

# Chapter 13

## Upscaling the Biogeochemical Role of Arbuscular Mycorrhizal Fungi on Metal Mobility

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### Abstract

In this chapter we introduce a concept relating the biogeochemical role of microorganisms explicitly to cross-scale effects in the frame of an approach we termed *objective scale integrated biogeochemistry*. By *objective*, we mean that the scale of analyses is that of the environmental objects involved in the cycling, and is not assumed *a priori* based on human (institutional) interests. By *integrated*, we refer to the consideration of multi-element fluxes (of nutrients and toxic elements) through the biotic and abiotic compartments controlling productivity of the system. After a critical analysis of the knowledge on arbuscular mycorrhizal fungi (AMF) relevant for estimating their biogeochemical role in the mobility of metals, we propose a methodology for characterizing this role and underline the practical limitations linked to current state of knowledge concerning AMF. These limitations are due to basic issues such as estimating the dimension of a physiological individual, the size in space of a population of AMF, and the species diversity of AMF in the hyphal compartment. We then focus on an example of myco-phyto-remediation using selected plants and commercial inocula. A multi-scale (pot, lysimeter, field plot) experimental approach for studying the biogeochemical role of AMF in metal mobility was developed, tackling scale-specific issues. The main findings of the operational research program are summarized.

**Key words:** arbuscular mycorrhizal fungi, biogeochemistry, metals, scale

### 13.1 Introduction

The target of environmental management is to optimize the production of natural resources and services at scales relevant for humans (usually environmental management units like ecosystems -  $10^4$ - $10^6$  m<sup>2</sup>, simple landscapes -  $10^6$ - $10^8$  m<sup>2</sup>, and larger landscapes - river basins and ecoregions). The operational measures of such management require knowledge about the role of each species. In order to describe this role, one can use the term service production unit (SPU, Luck et al. 2003) referring to an aggregate of populations of a certain species, or to a part of such a population directly involved in the production of a certain natural service or resource. The scale of an SPU is usually different from that of the environmental management units (either smaller or larger), and when the scale is of the same order, the SPU does not exactly overlap in space with the institutionally delineated environmental management unit. In the case of small scale organisms like fungi, one is additionally confronted with the problems inherent to upscaling the scientific knowledge on the role of fungi from the scale of the SPU to the scale of the management units.

Usually, natural services are related to the production of natural resources as structural elements of the ecosystems (e.g. renewable resources provided by a forest), and about services related to other

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functions of the ecosystems (e.g. hydrological or biogeochemical services). In this chapter, we focused on some of the biogeochemical services supported by AMF and on the methodology of their evaluation. However, the mentioned analytical and managerial distinction between types of services is not supported by a more basic insight in what happens in an ecosystem, because the production of biomass (supporting the exploitation of renewable resources) is inseparable from the circulation of substances, as well as energy between abiotic and biotic compartments (supporting the biogeochemical services).

Scientific disciplines dealing with element cycling and its effects on ecosystems can be seen to have developed in two historical phases. During the first, biogeochemistry has been conceived as a discipline dealing with ecosystem element cycling (pool and flux approach), where the cycling of each element was analyzed separately. In the particular case of toxic elements, like heavy metals or organic pollutants, one would have to firstly describe the cycling of these substances in ecosystems, and then (in the frame of a separate scientific discipline, ecotoxicology) to describe their effects on the functioning of ecosystems. The basic problem with this approach is that the circulation by organisms (and their role as reservoirs of elements in the cycling of elements) is not separable from the effects of the elements taken up on the production of biomass, in particular from the ecotoxicological effects of toxic elements or substances. As a reaction to the limitations of this approach, there are holistic proposals (in systems ecology line of thought) that biogeochemistry is a part of ecotoxicology (or vice-versa, depending on the institutional location of the researchers developing the ideas), and that the methodology should approach at the ecosystems scale both the circulation and the effects of elements. From a basic science point of view the problem with this second approach is that ecosystems are concepts imposing a scale of analyses relevant for human management interests, and not giving the attention due to the scale of each group of organisms (the role of organisms are evaluated directly at the scale of management units without an explicit upscaling or downscaling from the specific scale of the SPU, Iordache et al. 2011). Also, the partial decoupling between processes occurring at different scales in an environmental management unit, and the multiscale character of the ecosystems are ignored in the traditional (holistic systems analyses) research methodology of this approach (Iordache et al. 2012). From a practical point of view, this holistic variant of biogeochemistry (or ecotoxicology) is not workable because it tends to over-concentrate the existing resources in single large scale projects (and for this reason faces institutional resistance) and, in the frequent case of resource scarcity, may also lead to a superficial (from a good science standards perspective) approach of the SPU scale mechanisms involved in the functioning of ecosystems.

In this context, we introduced elsewhere (Iordache et al. 2012) a concept for the role of an organism in the mobility of elements giving attention to its specific scale as follows: “By *role* of a variable in the mobility of elements we understand the causal influence of a variable in a coupling mechanism, in producing the outcome of a process involving it. The *role* of a subsystem of the coupled entities (characterized by a variable) is specific to the coupling scale, The fluxes resulted from this role at the coupling scale propagate to larger or smaller scales (these effects at distance could eventually be labeled as indirect roles)”. Characterizing the direct role is a matter of understanding the functioning of the SPU, and characterizing the indirect role at ecosystem scale is a matter, for small scale organisms like fungi, of up-scaling from the SPU scale to the ecosystem scale. In this framework, one can recover a part of the holistic idea. Characterizing the direct role supposes the construction of a minimal homomorphic model of the SPU (e.g. Iordache et al. 2011 for ectomycorrhizal fungi), much less complex than a model of an environmental management unit (ecosystem), which makes the approach workable from a practical point of view. It also supposes the integrated research of the circulation of elements as resources (or toxicants) by the target organisms and the other environmental objects directly interacting with the target organisms. The study of the circulation of elements and substances is put in the frame of their effects on the biomass production of the target organisms. In the particular case of heavy metals (HM) from contaminated areas, implications are that the ecotoxicological effects of metals on mycorrhizal plants are not studied separately from their circulation and for instance, from the effects of macronutrients like nitrogen and phosphorus (at least as a research program), or any other significant resources needed for the functioning of the fungi-plant systems. To give a name to

