REVIEW

Mushroom cultivation for soil amendment and bioremediation

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Abstract

Intensive crop production, use of pesticides, and unsustainable farming practices are known to cause land degradation and soil contamination. Both have led to a decline in biodiversity and changes in the functional groups of soil microorganisms. Although physicochemical methods have been used to apply soil amendments to agricultural land, mushroom cultivation in agricultural land for soil improvement have been poorly studied. In-field mushroom cultivation is considered a good strategy for improving soil quality by reducing the input of chemical fertilizers. In this paper, we list the edible mushroom species suitable for growing in fields and summarize the important role that mushroom field cultivation can play in soil erosion control, nutrient cycling, and the bioremediation of contaminants. Decomposition, symbiosis, assimilation, degradation, bioweathering, oxidation, biosorption, and bioconversion are all critical components of mushroom field cultivation. Research has shown that field mushroom cultivation contributes to nutritional bioavailability while also promoting the degradation of pollutants and formation of soil aggregates. Through soil amendment practices, a portion of agricultural waste can be converted into high-quality food and nutraceutical sources, and the remaining organic matter improves soil quality via fungal mycelial networks and the re-use of spent mushroom substrates. Only a small number of mushroom species have been used in the application of soil amendments in field conditions. This review shows the need for further research into specific mushroom species for achieving different soil amendment goals in order to balance agricultural development with sustainable land management.

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Introduction

Agricultural activities degrade soil quality due to soil erosion, contamination of soil with pesticides and agrichemicals, depletion of soil nutrients and a decline in soil microbial diversity caused by predatory exploitation and low cropping system diversity^[1]. Soil erosion presents a severe threat to soil health^[2], exacerbating existing agricultural problems, such as limited land for food production^[3]. Contamination of agricultural soils not only negatively impacts soil ecosystems, it is also a threat to human health and water systems^[4–6]. Depletion and leaching of soil nutrients result in land desertification and water eutrophication^[1]. A decline in soil microbial diversity and activities impairs the functioning of soil ecosystems^[1,3]. Given these challenges, sustainable solutions are required in order to maintain agricultural productivity over the long-term.

One such solution is the use and integration of crop residues into agricultural systems. Agricultural organic waste could be transformed into nutrient-rich fertilizers and used as a soil amender during the soil amendment process. In this process, organic amendments increase total soil organic matter^[7–11]. At the same time, organic amendments improve soil structure and physiochemical properties^[12,13], thereby preventing soil from easily eroding and strengthening field capacity for agricultural production. In addition, organic

amendments provide abundant substrates to soil microorganisms, enhancing the natural habitat of soil microorganisms that play pivotal roles in soil improvement via increasing nutritional availability, mineralization, aggregate formation, degrading pollutants, and nutrient cycling^[14,15].

Fungi are a valuable group of organisms, providing important ecosystem services, such as nutrient cycling, symbioses, and maintenance or improvement of soil structure. Accordingly, they are used in numerous industrial and agricultural systems^[16]. In soil ecosystems, fungi improve soil health through distinct hyphal structures and nutrient-rich fungal secretions^[17]. Fungi hyphal networks bind soil particles and promote the formation of soil aggregates^[18,19]; moreover, mycelia produce chemical compounds capable of degrading organic material as well as pollutants^[20,21]. Many mushroom species from Basidiomycota, such as Agaricus bisporus, Agaricus subrufescens, Phallus impudicus, Stropharia rugosoannulata, and Volvariella volvacea can be cultivated on agricultural land, using composted materials originating from crop residues^[22-26]. The cultivation process not only encourages the reuse of crop residues, but also has the added gain of yielding mushrooms as a secondary crop as well as enhancing interactions between fungal hyphae, substrates, and soil systems^[27]. Fungal hyphae degrade different kinds of agricultural residues, such as crop straw, corn cobs, animal manure, and sugarcane bagasse, converting them into carbohydrates,

proteins, fatty acids, and other compounds^[28–30]. In addition, spent mushroom substrates left over after the harvesting of fruiting bodies contain high levels of organic matter, nitrogen, phosphorus, potassium and other nutrients, which are byproducts of edible mushroom cultivation and important agricultural resources usable for soil amendment and biore-mediation^[31,32]. Spent mushroom substrates are not considered agricultural waste but are rather considered a renewable resource in the mushroom industry, as the recovered enzymes are potentially valuable for the bioremediation of pollutants, animal feeding, dye decolourisation, and alternative energy^[33]. Spent mushroom substrates also enhance the sustainable recycling of organic matter, increasing soil quality while potentially degrading pesticides residing in the soils^[34].

In-field mushroom cultivation includes culture preparation, spawn production, composting of agricultural waste, inoculation, incubation, and harvest (Fig. 1). Compared to indoor cultivation, field-based mushroom cultivation occurs in a more varied environment more difficult to control while also providing convenient vegetation and soil conditions, such as the effective use of tree canopy as shade and soil as casing materials^[16,35]. Pure fungal cultures can be acquired from spore or mushroom tissue isolation, and the composting process starts after raw materials absorb water and attain a water content of 60%–70%^[36]. The composting process is carried out in field and involves two main phases. In phase I, meso- and thermophilic microbiota decompose the raw materials, causing a rise in temperature to 80 °C and the release of ammonia. In phase II, most of the ammonia evaporates via compost turning, and microorganisms consume the remaining 40% of ammonia^[37]. After two composting phases, compost is available for mycelium grown in field conditions, and mycelial mass coupled with compost is applied to the field and cultivation 'beds' for incubation of fungi (Fig. 1).

