MYCORRHIZAL FUNGI AS HELPING AGENTS IN PHYTOREMEDIATION OF DEGRADED AND CONTAMINATED SOILS

MIROSLAV VOSÁTKA, JANA RYDLOVÁ, RADKA SUDOVÁ AND MARTIN VOHNÍK
Institute of Botany, Academy of Sciences of the Czech Republic, 252 43 Průhonice, Czech Republic, E-mail: vosatka@ibot.cas.cz

1. Introduction

Plant roots were defined from phytoremediation point of view as "exploratory, liquid-phase extractors that can find, alter and/or translocate elements and compounds against large chemical gradients" [1]. Since the roots of majority of higher plants live naturally in symbiosis with different types of mycorrhizal fungi [2], this association should be regarded as an organic component of the phytoremediation systems [3, 4, 5]. However, relatively few studies have focused on the effects of mycorrhiza on phytoremediation and *vice versa*, despite the widely acknowledged importance of mycorrhizal symbionts for plant growth and fitness particularly in harsh environments.

By various mechanisms mycorrhizal fungi are able to take either direct or indirect part in different processes of phytoremediation of contaminated soils including phytostabilisation, phytoextraction or phytodegradation. Indirectly, mycorrhiza can increase plant ability to withstand soil phytotoxicity due to improved nutrition, particularly in the soils with relatively immobile phosphorus, protect plants against root pathogens and drought stress and enhance soil aggregation and consequently increase retention of xenobiotics. These functions are of particular importance mainly in degraded and contaminated soils that are often poor in nutrients, with low water holding capacity and adverse physical conditions. Through altered root exudation, mycorrhiza may also affect composition and activity of microbial communities in the rhizosphere towards the microflora more effective in xenobiotics degradation or microflora, which stimulates plant growth (plant growth promoting rhizobacteria such as nitrogen-fixing bacteria). Furthermore, mycorrhizal fungi also directly help the plant to escape from the build-up of phytotoxic concentrations of certain pollutants by secreting specific detoxifying compounds (e.g. organic acids) or by binding the pollutants into fungal tissues associated with the roots and thus creating a physical barrier against their translocation to the shoots of the host plant. Important role in direct interactions of all types of mycorrhiza with soil contamination plays so called extraradical fungal mycelium (ERM) radiating from the colonised root cortex far into the surrounding soil. This mycelial network represents extensive interface between roots and pollutants

M. Mackova et al. (eds.), Phytoremediation Rhizoremediation, 237–257.

dispersed in soil. Until now, some experimental data were published on possible role of different types of mycorrhiza in phytoremediation of xenobiotics, however, majority of those represents results of microcosm experiments and is focused mainly on heavy metals. This chapter is not a detailed review of the literature which is rather extensive in particular for ectomycorrhizal symbiosis, but it focuses on basic features of the role of mycorrhizas in phytoremediation, shifts in occurrence of mycorrhizal fungi in degraded and contaminated soils, the effects of xenobiotics (heavy metals – HMs, polyaromatic hydrocarbons – PAHs and polychlorinated biphenyls – PCBs) on development of symbioses and the effects of symbioses on plant tolerance and fitness in contaminated environment.

The role of mycorrhiza in phytoremediation should be viewed from the perspective that there are different types of mycorrhizal symbiosis varying in host plant species and each mycorrhizal type can also exhibit different mechanisms of interaction with xenobiotics. Two basic types of mycorrhizal symbiosis are endomycorrhiza and ectomycorrhiza. The endomycorrhiza is further divided into several subtypes among them arbuscular mycorrhizal and ericoid mycorrhizal being the most important and having a relevant role in phytoremediation, other subtypes such as orchideoid or arbutoid mycorrhizas are rather marginal from this point of view.

2. Potential of mycorrhizal fungi in phytoremediation of xenobiotics

2.1. ARBUSCULAR MYCORRHIZAL (AM) FUNGI

The arbuscular mycorrhiza is the most ubiquitous as the arbuscular mycorrhizal fungi belonging to the phylum *Glomeromycota* [6] form symbiosis with more than 80% of vascular plant species [2]. This type of mycorrhiza occurs in majority of the terrestrial ecosystems, however, it is difficult to be observed by naked eye in nature as the AM fungi form only spores in the soil and not the fruiting bodies and symbiosis does not change morphology of the colonised roots.

The AM fungi have not been considered as an important component of HM phytoremediation protocols in early studies because many metal hyperaccumulators, often small and slowly growing, belong to plant families *Brassicaceae* or *Caryophyllaceae* that predominantly do not form mycorrhizal symbiosis [7]. However, a range of plant species intended for phytoremediation practices has been extended also to the plants capable of forming AM symbiosis and readily producing large biomass (e.g. maize, tobacco, hemp, sunflower or some hardwood trees), partly along with the progress in genetic engineering and possibility to introduce genes inducing hyperaccumulation of xenobiotics [8]. Regarding different phytoremediation strategies feasible for HM contaminated soils, AM fungi are of interest especially for phytoextraction and phytostabilisation, whereas their potential for rhizofiltration technique is negligible due to a limited ability of AM fungi to survive under long-term flooding [4].

2.2. ERICOID MYCORRHIZAL (ERM) FUNGI

Ericoid mycorrhiza is a distinctive subtype of endomycorrhiza formed mostly by ascomycetous fungi inhabiting fine roots of the members of *Ericaceae* [9]. Ericaceous species have worldwide distribution occurring and sometimes dominating over large areas in both Northern and Southern Hemisphere. Their habitats are characterized by challenging environmental conditions including acidic, nutrient poor substrates with high carbon/nitrogen ratio, low decomposition rate, poor drainage and not least by elevated level of toxic compounds including heavy metals [2, 9].

The key role of the ErM fungi for the establishment of ericaceous vegetation at HM polluted habitats is widely accepted [10, 11, 12], as ericoid endophytes show high resistance to metal toxicity as compared to other mycorrhizal fungi [13]. Since ericaceous species occurring at HM contaminated sites are relatively slowly growing dwarf shrubs, their role in phytoextraction is unlikely to reach significant levels on industrial scale. However, the ErM fungi are suggested to be the key factors enabling ericaceous dwarf shrubs to dominate at HM polluted sites [11]. The ericaceous plants are often the first colonisers of such habitats [12], which together with their ability to grow at nutrient poor substrates underline their phytostabilisation effect in natural succession on contaminated sites.

2.3. ECTOMYCORRHIZAL (ECM) FUNGI

Ectomycorrhiza occurs in majority of coniferous trees and also in numerous broadleaved trees mainly from the families *Fagaceae*, *Betulaceae* and *Ulmaceae*. The EcM associations are formed mainly by basidiomycetous or ascomycetous fungi, most of them produce fruiting bodies known as mushrooms. Unfortunately, the diversity of fruiting bodies aboveground is not necessarily connected with the diversity of fungi forming ectomycorrhizas underground. In contrast to other types of mycorrhiza, these associations change distinctly morphology of the root system by forming typically thickened ectomycorrhizal root tips, from which dense fungal mycelium spreads into surrounding soil exploiting its nutrient sources. Extraradical ectomycorrhizal mycelium often forms thick and dense hyphal cords called rhizomorphs serving for water and nutrient transport between distant parts of mycelium.

Plants growing on contaminated substrates benefit from the associations with the EcM fungi, which can support their growth by improving their nutrient and water uptake and also alleviate HM toxicity. Areas polluted by HM are often re-vegetated with trees and EcM fungi are regarded as positive factors influencing survival of tree species at such areas [14] thus significantly affecting site phytostabilisation.

3. Effect of xenobiotics on occurrence of mycorrhizal fungi and development of mycorrhizal symbioses

3.1. ARBUSCULAR MYCORRHIZAL FUNGI

There are relatively scarce data on the effects of soil contamination on field abundance and diversity of populations of AM fungi. It was found that contamination of soils with heavy metals decreased numbers of AM propagules and reduced mycorrhizal infectivity of soils as compared to uncontaminated sites [15, 16, 17]. Nevertheless, spores of the AM fungi and relatively high levels of root colonisation were reported even from highly contaminated mine spoils as well as polluted agricultural soils [18, 19, 20, 21, 22]. A great variability in HM tolerance of different AM fungi isolates have been shown [23, 24, 25], with higher HM tolerance often reported for indigenous isolates obtained from polluted soils as compared with non-indigenous ones [26, 27, 28]. Especially the isolates capable to tolerate extreme soil contamination represent a valuable material for potential inoculation of plants within phytoremediation programmes. More attention should be, however, paid to the stability of high HM tolerance of these isolates during sub-culturing process since significant shifts in tolerance to contamination have been recently reported under keeping in conditions without selection pressure. For example, a decline in Mn tolerance of a *Glomus* sp. isolate from a Mn contaminated substrate was shown after its 2-year maintenance in metal-free substrate, compared with the lineage grown constantly under HM stress in the original substrate [28]. A similar decrease in Al tolerance of *Glomus clarum* isolates was reported, with the tolerance decreasing with increasing time under conditions without metal exposure [25].

Negative effects of heavy metals were observed at any ontogenetic stage of AM development, from spore germination, germ tube growth, root penetration and colonisation to proliferation of the extraradical mycelium into surrounding soil and formation of new spores. Considerable sensitivity of spore germination to HMs was firstly described almost thirty years ago [29, 30] and this stage was repeatedly shown as more sensitive than subsequent germ tube growth [23, 31]. A majority of results on HM effect on AM development refers, however, to the level of root colonisation in HM contaminated substrate. Generally lower percentage of root colonisation in contaminated soil is a complex phenomenon caused by inhibition of spore germination, lower extension of hyphae, unsuccessful root penetration and disruption of the internal hyphae [11]. In comparison to intraradical phase of colonisation, only little attention has been paid to the effect of HMs on the development of extraradical mycelium. Both higher [17, 32] and lower [33] sensitivity of ERM to HM exposure has been reported in comparison to root colonisation.

