statistically significant difference in plant heights between individual cereals, the significance level was 0.05, p-value was less than the predetermined significance level. The height of individual bacteria-treated plants differed from plants not treated with bacteria. Compared to the control, the highest difference in plant growth was observed for soy plants (increase by 28.68%) after inoculation with bacterial consortium (isolates 90, 96 and Dv123) and after inoculation with isolate Dv123 (25.9%). For triticale, the highest difference was noted for the consortium (17.76%) (isolates Om030, Om046, Dv097) and for isolate Dv097 (11.54%). For oats, the highest differences were also recorded for bacterial consortium (Om030, Om046, Dv097) (increase by 7.58%) and for isolate Om030 (7.37%). For wheat, the highest differences were recorded for bacterial consortium (Om030, Om046, Dv097) (5.59%) and for Om046 (3.35%). For barley, the highest differences were recorded for isolate 90 (4.39%) (Table 3).

#### Weight of the aerial parts

For all tested plants, except for barley and soy, the difference in the weight of the aerial parts was statistically significant when inoculated with selected bacterial strains. Compared to the control group, the highest differences were observed for oats after inoculation with Om046 (increase by 88.98%) and Om030 (73.6%). For soy, the highest differences were recorded for isolate 96 (53.79%) and for bacterial consortium (includes 90, 96 and Dv123) (18.99%). For triticale, the highest differences were recorded for bacterial consortium (Om030, Om046, Dv097) (36.9%) and for isolate Om46 (16.34%). For wheat, the highest differences were recorded for isolate Dv097 (31.43%) and for bacterial consortium (Om030, Om046, Dv097) (27.66%). For barley, none of the isolates included in the bacterial consortium had positive effects on plants (Table 4).

Based on the conducted statistical analyses, there were no statistically significant differences in plant height for all individual cereals. Wheat, triticale and oats inoculated with individual isolates did not show higher growth than the control group. For each cereal, the weight of above-ground parts of plants differed statistically significantly between the analyzed groups. Comparing the weight of the aerial parts of wheat plants between individual isolates and the control group, we obtained significant differences for the Dv097 isolate and the consortium. The above-ground parts of the wheat plants in isolate Dv097 and the consortium were statistically significantly heavier than in

	Variable	Om030	Dv097	Om046	Consortium	Control	p-value* for all individual variants
	stalk length [cm]	49.8 ± 3.8	$48.2 \pm 2.9$	50.8 ± 1.9	51.9 ± 2.5	$49.2 \pm 3.5$	0.0746
Wheat	% increase compared with control	1.32%	-1.93%	3.35%	5.59%	-	-
	stalk length [cm]	41.6 ± 3.5	$43 \pm 4.4$	41.1 ± 4.9	45.4 ± 4.1	$38.7\pm8.4$	0.0783
Triticale	% increase compared with control	7.91%	11.54%	6.61%	17.76%	-	-
	stalk length [cm]	$52.4 \pm 4.9$	50.8 ± 5.9	50.8 ± 4.8	52.5 ± 4.8	$48.8 \pm 5.5$	0.506
Oats	% increase compared with control	7.37%	4.09%	4.09%	7.58%	49.2 ± 3.5 - 38.7 ± 8.4 -	-
	Variable	90	96	Dv123	Consortium		<i>p</i> -value
	stalk length [cm]	29.9 ± 1.98	34.55 ± 5.728	38.4 ± 5.515	39.25 ± 8.839	30.5 ± 0.707	0.1131
Soy	% increase compared with control	-1.96%	13.27%	25.9%	28.68%	-	_
	stalk length [cm]	73.6 ± 0.566	70.3 ± 1.697	68.05 ± 0.7	68.308 ± 14.869	70.05 ± 9.829	0.5035
Barley	% increase compared with control	4.39%	0.35%	-2.85%	-2.49%	-	_

**Table 3.** Influence of phosphate solubilizing bacteria on plant growth and condition – stalk length. Averages of ten measurement repetitions are presented. The highest values are bolded

\*p-value – the significance level was 0.05. If the p-value is less than the predetermined significance level, the null hypothesis is rejected and it is concluded there are statistically significant differences between the groups. There is no statistically significant difference in plant heights among individual cereals

**Table 4.** Influence of phosphate solubilizing bacteria on over-ground plant parts weight. Averages of ten measurement repetitions are presented. The highest values are bolded