A range of mushroom species have been cultivated in fields that facilitate interactions between soil systems and compost through fungal hyphae (Fig. 1, Table 1). *Agaricus bisporus* is the world's fourth-most consumed mushroom species, with a global production weight reaching 4.43 billion kg in 2013^[38]. *A. bisporus* is cultivated on a cereal straw-manure compost mixture consisting of inocula and substrate covered with soil. However, mushroom species like *Volvariella volvacea* and *Phallus impudicus*, substrate, and solid inocula are inoculated



Profile of cultivation land

Fig. 1 Field mushroom cultivation process. The fungal fruiting bodies are collected to prepare pure cultures, spawn and inoculum bags in lab conditions. Wood sawdust and agricultural wastes from farmlands are used to prepare compost. Inoculum bags and compost are applied in fields for mushroom production.

Species	Raw materials for compost	Yield/biological efficiency	Nutritional value/bioactive compounds (dry weight)	References
Agaricus bisporus	Wheat straw; chicken manure	107.3 ± 5.37 kg per ton of dry weight compost	Crude protein 194.1 \pm 11.65 g/kg, crude fat: 17.8 \pm 1.25 g/kg, total carbohydrates: 686.4 \pm 41.18 g/kg, crude fibre: 73.1 \pm 6.58 g/kg, ash: 101.7 \pm 6.10 g/kg, energy value: 345 \pm 27.60 kcal/100 g	[26]
Agaricus subrufescens (Syn. Agaricus blazei, Agaricus brasiliensis)	Wheat straw, horse manure	40.0–241.4 g/kg of dry weight compost	O-alkyl-C group: 51.39–62.61 ppm, antioxidant activity: 36.48%–90.07% (scavenging ability of 1,1-diphenyl-2-picrylhydrazyl radicals) and 43.94%–98.47% (scavenging ability of 2,2-azino-bis-(3-ethyl-benzothiazoline-6-sulfonic acid))	[25]
Coprinopsis cinerea (Syn. Coprinus cinereus)	Sisal decortications residue, calcium sulfate	Yield: 238 ± 2.1 g/kg wet weight compost, biological efficiency: $68 \pm 0.72\%$	nd	[55]
Phallus impudicus (Syn. Dictyophora indusiata)	Formula 1: Bamboo chips (100%), formula 2: sugarcane bagasse (78%), wood sawdust (20%), others (2%).	Yield: 124.77 g/m ² (formula 1), 104.33 g/m ² (formula 2)	Protein: 17.87 (g/100 g), total carbohydrate: 54.98 (g/100 g), crude fat: 0.63 (g/100 g), crude fibre: 11.47 (g/100 g), ash: 8.54 (g/100 g), total amino acids: 16.32 (g/100 g), the proportion of total amino acids in the protein: 91.33%	[23,56]
Lepista sordida	Rice straw 89% ammonium phosphate 2%, calcium carbonate 1%, calcium sulfate 3%, rice bran 4%, urea 1%.	Yield: 93.1–287.5 g/kg	nd	[57]
Stropharia rugosoannulata	Wood sawdust 68%, wheat straw 22%, Corncobs 10%.	Yield: 4,836.52 ± 186.86 g/m ²	Protein: 25.75 (g/100 g), fat: 2.19 (g/100 g), carbohydrates: 53.92 (g/100 g), crude fiber: 7.99 (g/100 g), ash: 8.72 (g/100 g), free amino acid: 16.72 (g/100 g), the ratio of essential amino acid to non-essential amino acid: 64.00%. potassium: 34,750.0 mg/kg, phosphorus: 8,168.40 mg/kg, manganese: 40.60 mg/kg, Calcium: 151.90 mg/kg, iron: 244.1 mg/kg, copper: 16.00 mg/kg, zinc: 54.40 mg/kg, sodium: 47.54 mg/kg	[24]
Pleurotus flabellatus	Sisal decortications residue, calcium sulfate	Yield: 290 ± 1.23 g/kg wet weight compost, biological efficiency: 65 ± 1.37%	nd	[55]
Volvariella volvacea	Rice straw; animal manure	Yield: 92–482 g/kg substrate	Ash: 8.6%-11.5%, protein: 37.2%-48.9%, carbohydrate: 19.0%-26.9%, fat: 9.3%-12.2%, fiber: 9.0%-18.6%, potassium: 4.8%-5.68%, phosphorus: 1.18%-1.27%, sodium: 0.23%-0.58%, Calcium: 49.8-152.6 mg/kg, iron: 230-301 mg/kg, copper: 30.7-73.3 mg/kg, zinc: 94-123 mg/kg, manganese: 45.9-52.9 mg/kg.	[22]

Table 1. Compost-based field cultivation of edible mushroom species, including growth substrate, yield/biological efficiency, and nutritional value for listed species.

nd, not determined; Syn, synonym.

in a field, and mushroom 'beds' are formed and covered with rice straw^[39,40]. After compost is applied and each 'bed' is prepared for in-field mushroom growth, the plots are drained well, and lime (calcium oxide) is used for controlling contamination between grids. The casing layer is one of the most important steps for field mushroom cultivation due to it precluding drying, pests, and diseases^[41]. Mushroom growers cover mushroom substrates with soil, rice straw, or pine needles. In the modern mushroom industry, the indoor static composting method has been applied for *A. bisporus*, while *Stropharia rugosoannulata* has been grown in the field, and composting processes were conducted on cultivated land prior inoculation. Soil casing was used for maintaining moisture and stimulating the formation of fruiting bodies.