this approach we call it *objective scale integrated biogeochemistry* (OSIB). We mean here by “objective” that the scale of analysis is imposed by the environmental objects involved in the cycling, and not by an a priori delineation of environmental management units (ecosystems) based on human (institutional) interests. By integrated we refer to the integrated investigation of the fluxes of nutrients and toxic elements through the target organisms and through the biotic and abiotic compartments directly connected with them. OSIB is contrasted to institutional scale integrated biogeochemistry (the holistic approach described above), and with classic biogeochemistry (by element).

The question tackled is to what extent the existing knowledge on AMF allows an OSIB approach of the role of AMF in the mobility of metals in contaminated areas. We start by surveying the existing knowledge about AMF, describe the structure of an ideal methodology for investigating the biogeochemical role of AMF, show how the limits of the existing knowledge impact on the implementation of the ideal methodology, and propose an operational methodology and illustrate it with some of our research results.

### **13.2 Survey of the Literature on AMF**

The recent secondary literature (review type and meta-analyses) directly and indirectly relevant for an assessment of the biogeochemical role of AMF is large (Tab. 13.1). From taxonomic, to structural and functional aspects, comprehensive reviews are available. Especially striking is the large body of recent reviews concerning the influence of AMF on plants growing in areas contaminated with metals, in the context of phytoremediation studies, the focus of our interest in this chapter.

*Table 13.1 about here*

On the other hand, if one looks only at biogeochemical studies done in an ecosystem (holistic) paradigm, for instance by searching for the key word “arbuscular” in the on-line versions of the journals *Biogeochemistry* and *Ecosystems*, with the purpose to identify articles about the role of AMF in metal biogeochemistry, the picture is different. At the date of our search, there were 24 primary literature articles dealing with AMF in the whole collection of *Biogeochemistry*, of which 12 related to nitrogen, 3 to organic matter and carbon, 4 to carbon and nitrogen, one to organic matter and minerals, 1 to carbon and phosphorous, 2 to carbon, nitrogen and phosphorus, and one to nitrogen, phosphorous and sulphur. In the journal *Ecosystems* we found 15 articles, most of them dealing with nitrogen and carbon, and several with disturbances not related to the contamination with metals. Complementary, we searched for the same key term in two ecotoxicological journal, *Ecotoxicology*, and *Environmental Toxicology and Chemistry*. We found only 8 articles in the first journal and 13 in the second one, of which about half were dealing with metals, usually in an experimental setting. One can conclude that the information about the role of AMF in holistic (large scale) type approaches of metal biogeochemistry was lacking at the level of January 2011. Despite the large apparent interest on their use in phytoremediation of contaminated areas, most of the information is at small scale. The roles of AMF in the mobility of metals based on this literature can be synthesized in Tab. 13.2 (adapted from Neagoe et al. 2011; details in part 13.2.1 of this chapter).

*Table 13.2 about here*

The problematic situation of basic issues like identifying individuals, populations and communities (reviewed by Rosendahl 2008) should also be underlined, because it has profound effects on the practicability of a systems ecology type approach with respect to the role of AMF, and on the methodology of upscaling the information about functions at small scale to functions at large scale. Currently, we do not have methodological access to the delineation of AMF physiological individuals in space in real field ecosystems, and implicitly we cannot have true estimations of the number of individuals in populations and the numeric and biomass abundances in communities needed for characterizing succession changes, as we do for aboveground communities. The situation seems to be worse than that for ectomycorrhizal fungi (Iordache et al. 2011a). In this context, the discussions about the succession of AMF, and the influence of AMF on plant succession, should be interpreted keeping

in mind the basic problems outlined above. Although soil pH, nutrients and organic matter, as well as plant community structural changes are considered to be the most important drivers of AMF succession (Piotrowski and Rillig 2008), and the role of AMF especially in primary succession has been proven (Gange et al. 1993), it is not yet clear at what scale these statements hold up in real systems.

Before exploring the consequences of these limitations in knowledge on the possibility to characterize the role of AMF in the frame of an objective scale integrated biogeochemistry, we provide some extra information on the available knowledge concerning the influence of AMF on the transfer of metals to plants, and to lower soil layers.

### **13.2.1. Influence of AM fungi on the bioaccumulation of heavy metals in plants**

In the last decade, a vast number of publications on the effect of AMF on the uptake of HM by plants became available. Interestingly, this effect is not uniform, both stimulation and inhibition of uptake have been reported. The outcome depends on the selected plants, the species and strain of the fungus used, on the degree of pollution, and on the pollutant's binding capacity to soil constituents. In particular, heavy metals (HM) have been shown to have positive, negative or neutral effects on mycorrhizal colonization in soil or culture solution, depending on their host plants. Metal accumulation by plant shoots is reported to be lower under elevated soil metal concentrations or higher under normal metal conditions (Toler et al. 2005), when this is applied to phytoremediation technologies using AMF, HM from polluted areas, in the majority of cases, were retained in the rhizosphere. The retention capacity differs as a function of the degree of pollution and of the nature of the element. In such cases, HM are not accumulated in big quantities in the above-ground part of plants, although the root absorption area can increase up to 47-fold using mycorrhizal fungi (Turnau et al. 2006 after Smith and Read 1997, Soares and Siqueira 2008). Metal acquisition by plants is reduced, and plant growth is enhanced, thus metal dilution occurs in plant tissue as a consequence of increased root or shoot growth, but also due to the HM uptake, reduction, exclusion by precipitation, or chelation in the rhizosphere system, and also due to the phosphorus (P) mediated effects on the host plants (Soares and Siqueira 2008).

