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Review Article

The Impact of Microbial Communities on *Agaricus bisporus* and *Pleurotus ostreatus* Mushroom Cultivation

Bolem Biswajith, Sanidhya Gupta,

Roochie Gautam and *Garima Gupta

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University Institute of Agricultural Sciences, Chandigarh University, Mohali, Punjab, 140413, India
*Corresponding author: hod.agri@cumail.in
Tel: +919569409099

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Abstract

This paper provides an in-depth analysis of how microbes play a crucial role in improving the cultivation of two commercially important mushrooms: button mushroom (*Agaricus bisporus)* and oyster mushroom (*Pleurotus ostreatus*). It focuses on the interaction between beneficial bacteria and fungi at different stages of mushroom production, such as compost preparation, substrate colonization, and forming fruiting bodies. The variety and structure of microbial communities involved in mushroom farming are essential for enhancing substrate use. The relationship between microbes and mushrooms becomes particularly clear during composting, where microbial activities convert raw materials into a nutrient-dense environment favorable for mycelium growth. The changes in microbial populations seen throughout the different phases of composting, especially the rise in bacteria during the later stages, greatly influence the yield and quality of mushrooms. Additionally, the dynamics of microbes in the casing layer are crucial for helping mushrooms progress from the vegetative phase to the reproductive phase, aiding in the development and maturity of fruiting bodies. The paper emphasizes the contribution of microorganisms in enhancing mushroom yield by increasing nutrient availability in the substrate, facilitating mycelial growth, and offering protection against fungal pathogens. Furthermore, cellulases, xylanases, and ACC deaminase, which are microbial enzymes, increase nutrient accessibility and support hyphae extension which is crucial for the strong development of mycelium and the eventual formation of fruiting bodies. It also highlights the role of bacteria such as Azotobacter, Bacillus, and Pseudomonas in promoting substrate breakdown and mycelium development, as well as in suppressing diseases, particularly against pathogens like *Trichoderma aggressivum* and *Pseudomonas tolaasii.* The paper emphasizes the significance of microbial diversity in compost and casing layers and discusses how microbes contribute to substrate decomposition through enzymatic activities.

Keywords: *Agaricus bisporus*, *Pleurotus ostreatus*, microbial communities, bacteria, fungi, microbial enzymes, disease suppression.

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Introduction

Mushrooms are widely recognized as a food source and are consumed extensively around the globe. The most commercially cultivated mushrooms are *Agaricus bisporus*, *Pleurotus species*, and *Volvariella volvacea* [1]. The primary commercially grown edible mushroom is *Agaricus bisporus*being the most prevalent, constituting approximately 30% of the global market. Another significant edible mushroom is Pleurotus, which includes 5-6 species i.e., *Pleurotus ostreatus*, *Pleurotus djamor*, *Pleurotus pulmonarius*, *Pleurotus eryngii*, *Pleurotus sajor-caju*, and *Pleurotus citrinopieatus*. Unlike some other mushrooms, Pleurotus and Agaricus rely not only on the mushrooms themselves but also on the presence of bacteria and other fungi in the substrate. These bacteria and fungi play crucial roles at various stages of production [2, 3]. Commercial mushroom production generally involves several solid fermentation stages conducted in controlled conditions, where microbes like bacteria and fungi play significant roles in processing sugars, reducing infestation of pathogenic fungus, and stimulating fruiting. Numerous interactions between bacteria and cultivated mushrooms result in beneficial or detrimental effects on the fungus, depending on the specific bacterial isolate and the developmental stage of the fungus [4]. In mushroom farming, effective microorganisms can be utilized as an additional substance which serves as a supplement to enhance the variety of microorganisms in the substrate ecosystem in mushroom cultivation. These microorganisms are called mushroom growth-promoting bacteria encompassing various species like Bradyrhizobium, Pseudomonas, and Bacillus [5]. The microbial population is crucial for the growth of mycelium and other stages of mushroom cultivation, including the development of fruiting bodies. These bacteria promote mushroom growth and enhance productivity by producing growth hormones, breaking down inhibitory compounds released by the mycelium, solubilizing phosphate, and producing siderophores [6]. Azotobacter, Bacillus, Paenibacillus, and Pseudomonas are known to be utilized as bio supplements in the cultivation of mushrooms. Incorporating these bacteria into the growing media for mushrooms enhances the growth and fruiting of *Pleurotus spp.* and *Agaricus bisporus*mushrooms [7].

In the cropping stages of A. bisporus, the fungus mycelium will directly interact with the microbial community (compost colonization and mushroom formation). Another microenvironment is the casing layer, which creates a favorable environment for mushroom formation. The casing materials harbor bacteria that play a role in converting vegetative mycelial growth into the formation of fruiting bodies [8]. Bacteria significantly impact the various stages of mushroom development, including the transformation and adjustment of substrates, the elongation of mycelial hyphae in the substrate, and the initiation of the fruiting body. Research shows that bacteria encouraging mycelial growth positively influence fungal strains like A. bitorquis, A. bisporus, and P. ostreatus. They stimulate mycelium growth, boost fructification, and help control pathogenic microbes. [9].