For the field cultivation of mushroom species, the yield per unit weight of compost reflects the degree to which space is efficiently used. Biological efficiency is one variable useful for evaluating mushroom cultivation activities, such as substrate formula, quality of mycelial spawn, and management^[42]. During field mushroom cultivation, fruiting bodies contain nutrients originating from compost, soils, and exogenous sources. Table 1 lists the compost-based cultivated mush-room species suitable for field growth.

Previous studies have focused on the effects of spent mushroom substrates and additives on soil amendments as well as the removal of soil pollutants^[43-47]. However, the effects of field mushroom cultivation on soil quality improvement have received little attention, and no research has reported the benefits of growing mushrooms in agricultural fields. Given this knowledge gap, and the huge potential of mushroom cultivation on agricultural diversification and soil remediation, the aim of this review is to summarize the current state of knowledge regarding the field cultivation of mushrooms and how field cultivation of mushrooms can be used for soil rehabilitation. We also listed mushroom species that are best suited for this style of cultivation, and the positive impacts that field cultivation of mushrooms can have on soil systems. Furthermore, we highlighted field-grown mushroom production systems as important components of sustainable agriculture.

Soil erosion control

Soil erosion is a key factor resulting in poor soil health and loss of agricultural productivity, especially in areas prone to heavy rainfall. As such, erosion control remains a priority in landscape management, and numerous agricultural and engineering practices have been developed and utilized for mitigating soil erosion. These can be briefly stated as follows: reducing rainfall impact via forest canopy/use of shade cloth; carrying water out of the field through runoff drainage lines; stabilizing soil aggregates; terracing in mountains landscapes; and conservation tillage^[48–50]. Biological methods are also economical and practical to control soil erosion^[51]. An alternatively increasing viable strategy is to enhance the amount of fungal mycelium, with mushrooms as a byproduct, into agricultural soils.

Growing mushrooms in agricultural fields can benefit soil erosion control through direct and indirect mechanisms. In the direct mechanism, mushroom mycelia bind soil particles and establish strong cord-forming mycelial networks that comprise the formation of soil aggregates^[51]. In the indirect mechanism, fungal hyphae exude hydrophobins such as glomalin and other extracellular compounds including mucilages and polysaccharides into the soil, thereby bolstering soil organic matter^[52,53]. Accordingly, soil aggregate clumps form through the composition of fungal hyphae, organic matter, nutrients, water, lipids, protein, and minerals^[54], limiting soil erosion.

Cord-forming mycelial networks

Almost all mushroom species selected for outdoor cultivation are saprobic fungi, living off organic matter found in soils or compost layers. The life of mushrooms starts with a spore which has a diameter of a few microns. The spore swell, germinate, and elongate to form a filamentous cell in a humid and nutrient-rich environment, called a hypha. After the hypha grows, it elongates and forms a network of interconnected hyphal threads called a mycelium^[58]. During the field-based mushroom cultivation process, the mycelium runs in the compost to obtain nutrients and eventually form the 'cord-forming mycelial network'. Once the compost layer has been fully colonized by the fungal mycelial network, the mycelia grow into the soil layers, obtaining carbon and nutrients from the soil and releasing fungal-based organic matter into the soil^[58]. The carbon and nutrients gained by the mycelia allow for the formation of mushrooms^[59].

As the fungal hyphae penetrate the soil layers, the hyphal networks can physically or chemically bind soil particles, thus aiding in the formation of soil aggregates^[60]. Phallus impudicus and Stropharia rugosoannulata (Table 1) are two examples of field cultivated mushrooms that perform these functions. Research from Thompson and Rayner^[61] and Donnelly and Boddy^[62] show how Phallus impudicus form cord-like mycelial networks when grown in field conditions. Similarly, during the field cultivation of Stropharia rugosoannulata, soils were observed to contain abundant hyphae after the cultivation process^[63] (Fig. 2). The increasing abundance of hyphae in soils, and especially cored-forming mycelial networks, enhance the aggregation of soils, and thus improve overall soil quality. Soil aggregation not only reduces soil erosion, but increases gaseous movement within the soil, and improves the ability of roots to penetrate the soil systems^[64]. Moreover, aggregates provide habitats for microbial dynamic processes, including soil carbon sequestration^[65], microbial evolutionary^[66], nutrient turnover, and trace gas emissions^[67].

Soil organic matter

A key mechanism for mitigating soil erosion is to increase the levels of soil organic matter. The soils with higher organic carbon contents offer good protection against erosion^[68]. Conservation tillage and organic farming help to reduce soil erosion since they could increase soil fertility and soil organic matter^[50,69]. Organic matter binds soil particles, and increases soil moisture levels, thus preventing soil from drying out and soil particles being washed away during heavy rain events or strong winds^[70,71]. The increase in organic matter fosters the development soil structure, water-storage capacity, formation of aggregation, biota biomass, and biodiversity in soil ecosystems^[72]. Research has shown that field-based mushroom cultivation is an effective means for improving the organic matter content in soils, either via the addition of fungal based organic material (mycelium, hyphal exudates) or through the addition of compost and spent mushroom substrates into the soil.

