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Function of Phosphorus-Solubilizing Bacteria in Nutrient Mobilization and Pathogen Suppression (*Trichoderma spp.*) during *Pleurotus Ostreatus* Cultivation: A Systematic Review

Udugalage Isuru Harsha Kumara[1], Gunavathy Selvarajh[1*]

[1]Department of Agriculture, School of Health and Applied Science, Lincoln University College, Selangor, Malaysia.

***Corresponding Author's E-mail**:*gunavathy@lincoln.edu.my

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Abstract
Cultivation of oyster mushroom (*Pleurotus ostreatus*) is a significant portion of the overall mushroom crop of the planet, but it has been persistently subject to contamination by *Trichoderma* and wastefulness of nutrients. This is a systematic review of the multi purpose of phosphorus-solubilizing bacteria (PSB) to act as a biocontrol agent against *Trichoderma* species and a nutrient mobilizer in oyster mushroom production systems. The critical review of the literature published since 2017 indicates that PSB, particularly the species of the genera *Pseudomonas, Bacillus,* and *Paenibacillus*, can be used with a high probability to increase the yield of mushrooms and, simultaneously, neutralize the pathogenic species of *Trichoderma* in numerous ways, e.g., antibiosis, competition, and the production of antimicrobial metabolites. The review gives a summary of available data on phosphorus solubilization processes, Efficacy of biocontrol, and various methods of application, and the synergistic interaction between PSB and the parameters of mushroom growth. It has been demonstrated that the strategic use of PSB can be used to improve biological performance by 15-35%, and *Trichoderma*-contaminated products can be reduced by 40-85% in comparison to the traditional methods. The research gaps identified in this review have recommended areas in which future research can be conducted in a bid to maximize PSB-based integrated management strategies in a sustainable oyster mushroom production system.
Keywords: *Pleurotus ostreatus*, phosphorus-solubilizing bacteria, *Trichoderma*, biocontrol, green mold, mushroom cultivation, nutrient mobilization, biological efficiency

1.0 Introduction

1.1 Background and Significance

Amongst all mushrooms grown in the world, the oyster mushroom is obtained 19%. Oyster mushroom (*Pleurotus ostreatus*) can be considered as one of the most popular edible mushrooms that is cultured all over the world (Kumara *et al.,* 2025). It has an amazing ability to expand with farming, excellent organoleptic, and a great extent of nutraceutical advantages, and has a high business worth in varied geographical areas (Hultberg *et al.*, 2023). The oyster mushrooms are particularly significant in the context of Asian countries since they form a significant part of the

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agricultural waste valorization systems and contribute to the food security systems and rural economy. Agri waste is abundant and can be utilized for a sustainable and long-term use (Selvarajh *et al.*, 2024)

The presence of high protein content (19-35% dry mass), essential amino acids, dietary fiber, vitamins, and minerals, including high phosphorus content, makes the *P. ostreatus* a functional food (Wal *et al.*, 2023). However, two problems tend to be unproductive to the cultivation success: nutrient denial of the substrates and, in particular, infection with the other competing fungi, specifically *Trichoderma* species that induce the green mold disease.

1.2 The Challenge of *Trichoderma* Contamination

The most problematic species in the mushroom farming industry are *Trichoderma*, which cause disastrous losses in *P. ostreatus* and other mushrooms cropped in commercial farms (Kredics *et al.*, 2022). These mycoparasites can rapidly settle down on the surface of their prey, competing with mushroom mycelium not only for nutrients but also for space and producing enzymes to degrade the walls of fungi, including chitinases and glucanases (Kredics *et al.*, 2022). The *Trichoderma* contamination is usually green; failure of the crop might be absolute when not checked.

Over the last few years, a number of *Trichoderma* species that lead to harm to the mushroom production process have been identified, including *T. harzianum, T. aggressivum, T. asperellum, T. atroviride and T. pleurotum* (Chen *et al.*, 2023) [Figure 1]. The *Trichoderma* problem in mushroom farms is nauseating, and as indicated by some sources, the fungi constitute up to 20 percent of all air-borne fungi in mushroom houses (Kim *et al.*, 2019). Traditional methods of control that are founded on the application of chemical fungicides like benomyl, prochloraz, and carbendazim, although successful, have environmental and food safety issues and contribute to the development of resistant strains of fungi.

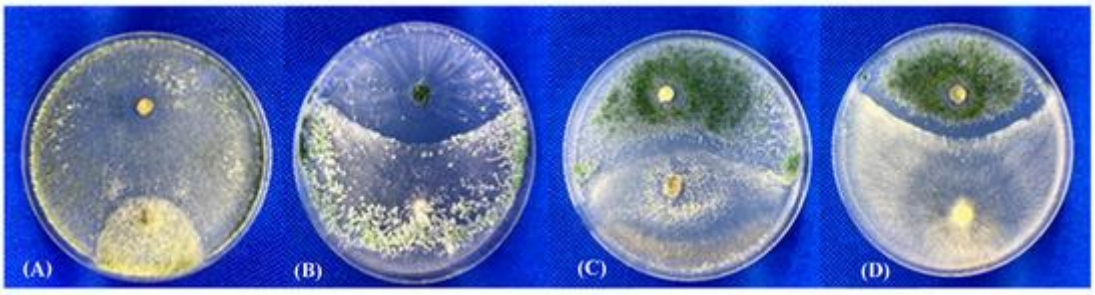

Figure 1 Dual culture assay of *Trichoderma-Trichoderma* interaction. (**A**) *T. pleuroticola (*bottom) vs. *T. atroviride* (top); (**B**) *T. atroviride* (bottom) vs. *T. pleuroticola* (top); (**C**) *T. pleuroticola* (bottom) vs. *T. afroharzianum* (top); (**D**) *T. atroviride* (bottom) vs. *T. afroharzianum* (top). (Lombardi *et al.*, 2023)