Survival and propagation of mushrooms depend on various factors, which can have individual or interactive effects. High-intensity cultivation of edible mushrooms is frequently impacted by fungal and bacterial diseases, leading to significant production losses [10]. Fungi like *Pseudomonas tolaasii*, *Sclerotium rolfsii*, and *Cephalothecum roseum* are identified as causing infections in mushroom cultivation at various growth stages, from the spawn run to the fruiting maturation. These fungi reduce yield and compromise the formation of mushroom fruiting bodies, resulting in economic losses [11]. Throughout different stages of growth, Agaricus faces attacks from pathogens that can disrupt

various stages of cultivation. These include *Trichoderma aggressivum, Verticillium fungicola*, and *Pseudomonas tolasii,* which causes diseases like green mould, dry bubble, and brown blotch [12]. Selected bacterial strains can be utilized for biocontrol to tackle these issues in an environmentally friendly manner. The biocontrol activity of most bacterial strains has been assessed against pathogens of A. bisporus [13].

Literature Review:

1. Action of microbes on mushroom cultivation

The study of microbial community dynamics is primarily undertaken during substrate preparation for mushroom production, and a few studies have focused on the overall cultivation cycle. Microbes' metabolic activity involves fermenting the cultivation substrate and changing it to enhance mycelial growth. *Agaricus bisporus*relies ecologically on microbes present in compost [2, 14]. Microbes like Azotobacter, Bacillus, Paenibacillus, and Pseudomonas increase Pleurotus and Agaricus mushroom yield by interactions like shortening the composting process and degrading lignocellulose, promoting mycelial growth by releasing nutrients in compost substrate and stimulating pinhead formation [7]. Microbes present in compost and casing play an important role in providing mycelium nitrogen, inducing fruit bodies' development, and releasing sugar residue from the straw substrate for *Agaricus bisporus*[15]. The microbial ecosystem in the compost undergoes significant changes throughout the various stages of fermentation in mushroom crop production. As the process advances, the bacterial community experiences a steady increase compared to the fungal community in the mushroom cropping process [8]. Factors like temperature, moisture, oxygen, materials used in composting, and C/N ratio, affect the microbial community in the cultivation and development of mushrooms. Bacterial communities help in fruit body formation, providing growth-promoting hormones and antagonizing pathogens [1].

Plant growth-promoting bacteria like *Pseudomonas fluorescens, Rhizobium leguminosarum,* and *Sinorhizobium meliloti* increased the yield of button *Agaricus bisporus*fruit body and efficiently increased the fresh matter yield and reduced harvesting time of *Agaricus blazei* [16]. The presence of microbes in the mushroom substrate of *Pleurotus ostreatus* decreased substrate contamination and increased carbohydrate utilization by the P. ostreatus during fruiting body formation. They also produce antimicrobial compounds, reducing competition between active microbes [17]. Some Pseudomonas species cause blotch in mushrooms, P. putida and P. fluorescens control blotch up to 100% [18]. *Pseudomonas tolaasii* inhibits the green mould disease-causing pathogen i.e., *Trichoderma aggressivum* up to 57% by releasing tolaasin toxin [19]. Dry bubble disease is caused by *Lecanicillium fungicola,* which causes disease in button and oyster mushrooms. Different Bacillus species act as control agents showing antagonistic effects against L. fungicola [20]. Azotobacter can be used as a biofertilizer for mushroom growth. Applying Azotobacter with phosphate-solubilizing bacteria increases oyster mushroom fruit size and nutritional value [5]. *Agaricus bisporus*growth is increased in the presence of *Pseudomonas putida.* P. putida increases the internode length of hyphae, transport ability of water and nutrients through the mycelium, and decreases the branching of the mushroom [21].