The compost used in field-based mushroom cultivation can contribute towards sustainable production systems; utilizing agricultural waste, such as crop residues, for compost production ensures a circular system and limits the use of additional external resources to be used for the production of mushrooms^[73] (Fig. 3). During the cultivation process, compost from mushroom production provides a growth



Fig. 2 Cord-forming mycelial network observed during field cultivation of *Stropharia rugosoannulata* in Honghe, China. (a) Mycelium colonized on substrate. (b) Mycelium invade to soil from growing substrate. (c) Mycelium transmission in soil. Scale bars: 1 cm. Photo credit: Yuwei Hu.



Fig. 3 Roles of field cultivation of mushrooms in soil nutrition cycling. In the first step of the field mushroom cultivation process, various kinds of waste from agricultural activities are gathered and used as raw material for mushroom-growing compost. The final fruiting bodies provide food and medicinal resources, and the spent mushroom substrate could be used in soil remediation, enhancing agricultural activities. Finally, the soil organic matter increases, helping to restore soil ecosystems.

substrate for mushroom hyphae and cord-forming mycelia that can colonize soil systems. A portion of mycelia is responsible for the formation of mushroom fruiting bodies, while the remainder resides in the soil, and as this portion dies off and is replaced, so the levels of soil organic matter increase. Cultivation studies conducted by Gong et al.^[74] using *Stropharia rugosoannulata* showed that soil organic matter significantly increased after cultivation of *S. rugosoannulata* compared with soil systems not exposed to compost based mushroom cultivation in field conditions. Furthermore, intercropping *S. rugosoannulata* and citrus trees significantly improved soil organic carbon, which is a valuable indicator in assessing soil quality in agroforestry systems^[75].

In addition to the organic matter derived from fungal mycelium, mushroom substrate materials such as crop straw or woodchips have been shown to improve soil organic matter as well as soil mineral nutrition. For example, the work of Lou et al.^[76] showed that organic matter in spent mushroom substrates is converted into humus within the soil, thus improving soil organic matter content. Tan et al.[77] investigated the field cultivation practices of Morchella importuna (Black morel), in particular examining the nutritional acquisition of morel mycelium from exogenous nutrient bags through soil media. During the cultivation process, the exogenous nutrient bags were decomposed by mycelia of *M. importuna*, and the soil organic carbon content of the surface soils increased significantly. These studies provide clear evidence that field-based cultivation of a variety of mushroom species enhances soil organic matter levels, thereby mitigating soil erosion.

Contribution of field-based mushroom cultivation to soil nutrition

During the mushroom production process, a portion of the substrate is transferred to mushroom products, and the

remaining substrate is recognized as spent mushroom substrate; accordingly, every kilogram of fresh mushroom production results in around 5-6 kilogram of spent mushroom substrate^[78,79]. Spent mushroom substrates also contains various nutrients and organic matter, such as neutral detergent fiber, acid detergent fiber, lignin, hemicelluloses, cellulose, carbohydrate, ether extract, crude protein, nitrogen, calcium, and phosphorus^[80,81]. Currently, the majority of spent mushroom substrates are disposed of via dumping or incineration^[82], but innovative techniques can allow these substrates to add value in integrated agricultural systems. Examples include energy production, composting, cultivation substrate of new mushroom species, animal feed, enzyme production, packing, and construction materials^[81,83]. For field-based cultivation of mushrooms, there are two main ways to dispose of spent mushroom substrates (Fig. 3): 1) composting for bio-fertilizer use; and 2) in situ amendment for degraded soil^[84].

Spent mushroom substrates contain essential nutrients and microbial biomass resources, which could be utilized as fertilizer for further agricultural activities, such as promoting seedling growth and growing other mushroom varieties. Based on studies by Demir^[85] and Meng et al.^[86], spent mushroom compost can be used as a substitute for peat (a non-renewable resource) in seedling growth, and an appropriate composting formulation will affect seedling growth parameters like germination and seedling morphology. Demir^[85] showed that a mixture of 70% spent mushroom compost +30% perlite as well as only aged spent mushroom compost are both effective for widening seedling growth parameter of Charleston pepper (Capsicum annuum L), a widely cultivated crop variety. It was additionally found that aged spent mushroom compost (at least six months under natural condition) is better than fresh spent mushroom compost due to higher macro nutrient contents. According to Meng et al.^[86], compost (consisting of spent mushroom

substrate, pig manure, and biogas production residue) presents a good alternative to peat for encouraging seedling growth of tomato and pepper. Besides seedling growth, spent mushroom substrates are a stable organic amender for plant growth-promotion in agricultural and horticultural sectors, with the support of spent mushroom substrates of *Lolium multiflorum* (Italian ryegrass) increasing total biomass by 300% when compared to non-spent mushroom substrates treatment^[31]. Spent mushroom substrates mixed with alluvium soil or garden soil had significant positive effects on traits of marigold (*Calendula officinalis*)^[87].

Limited nutrients in spent mushroom substrates are unable to support further mushroom production of the same species^[88], but they could be used for the cultivation of other mushroom species through nutrient addition or substrate refining (pyrolysis of substrate into biochar)^[78,89]. The microwave vacuum pyrolysis method has been used to test the properties and effects of spent mushroom substratesderived biochar on mycelia growth and mushroom production^[89]. The control experiment based on biochar additions showed that the surface area of biochar is a key factor for mycelium growth due to water retention, nutrient availability, fast mycelium growth, and higher mushroom yield^[89]. In addition, spent mushroom substrates have been examined for potential uses as a feed additive to increase the blood metabolism of different animals^[90,91]. Similar studies regarding different mushroom species suitable for in-field cultivation, such as Agaricus bisporus^[92], Agaricus subrufescens^[93], and Volvariella volvacea^[81] have been conducted to evaluate the performance of crop plants using spent mushroom substrates as a soil conditioner.

