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Review

The input of microorganisms to the cultivation of mushrooms on lignocellulosic waste

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Abstract: Lignocellulosic crop waste is the world's most abundant renewable raw material. Its burning leads to the loss of an energy valuable resource and causes enormous environmental damage. An environmentally friendly and promising biotechnological process for such waste utilization is the production of mushrooms for food and medicine. However, the energy intensity of substrate preparation hinders the development of work in this direction. Another significant challenge in this field is to increase the biological efficiency of substrate processing. The purpose of our investigation was to reveal the contribution of microorganisms to solving this and other problems of mushroom cultivation based on a review of the latest scientific research on the topic. The literature from databases of Google Scholar, Scopus, and Web of Science was selected by various combinations of search queries concerning mushrooms, substrates, microbial communities, and their effects. The current state of the issue of mushrooms and microorganisms' interactions is presented. The review considers in detail the contribution of microorganisms to the substrate preparation, describes microbial communities in various phases of the mushroom cultivation process, and identifies the main groups of microorganisms associated with lignocellulose degradation, mushroom growth promotion, and protection against pathogens. The significant contribution of bacteria to mushroom cultivation is shown. The review demonstrates that the contribution of bacteria to lignin degradation in lignocellulosic substrates during mushroom cultivation is largely underestimated. In this process, various genera of the bacterial phyla *Bacillota*, *Pseudomonadota*, and *Actinomycetota* are involved. The correct combinations of microorganisms can provide controllability of the entire cultivation process and increase required

indicators. However, expanding research in this direction is necessary to remove gaps in understanding the relationship between microorganisms and mushrooms.

Keywords: lignocellulosic crop residue; substrate composting; microbial community; lignin degradation; higher fungi; bacterial-fungal interactions; mushroom growth-promoting; antagonistic activity; endofungal bacteria

1. Introduction

Lignocellulosic agricultural residues, primarily rice and wheat straw and the remains of corn and sugar cane are the most widespread renewable raw materials on the planet [1]. Their global production, along with the wastes from industrial processing of plant biomass, reaches 200 billion tons per year [2]. The widespread burning of these residues is one of the main contributors to dangerously high levels of greenhouse gas production and health-related air pollution. In addition, the high concentration of ash makes straw less attractive than pure wood as a fuel. The problem requires the development and implementation of other approaches for climate-friendly waste disposal.

The collection, processing, and transportation of straw are associated with high costs. The technology of involving it in the production of high-value-added products is the most justified thereby. Even though lignocellulosic biomass is a renewable and available source for feeding farm animals, its hydrolysis is the limiting step in the process of anaerobic digestion. Various pretreatment methods, such as physical, chemical, thermochemical, and biological, have been studied to increase lignocellulose availability. The biological transformation of lignocellulosic wastes is found to be more economically viable [3] since the process of chemical transformation of polymers takes place with the help of living organisms and does not require complex methods and the construction of highly equipped factories [4]. The higher fungi have proved to be the most active in this regard since they have the highest laccase activity among bacteria and fungi [5]. The use of mushrooms, the key enzymes of which, including laccase and universal peroxidases, can unlock indigestible lignocellulosic compounds [6–8], is recognized to be the most effective and low-cost. Several reviews [9–12] present an encouraging prospect for the future of environmentally friendly transformation of low-value by-products into new high-value-added resources. The use of bioactive ingredients in macrofungi can also increase market value. The development and implementation of new systems for the mass production of macrofungi and their active substances, including cultivation conditions, deserve great attention [13]. A large list of diverse cellulose-containing wastes can be used for the production of mushrooms, among them: wheat, barley, oats, rice, or millet straws, bran, rice husks, grape pomace, corn cobs, forestry by-products (sawdust and shavings) [7,14–19], cotton residues [16,19–21], sugarcane bagasse [16], olive wastes [19,22], a combination of sawdust and bagasse [23], coffee waste [24,25], spent brewery grains [26], faba bean hulls [27], sisal shredded leaf, dry fiber powder waste [28], and other. Such less traditional wastes like banana residue [29], beans straw, *Melia volkensii* leaves [30], and palm empty fruit bunch [31] are applicable for mushroom cultivation as well. Substrates for the growth of *Pleurotus* fungus are reviewed in detail by Ritota and Manzi [17] and Raman et al. [7].

More than 2189 species of mushrooms from 99 countries are edible [32]. According to the FAOSTAT database [33], the world production of mushrooms and truffles has increased from 25.0 to

42.8 million tons from 2010 to 2020, which indicates a great consumer demand for them. The productivity of mushrooms reaches 4.8–6.2 tons of dry protein per hectare in a year [34]. Mushroom farming is a good substitute for meat production [35] and has a great impact on poverty alleviation programs [36]. At the same time, mushrooms are a rich source of biologically active and medicinal compounds [37–39]. The main producer of edible mushrooms in the world for many centuries has been China. It produced almost 87% of the world-level mushrooms and truffles in 2019 [40] and 93% in 2020. The size of the global medicinal mushroom market is projected to grow significantly [41]. By 2050, a third of the proteins consumed by humans are supposed to come from the fungal origin [42]. The rapid growth of the population and demand for meat products create problems of land and water shortages, animal welfare, and climate change [43]. The use of mushroom protein is one of the alternatives to increase meat production. Basidiomycetes of various species and their wide range of pharmaceutically interesting products represent one of the most attractive natural product groups in Asia and North America in recent decades. The production of mushrooms as a new generation of human food sources is steadily increasing throughout the world. This is especially true regarding climate change issues, the water crisis, land degradation, and desertification [44]. However, the production of fruiting bodies of mushrooms using agricultural technology practically does not cover the market [45]. Currently, even the creation of a lunar base for the production of mushrooms is being considered [38].

The efforts of researchers in the field of mushroom production are aimed at improving their growth and productivity on available lignocellulosic substrates and protection against pathogens. A promising direction in this area is the study of the relationship of mushrooms with various microorganisms, both associated with the substrate used and living on the surface or inside the fungal mycelium and fruiting bodies. To date, the huge contribution of microorganisms to all aspects of plant life has already been proven, while the relationship between microorganisms and higher fungi is very poorly understood.

The purpose of our investigation was to reveal the contribution of microorganisms to mushroom cultivation on lignocellulosic substrates based on a review of the latest scientific investigations on the topic. The literature was explored in the databases of Scopus, Web of Science, and Google Scholar for various combinations of search queries: mushroom, microorganisms/bacteria, lignocellulose, compost, “mushroom cultivation”, “microbial community”, “substrate composting”, “lignocellulosic substrate”, “lignocellulose degradation”, “mushroom growth-promoting bacteria/microorganisms”, “endofungal/endohyphal bacteria”, and “bacterial-fungal interactions”. If necessary, the narrowing of the search circle in the closest directions and the exclusion of the most common matches that are not related to microorganisms and mushrooms interrelations were used. Not related sources were excluded by the abstract content.

2. Lignocellulosic substrate and biological efficiency

Most macrofungi are obtained by large-scale solid-state fermentation – the simplest and most valuable method ensuring higher productivity, enzyme efficiency, and stability, as well as reduced production costs and environmental pollution [19,46,47]. Solid-state fermentation allows the utilization of various lignocellulosic agro-industrial wastes. The degree of utilization of lignocellulosic substrates by mushrooms varies over a wide range and depends on the fungal species and composition of the substrate. Thus, the biological efficiency of the use of rice straw by *Pleurotus ostreatus* (oyster

mushroom) varied between 25.6%–84.6% and by *Volvariella volvaceae* only 10%–15% [10]. The utilization efficiency of rice husk by *P. ostreatus* was 9.5% [10], which may be due to the tough structure of rice husks despite the similar established ratio of cellulose, hemicellulose, and lignin in straw and husk used. Studies have shown that grinding cotton straw to a particle size of 0.75 mm maximized the lignocellulose degradation by *P. ostreatus* [48]. In practice, however, such a procedure cannot be implemented for economic reasons; therefore, other ways to increase the biological efficiency of substrate use are required.

Currently, various technologies for growing mushrooms are being considered, including the traditional cultivation of fruiting bodies on tree logs and beds, as well as on other substrate media, such as growing in bags, bottles, etc. Numerous mushroom cultivation substrates can be used in both composted (champignon *Agaricus bisporus* and straw mushroom *Volvariella volvaceae*) and non-composted (*Pleurotus* spp., *Lentinus* spp., *Ganoderma* sp., *Auricularia* sp., *Hypsizygus marmoreus*, *Pholiota* sp.) form [49]. However, *Pleurotus ostreatus* can also be cultivated on fermented rice straw [14] or short-term composted substrate [50]. The rate and efficiency of substrate utilization depend on the mushroom species and the type of substrate, its structure, and chemical composition. For example, *V. volvaceae* can grow without special substrate preparation [51], but the level of biological efficiency remains extremely low under such conditions [52]. Substrate composting in many cases makes it possible to increase the selectivity of the substrate for several fungi and thereby affect their growth parameters and the efficiency of the use of lignocellulosic compounds. The most significant and complex stage is the selective pre-treatment of the substrate by two-phase composting for the cultivation of the fungus *A. bisporus* [51]. Substrate composting is a prerequisite for the cultivation of mushrooms of the *Agaricu*s genus. The degradability of lignocellulosic substrates and their availability to compost microbiota and *A. bisporus* were shown to be the overriding factors for optimizing the composting process with different straw types and carbon/nitrogen ratio [15,49,53,54]. Under the same composting conditions, the rice straw with the soft texture was decomposed significantly and lost availability to the mushroom lignocellulose as compared to wheat straw. Reed straw, on the other hand, due to its structure and low water holding capacity, turned out to be not favourable for the use of a carbon resource by the mushroom. Composted wheat straw was the best substrate for *A. bisporus* and one-year-fermented horse manure for other *Agaricus* species [49]. A study of the composting process of the six most common types of agro-industrial waste in China [54] showed that they differ in decomposition activity under the same composting conditions, wherein wheat, rice, and cotton straws caused significantly higher *A. bisporus* yields than other wastes. Wang L et al. [15] also showed that rice straw compost is as effective for *A. bisporus* growth and productivity as conventional wheat straw compost.