Table 1: Influence of microbes on mushroom growth and yield during cultivation

Microbes	Effect on growth and yield	References
Glutamicibacter arilaitensis	Cocultivation with bioinoculant *Glutamicibater arilaitensis* stimulated fruit body yield and biological efficiency of oyster mushroom	[6]
Pseudomonas sp	Bacteria present in compost and casing like *Pseudomonas putida* promote fruit body yield, mycelium growth, and mushroom initiation of A. bisporus, P. ostreatus, and P. eryngii	[21]
Azotobacter	Supplementation of biofertilizer treatment with *Azotobacter* and PSB during casing enhanced the mycelium run, pinhead formation, maximum fruiting body size, number of fruiting bodies, weight, and yield of oyster mushroom	[22]
Bradyrhizobium japonicum	Inoculation of B. japonicum on substrate and casing increased the number of mushrooms per tray under control, mushroom weight per tray, biological efficiency, nitrogen, and potassium content	[23]
Azospillum lipoferum	Bacteria inoculated along with mycelium and incubated increased yield by 33% by enhancing mushroom number per unit area in white button mushroom	[24]
Bacillus subtilis	A bacterial inoculant of B. subtilis with FYM + SMS in casing improved the fruit body yield of A. bisporus. It also inhibited the growth of green mould.	[25, 26]
Micromonospora lupini	Bacteria from spawn, mycelial colonized straw, and the fruiting body were isolated and tested that M. lupini reduced the spawn running time and had a positive effect on mycelium growth on P. ostreatus	[9]
Bacillus cereus, Bacillus aryabhattai, and Acinetobacter pittii	Bacteria were inoculated in PDA media and P. ostreatus mycelium was inoculated into the media containing bacteria, and it was observed that mycelium growth was promoted	[27]
Bacillus amyloliquefaciens and Streptomyces flavovirens	Bacteria isolated from compost were inoculated with *Agaricus bisporus*, which increased the yield by 5% and Controlled green mould disease-causing pathogen *Trichoderma aggressivum*	[28]
Pseudomonas taiwanensis and Bacillus thuringiensis	They show antagonistic behaviour against bacterial pathogens like *Pseudomonas tolaasii* and *Ewingella americana*	[29, 30]

2. Microbial communities in mushroom substrate

In white button cultivation, microbes of different phyla i.e., Proteobacteria, Actinobacteria, Firmicutes, Bacteriodetes, Verrucomicrobia, Deltaproteobacteria, Thermodesulfobacteria are dominant in substrates [1]. Some bacterial genera like *Caldibacillus*, *Thermobispora*, *Thermopolyspora*, *Ureibacillus*, and *Thermobacillus* degrade organic matter when composting oyster mushrooms' substrate. The time taken for the composting process impacted the bacterial population, rate of cellulose degradation, and biological efficiency [31]. While preparing compost substrate for A. bisporus, pasteurization resulted in a stable community mainly dominated by *Mycothermus thermophilus, Pseudoxanthomonas taiwanensis*, and other Proteobacteria. These taxa experienced a decrease in spawn run which

might serve as a direct source of nutrition for the rapidly growing mycelia [32]. The compost and casing materials had unique bacterial communities, but in both microenvironments, the alpha diversity generally increased and reached a stable level over time in regular and passaged substrates. After the fungus colonization, the community composition within the compost and casing microenvironments became more uniform. The passaging of casing led to increased bacterial alpha diversity and a shift in community composition, whereas such changes were not seen in passaged compost [33].

The coexistence and interaction of microorganisms in compost and casing microenvironments signifies the A. bisporus growth and development. These ecological relationships are considered crucial factors for the mycelial growth and formation of fruiting bodies. The cultivation process begins with substrate preparation, specifically composting, which significantly influences the shifts in bacterial communities within the compost microenvironment [8]. Phyla of bacteria like Bacteroidetes, Firmicutes, and Proteobacteria were most prevalent in the millet straw-based substrate, with Prevotella being the predominant genus. In the Phase I composting process, the dominant phyla were Firmicutes, Bacteroidetes, Proteobacteria, Deinococcus-Termus, and Actinobacteria. Phase II had the most abundant bacteria taxa, including Proteobacteria, Chlorofexi, Actinobacteria, and Firmicutes [34].