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1.3 Phosphorus Dynamics in Mushroom Cultivation

Phosphorus (P) is also a required essential macronutrient that supports the growth and development of mushrooms because it is an important component of energy metabolism, the construction of nucleic acids, and cell membranes. Though present in large amounts, phosphorus is not necessarily present in high amounts in mushroom feeds, and most of it may be insoluble inorganic (caustic phosphates, iron phosphates) or trapped within organic acids, of which it is unavailable to the mushroom mycelium (Silva *et al.*, 2023). Agricultural wastes, which are utilized in a relatively fair manner as mushroom feeds, such as rice straw, wheat straw, and cotton wastes, tend to have low quantities of bioavailable phosphorus (Costa *et al.*, 2024; Selvarajh *et al.*, 2023). Nutrition plans to enhance the ratio of carbon to nitrogen and enhance nutrient profiles do not normally take into consideration phosphorus bioavailability, but rather they emphasize nitrogen addition. Such negligence can limit mushroom biological activity and the quality of fruiting bodies, particularly when large cultivation intervals are to be considered.

1.4 Phosphorus-Solubilizing Bacteria: Dual Functionality

Phosphorus-solubilizing bacteria (PSB) represent a heterogeneous group of microorganisms capable of converting insoluble phosphorus into absorbable forms that can be absorbed by the host through the production of organic acids, chelation, and enzymes (Enriquez-Leon *et al.*, 2025). Most PSB species, besides their biofertilizing functions, possess strong biocontrol abilities and produce antimicrobial compounds, siderophores, lytic enzymes, and volatile organic compounds with an anti-phytopathogenic impact (Pan & Cai, 2023).

The phosphorus-solubilizing bacteria applied in mushroom production are a new integrated management tool, which not only overcomes the nutrient deficiency but also prevents pathogens. The most common representatives of such a dual activity are *Bacillus, Pseudomonas, Paenibacillus, Burkholderia, Serratia* and *Streptomyces* (Silva *et al.*, 2023). These organisms also grow on growth mediums and form a mutualistic association with the mushroom mycelium and an antagonistic association with *Trichoderma* species.

1.5 Scope and Objectives

Although in the view of the growing interest in the application of useful microbes in mushrooms, there are no detailed reviews that solely examine the duality of PSB in the manufacture of *P. ostreatus* as nutrient mobilizers and biocontrol agents. This knowledge gap will be sealed by such a systematic review, which will:

1. Combining the available information on how bacteria are expected to dissolve phosphorus in the conditions of mushroom growth.
2. Comparison of the biocontrol efficiency of PSB in the control of *Trichoderma* species that infest an oyster mushroom.
3. Comparison of the effect of PSB application on parameters, which include mushroom growth, yield, and biological efficiency.
4. Evaluation of the use methods, time, and maximization of dosage of PSB on the growth of *P. ostreatus*.
5. Establishing synergies of PSB in association with mushroom mycelium.
6. Denoting gaps in research and the direction of future research.

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2.0 Methodology

2.1 Literature Search Strategy

The literature search was systematic and carried out in other scientific databases, including PubMed, Web of Science, Scopus, Google Scholar, and certain repositories (ScienceDirect, Springer Link, Frontiers). The search covered the articles published since January 2018 till December 2025, prioritizing peer-reviewed articles, conference proceedings, and authoritative reviews. Search terms were phosphorus-solubilizing bacteria (AND), Pleurotus ostreatus, oyster mushroom, *Trichoderma*, green mold, biocontrol, mushroom cultivation, nutrient mobilization, biological efficiency, mushroom growing, promoting bacteria etc. Boolean operators (AND, OR) were used to reduce the search results.

3.0 Phosphorus-Solubilizing Bacteria in Mushroom Cultivation

3.1 Diversity and Characterization of PSB

PSB (Table 1) is a functionally diverse group, and the reports show that 1-50 percent of all bacteria in soils carry the ability to solubilize phosphate (Sharma *et al.*, 2013). PSB have been isolated in mushroom cultivation settings in different sources, including compost, casing soil, spawn, colonized substrate, and fruiting body tissues (Suarez *et al.*, 2019).

Table 1
Major PSB Genera in Mushroom Cultivation Systems

Bacterial Genus	Representative Species	Key Characteristics	References
Bacillus	*B. subtilis, B. pumilus, B. amyloliquefaciens, B. velezensis, B. paramycoides*	Endospore-forming, environmental resistance, antimicrobial lipopeptide production	Nikolić *et al.*, 2019; Dimkić *et al.*, 2022
Pseudomonas	*P. fluorescens, P. putida, P. chlororaphis, P. protegens, P. synxantha*	Gram-negative, phenazine production, siderophore synthesis	Dimkić *et al.*, 2022
Paenibacillus	*P. polymyxa*	Nitrogen fixation, phosphorus solubilization, and antimicrobial activity	Silva *et al.*, 2023
Actinobacteria	*Micromonospora lupini, Streptomyces* spp.	Mycelial growth promotion, spawn colonization enhancement.	Suarez *et al.*, 2019; Chouyia *et al.*, 2022

Molecular characterization based on 16S rRNA gene sequencing revealed high species diversity within mushroom cultivation microbiomes, with *P. ostreatus* isolation studies identifying 38 bacterial isolates predominantly from Firmicutes and Actinobacteria phyla (Suarez *et al.*, 2019).

