

Ectomycorrhizal Mushrooms

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Environmental changes and heavy metal pollution are some of the consequences of anthropogenic activities. Many ecosystems, including edaphic ecosystems, suffer from the effects of pollution. The accurate assessment of soil heavy metal contamination leads to better approaches for remediating soils. The exploration of different ways, including biological methods, to conduct environmental monitoring is still ongoing.

Keywords: contamination ; ectomycorrhiza ; heavy metal

1. Introduction

Heavy metals (HM) and metalloids are metallic elements having a specific density of more than 5 g cm^{-3} , such as mercury (Hg), chromium (Cr), cadmium (Cd), arsenic (As), and lead (Pb) ^[1]. Heavy metals are adversely affecting living organisms even at low concentrations through bio-accumulation in the food chain ^{[2][3]}. Heavy metals are characterized by a long half-life, and they are highly persistent in the environment with the potential for accumulation ^[4]. The artificial radionuclides or isotopes of different heavy metals cause significant hazards in terms of soil pollution. There are two main sources globally, which are responsible for the presence of different radionuclides in the environment ^[5]. Nuclear weapon tests and nuclear reactor catastrophes such as Chernobyl in 1986 are the main sources that emitted considerable amounts of α , β , and γ -radionuclides into the atmosphere. For instance, the long-life gamma radioisotope cesium ^{137}Cs is considered an important indicator of radioactive pollution due to its long half-life (30.07 years) ^{[5][6]}. Caridi et al. ^[7] explain that radionuclides are strongly absorbed into the sediments and retained for a long time, resulting in genetic mutations, the development of diseases, and soil infertility.

Although cobalt (Co), copper (Cu), iron (Fe), manganese (Mn), molybdenum (Mo), nickel (Ni), and zinc (Zn) are also grouped under the HM category, at optimum concentrations, they are beneficial for plant growth and development ^[8]. Nevertheless, the same metals become toxic when they exceed certain threshold concentrations ^{[8][9]}. Even though HM occurs naturally in the crust of the Earth, anthropogenic activities mostly contribute to the HM prevalence in air, soil, and water ^{[10][11]}. Since these metals are non-biodegradable, they persist in the environment ^[12]. Therefore, heavy metal contamination and pollution are major environmental hazards, which, when amplified by inadequate human intervention, could become a serious concern.

Conventional farming practices, increasing industrialization, and the substantial use of fossil fuels have led to high concentrations of heavy metals in the environment ^[13]. Furthermore, the large quantities of synthetic fertilizers and other agro-chemicals used in farming systems lead to substantially high concentrations of heavy metals in soil and water ^[1]. In acidic soils, HM becomes highly bioavailable due to competition with H^+ for binding sites and increased solubility ^{[14][15]}. Considering these threats, scientists have focused on finding solutions to minimize the adverse effects caused by heavy metals. In the HM remediation processes in contaminated environments, demarcation of the contamination, identification, and quantification of the HM, specifically in their ionic form, are inevitably important ^{[16][17][18]}.

From an ecological perspective, different organisms, including microorganisms, are naturally occurring bioindicators. Bioindicators are used to assess the environmental quality and detect positive or negative changes and their subsequent effects on biotic and abiotic components of the environment ^[19]. Bioindicator organisms possess the potential to absorb particular pollutants from the surrounding environment and indicate the presence of a particular pollutant within the organism ^[20]. Although different types of organisms are used as bioindicators in ecological monitoring, ectomycorrhizal mushrooms are well known among them due to their capability of absorbing heavy metals from the surrounding environment ^[18].

Mycorrhizae are generally considered mutualistic symbioses between plant roots and some fungi ^[21]. These symbioses are characterized by the bi-directional movement of nutrients where carbon flows to the fungus from the plant and inorganic nutrients move to the plant from the fungus, thereby providing a critical bond between the plant root and soil ^[22].

In the humid tropics, the following two major types of mycorrhizal associations of trees have been reported: ectomycorrhiza (EM) and arbuscular mycorrhizal fungi (AM) [23]. Both EM and AM are recognized as heavy metal accumulators [24][25][26].