Spent mushroom substrates are helpful soil amenders in degraded lands, enhancing physical properties, nutrients, and microorganism activities^[94]. Application of spent mushroom compost is suitable for soil structure restoration based on soil physiochemical properties determination by Gümüş and Şeker^[95]. Soil organic carbon and nitrogen significantly increased among different spent mushrooms substrates treatments under both field and laboratory conditions. Furthermore, spent mushroom compost increased soil electrical capacity, which is an important parameter in soil health^[95]. Beside organic carbon, nitrogen mineralization is also a crucial process in spent mushroom compost-amended soils^[96]. Laboratory experiments have been conducted to monitor soil amendments primarily comprised of spent mushroom compost, and results have shown that spent Agaricus bisporus compost treatment accumulated a higher level of mineral nitrogen in soil compared to a farmyard manure treatment and no treatment control^[96]. Research into nitrogen mineralization in soils under continuous cultivation and composting processes has been conducted by Lou et al.^[76]. In this study, relative moisture and polysaccharide content of spent mushroom substrates decreased while protein increased. It was also found that use of spent mushroom compost and urea represents a good strategy for nitrogen mineralization in soils^[76].

The use of spent mushroom substrates as a soil amender may deliver a long-term positive impact on microbial communities and functional diversity^[97]; furthermore, the continuous application of spent *Agaricus bisporus* substrates can change the soil organic carbon, humus composition, microbial community, and functional diversity. The proper amount of spent mushroom substrates can benefit highly efficient soil microorganisms seeking carbon sources^[97]. Besides the continuous application of spent mushroom substrates as a soil amendment, crop rotations can also improve soil conditions. Research by Yang et al.^[98] revealed that rotating Volvariella volvacea with cucumber increases soil nutrients for cucumber growth while also improving bacterial diversity near cucumber root systems. Crop rotation could thereby reduce the number of soil pathogens and increase microbial diversity near plant rhizospheres. In addition, according to sampling and test results, Fusarium spp., a type of soil pathogen, decreases, while at the same time catalase, dehydrogenase, polyphenol oxidase, and alkaline phosphatase increased in the treated land, boosting crop yield^[98]. Accordingly, both soil beneficial microbial biomass and diversity increased and soil conditions improved through crop rotation.

Both compost and spent mushrooms substrates contain an abundance of nutrients, much of which go unutilized during the field-based cultivation process. Thus, field-based cultivation of mushrooms contributes towards improved soil nutrient cycling via two routes: first, the increased presence of fungal mycelium in the soils enhances nutrient and carbon turnover; and second, the use of compost based substrates inevitably leads to improved soil nutrition. Key elements that have been shown to increase in soils associated with field grown mushrooms are carbon, nitrogen, phosphorous, and potassium.

Carbon cycling

In most agricultural waste substrates used in field mushroom cultivation, carbon exists mainly in the form of fermentable sugars such as lignin, hemicelluloses, and cellulose. After the inoculation of compost and mushroom spawn, lignocelluloses are degraded with the aid of extracellular enzymes such as lignin peroxidases, manganese peroxidase, and versatile peroxidases^[99,100]. In field mushroom cultivation, the carbon cycle features heavily in many close interactions between soil layers and the mushroom cultivation layer. During the mushroom farming process, carbon, mainly microbial carbon, is transferred from the growth substrate to soil through physical processes such as weathering and leaching^[101]. Spent mushroom substrates used as bio-fertilizer increases organic matter content of in situ soil, and spent mushroom substrate is also a useful resource for the generation of biochar that can be fed back into soil systems^[102-104]. Thus, it can be summarized from above that the metabolites of carbon sources travel through four primary pathways: 1) conversion of mycelium biomass and formation of fruiting bodies; 2) carbon dioxide emissions through the respiration of mushroom mycelia and other microbes; 3) participation of soil formation in the form of humus; and 4) microbial carbon and lignocelluloses contained in spent mushroom substrates (Fig. 4).

Nitrogen, phosphorus, potassium cycling

Currently there is limited available data on the direct impact of field grown mushrooms on soil nutrition; therefore we rely on evidence from research using spent mushroom



Fig. 4 Carbon cycling in soil during field mushroom cultivation. Fungal mycelium in mushroom-growing substrates enable carbon to enter soils and facilitate carbon cycling. Carbon flows to fruiting bodies and becomes food; to carbon dioxide through microbial respiration; to spent mushroom substrates post-harvest; and to soil organic matter through weathering. In addition, agricultural waste produced by agricultural activities functions as the source of carbon in growth substrates.

substrates as compost for agricultural fields. Lou et al.^[76] reported that by incorporating composted spent mushroom substrates into agricultural fields, it is possible to improve soil nutrition and health. The authors reported a greater than 5-fold increase in soil mineral nitrogen in fields composted with spent mushroom substrates. Similarly, Yu et al.^[105] reported high levels of soil organic matter and available nitrogen, phosphorus, and potassium in agricultural fields treated with spent mushroom substrates. Though these results are not directly derived from field-based cultivation experiments, they do indicate the potential of mushroom compost for improving soil nutrient content.