	Variable	Om030	Dv097	Om046	Consortium	Control	<i>p</i> -value* for all individual variants
	overground plant parts weight [g]	2 ± 0.2	2.6±0.4	2.1 ± 0.4	2.5 ± 0.4	2 ± 0.4	0.001
Wheat	% increase compared with control	3.97%	31.43%	7.94%	27.66%	-	-
	<i>p</i> -value; comparison between isolate and control	0.9727	0.0024	0.7629	0.0086	-	-
	overground plant parts weight [g]	2.1 ± 0.3	1.9 ± 0.3	$2.2\pm0.3$	2.5 ± 0.4	1.8 ± 0.2	0.0002
Triticale	% increase compared with control	11.09%	4.38%	16.34%	36.9%	-	-
	<i>p</i> -value; comparison between isolate and control	0.4072	0.9426	0.1189	0.0001	-	-

	Variable	Om030	Dv097	Om046	Consortium	Control	<i>p</i> -value* for all individual variants
	overground plant parts weight [g]	$2.3\pm0.6$	$2.3 \pm 0.4$	2.5 ± 0.6	1.6 ± 0.4	1.3 ± 0.6	< 0.0001
Oats	% increase compared with control	73.6%	70.43%	<b>88.98</b> %	19.75%	-	-
	<i>p</i> -value; comparison between isolate and control	0.0005	0.0009	<0.0001	0.6294	-	-
	Variable	90	96	Dv123	Consortium	Control	<i>p</i> -value
( au	overground plant parts weight [g]	6.61 ± 0.57	10.12±0.74	$5.54 \pm 0.8$	$8.56\pm0.52$	6.58 ± 0.77	0.8395
Soy	% increase compared with control	0.45%	53.79%	-15.8%	18.99%	_	-
Parloy	overground plant parts weight [g]	$9.69\pm0.23$	$8.52\pm4.67$	9.53 ± 2.24	9.73 ± 2.55	12.07 ± 0.31	0.3317
Barley	% increase compared with control	-19.71%	-29.41%	-21.04%	-19.38%	-	-

**Table 4.** Influence of phosphate solubilizing bacteria on over-ground plant parts weight. Averages of ten measurement repetitions are presented. The highest values are bolded – continuation

\*p-value – the significance level was 0.05. If the p-value is less than the predetermined significance level, the null hypothesis is rejected and it is concluded there are statistically significant differences between the groups

the control group (p = 0.0024; p = 0.0086 respectively). Comparing the weight of the aerial parts of triticale plants between individual isolates and the control group, we obtained significant differences in the consortium. The above-ground parts of the triticale plants in the consortium were statistically significantly heavier than in the control group (p = 0.0001). Comparing the weight of the aerial parts of oat plants between individual isolates and the control group, we obtained significant differences in isolate Om030, Dv097 and Om046. The above-ground parts of oats in isolates Om030, Dv097 and Om046 were statistically significantly heavier than in the control group (p = 0.0005; p = 0.0009; p < 0.0001, respectively).

#### Phosphatase activity in rhizosphere soil

The phosphatase activity expressed in mg of released p-nitrophenol per 1 kg of soil for 1 hour and determined on the basis of the standard curve is presented in Table 5. The standard curve is available in the Supplement (Fig. S1).

Regarding the phosphatase activity in rhizosphere soil, in oats, the consortium treatment resulted in a maximum increase in phosphatase activity, which was 165% higher than in the uninoculated control. In wheat, inoculation with the Dv097 strain resulted in a maximum increase of phosphatase activity of 103% higher than the control. The effect of inoculation with the Om046 isolate in triticale plants caused the highest increase in the activity of rhizosphere phosphatase by 114% compared to the control. In soybean, the maximum increase in activity was obtained when inoculated with the bacterial consortium compared to the control by 36%, while the maximum increase of over 275% was observed in barley after inoculation with strain 90 (Table 5).