For the cultivation of oyster mushrooms, wheat straw is usually noted as the best substrate [49]. Good results have also been obtained using composted sawdust. The highest yield of *Pleurotus eryngii* biomass was noted when using wheat straw, corn cobs, and ramie and kenaf stalks, and for *Pleurotus cysidiosus*, the corn cobs and sugar cane cake were the optimal substrates. *Lentinus edodes* demonstrated better growth results with the use of sugarcane bagasse and leaves, as well as barley straw, while *Lentinus sajor-caju* grew better with soya stalk and rice straw. For *Ganoderma lucidum* the type of wood from which the sawdust was made mattered much [49]. Wheat straw was optimal for *Agrocybe cylindracea* and rubber tree sawdust with rice straw in equal parts showed very good efficiency in *Flammulina velutipes* production. The combination of various substrates and the introduction of additives, for example urea, leads in many cases to a significant increase in the

biological efficiency of lignocellulose utilization. Such additions are largely based on the optimal C/N ratio for various mushrooms. Thus, the optimal C/N ratio for *Agaricus* mushrooms is 19–28, for *Flammulina* 30, *Pleurotus* 45–60, *V. volvaceae* 40–60, and *Ganoderma lusidum* 70–80 [10]. Often, the use of non-traditional substrates in the form of additives to the optimal substrates shows good results [49]. Thus, wheat straw, both alone and in combination with spent coffee grounds and composted sawdust, showed the best results in the accumulation of *P. ostreatus* biomass. Wherein, woodchips were the most effective as additives to *A. bisporus* substrates. For *Auricularia polytricha*, the supplements of oil palm frond and empty fruit bunch were better than the sawdust only.

The chemical composition and biological value of cultivated mushrooms are, in turn, highly dependent on the constitution of the substrate and the growing technique [7,55–60]. The optimal growth conditions required by mycelium to improve quality and yield are considered, as well as the biological mechanisms responsible for their therapeutic properties and their application [61]. It is shown that mushroom yield can be increased by 5%–20% using millet straw and additives balancing the nitrogen content [62]. One of the main directions for increasing the agronomic potential of fungi is currently enriching the cultivation medium with various nutrient additives that cover the lack of nutrients [63,64]. Thus, the use of nano-urea can increase the protein content in fungal cells [65] and the addition of nano fertilizer containing amino acids helps to increase the yield of mushrooms and enrich them with protein and essential amino acids [66].

In solid-state fermentation, the amount of inoculum, moisture content, and cultivation time also must be considered [67]. The critical environmental factors for the induction of fruiting, are nutrients, temperature, and lighting conditions. Higher levels of nitrogen and carbon in the medium inhibit the fruiting bodies' incipience in many fungi, while their induction is triggered by lower concentrations of these nutrients [68].

The possibility of maximizing the value and profitability of macrofungi production is currently being considered [13]. In this regard, much attention from researchers in this direction is drawn to the effect of microorganisms on the growth and production of mushrooms.

3. Input of microorganisms into mushrooms cultivation

When cultivating mushrooms, three groups of microbial communities should be taken into account, namely: communities associated with substrate preparation, its colonization by mushroom mycelium, and fruiting [49].

3.1. Substrate processing for mushroom cultivation

The need for pre-treatment of the substrate for growing mushrooms is one of the main problems of mushroom cultivation. Cellulose-containing raw materials, even of the best quality, contain numerous dormant forms of mold fungi that become active when moistened and compete with the higher fungus for food sources, inhibiting its development and accumulating mycotoxins that are not destroyed even when exposed to high temperatures for many hours. The methods of mushroom production involving substrate sterilization are energy-intensive, economically disadvantageous, and require adherence to strict asepsis during further cultivation. Failure to comply with strict aseptic rules leads to a significant decrease, up to a complete loss, of the yield. Reducing energy consumption is the main direction of further work in mushroom cultivation areas to receive more profit and decrease

environmental impact [69]. The use of fungicidal preparations has a positive effect but significantly lengthens the growing period, increases the cost of the final product, and also poses an environmental threat due to the emergence of resistant forms (Figure 1).

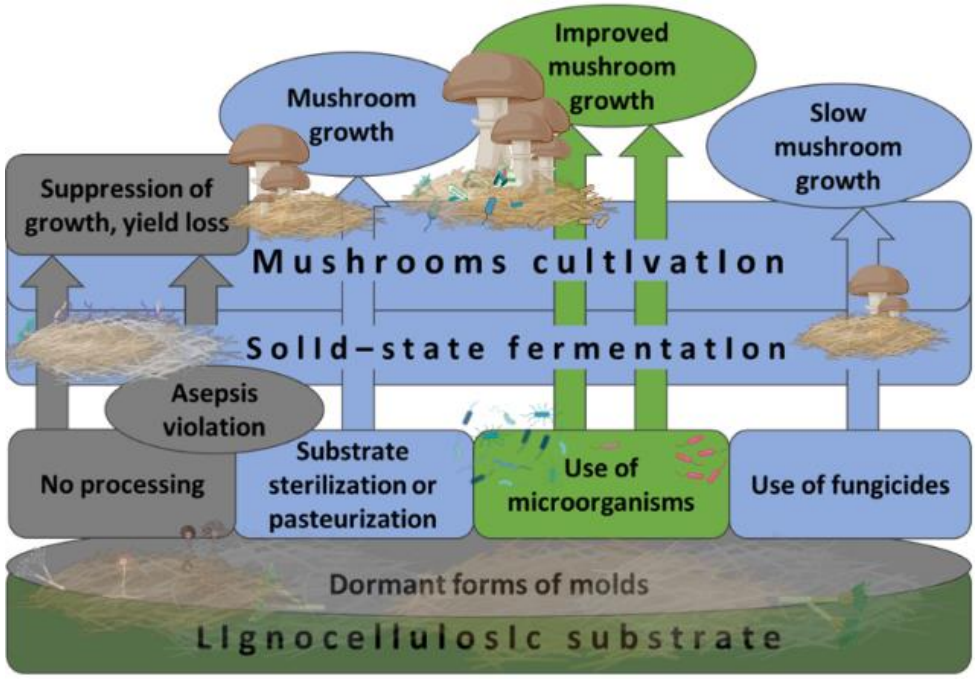

Figure 1. Various strategies for protecting the substrate from competing molds (Created using BioRender.com).

Microorganisms creating a selective substrate that provides mushrooms with nutrients and protects them from competitors are of particular interest to ensure a controlled cultivation process.

3.1.1. Microbial communities associated with substrate composting for *Agaricus bisporus*

Substrate composting is a prerequisite for the cultivation of mushrooms of the genus *Agaricus*, as it inhibits the development of competing microflora and leads to the transformation of the substrate into a nutrient-rich humus-containing medium. Therefore, microbial successions associated with the composting of the substrate for their cultivation have been studied in the most detail. *Agaricus* cultivation compost is traditionally made from wheat straw, manure, and gypsum [70]. The components are mixed to achieve an optimal C/N ratio (25:1). Composting is divided into several stages: straw moistening (3–10 days), thermophilic composting (Phase I, 70–80 ℃, 6–14 days), pasteurization (Phase II, 58–60 ℃, 2 days), and conditioning at mesophilic temperatures (45 ℃, 2–3 days) [71]. At a higher pasteurization temperature (68 ℃), the growth of the mycelium of the fungus is slowed down due to too high ammonia emissions [72]. *A. bisporus* is added to the prepared substrate in the form of grain spawn. The complete colonization of the compost by *Agaricus* mycelium lasts about 16 days, after the growth of fungal mycelium, compost is covered with a peat casing layer (usually commercial) [18,73]. Microorganisms (beneficial or not) coexist with *A. bisporus* in two heterogeneous microenvironments; compost and cover layer, which differ in nature and function.

Various populations of bacteria and fungi are involved in the processing of various lignocellulosic agricultural waste into a selective substrate by thermophilic composting (Table 1). First, they break down easily accessible compounds (free sugars and amino acids) and release ammonia. Then, during the composting process, 50%–60% of cellulose and hemicellulose is degraded [74] and excess ammonia is assimilated [51]. Consumed components are converted into microbial compost biomass, which is the main source of nutrition for the mycelium of the mushroom [51,62,74,75] at the initial stages of its growth. In the future, there is a gradual destruction of more than 50% of the lignin of the lignocellulosic substrate by the basidiomycete fungus with the production of fruiting bodies [51,74,76].

In recent years, detailed studies of the microbiomes of *A. bisporus* intended compost have been carried out. The greatest differences in the representation and abundance of microbial taxa are noted in the phase of mixing and moisturizing the components. However, these fluctuations are mainly related to the initial substrate microbiota. During this period, the utilization of soluble sugars, starch, and proteins along with the active reproduction of various groups of microorganisms takes place [70]. Later, in the first and second phases of composting, most researchers note the dominance of three main phyla: *Bacillota* (synonym *Firmicutes*), *Pseudomonadota* (synonym *Proteobacteria*), and *Actinomycetota* (synonym A*ctinobacteria*) (Table 1).