Mushrooms and spent substrate compost for soil bioremediation

Various pollutants emerging as a result of industrial and agricultural activities entering soil or water pose a serious threat to human health and natural ecosystems^[106-116]. The polycyclic aromatic main soil pollutants include hydrocarbons, chlorinated hydrocarbons, petroleum and related products, pesticides, and heavy metals. Various techniques have been developed to improve the health of polluted soils; however, among these technologies, soil bioremediation is an emerging and innovative practice, showing potential as an effective means of the use of natural processes to remove pollutants from soil systems^[117].

Applications using fungi and mushroom cultivation in the bioremediation process have been extensively studied over the last two decades^[32,118–123]. Fungi have shown promising results in the degradation or absorption of soil pollutants, including petroleum-based products, heavy metals, chlorinated insecticides, and other agrichemicals^[124,125]. Mushroom-forming fungi are capable to degrade large amounts of environmental pollutants into less toxic forms or into non-toxic metabolites via mineralization and degradation processes, with the aid of various oxidative enzymes, organic acids, and chelators^[16,126,127]. For example, laccase and peroxidase enzymes secreted by Agaricus bisporus can degrade three-ringed polycyclic aromatic hydrocarbons commonly found in petroleum^[128]. During the degradation of polycyclic aromatic hydrocarbons, laccase

catalyzes the initial reaction of polycyclic aromatic hydrocarbon molecules. Further, peroxidase catalyzes the oxidation through complex reactions with combinations of bacteria, and high-molecular mass polycyclic aromatic hydrocarbons were converted into low-molecular mass and low toxic compounds^[129]. In a pilot experiment conducted by Anasonye et al.^[100], fungal enzymes manganese peroxidase and laccase of Stropharia rugosoannulata have been detected and show the potential for degrading 2,4,6-trinitrotoluene, a commonly used explosive from the military and private companies such as mining industry. Moreover, lignocellulose enzymes such as laccase from the spent mushroom compost of Agaricus subrufescens are involved in the degradation of metsulfuron methyl, a herbicide that can contaminate agricultural soils^[130]. In addition to the biodegradation and bioconversion capabilities of fungi, spent mushroom compost of A. bisporus could be used as a biosorbent of textile dyes^[131] and heavy metal biosorption from soils^[132]. These activities have been attributed to the plentiful organicactivated carbon found on the large surface area, surface reactivity, and the microporous structure of the spent mushroom substrate.

Based on the above evidence, the three main roles of mycoremediation in field based mushroom cultivation are biodegradation, bioconversion, and biosorption. Numerous research projects provide proof of concept and the potential for application (Table 2). However, despite the wide variety of fungal species showing potential for use in mycoremediation, few studies have investigated the role of fungi in bioremediation during field cultivation of mushrooms, and thus this remains an avenue for future studies and research.

Degradation of polycyclic aromatic hydrocarbons

Polycyclic aromatic hydrocarbons (PAHs) are organic-based pollutants found in soils, typically originating from natural emissions like wood fires and volcano eruptions or anthropogenic activities such as petroleum-refining processes and pesticide use on agricultural lands^[151,152]. PAHs are carcinogens, mutagens, and teratogens that threaten human health from soil ecosystems. Exposure to PAHs may cause acute or chronic diseases of the immune system^[153]. Although PAHs are hydrophobic and found predominantly on particulate