Nevertheless, the ectomycorrhizal fungi have been identified as a group of organisms that intensely affect ecosystems by facilitating nutrient and water uptake, structuring soil, maintaining food webs, protecting the root systems of trees from pathogenic organisms, extreme environmental conditions, and phytoremediation of contaminated soils [27][28][29]. Besides that, the vast diversity of EM fungi helps nature to withstand changes in environmental factors due to heavy pollution and global climate change. Moreover, many EM fungi play a major role in bearing commercial value for edible fruiting bodies and in producing metabolites useful in industries [28][30]. Therefore, conservation, broader appreciation, and widening applications of EM fungi are necessary due to their extensive intervention in the successful functioning of ecosystems.

2. Ectomycorrhizal Fungi

Ectomycorrhizal mushrooms include approximately 10,000 species, mainly belonging to Basidiomycetes, Ascomycetes, and Zygomycetes that form associations with host plants [31][32] and were found to have evolved 130 million years ago [31]. Caesalpiniaceae, Pinaceae, Fagaceae, and Dipterocarpaceae are the major families known to host EM mushrooms in tropical, subtropical, temperate, and boreal forests [33]. Among the different classes of EM fungi, Agaricomycetes are found to be the dominant class in forming mycorrhizal symbiosis [34].

Ectomycorrhizal mushrooms possess a dual lifestyle in soil, being symbionts and facultative saprotrophs [35]. Due to the ecological symbiosis maintained by EM mushrooms with the root systems of trees, the number of interactions maintained with the inhabited environment is higher compared to purely saprotrophic mushrooms [36].

Ectomycorrhizal fungi are capable of enclosing their hyphae, convolving the root tips, and creating a hyphal mantle. Within the mantle, hyphae grow between cortical and epidermal cells where the lumen of roots is not penetrated [37]. This formation results in a structure called the Hartig net (Figure 1). A Hartig net makes an interface for nutrient and water exchange between fungi and roots [35]. Meanwhile, the hyphae extend out of the fungal mantle to the soil and explore the faraway regions of the rhizosphere, and increase the nutrients available for the host [35]. Hence, EM mushrooms act as an integral part of plant nutrition. The plants intern, transferring carbohydrates to the fungus [35]. Apart from sharing nutrients, the host plant also receives benefits, including increased tolerance for salt and drought stresses [38], tolerance to heavy metals [38][39], and resistance to plant pathogens [40][41]. Furthermore, EM mushrooms protect their hosts [42][43], mitigating drought stress and producing vitamins and hormones for plant development [31][44].

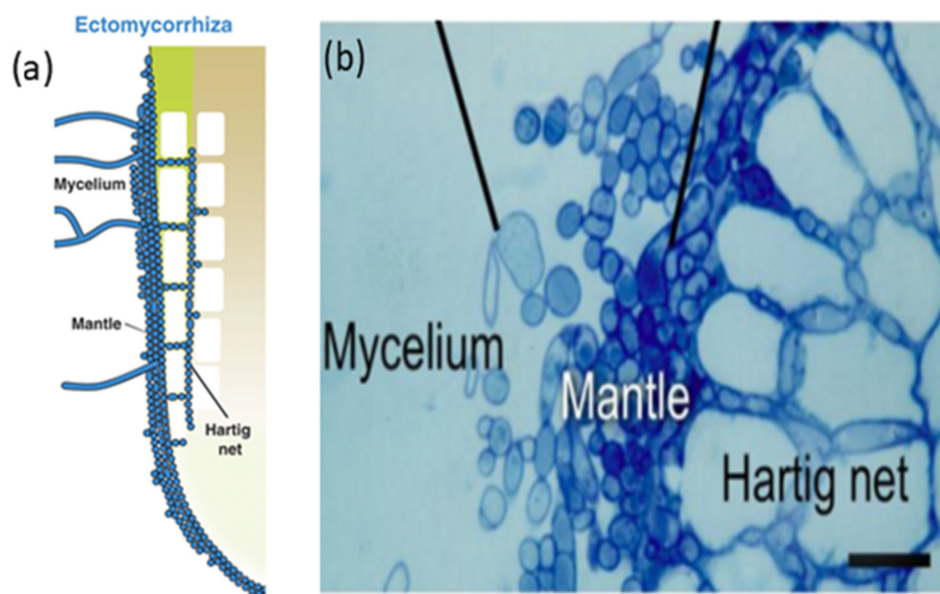


Figure 1. (a) Illustration of root colonization structures in ectomycorrhiza (b) Hartig net formation of EM fungi. Outbreak of hyphae of mycelium in intracellular space with no penetration in lumen [37] Mechanisms underlying beneficial plant-fungus interactions in mycorrhizal symbiosis.