3.2 Mechanisms of Phosphorus Solubilization

Phosphorus-solubilizing bacteria employ multiple mechanisms to mobilize insoluble phosphorus compounds (Table 2):

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Table 2
Mechanisms of Phosphorus Solubilization by PSB

Mechanism	Process	Key Compounds/Enzymes	Effects	References
Organic Acid Production	Secretion of low-molecular-weight organic acids	Gluconic acid, citric acid, oxalic acid, lactic acid, succinic acid, 2-ketogluconic acid	pH reduction, cation chelation (Ca^{2+}, Fe^{3+}, Al^{3+}), competitive displacement	Wei *et al.*, 2018
Enzymatic Hydrolysis	Extracellular phosphatase production	Acid phosphatases, alkaline phosphatases	Hydrolysis of organic P compounds (phytates, phosphoesters, phosphodiesters)	Pan & Cai, 2023
Chelation	Metal complex formation	Siderophores, organic acids	Dissolution of phosphate through metal complexation	Ali *et al.*, 2022

Carbon Source Effects: Using glucose and maltose, *Citrobacter* sp. synthesized gluconic acid (~20 mM) and solubilized 520-570μM phosphate, whereas sucrose produced ~49 mM acetic acid with lower phosphate levels (170μM) (Silva *et al.*, 2023). Research on *Trichoderma harzianum* T-22 showed phosphate solubilization via chelation and reduction rather than acidification, as pH did not drop below 5.0 (Ali *et al.*, 2022).

3.3 PSB Effects on Nutrient Availability in Mushroom Substrates

Phosphate-solubilizing bacteria are important in radically changing the nutrient dynamics in mushroom-growing substrates via a series of combined biological pathways. Upon addition of these useful microorganisms into the growing medium, the media undergoes drastic enhancement of phosphorus bioavailability, and effective phosphorus and total phosphorus increases of 6.84% and 11.05% in spent mushroom substrate compost, respectively (Sun *et al.*, 2023). Multilocational trials have shown that the use of PSB biofertilizer raised crop yields by 10% to 40% based on crop type and soil conditions and had the potential to save 30 to 50 kg P_2O_5/ha equivalent of phosphate fertilizers (Alori *et al.*, 2017). This improvement is directly correlated with faster mycelial growth, higher substrate penetration efficiency, and an eventual increase in mushroom production (Li *et al.*, 2023). Besides the primary phosphorus-mobilizing function, bacterial communities set the world's metabolic nutrient changes through specific biochemical processes. They also generate siderophores, powerful chelating molecules containing extraordinarily high ferric iron affinity, with formation constants between 10^{23} and $10^{52M\ -1}$, and solubilize hitherto inaccessible metallic components like iron, zinc, and copper and convert them to forms accessible to fungal and plant tissues (Kretschmer & Osgood, 2020; Hussain *et al.*, 2021). Certain bacteria, particularly those of the genus *Paenibacillus*, such as *P. polymyxa*, also have some extra-fixed nitrogen-binding ability,

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and strains have been observed to fix as much as 25.93% of foliar nitrogen in plant systems (Li *et al.*, 2022).

Phosphorus-solubilizing bacteria communities are also actively involved in the production of plant growth-regulating compounds such as indole-acetic acid, cytokinins, and gibberellins (Figure 2). These phytohormones are biological signaling molecules that trigger fungal development pathways and stimulate cellular division, hyphal extension, and metabolic activation. Phosphate solubilization results in the synthesis of low molecular weight organic acids that concomitantly acidify the substrate microenvironment by chelating cations attached to phosphate to form an environment that facilitates even stronger mineral dissolution and nutrient movement (Zhang *et al.*, 2023). The positive feedback between these processes creates an optimal nutritional environment in the substrate matrix, which is a sustainable cultivation approach that helps to eliminate the use of synthetic fertilizers and, at the same time, enhances the yield of mushrooms.