Mushroom species	Inoculum type	Roles as remediator and target pollutants	References
Agaricus bisporus	Fungal culture	Degradation of three-ringed PAHs, metabolism process occurred with the aid of laccase and versatile peroxidase.	[128]
	Spent mushroom compost	Biosorption of textile dye by spent mushroom compost was attributed to the activated carbon contained in spent mushroom compost, and the process is spontaneous and exothermic.	[131]
	Spent mushroom compost	Inoculation of spent mushroom substrate without previous treatment showed certain PAH biodegradation in Pb-PAH co-polluted soil, and the re-inoculation of fungus exhibited high levels of ligninolytic activity, while the application of spent mushroom substrate produced slight Pb mobilization (< 0.3%).	[133]
	Spent mushroom substrates/raw materials	Adsorption of Cd, Pb and Cu by spent mushroom substrates and their raw materials removed heavy metals from polluted soils, and the process could be attributed to electrostatic attraction, complexation, carboxyl group and N-alkyl effects.	[132]
Agaricus subrufescens	Spent mushroom compost	Crude enzymes extracted from spent mushroom compost were used to test the degradation of metsulfuron methyl, and oil rape (<i>Brassica napus</i> L.) was used as a plant indicator species in the growing medium. It was concluded that complex enzyme fractions degraded metsulfuron methyl significantly when incubation time is over 72 h.	[130]
Flammulina velutipes	Liquid culture/ quartz culture	Biodegradation of polyvinyl alcohol examination in both liquid and quartz sand culture, and the results showed that unsubmerged cultivation is more suitable for the biodegradation of polyvinyl alcohol.	[134]
Coprinus comatus & Pleurotus eryngii	Mycelium substrate bags	Co-incubation exerted the best remediation effect on co-contaminated soil. High yield of mushroom production (1.04–2.60 mg/kg of Cd concentration in different treatments), the removal rates of endosulfan in all treatments were over 87%.	[135]
Ganoderma lucidum	Mycelium with potato dextrose agar	Sufficient amount of ligninolytic enzymes were produced for lindane degradation <i>in vivo</i> , which shows the potential for bioremediation <i>in situ</i> . A maximum of 75.50% lindane degradation after a 28-day incubation period under liquid state fermentation, and 37.5% lindane degradation under solid state fermentation were measured in the experiment.	[136]
lrpex lacteus/Pleurotu s ostreatus	Mycelium with wheat straw-based pellets spawn	Both fungi could oxidize and decompose the aromatic moiety of polychlorinated biphenyls in soils, and results showed contaminant removal rates of 18.5%, 41.3%, and 50.5% from the bulk, surface, and rhizosphere soils respectively. This experiment showed the potential for large-scale remediation of polychlorinated biphenyls contaminated soil using these fungal species.	[137]
Lentinula edodes	Spent mushroom substrate	Spent mushroom substrate and acclimated sewage sludge show degradation rates beyond 94% of PAHs in soil and acclimated sewage sludge improved bacterial abundance, while spent mushroom substrate improved the fungal population and had a better effect on degradation by ligninolytic enzyme	[138]
	Spent mushroom substrate	Organic amendment of cadmium-dichlorophen co-contaminated soil, pollutants removal of soil linked to microbial properties, soil respiration, and ligninolytic enzymes.	[139]
Lentinus sajor- caju/ Pleurotus ostreatoroseus	Mycelium with potato dextrose agar	The mycelium growths in agar medium were affected by different concentration of irons, and <i>L. sajor-caju</i> was able to produce the largest mycelial dry mass (20 ppm of iron), while <i>P. ostreatoroseus</i> also has potential in the iron remediation process.	[140]
Lentinus squarrosulus	Mycelium with sawdust spawn substrate	Inoculation of mushroom spawn was found to reduce the amount of heavy metals and total petroleum hydrocarbon, 85% to 36.94% of petroleum hydrocarbon degradation with 5 ml of crude oil treatment, 86% to 47.58% of petroleum hydrocarbon degradation with 10 ml of crude oil treatment.	[141]
Pleurotus eryngii	Substrate bag with mycelium	Fluoranthene significantly decreased in soil inoculated with mushroom bags, accounting for 86.39%–91.95% of initial concentration in soils; also, <i>P. eryngii</i> could uptake Ni (4.88–39.53 ppm) in Ni-fluoranthene co-contaminated soils.	[142]
Pleurotus ostreatus	Mycelium with potato dextrose agar	Oxo-biodegradable plastic degraded because of the formation of hydroxyl groups and carbon-oxygen bonds.	[143]
	spent mushroom substrate	Inoculation of spent mushroom substrate degraded 48% of (1,1,1-trichloro-2,2-bis(4- chlorophenyl)ethane), and 5.1% of contaminant was mineralized in soil during 28 days incubation.	[120]
	Spent mushroom compost	Bioaugmentation helped for dissipation of endosulfan treating by spent mushroom compost and soil.	[144]
Pleurotus pulmonarius	Fungal mycelium culture	With a period of 62 days of mycoremediation for hydrocarbon polluted soil, heavy metals (manganese, copper, and zinc) decreased significantly in treated soils. Percentage loss for 2.5%, 5%, 10% and 20% concentration are 52.60%, 38.71%, 27.20% and 8.31%.	[145]
Pleurotus tuber- regium	Substrate with fungal mycelium	The growth of fungal mycelium showed high bioavailability for manganese and cobalt and low bioavailability for nickel and iron. It has the potential to increase the release of metals into bio-available states in crude oil-contaminated soil.	[146]
Stropharia coronilla	Mycelium with malt extract liquid	It was found to metabolize and mineralize one kind of PAH benzo[a]pyrene through oxidation, which attributed to the ligninolytic enzyme manganese peroxidase.	[147]
Stropharia rugosoannulata	Fungal inoculum on bark	16 kinds of PAHs were degraded significantly in soil piles after inoculation of fungal inoculum in soil-compost mixtures.	[148]
5	Mycelium with malt extract liquid	Litter-degrading fungal species was chosen for bioremediation experiment in PAH contaminated soil, and the results showed excellent fungal growth and enzyme (laccase and manganese peroxidase) production.	[149]
Trametes versicolor/Bjerka ndera adusta	Mycelium with malt agar culture	Two fungal species were investigated regarding the biodegradation of petroleum residues in soil, and the expression of functional genes were studied after treatment process. Results showed both species are conducive in biodegradation, and <i>T. versicolor</i> is more effective than <i>B. adusta</i> . The expression of <i>nah</i> and <i>phnAc</i> genes increased, while the <i>alkB</i> gene did not increased	[150]

Table 2. Roles of mushroom species in the bioremediation of pollutants after the bioaugmentation of fungal inocula.

&, co-incubation; /, incubation separately; PAHs, polycyclic aromatic hydrocarbons.

matter, they enter the food we eat through the food web and cripple crop productivity^[154].

Due to their chemical structure and low solubility. PAHs are resistant to environmental degradation^[148,155,156]. Fungi are promising organisms that can degrade PAHs in soil ecosystems due to the distinct extracellular enzymes secreted by fungal hyphae^[157]. Field mushroom cultivation facilitates the growth of substantial mushroom mycelia throughout the soil, producing an abundant amount of enzymes such as laccases and peroxidases, which foster the catalytic degradation of hydrocarbons in agricultural lands^[99]. The two main bioremediation approaches for recalcitrant toxic PAHs are the microbial-substrate based remediation method and the phyto-microbial remediation method. Field mushroom cultivation refers to the fungi-substrate method can improve soil health by reducing PAH content in agricultural soil ecosystems^[149,133]. For example, biostimulation and bioaugmentation resulting from the use of spent mushroom substrate of Agaricus bisporus can degrade PAHs; previous research showed that the addition of spent mushroom substrates stimulates the growth of resident soil microbes removes 3-ringed PAHs^[133]. Benzo[a]anthracene, and benzo[a]pyrene and dibenzo[a,h]anthracene in soils can be effectively degraded by eight mushroom species (Agrocybe dura, A. praecox, Hypholoma capnoides, Kuehneromyces mutabilis, Pleurotus ostreatus, Stropharia. coronilla, S. hornemannii, S. rugosoannulata)^[149], and the mycelia of S. coronilla and S. rugosoannulata grow into the soil and are the most efficient at degrading PAHs. Based on the above application, a combination of fungal species and agro-waste during field mushroom cultivation is technically feasible for environmental in situ PAH remediation.