The increase in the abundance of thermophilic *Deinococcota* (synonym *Deinococcus-Thermus*) is also characteristic during the heating of the compost to 70–80 °C with a further decrease in the abundance of this phylum [70]. The most common genera of microorganisms in different periods of the first thermophilic phase are *Thermobispora*, *Thermopolyspora* (*Actinomycetota*), *Ruminiclostridium*, *Thermobacillus*, *Bacillus* (*Bacillota*), *Pseudoxanthomonas* (*Pseudomonadota*), *Thermus* (*Deinococcota*) [18,77,78]. Fungi are usually dominated by various *Ascomycota* [70,76,78–80], often from the *Chaetomiaceae* family (*Mycothermus*, *Humicola*).

In phase II (pasteurization), microbial communities change. The abundances of *Deinococcota* and *Bacillota* decrease [18,72,73,78,81], while the thermophilic fungus *Mycothermus* [70] and *Actinomycetota* phylum abundances increase [18,73,78]. Some authors note an increase in *Chloroflexota* (synonym *Chloroflexi*) [18,82]. The most frequent genera in the pasteurization phase are *Thermobispora*, *Thermopolyspora*, *Thermobifida*, *Microbispora* (*Actinomycetota*), *Thermobacillus* (*Bacillota*), and *Pseudoxanthomonas* (*Pseudomonadota*) [77–79,83].

When using other straw types, except for wheat, the same dominant phyla and genera of microorganisms were noted. There are also some indications of a higher content of *Bacteroidota* in the 2nd phase of composting and the abundance of some other genera. However, more research is needed to clarify the contribution of these microorganisms to substrate composting.

The growth of thermophilic microorganisms in phase I is associated with an increase in cellulase/β-glucosidase, xylanase, protease, chitinase, and overall microbial activities [70]. The gradual growth of these enzyme activities continues until the end of the conditioning phase. The dominant groups of microorganisms in the first two phases of composting are associated with the degradation of cellulose and hemicellulose of the substrate [79]. The major enzymes involved in lignin degradation are known to be laccase, dye peroxidase, and class II peroxidases including lignin peroxidase, manganese peroxidase, and versatile peroxidase. Out of them, only laccase and manganese peroxidase can directly oxidize phenolic lignin components [84]. Several researchers have shown that the degradation of lignin is caused exclusively by the higher basidiomycete fungus and is not associated with compost microorganisms. Thus, in the works of Jurak et al. [74], and Carrasco et al. [76], lignin was not degraded during composting before inoculation of *Agaricus* mushroom. Similar

data were obtained by Qin et al. [85] and Zhang et al. [18] on the absence of laccase and manganese peroxidase activity in the compost by the end of phase 2 of composting. However, studies by Zhang et al. [18] also showed a decrease in the total lignin content in the millet straw substrate by 8%–17% by the end of the 2nd phase of composting. An assumption was made that the compost microbiota had other enzymes that degrade lignin, in addition to laccase and manganese peroxidase. In studies by [86], the lignin loss was between 20% and 30% during weed composting and between 16% and 21% during *A. bisporus* cultivation. The dominant bacteria were *Prevotella* (*Bacteroidota*), *Bacillus* (*Bacillota*), *Thermus*, *Truepera*, *Caldicoprobacter* (*Deinococcota*), *Thermopolyspora* (*Actinomycetota*), and *Pseudoxanthomonas* (*Pseudomonadota*). According to Duran et al. [81], delignification by the end of phase II of composting was 30%. Various researchers have noted the production of ligninolytic enzymes by *Bacilli*, *Alpha*- and *Gammaproteobacteria*, and *Actinomycetes* and their contribution to the dissolution and decomposition of lignin in lignocellulosic waste [77,81,83,87,88]. Shen et al. [89] showed a positive correlation between lignocellulose degradation and *Sphingobacterium*, *Pseudomonas*, *Bacillus*, and *Actinomycetota* content during pig manure and straw fermentation. The importance of microbial functional diversity in the production of auxiliary lignocellulose degrading enzymes is emphasized. Chauhan (2020) carried out a detailed analysis of the roles of various bacterial enzymes in the complete depolymerization of lignin [90]. Chauhan described a whole range of lignin-depolymerizing auxiliary enzymes and lignin-modifying enzymes produced by various bacterial genera. The discovery of new bacterial enzymes within known families [90] also requires closer attention from researchers.

Considering the above data, the generally accepted ideas about the weak contribution of bacteria to the decomposition of lignocellulosic waste seem to be largely underestimated. A possible reason for the discrepancies in investigations of different authors regarding the lignin content may be the various duration of the composting phases. It should be taken into account that the relative lignin content increases as a result of cellulose and hemicellulose utilization and cannot be evidence of the absence of its decomposition. It should also be noted that most of the experimental research is mainly focused on the assessment of laccase production, the level of which, according to numerous data, increases with the development of higher fungus mycelium. However, the absence of laccase synthesis genes in the macro genome of *A. bisporus* indicates the other origin of this enzyme. The investigations aimed at elucidating the genetic origin of laccase and studying the activity levels of a wide range of enzymes associated with lignin degradation in varying conditions will help shed light on the true contribution of individual representatives of bacterial and fungal organisms to the degradation of lignocellulose.

Table 1. Involvement of microorganisms in bioconversion and substrate pretreatment during *Agaricus bisporus* cultivation.

Substrate	Predominant and abundant microbial taxa		Reference
	Phase I (PI), thermophilic	Phase II (PII), pasteurization	
Raw wheat straw, manure, and gypsum	9th day: *Actinomycetota – Corynebacterium* (more abundant at 30 cm), *Firmicutes* (*Clostridia*), Fungi (more abundant at 30 cm). Fungi: subsurface (30 cm) - *Thermomyces* 38%, *Aspergillus* 15%; 60 cm - *Acremonium* 22%, *Humicola* 15%. *Deinococcota* are present.	After conditioning: *Actinomycetota – Thermopolyspora* 46%, *Microbispora* 21%. Fungi: *Humicola* 75%, *Chaetomium* 15%.	[79]
Wheat straw-bedded horse manure, dried poultry manure, dried distiller's grain, and gypsum.	*Bacillota* - *Caryophanales* (synonym *Bacillales*), followed by *Pseudomonadota* and *Actinomycetota*.	*Pseudomonadota*, *Actinomycetota*, and *Bacteroidota* (*Bacteroidetes*). *Clostridiales*, *Lactobacillales*, and *Micrococcales. Caryophanales* decreased but are still predominant. During conditioning: an increase of unclassified phylum.	[72]
Wheat straw, rapeseed cake, gypsum, mono-calcium phosphate, ammonium sulfate, and urea.	Bacteria: *Bacillota*, *Pseudomonadota*, *Actinomycetota.* Fungi: *Ascomycota*, and *Basidiomycota*. 9th day: *Thermobispora bispora*, *Pseudo-xanthomonas taiwanensis*, and *Chytridiomycota.* 12th day: *Thermobispora*, *Thermopolyspora*, *Ruminiclostridium*, *Thermobacillus*, *Bacillus*, and *Chytridiomycota*.	Bacteria: *Bacillota* (*Ruminiclostridium*, *Thermobacillus*, and *Bacillus*), *Pseudomonadota* (*Thermobispora*, *Thermopolyspora*), *Actinomycetota.* Fungi: *Ascomycota* (*Mycothermus thermophilus* and *Phaeophleospora eugeniae*), *Basidiomycota*, and *Chytridiomycota* (*Gonapodya polymorpha*).	[80]
Wheat straw-bedded horse manure, dried poultry manure, and gypsum; after 3 days - dried distiller's grain.	PI end: *Bacillota* (*Bacilli* and *Clostridia*), and *Deinococcota* (*Thermus)*. Reduction in *Actinobacteriota* (large amounts of *Thermobifida*), and *Pseudomonadota* (with 40% of *Rickettsiales*, then *Leitomonas* and *Chelativorans*).	*Pseudomonadota*. Reduction of *Bacillota* (twice) and *Deinococcota* (sharply). Growth of *Actinobacteriota*.	[73]

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Substrate	Predominant and abundant microbial taxa		Reference
	Phase I (PI), thermophilic	Phase II (PII), pasteurization	
Wheat straw, gypsum, chicken manure, and additives.	*Bacillus*, *Paenibacillus*, unclassified *Clostridia* (*Bacillota*), and *Pseudomonadota* followed by *Ruminofilibacter* (*Bacteroidota*). PI end: *Thermus*, thermophilic *Sphingobacterium*, and *Luteimonas* made up 6% of the bacterial community. Fungi: *Mycothermus thermophiles* (*Ascomycota*, *Chaetomiaceae*).	Mid-PII: *Mycothermus thermophilus* - 80% of the fungal population.	[70]
Various conditions	*Bacillota* (*Bacillus*, *Ruminiclostridium*, and *Thermobacillus*), *Pseudomonadota*, *Actinomycetota*, and *Deinococcota*. Fungi: Domination of Ascomycota; *Gibellulopsis*, *Alternaria*, *Microidium*, *Chaetomium*, *Gonapodya*, and *Trichoderma*.	Domination of ascomycetes, *Bacillota*, *Pseudomonadota*, and *Actinomycetota*. Decrease in *Bacillota*, increase in *Actinomycetota*. *Pseudoxanthomonas* (*Pseudomonadota*), *Thermobacillus* (*Bacillota*), *Thermopolyspora*, *Thermobifida*, and *Thermobispora* (*Actinomycetota*) are the most frequent. Fungi: *Microidium*, *Chaetomium*, *Mycothermus*, and *Gonapodya*.	[78]
Commercial crop production	*Bacillota*, *Pseudomonadota*, *Deinococcota*, and *Ascomycota*.	*Pseudomonadota*, *Bacteroidota*, and *Actinomycetota* (*Actinomadura*). Fungi - *Ascomycota*.	[76]
Wheat straw, chicken manure, peanut meal, and gypsum.	-	Bacteria 93,17%: *Pseudomonadota* (*Pseudoxanthomonas*), *Actinomycetota* (*Thermobifida*, *Thermostaphylospora*, *Thermopolyspora*), *Chloroflexota* (synonym *Chloroflexi*), *Planctomycetota* (synonym *Planctomycetes*), *Bacteroidota* (*Bacteroidetes*), and *Bacillota*. Genera *Sphaerobacter* (*Thermomicrobiota*), *and Rhodothermus* (*Rhodotermota*).	[82]