The influence of AMF on metal plant uptake depends on many factors such: “fungal genotype, uptake of metal by plant *via* AM symbiosis, root length density, competition between AMF communities, seasonal variation in AM, association with soil microorganisms, chemical properties of the soil outside the rhizosphere (pH, CEC, etc.), the metal itself, concentrations of available metals, soil contamination conditions (contaminated or artificially contaminated vs non-contaminated soil, interactions between P and metals (addition of P fertilizers), experimental conditions (light intensity, plant growth stage, available N and P), litter inputs, plant species and plant size” (Giasson et al. 2008). The toxic effect could be diminished by covalent binding, compartmentalization, or extrusion; moreover, a physico-chemical barrier can be formed to protect crucial organs from toxicity (avoidance), or prevention of HM uptake by excluder plant species, HM precipitation on the surface of extraradical mycelium, production of metallothioneins (metal binding proteins), metabolism alterations like increasing production of scavengers for reactive oxygen such as proline through symbiotic fungi are known. None of these mechanisms so far have been proven with molecular techniques (Giasson et al. 2008, Turnau et al. 2010).

According to Gadd (2005), both live and dead components of the fungal cell wall can be involved in HM binding with help of free amino, hydroxyl, carboxyl and other groups. AMF form extraradical mycelium and intraradical hyphae that penetrate the intercellular spaces and enter cortical root cells. In the case of reduction of HM uptake, an important role in retention, binding and immobilization seems to be associated to *fungal vacuoles*. They are involved in the regulation of cytosolic metal ion concentrations and the detoxification of potentially toxic metal ions (Gadd 2005). The *fungal cell wall*, respectively chitin and glomalalin from the fungal wall (Christie et al. 2004), are also important due to the presence of free amino, hydroxyl, carboxyl and other functional groups (Gadd 1993 and 2005,

Kapoor and Viraraghavan 1995). While chitin is an important component of fungal cell walls acting as an effective biosorbent for radionuclides (Tobin et al. 1994), glomalin is a glycoprotein produced by the hyphae of AMF. It plays an important role in fungal physiology and in the soil environment with a negative effect on soil aggregate stability. It seems to be efficient in sorbing potentially toxic elements by sequestering As, Cu, Cd, Zn, Pb (Alexander 1994, Gonzales-Chavez et al. 2004, Carrasco et al. 2009), Cr (Alexander 1994, Estaún et al. 2010), Hg (Alexander 1994, Yu et al. 2010) etc., and reducing the level of toxicity in soil by converting HM into their organic form thus making them more bioavailable. As already noted, the toxic effect of metals entering into the cells can be counteracted by synthesizing complex organic molecules such as metallothioneins and phytochelatins, or HM transporters of various families (Turnau et al. 2010 citing Hall 2002). Van Keulen et al. (2008) described some advanced proteomic studies in which an array of proteins was found to be expressed under stress conditions including chitinases.

HM enter the roots, where are deposited mainly in the inner root parenchyma cells. There also are most of the fungal structures (intraradical hyphae, arbuscules and vesicles) in which metals can be stored (Turnau 1998). Due to their potential in sequestering HM, AM fungi play a significant ecological role in phytostabilization of toxic HM in polluted soils and, at the same time, help mycorrhizal plants to survive in these hostile soils. The migration of HM is prevented also by microbial production of organic acids, acid phosphatases, or pigments which precipitate HM outside of the mycelium (Turnau and Dexheimer 1995). To that end, chelation of metals is possible with the help of different compounds excreted from the extraradical mycelium of mycorrhizal fungi (Turnau et al. 2006), or by metal retention in the root system, a result of surface complexation of metals with cysteine-containing ligands of fungal proteins, a phenomenon which seems to play an important role in resistance of plants to heavy metals (Christie et al. 2004).

Water deficiency is a parameter which may affect the intra- and extraradical development of AMF through a decrease in plant photosynthesis and stomatal closure, leading to a decreased supply of the fungal symbiont with carbohydrates. A low soil moisture regime leads also to a decrease in phosphorus and other major nutritional elements in plants lowering in turn plant biomass production and increasing concentrations of HM *in planta*. In this case, HM can be bound within the AMF cells to metallothionein, or be stored in vacuoles (Neumann et al. 2009).

In conclusion, as Vamerali et al. (2010) underlined, the beneficial effect of AMF on HM uptake into plants consists of a higher biomass production which could lead to a metal “dilution effect”, an increase in HM plant tolerance, as well as a greater HM concentrations in plant tissues. However, information about the variability in space of these effects in large scale contaminated ecosystems is lacking.