As regards the interaction of AM fungi with organic pollutants, in one of the few studies [34] there was found that mycorrhizal colonisation of several plant species by indigenous AM population was not significantly affected by addition of a single PAH (anthracene) in concentrations up to 10 $g.kg^{-1}$. However, colonisation of clover and leek decreased when industrial PAH polluted soil was added into unpolluted soil, while maize and ryegrass colonisation was not affected. Spiking of soil with a mixture of three PAHs reduced colonisation of clover by a non-adapted AM fungus *Glomus mosseae*

BEG69 to a half of that in non-spiked soil [35]. Uptake of phosphorus was maintained in mycorrhizal clover when PAHs were added, but was reduced in non-inoculated clover and in inoculated clover plants that received surfactant to increase PAH availability. This may indicate higher PAH sensitivity of clover as compared to the AM fungus. No such effects were observed for ryegrass. By contrast to the previous results, the colonisation of alfalfa by *G. caledonium* was not significantly affected in soil artificially contaminated with a single PAH (benzopyrene) up to 10 mg.kg^{-1} but significantly decreased at 100 mg.kg^{-1} [36]. In two pot experiments with PCB contaminated soils (mixture of Delor 103 and Delor 106, total PCB concentrations 25 and 94 g.kg^{-1}, respectively), relatively high colonisation of tobacco (up to 98%) and alfalfa (up to 52%) roots by two non-adapted AM isolates was observed, depending on plant species, cultivar and AM fungal isolate [37].

3.2. ERICOID MYCORRHIZAL FUNGI

The data on the effects of HMs on occurrence of ericoid mycorrhizal fungi in the soil are very limited due to rather difficult quantification of ericoid mycorrhiza in the field samples – the ErM fungi generally do not form spores or fruiting bodies. However, occurrence of ericoid mycorrhizal fungi can be linked together with occurrence of their ericaceous hosts, which are usually highly mycorrhizal at both disturbed and undisturbed sites.

For the ErM fungi, there are only few reports on how heavy metals influence development of symbiosis and growth of the host plants. Screening the effects of lead on the growth of ericoid mycorrhizal mycobiont *Hymenoscyphus ericae* cultivated *in vitro* showed that this fungus was able to grow on media containing up to 400 μg.ml^{-1} Pb [38]. The same fungus was able to grow over all iron concentrations tested (0-144 μg.ml^{-1}), exhibiting greater resistance than its host plants [39]. The growth of another ErM fungus *Oidiodendron maius* isolated from mycorrhizal roots of *Vaccinium myrtillus* growing in heavily contaminated soil was investigated in the presence of zinc ions [40] and the authors found strong specificity of HM tolerance for each fungal strain. In the presence of increasing concentrations of Zn salts (especially at higher ion concentrations), better performance of the mentioned isolate was observed in comparison with isolates from unpolluted soils. Differential resistance was also observed among populations of *H. ericae* isolated from *Calluna vulgaris* from natural heathland soils and mine-site soils contaminated with AsO_4^{3-} and Cu^{2+} [41]. *H. ericae* populations from the mine sites demonstrated resistance to AsO_4^{3-} compared with the heathland population; the mine-site populations produced significant growth at the highest AsO_4^{3-} concentrations (4.7 mol.m^{-3}), whereas growth of the heathland population was almost completely inhibited. All isolates produced identical responses to increasing copper concentrations with no differences observed between mine-site and heathland fungal populations. Thus, *H. ericae* on the contaminated sites has developed an adaptive resistance to arsenate whereas resistance to copper appears to be constitutive.

3.3. ECTOMYCORRHIZAL FUNGI

Negative effects of heavy metals on the development of EcM symbiosis have been repeatedly reported, both *in vitro* as well as in association with host plants. Decreasing abundance and diversity of Ectomycorrhiza morphotypes with increasing concentration of heavy metals was observed in a vicinity of the fertiliser factory [42]. Similarly, lower average number of EcM root tips in *Pinus sylvestris* was reported from site polluted with acid rain and with high aluminium availability than from a reference unpolluted site [43]. On the contrary, no evidence for a reduction of the genetic variation of subpopulations of the EcM fungus *Suillus luteus* caused by HM contamination was revealed in another field study [44]. High chromium and nickel concentrations were reported to decrease EcM colonisation by *Pisolithus tinctorius* in *Eucalyptus urophylla* [45]. Five different heavy metals were shown to negatively influence nitrogen acquisition efficacy of ectomycorrhizal birch seedlings [46]. On the contrary, no adverse effects of lead exposure on development of association of two EcM fungi with Norway spruce were found in another study [47]. Increased concentrations of cadmium and zinc reduced EcM colonisation of Scots pine with *Paxillus involutus* and EcM colonisation was found to be more sensitive to elevated HM levels than host *Pinus sylvestris* itself [48]. The authors also showed that both metals negatively influenced not only root colonisation but also dispersal of EcM fungi from colonised roots towards non-mycorrhizal roots. This was prominent mainly in the case of cadmium, which suppressed cross-colonisation of non-mycorrhizal roots with mycelium from roots already colonised by EcM fungi to a greater extent than the colonisation of already EcM roots. However, it should be noted that HM tolerance of ectomycorrhizal fungus in pure culture and symbiotic state does not always correlate. For example, strains of *Paxillus involutus* and *Laccaria bicolor* exhibited similar HM tolerance in pure culture, but in association with Norway spruce roots only the colonisation by *L. bicolor* but not by *P. involutus* was decreased by cadmium [49].

Similarly as for the other mycorrhizal types, a strong inter- and intraspecific variation in HM tolerance has been reported for the EcM fungi [46, 50, 51]. The isolates of EcM fungi originating from polluted soils with high selection pressure were repeatedly shown to perform better in the presence of increasing concentrations of heavy metals when compared to isolates from unpolluted soils [50, 52, 53, 54]. For example, experiments screening HM tolerance of ectomycorrhizal strains of *Amanita muscaria*, *Paxillus involutus*, *Pisolithus tinctorius*, *Suillus bovinus*, *S. luteus* and *Thelephora terrestris* isolated from polluted or unpolluted soils revealed that the strains originating from unpolluted soils were strongly inhibited by HM amendment into growth media, whereas most of the strains isolated from sporocarps growing in polluted soils exhibited tolerance to HMs. Some of these strains were able to grow at zinc concentrations up to 1 $mg.g^{-1}$ in medium [55]. The authors supposed EcM strains to be naturally selected for HM tolerance in polluted soil, but at the same time noted the occurrence of HM sensitive EcM strains at polluted sites, which was attributed to unequal distribution of HMs in polluted soils. However, HM tolerance of different geographical strains of the EcM fungi from polluted and unpolluted sites is not always predetermined by their origin, as it was the case of different *Paxillus involutus* strains screened for alleviation of aluminium stress [56].

4. Effect of mycorrhizal fungi on xenobiotics uptake and tolerance of the host plants

4.1. ARBUSCULAR MYCORRHIZAL PLANTS

Inoculation with AM fungi has been repeatedly reported to modify HM uptake by host plants, however, the results are contradictory [4, 11]. In general, AM plants are more efficient than non-mycorrhizal in the acquisition of micronutrients such as copper, iron, manganese and zinc when available at low concentrations [57, 58, 59, 60, 61]. However, when grown in excess of micronutrients or in soils contaminated by HMs with unknown biological function such as cadmium, chromium or lead, both AM-mediated increases [62, 63, 64, 65, 66] and decreases [57, 60, 67, 68] of HM concentrations in plant tissues were observed, depending strongly on plant-fungus combination and cultivation conditions.

Protective role of AM fungi for plants growing in HM contaminated soils together with lower HM concentrations in plant tissues were frequently reported for inoculated plants [59, 69, 70], although the opposite observations, i.e. growth inhibition connected with higher HM concentrations were also shown [62, 66, 71]. Growth stimulation induced by inoculation with AM fungi is not always connected with lower HM concentrations in plant tissues, for example alleviation of zinc phytotoxicity in mycorrhizal plants without any effect of inoculation on Zn concentrations was observed [72]. In some cases, AM can be of fundamental importance for plant survival in heavily contaminated substrate: non-inoculated plants of several species (maize, barley, alfalfa) were not able to survive long-term without inoculation with an isolate from the rhizosphere of a metallophyte species *Viola calaminaria* [21]. When inoculated with reference fungal isolate of the same species from unpolluted soil, the positive effect on plant growth and HM uptake was less pronounced [73]. Differences between AM fungal isolates of different origin were reported also in other study [74] where AM fungi from a zinc contaminated site were more effective in increasing *Adropogon gerardii* biomass at higher levels of Zn in the soil whereas plant growth at lower levels of soil Zn was better with mycorrhizal fungi from an uncontaminated site. In some cases, positive effect of AM inoculation on host plant growth is more pronounced under conditions of HM contamination than in control conditions or under slight contamination levels [75, 76]. It was observed that only an obligately mycotrophic species *Andropodon gerardii* but not facultatively mycotrophic *Festuca arundinacea* benefited from AM in uncontaminated soil whereas both species benefited from inoculation under HM contamination [77]. Protective effect of AM can vary not only among plant species but even varieties [69]. Recently, also indigenous soil bacteria were shown to significantly modify the effect of AM on HM uptake by host plants [78, 79]. Therefore, fungal isolates should be thoroughly screened prior to the final inoculation of a particular host plant species not only in greenhouse experiments, but also directly on contaminated sites where AM fungi inocula interact with the whole microbial community.