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Substrate	Predominant and abundant microbial taxa		Reference
	Phase I (PI), thermophilic	Phase II (PII), pasteurization	
Industrial PII substrate	PI end: *Bacillota*, *Deinococcota*, *Actinomycetot*a, and *Pseudomonadota.*	PII end: *Bacillota* (*Bacilli*) and *Deinococcota* decreased; *Pseudomonadota* (*Gammaproteobacteria* and *Alphaproteobacteria*) became most abundant followed by *Bacteroidota* (*Bacterioidia*).	[81]
Cotton straw/wheat straw/rice straw/corncob substrate/corn straw substrate/bagasse substrate, rapeseed cake, gypsum, mono-calcium phosphate, ammonium sulfate, and urea.	3d day: *Bacillota*, *Pseudomonadota* (*Pseudoxanthomonas; Vulgatibacter - Deltaproteobacteria*), and *Actinomycetota* (*Thermopolyspora*, *Thermobifida*, *Thermobispora*), and *Bacteroidota*. Top 5 genera during 6 days: *Pseudoxanthomonas*, *Thermobispora*, *Thermo-polyspora*, *Thermobifida*, and *Thermobacillus;* and after 10 days: *Thermobispora*, *Pseudomonas*, *Thermopolyspora*, *Thermobifida*, and *Ruminiclostridium*.	*Bacillota*, *Pseudomonadota*, *Actinomycetota*, *Gemmatimonadota*. Top 5 genera: *Thermobispora*, *Thermo-polyspora*, *Thermobifida*, *Microbispora*, *and Thermobacillus.*	[77]
Millet straw, chicken manure, bean meal, and gypsum.	*Actinomycetota*, *Deinococcota*, and *Pseudomonadota* were increased during the phase, *Firmicutes* were stable, and *Bacteroidetes* decreased. Genera: *Ruminiclostridium*, *Bacillus*, *Thermobacillus*, *Lactobacillus* и *Caldicoprobacter* (*Bacillota*), *Thermus* (*Deinococcota*), *Bacteroides*, *Rhodothermus* (*Bacteroidota*), *Thermobifida*, and *Salinispora* (*Actinomycetota*).	*Proteobacteria* and *Chloroflexi;* some increase in *Actinomycetota*, gradual reduction in *Deinococcus-Thermus*, and a decline in *Bacillus* abundances.	[18]
Rice straw/ corn stalks, cow dung, soy flour, superphosphate, gypsum, and lime/corn flour.	*Pseudomonadota* (*Pseudomonas*, *Cellvibrio*), *Bacillota* (*Bacillus*, *Paenibacillus*), *Actinomycetota* (*Thermomonospora* and *Thermasporomyces*).		[83]

3.1.2. Substrate preparation for *Pleurotus ostreatus* cultivation

Table 2. Microbial communities during short-term composting of *Pleurotus* intended substrates.

Substrate	Conditions	Phase I (PI) thermophilic	Reference
Crude wheat straw, alfalfa	PI: 7 days, 65-70°C; PII 65°C 18 h, 48C for 48 h.	Fungi: *Thermomyces lanuginosus*, *Myceliophthora thermophile*, *Rhizomucor pusillus*, and *Aspergillus fumigatus.*	[92]
Sugarcane straw, wheat bran (C/N 65:1), limestone, and gypsum.	PI 5, 10, or 15 days; PII 59.5°C for 8h, conditioning for 3 days.	*Pseudomonadales*, *Bacillales.* In the beginning: *Pseudomonas* dominated In the end: *Acinetobacter* was near 80%.	[93]
Peach sawdust, wheat bran, corncob, and quicklime, moisture 70%.	58°C for 4-5 days.	2nd day: *Bacillota* (dominated), *Actinomycetota*, *Pseudomonadota*, and *Chloroflexota*. Genera - *Caldibacillus* and *Thermobacillus* (*Bacillota*), *Thermobispora* (*Actinomycetota*). 4th day – a decrease in total *Bacillota*. Genera: *Ureibacillus*, *Symbiobacterium*, *Thermobispora*, *Thermopolyspora.* 5th day – *Thermopolyspora*, *Thermobispora*, unclassified *Limnochordaceae*. Fungi: *Ascomycota* - *Candida*, *Mycothermus*, and *Aspergillus*.	[50]
Peach sawdust, corncob, cotton seed hull, corn flour, and lime. Moisture 60%.	11 days, 57-67°C from 3d till 10th day, turning every 3 days.	Bacteria most abundant during the whole period: *Bacillota*, *Actinomycetota*, *Pseudomonadota*, *Chloroflexota*, and *Bacteroidota*. Fungi: *Ascomycota* (*Mycothermus*, *Aspergillus*, *Thermomyces*, and *Issatchenkia*). At 9th day: genera *Caldibacillus*, *Symbiobacterium*, *Thermobacillus*, and *Ureibacillus*.	[94]
Corncob, bran, lime, and urea. Raw materials: water 1:2.5.	4th day 71°C, followed by a gradual decrease.	*Bacillota* replaced *Pseudomonadota* after 2nd day and was maximal during 4-6 days. At 8-10 days *Pseudomonadota* and *Actinomycetota* increased.	[95]
Cottonseed hull 38.6%, corn cob 46.5%, bran, fertilizer, lime (C/N 40:1, 50:1), moisture 65%.	7 days	*Bacillota*, *Pseudomonadota*, *Bacteroidota*, and *Actinomycetota*. 2 days: *Kurthia*, *Acinetobacter*, and *Sphingobacter*; 7 days: *Caldibacillus* (class *Bacilli*), *Limnochordaceae* (*Limnochordia*), and *Caproiciproducens* (*Clostridia*).	[96]

Mushrooms of the genus *Pleurotus* attract a lot of attention as an object of cultivation because

they require a shorter growth time than other edible mushrooms. The substrate for their growth does not require sterilization, only pasteurization is sufficient, which is cheaper. *Pleurotus ostreatus* needs little environmental control as their fruiting bodies are less susceptible to pest attacks [91]. As a consequence, microbiome studies associated with *P. ostreatus* substrate composting are limited.

For *Pleurotus* mushrooms cultivation, the short-term 7–11 days composting method with a thermophilic phase duration of 4–9 days is most often used (Table 2).

The data obtained by various authors are heterogeneous, which is explained by differences in the substrates used and the timing of composting. The use of sugarcane straw as a substrate resulted in the dominance of *Acinetobacter* [93]. When using peach sawdust, *Bacillota*, *Actinomycetota*, *Pseudomonadota*, *Chloroflexota*, *Bacteroidota*, and thermophilic *Ascomycota* were present during composting. *Thermopolyspora* and *Thermobispora* were noted after 5 days, and the dominance of bacterial genera belonging to *Bacillota* (*Caldibacillus*, *Thermobacillus*, *Ureibacillus*, and *Symbiobacterium*) was shown after 9 days [50,94]. The absence of *Actinomycetota* genera among dominated species and the appearance of *Symbiobacterium* (class *Clostridia*) may indicate the creation of anaerobic conditions. Cottonseed hull composting also led to the dominance of *Bacillota*, belonging to three different classes. The reason seems to be the use of finely structured substrates such as sawdust and cottonseed, which favor anaerobic conditions when wet.

The study of correlations between physicochemical properties and microbial communities carried out by Guo et al. [941 showed, that *Actinomycetota*, *Pseudomonadota*, and *Eurotiomycetes* fungi played key roles in hemicellulose and lignin degradation. *Bacillota's* role was positive in cellulose degradation but dual in hemicellulose destruction. Among fungal microorganisms, *Sordariomycetes* made a positive contribution to the destruction of cellulose and a negative contribution was made by *Eurotiomycetes*. Kong et al. [95] showed a negative correlation between laccase activity and pH, water content, organic matter, and C/N ratio. The reduction in carbon content during the decomposition of cellulose and hemicellulose creates conditions for the further decomposition of lignin. Therefore, the dissimilarity in the degrees of lignin utilization by different authors during the preparation of the substrate for *A. bisporus*, noted in the previous section, can come both from differences in cultivation conditions and from different carbon-to-nitrogen ratios. The use of various substrates for mushroom cultivation also leads to a significant discrepancy in results. Studies by Vajna et al. [92] conducted during substrate production did not reveal characteristic bacterial microorganisms for the substrate preparation period. A conclusion was made about the "functional redundancy" of bacterial communities and the decisive importance of cultivation conditions in increasing the yield of the fungus. However, it should be noted that in Vajna's experiments, compost microbial diversity was investigated in comparison with the mushroom yield, while the studies of microbiomes associated with mycelial growth and formation of fruiting bodies were not carried out.

The other effective way to prepare a substrate for *P. ostreatus* cultivation is an anaerobic fermentation with the use of antagonistically active antifungal bacillary strains eliminating the need for sterile conditions [97]. The use of such "protection" not only minimizes the risk of contamination of the substrate with competitive microorganisms but also makes it possible to obtain a high-quality nutrient medium for mushrooms. The selectivity of the medium increases the yield of *Pleurotus* fruit bodies by 5%–10%. However, this method does not exclude thermostatic heating (pasteurization). The pre-processing of raw materials by solid phase fermentation using cellulolytic bacteria *Bacillus coagulans* can eliminate the stage of substrate sterilization when growing the oyster mushroom [98] preventing the development of extraneous microflora including molds. To grow the mycelium of the

mushroom for obtaining a protein feed product, it was proposed to use the method of solid-state fermentation of cellulose-containing crop waste (straw - wheat or rice, sunflower husks, cereal husks, etc.) implemented by the type of ensiling [99,100], which helps to increase its palatability and digestibility. Facultative anaerobic acid-tolerant cellulolytic bacteria of the genus *Bacillus*, which are antagonistic to molds, were used as a starter culture [98,101–104]. After 25–30 days of ensiling in standard conditions, the resulting substrate was neutralized and used as a selective medium for *P. ostreatus*, contributing to the protection of the process from extraneous microflora. At the same time, the efficiency of accumulation of mushroom mycelium when using multistrain starter cultures, including lactic acid bacteria and propionibacteria (after neutralization with gypsum) was significantly higher.