### Discussion

Plant growth promoting bacteria (PGPB) have been shown to serve as biofertilizers in sustainable agriculture (Magnusson *et al.* 2003; Pandey *et al.* 2006; Kim and Indiragandhi 2008; Hussain *et al.* 2013;). Their use has become a tangible alternative for chemical fertilizers. The vast majority of PGPB have been isolated from phyllosphere, rhizosphere, cattle manure, and soil (Kim and Indiragandhi 2008). Amongst the PGPB, phosphate solubilizing bacteria are one of the

		Oats			Wh	eat			Tritica	ale	
lsolate	average of mea- surements (DTX read- ing)	released p-nitro- phenol ap- proximate value [µg]	% increase compared with con- trol	average of mea- surements (DTX read- ing)	relea p-ni pheno proxii value	tro- ol ap- mate	% increase compared with con- trol	average of mea- surements (DTX read- ing)	releas p-nitr phenol proxim value [	o- ap- ate	% in- crease com- pared with control
Dv097	0.53222	12.5	119%	0.63404	15.	05	103%	0.56038	13.0	5	70.5%
Om030	0.55972	13.2	131.5%	0.39534	9.	1	23%	0.5393	12.2	5	60%
Om046	0.43584	10.1	77%	0.40282	9.2	25	25%	0.67486	16.3	5	114%
Consortium	0.637	15.1	165%	0.43002	10.	04	35.5%	0.4949	11.45		50%
Control	0.24728	5.7	-	0.33072	7.	4	-	0.339	7.65	5	-
						Barley					
Isolate	average of measurer (DTX readi	e p-nit nents prox	released rophenol ap- imate value [µg]	% increase pared with c		of me	average easurements 'X reading)	release p-nitroph approximate [µg]	enol	con	ncrease npared control
90	1.416		35.5	-12.3%	)	overflow		> 90		> 275%	
96	2.0517 52.5		29.5%	29.5% 1.447		1.447	37.5		1	56%	
Dv123	1.3 32.5		19.5%	19.5% 1.103		1.103	27		1	2.5%	
Consortium	2.2126 55		36%	<b>36%</b> 1.582		1.582	41		71%		
Control	1.546		40.5		- 1.001			24	24		-

**Table 5**. Spectrophotometric reading (400 nm) – measurement of phosphatase activity in rhizosphere soil inoculated with phosphate solubilizing bacteria (PSB) isolates and approximate value of released p-nitrophenol. The highest values are bolded

most important groups due to the significant role of phosphorus in plant growth and development (Alam et al. 2002). Although phosphate solubilizing bacteria have been reported in many types of soil, various phyllospheres, and sometimes even in environmentally hostile ecological niches like sub-alpine locations in the Himalayas (Pandey et al. 2006), the need for new sources of plant growth promoting bacteria remains significant. That is why we directed our attention to microbial communities isolated from insects because of the well-documented associations between insects and plants. It is known that bacteria inhabiting insects' guts affect the fitness of their hosts. The insect gut provides suitable conditions for bacterial development and gene transfer, as demonstrated through genome analysis (Dillon and Dillon 2004). Bacteria-insect relationships are complex and involve both commensalism and mutualism (Araujo 2004). Therefore, we investigated insects' guts to determine if they contain phosphate solubilizing bacteria, especially since plantfeeding insects consume large amounts of plant tissue with already assimilated phosphates that needs to be dissimilated, potentially with the aid of bacteria.

In our study, out of the 171 strains we tested, only 20 were not able to solubilize phosphate at all, confirming the common occurrence of this feature among bacteria. We used bacterial strains isolated from representatives of four distinct insects: two representatives

of the Coleoptera order, belonging to the same Chrysomelidae family - the Western corn rootworm D. virgifera and the cereal leaf beetle O. melanopus; a butterfly (Lepidoptera) belonging to the Pyralidae family - the European corn borer O. nubilalis; and black fly (Diptera) from Stratiomyidae family - H. illucens. We observed the phosphate-solubilizing effects of several bacterial genera isolated from insects. Our results are consistent with another study in which the phosphate-solubilizing effects of insect derived Pseudomonas sp. PRGB06, isolated from Plutella xylostella (Lepidoptera), were reported (Kim and Indiragandhi 2008). In our study, phosphate-solubilizing effects were observed for Acinetobacter guillouiae, Lactococcus garvieae, L. lactis and Rothia kristinae (Table 1). Tests conducted in the greenhouse demonstrated the effectiveness of bacteria isolated from insects and their ability to produce phosphatase, thereby increasing the availability of desired, plant-assimilable forms of phosphorus in the soil. There are reports of mycorrhizal and saprotrophic fungi and plant roots as sources of phosphatases in the soil (Tarafdar et al. 2001; Margalef et al. 2021). However, the only difference between the tested samples and the control samples was the presence of the tested bacterial strains. Therefore, the increased amounts of phosphatase in the tested rhizosphere soil are very likely to indicate the activity of the bacteria used in the experiment. Our research