### **13.2.2 Particular effects of AM fungi on different HM**

AMF inoculation with or without fertilizer application leads to a decrease of toxicity symptoms of plants. It is well documented that AMF and P nutrition can produce larger plant biomass with a resulting ‘growth dilution’ effect. Thus, shoots As concentrations are slightly reduced and soil inorganic As is transformed into the less toxic organic form by AMF (Adriano 2001, Ultra et al. 2007). Inorganic arsenic (e.g. arsenite, arsenate, etc.) is very toxic for membranes and can also inhibit seed germination or lead to death of plant cells (Barua et al. 2010 after Carbonell et al. 1998). Giasson et al. (2008) noted that arsenate may be accumulated in the cytoplasm in the same way as polyphosphates. There are more studies in which clear indications are given for mycorrhizal inoculation reducing harmful effects of arsenic on the initial growth of different plant species improving plant tolerance to toxicity (Sanon et al. 2006, Chern et al. 2007, Ultra et al. 2007). The tolerance to arsenic toxicity is variable from one plant species to another. Moreover, a low level of As has been found to stimulate plant growth in spite of the fact that As is not a nutritional element for plants. Barua et al. (2010) underlined that plant roots contain higher proportion of arsenic than any other plant parts. Under As exposure, the length of roots are reduced and thus the spreading of plants is disturbed. High arsenic

contamination in soil, however, lead to a strong growth suppression, stopping the normal functioning of roots (e.g. water transport, gas diffusion, nutrient uptake, etc.) in addition to the shorter roots and disassembled root cap (Ahmed et al. 2006). In the presence of AMF, the biomass production was increased up to 2.4 times due to a better root development, Chemical changes of root exudates under AMF action provided conditions for more mycelium to develop, while they act as nutrient source for rhizosphere microorganisms (Leung et al. 2006, Ultra et al. 2007). Barua et al. (2010) underlined the increase of roots as a results of AMF association with plants, after the transformation of As from inorganic to organic forms by biomethylation. Dimethylarsine was detected in colonized *Petris vittata* but also in other plant species, and the mycorrhization was not inhibited by As (Liu et al. 2005, Gadd 2005, Ultra et al. 2007, Giasson et al. 2008).

The alleviation of **Zn** toxicity towards plants by using AMF was reported in Christie et al. (2004) and Chen et al. (2004), and this phenomenon was shown to be dependent on direct and indirect mechanisms. As an example for a direct mechanism, Zn was bound in mycorrhizal structures and immobilized in mycorrhizosphere, while for an indirect effect, an influence of mycorrhiza on the plant's mineral nutrition, especially for P, lead to increased plant growth and enhanced metal tolerance. The mobility of Zn is greatly affected by the changes in soil pH. The Zn immobilization through the fungal activity might be an effect of these changes, contributing to the inhibition of Zn uptake into the mycorrhizal plant by storage in the arbuscles, but also in hyphae (Christie et al. 2004). In highly contaminated soil, Zn was found in higher concentration in roots while a decrease in the shoots was seen as effect of AMF. When Zn amounts in soil increased, a critical threshold exists, below which Zn uptake is enhanced, while above this level Zn translocation to the above-ground parts of host plants is inhibited. In some plant species, higher translocation rates may occur, but at the cost of poor plant biomass development and probable early death of the individuals (Chen et al. 2005). Giasson et al. (2008) found that ZnCO<sub>3</sub> can be solubilized by hyphae and Zn is then translocated into the plant roots. Chen et al. (2004) provided information about the effects of chelating agents such EDTA on mycorrhizal development and on Zn uptake in plants. It is known that EDTA application on a polluted soil leads at the release of absorbed HM increasing the mobility of metals in the soil. In the case of AMF inoculation, the uptake differed in function of the soil Zn. In general, mycorrhizal colonization decreased both deficiency and the effects of pollution with Zn. However, neither EDTA, nor AM colonization, stimulated Zn translocation from roots to shoots. In conclusion, the combined effects of both did not promote metal removal from the soil. Zn depositions were found in spores of *Glomus intraradices* in the periplasmic space between the inner layer of the wall and the plasmalemma. The fungal alkaline phosphatase activity as an indicator of fungal viability was strongly reduced in the presence of EDTA, also affecting Zn uptake (Turnau et al. 2006). Göhre and Paszkowski (2006) and Cavagnaro (2008) explored the effects of Zn on the colonization of roots by AMF and the molecular Zn physiology for bothm, plant and fungal gene products. These authors concluded that the changes in the Zn status of plants due to AMF colonization were influenced by the expresion of a specific gene of *Glomus intraradices*. They recommended the identification of further genes involved in interactions between AMF and Zn, as well of the factors which control their expression.

Yu et al. (2010) reported that in the case of **Hg**, the uptake is lower by mycorrhizal than by non-mycorrhizal roots of maize, and AMF inoculation significantly decreased the total and extractable Hg concentrations in soil as well as the ratio of extractable to total Hg. Calculating mass balances for Hg in soil indicated a loss of Hg which can be attributed to Hg volatilization as a result of AMF influence. No significant difference of Hg concentrations was found between mycorrhizal and non-mycorrhizal shoots of maize which suggest that contribution of root uptake to shoot accumulation of Hg is very limited. The release of Hg into soil gases or into the atmosphere is a result of methylation (CH<sub>3</sub>Hg<sup>+</sup>), which leads to phytovolatilization, seen also with As and other metalloids (Giasson et al. 2008).

Various studies show that AM symbiosis may alleviate also **Cd** stress and decrease Cd uptake by plants growing in contaminated soils. A negative effect of Cs on root colonization and the development of extraradical mycelium was seen (Rivera Becerril et al. 2002; Janoušková et al., 2006;

Biró and Takács 2007, de Andrade and da Silveira 2007, Rashid et al. 2009, Janoušková and Pavlíková 2010, Regvar et al. 2010). Redon et al. (2008), as well as Janoušková and Pavlíková (2010) reported that in the mycorrhizosphere the concentration of Cd was lower as compared to non-mycorrhizal plants with extraradical hyphae being responsible for the decrease of Cd toxicity. Janoušková et al. demonstrated in 2006 that extraradical hyphae have a high Cd binding capacity which is specific for HM (Hildebrandt et al. 2007). The toxic and non-essential metal Cd is bound more strongly to ligands compared with essential metals. This phenomenon leads to the displacement of essential metals from their normal sites, and the Cd toxic effect is exercised by binding to other sites. The small plant peptides called phytochelatins (PC) which have a protective role in plant cells help Cd to be sequestered *via* cysteinyl residues. Similarly, the sequestration of Cd in fungal structures could be responsible for the retention of Cd in the roots. The molecular responses of AMF plants to Cd was a research subject for Aloui et al. (2009) who worked at the proteomic level and found down-regulation of several proteins upon Cd stress. Cd can be also adsorbed on the spores. After saturation of fungi with Cd, increased translocation of this metal to shoots occurred (Giasson et al. 2008).