Based on the published data, the preparation of the substrate for oyster mushrooms can be carried out without observing aerobic conditions, in contrast to the composting of the substrate for *A. bisporus*. This greatly simplifies the process of preparing the substrate. However, further studies are required to confirm this conclusion.

3.2. Microorganisms associated with mushrooms' mycelial growth and fruiting bodies formation

At the stage of filling the substrate with *Agaricus* mycelium, some changes were noted in the structure of microbial communities. In the phase of colonization of the substrate by mycelium, the bacterial communities also dominated. The main part of them was comprised of *Actinomycetota*, *Bacteriodota*, *Chloroflexota*, *Deinococcota* (genus *Thermus*), *Bacillota*, *Pseudomonadota* (genera *Pseudomonas*, *Rhizobium*, and *Stenotrophomonas*), and the Unclassified bacterial phylum [105]. Throughout the growing process of *A. bisporus*, a decrease in the abundance and activity of *Bacteriodota* and *Deinococcota* and an increase in the abundance and activity of *Actinomycetota* and *Bacillota* were noted in the composted substrate. *Planctomycetota* and *Verrumicrobia* also significantly increased [82,105]. Phyla *Chloroflexota* and *Pseudomonadota* remained active despite reduced abundances. Genera *Thermobifida*, *Thermostaphylospora*, *Thermomonospora* (*Actinomycetota*), *Sphaerobacter* (*Thermomicrobiota*), and *Chelatococcus* (*Pseudomonadota*) were the most abundant in Chang et al. [82] research group investigations, but *Thermopolyspora*, *Rhodothermus*, and *Pseudoxanthomonas* decreased. *Sandaracinaceae* bacterium (*Myxococcota*) and fungi *Spizellomyces*, *Rozella*, and *Basidiobolus* were also enhanced. However, in the study of Thai et al. [70], *Pseudoxanthomonas taiwanensis* was the dominant microorganism until the end of mycelial growth. Other studies indicate an increase in the abundance of *Bacillota* and *Pseudomonadota* in the process of substrate colonization by the mushroom [106].

At the stage of filling the substrate with mycelium, a sharp increase in laccase production was noted; the enzyme level was maximal during pinning, and then fell after cropping flushes [18,85]. These data are consistent with the detection of laccase production during the growth of the fungus *A. bisporus* under in vitro conditions [107]. However, whole genome sequencing of *A. bisporus* indicates the absence of laccase synthesis genes in the macro-genome of the fungus [108]. According to data from Morin and coauthors [108], *Agaricus* mushrooms are adapted to partially degraded and humified plant litter. They have only two genes (coding manganese peroxidases) of 6-26 ligninolytic enzymes characteristic of white rot lignin-degrading fungi. At the same time, *Agaricus* has a wide set of enzymes of protein families for metabolizing derivatives of lignin and other polymers abundant in humicolous habitats. Chang et al. [82] showed that the increase in laccase activity in the compost during mycelial

growth is mainly associated with bacteria from the genus *Thermostaphylospora*. These data suggest that these actinobacteria may play a synergistic role in lignin degradation along with *A. bisporus* mycelium. Other studies indicate a synergistic relationship between *Agaricus* and Gram-negative bacteria of the genus P*seudomonadota* [106]. It is known that *A. bisporus* is not capable of fruiting under axenic conditions and without applying a cover layer of peat to the surface of the substrate overgrown with mycelium [109]. The addition of a cover layer containing microorganisms that are not present in the composted substrate contributes to the fruiting of the fungus. It has also been shown that the introduction of *Agaricus* spawn stimulates the active reproduction of microorganisms in the cover layer [109–111], indicating syntrophy between the bacterial microorganisms of the integumentary layer and the higher fungus. According to Zarenejad et al. [111], fluorescent *Pseudomonas* spp. accounted for 14%–41% of the total number of bacteria present in the cover layer, and their populations increased during the cultivation of *A. bisporus*, which positively affected the yield of the mushroom. It has been shown that *Pseudomonas putida* and *Pseudomonas tolaasii* form a close association with *A. bisporus* hyphae [109,112].

The number of pseudomonads declines towards the end of the second flush. The other microorganism associated with mycelial strands is *Pedobacter* (*Sphingobacteriaceae*, *Bacteroidota*) [109]. Data on the quantitative content of *Pseudomonas* during colonization of the *A. bisporus* substrate [105,106], which at first glance appear to be inconsistent, are most likely associated with differences in the time intervals of the studies since the introduction of the fungus inoculum simultaneously promotes the growth of individual microorganisms and reduces their abundance in the substrate due to their attachment to the surface of the mycelium.

Interestingly, in contrast to the decrease of *Bacteroidota* abundance in the substrate, there was a simultaneous increase in the abundance of this taxon in the mushroom caps [73]. The dominant genera of this phylum were *Flavobacterium* and *Pedobacter*. *Pseudomonadota*, along with *Bacteroidota*, constituted the majority of bacterial communities in mushroom caps, and *Pseudomonas* was the most numerous genus (33%) followed by *Flavobacterium* and *Pedobacter*. A closer attachment to the hyphae of individual *Bacteroidota* and *Pseudomonadota* with further penetration into the fruiting bodies is the most likely explanation for the reduction of these phyla in the substrate in the phase of *Agaricus* mycelium colonization.

In the casing layer, four main bacterial phyla (*Psudomonadota*, *Actynomycetota*, *Bacillota*, and *Bacteroidota*) are present [78,113]. The most abundant genera are *Sphingobium*, *Pseudomonas* (*Pseudomonadota*), and *Flavobacterium* (*Bacteroidota*) [78]. Siyoum et al. [114] also showed the presence of not only *Gammaproteobacteria* but also *Alpha*-, *Beta*-, and *Deltaproteobacteria*.

An increase in the relative abundance of *Enterobacteriaceae* and *Pseudomonadaceae* in *P. ostreatus* was shown by Ban et al. [115]. The study of bacterial diversity in *Pleurotus eryngii* revealed the different distributions of microbial species in the cap and stem [116]. This suggests that they probably represent different microbial niches. *Bacillota* predominated in the mushroom cap, and *Actinomycetota* abounded in the stipe. It can be assumed that the identified endobacteria play a symbiotic role, similar to endophytic bacteria in plants.

Microorganisms living in the fruiting bodies of higher fungi are poorly studied. The compost and casing layer are the two main possible sources of fungal colonizing bacteria [117]. Bacteria from the soil can colonize the hyphae and then enter the fruiting body. Vieira and Pecchia [73] showed that compost, casing soil, and fruiting bodies represented different niches for the bacteria in the cultivation system, but at the same time, bacterial exchange between microenvironments could occur for part of

the community. Bacteria can associate with mushrooms both as hyphae surface colonizers and as endohyphal symbionts. Hyphae surface colonizers form multispecies biofilm communities that feed on either fungal exudate [118] or fungal cell wall components and cytoplasmic substances [119,120]. In contrast, endohyphal bacteria colonize the interior of fungal hyphae. One way they can enter is through the production of chitinases, which break down chitin oligomers in the fungal cell wall and thus facilitate bacterial entry [121].

The casing layer is the main source of microorganisms that stimulate fruiting and subsequently populate mushroom caps. The cultivation substrate is also the main source of fungal infections, which can lead to losses of up to 100% of the yield of fruiting bodies. Many *Ascomycot*a fungal pathogens like *Cladobotryum dendroides*, *Lecanicillium fungicola*, *Moniliophthora perniciosa*, and *Trichoderma* spp. are found in the casing layer [113].

3.3. Antagonistic and pathogenic microorganisms during mushroom cultivation

Mycoparasites cause great damage to commercial mushroom farms around the world. The diseases caused by *Lecanicillium* spp., *Cladobotryum* spp., *Mycogone* spp., *Trichoderma* spp., *Coprinus* spp., *Sependonium* spp., *Sclerotium rolfsii*, *Cephalothecum roseum*, *Gliocladium roseum*, and *Diehliomyces microsporus* limit the yield and quality of the crop, reducing the area under cultivation [122–124]. However, such an infecting fungus as *Trichoderma* can also be hemibiotrophic, existing for a long time in the host cells and causing minimal damage [125]. Among the bacterial pathogens, species of the genus *Pseudomonas* dominate [126–128]. The most frequent is *Pseudomonas tolaasii* causing brown blotch disease. However, some other bacteria, namely Pantoea and Ewingella, are also characterized as causative agents of mushroom diseases [122,123]. According to the data of Suarez et al. [124], nearly all isolates from mycelial-colonized straw and healthy spawn inhibited the growth of *P. ostreatus*. Currently, the emergence of new species and genera of pathogens that infect fungi, such as *Arthrobacter arilaitensis* and *Pseudomonas yamanorum*, is noted [125]. There is also a known case of infection of the edible mushroom *Coprinus comatus* by the cross-kingdom pathogen *Achromobacter xylosoxidans* [126]. This makes controlling pathogens essential in the production of mushrooms for human consumption.