Ectomycorrhizal fungi possess crucial symbiotic relationships with plants that grow on heavy metal contaminated sites such as AM and influence plants to alleviate heavy metal toxicity [45][46]. The enhanced Cd tolerance of *Paxillus involutus* by *Populus canescens* [38] and Cu and Cd tolerance of *Eucalyptus tereticornis* by *Pisolithus albus* [47] were some of the

evidences that EM helped for host heavy metal tolerance. Furthermore, the alleviated Cd toxicity of *Pinus pinaster* seedlings was found with the EM fungi *Suillus bovinus* and *Suillus granulatus* [48]. *Inocybe curvipes* enhanced the Pb and Zn tolerance of the Masson pine trees [49]. According to Krzmaric et al. [50], pine trees that have an association with *Suillus luteus* possess the ability of heavy metal tolerance.

In contrast to AM, the symbiotic compatibility and stress tolerance of EM are species-specific to some extent, and therefore, knowing EM fungal community dynamics can lead to understanding the processes of forest ecosystems and help to facilitate the tools of bioindicators in different environmental stress conditions, including heavy metal toxicity due to contamination of soil [51]. Furthermore, the changes in EM fungal dynamics can therefore be correlated with altered tree responses to stress conditions, including heavy metal toxicity [52]. According to Milenge et al. [53], environmental stress factors could affect photosynthesis and, hence, reduce the sugar availability to EM, which might lead to changes in EM dynamics. Similarly, due to stress factors, the changes in the EM community might alter plant nutrient uptake and photosynthesis and affect plant performance [52]. As a consequence, both EM fungi and the host plant together can act as bioindicators.

3. The Role of Ectomycorrhizas in Heavy Metal Stress Tolerance of Host Plants

3.1. Heavy Metal Deposition in EM Fungi

Heavy metals are absorbed by EM fungi from soil solutions. Soil contamination by heavy metals occurs mainly due to natural phenomena and anthropogenic activities. Heavy metal deposition of Basidiomycetes varies depending on temperature, humidity, nature of metal, soil pH, substrate, mushroom species, and also ecosystem processes [54][55][56]. Due to the sensitivity of EM fungi to heavy metal contaminants, EM mushrooms can be used as an active and passive biomonitoring tool for metal deposition [57][58]. The estimations of biological effects caused by heavy metals are measured by monitoring the population dynamics of EM mushrooms, community variations, and morphological changes [59][60]. Reduced hyphal extension, morphological changes in mycelia, biomass reduction, and increased hyphal branching are major indications of declines of some EM species due to metal stress [61][62].

The mobility of the heavy metal changes due to the nature of metallic compounds since the availability of cations depends mainly on the anions. Ni, Co, Pb, and Cr have less mobility compared to Cd and Hg [9][63][64]. The ectomycorrhizal fungi *Suillus granulatus*, *Lactarius deliciosus*, *Tuber melanosporium*, and *Tuber brumale* showed higher Cu biosorption with surplus supplies of potassium (K) and three [65].

The EM mushrooms are capable of withholding heavy metals absorbed by soil solutions and, hence, protecting the host plants. This mechanism of the EM mushrooms relies mainly on the capacity of the fungus to continue proliferation through the substrate, producing new biomass in the presence of high metal concentrations [65][66][67][68]. The deposition levels of heavy metals in EM fungi have been extensively studied in different regions and contamination levels [64][69]. *Lactarius deliciosus*, *Russula delica*, and *Russula albidia* from Canakkale, Turkey were found to have deposited the higher concentrations of Cd, Cu, and Pb [24][64][70][71], while Zn was deposited in *Russula delica*. A higher level of Cr was recorded in *Lactarius deliciosus* [64][70][71][72]. *Russula albidia* was found to absorb higher Ni, Cr, Mn, and Zn concentrations, and it was in the range of 1–5 mg kg⁻¹ [72].

Akin et al. [64] carried out two different experiments to compare the absorption of Cu and Zn by *Baorangia bicolor* in Çanakkale, Turkey. *Baorangia bicolor* was compared with *Retiboletus fuscus*, *Russula delica*, and *Russula crustosa* for Cu absorption and found that *R. fuscus* and *R. delica* absorbed more Cu compared to *B. bicolor*. A comparison of *B. bicolor* with *R. crustosa* and *Lactarius representaneus* for Zn absorption resulted in a higher absorption rate of *R. crustosa* and *L. representaneus*. Further, *Imleria badia* showed higher sensitivity to Pb by absorbing a concentration of 0.448 ± 0.03 mg kg⁻¹ of biomass [64][70][71][73].