showed that the overall growth and condition of plants were more influenced by a consortium consisting of several strains of bacteria rather than by single isolates of bacteria. The same result, which is the positive effect of inoculation with phosphate-solubilizing bacteria on plant growth, was also reported for maize plants by using soil-derived Burkholderia sp., Bacillus sp., Pseudomonas sp., and Flavobacterium sp. (Hussain et al. 2013), where a significant increase in maize height, root length, dry weight of shoots, dry weight of roots, and grain yield was observed in response to inoculation with selected rhizobacteria. This is congruent with our study, where using insect-derived bacteria, we were able to elicit the effect of plant growth promotion. Other reports on the positive effects of inoculation with PSB on plant growth were reported for multiple crops, e.g., for wheat (Sarker et al. 2014; Munir et al. 2019), cotton (Egamberdiyeva et al. 1996), strawberries (Güneş et al. 2009) or rice (Bakhshandeh et al. 2015). The PSB bacteria were also applied with arbuscular mycorrhizal fungi (Yousefi et al. 2011). However, those reports involved using bacteria of rhizosphere origin, not insect-derived bacteria, as in our study.

Plants are able to uptake only the inorganic forms of phosphorus. Importantly, a significant portion of organic phosphorus compounds is mineralized by rhizosphere-associated bacteria phosphatase enzymes (Rodríguez and Fraga 1999; Gupta et al. 2014). There are reports of different phosphatase activities observed in different types of soil (Ponmurugan and Gopi 2006; Jorquera et al. 2008; Tang et al. 2018; Bautista-Cruz et al. 2019). In all cases, the use of certain strains of PSB contributes to the reduction of the amount of mineral fertilizers used. For example, by facilitating plants with phosphorus uptake, the yield of crops, such as oats, barley, soybeans, mustard, or corn was increased by up to 20% (Gupta et al. 2014), which is consistent with our results obtained with insect-derived bacteria isolates.

It is interesting that we observed that all tested strains of H. illucens and O. nubilalis derived-bacteria showed low phosphate solubilizing activity (PSI < 3) (Table S1). None of them qualified to be used in the greenhouse test. In H. illucens, a possible explanation could be that the larvae of this insect breed primarily on various organic debris of both plant and animal origin. Such debris are often initially decomposed, which makes the presence of bacteria-donated phosphatase enzyme not essential for the insect to obtain an optimal nutrient level. However, this explanation fails in the case of O. nubilalis which feeds on crops, including maize, just like D. virgifera and O. melano*pus*, in which we reported the presence of phosphatesolubilizing bacteria. It is possible that O. nubilalis has its own endogenous phosphatase production and does not require bacteria-donated phosphatase.

We also recorded differences in the influence of phosphate solubilizing bacterial strains on aboveground plant parts weight (Table 3 and 4). The main factor that might have contributed to the varying efficacy of different bacterial strains across plant species is most probably the influence of plant root exudates. It is known that plant root exudates, such as long-chain fatty acids and amino acids, recruit beneficial bacteria like Pseudomonas, enhancing plant defense against foliar pathogens by promoting their growth and resistance capabilities (Wen et al. 2021). The exudates select beneficial soil microbes, aiding in plant-microbial communication. This phenomenon was documented under drought conditions which alters exudation, impacting microbial recruitment and ecosystem functioning, particularly in fast-growing plants (Williams and de Vries 2020). Furthermore, the plant root exudates contain specific organic acids like citric and fumaric acid, which attract and influence chemotaxis and biofilm formation of beneficial bacteria, aiding in their preferential colonization (Zhang et al. 2014). Various plant root exudates select beneficial bacteria by attracting them through specific metabolites, aiding in stress alleviation and nutrient uptake (Vives-Peris et al. 2020). Each plant individually selects and recruits bacteria and the performance of the tested bacteria itself might be preferential towards e.g., wheat, oat, barley or soy. Further studies are required on this subject to better understand insect-plant-bacteria relationships. We demonstrated that inoculation with phosphate-solubilizing bacteria had a positive effect on plant growth parameters such as shoots length and the weight of plants. This effect is universal, although its level for each plant is different, as it was observed for wheat, barley, triticale, soy and oats. Furthermore, the plants selected for inoculation - barley, oats, wheat, triticale and soybeans - are among the most economically important crops cultivated in Poland. For years, they have been of utmost importance in the sowing structure. Moreover, soybeans are gaining more and more popularity, and their cultivation in Poland is constantly expanding. This demonstrates that the plant growth-promoting features of bacteria, in this case phosphate-solubilization, are not species-specific or soil-type dependent. This makes the insect-derived bacteria a promising new source of plant growth-promoting bacteria.