The data on the uptake of organic xenobiotics by AM plants are very scarce. Amendment of soil with up to 5% of a heavily PAH polluted soil (8.1 g PAHs kg^{-1}) reduced growth of ryegrass but AM colonisation with a non-adapted fungus (*G. mosseae* BEG69) was not affected [34]. At 5 g of PAHs kg^{-1} only mycorrhizal plants survived. The fate of PAHs in the rhizosphere and mycorrhizosphere of ryegrass inoculated with *G. mosseae* BEG69 was investigated in soil spiked with 5 $g.kg^{-1}$ of anthracene or with 1 $g.kg^{-1}$ of a mixture of eight PAHs [80]. Proportion of the total PAH amount that was taken up to plant tissues or adsorbed to roots was negligible and major part of PAH dissipation in the rhizosphere was due to biodegradation or biotransformation. The authors found no difference between inoculated and non-inoculated ryegrass in PAH dissipation, however, shoot concentrations of PAHs and their adsorption to roots were lower in mycorrhizal than in non-mycorrhizal plants.

4.2. ERICOID MYCORRHIZAL PLANTS

Results of the studies confirmed mycorrhizal colonisation with the ErM fungi as an important factor positively influencing the resistance to heavy metals. Ericaceous plant species themselves display HM resistance [81], but it is supposed that successful colonisation of certain HM polluted sites requires adaptations from both host plant and ericoid mycorrhizal fungus [12]. In general all reports on experiments with the ErM fungi showed lower content of heavy metals in shoots of mycorrhizal plants as compared to non-mycorrhizal plants but often increased HM accumulation in the roots. Seedlings of *Vaccinium macrocarpon* colonised by *Hymenoscyphus ericae* showed increased tolerance to lead expressed in reduced translocation of Pb to the shoots when compared to non-mycorrhizal seedlings [38]. In another study, two races of *Calluna*, one from a HM polluted site, the other from an unpolluted natural heathland, were compared under mycorrhizal and non-mycorrhizal conditions in sand cultures with different levels of copper and zinc [82]. The colonisation by ErM fungi lead to significant reduction of the HM content in shoots of experimental plants. The ErM fungi from the study were Cu resistant regardless of the site of their origin. Mycorrhizal endophytes isolated from *Calluna vulgaris*, *Vaccinium macrocarpon* and *Rhododendron ponticum* were reported to protect their host plants against metal toxicity when grown together in sand with addition of copper (concentrations from 0 to 75 $mg.l^{-1}$) and zinc (concentrations from 0-150 $mg.l^{-1}$) [83]. All ErM fungal endophytes were able to grow even at the highest concentrations of both elements in pure cultures. Mycorrhizal plants also showed at least some growth in all treatments, whereas non-mycorrhizal plants failed to grow at all but the lowest Cu and Zn concentrations. Mycorrhizal plants had lower concentrations of metals in their shoots than non-mycorrhizal but higher metal concentrations in roots. The role of the ErM colonisation in the regulation of iron uptake was investigated in a study where ericaceous plants were exposed to various Fe concentrations corresponding to those occurring in the extracts from heathland soil (0-144 $\mu g.ml^{-1}$) [39]. The authors observed very high affinity of mycorrhizal roots of *V. macrocarpon* and *C. vulgaris* for absorption of Fe at low concentrations, which was not observed for non-mycorrhizal roots. They suggested the involvement of a hydroxamate siderophore in the absorption of Fe by mycorrhizal plants at low external concentrations. At higher concentrations, the presence of fungal endophyte decreased Fe uptake to shoots resulting in lower concentrations of Fe in shoots comparing to non-mycorrhizal plants. A strain of *H. ericae* decreased Fe content in shoots of *Vaccinium macrocarpon* and reduced HM toxicity symptoms of the host plant [84].

4.3. ECTOMYCORRHIZAL PLANTS

Regarding heavy metal uptake by host plants, EcM fungi can decrease the uptake of range of elements, e.g. aluminium [85], cadmium [50], copper [86], lead [87] and zinc [50] and thus alleviate HM toxicity to the host plants. For example, the seedlings of birch, pine and spruce were reported to be less susceptible to toxic concentrations of zinc, copper, nickel and aluminium when formed associations with several EcM fungi [88]. In another study, *Paxillus involutus* ameliorated the toxicity of cadmium and zinc to Scots pine seedlings in terms of root length [89]. Even though cadmium inhibited ectomycorrhiza formation in seedlings, colonisation with *P. involutus* decreased cadmium and zinc transport to the plant shoots and also altered the ratio of zinc transported to the roots and shoots, with higher amount of cadmium retained in the roots of the seedlings. Investigations on the effect of *Paxillus involutus*, *Suillus luteus* and *Thelephora terrestris* on the copper resistance of *Pinus sylvestris* revealed that although *Suillus luteus* was more sensitive to increased copper concentrations than the other two fungi, it prevented HM accumulation in the needles of *Pinus sylvestris*; this ability was absent in *T. terrestris* [86]. Alleviating effect of the EcM fungi on HM toxicity was observed across wide range of fungal species, therefore, it seems to be universal feature: protective effects of *Thelephora terrestris*, *Laccaria laccata*, *Scleroderma citrinum*, *Paxillus involutus*, *Suillus luteus* and *S. bovinus* against cadmium in *Pinus sylvestris* seedlings were demonstrated [50].

On the other hand, some studies report that EcM fungi do not limit uptake of heavy metals by their host plants, moreover, they can increase such an uptake, which was the case of zinc in *Pinus sylvestris* inoculated with *Thelephora terrestris* [54]. Increased uptake of aluminium by host plants mediated by EcM fungi was show as well [90]. EcM fungi can affect HM stress in host plants differently according to the metal screened: *Laccaria proxima*, *Lactarius hibbardae, L. rufus* and *Scleroderma flavidum* increased tolerance of *Betula papyrifera* to different concentrations of nickel but negative growth effect of ectomycorrhizal fungi were observed at elevated levels of copper [91]. Also the concentration of the metal in the medium plays a significant role: regulation of zinc uptake by EcM fungi in *Pinus sylvestris* was dependent on the concentration of metal in the mycorrhizosphere [92]. At low Zn concentrations, the EcM fungi increased its uptake, whereas at high external Zn concentrations, the EcM fungi were able to maintain shoot Zn concentrations at relatively low levels. This effect of EcM fungi was hypothesised to be involved also in uptake of other heavy metals and it might explain also contradictory data reported on HM uptake [93].

Little information is available on EcM effects on host tolerance to organic pollutants. Tolerance of pine seedlings to m-toluate was unaltered regardless of the presence or absence of the EcM fungus *Suillus bovinus* or biodegradative bacteria in microcosms containing expanded clay and growth media [94]. On the contrary, fungus tolerance was significantly increased when grown in symbiosis with pine: it was able to withstand two-order higher concentration of m-toluate as compared to the pure culture on agar plates (0.02 vs. 2.0 $mg.kg^{-1}$). Fungal survival on agar was increased in a co-culture with the degradative bacterial strain.

5. Possible mechanisms of the interaction of mycorrhizal fungi and their host plants with xenobiotics

5.1. HEAVY METALS

Most of the references on potential mechanisms of plants-mycorrhizae-xenobiotics interaction are again related to heavy metals. It is generally acknowledged that mycorrhizal amelioration of metal toxicity is achieved via several physiological processes rather than through a single mechanism and that participation of single mechanisms in metal detoxification is metal- and species-specific [4, 95, 96].

Firstly, extraradical fungal mycelium radiating from the roots and exploiting non-rhizosphere soil enables the mycorrhizal plants to capture nutrients, mainly immobile ones such as phosphorus, zinc, copper and ammonium, also from sources non-available to non-mycorrhizal plants. Due to better nutrition, growth stimulation is often observed in mycorrhizal plants, sometimes connected with lower concentrations of HMs in plant biomass [e.g. 68, 97]. However, this “growth dilution effect” cannot explain all the experimental results and also another, direct mechanisms must be involved.