It is known that **Pb** has low mobility (even less than P and Zn) and is strongly complexed with the organic matter in soil, forming organic complexes which are unavailable for plants. Similarly, plants possess mechanisms to precipitate Pb in the rhizosphere, in highly insoluble forms such as PbSO<sub>4</sub>. However, Pb that has entered the roots can be sequestered in fungal vesicles, which can provide an additional detoxification mechanism. However, sequestration of Pb in roots was not found to be correlated with an increase in the number of vesicles (Göhre and Paszkowski, 2006). Similar results were found by Chen et al. (2005) where, after growth of plants in the presence of AMF in an artificially polluted soil, Pb had a positive effect on vesicular abundance which was not correlated with a lower concentration of Pb as it was expected. At the same time, enhanced Pb concentrations both in roots and shoots, and a higher root/shoot ratio was found for highly mycorrhizal plant species (*K. striata*, *I. denticulate*, and *E. crusgalli* var. *mitis*). Marschner (1995) reported lower Pb concentration in the cortical cell walls of Norway spruce (*Picea abies* L. var. *Karst*), while Chen et al. (2005) reported the contrary, an elevated Pb concentration, and suggested that under this higher concentration of Pb, mycorrhiza could promote plant growth by increasing P uptake and mitigate Pb toxicity by sequestering more Pb in roots. Also, a higher amount of Pb absorbed and accumulated also in *Eucalyptus* mycorrhizal variants (Bafeel 2008). The shoot biomass was higher, while roots biomass was significantly lower than those of non-mycorrhizal trees. Other experimental variants included the growth of *Eucalyptus* together with legumes (*F. vulgaris*) and AMF. This association with heavy-metal-resistant legume varieties and AMF further increased the positive effects on shoot biomass and helped to improve the resistance of *Eucalyptus* to HM. This effect was correlated to an increase of Pb absorption and accumulation. An explanation was given with the statement that AMF lead to increased plant biomass, and thus a larger potential absorption area for Pb, of accessible soil, and a higher efficiency in hyphal translocation. Similar studies were described in Chen et al. (2009) and Regvar et al. (2010) who found, however, that the indirect ordination analysis of restriction fragment length polymorphisms data showed no statistically significant correlations with environmental gradients.

Estaún et al. (2010) investigated the influence of the AMF *Glomus intraradices* (BEG 72) on the transfer of **Cr** in *Plantago lanceolata* grown in a high Cr soil. Although *Plantago lanceolata* is known to be tolerant towards many environmental stress factors while showing a high degree of mycorrhization, under Cr pollution the plants' survival decreased quickly. When Cr was supplied as CrCl<sub>3</sub>, this mycorrhizal model plant accumulated Cr, both in the shoots and roots. Therefore, AMF seem to act as a barrier, decreasing Cr uptake, in comparison to non-mycorrhizal plants. The effect consisting in a decrease of HM stress is due to selective immobilization in the roots system colonized by the fungus, or to a very high Cr sorption capacity of the extraradical mycelium of the AMF. This mechanism may explain the decrease of HM concentrations in root cells and through a different allocation of the metal within the root cells may have an effect on fungal colonization. Similar research was performed also on *Helianthus annuus* in the presence of Cr(III) and Cr(VI) with similar results: the uptake of Cr decreased both in shoots and roots upon mycorrhization (Davies et al. 2001). On the other part, the non-hyperaccumulator plants tend to avoid Cr uptake and translocation, and in this case,

the higher concentrations are distributed in roots, rather than leave or stem (Estaún et al. 2010, after Glosch and Sigh 2005). Similar investigations were performed by Carrasco et al. (2009) who remarked that the soluble content of Cr in soil was negatively correlated with the glomalin concentration. Testing the synergistic effect of mycorrhizal and saprobic fungi (*Trichoderma pseudokoningii*) on HM uptake into *Cynodon dactylon*, it was found that the amount of Cr uptake was highest in dual inocula. Nevertheless, the amount of Cr uptake in single saprobic fungi was more significant as compared to the mycorrhizal treatment alone (Bareen and Nazir 2010).

Studies related by Rufyikiri et al. (2004) demonstrated that the mobility of U in soil depends on the organic compound content, the bioavailability being highly dependent on soil pH. The same author found that the most mobile U forms are U(VI) salts, predominantly as  $UO_2^{2+}$  and carbonate complexes, while other forms are less bioavailable and remain bound to soil particles. The role of AM fungi in translocating U as uranyl cations to roots through fungal tissues is related to fungal mycelium HM binding capacity (Chen et al. 2005a,). Chen et al. (2005b, cited by Babula et al. 2008) performed and confirmed such studies using *Medicago trunculata* as a model plant, inoculated with *Glomus intraradices*. They found higher concentrations of U in roots than in shoots of mycorrhizal plant, suggesting that the AM fungus has a potential to reduce the translocation of U from roots to shoots.