Edible mushrooms are most damaged by the green mold caused by *Trichoderma* spp., especially *Trichoderma harzianum* and *Trichoderma aggressivum* [127], as well as *Pseudomonas* spp. [125,128]. Therefore, their antagonists are of particular interest in mushroom disease control. Bacteria of the genera *Bacillus*, *Paenibacillus*, *Pseudomonas*, and the fungus *Mycetocola* are most often noted as antagonists of fungal pathogens (Table 3).

Table 3. Inhibition of competitive and pathogenic microflora.

Mushroom	Microorganism	Influence	Reference
Agaricus bisporus	Fluorescent *Pseudomonas* spp.	Inhibited *in vitro* bubble disease caused by *Lecanicillium fungicola*	[129]
	Pseudomonas putida, *Pseudomovas reactants*, *P. fluorescens*, and *Bacillus subtilis*	Antagonists of *Pseudomonas tolaasii*, the causative agent of brown blotch disease	[130]
	Bacillus subtilis	Inhibits the growth of green mold	[131]

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Mushroom	Microorganism	Influence	Reference
	Bacillus, *Lysinibacillus*, *Paenibacillus*, *Pandorea*, *Streptomyces*, *Alcaligenes*, and *Pseudomonas* from fruiting bodies	A broad spectrum of antimicrobial activity	[117]
	Streptomyces flavovirens	Inhibits the growth of *Trichoderma aggressivum* and *Trichoderma harzianum*	[132]
	Endofungal bacteria *Pseudomonas*, *Bacillus*, *Serratia*, *Stenotrophomonas*, and *Brochothrix* from wild mushrooms	Inhibit *P. tolaasii* (brown blotch disease) and *Ewingella americana* (internal stipe necrosis disease)	[133]
	Halotolerant *Bacillus sp.* from saline soils	Produced extracellular antifungal metabolites in butanol extract against *T. harzianum* and, in chloroform extract, against *L. fungicola*	[134]
	Bacillus velezensis	Inhibits *T. aggressivum*	[135,136]
	Bacillus velezensis	Inhibits the growth of *T. aggressivum* without stressing the mushroom	[137]
	Mycetocola tolaasinivorans and *Mycetocola lacteus*	Can protect their host against brown spot disease caused by *P. tolaasii* via a detoxification mechanism (inactivate tolaazine by lipocyclopeptide linearization)	[138]
	Pseudomonas, *Bacillus*, and *Pantoea*	Reduced mushroom brown blotch symptoms	[139]
	Pseudomonas putida, *P. fluorescens*, *P. reactans*, *Mycetocola*, *Bacillus*, *Pedobacter*, and *Sphingobacterium* associated with wild mushrooms	Detoxify *P. tolaasii* virulence factor tolaasin	[78]
Pleurotus *ostreatus*	*Paenibacillus polymyxa*	Inhibits T. harzianum	[140]
	Pseudomonas, *Sphingomonas*, *Bacillus*, *Pseudoxanthomonas*, *Thermobispora*, *Actinobacteria*, *Thermus*, and *Bacillus* from the substrate	Production of antibiotics that create substrate selectivity	[92]
	Bacillus coagulans	Inhibition of competing molds	[98]
Paxillus (*Boletales*)	Yeast *Kluyveromyces dobzhanskii*	Inhibit mycoparasitic fungus *Sepedonium chrysospermum*	[141]
Ectomycorrhizal truffles	Endogenous microorganisms	Produce volatile substances with antimicrobial activity	[142]

Antagonism against *P. tolaasii*, the causative agent of brown blotch disease, has been noted among *Bacillus*, *Pseudomonas*, *Serratia*, *Pantoaea*, *Stenotrophomonas*, *Brohotrix*, *Mycetocola*, *Pedobacter*, *Sphingobacterium*. Green mold was inhibited by *Bacillus* (*Bacillus subtilis*, *Bacillus velezensis*), *Paenibacillus*, *Lysinbacillus*, *Pandorea*, *Streptomyces*, and *Alcaligenes*. While yeast *Kluyveromyces dobzhanskii* inhibited the mycoparasitic fungus *Sepedonium chrysospermum*. Various species of the genus *Bacillus*, due to their antagonistic activity, are currently successfully used as biocontrol agents in agriculture, including for the prevention of gray mold and other post-harvest diseases of agricultural products during storage, for the control of nematodes and other parasites [143,144]. Microorganisms of the genera *Bacillus* and *Paenibacillus* are involved in increasing the selectivity of mushroom cultivation substrates by inhibiting the growth of *T. harzianum*. Thus, the management of microbial communities during mushroom cultivation - preparing a substrate to support the growth of *P. polymyxa* and other *Bacillus* spp., may serve as a way to optimize mushroom production [140]. It is interesting to note that the maximum antagonistic activity against *T. harzianum* and other pathogens was demonstrated by *Bacillus* spp. isolated from the saline soils of Goa [134]. Along with free-living bacterial and yeast microorganisms, producers of antagonistically active substances, and a significant number of antagonists of fungal pathogens have been isolated from fruiting bodies and fungal cells [78,117,133]. Bacteria of various species of the genus *Pseudomonas*, along with the genus *Bacillus*, are the most frequent antagonists of edible mushroom diseases [130,139]. The mechanism of action of microorganisms protecting fungi can be both the suppression of the pathogen and the neutralization of toxins produced by the pathogen. The received results allowed the researchers to recommend the listed microorganisms as a natural alternative to synthetic fungicides in mushroom cultivation. Nevertheless, preliminary studies on the effect of antagonistically active microorganisms on the growth of edible fungus should be carried out, since antagonists can also have an inhibitory effect on the higher fungus [145].

3.4. Mushroom growth promotion

Antagonistic microorganisms potentially promote mushroom growth by suppressing the development of pathogens and thereby increasing the yield and efficiency of substrate use. However, other mechanisms of mushroom growth promotion by microorganisms have also been identified. The interaction of bacteria with mushrooms contributes not only to protecting the substrate, improving its quality, and reducing the composting time but also to promoting mushroom growth by establishing symbiotic interactions [146] increasing hyphal growth [62,147–149], and inducing the pinning and fruiting bodies formation [51,148,149] (Table 4), which ultimately leads to an increase in yield, biological efficiency and the degree of processing of the substrate.

Analysis of the data presented in Table 4 showed that representatives of *Alphaproteobacteria* were noted as the main growth stimulators of *A. bisporus*: *Agrobacterium*, *Bradyrhyzobium*, *Rhizobium*, *Azospirillum*, and R*hodopseudomonas*. Fewer genera belonged to *Betaproteobacteria* (*Alcaligenes*, *Pandoraea*), *Gammaproteobacteria* (*Pseudomonas*, *Azotobacter*), *Bacilli* (*Bacillus*, *Paenibacillus*, and *Lysinbacillus*), and *Actinomycetes* (*Streptomyces*). The list of microorganisms stimulating the growth of *Agaricus* is consistent with the data of Siyoum et al. [114] on the presence of *Alpha*- and *Betaproteobacteria* in the casing layer, which is the main source of mushroom growth-promoting microorganisms in mushroom caps. Interestingly, *A. blasei* and *A. subrufescens* growth promoters differ sharply from those of *A. bisporus*. They are predominantly represented by *Actinomycetes*

(*Arthrobacter*, *Microbacterium*, *Advenella*, *Curtobacterium*, and *Gordonia*) but include also *Bacilli* (*Exiguobacterium*), and *Alphaproteobacteria* (*Agaricicola*). In the studies of Young et al. [157], similar data were obtained on microorganisms from the casing layer stimulating the growth of *A. blasei* (Table 4). For both mushroom species, the participation of microalgae in growth stimulation has also been shown. Baars et al. [109] emphasize the need to study the early stages of primordia formation to determine the influencing factors and mechanisms of their action.

The composition of microorganisms that stimulate the growth of oyster mushrooms is somewhat more diverse. It includes *Gammaproteobacteria*, *Alphaproteobacteria*, *Bacilli*, and *Actinomycetes* (Table 5). The mode of action of the microorganisms listed in the table has not always been investigated. There is information about the production of plant growth hormone indoleacetic acid by microorganisms of the genera *Bacillus* and *Pseudomonas* (124,159), and the use of microorganisms by mushrooms as a source of nutrition in conditions of nutrient deficiency [78,111]. The contribution of these microorganisms to the increase in laccase, cellulose, and amylase activities by oyster mushrooms was also noted [159,160]. A study of 35 bacterial isolates from *P. ostreatus* mycelium showed that only fluorescent pseudomonads promoted fungal growth, and only if they were firmly attached to the mycelium of the mushroom [161]. The *Pleurotus* beneficial microorganisms contribute both to the growth of mycelium [160,162,163], and to increase the yield, reduce the time of its production and increase the biological efficiency of the substrate use [124,158,163–165]. It was shown with *P. ostreatus* that fruiting bodies were the best source for the isolation of mycelial growth-promoting bacteria [124].

Table 4. *Agaricus* growth-promoting microorganisms.