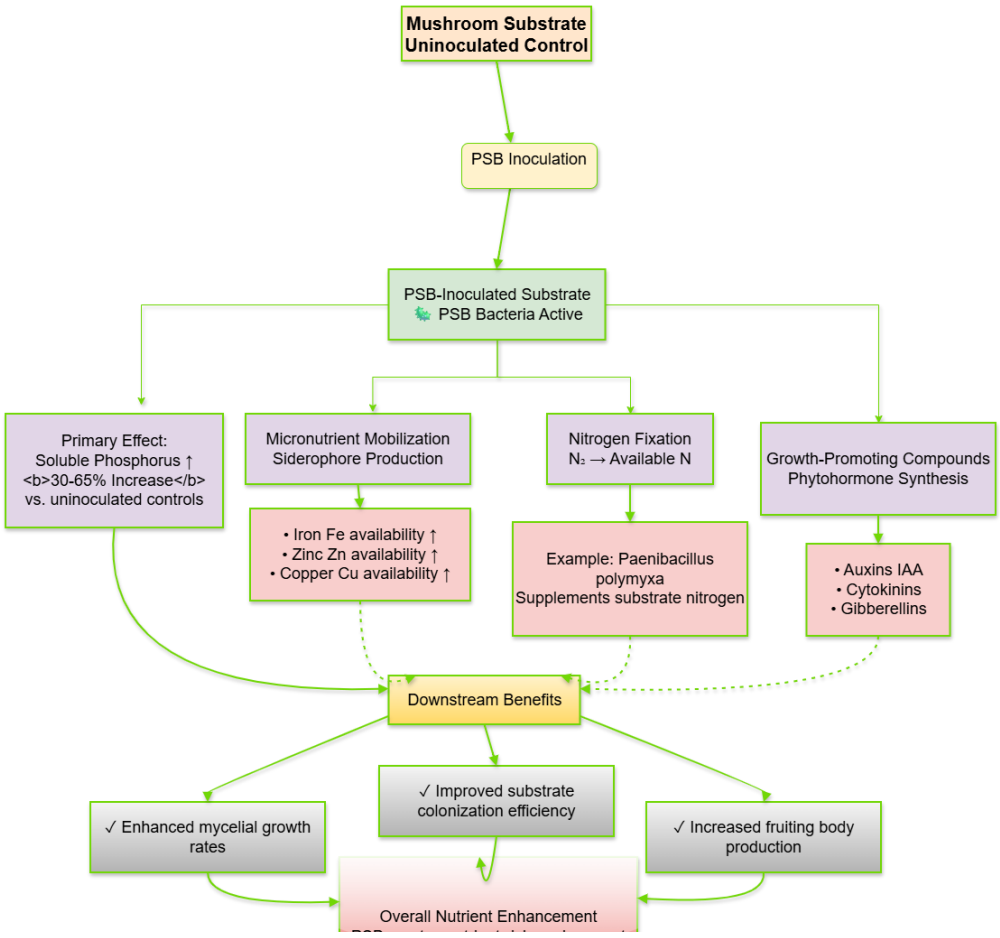

Figure 2 Integrated mechanisms of phosphate-solubilizing bacteria (PSB) in enhancing mushroom substrate productivity. PSB inoculation triggers four complementary pathways: phosphorus solubilization (30-65% increase), micronutrient mobilization (Fe, Zn, Cu)

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3.4 Specific Roles in Pleurotus ostreatus Cultivation

Phosphorus-solubilizing bacteria have been shown to have the following positive impacts in *P. ostreatus* systems of cultivation.

Reduction of spawn running time: *Micromonospora lupini* strain M46F greatly reduced the spawn running time in P. ostreatus, and it had a faster rate of substrate colonization (Suarez *et al.*, 2019). This acceleration is economical, as it shortens production periods and reduces contamination.

Improvement of mycelial growth: Co-cultivation experiments indicate that some bacterial isolates favor mycelial density and growth rate. Yet, the effect differs; not every phosphorus-solubilizing bacterium can show growth-promoting potential on mushroom mycelium (Kaur *et al.*, 2025).

The association of PSB with the *P. ostreatus* mycelium seems to be complicated and strain-dependent. The vast majority of bacteria do not kill their host by growing on the surface of the mycelium and becoming a part of the fungal microbiome, but affect the latter either by diffusible metabolites or volatile substances. These interaction dynamics are important in order to maximize PSB application strategies.

4.0 *Trichoderma* Species as Pathogens in Oyster Mushroom Cultivation

4.1 *Trichoderma* Species Affecting *Pleurotus ostreatus*

The *Trichoderma* species that cause green mold disease during the growth of *P. ostreatus* consists of more than one species whose phylogenetic lineages are phenotypically similar.

Table 3 shows that the *Trichoderma* species are phenotypically divergent yet genetically closely related to each other, which, in turn, is the cause of green mold disease in oyster mushroom farms all over the world, and proves the outstanding adaptability and pathogenicity of the genus (Ajis *et al.*, 2024).

Table 3
Pathogenic *Trichoderma* Species in *P. ostreatus* Cultivation

Species	Characteristics	Geographic Distribution	References
T. harzianum	Most common, highly aggressive	Worldwide	Chen *et al.*, 2023
T. aggressivum f. europaeum	Particular concern in commercial facilities	Europe, North America	Kredics *et al.*, 2022
T. pleurotum & *T. pleuroticola*	Specific to *Pleurotus* species	Widespread	Chen *et al.*, 2023
T. asperellum	Emerging contaminant	Asia is increasing globally	Chen *et al.*, 2023
T. atroviride	Significant yield losses	Widespread	Chen *et al.*, 2023

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4.2 Disease Epidemiology and Economic Impact

Contamination with *Trichoderma* can be performed at different points of mushroom growth. The first one is the preparation of substrates phase. Small *Trichoderma* spores are capable of surviving because of the lack of sterilization or pasteurization. The fungi are then left to cultivate in the cooling process, competing with the spawn to colonize.

Second is the spawning and colonization stage. In this stage, contamination of the spawning process takes place with the assistance of airborne spores, contaminated equipment, or infected spawn. *Trichoderma* has an approximate 20 percent prevalence of the fungi in the air of mushroom-growing houses (Table 4). The third one is the Fruiting stage. Humidity prefers *Trichoderma* sporulation; therefore, the secondary contamination of the environmental sources takes place (Kim *et al.*, 2019).

Contamination of *Trichoderma* may result in a major loss to the economy. In extreme cases of the outbreak, there will be losses of 30-100 percent of the yield, and the bags that contain the infected crops must be disposed of completely. Not only does contamination lead to loss of yields, but it also involves strict sanitation, additional manpower, and even closure of the facilities in order to be fumigated.