As the main mechanism, immobilisation of HMs in both intra- and extraradical fungal structures and resulting restriction of metal transfer into plant tissues has been suggested [4, 98]. In accordance with this theory, it was shown that inoculation with different EcM strains decreased zinc and cadmium uptake into pine shoots and the fungus producing more extensive extraradical mycelium showed greater effect on overcoming metal toxicity and lowering shoot metal concentrations [50, 54]. Non-mycorrhizal pine seedlings were reported to transport more copper to above-ground parts, however, roots and extraradical mycelium of inoculated plants accumulated up to two times more metal than non-mycorrhizal roots [99]. Similarly, EcM colonisation decreased Zn and Cd transport to the plant shoots and influenced the proportion of Zn transported to the roots and shoots, with a higher proportion retained in the roots of the seedlings [100]. Recently, accumulation of large amounts of aluminium at the fungal mantle and in areas with the Hartig net was described in the pine roots colonised by an EcM fungus [101]. Increased root but decreased shoot HM concentrations were also reported for three ericoid mycorrhizal plant species [83] and the authors hypothesised that fungus provided adsorptive surfaces for binding of metals and thus facilitated exclusion of metals from the shoots. Concerning AM fungi, metal immobilisation in fungal tissues and lower metal partitioning to the shoots of inoculated plants was also repeatedly demonstrated [57, 102]. For example, root-to-shoot ratio of Cd concentrations of 3.15 was reported in mycorrhizal clover plants compared to only 1.66 in non-mycorrhizal plants [67]. However, retention of the HMs in fungal structures does not seem to be a universal phenomenon as inoculation was shown to lead to the completely opposite results in some cases and significantly enhanced translocation of HMs from roots to shoots of mycorrhizal plants was observed [68, 103]. Retention of HMs in fungal structures inside colonised roots was supported also by several microanalytical studies. Accumulation of metals within intracellular AM hyphae, mainly in phosphate-rich materials in the vacuoles, was reported in the mycorrhizal roots of the fern *Pteridium aquilinum* from a contaminated soil [104]. A massive accumulation of heavy metals in inner cortical cells of AM colonised maize roots where arbuscules and intraradical hyphae were located was also confirmed using different microbeam techniques [73]. Further, a high cadmium and zinc sorption capacity of the ERM of AM fungi in comparison with other microorganisms was shown [105] and a metal tolerant *Glomus mosseae* isolate showed significantly higher binding capacity than non-tolerant isolate of the same species. Similarly, a very high cation exchange capacity for lead absorption was reported for the fungal mycelium of two EcM fungi [106]. Different HMs can be detoxified *via* different mechanisms, as shown by a study where Cd was complexed predominantly extracellularly in the Hartig net hyphae, whereas zinc was sequestered also in the cytosol of mantle hyphae [107]. Binding of cadmium onto fungal cell walls as well as accumulation of Cd in the vacuolar compartments was described for *in vitro* grown EcM fungus *Paxillus involutus* [108]. Cytoplasmatic sequestration of metals may be realised *via* different thiol compounds, including reduced glutathione, phytochelatins and metallothioneins that are essential components of HM detoxification pathways in various organisms. Using a specific histochemical staining, induction of protein-bound thiolate clusters in EcM hyphae in response to cadmium was detected [109] and the sulphur-rich clusters were hypothesised to be derived from metallothionein or metallothionein-like proteins. Later, a metallothionein-like protein was detected in two tolerant EcM fungi in response to copper exposure and this compound associated with as much as 90% of the total copper [110]. Recently, a drastically increased production of the Cd-modulated compound most probably related to a metallothionein was detected in Cd-exposed EcM mycelium of *Paxillus involutus* [111]. In contrast, neither phytochelatins nor metallothioneins were detected in EcM fungus exposed to Cd, in spite of increased glutathione levels [112] and the authors concluded that rather glutathione and glutamylcystein were involved in metal detoxification. Similarly, increased contents of glutathione and lack of phytochelatin induction in two different EcM fungi exposed to cadmium were reported recently [111, 113]. As far as AM fungi, increased synthesis of metallothioneins by mycorrhizal plants was also proposed [114, 115], however, higher synthesis of peptides containing thiol groups was not revealed in roots of AM-inoculated plants exposed to high Cd and Cu concentrations, in spite of increased concentrations of cysteine, glutathione and glutamycysteine. Recently, a novel metallothionein-like gene that was selectively up-regulated by Cu exposure was identified in the ERM of AM fungi [116].

Apart from metal binding onto cell walls, accumulation of copper in the mucilaginous outer hyphal wall zone of the ERM of AM fungi was reported [117] and the authors suggested an employment of extracellular glycoprotein glomalin into HM detoxification. Similarly in EcM fungi, zinc was shown to be bound not only to extraradical hyphal walls, but also to extrahyphal slime polymers [53]. In accordance with this finding, a frequent excretion of extracellular mucilaginous substances by EcM fungal cultures exposed to higher metal concentrations was observed [118]. The correlation between excretion of loosely adhering extrahyphal slime and zinc tolerance of fungal strains and the degree of amelioration of zinc toxicity to mycorrhizal host plants was reported also for ErM fungi [119]. A significantly higher production of oxalic acid by EcM pine seedlings than non-mycorrhizal controls was reported in response to aluminum exposure [120] and it was assumed that ectomycorrhizae produce or stimulate the roots to secrete organic acids that bind Al and prevent its absorption. Study on a Zn and Cd tolerant strain of ErM fungus *Oidiodendron maius* showed that the increase in concentration of Zn ions in cultivation medium induced a shift in the spectrum of proteins secreted by the fungus towards more basic, low molecular weight polypeptides [121]. Among other products, two superoxide dismutase isoforms were found as well. These are known to act in HM response in plants, animals and microorganisms and the authors hypothesised that they could play similar role also in ErM fungi. As another option how mycorrhizal plants may influence metal uptake, modification of metal solubility mediated by changes in pH of soil solution was suggested [122] as higher pH values and lower zinc concentrations in soil solution were observed in mycorrhizal treatments.

Interesting mechanism of eliminating arsenate toxicity was reported for the ErM fungi growing in arsenate-polluted soils. Arsenate is analogical to phosphate and can be transported across the plasma membrane *via* the phosphate co-transporter [123]. The ErM accumulating arsenate in their hyphae would thus transport phosphorus together with arsenate into plant tissues resulting in negative consequences to host plants. But *Hymenoscyphus ericae* strains from arsenic-polluted sites had the ability to reduce arsenate to arsenite and excrete the latter from their hyphae [124, 125]. By this way, *H. ericae* actively accumulated phosphate while eliminating arsenate and transported phosphate to the host plant. Ericaceous host plants appear to lack altered phosphate-arsenate uptake system and seem to be dependent on their mycobionts regarding alleviation of arsenate toxicity [125].

Also other mechanisms how mycorrhizal fungi cope with elevated concentrations heavy metals in their environment have been proposed (e.g. chelating by pigments with metal binding ability such as melanin, enzymes resistant to inactivation by metal binding, modified uptake systems at the plasmalemma, ability of membranes to withstand attack from oxygen radicals), their role, however, remains unravelled [12, 96, 126].

5.2. ORGANIC COMPOUNDS

It was shown that dissipation of condensed PAHs might be enhanced in the presence of AM fungi in the soil spiked with a mixture of different PAHs [127]. These results were consecutively verified in pot experiments conducted in two different industrially polluted soils [128]. In general, following explanations were suggested by the authors to elucidate the contribution of AM to PAH degradation: i) mycorrhiza modifies root enzyme activity, exudation and architecture in a manner that stimulates PAH degradation, either by root-derived enzymes or by rhizosphere microorganisms, ii) mycorrhizal colonisation affects root surface or rhizosphere soil properties that act on PAH availability through adsorption. Several examples of above mentioned capabilities of AM fungi can be found in the literature. Mycorrhiza was reported to enhance amount of hydrogen peroxide in the roots [129] and to stimulate oxidoreductase activities in the roots and the rhizosphere [130]. These mechanisms may contribute to increase of PAH dissipation associated with mycorrhizal roots. Mycorrhizal colonisation also modifies root exudation both quantitatively and qualitatively [131, 132], which could have further effects on the composition and activity of microbial communities in the rhizosphere [133, 134]. This mycorrhiza-associated microflora may be more effective in organics degradation in comparison with that related to non-mycorrhizal roots. Accumulation of phenolics in the roots or rhizosphere soil of mycorrhizal plants could induce degradation of more complex aromatic compounds [135].

Effects of AM on root longevity and proportion of higher order lateral roots with short life span was documented for several plant species [136]. Accumulation of root debris together with the ability of mycorrhizal plants to enrich the soil in organic matter [137] may contribute to enhanced PAH adsorption in plant rhizosphere. Finally, AM colonisation results in formation of an extensive network of extraradical mycelium, which can modify surrounding environment by extrusion of glycoproteins [138] and extracellular enzymes [139]. Hyphal biomass together with the two latter substances can serve as substrates for microbial growth. Nutrients derived from extraradical hyphae of AM fungi were hypothesised to drive co-metabolic degradation of PAHs within small soil pores where PAHs are spatially unavailable to roots [127].

Most of the ectomycorrhizal fungi have some limited ability to use polymers such as lignin and cellulose as substrates for their growth [2], however, their ability to degrade polymers of this kind was supposed to be much lower as compared to wood decomposers or even of some ericoid mycorrhizal fungi [140, 141, 142]. As it was recently reviewed, most of the EcM fungi screened for degradation of persistent organic pollutants are able to transform these compounds [143]. On the other hand, most reports concern degradation in pure cultures, rather than in symbiosis with plants. It has been demonstrated that EcM fungi can degrade e.g. trinitrotoluene [144], dichlorphenol [145], atrazine [146] and several 3-5 ring PAHs [147]. Only limited PAH degrading abilities of EcM fungi and decreased mineralisation of some PAHs in microcosms with EcM pine seedlings vs. unplanted microcosms inoculated with ectomycorrhizosphere soil were documented [148]. On the contrary, mineralisation of dichlorphenol was stimulated when EcM fungi were cultivated in symbiosis with pine than when grown in absence of the host [145].

Also degradation of lower chlorinated PCBs by eight of 13 studied species of EcM fungi was reported, however, only two species were able to degrade 4 and 5 chlorinated biphenyls [149]. While EcM fungi could sequentially hydroxylate a halogenated biphenyl ring (parent compound is then more polar and bioavailable), they were unable to cleave the ring [150]. However, hydroxylation of the biphenyl ring can be an important initial metabolic step facilitating degradation of PCBs by other rhizosphere organisms that have the capacity to degrade compounds further [143]. In this context it can be hypothesised that the presence of EcM fungi may negate the need for the presence of co-substrates. Although the tolerance of EcM fungi to different aromatic compounds is lower as compared to white rot fungi and depends on the compound type, its external concentration and the fungal species, the degradative capabilities of different fungi varied between species but not generally between the biotrophic and saprotrophic fungi [151].