Microorganisms	Substrate	Influence	Mode of action	Reference
Agaricus bisporus				
Pseudomonas, *Agrobacterium*	Water agar	MP	Nutrient source for feeding mushrooms.	[150]
Pseudomonas putida, *Bradyrhizobium japonicum*, *Rhizobium leguminosarum*	Compost	Y, BE	Primordia initiation and development.	[151]
Azospillum lipoferum	Compost	Y, FB	Presumably promoting nitrogen transport.	[152]
Azotobacteria, *Bacillus*, *Paenibacillus*, *Pseudomonas*	Compost	MP	Bio-fertilizer: indoleacetic acid (IAA), siderophores, and ACC-deaminase production; phosphate solubilization	[153]
Pseudomonas putida	Compost	MP	Phosphates solubilization and siderophores production	[111]
Some Gram-negative bacteria.	Compost	FB	Initiation of fungal sporophores	[110]
Azotobacter chroococcum, *Bacillus megaterium*	-	Y	Bio-fertilizers (N, P)	[148]
The consortium of *Mycothermus thermophiles*, thermophilic *Proteobacteria* and A*ctinobacteria*	Compost	MP, FB	Elongation of fungal hyphae; induction of fruiting body formation.	[51]

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Microorganisms	Substrate	Influence	Mode of action	Reference
Pseudomonas sp.	Compost	MP, FB	Reduction of ethylene synthesis by bacterial acdS gene, which inhibits mycelium growth and primordia formation.	[154]
Pseudomonas putida, *P. veronii*, *P. poae*, and *Pseudomonas* sp..	Ca-sing	FB, Y	Metabolized 2-Ethyl-1-hexanol and 1-octen-3-ol and removed C8 compounds inhibiting primordium formation	[155]
Bacillus, *Lysinibacillus*, *Paenibacillus*, *Pseudomonas*, *Streptomyces*, *Alcaligenes*, and *Pandoraea* from the fruiting bodies.	In vitro	MGP	Antimicrobial activity, phosphates solubilization, IAA production, and cellulase production.	[117]
P. putida, *Alcaligenes sp.*, *Bacillus sp.*, *Rhodopseudomonas palustris*, *Azotobacter vinelandii*, *Rhizobium sp.*, green algae *Scenedesmus quadricauda*, and yeast *Lipomyces starkeyi*	No data in this review	MGP	No data	[109]
Not identified bacteria		MP, FB	The source of nitrogen and sugar for fungal mycelium.	[113]
Gram-negative bacteria		MGP	A nutrient source for feeding mushrooms	[78]
Agaricus blazei				
Arthobacter sp., *Microbacterium esteraromaticum*, *Exiguobacterium* sp., *Pseudomonas resinovorans*		RGP, Y		[156]
Bacteria from casing soil: *Actinomycetota* 60%, *Bacillota* 20%, and *Pseudomonadota* 20%.	Potato dextrose agar PDA	MP	Cellulase secretion, phosphates solubilization, nitrogen fixation.	[157]
Agaricicola taiwanensis, *Microbacterium humi*	PDA	MP	No data	[157]
Agaricicola taiwanensis, *Advenella incenata*, *Curtobacterium citreum*, *Microbacterium humi*, *Gordonia hydrophobica*	Sterilized sawdust and casing	RGP, Y	No data	[157]
Cyanobacteria and *Microalgae*		RGP		[158]
Agaricus subrufescens				
Microbacterium humi		RGP, Y		[106]

Note: MP: mycelium promotion; FB: induction of the formation of fruiting bodies; Y: yield increase; MGP: mushroom growth-promoting ability; RGP: Reduction of the growing period.

Table 5. *Pleurotus* growth-promoting microorganisms.

Microorganisms	Influence	Reference
Pseudomonas and *Agrobacterium*	Growth promotion	[111]
7 strains of fluorescent *Pseudomonas* spp.	GP	[161]
Bacillus, *Paenibacillus*, and *Micromonospora*	MP, GP	[124]
Bacillus cereus, *Bacillus megaterium*, *Kurthia gibsonii*, *Enterobacter asburiae*, *Enterobacter cloacae*, *Pseudomonas pseudoalcaligenes; Saccharomycetes Meyerozyma guilliermondii.*	MP, Y	[164]
Bacillus cereus, *Bacillus aryabhattai*, and *Acinetobacter pittii*	MP	[166]
Glutamicibacter arilaitensis from rhizosphere	MP, Y, BE	[165]
Micromonospora lupini from fruiting bodies	MP, RGP	[124]
Pseudomonas and *Agrobacterium*		[78]
Azospirillum brasilense	MP	[162]
Cyanobacteria and *Microalgae*	RGP	[158]
Pseudomonas sp.	MP, MGP, RGP	[163]
Pseudomonas sp.	MP	[159]
B. cereus	MP	[160]

Note: MP: promotion of mycelial growth; FB: induction of the formation of fruiting bodies; Y: yield increase, MGP: mushroom growth-promoting ability; RGP: reduction of the growing period; BE: biological efficiency.

The data on microorganisms stimulating the growth of other fungi are largely limited (Table 6). However, *Serratia odorifera* promoted the growth of *H. marmoreus* [167,168], *Pseudomonas* and *Agrobacterium* influenced the growth of *Coprinus* and *Lepista* mycelium [111], and various *Bacillus* species influenced the growth and production of fruiting bodies by *Volvariella volvaceae* [169,170]. *Lentínula edodes* was influenced by *Azospirillum*, microalgae, and cyanobacteria [171,158], while *Rhizobium* stimulated the growth of *Armillaria* and *Polyporus* [172]. Many studies have been carried out under in vitro conditions. The use of *Pseudomonas* and *Agrobacterium* as a nutrient source for feeding mushrooms has been shown on Water agar [111]. The mechanisms of action of microorganisms are not always understood. However, *Azospirillum* is known to contribute to the accumulation of mannitol as a fruiting precursor in *Lentínula edodes* [171], and *Rhizobium* showed phosphate solubilization and xylanase activity, resulting in better substrate utilization. *Serratia odorifera* increases gene transcription and activity of lignin-decomposing enzymes in *Hypsizygus marmoreus* [168].

Table 6. Other *Agaricomycetes* mushrooms growth-promoting microorganisms.

Mushroom	Microorganisms	Reference
Coprinus quadrifidus (*Agaricales*, *Agaricaceae*)	*Pseudomonas* and *Agrobacterium*	[111]
Lepista nuda (*Agaricales*, *Tricholomataceae*)	*Pseudomonas* and *Agrobacterium*	[111]
Volvariella volvacea (*Agaricales*, *Pluteaceae*)	*Bacillus thuringiensis serovar konkukian*	[170]
Volvariella volvaceae (*Agaricales*, *Pluteaceae*)	*Bacillus cereus*	[169]
Hypsizygus marmoreus (*Agaricales*, *Lyophyllaceae*)	*Serratia odorifera*	[167]
Hypsizygus marmoreus (*Agaricales*, *Lyophyllaceae*)	*Serratia odorifera*	[168]
Lentínula edodes (*Agaricales*, *Omphalotaceae*)	*Azospirillum*	[171]
Lentínula edodes (*Agaricales*, *Omphalotaceae*)	*Cyanobacteria* and *Microalgae*	[158]
Armillaria gallica (*Agaricales*, *Physalacriaceae*)	*Rhizobium*, new species	[172]
Tricholoma matsutake (*Agaricales*, *Tricholomataceae*)	*Dietzia*, *Ewingella*, *Pseudomonas*, *Paenibacillus*, and *Rodococcus*	[173]
Polyporus umbellatus (*Polyporales*, *Polyporaceae*)	*Rhizobium*, new species from *P. umbellatus* sclerotia	[172]
Trametes (*Polyporales*, *Polyporaceae*)	*Cyanobacteria* and *Microalgae*	[158]
Hericium erinaceus (*Russulales*, *Hericiaceae*)	*Arthrobacter humicola*	[174]
Rhizopogon roseolus (*Boletales*, *Rhizopogonaceae*)	*Paraburkholderia* spp. from sporocarp on the mycelial growth	[175]

Many interactions, from antagonism and competition to mutualism, have been established between bacteria and fungi [176]. The mechanism of their interaction depends on the characteristics of the host fungus and the specifics of the microorganism used, as well as environmental conditions. The positive effect of microorganisms on mushrooms is largely analogous to their effect on plants. The ability of microorganisms to produce phytohormones also enhances the growth of fungi [169]. Phytohormones can have a positive effect on the germination of spores, the growth of vegetative mycelium, and the formation of fruiting bodies of basidiomycetes [177–179]. According to Kertesz and Thai [51], microorganisms promoting mushroom growth act on the soil, substrate, casing layer, or mycelium increasing yield and reducing cultivation time. At the same time, they not only secrete enzymes supplying nutrition to the host [180] and solubilize phosphate from insoluble compounds [117] but also increase the availability of metal ions, such as iron and manganese, owing to metal reduction activity and siderophore production [181,182].

The literature analysis shows that microorganisms can affect mushrooms by improving nutrient availability for them, by being directly used by the fungi as a source of nutrition under nutrient-deficient conditions, by producing growth hormones, up-regulation the production of lignocellulosic decomposing enzymes, and removal the inhibiting products of fungal metabolism accumulated in the

environment. Such substances are calcium oxalate, and various C8 compounds, including mushroom alcohol 1-octen-3-ol, hypocrellin, and presumably ethylene, although data on the effect of the last one on fungal growth is ambiguous [109,183]. The use of scanning electron microscopy has shown abundant calcium oxalate crystals from the hyphae of the substrate mycelium [112]. At the same time, the mycelium of the cover layer was a wide strand without calcium oxalate crystals but with densely attached bacteria, a significant part of which belonged to the genus *Pseudomonas*. Sun et al 2020 studies with *Hypsizygus marmoreus* showed the dominance of *Serratia odorifera*, which stimulated the growth of the fungus, shortened the fruiting cycle, and increased the yield of fruiting bodies. An increase in the abundance of these microorganisms correlated with the growth of fungal hyphae.