In our study we confirmed the presence of the following bacteria: *Acinetobacter* sp., *Lactococcus lactis*, *L. garvieae*, and *Rothia kristinae* in the body of the tested insects. Moreover, we confirmed the ability of those bacteria to solubilize phosphate in the soil, making it more accessible to plants. Identifying those bacterial strains has a new significance and will be discussed more comprehensively.

Acinetobacter sp. has been identified as a beneficial plant growth-promoting bacterium in various studies.

Research has shown that *Acinetobacter* strain SuKIC24 exhibited significant phosphate solubilization and indole-3-acetic acid production, leading to enhanced growth in *Basilicum polystachyon* plants (Minuţ *et al.* 2023). Additionally, the application of *Acinetobacter lwoffii* A07, a rhizosphere bacterium, resulted in increased plant biomass, root structure, nutrient content, and soil enzyme activity, promoting the growth of *Pinus sylvestris* var. *mongolica* seedlings and enhancing soil microbial communities (Song *et al.* 2022b). These findings highlight the potential of *Acinetobacter* species in promoting plant growth through various mechanisms, such as nutrient solubilization and enhancing soil health, making them valuable candidates for sustainable agricultural practices (Minuţ *et al.* 2023).

Lactobacillus lactis, a type of lactic acid bacteria, has shown potential as a plant growth-promoting bacteria. Studies have highlighted the abilities of lactic acid bacteria, including Lactobacillus species, to promote plant growth through various mechanisms (Abhyankar et al. 2022; Panetto et al. 2023). These bacteria can produce plant growth hormones, enzymes, and exhibit antifungal activity, making them suitable for enhancing plant growth. Additionally, lactobacilli have been recognized for their role in soil nutrient regulation and promoting plant growth in various plant hosts. The use of non-N-fixing lactobacilli inoculants have shown positive effects on plant attributes, such as increased plant biomass and total plant nitrogen, especially in soils treated with compost (Al-Tammar and Khalifa 2022). Therefore, L. lactis holds promise as a plant growth-promoting bacteria, contributing to sustainable agriculture practices.

Lactococcus garvieae, traditionally known for its role in animal infections, has recently garnered attention for its potential as a plant-promoting bacterium. While primarily studied in the context of animal diseases like bovine mastitis (Abhyankar et al. 2022), L. garvieae has also been identified as an emerging zoonotic pathogen (Jaffar et al. 2023). Research on L. garvieae's plant-promoting capabilities is limited, with most studies focusing on its pathogenicity in animals. However, given the rise in interest in using lactic acid bacteria (LAB) for plant growth promotion (Lima et al. 2022; Lin et al. 2023), exploring the potential of L. garvieae in this area could be beneficial. Further investigations are needed to understand the mechanisms through which L. garvieae could promote plant growth and its potential applications in agriculture and horticulture.

Plant growth-promoting bacteria (PGPB) enhance soil fertility, plant growth, and productivity through various mechanisms (Cropotova *et al.* 2020; Gond *et al.* 2021; Al-Tammar and Khalifa 2022). PGPB play a crucial role in nutrient availability, phytohormone production, and stress mitigation, contributing to sustainable agriculture (de Souza *et al.* 2015). While knowledge about *Rothia kristinae* as PGPB is scant, the broader concept of PGPB aligns with the potential benefits associated with such bacteria, emphasizing their role in sustainable agriculture and food security.

To summarize, insect-derived bacterial strains have significant implications as plant growth-promoting bacteria (PGPB) in agriculture (Huazhong et al. 2023; Wang et al. 2023). These strains, particularly those capable of phosphate solubilization, offer sustainable solutions by enhancing phosphorus availability to plants, thus improving crop productivity and reducing reliance on costly phosphatic fertilizers (Hyder et al. 2023; Li et al. 2023). Challenges like high fertilizer costs and low efficiency can be addressed by utilizing these bacteria for efficient phosphorus uptake by plants (Yadav et al. 2023). Future research can focus on optimizing the use of insect-derived bacterial strains for enhanced phosphate solubilization, exploring their interactions with plants, and developing tailored microbial inoculants for specific agro-ecosystems. This approach holds promise for sustainable agricultural practices, environmental protection, and improved crop yields in the future.

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