Table 4
Stages of *Trichoderma* Contamination in Mushroom Cultivation

Cultivation Stage	Contamination Source	Risk Factors	Impact
Substrate Preparation	Surviving spores	Insufficient sterilization/pasteurization	Competitive colonization during cooling
Spawning & Colonization	Airborne spores (~20% of air fungi), contaminated equipment, and infected spawn	Poor hygiene, inadequate air filtration	Direct competition with the mushroom mycelium
Fruiting	Environmental sources	High humidity favors sporulation	Secondary contamination, crop failure

Economic Impact: Severe outbreaks cause 30-100% yield loss, requiring complete disposal of infected bags, rigorous sanitation, additional labor, and potential facility shutdown for fumigation (Kim *et al.*, 2019).

4.3 Pathogenicity Mechanisms

The *Trichoderma* species use several methods to parasitize the mycelium of mushrooms. *Trichoderma* has fast growth rates (23 times faster than the mushroom mycelium), and it has a quick appearance on the surfaces of available substrates, as well as it consumes nutrients (Table 5). They can use a wide range of carbon and nitrogen supplies because of their bifurcated metabolism, which results in the development of resource competition that disadvantages the slower-growing mushroom fungi. *Trichoderma* releases cell-degrading enzymes such as chitinases, β-3: 1-glucanases, and proteases, which directly assault mushroom mycelium. The parasite has hyphae that coil and penetrate the host cells, resulting in cell lysis and demise. Some

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of the *Trichoderma* strains form toxic secondary metabolites (peptaibols, trichorzianines) that suppress mushroom growth and lead to physiological damage to fungi cells. These substances can have an antifungal effect at a concentration not lethal to *Trichoderma* itself (Mukherjee *et al.*, 2022).

Table 5
Trichoderma Pathogenicity Mechanisms Against Mushroom Mycelium

Mechanism	Description	Key Factors	References
Aggressive Competition	Fast growth rate (23× faster than mushroom mycelium); rapid substrate colonization	Versatile metabolism utilizing a wide range of C and N sources	Mukherjee *et al.*, 2022
Mycoparasitism	Direct parasitism via hyphal coiling and penetration	Cell-degrading enzymes (chitinases, β-1,3-glucanases, proteases); hyphal lysis	Kredics *et al.*, 2022
Antibiosis	Production of toxic secondary metabolites	Peptaibols, trichorzianines with antifungal activity	Mukherjee *et al.*, 2022

4.4 Current Control Measures and Limitations

Fungicides like benomyl, prochloraz-manganese, carbendazim, and mancozeb are used to treat the *Trichoderma*. Even though it is effective in growth retardation of the pathogen, one can raise the following concerns: environmental and food safety issues, the emergence of *Trichoderma* strains resistant to fungicides, adverse effects on the mushroom mycelium at higher concentrations, and the regulation of fungicide use in organic production (Table 6). It was shown that the inhibitory level of prochloraz and carbendazim on Trichloraz isolates is high, and the minimum effective concentration (EC50) varies between 2.1 and 15 ppm depending on the isolate (Ye *et al.*, 2023).

Table 6
Current *Trichoderma* Control Methods and Limitations

Control Method	Approach	Effectiveness	Limitations	References
Chemical Fungicides	Benomyl, prochloraz-manganese, carbendazim, mancozeb	High (EC50: 2.1-15 ppm)	Environmental/food safety concerns, resistance development, potential mushroom mycelium damage, and organic production restrictions	Ye *et al.*, 2023

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Control Method	Approach	Effectiveness	Limitations	References
Heat Treatment	Sterilization (121°C), pasteurization (60-80°C), hot water immersion (60°C, 30 min), alkalinized water (36 hrs)	Very high for initial contamination	Post-treatment contamination during handling/spawning	(Grimm *et al.*, 2024)
Environmental Management	Hygiene protocols, ventilation control, humidity management, HEPA filtration	Moderate to high	Ubiquitous *Trichoderma* spores in the environment require constant vigilance.	Kim *et al.*, 2019

The inefficiency of traditional control practices, alongside the growing demand for sustainable and organic mushroom production, highlights the pressing necessity of efficient biological control solutions. PSBs are highly promising agents, providing two advantages in terms of pathogen repulsion and nutrient content, with no drug residues and minimal environmental issues.

5.0 Biocontrol Mechanisms of Phosphorus-Solubilizing Bacteria Against *Trichoderma*

5.1 Direct Antagonism Through Antibiosis

The PSB antimicrobial compounds and mechanisms against *Trichoderma* are shown in Table 7.

Table 7
PSB Antimicrobial Compounds and Mechanisms Against *Trichoderma*

Compound Class	Producing Bacteria	Key Compounds	Mode of Action	References
Lipopeptides	*Bacillus* spp.	Surfactin (membrane disruption), Iturin A (pore formation, K^+ leakage), Fengycin (phospholipase A inhibition)	Fungal membrane integrity disruption, cell lysis, and synergistic effects	Nikolić *et al.*, 2019; Wu *et al.*, 2020
Phenazines	*Pseudomonas* spp.	Phenazine-1-carboxylic acid (PCA), phenazine-1-carboxamide, pyocyanin	ROS generation, respiration disruption, and spore germination inhibition	Cossus *et al.*, 2021

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Compound Class	Producing Bacteria	Key Compounds	Mode of Action	References
Siderophores	*Bacillus*, *Pseudomonas* spp.	Catecholates, hydroxamates, carboxylates	Iron sequestration, nutritional competition	Silva *et al.*, 2023
Volatile Organic Compounds (VOCs)	*Bacillus subtilis*, *B. amyloliquefaciens*, *B. pumilus*	Alcohols, aldehydes, ketones, terpenes, sulfur compounds	Distance inhibition without contact, spore germination inhibition	Poveda, 2021

Genomic Evidence: *Bacillus subtilis* A9 genome analysis revealed 13 gene clusters for antimicrobial compound production, including surfactin, iturin, and fengycin biosynthesis pathways (Chen *et al.*, 2022).