6. Conclusion

Application of mycorrhizal fungi as supportive agents for phytoremediation can generally eliminate or reduce some known limitation of phytoremediation processes. Mycorrhizal fungi can help plants to acquire nutrients more effectively, increase their tolerance to edaphic stress and change accumulation of pollutants in plant tissues.

Reduced HM concentrations in plant tissues of mycorrhizal plants, together with an amplified barrier against metal translocation from plant roots to shoots, are favourable for phytostabilisation that is aimed at prevention of contamination spreading into the surroundings. The presence of AM fungi leading to decreased HM concentrations in plant shoots can be also an important factor for quality and safety of plants which enter food chains such as forage crops, medicinal herbs and vegetables. For example, tobacco was found to accumulate significantly less cadmium in the leaves when inoculated with selected AM fungi [8].

On the other hand, enhanced HM concentrations in the shoots of mycorrhizal plants induced by some mycorrhizal fungal isolates represent optimal conditions for phytoextraction technique. In some cases, elimination of present AM fungi populations (in particular if they involve strains decreasing HM translocation to the shoots) might be recommended before phytoextraction beginning. For example, application of the fungicide benomyl detrimental to mycorrhiza was shown to significantly decrease root colonisation and simultaneously to increase Pb concentrations in plant shoots [153]. Mycorrhizal fungi may be crucial also for re-vegetation efforts after heavy metal removal as the rate of site re-vegetation may be accelerated when AM fungi are present in soil. However, little is known about mycorrhiza functioning under conditions imposed by particular metal remediation protocols. First investigations have appeared showing that the quantity and species composition of glomalean propagules and the functioning of AM symbiosis could be significantly influenced by phytoextraction treatments (the choice of plant species, i.e. non-mycotrophic vs. mycotrophic, soil supplements etc.) [7]. Recently, negative effects of synthetic chelates used for chelate-induced HM phytoextraction such as EDTA on AM development were also described [102, 152].

Based on the intended phytoremediation strategy, the appropriate management of native fungi and/or application of artificial inocula should be chosen. For the introduction of artificial inocula, it seems to be essential to formulate specific products (mixtures of strains compatible with target plants and environment) rather than to use generic products all over the scale of edaphic conditions. However, it should considered that the effect of mycorrhizal inoculation may interact e.g. with fertilisation regime as demonstrated for the grasses grown in mine tailings containing high levels of zinc: plant growth was best after inoculation combined with nitrogen and phosphorus fertilisation, whereas neither mycorrhiza nor fertilisation alone had any effect on plant biomass [77]. Therefore, mycorrhizal inoculation cannot be considered as panacea and should be combined with other practices such as appropriate fertilisation or soil amendments to maximise re-vegetation success.

To conclude, an extension of knowledge on the involvement of mycorrhizal fungi in phytoremediation should still be achieved. Great attempt should be also undertaken to increase awareness of potential users of mycorrhizal inoculants regarding all possible functions and impacts of mycorrhiza applications in phytoremediation processes.

Acknowledgement

Presentation of this contribution was supported by the grant 526/04/0996 of the Grant Agency of the Czech Republic and by the Research Centre for Bioindication and Revitalisation funded by the Ministry of Education, Youth and Sports of the Czech Republic (grant 1M67985939).

References

[1] Cunningham, SD; Berti, WR and Huang, JW (1995) Phytoremediation of contaminated soils. Trends Biotechnol 12: 393-397
[2] Smith, SE and Read, DJ (1997) Mycorrhizal symbiosis. Academic Press, London.
[3] Donnelly, PK and Fletcher, JS (1994) Potential use of mycorrhizal fungi as bioremediation agents. In: Anderson T.A. (ed.) Bioremediation through Rhizosphere Technology. ACS Symposium series No. 563, American Chemical Society, pp. 93-99
[4] Leyval, C; Turnau, K and Haselwandter, K (1997) Effect of heavy metal pollution on mycorrhizal colonization and function: physiological, ecological and applied aspects. Mycorrhiza 7: 139-153
[5] Gaur, A and Adholeya, A (2004) Prospects of arbuscular mycorrhizal fungi in phytoremediation of heavy metal contaminated soils. Curr Sci 86: 528-534
[6] Schüssler, A; Schwarzott, D and Walker, C (2001) A new fungal phylum, the *Glomeromycota*: phylogeny and evolution. Mycol Res 105: 1413-1421
[7] Pawlowska, TE; Chaney, RL; Chin, M and Charvat, I (2000) Effects of metal phytoextraction practices on the indigenous community of arbuscular mycorrhizal fungi at a metal-contaminated landfill. Appl Env Microbiol 66: 2526-2530
[8] Janoušková, M; Pavlíková, D; Macek, T and Vosátka, M (2005) Arbuscular mycorrhiza decreases cadmium phytoextraction by transgenic tobacco with inserted metallothionein. Plant Soil 272: 29-40
[9] Read, DJ (1996) The structure and function of the ericoid mycorrhizal root. Ann Bot 77: 365-374
[10] Cairney, JWG (2000) Evolution of mycorrhiza systems. Naturwissenschaften 87: 467-475
[11] Meharg, AA and Cairney, JWG (2000) Co-evolution of mycorrhizal symbionts and their hosts to metal-contaminated environments. Adv Ecol Res 30: 69-112
[12] Cairney, JWG and Meharg, AA (2003) Ericoid mycorrhiza: a partnership that exploits harsh edaphic conditions. Eur J Soil Sci 54: 735-740
[13] Shaw, G and Read, DJ (1989) The biology of mycorrhiza in the Ericaceae. XIV. Effects of iron and aluminium on the activity of acid phosphatase in the ericoid endophyte *Hymenoscyphus ericae* (Read) Korf and Kernan. New Phytol 113: 529-533
[14] Wilkinson, DM and Dickinson, NM (1995) Metal resistance in trees: the role of mycorrhizae. Oikos 72: 298-300
[15] Boyle, M and Paul, EA (1988) Vesicular-arbuscular mycorrhizal associations with barley on sewage-amended plots. Soil Biol Biochem 20: 945-948
[16] Leyval, C; Singh, BR and Joner, EJ (1995) Occurrence and infectivity of arbuscular mycorrhizal fungi in some Norwegian soils influenced by heavy metals and soil properties. Water Air Soil Poll 84: 203-216
[17] del Val, C; Barea, JM and Azcón-Aguilar, C (1999) Assessing the tolerance to heavy metals of arbuscular mycorrhizal fungi isolated from sewage sludge-contaminated soils. Appl Soil Ecol 11: 261-269

[18] Ietswaart, JH; Griffioen, WAJ and Ernst, WHO (1992) Seasonality of VAM infection in three populations of *Agrostis capillaris* (Graminae) on soil with or without heavy metal enrichment. Plant Soil 139: 67-73

[19] Weissenhorn, I; Mench, M and Leyval, C (1995) Bioavailability of heavy metals and arbuscular mycorrhizas in a sewage sludge amended sandy soil. Soil Biol Biochem 27: 287-296

[20] Pawlowska, TE; Blaszkowski, J and Rühling, A (1996) The mycorrhizal status of plants colonizing a calamine soil mound in southern Poland. Mycorrhiza 6: 499-505

[21] Hildebrandt, U; Kaldorf, M and Bothe, H (1999) The zinc violet and its colonization by arbuscular mycorrhizal fungi. J Plant Physiol 154: 709-717

[22] Turnau, K; Ryszka, P; Gianinazzi-Pearson, V and van Tuinen, D (2001) Identification of arbuscular mycorrhizal fungi in soils and roots of plants colonizing zinc wastes in southern Poland. Mycorrhiza 10: 169-174

[23] Weissenhorn, I; Leyval, C and Berthelin, J (1993) Cd-tolerant arbuscular mycorrhizal (AM) fungi from heavy-metal polluted soils. Plant Soil 157: 247-256

[24] Bartolome-Esteban, H and Schenck, NC (1994) Spore germination and hyphal growth of arbuscular mycorrhizal fungi in relation to soil aluminium saturation. Mycologia 86: 217-226

[25] Kelly, CN; Morton, JB and Cumming, JR (2005) Variation in aluminium resistance among arbuscular mycorrhizal fungi. Mycorrhiza 15: 193-201

[26] Gildon, A and Tinker, PB (1983) Interactions of vesicular-arbuscular mycorrhizal infection and heavy metals in plants. I. The effects of heavy metals on the development of vesicular-arbuscular mycorrhizas. New Phytol 95: 247-261

[27] Weissenhorn, I and Leyval, C (1995) Root colonization of maize by a sensitive and a Cd-tolerant *Glomus mosseae* and cadmium uptake in sand culture. Plant Soil 175: 233-238

[28] Malcová, R; Rydlová, J and Vosátka, M (2003) Metal-free cultivation of *Glomus* sp. BEG 140 isolated from Mn-contaminated soil reduces tolerance to Mn. Mycorrhiza 13: 151-157

[29] Hepper, CM and Smith, GA (1976) Observations on the germination of *Endogone* spores. Trans Br Mycol Soc 66: 189-194

[30] Hepper, CM (1979) Germination and growth of *Glomus caledonius* spores: the effects of inhibitors and nutrients. Soil Biol Biochem 11: 269-277