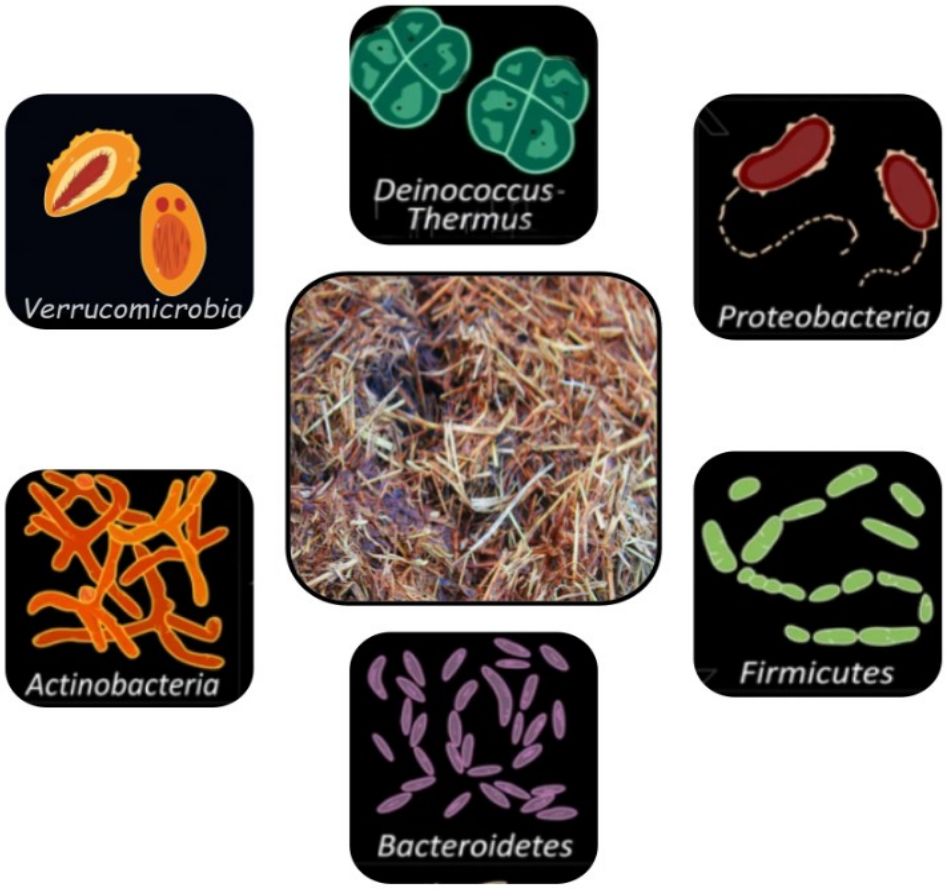

Fig 1: Different phyla of microbes found in substrate.

3. Interaction between bacteria and mushroom

The compost's bacterial biomass is a significant nutrient source for promoting A. bisporus and P. ostreatus mycelium growth. In vitro, *Pleurotus ostreatus* hyphae actively infiltrated in groups of *Pseudomonas fluorescens*, leading to extensive expansion of hyphae and the breaking down of colonies. A. bisporus mycelium decomposed *Bacillus subtilis* cells by releasing extracellular enzymes to disintegrate the bacterial cell wall made of peptidoglycan [35]. During the mycelial growth of mushrooms in compost, there was an increase in populations of Gram-positive bacteria and a decrease in Gram-negative bacteria. This suggests that the compost nutrient environment may support the proliferation of Gram-positive bacteria or that the Agaricus mycelium may selectively break down Gram-negative bacteria [36]. Bacteria that stimulated mycelium growth were also observed to secrete chitinase. It strongly indicates bacteria promote growth function by partially breaking down the hyphal cell walls to extract sugars and amino acids from the mushroom mycelium while offering nutrients [9]. *Pseudomonas putida* and Bacillus species isolates from compost induced mycelial extension in *Pleurotus ostreatus*, bacterial isolates found in the fruiting body of P. ostreatus, which improved mycelial growth, did not produce IAA.