5.2 Competition for Nutrients and Ecological Niches

PSB also competes well with *Trichoderma* using:

- **Rapid colonization:** Phosphorus-solubilizing bacteria propagate at rapid rates and settle on the substrates before the colonization by the pathogen, gaining access to ecological niches and eating the available nutrients. The competitiveness of Bacillus species is improved by the formation of protective biofilms (Xu *et al.*, 2023).
- **Effective nutrient uptake:** Phosphorus-solubilizing bacteria can acquire phosphorus solubility, which is competitively advantageous and can access phosphorus unattainable to *Trichoderma*. Mobilization of nutrients increases well-developed mushroom mycelia, which continues to the detriment of pathogens.
- **Substrate acidification:** organic acid production by PSB reduces substrate pH, which results in inopportune *Trichoderma* growth and favorable mushroom mycelium growth.

5.3 Production of Lytic Enzymes

Table 8 shows the lytic enzymes produced by PSB.

Table 8
Lytic Enzymes Produced by PSB

Enzyme Type	Target	Example Activity	Effect on *Trichoderma*	References
Chitinases	Chitin polymers in fungal cell walls	*B. subtilis* JN032305: 2.84 U/mL	Cell wall degradation, growth inhibition	Das *et al.*, 2024
β-1,3-glucanases	β-glucan components	Synergistic with chitinases	Mycolytic effects, cell wall breakdown	Mohamed *et al.*, 2025
Proteases & Cellulases	Proteins and cellulose	50% of growth-promoting bacteria produce cellulases	Overall antagonistic contribution	(Cheng *et al.*, 2023)

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Note: Lytic enzyme production is often induced by fungal biomass presence, representing an adaptive response enhancing biocontrol efficacy during pathogen encounters.

5.4 Induced Systemic Resistance in Mushroom Mycelium

While primarily documented in plant systems, emerging evidence suggests PSB may trigger defense responses in mushroom mycelium:

Signaling molecule production: Bacterial lipopeptides and VOCs can activate fungal defense pathways, potentially enhancing mushroom resistance to *Trichoderma* attack.

Priming effects: Pre-exposure to PSB or their metabolites may prime mycelium for more rapid and robust responses to subsequent pathogen challenge.

This mechanism requires further investigation in mushroom systems, as most current understanding derives from plant-microbe interactions.

5.5 Synergistic and Antagonistic Interactions

PSB biocontrol efficacy can be modulated by:

Consortium effects: Co-application of multiple PSB strains may provide broader spectrum activity and enhanced efficacy through complementary mechanisms. Studies show bacterial-fungal consortia (SynCom) combining *Pseudomonas* and beneficial fungi effectively control plant pathogens (Yang *et al.*, 2025).

Environmental factors: Temperature, humidity, pH, and substrate composition influence PSB performance. Optimization of these parameters is crucial for maximizing biocontrol effectiveness.

Mushroom-bacteria interactions: Positive associations between PSB and mushroom mycelium can enhance overall system resilience against pathogens. However, strain-specific variations exist, with some bacteria showing neutral or even negative effects on mycelial growth.

6.0 Application of PSB in Pleurotus ostreatus Cultivation Systems

6.1 Isolation and Screening of Effective PSB

A successful PSB application begins with isolation and rigorous screening:

6.1.1 Isolation Sources

Effective PSBs have been isolated from diverse sources, including:

- Mushroom compost and substrates
- Casing soil from mushroom facilities
- Rhizosphere soil from agricultural systems
- Fruiting body tissues of healthy mushrooms
- Spawn and colonized substrate samples

Studies isolating bacteria from different stages of *P. ostreatus* cultivation identified fruiting bodies as particularly good sources for mycelial growth-promoting isolates (Suarez *et al.*, 2019).

6.1.2 Screening Criteria

Multi-trait screening approaches select optimal PSB candidates:

- **Phosphorus solubilization ability:** Determined by the use of Pikovskaya agar medium with tricalcium phosphate. The appearance of distinct halos around colonies of bacteria is a sign of the P-solubilization phenomenon, and the ratios of halo to colony (d/d) are used to measure the activity (Chouyia *et al.*, 2022).

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- **Antagonistic activity:** *Trichoderma* species dual-culture assays determine the percentage growth inhibition. Effective biocontrol candidates are generally >40% active in vitro (Stanojevic *et al.*, 2019).
- **Siderophore production:** Siderophore activity is detected by chromazine azurol sulfonate (CAS) agar assays, which form orange halos on blue media.
- **Production of growth-promoting substances:** IAA production, ACC deaminase activity, and other plant growth-promoting characteristics tests.
- **Mushroom mycelium compatibility: Co-cultivation assays:** The PSB of interest must not prevent the growth of mushrooms. This is a very crucial step, and it removes candidates that have antagonistic effects on target mushrooms.

6.2 Application Methods and Timing

Table 9 shows the PSB Application Methods in Oyster Mushroom Cultivation.