Some research has been carried out on Cs, with, e.g., Leyval et al. (2002) reporting that  $^{134}Cs$  radioactivity increased twofold in leaf tissue of *Paspalum notatum* in symbiosis with AMF while, in the case of mycorrhizal *Mellilotus officinalis* 1.7 to 2 times increased  $^{137}Cs$  was found. *Sorgum sudanese* revealed only insignificantly increase. A significant decrease of  $^{137}Cs$  in mycorrhizal *Festuca ovina* and *Agrostis tenuis* was found; this finding underlining that soil fungi represent a potential for Cs immobilization. On the other hand, Rosén et al. (2005) working with mycorrhizal ryegrass and leek found an enhanced  $^{137}Cs$  uptake by leek, but no effect on the uptake by ryegrass. Similar studies were performed on mycorrhizal *Festuca ovina* in which shoots showed higher  $^{137}Cs$  concentration than roots, as well as on *Trifolium repens*, and AM plants took up less Cs with no increase in translocation of  $^{137}Cs$  to the shoots being found. In conclusion, AMF seems to play a role, with regard of both immobilization and phytoextraction being represented depending on plant species. Specifically grasses seem to respond with decreased uptake into shoot biomass.

Turnau and Mesjasz-Przybyłowicz (2003) have found an increased Ni content in shoots of *Berkheya coddii*, a hyperaccumulator from the Asteraceae family, with well-developed mycorrhization. There is only very scarce literature relating details on other elements, excepting the nutrients P, Ca, or Mn.

### **13.2.3 The effects of poly-metal pollution on HM uptake in plants inoculated with AMF and combination to other microbial communities**

When research focusses on a single pollutant, the response of AMF on HM uptake into plants is much more clear as compared to soil containing more than two pollutants (poly-metal pollution). In such cases, it is very useful to include mechanisms of HM toxicity like the producing of ROS, which can damage biomolecules such as membrane lipids, proteins, chloroplast pigments, enzymes and nucleic acids. Normally, plants have mechanisms for protecting against oxidative stress. As an effect of AMF inoculation, decreased oxidative stress could be shown either by assaying enzymatic activity (of, e.g., SOD – superoxide dismutase, POD – peroxidases, CAT – catalase, etc.) or non-enzymatic systems acting as free radical scavengers (e.g., soluble protein or pigments such as chlorophyll and carotenoids). Zhang et al. (2006) found that inoculation with *Glomus mosseae* decreased POD activity and DNA damage in AM *Vicia faba* plants. The high level of such antioxidative systems as well as non-enzymatic antioxidants in mycorrhizal plants could be an effect of arbuscle senescence (Fester and Hause 2005).

It is well documented that AMF coexist with other soil microorganisms which might have positive or negative effects on HM uptake (Giasson et al. 2008). When the inoculation with AMF is combined with saprobic fungi, there is a synergistic effect. Bareen and Nazir (2010) used a dual inoculation with

mycorrhizal fungi and a saprobic fungus (*Trichoderma pseudokoningii*) applied in a poly-metal soil using the host plant *Cynodon dactylon*. The results showed an increased plant biomass and phytoextraction ability for metals like Cd, Cr, Cu, as well as Na, with a greater volume of HM being stored in the mycorrhizal structures and spores. These studies were performed using autochthonous fungi, because it is known that the results are much better than in the case of using allochthonous fungi. Similar results using saprobic fungi and *Glomus deserticola* in symbiosis with tomato and alfalfa were related by Sampedro et al. (2008).

Wang et al. (2005) used only one fungal strain (*Glomus caledonium* 90036) and compared that to a consortium of AMF *Gigaspora margarita* ZJ37, *Gigaspora decipens* ZJ38, *Scutellospora gilmori* ZJ39, *Acaulospora* spp. and *Glomus* spp. The results indicated that the inoculation with the consortium led to a significant increase of shoot biomass and shoot P, Cu, Zn, Pb concentrations, but did not alter shoot Cd concentrations, resulting in higher Cu, Zn, Pb, Cd extracted by *E. splendens*. In poly-metal pollution, it has been documented that Cu mainly accumulated in the spore vacuoles, while Cd was contained in vacuoles of the mycelium (Turnau et al. 2010). Barea et al. (2005) described the tripartite symbiosis among legume-mycorrhiza-rhizobia underlining that they established positive interactions reflected in the increase of Zn, Cu, Mo, Ca, and P uptake in plants, making it possible to use the combination in revegetation programs to restore HM polluted sites.

#### **13.2.4 Influence of succession on AMF communities and bioaccumulation of HM in plants**

It is known that at HM polluted sites, either individual plants or the entire communities and populations are affected. It is assumed that the response includes changes in species composition and diversity in terms of *succession*, and higher stress tolerance in terms of natural *selection*, both of them being processes at the long time scale (Turnau et al. 2010). According to these authors, at polluted sites first appeared the non-mycorrhizal plant species, which are not able to establish a vegetative cover, while second stages are dominated by facultative mycorrhizal species. A very pure vegetation cover could be developed only after several decades with spontaneous succession. The succession is thought to influence parameters like relative mycorrhizal colonization, relative arbuscule formation, or arbuscule richness, which could affect HM bioaccumulation in plants allowing a differentiation between restored and non-restored sites. Rowe et al. (2007) suggested using native inoculum rather than commercial ones since they seem to be more effective in establishing the late-successional associations. However, all discussions on succession should be considered with care, because of the methodological limitations underlined in the end of part 13.2.

#### **13.2.5 Influence of AMF on leaching in the soil column**

There are few articles looking for the effects of plants on the leaching of elements with the seepage water (Dudley et al. 2008), and even fewer about the effect of AMF on leaching in mesocosms extracted from the field (Heijden 2010). Several studies on the effect of AMF on metal leaching were performed in the context of investigations dealing with contaminated sites (Banks et al. 1994, Iordache et al. 2006, Neagoe et al. 2009).