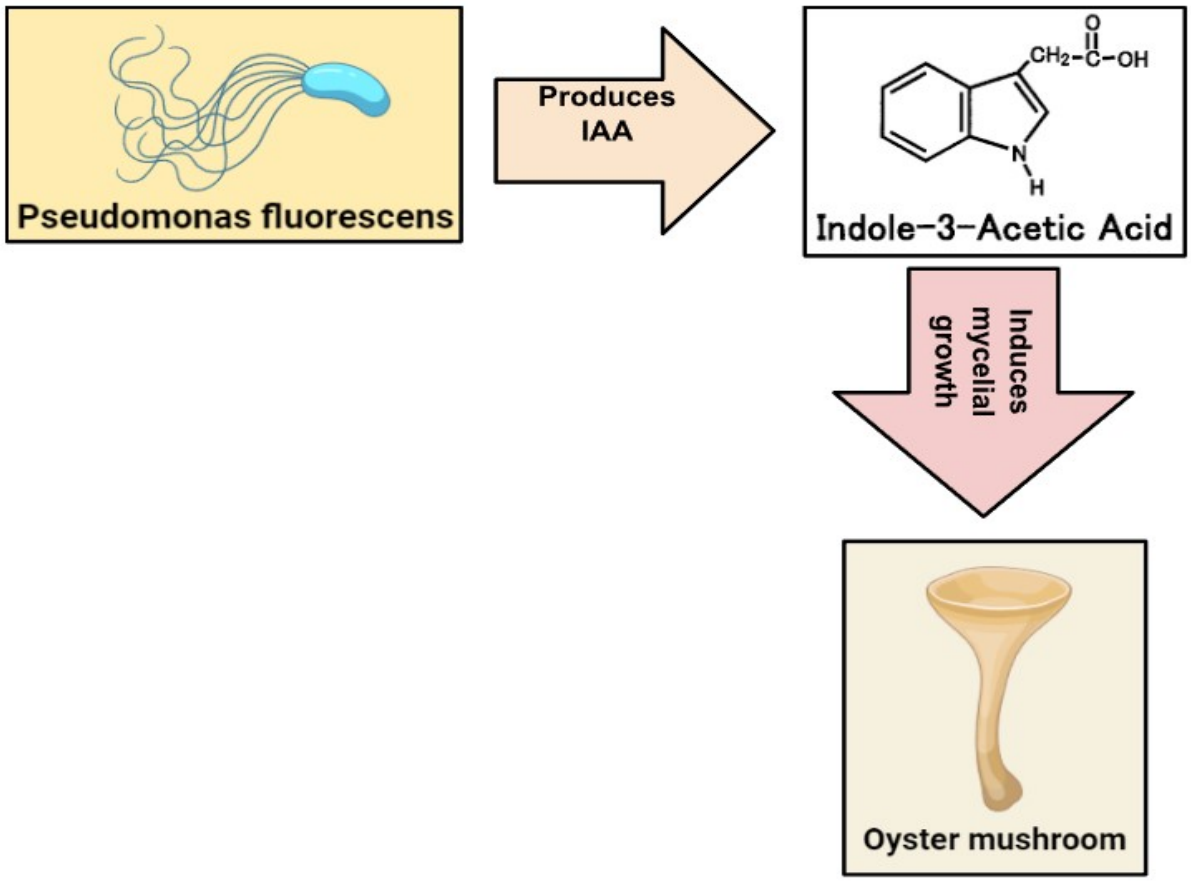

Fig 2: Production of IAA by P. putida in *Pleurotus ostreatus* promoting mycelium growth.

This highlights the diverse mechanisms for promoting mycelium growth and the phenotypic distinctions between bacteria from casing and fruit bodies and those from compost. It is noteworthy that *Pseudomonas fluorescens* strains isolated from P. ostreatus fruiting bodies are considered mushroom growth-promoting bacteria due to bacterial IAA production, while *Pseudomonas fluorescens* strain from *Agaricus bisporus*from the casing soil did not impact the mycelium growth rate [37, 38].

The P. ostreatus substrate is mainly associated with Bacillus, Paenibacillus, and Lysinibacillus spp. Bacillus spp. are known for producing antifungal peptides that selectively inhibit the growth of Trichoderma spp., the cause of green-mould disease, without affecting P. ostreatus. Additionally, *Paenibacillus polymyxa* contributes to the competitiveness of P. ostreatus. Bacillales, Thermus spp., and Halomonas spp. play a role in reducing substrate contamination and enhancing cellulase and hemicellulase activity during the fruiting body production of *Pleurotus ostreatus* [17]. When *Pleurotus ostreatus* was cultivated alongside a *Bradyrhizobium elkanii*, both colonization of mycelium by bacteria and active nitrogen fixation on hyphae within biofilm occurred. *Sinorhizobium meliloti* and *Rhizobium leguminosarum* were used in *Agaricus bisporus*cultivation on compost, resulting in increased yield and improved quality of the mushroom fruiting bodies [16]. Azotobacter with phosphate-solubilizing bacteria as mushroom growth-promoting bacteria (GPB) showed the fastest mycelium inoculation in the substrate from the spawn, harvesting stage, initiation of pinheads, maximum number of fruiting bodies of Pleurotus sp. [22].

4. Enzymatic contributions of microbes:

*Agaricus bisporus*mycelium showed reduced ethylene production due to the release of ACC deaminase (AcdS) by *Pseudomonas putida* strains. The ethylene produced by *Agaricus bisporus*mycelium inhibited its growth. AcdS-producing *Pseudomonas putida* strain, when inoculated with *Agaricus bisporus*mycelium, directly attaches to hyphae and ACC (1-aminocyclopropane-1-carboxylic acid), the immediate precursor of ethylene which is produced by the mycelium, is cleaved through bacterial ACC deaminase activity [35]. Microbispora demonstrates cellulase, xylanase, and mannanase enzymatic activities, suggesting their potential involvement in the degradation of cellulolytic and hemicellulolytic processes in wheat straw compost during composting [39].

The bacterial isolates from fruiting bodies in P. ostreatus showed decreased enzymatic activities but stimulated hyphal extension. On the other hand, bacteria isolated from the mycelium displayed elevated levels of peptidase and lipase enzymes and suppressed hyphae growth and development [9]. The conversion of macromolecular components in compost feedstocks, such as proteins, cellulose, hemicellulose, and lignin, is primarily facilitated by enzymes produced by bacteria and fungi of mesophiles and thermophiles. Mesophilic compost organisms quickly utilize starch and protein through the wetting period of the composting process due to invertase, amylopectinase, and protease activity [32]. However, invertase and amylopectinase show reduced activity in the compost. Enzymes like cellulase, β-glucosidase, and xylanase are highly active at the beginning of the composting process and decrease the activity of the pre-wet period. These enzymatic activities associated with mesophilic microbes initially benefit from increased nutrient availability due to substrate degradation [32].