[31] McIlveen, WD and Cole, H (1978) Influence of zinc on development of the ectomycorrhizal fungus *Glomus mosseae* and its mediation of phosphorus uptake by *Glycine max* "Amsoy 71". Agric Environm 4: 245-256

[32] Batkhuugyin, E; Rydlová, J and Vosátka, M (2000) Effectiveness of indigenous and non-indigenous isolates of arbuscular mycorrhizal fungi in soils from degraded ecosystems and man-made habitats. Appl Soil Ecol 14: 201-211

[33] Arines, J; Porto, ME and Vilariño, A (1992) Effect of manganese on vesicular-arbuscular mycorrhizal development in red clover plants and on soil Mn-oxidizing bacteria. Mycorrhiza 1: 127-131

[34] Leyval, C and Binet, P (1998) Effect of polyaromatic hydrocarbons in soil on arbuscular mycorrhizal plants. J Environ Qual 27: 402-407

[35] Joner, EJ and Leyval, C (2001) Influence of arbuscular mycorrhiza on clover and ryegrass grown together in a soil spiked with polycyclic aromatic hydrocarbons. Mycorrhiza 10: 155-159

[36] Liu, SL; Luo, YM; Cao, ZH; Wu, LH; Ding, KQ and Christie, P (2004) Degradation of benzo[a]pyrene in soil with arbuscular mycorrhizal alfalfa. Environ Geochem Hlth 26: 285-293

[37] Rydlová, J; Stárek, L; Macková, M; Vosátka, M and Macek, T (2005) Interactions of arbuscular mycorrhizal fungi and PCB degrading bacteria in two soils contaminated with PCB. Biodegradation (submitted)

[38] Hashem, AR (1990) *Hymenoscyphus ericae* and the resistance of *Vaccinium macrocarpon* to lead. Trans Myc Soc Jap 31: 345-353

[39] Shaw, G; Leake, JR; Baker, AJM and Read, DJ (1990) The biology of mycorrhiza in the *Ericaceae*. XVII. The role of mycorrhizal infection in the regulation of iron uptake by ericaceous plants. New Phytol 115: 251-258

[40] Martino, E; Turnau, K; Girlanda, M; Bonfante, P and Perotto, S (2000) Ericoid mycorrhizal fungi from heavy metal polluted soils: their identification and growth in the presence of zinc ions. Mycol Res 104: 338-344

[41] Sharples, JM; Meharg, AA; Chambers, SM and Cairney, WG (2001) Arsenate resistance in the ericoid mycorrhizal fungus *Hymenoscyphus ericae*. New Phytol 151: 265-270

[44] Stankenkevičiene, D and Pečiulyte, D (2004) Functioning of ectomycorrhizas and soil microfungi in deciduous forests situated along a pollution gradient next to a fertilizer factory. Pol J Environ Stud 13: 715-721

[45] Rudawska, M; Kieliszewska-Rokicka, B and Leski, T (1996) Effect of acid rain and aluminium on the mycorrhizas of *Pinus sylvestris*, in Azcón-Aguillar C and Barea JM (Eds.), Mycorrhizas in integrated systems. From genes to plant development. European Commission, Luxembourg, pp. 452-454

[46] Muller, LAH; Lambaerts, M; Vangronsveld, J and Colpaert, JV (2004) AFLP-based assessment of the effects of environmental heavy metal pollution on the genetic structure of pioneer populations of *Suillus luteus*. New Phytol 164: 297-303

[47] Aggangan, NS; Dell, B and Malajczuk, N (1989) Effects of chromium and nickel on growth of the ectomycorrhizal fungus *Pisolithus tinctorius* and formation of ectomycorrhizas on *Eucalyptus urophylla* Blake. S.T. Geoderma 84: 15-27

[48] Blaudez, D; Jacob, C; Turnau, K; Colpaert, JV; Ahonen-Jonnarth, U; Finlay, R; Botton, B and Chalot, M (2000) Differential reponses of ectomycorrhizal fungi to heavy metals *in vitro*. Mycol Res 104: 1366-1371

[49] Jentschke, G; Fritz, E and Godbold, DL (1991) Distribution of lead in mycorrhizal and non-mycorrhizal Norway spruce seedlings. Physiol Plantarum 81: 417-422

[50] Hartley, J; Cairney, JWG and Meharg, A (1999) Cross-colonization of Scots pine (*Pinus sylvestris*) seedlings by the ectomycorrhizal fungus *Paxillus involutus* in the presence of inhibitory levels of Cd and Zn. New Phytol 142: 141-149

[51] Jentschke, G; Winter, S and Godbold, DL (1999) Ectomycorrhizas and cadmium toxicity in Norway spruce seedlings. Tree Physiol 19: 23-30

[52] Colpaert, JV and van Assche, JA (1993) The effects of cadmium on ectomycorrhizal *Pinus sylvestris* L. New Phytol 123: 325-333

[53] Vodnik, D; Byrne, AR and Gogala, N (1998) The uptake and transport of lead in some ectomycorrhizal fungi in culture. Mycol Res 102: 953-958

[54] Egerton-Warburton, LM and Griffin, BJ (1995) Differential responses of *Pisolithus tinctorius* isolates to aluminium *in vitro*. Can J Bot 73: 1229-1233

[55] Denny, HJ and Wilkins, DA (1987) Zinc tolerance in *Betula* spp. 4. The mechanism of ectomycorrhizal amelioration of zinc toxicity. New Phytol 106: 545-553

[56] Colpaert, JV and van Assche, JA (1992) Zinc toxicity in ectomycorrhizal *Pinus sylvestris*. Plant Soil 143: 201-211

[57] Colpaert, JV and van Assche, JA (1987) Heavy metal resistance in some ectomycorrhizal fungi. Funct Ecol 1: 415-421

[58] Rudawska, M and Leski, T (1998) Aluminium tolerance of different *Paxillus involutus* Fr. strains originating from polluted and non-polluted sites. Acta Soc Bot Pol 67: 115-122

[59] Dehn, B and Schüepp, H (1989) Influence of VA mycorrhizae on the uptake and distribution of heavy metals in plants. Agr Ecosyst Environ 29: 79-83

[60] El-Kherbawy, M; Angle, JS; Heggo, A and Chaney, RL (1989) Soil pH, rhizobia, and vesicular-arbuscular mycorrhizae inoculation effects on growth and heavy metal uptake of alfalfa (*Medicago sativa* L.). Biol Fertil Soils 8: 61-65

[61] Heggo, A; Angle, JS and Chaney, RL (1990) Effects of vesicular-arbuscular mycorrhizal fungi on heavy metal uptake by soybeans. Soil Biol Biochem 22: 865-869

[62] Loth, FG and Höfner, W (1995) Einfluss der VA-Mykorrhiza auf die Schwermetallaufnahme von Hafer (*Avena sativa* L.) in Abhängigkeit vom Kontaminationsgrad der Böden. Z Pflanzenernaehr Bodenk 158: 339-345

[63] Liu, A; Hamel, C; Hamilton, RI; Ma, BL and Smith, DL (2000) Acquisition of Cu, Zn, Mn and Fe by mycorrhizal maize (*Zea mays* L.) grown in soil at different P and micronutrient levels. Mycorrhiza 9: 331-336

[64] Killham, K and Firestone, MK (1983) Vesicular arbuscular mycorrhizal mediation of grass response to acidic and heavy metal depositions. Plant Soil 72: 39-48

[65] Carneiro, MAC; Siqueira, JO and Moreira, FMD (2001) Establishment of herbaceous plants in heavy metal contaminated soils inoculated with arbuscular mycorrhizal fungi. Pesqui Agropecu Bras 36: 1443-1452

[66] Jamal, A; Ayub, N; Usman, M and Khan, AG (2002) Arbuscular mycorrhizal fungi enhace zinc and nickel uptake from contaminated soil by soybean and lentil. Int J Phytorem 4: 205-221

[67] Liao, JP; Lin, XG; Cao, ZH; Shi, YQ and Wong, MH (2003) Interactions between arbuscular mycorrhizae and heavy metals under sand culture experiment. Chemosphere 50: 847-853

[68] Yu, X; Cheng, J and Wong, MH (2005) Earthworm-mycorrhiza interaction on Cd uptake and growth of ryegrass. Soil Biol Biochem 37: 195-201

[69] Joner, EJ and Leyval, C (1997) Uptake of ^{109}Cd by roots and hyphae of a *Glomus mosseae*/*Trifolium subterraneum* mycorrhiza from soil amended with high and low concentrations of cadmium. New Phytol 135: 353-360

[70] Weissenhorn, I; Leyval, C; Belgy, G and Berthelin, J (1995) Arbuscular mycorrhizal contribution to heavy metal uptake by maize (*Zea mays* L.) in pot culture with contaminated soil. Mycorrhiza 5: 245-251

[71] Rivera-Becerril, F; Calantzis, C; Turnau, K; Caussanel, JP; Belimov, AA; Gianinazzi, S; Strasser, RJ and Gianinazzi-Pearson, V (2002) Cadmium accumulation and buffering of cadmium-induced stress by arbuscular mycorrhiza in three *Pisum sativum* L. genotypes. J Exp Bot 53: 1177-1185

[72] Chen, BD; Li, XL; Tao, HQ; Christie, P and Wong, MH (2003) The role of arbuscular mycorrhiza in zinc uptake by red clover growing in a calcareous soil spiked with various quantities of zinc. Chemosphere 50: 839-846

[73] Dosskey, MG and Adriano, DC (1993) Trace element toxicity in VA mycorrhizal cucumber grown on weathered coal fly ash. Soil Biol Biochem 25: 1547-1552