The mechanisms underlying the effects of plants on leaching are the creation of preferential flow paths (by roots) and the direct and indirect influence of soil pore size distribution (Halabuck 2006). Simulation of metal transport in the soil profile as a result of plant influences is a matter of current research (Dusek et al. 2010), but in principle, AMF might exert an influence which can be modeled by their effects on preferential flow paths and pore size distribution. Such effects have not been studied explicitly to our knowledge. A synthesis of the knowledge on the influence of organic matter on soil profile leaching, which can be eventually related to the role of AMF on the distribution of organic matter in soil, can be found in Neagoe et al. (2012).

The main problem of the existing studies in terms of up-scaling is that the scale of these experiments is not explicitly related to the size of AMF populations in natural ecosystems. Thus, it cannot be used to extrapolate the function of control variables in the field distribution. In the existing studies, the development of AMF was restricted in space by the experimental design, and the results cannot

meaningfully be used to predict the effects in the field under variable soil and vegetation conditions. A need for an integrated study of the role of AMF on metal mobility *in situ* by both leaching to lower soil horizons and bioaccumulation in plants is in need.

### 13.3 Methodology for Investigating the Biogeochemical Role of AMF

Upscaling the role of AMF depends, in general terms, on the development of community-environment relationships (where the environment is “stratified by multiple gradients”; Lilleskov and Parrent 2007). In particular, exactly how this stratification should be set up (which is the scale of the elementary unit of extrapolation, and implicitly the sampling scale for characterizing the gradients) is to be described. Graham (2008) states that “experimental design should either integrate multiple mechanisms of the landscape scale and include such measures as mycorrhizal influences on net primary production, evapotranspiration and nutrient cycling, or integrate measures of [ . . . ] fungal diversity into assessment of ecosystem function.” We believe that a functional dynamic approach (already applied to ectomycorrhizal fungi – Iordache et al. 2011) would be useful also for AMF.

Pool-flux classical ecosystem type research can be associated with this method by the construction of a minimally complex homomorphic model, and it is also compatible with the stoichiometric approach proposed by Johnson (2010), who considers that a “stoichiometric perspective of C, N and P fluxes through mycorrhizas may provide a ‘common currency’ to facilitate cross-scale communication among a diversity of scientists interested in understanding AM symbioses from genes to ecosystems”. Instead of C, N, and P fluxes studied separately, and metals studied separately (Audet and Charest 2007a), the integrated research of macronutrients, micronutrients, and toxic metals influence on soil-plant-AMF system would be of greater relevance.

An ideal methodology for investigating the biogeochemical roles of AMF is based on a conceptual model of productive systems involving both biotic and abiotic objects that would involve the following steps:

1. Identification of the system of productive objects at the source scale. Description of the space-time scales of the biotic and abiotic objects involved in the productivity of AMF and of the main processes coupling these objects. The result of this step is a homomorphic model of minimal multi-scale complexity needed to understand the processes occurring at the time and space scale of AMF.
2. Characterizing the functioning of the system identified in step 1 in terms of relationships between the productivity of AMF-plant systems and macronutrients, micronutrients, and toxic elements and substances. The result of this step is a model of the circulation of elements and substances due to biological processes).
3. Characterizing the transport of elements and substances by larger scale abiotic objects (e.g. hydro-systems) coupled to the productive objects investigated in step 2. The result of this step is a model of the effects at distance in space-time (at the target scale) of the relatively smaller scale processes occurring at the source scale. For more details on effects at large distance see Iordache et al. (2012).

Within step 1 by applying the methodology described in detail in Iordache et al. (2011), one would obtain the structural model presented in Fig. 13.1.

*Figure 13.1 about here*

Step 2 involves performing the following activities (adapted from Iordache et al. 2011): (1) describing the biomass production functions of the plant-AMF systems at source scale (2) characterizing the mathematical functions describing the influence of larger scale biological objects on the productivity of the original objects (e.g. plant consumers), (3) characterizing the mathematical relationships underlying the influence of large scale abiotic parameters on productive system at the original scale, the space distribution of the abiotic parameters in the system of target scale with a resolution of original scale, and the mathematical functions predicting their space-time dynamic and the abiotic

processes involved at the target scales), (4) estimating the large scale abiotic factor's influence on large scale DSs connected to the source scale (the same as at point 1 done for the large scale biological objects mentioned at point, (5) stratifying the system of target scale system into strata having the scale of the system identified as in figure 1) (6) characterizing the production function by strata as controlled by large scale biotic and abiotic factors, and (7) model upscaling (extrapolation of production function to the target area of interest by types of strata).

The problems with putting this ideal methodology into operation start from the very beginning, with the system identification. As seen from the previous chapter, we do not know the exact size in space of the AMF physiological organisms, which means that we will not be able to quantify the surface occupied by the extraradical parts of the individuals (F3 compartment in figure 1). Based on the current information in literature, F3 compartment in Fig. 1 can be limited in space to several meters around the plants, or (based on experimental work - Mikkelsen et al. 2008, or field observations like those summarized by Jakobsen 2004) could link plants of the same or different species as far as 10 m apart, although usually the distance would be smaller. It seems reasonable at the current state of knowledge to assume that the source for upscaling has to be a plot of a maximum of 100 m<sup>2</sup>, preferably smaller, down to 10 m<sup>2</sup>. As we go to smaller discretization units, the quantity of data needed will increase accordingly. Another problem is related to the estimation of species diversity of AMF in the extraradical (hyphal) compartment (Taylor et al. 2000, Rosendahl 2008).