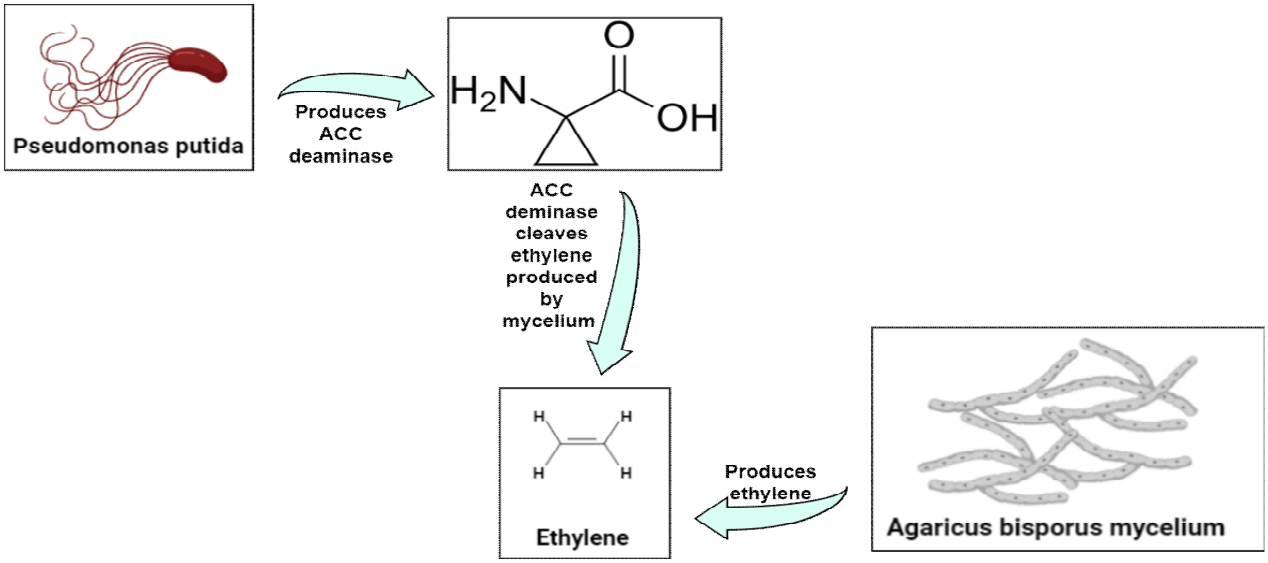

Fig 3: Inhibition of ethylene effect on the growth of *A. bisprous* due to the presence of ACC deaminase produced by inoculant *Pseudomonas putida* strain.

5. Microbial impact on primordia and fruiting body formation

P. putida and P. tolaasii are the bacteria closely associated with the *Agaricus bisporus*mycelium. They are attached to the *Agaricus bisporus*hyphae and display chemotaxis. The presence of glucose, mannose, and rhamnose in the exudate is of less percentage; bacteria mainly respond to amino acids like glutamine, alanine, leucine, phenylalanine, and proline in the exudate [40]. The P. putida strain UW3 shows chemotaxis against arginine, succinic acid, and ACC. Furthermore, it has been demonstrated that bacteria consume water-soluble compounds in *Agaricus bisporus*exudate and gaseous compounds produced in the mycelia [41]. During the cropping process, the fungal community shows higher abundance than the bacterial community in the casing. The abundance of the fungal community in the casing increases almost exponentially between the first and second mushroom flushes, likely dominated by *Agaricus bisporus*. On the other hand, bacterial abundance, as assessed in phospholipid fatty acid analysis (PLFA), was observed to rise in the casing layer during the first and second mushroom flushes while decreasing during other stages of mushroom growth [15].

The presence of the acdS gene of *Pseudomonas sp.* in the *Agaricus bisporus*-acdS transformants decreased ACC and ethylene levels, ultimately enhancing mycelial growth and primordial development [42]. The highest primordia formation and enhanced fruit body development of P. ostreatus were promoted by inoculating pure bacterial cultures of *Pseudomonas fluorescens* isolated from the mycelial plane. The biological efficiency of mushroom cultivation was increased by supplementing with *Pseudomonas putida*. Bacteria inoculation accelerated fungal mycelia, increased basidium development, and mushroom biological efficiency.