[74] Dueck, TA; Visser, P; Ernst, WHO and Schat, H (1986) Vesicular-arbuscular mycorrhizae decrease zinc-toxicity to grasses growing in zinc-polluted soil. Soil Biol Biochem 18: 331-333

[75] Kaldorf, M; Kuhn, AJ; Schröder, WH; Hildebrandt, U and Bothe, H (1999) Selective element deposits in maize colonized by a heavy metal tolerance conferring arbuscular mycorrhizal fungus. J Plant Physiol 154: 718-728

[76] Shetty, KG; Hetrick, BAD and Schwab, AP (1995) Effects of mycorrhizae and fertilizer amendments on zinc tolerance of plants. Environ Pollut 88: 307-314

[77] Davies, FT; Puryear, JD; Newton, RJ; Egilla, JN and Grossi, JAS (2001) Mycorrhizal fungi enhance accumulation and tolerance of chromium in sunflower (*Helianthus annuus*). J Plant Physiol 158: 777-786

[78] Chen, BD; Liu, Y; Shen, H; Li, XL and Christie, P (2004a) Uptake of cadmium from an experimentally contaminated calcareous soil by arbuscular mycorrhizal maize (*Zea mays* L.). Mycorrhiza 14: 347-354

[79] Hetrick, BAD; Wilson, GWT and Figge, DAH (1994) The influence of mycorrhizal symbiosis and fertilizer amendments on establishment of vegetation in heavy metal mine soil. Environ Pollut 86: 171-179

[80] Vivas, A; Barea, JM and Azcon, R (2005) Interactive effect of *Brevibacillus brevis* and *Glomus mosseae*, both isolated from Cd contaminated soil, on plant growth, physiological mycorrhizal fungal characteristics and soil enzymatic activities in Cd polluted soil. Environ Pollut 134: 257-266

[81] Vivas, A; Vörös, A; Biró, B; Barea, JM; Ruiz-Lozano, JM and Azcón, R (2003) Beneficial effects of indigenous Cd-tolerant and Cd-sensitive *Glomus mosseae* associated with a Cd-adapted strain of *Brevibacillus* sp. in improving plant tolerance to Cd contamination. Appl Soil Ecol 24: 177-186

[82] Binet, P; Portal, JM and Leyval, C (2000) Fate of polycyclic aromatic hydrocarbons (PAH) in rhizosphere and mycorrhizosphere of ryegrass. Plant Soil 227: 207-213

[83] Marrs, RH and Bannister, P (1978) The adaptation of *Calluna vulgaris* (L.) Hull to contrasting soil types. New Phytol 81: 753-761

[84] Bradley, R; Burt, AJ and Read, DJ (1981) Mycorrhizal infection and resistance to heavy metal toxicity in *Calluna vulgaris.* Nature 292: 335-337

[85] Bradley, R; Burt, AJ and Read, DJ (1982) The biology of mycorrhiza in the *Ericaceae*. VIII. The role of mycorrhizal infection in heavy metal resistance. New Phytol 91: 197-209

[86] Hashem, AR (1995) The role of mycorrhizal infection in the tolerance of *Vaccinium macrocarpon* to iron. Mycorrhiza 5: 451-454

[87] Hentschel, E; Godbold, DL; Marschner, P; Schlegel, H and Jentschke, G (1993) The effect of *Paxillus involutus* Fr. on aluminium sensitivity of Norway spruce seedlings. Tree Physiol 12: 379-390

[88] van Tichelen, KK; van Straelen, T and Colpaert, JV (1999) Nutrient uptake by intact mycorrhizal *Pinus sylvestris* seedlings: a diagnostic tool to detect copper toxicity. Tree Physiol 19: 189-196

[89] Dixon, RK (1988) Response of ectomycorrhizal *Quercus rubra* to soil cadmium, nickel and lead. Soil Biol Biochem 20: 555-559

[90] Cumming, JR and Weinstein, LH (1990) Aluminum-mycorrhizal interactions in the physiology of pitch pine seedlings. Plant Soil 125: 7-18

[91] Hartley-Whitaker, J; Cairney, JWG and Meharg, AA (2000) Sensitivity to Cd or Zn of host and symbiont of ectomycorrhizal *Pinus sylvestris* L. (Scots pine) seedlings. Plant Soil 218: 31-42

[92] Schier, G and McQuattie, C (1995) Effect of aluminium on the growth, anatomy, and nutrient content of ectomycorrhizal and nonmycorrhizal eastern white pine seedlings. Can J For Res 25: 1252-1262

[93] Jones, MD and Hutchinson, TC (1986) The effect of mycorrhizal infection on the response of *Betula papyrifera* to nickel and copper. New Phytol 102: 429-442

[94] Bucking, H and Heyser, W (1994) The effect of ectomycorrhizal fungi on Zn uptake and distribution in seedlings of *Pinus sylvestris* L. Plant Soil 167: 203-212

[95] Khan, AG; Kuek, C; Chaudhry, TM; Khoo, CS and Hayes, WJ (2000) Role of plants, mycorrhizae and phytochelators in heavy metal contaminated land reclamation. Chemosphere 41: 197-207

[96] Sarand, I; Timonen, S; Koivula, T; Peltola, R; Haahtela, K; Sen, R and Romantchuk, M (1999) Tolerance and biodegradation of m-toluate by Scots pine, a mycorrhizal fungus and fluorescent pseudomonads individually and under associative conditions. J Appl Microbiol 86: 817-826

[97] Hartley, J; Cairney, JWG and Meharg, AA (1997) Do ectomycorrhizal fungi exhibit adaptive tolerance to potentially toxic metals in the environment? Plant Soil 189: 303-319

[98] Jentschke, G and Godbold, DL (2000) Metal toxicity and ectomycorrhizas. Physiol Plantarum 109: 107-116

[99] Kucey, RMN and Janzen, HH (1987) Effects of VAM and reduced nutrient availability on growth and phosphorus and micronutrient uptake of wheat and field beans under greenhouse conditions. Plant Soil 104: 71-78

[100] Godbold, DL; Jentschke, G; Winter, S and Marschner, P (1998) Ectomycorrhizas and amelioration of metals stress in forest trees. Chemosphere 36: 757-762

[101] van Tichelen, KK; Colpaert, JV and Vangronsveld J (2001) Ectomycorrhizal protection of *Pinus sylvestris* against copper toxicity. New Phytol 150: 203-213

[102] Hartley-Whitaker, J; Cairney, JWG and Meharg, AA (2000) Toxic effects of cadmium and zinc on ectomycorrhizal colonization of Scots pine (*Pinus sylvestris* L.) from soil inoculum. Environ Toxicol Chem 19: 694-699

[103] Moyer-Henry, K; Silva, I; Macfall, J; Johannes, E; Allen, N; Goldfarb, B and Rufty, T (2005) Accumulation and localization of aluminium in root tips of loblolly pine seedlings and the associated ectomycorrhiza *Pisolithus tinctorius*. Plant Cell Environ 28: 111-120

[104] Chen, B; Shen, H; Li, X; Feng, G and Christie, P (2004) Effects of EDTA application and arbuscular mycorrhizal colonization on growth and zinc uptake by maize (*Zea mays* L.) in soil experimentally contaminated with zinc. Plant Soil 261: 219-229

[105] Citterio, S; Prato, N; Fumagalli, P; Aina, R; Massa, N; Santagostino, A; Sgorbati, S and Berta, G (2005) The arbuscular mycorrhizal fungus *Glomus mosseae* induces growth and metal accumulation changes in *Cannabis sativa* L. Chemosphere 59: 21-29

[106] Turnau, K; Kottke, I and Oberwinkler, F (1993) Element localization in mycorrhizal roots of *Pteridium aquilinum* (L.) Kuhn collected from experimental plots treated with cadmium dust. New Phytol 123: 313-324

[107] Joner, EJ; Briones, R and Leyval, C (2000) Metal-binding capacity of arbuscular mycorrhizal mycelium. Plant Soil 226: 227-234

[108] Marschner, P; Jentschke, G and Godbold, DL (1998) Cation exchange capacity and lead sorption in ectomycorrhizal fungi. Plant Soil 205: 93-98

[109] Frey, B; Zierold, K and Brunner, I (2000) Extracellular complexation of Cd in the Hartig net and cytosolic Zn sequestration in the fungal mantle of *Picea abies – Hebeloma crustaliniforme* ectomycorrhizas. Plant Cell Environ 23: 1257-1265

[110] Blaudez, D; Botton, B and Chalot, M (2000) Cadmium uptake and subcellular compartmentation in the ectomycorrhizal fungus *Paxillus involutus*. Microbiology 146: 1109-1117

[111] Morselt, AFW; Smits, WTM and Limonard, T (1986) Histochemical demonstration of heavy metal tolerance in ectomycorrhizal fungi. Plant Soil 96: 417-420

[112] Howe, R; Evans, RL and Ketteridge, SW (1997) Copper-binding proteins in ectomycorrhizal fungi. New Phytol 135: 123-131

[113] Courbot, M; Diez, L; Ruotolo, R; Chalot, M and Leroy, P (2004) Cadmium-responsive thiols in the ectomycorrhizal fungus *Paxillus involutus*. Appl Environ Microb 70: 7413-7417

[114] Galli, U; Meier, M and Brunold, C (1993) Effects of cadmium on non-mycorrhizal and mycorrhizal Norway spruce seedlings [*Picea abies* (L.) Karst.] and its ectomycorrhizal fungus *Laccaria laccata* (Scop. Ex Fr.) Bk. & Br.: Sulphate reduction, thiols and distribution of the heavy metal. New Phytol 125: 837-843