Pesticide and herbicide degradation

Many chemical pesticides are now widespread throughout global ecosystem^[158]. Chemicals resulting from the use of pesticides, herbicides and fungicides create environmental hazards that influence soil chemistry and biology. The mycoremediation of contaminated soils is considered a good method to adapt to the current predicament, especially as the use of mushrooms has drawn considerable research attention and interest. Many mushroom species or spent mushroom substrates are effective for the degradation of pesticides, such as endosulfan, lindane, methamidophos, cypermethrin, dieldrin, methyl parathion, chlorpyrifos, and heptachlor^[20]. With the involvement of different enzymes, pesticides have been degraded by fungal strains through biological processes including oxidation, hydroxylation, and demethylation across both laboratory and field scales. Moreover, the degradation rates in soils are affected by abiotic factors, including pH, temperature and moisture. For instances, Ribas et al.[159] reported that Agaricus subrufescens can degrade 35% of atrazine, a kind of carcinogenic herbicide when pH at 4.5, and a lower reduction of atrazine occurs at pH is higher than 4.5. Jin et al.^[160] investigated fungal degradation for laccasecatalyzed pesticide, and results showed the optimum condition for highest activity of laccase is pH at 5.0 and temperature at 25 °C; also the laccase is stable at a pH range of 5.0-7.0 and temperature range of 25-30 °C. In the experiment conducted by García-Delgado et al.[133], spent Agaricus bisporus substrate was used to remediate polycyclic aromatic hydrocarbons contaminated soils, and soil moisture content was adjusted to 70% to maintain the activity of spent mushroom substrate microbiota for removing soil contaminates. Key examples of laboratory based degradation of pesticides using fungi include: the degradation of endosulfan, a highly toxic organochlorine pesticide, by *Pleurotus ostreatus*^[161] and the degradation of an organochlorine-based pesticide, Lindane, by the white rot fungus *Ganoderma lucidum*^[136]. This research also highlighted that a dialyzed crude extract of ligninolytic enzymes, derived from mushroom culture, was efficient in lindane degradation.

However, most mushroom species used for the degradation of pesticides and herbicides are not related to field-cultivated mushrooms, and most experiments regarding the biodegradation of pesticides have only been conducted at the lab scale. Only Agaricus bisporus and A. subrufescens are reported to possess the ability to degrade pesticides in field conditions^[130,162]. Matute et al.^[130] investigated the degradation of metsulfuron methyl by using spent A. subrufescens substrate, and results showed metsulfuron methyl is degraded by spent mushroom compost enzymes, and high laccase activity has also been detected in the experiment. Furthermore, Ahlawat et al.[162] reported that the spent mushroom substrate of A. bisporus is effective in the degradation of Carbendazim and Mancozeb, two commonly used fungicides, providing further evidence of the potential for fungi to breakdown pesticides and agrichemicals.

Bioremediation of heavy metal contaminated soils

Recent reviews by Bosco and Mollea^[21] and Raina et al.^[163] look into the mechanisms behind mycoremediation of metalcontaminated soils, providing detailed insight into these processes and emphasizing the emerging role the fungi can play in the bioremediation of heavy metal-contaminated soils. However, the work of Stoknes et al.^[164] provides a good example of the reduction of soils heavy metals under fieldbased mushroom cultivation. The authors reported that the cultivation of Agaricus subrufescens in soil contaminated with Cd results in an 80% decline in Cd levels. The majority of this accumulated Cd was stored in the first batch of mushrooms that were harvested, and as such, had to be disposed of. However, subsequent mushroom harvests were shown to be safe for human consumption. Similarly, Liagat^[165] reported that the spent mushroom substrate of Volvariella volvacea is also a good candidate for the bioremediation of Pb- and Hgcontaminated soils^[163]. Therefore, the field mushroom cultivation of mushrooms shows promising applications in the bioremediation of heavy metal-contaminated soils and improved soil health through biosorption in both the cultivation process and spent mushroom substrates.

Conclusion and perspectives

There is evidence showing the potential of fungi to improve soil health in agricultural systems by increasing carbon and nutrient levels, preventing soil erosion, and breaking down pollutants. However, much of this evidence is indirect or has not been tested at scale. Thus, this field of study remains wide open, with opportunity for field practitioners and scientists to provide scaled research investigating which fungal species have the most significant impact on soil health, which species degrade, bind, or accumulate toxins and heavy metals, and ultimately which fungal species still provide a harvest of mushrooms considered safe for human consumption. Currently, land use diversification, soil health, and sustainable agriculture are important topics, all of which need to be researched in greater detail if we are to address the challenges facing modern agriculture. We hope our review provides evidence that solutions to many of these challenges already exist. Incorporating mushroom production systems into existing agricultural lands will be a good first step in implementing such changes.

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Conflict of interest

The authors declare that they have no conflict of interest.

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