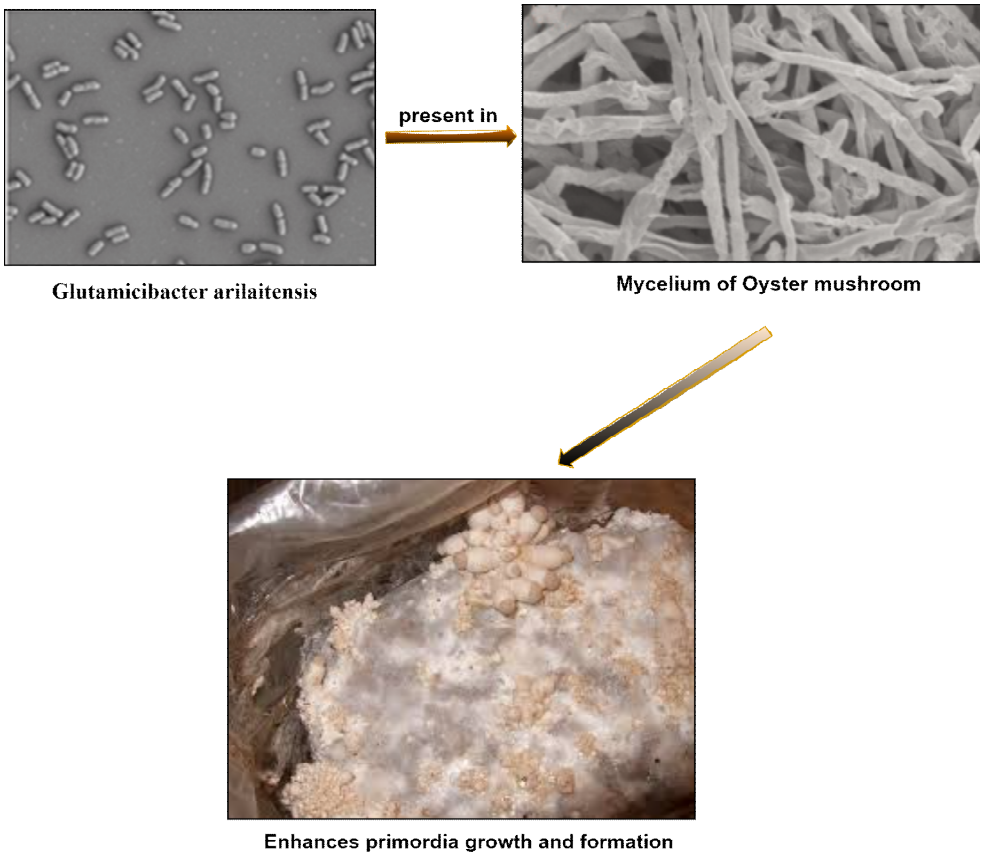

Fig 4: *Glutamicibacter arilaitensis* enhancement of primordial formation of oyster mushroom.

Glutamicibacter arilaitensis and its culture filtrate played a crucial role in achieving higher yields of oyster mushrooms increasing primordial formation [6]. The casing layers in A. bisporus cultivation correspond to 75–85% of the Pseudomonas sp population, with P. putida accounting for 12%. When P. putida interacts with A. bitorquis mycelia, it can promote primordial formation compared to non-living bacterial suspensions. The promotion of A. bitorquis primordia does not hinder mycelial growth but rather indicates a hierarchical relationship in the succession and development of primordia [43].

6. Microbial roles in disease suppression:

Pseudomonas tolaasii, a bacterial pathogen, causes severe damage to *Agaricus bisporus*mushrooms releasing the toxin tolaasin, the main virulence factor causing brown blotch disease. However, *Mycetocola tolaasinivorans* and *Mycetocola lacteus*, associated with the fungus, deactivate tolaasin by straightening the lipocyclopeptide. Mycetocola sp hinders the pathogen spread by breaking the lactone ring of pseudodesmin [44]. Blotch disease is caused by several Pseudomonas species, where *Pseudomonas tolaasii* is the most dominant one for its role in causing brown blotch disease in *Agaricus bisporus*. It is challenging to control this pathogen because it is commonly found in compost and quickly transforms from a saprotroph to a pathogen [45, 2]. Pseudomonads can lead to bacterial blotch, but certain Pseudomonas species can manage these pathogens, like *Pseudomonas tolaasii. Pseudomonas putida, Pseudomonas fluorescens,*

and *Pseudomonas reactans* achieve up to 100 percent control in bacterial blotch [46, 29].

Trichoderma aggressivum causes green mould in A. bisporus. The interaction between *Pseudomonas putida* and *Pseudomonas tolaasii* affects *Trichoderma aggressivum*. The growth of Trichoderma is inhibited by 57% when exposed to P. tolaasii culture supernatant, possibly due to the presence of the tolaasin toxin [21, 19]. Using biological methods for disease management is a superior alternative to other methods. *Bacillus velezensis* is commonly used as a biological control method to suppress diseases that produce two lipopeptides i.e., surfactin and fengycin which are increased in response to *Trichoderma aggressivum. Bacillus velezensis* and *Bacillus amyloliquefeciens* combat green mould disease and impact the growth of T. aggressivum [47, 12, 48]. *Streptomyces flavovirens* A06 effectively inhibited green mold in compost triggered by T. aggressivum. These findings suggest that S. flavovirens A06 could boost mushroom production and help manage the aggressive compost green mould caused by T. aggressivum [49].