[115] Ott, T; Fritz, E; Polle, A and Schützendübel, A (2002) Characterisation of antioxidative systems in the ectomycorrhiza-building basidiomycete *Paxillus involutus* (Bartsch) Fr. and its reaction to cadmium. FEMS Microbiol Ecol 42: 359-366

[116] Galli, U; Schüepp, H and Brunold, C (1994) Heavy metal binding by mycorrhizal fungi. Physiol Plantarum 92: 364-368

[117] Galli, U; Schüepp, H and Brunold, C (1995) Thiols of Cu-treated maize plants inoculated with the arbuscular-mycorrhizal fungus *Glomus intraradices*. Physiol Plantarum 94: 247-253

[118] Lafranco, L; Bolchi, A; Ros, EC; Ottonello, S and Bonfante, P (2002) Differential expression of a metallothionein gene during the presymbiotic versus the symbiotic phase of an arbuscular mycorrhizal fungus. Plant Physiol 130: 58-67

[119] Gonzalez-Chavez, C; D'Haen, J; Vangronsveld, J and Dodd, JC (2002) Copper sorption and accumulation by the external mycelium of different *Glomus* ssp. (arbuscular mycorrhizal fungi) isolated from the same polluted soil. Plant Soil 240: 287-297

[120] Tam, PCF (1995) Heavy metal tolerance by ectomycorrhizal fungi and metal amelioration by *Pisolithus tinctorius*. Mycorrhiza 5: 181-187

[121] Denny, HJ and Ridge, I (1995) Fungal slime and its role in the mycorrhizal amelioration of zinc toxicity to higher plants. New Phytol 130: 251-257

[122] Ahonen-Jonnarth, U; van Hess, PAW; Lundström, US and Finlay, RD (2000) Organic acids produce by mycorrhizal *Pinus sylvestris* exposed to elevated aluminium and heavy metal concentrations. New Phytol 146: 557-567

[123] Martino, E; Franco, B; Piccoli, G; Stocchi, V and Perotto, S (2002) Influence of zinc ions on protein secretion in a heavy metal tolerant strain of the ericoid mycorrhizal fungus *Oidiodendron maius*. Mol Cell Biochem 231: 179-185

[124] Christie, P; Li, X and Chen, B (2004) Arbuscular mycorrhiza can depress translocation of zinc to shoots of host plants in soils moderately polluted with zinc. Plant Soil 261: 209-217

[125] Meharg, AA and Macnair, MR (1992) Suppression of the high affinity phosphate uptake system: a mechanism of arsenate tolerance in *Holcus lanatus* L. J Exp Bot 43: 519-524

[126] Sharples, JM; Meharg, AA; Chambers, SM and Cairney, JWG (2000) Evolution: Symbiotic solution to arsenic contamination. Nature 404: 951-952

[127] Sharples, JM; Meharg, AA; Chambers, SM and Cairney, JWG (2000) Mechanism of arsenate resistance in the ericoid mycorrhizal fungus *Hymenoscyphus ericae*. Plant Physiol 124: 1327-1334

[128] Perotto, S and Martino, E (2001) Molecular and cellular mechanisms of heavy metal tolerance in mycorrhizal fungi: what perspectives for bioremediation? Minerva Biotecnol 13: 55-63

[129] Joner, EJ; Johansen, A; Loibner, AP; de la Cruz, MA; Szolar, OHJ; Portal, JM and Leyval, C (2001) Rhizosphere effects on microbial community structure and dissipation and toxicity of polycyclic aromatic hydrocarbons (PAHs) in spiked soil. Environ Sci Technol 35: 2773-2777

[130] Joner, EJ and Leyval, C (2003) Rhizosphere gradients of polycyclic aromatic hydrocarbon dissipation in two industrial soils and the impact of arbuscular mycorrhiza. Environ Sci Technol 37: 2371-2375

[131] Salzer, P; Corbiere, H and Boller, T (1999) Hydrogene peroxide accumulation in *Medicago truncatula* roots colonized by the arbuscular mycorrhiza-forming fungus *Glomus intraradices*. Planta 208: 319-325

[132] Criquet, S; Joner, EJ; Léglize, P and Leyval, C (2000) Anthracene and mycorrhiza affect the activity of oxidoreductases in the roots and the rhizosphere of lucerne (*Medicago sativa* L.). Biotechnol Lett 22: 1733-1737

[133] Mada, RJ and Bagyaraj, DJ (1993) Root exudation from *Leucaena leucocephala* in relation to mycorrhizal colonization. World J Microb Biot 9: 342-344

[134] Jones, DL; Hodge, A and Kuzyakov, Y (2004) Plant and mycorrhizal regulation of rhizodeposition. New Phytol 163: 459-480

[135] Secilia, J and Bagyaraj, DJ (1987) Bacteria and actinomycetes associated with pot cultures of vesicular-arbuscular mycorrhizas. Can J Microbiol 33: 1069-1073

[136] Kandeler, E; Marschner, P; Tscherko, D; Gahoonia, TS and Nieksen, NE (2002) Microbial community composition and functional diversity in the rhizosphere of maize. Plant Soil 238: 301-312

[137] Vierheilig, H; Gagnon, H; Strack, D and Maier, W (2000) Accumulation of cyclohexanone derivates in barley, wheat and maize roots in response to inoculation with different arbuscular mycorrhizal fungi. Mycorrhiza 9: 291-293

[138] Hooker, JE and Atkinson, D (1996) Arbuscular mycorrhizal fungi-induced alteration to tree-root architecture and longevity. Z Pflanzenernaehr Bodenk 159: 229-234

[139] Quintero-Ramos, M; Espinoza-Victoria, D; Ferrera-Cerrato, R and Bethlenfalvay, GJ (1993) Fitting plants to soil through mycorrhizal fungi – mycorrhiza effects on plant growth and soil organic matter. Biol Fert Soils 15: 103-106

[140] Wright, SF and Upadhyaya, A (1998) A survey of soils for aggregate stability and glomalin, a glycoprotein produced by hyphae of arbuscular mycorrhizal fungi. Plant Soil 198: 97-107

[141] Joner, EJ; van Aarle, IM and Vosátka, M (2000) Phosphatase activity of extraradical arbuscular mycorrhizal hyphae: A review. Plant Soil 226: 199-210

[142] Trojanowski, J; Haider, K and Hüttermann, A (1984) Decomposition of 14C-labelled lignin, holocellulose amd lignocellulose by mycorrhizal fungi. Arch Microbiol 139: 202-206

[143] Haselwandter, K; Bobleter, O and Read, DJ (1990) Degradation of 14C-labelled lignin and dehydroplymer of coniferyl alcohol by ericoid and ectomycorrhizal fungi. Arch Microbiol 153: 352-354

[144] Cairney, JWG and Burke, RM (1994) Fungal enzymes degrading plant cell walls: their possible significance in ectomycorrhizal symbiosis. Mycol Res 98: 1345-1356

[145] Meharg, AA and Cairney, JWG (2000) Ectomycorrhizas – extending the capabilities of rhizosphere remediation? Soil Biol Biochem 32: 1475-1484

[146] Meharg, AA; Cairney, JWG and Maguire, N (1997) Mineralization of 2,4-dichlorphenol by ectomycorrhizal fungi in axenic culture and in symbiosis with pine. Chemosphere 34: 2495-2504

[147] Meharg, AA; Dennis, GR and Cairney, JWG (1997) Biotransformation of 2,4,6-trinitrotoluen (TNT) by ectomycorrhizal basidiomycetes. Chemosphere 35: 513-521

[148] Donnelly, PK; Entry, JA and Craftword, DL (1993) Degradation of atrazine and 2,4-dichlorphenoxyacetic acid by mycorrhiozal fungi at three nitrogen concentrations *in vitro*. Appl Environ Microbiol 59: 2642-2647

[149] Braun-Lüllemann, A; Hüttermann, A and Majcherczyk, A (1999) Screening of ectomycorrhizal fungi for degradation of polycyclic aromatic hydrocarbons. Appl Microbiol Biot 53: 127-132

[150] Genney, DR; Alexander, IJ; Killham, K and Meharg, AA (2004) Degradation of the polycyclic aromatic hydrocarbon (PAH) fluorene is retarded in a Scots pine ectomycorrhizosphere. New Phytol 163: 641-649

[151] Donnelly, PK and Fletcher, JS (1995) PCB metabolism by ectomycorrhizal fungi. B Environ Contam Tox 54: 507-513

[152] Green, NA; Meharg; AA; Till, C; Troke, J and Nicholson, JK (1999) Degradation of 4-fluorbiphenyl by mycorrhizal fungi as determined by F-19 nuclear magnetic resonance spectroscopy and C-14 radiolabelling analysis. Appl Environ Microbiol 65: 4021-4027

[153] Dittmann, J; Heyser, W and Bucking, H (2002) Biodegradation of aromatic compounds by white rot and ectomycorrhizal fungal species and the accumulation of chlorinated benzoic acid in ectomycorrhizal pine seedlings. Chemosphere 49: 297-306

[154] Jurkiewicz, A; Orłowska, E; Anielska, T; Godzik, B and Turnau, K (2004) The influence of mycorrhiza and EDTA application on heavy metal uptake by different maize varieties. Acta Biol Cracov Bot 46: 7-18

[155] Hovsepyan, A and Greipsson, S (2004) Effect of arbuscular mycorrhizal fungi on phytoextraction by corn (*Zea mays*) of lead-contaminated soil. Int J Phytorem 6: 305-321