Table 9
PSB Application Methods in Oyster Mushroom Cultivation

Application Method	Procedure	Advantages	Limitations	Efficacy
Pre-spawn Mixing	Direct PSB addition (10^6-10^8 CFU/mL) before spawning	Consistent bacterial distribution	Heat treatment may inactivate bacteria	Moderate
Post-pasteurization Inoculation	PSB added after heat treatment	Maximum bacterial survival, sterile environment colonization	Requires careful timing	High (Recommended)
Layered Application	PSB is placed between the substrate layers and the spawn	Targeted at the mushroom-bacteria interface	Labor intensive	High
Spawn Inoculation	Direct spawn treatment with PSB	Simple application	Inconsistent benefits reported	Variable
Casing Soil Amendment	PSB added to casing layer	Targeted fruiting phase delivery	Species-dependent responses	Moderate

Dosage Recommendations: 10^7-10^8 CFU/g substrate; 1-5% of total substrate mass for liquid inoculum. Multiple applications during colonization and fruiting may sustain bacterial populations.

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6.3 Formulation and Dosage Optimization

Table 10 illustrates the PSB formulation types for commercial application.

Table 10
PSB Formulation Types for Commercial Application

Formulation Type	Description	Advantages	Disadvantages	Commercial Viability
Liquid Suspensions	Fresh cultures in protective media (glycerol, skim milk)	Rapid application, immediate availability	Short shelf-life, storage challenges	Low-Medium
Dry Preparations	Spray-dried, freeze-dried, granular forms	Extended shelf-life, simplified logistics	Production costs, viability maintenance	High
Carrier-based Systems	PSB immobilized on porous surfaces (bone charcoal)	Controlled release, enhanced survival	Complex production	Medium-High

Optimal Dosage: Literature suggests 10^6-10^9 CFU/g substrate, with most effective studies using 10^7-10^8 CFU/g. Application volumes: 1-5% of total substrate mass for liquid inoculum.

6.4 Environmental Factors Affecting PSB Performance

Table 11 shows the critical environmental parameters for PSB activity.

Table 11
PSB Formulation Types for Commercial Application

Parameter	Optimal Range	Effect on PSB	Compatibility with Mushroom Cultivation
Temperature	25-35°C	Maximum bacterial activity	Aligned with standard mushroom cultivation
pH	Substrate-dependent	Influences survival and activity	Requires monitoring
Moisture Content	60-70%	Critical for bacterial survival	Standard range for mushrooms
Oxygen Availability	Aerobic conditions	Essential for most PSB metabolism	Adequate in substrate systems

Note: Individual strain selection must consider specific temperature profiles and substrate conditions of cultivation systems.

6.5 Effects on Mushroom Growth Parameters and Yield

Table 12 shows the effects of PSB on mushroom growth and production parameters.

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Table 12
PSB Effects on Mushroom Growth and Production Parameters

Growth Parameter	PSB Effect	Magnitude of Improvement	Key Mechanisms	References
Spawn Run Time	Reduction	15-25% faster	Enhanced nutrient availability, growth hormone production	Suarez *et al.*, 2019
Mycelial Density	Increase	Significantly higher scores	Complete substrate colonization	Kaur *et al.*, 2025
Mycelial Growth Rate	Stimulation	10-30% increase	P-solubilization, fungal growth-promoting hormones, and improved substrate conditions	Multiple studies
Biological Efficiency	Enhancement	15-35% improvement	Nutrient mobilization, pathogen suppression	Review synthesis
***Trichoderma* Contamination**	Reduction	40-85% decrease	Biocontrol mechanisms	Review synthesis

Strain-Specific Variation: Extensive screening shows significant variation—some bacteria have strong promoting effects while others show neutral or inhibitory effects, emphasizing the importance of rigorous strain selection.

6.6 Integration with Current Cultivation Practices

In order to integrate phosphorus-solubilizing bacteria applications with the existing cultivation practices, compatibility with methods of sterilization or pasteurization of substrates, compatibility with any chemical additive such as fungicides, and development of quality-control measures to check the viability of bacterial populations in recipients should be given particular attention. Commercially designed PSB products specifically to suppress mushroom growth also emerge; these include registered biomineral bioinoculants for mushroom growing, including *Bacillus velezensis* QST713 and *Bacillus amyloliquefaciens* MBI600. The first biomineral products have been used in the mushroom industry.

7.0 Challenges and Limitations

7.1 Variability in Phosphorus-solubilizing Bacteria Performance

Significant challenges in the Phosphorus-solubilizing bacteria application stem from performance variability:

Phosphorus-solubilizing bacteria do not always succeed in mushroom growth or pathogen suppression. It requires extensive screening in order to discover better strains. Things that work in vitro do not necessarily reproduce in commercial cultivation conditions. Under complex conditions of the field, such as indigenous microbiomes, environmental variations, and heterogeneity of substrates, laboratory biocontrol activity can be undetected. The effects of PSB are substrate dependent. Strains that thrive well on wheat straw substrates might not be active on rice straw or cottonseed hull substrates. The presence and concentration of temperature, pH, moisture, and

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oxygen play a major role in the PSB survival and activity. Poor conditions may destroy the benefits of bacteria (Silva *et al.*, 2023; Cheng *et al.*, 2023).

7.2 Bacterial Survival and Establishment

Introduced Phosphorus-solubilizing bacteria have to compete with the existing microbial communities of substrates. The lack of competitive capacity may lead to a decrease in the number of bacteria and the loss of benefits. The sterilization or pasteurization procedures to get rid of pathogens in the case also kill the useful bacteria if they are applied after inoculation. Coordination of time is essential. Drying because of substrate colonization is sensitive to bacteria. Bacteria require sufficient moisture to survive. Protozoa, nematodes, and hostile microorganisms that are natives of the area may decrease the population of PSB.