Lecanicillium fungicola infects A. bisporus, A. bitorquis, and P. ostreatus as a pathogen. In the case of A. bisporus, it leads to dry bubble disease [21]. B. amyloliquefaciens, B. velezensis, B. pumilus, and B. subtilis were tested. In all in vivo trials, B. amyloliquefaciens exhibited comparable pathogen suppression results to the commercial bio-fungicide B. velezensis. B. amyloliquefaciens displayed the most potential for controlling green mould and dry bubble disease [20].

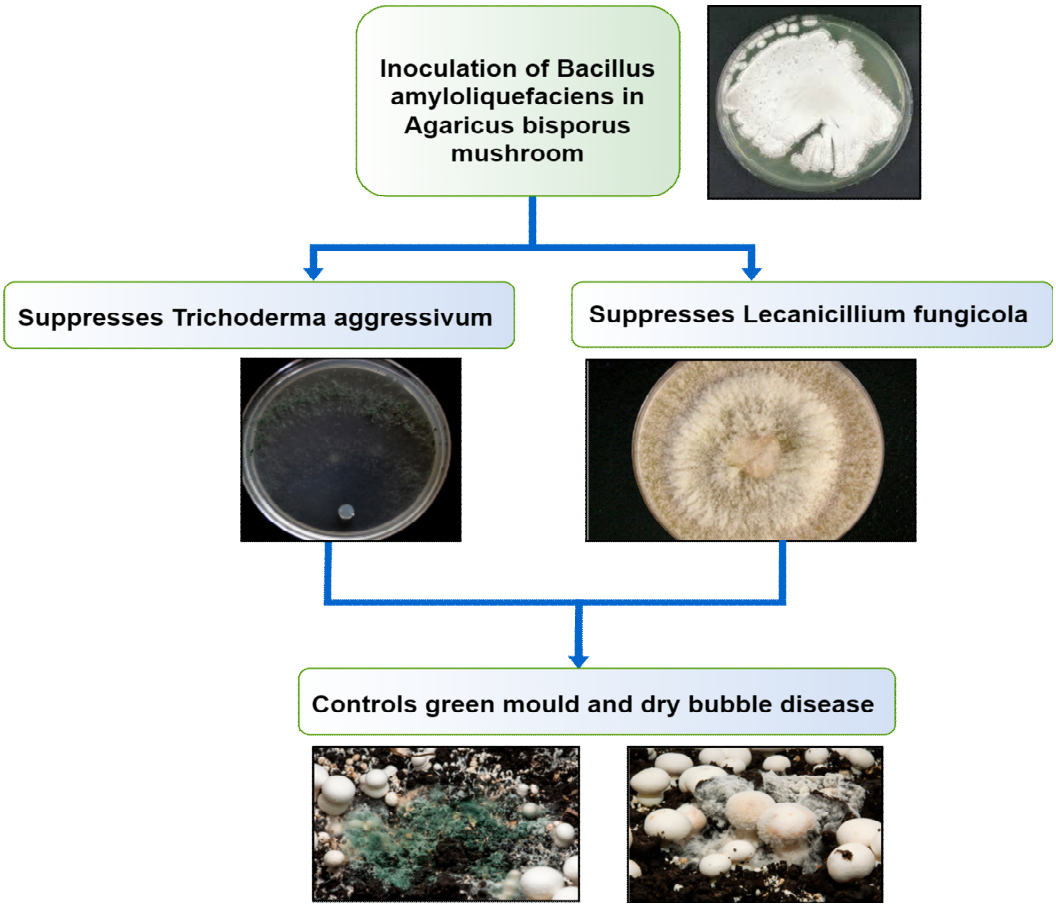

Fig 5: *Bacillus amyloliquefaciens* suppression and control of green mould and dry bubble disease.

Conclusion:

In conclusion, the cultivation of *Agaricus bisporus*and *Pleurotus ostreatus* is heavily influenced by the microbial community and substrate composition, which greatly contribute to mushroom yield and quality. The interaction between helpful microbes like Pseudomonas, Bacillus, and Azotobacter species and the mushroom mycelium helps make nutrients available, improving mycelial growth, and assisting in fruit body formation. These microbes produce important enzymes such as cellulase and xylanase, which aid in breaking down lignocellulosic materials, enriching the substrate, and facilitating strong mycelial colonization. Moreover, the diversity of microbes in compost and casing materials is essential for disease control. Certain bacteria support mycelial growth and act as biocontrol agents, managing pathogens like *Trichoderma aggressivum* and *Pseudomonas tolaasii*, which cause green mould and blotch diseases, respectively. Using bioinoculants such as *Bacillus velezensis* and *Pseudomonas putida* has been proven effective in enhancing mushroom productivity and ensuring crop health by reducing disease outbreaks. Therefore, combining microbial community management with substrate optimization presents a promising sustainable and high-yield mushroom cultivation. The ecological balance between microbes and mushrooms is crucial for maintaining substrate quality, promoting fungal growth, and ensuring a healthy, disease-free cultivation environment.

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