In the studies of Pion et al. with 13C probing [184], it was demonstrated that the fungus *Morchella crassipes* attracts bacteria *Pseudomonas putida* with its exudates and subsequently consumes them. The data indicating the direct use of microorganisms for the nutrition of mushrooms [113] are particularly noteworthy. The analysis of the scientific literature shows that Gram-negative bacteria and yeast can be used by mushrooms as a source of carbon and energy, especially in nutrient-poor substrates. After Barron's studies [150], various researchers noted the highest contribution of Gram-negative bacteria to the growth promotion of edible mushrooms (Tables 4–6). Carrasco et al. [76] demonstrated a negative correlation between total live bacterial biomass and crop mycelium of *A. bisporus*. Such a decrease may be a result of microbial biomass consumption by the mushroom mycelium [51]. Interestingly, only four mushroom species, namely *A. bisporus*, *P. ostreatus*, *Coprinus quadrifidus*, and *Lepista nuda* out of a hundred tested *Basidiomycota*, *Oomycota*, *Zygomycota*, *Deuteromycota*, or *Ascomycota* were capable of attacking and digesting bacterial colonies in nutrient-limiting conditions [150]. In this process mushrooms formed directional specialized haustorial-like absorptive hyphae colonizing bacterial colonies.

Feeding with yeast has also been noted in various mushrooms. Thus, Savelieva and Kamzolkina [185] observed an increase in mycelial branching in four species of the genus *Pleurotus* and the formation of various types of outgrowths (papillary and coral-shaped) for contact with the cells of basidiomycete and ascomycete epiphytic yeast. They also observed the trapping loops for capturing *Metschnikowia pulcherrima* by *Pleurotus citrinopileatus*. Novoselova [186] showed that to achieve the maximum growth rate of *Pleurotus* mushrooms on the substrate and obtain the maximum yield of fruiting bodies, live yeast cells are required, which are an additional source of nutrition for the mycelium during the entire growth and fruiting cycle on the substrate. A comprehensive study of mycelium micromorphology of *Pleurotus citrinopileatus*, *Pleurotus djamor*, *P. eryngii*, *P. ostreatus*, and *Pleurotus pulmonarius* revealed specialized structures for contact with dead and live yeast cells [187]. The range of asco- and basidiomycetous yeast food preferences for several *Pleurotus* species was determined. The commonly preferred yeast species for all studied mushrooms was *Saccharomyces cerevisiae*. The widest range of food preferences was typical for *Pleurotus djamor* and the narrowest one for *P. eryngii*. *Hanseniaspora uvarum*, *Rhodotorula minuta*, and *S. cerevisiae* were identified as trophic preferendum for *P. ostreatus* [188]. Kamzolkina et al. [189] developed a method for growing edible *Pleurotus* mushrooms on sunflower husks or wheat straw enriched with a suspension of *Cryptococcus albidus*, *H. uvarum*, or *S. cerevisiae* yeast, which helped to reduce the cultivation period and increased the yield of mushrooms.

The enzyme system of edible mushrooms capable of the lysis of yeast and bacterial cell walls can act as a nutrient release system to provide carbon, nitrogen, and minerals for the fungal mycelium. It can be part of an antimicrobial protecting system as well. Ibragimova et al. [190] showed that *P.*

ostreatus and *L. edodes* produced enzymes hydrolyzing the cell wall of baker's yeast *S. cerevisiae* during submerged cultivation. In 2021, Mazheika and Kamzolkina [191] suggested that macrovesicular endocytosis, which helps fungi quickly capture nutrient resources into the cells and minimize losses caused by the accompanying microorganisms, might be the mechanism for the uptake of microorganisms by fungi. The development of research in the field of optimization of optical microscopy [192] will contribute to the elucidation of the hidden sides of bacterial-fungal interactions.

Of particular interest is a study by Sun et al. [168], who found that the reason for the stimulation of fungal growth is the quorum sensing system of cyclic dipeptides of *Serratia odorifera* that increase the transcription level of lignin-degrading enzyme genes of *H. marmoreus*. Thus, cyclo(Pro-Phe) increases the activity of extracellular laccase 1.32-fold and manganese peroxidase by 20%. There is also evidence of overproduction of laccase by the fungus of the genus Trametes during co-cultivation with the yeast *Candida* sp. and *Rhodotorula mucilaginosa* due to glucose starvation [193,194]. High-throughput sequencing of the Chinese medicinal mushroom *Cordyceps militaris* has revealed an unexpectedly high diversity of microbial communities and their functions in the development and quality of *C. militaris* [195]. It was also found that the genes associated with metabolism were more numerous in soil bacteria, while the membrane transport genes were more numerous in the endophytic bacteria of *C. militaris*. Determination of the structure of bacterial communities of fruiting bodies of ectomycorrhizal and saprotrophic fungi revealed that the bacterial taxa involved in the decomposition of organic material were relatively more numerous in the fruiting bodies of saprophytic fungi, while the taxa involved in the release of minerals were in the fruiting bodies of ectomycorrhizal fungi [196]. The results of these studies provide evidence that bacteria can support the functional role of mushrooms in various ecosystems making an inseparable contribution to the destruction of various hardly decomposable substrates.

4. Conclusions

The interaction of humans, animals, and higher plants with microorganisms has been studied quite fully in many ways. It is known that numerous species of bacteria, in particular rhizobacteria inhabiting the soil near plant roots, play an important role in nutrient mobilization and plant growth by producing hormones, cellulases, and solubilizing phosphates, and protecting against phytopathogens and abiotic stresses. However, there are much fewer such studies, especially concerning microorganisms living on the surface and inside the mycelium. Bacterial–fungal interactions, while ubiquitous, remain largely unexplored to date.

Expanding research in mushroom production has revealed microorganisms significantly contributing to the mushroom cultivation process. Nevertheless, many gaps remain in understanding the role of microorganisms in substrate preparation, degradation of lignocellulose, and mechanisms of mushroom growth promotion and protection. It has been shown that the efficiency of lignocellulose utilization correlates positively with mushroom yield [53]. Therefore, works focused on increasing the yield of mushrooms simultaneously contribute to an increase in the utilization of hard-to-decompose lignocellulosic substrates. Therefore, it is important not only to prepare a high-quality substrate for cultivation but also to take measures to increase yields and protect fungi from pathogens. The review of the scientific literature on the topic has discovered a great underestimation of microbial input into mushroom production on hard-to-recycle lignocellulosic wastes and the decomposition of their most chemically stable component lignin. Further studies of microorganisms and their symbiosis with

mushrooms are required for the most complete use of substrate lignocellulose.

The microbiota of mushrooms, which largely determines the phenotype of fungi and their productivity, is becoming a priority object of research nowadays. As evidenced by numerous scientific data, the production of higher mushrooms, which contributes to the growth of human well-being, combined with the possibility of efficient disposal of one of the most numerous wastes of the agro-industrial complex, is very promising. The correct use of microorganisms for the preparation of the substrate, as well as further promotion of the fruiting bodies of mushrooms, makes it possible to develop management methods for growing them, as well as increasing their nutritional and biological value and more fully using renewable lignocellulosic raw materials.

Microorganisms that decompose cellulose and hemicellulose of lignocellulosic substrates are well studied. It is already known about the production of various ligninolytic enzymes by members of the genera *Bacillus*, *Pseudomonas*, *Streptomyces*, *Thermomonospora*, *Thermus*, *Serratia*, *Acinetobacter*, *Enterobacter*, *Paenibacillus*, *Pandoraea*, *Saccharomonospora*, *Thermobifida*, *Azospirillum* [90], which are associated with mushrooms during various phases of substrate preparation and mushroom growth. Representatives of these genera are characterized by different temperature optima of lignin-degrading enzymes and are dominant in different periods depending on conditions. The protective and mushroom growth-promoting activity of many of them has been shown. Some bacteria, such as *Pseudomonas*, *Serratia*, and *Actinomycetes*, are closely associated with the growth of fungal mycelium, colonize the surface of hyphae and move along them, getting into hard-to-reach places [197,198] and enter close metabolic relationships that contribute to the joint assimilation of hardly decomposable lignocellulose substrates. The endophytic existence of some bacteria inside fungal hyphae is probable due to the production of chitinolytic enzymes (for example, by actinomycetes) or possibly as a result of their capture by fungal hyphae. Part of the microorganisms is more associated with the fungal mycelium, others predominantly colonize fruiting bodies, while the microbial communities in the caps and stipes of mushrooms differ. The majority of mushroom growth promoters are isolated from the fruiting bodies. However, the proven connection of ligninolytic activity with fungal mycelium suggests that the primary contribution to the decomposition of lignocellulosic substrates is made by bacteria colonizing the surface of hyphae or/and by endophytic microorganisms.

The accumulated knowledge indicates the possibility of the successful use of microorganisms to increase mushroom yield and the degree of lignocellulosic substrate decomposition. However, the amount of scientific research on the relationship between mushrooms and microbes is largely limited. Further research in the field of the relationship between mushrooms and microorganisms should be directed to a more detailed analysis of microbial communities living both on the surface of fungal hyphae and inside mycelium or fruiting bodies, as well as to the molecular and genetic aspects of the bacterial-mushroom interactions during substrate processing. This will allow us to use the planet's renewable lignocellulosic raw materials with the greatest return.

A deeper understanding of bacterial-mushroom interactions could bring a significant increase in the profitability of this industry of food and medicinal products. The development of research in various directions, in particular in the field of optimizing optical microscopy [192], will help to elucidate the hidden sides of these interactions. Besides, the simpler organization of mushrooms in comparison with higher plants and animals can serve as a good model for studying the relationships of microorganisms in the composition of the holobiont and their contribution to the epigenetic regulation of host metabolism. Research in this area contributes to the manifestation of the latent potential for the synthesis of biologically active substances by stimulating the work of “silent

genes" [197] and can be widely used in various biotechnological solutions. Finally, it can be said that the solution of several tasks set for the successful cultivation of mushrooms will help to some extent to push back the problem of the impending shortage of food products in the world. The most attractive side to solving these issues is the fact that the production of mushrooms not only solves the problem of reducing waste and losses in agriculture but also increases the added value of agro-industrial waste, ensuring economic growth and environmental protection, contributing to the development of a circular economy.

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Conflict of interest

The authors declare that they have no conflict of interest.

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