Crane et al. [15] revealed the response of EM fungi towards Hg concentration and showed that *Amanita muscaria*, *Coccobotrys xylophilus*, *Laccaria laccata*, *Piloderma bicolor*, *Pisolithus arhizus*, and *Suillus decipiens* are influenced by Hg at the immature stage of their growth, reducing the growth of the fruiting bodies. The changes in morphology depend on the concentrations of Hg and the exposure time. Among hyper-accumulating mycorrhizal mushrooms, such as *Gomphidius glutinosus*, *Craterellus tubaeformis*, and *Laccaria amethystina*, which are all associated with pines, *G. glutinosus* has been seen to absorb the most via the mycelium and concentrate radioactive cesium (Cs) more than 10,000-fold over ambient background levels [74].

Studies carried out in Slovakia, Turkey, and Northern Poland revealed that different EM fungi such as *Boletus edulis* and *Paxillus involutus* hold considerably higher concentrations of Hg, Pb, Cd, and Cu [15][25][26][27]. Tuzen et al. [28] and Dermirbas et al. [58] revealed that *Tricholoma terreum* is one of the EM fungi studied for retention of different metal ions. Furthermore, Yilmaz et al. [79] explained that *T. terreum* tolerates and holds a higher number of metal ions compared to other EM fungi, and his results explained that the highest contents of HM were represented by Fe (744), Zn (179), and Cu (51) mg kg⁻¹. Durken et al. [80] demonstrated that *Paxillus rubicundulus* can hold Pb (0.69), Cd (0.78), Hg (0.21), Fe (37.0), Cu (51.0), Mn (10.8), Zn (16.8) mg kg⁻¹ in a study conducted in Turkey.

It was reported from Northern Greece and Turkey that *Boletus* sp. and *Hydnum repandum*, *Russula delica*, *Tricholoma terreum*, *Butyriboletus appendiculatus*, *Leccinum scabrum*, *Psilocybe coronilla*, *Tricholoma scalpturatum*, and *Suillus granulatus* are a few edible EM fungi that withhold Pb, Cd, Hg, Cu, Mn, Zn, and Fe in higher quantities compared to other edible EM fungi [80][81][82][83][84].

3.2. Heavy Metal Deposition in Edible EM Mushrooms

The deposition of heavy metals in mushrooms is an important concern for edible mushrooms. Wild edible fungi are belonging to several trophic groups as saprotrophic or termite associated (growing in mutualistic relation with termites) or ectomycorrhizal [84][85]. Some EM genera, i.e., edible *Amanita*., *Lactarius*, *Lactifluus*, and *Russula*, are common in some forests. These edible EM fungi are harvested and consumed by people [85]. *Boletus edulis* (Bull.), *Tricholoma matsutake* (S. Ito and S. Imai), *Lyophyllum shimeji*, *T. bakamatsutake* Hongo, *T. portentosum* (Fr.), *Rhizopogon roseolus* (Corda) Th. Fr., *Suillus grevillei* (Klotzsch) Singer, *Boletus edulis* Bull., *Amanita caesareoides* Lj. N. Vassiljeva, *Entoloma sepium* (Noulet and Dass.) Richon and Roze, *Cantharellus cibarius* Fr., and *Tuber indicum* Cooke & Massee, *Cantharellus cibarius*, and *Lactarius hatsudake* are some of the examples of edible mycorrhizal mushrooms [84]. Heavy metal pollution causes detrimental effects on humans, other organisms, and the environment. Hence, it is important to study and investigate the metal content and accumulation in local wild mushrooms since they are a significant nutritional source in many countries [70].

Heavy metal contents of six edible EM mushroom species viz. *Cyanoboletus pulverulentus*, *Cantharellus cibarius*, *Lactarius quietus*, *Russula xerampelina*, and *Suillus grevillea* were estimated by Arvay et al. [86]. The highest mean concentrations of some metal elements were recorded in *S. grevillei* as 107, 104, 81.6, and 434 mg/kg (dried mass basis) for Zn, Cu, Mn, and Fe, respectively. Furthermore, the highest content of Co was found in *L. quietus* at 0.90 mg/kg (dm). Mleczek et al. [81] stated that toxic metals (Al, Cr, Hg, Ni, As, and Pb) amounts are higher in wild mushrooms compared to cultivated mushrooms.

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