7.3 Potential Negative Effects

Production of organic acids solubilizes phosphorus over-acidification, which may suppress the growth of mushrooms. There should be a selection against extreme acid producers. Blistering bacterial increase can provisionally freeze the nutrient in bacterial biomass and limit the nutrient availability to mushroom mycelium at the most severe stages of growth. Certain bacterial secondary metabolites can have adverse impacts on mushroom flavor, aroma, or even safety. There is a need to characterize the bacterial metabolite profiles properly. The spores or components of bacteria may become an allergenic risk to workers or consumers, but there are no known incidences of this in mushroom farming.

7.4 Regulatory and Commercialization Barriers

Commercial sales of microbial inoculants are regulated and assessed for safety by many countries before commercial sales. The processes of registration may be tedious, costly, and discourage small-scale product development. It is technologically difficult to retain viable bacteria populations in commercial preparations during storage and distribution. Logistics may get complicated due to shelf-life restrictions. In most jurisdictions, natural sources of bacteria cannot be patented, and this limits the level of commercial interest in developing products. Perhaps a certain degree of IP protection is provided by proprietary formulations or strain of production. The conservative mushroom growers might be reluctant to change to new biological inputs, and they can stick to the already known chemical methods.

7.5 Knowledge Gaps

Although general biocontrol and nutrient mobilization are familiar, the molecular knowledge about PSB-mushroom-pathogen interactions is still insufficient. Design principles of effective multi-strain bacterial consortia to be used in mushroom production are not clearly defined. The impact of repeated PSB use on substrate and facility microbiomes across repeated cultivation should be explored. The economic models that involve variable costs, yield gains, and risk reduction should be comprehensive to support decisions by the commercial sector. The absence of standardized methodological procedures in the screening of PSB prevents cross-study comparisons and the determination of universal best practices.

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8. Future Research Directions

Higher throughput screening platforms were developed that are automated and high-throughput in order to screen large collections of bacteria in a rapid fashion in terms of P-solubilization, biocontrol activity, and mushroom growth promotion. This would be facilitated by identifying genetic markers linked to desirable PSB traits, which would be used in high-speed screening and prediction of bacterial performance via PCR. The machine learning models incorporating both genomic, phenotypic, and environmental data sets could be used to forecast the best PSB strains to use under certain growth environments. The strategies of adaptive laboratory evolution would improve desired PSB properties, including stress resistance, P-solubilization efficiency, or antimicrobial compound production.

Effective and ineffective PSB strains can be sequenced in their entire genome, and this can help identify the genetic determinants of beneficial traits. The analysis of the Bacillus subtilis A9 genome revealed 13 antimicrobial biosynthetic gene clusters, which proves the strength of genomic approaches (Chen *et al.*, 2022). By analyzing RNA-seq of PSB in the mushroom co-cultivation, it will be possible to show the pattern of gene expression that is related to the beneficial interaction and biocontrol activity. The use of a comprehensive profiling of PSB secondary metabolites under different conditions can discover bioactive compounds and optimize the conditions of production. Community-level effects and interactions Shotgun metagenomic sequencing of substrate microbiomes prior to and following PSB application can provide information on community-level effects and interactions. Multi-omics data would be utilized to inform systems biology models, which predict the PSB behavior in complex cultivation environments. Development of automated, high-throughput screening platforms to evaluate large bacterial collections rapidly for P-solubilization, biocontrol activity, and mushroom growth promotion. Identification of genetic markers associated with desirable PSB traits would enable PCR-based rapid screening and prediction of bacterial performance. Machine learning models integrating genomic, phenotypic, and environmental data could predict optimal PSB strains for specific cultivation conditions. Adaptive laboratory evolution strategies could enhance desired PSB traits such as stress tolerance, P-solubilization efficiency, or antimicrobial compound production.

Whole-genome sequencing of effective and ineffective PSB strains can reveal genetic determinants of beneficial traits. *Bacillus subtilis* A9 genome analysis identified 13 antimicrobial biosynthetic gene clusters, demonstrating genomic approaches' power (Chen *et al.*, 2022). RNA-seq analysis of PSB during mushroom co-cultivation can reveal gene expression patterns associated with beneficial interactions and biocontrol activity. Comprehensive profiling of PSB secondary metabolites under various conditions can identify bioactive compounds and optimize production conditions. Shotgun metagenomic sequencing of substrate microbiomes before and after PSB application can reveal community-level effects and interactions. Integrated multi-omics data can inform systems biology models predicting PSB behavior in complex cultivation environments.

Conclusions

This is a systematic review study that exhaustively examined the dual capacity of phosphorus-solubilizing bacteria to act as both nutrient mobilizers and biocontrol agents in oyster mushroom (*Pleurotus ostreatus*) production, targeting *Trichoderma* contamination. Phosphorus-solubilizing

bacteria are an effective biotechnological answer to the severe problem in the production of oyster mushrooms. Their dual-purpose as nutrient mobilizers and biocontrol agents will be consistent with the growing pressure to develop sustainable agricultural activities with reduced chemical use. Although the optimization of applications and maintaining the same level of performance is problematic, the evidence of the large scale presented in this paper confirms the new direction of PSB-based management strategies development and implementation in the Pleurotus ostreatus cultivation systems. As the mushroom industry in the world, especially in the developing areas where the technologies of sustainable production are highly demanded, PSB provides the scientifically correct, economically justified, and environmentally friendly ways to make the production more productive and to save the ecological integrity at the same time.

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