As for the practical delineation in space of the types of strata to be studied separately for the final purpose of up-scaling the productivity to target scale, they can be obtained by a mapping of the main entities with values for AMF, at the needed resolution. The strata will result from an intersections of the (10-100 m<sup>2</sup> scale) maps for C, N, P, micronutrients and toxic substances, pH and other soil parameters, as well as the map of plant associations, if plant cover is present (in the case of soils impacted by pollution it may lack). The intersection of layers leads to types of areas to be studied for effects of AM on mobility of metals, with an associated homomorphic model for each one, or to potential effects in case of myco-phyto-remediation.

According to our knowledge there is no article yet dealing with such a locally integrated approach, useful for farther extrapolation at ecosystem scale of the processes occurring in contaminated sites still covered by plants. Characterizing the AMF source scale system structurally, systems of two smaller and larger scales (Fig. 13.1), and mapping the target scale system in discretization units relevant for system identification is simpler than an institutional scale (ecosystem, site) integrating biogeochemistry for a truly holistic approach, but still sufficiently complex. It is an important research direction in objective scale integrated biogeochemistry and provides a framework for testing research hypotheses resulting from meta-analyses of existing results on nutrient dependent plant response to AMF (Hoeksema et al. 2010) and from field studies of the relative role of AMF and ectomycorrhiza in highly dynamic systems (Piotrovski et al. 2008).

Step 3 is not a matter of ecological research, but rather of modelling the larger scale abiotic processes of transport to distance (e.g. by vertical flow to groundwater, or by runoff) with the right resolution using the results from step 1, by type of strata as input variables in the discretization units needed for modelling the abiotic process.

What is possible at present based on existing knowledge about AMF biology and ecology? A research opportunity is provided by the challenge of myco-phyto-remediation of contaminated areas using selected plants and commercial inoculums. In this case, the problem of characterizing the species diversity and scale of AMF is eliminated (although the functional diversity within the same species will still be potentially existing – Munkvold et al. 2004), at least in the first part of the experiments. Using this opportunity, we devised an operational, three scale experimental approach as described in table 2. A research program started in 2003 allowed us to investigate patterns and processes mentioned in this table, including the relative role of AMF in the export of metals by plants and leaching from soil columns. A preliminary synthesis of the results of this approach was performed by Kothe et al. (2005).

We summarize here only the main findings of the program (methods and extended results can be found in the sources mentioned in Tab. 13.3): 1) the plant response to inoculation is species specific, but there is a general pattern of positive response in terms of biomass increase and decrease of oxidative stress (illustrated in Fig. 13.1), 2) the plant specific response depends on environmental conditions and plant community structure; plants classified as non-host may benefit from inoculation in highly contaminated soils, 3) large scale (field plot) response to artificial inoculation and mono-specific cultivation is modulated by seed bank and natural inoculation from clean soil amendment, 4) the inoculation may increase the relative importance of plants compared to leachate in the export of metals, but this depends on the rhizosphere microbial community structure (bacteria co-inoculated with AMF influenced the dynamics of soil redox potential and metal toxicity) and on soil variable heterogeneities at meter scale.

*Table 13.3 about here*

### 13.4 Conclusions

We introduced a concept of the biogeochemical role explicitly related to cross-scale effects in the frame of an approach labelled as *objective scale integrated biogeochemistry*. By objective, we mean that the scale of analyses is that of the environmental objects involved in the cycling, and is not assumed *a priori* based on human (institutional) interests. By integrated, we refer to the consideration of multi-element fluxes (of nutrients and toxic elements and substances) through the target organisms and through the biotic and abiotic compartments directly connected with them, as control factors of the productivity of the system. After a critical analysis of the knowledge on AMF relevant for estimating their biogeochemical role in the mobility of metals, we proposed a methodology for characterizing this role and underlined the practical limitations linked to current state of knowledge concerning AMF. These limitations are linked to basic issues such as estimating the dimension of a physiological individual, the size in space of a population of AMF, and the species diversity of AMF in the hyphal compartment. We underlined then a research opportunity provided by the challenge of myco-phyto-remediation of contaminated areas using selected plants and commercial inoculums. Operationally we developed a multi-scale (pot, lysimeter, field plot) experimental approach of the biogeochemical role of AMF in metal mobilities tackling scale-specific issues. The main findings of the operational research program are summarized.

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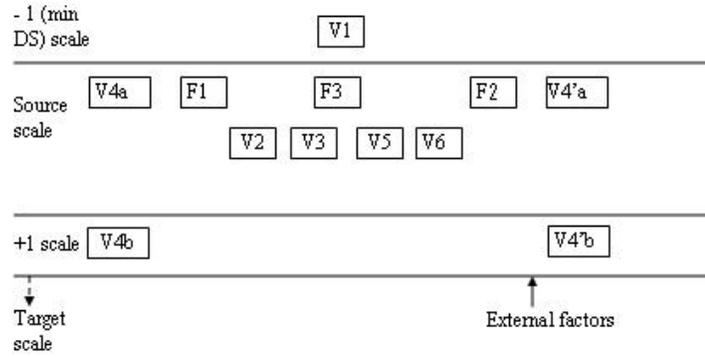
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**Figure legends**



**Figure 13.1** Homomorphic model of a community of arbuscular mycorrhizal fungi with the entities with value for them - biotic and abiotic objects influencing them (relationships not represented for reason of visibility; a connectivity matrix can be easily constructed using the information presented in the text). The scale refers to scale in space, not in time. The physical part is not represented. The part of the model within the source scale (within a stratum) is the homomorphic model for up-scaling under the constraints from organisms of different scales and external factors external to the AM functional dynamic modules. F1, fungal parts on plant roots 1; F2, fungal parts at plant roots 2; F3, hyphae in the extraradical mycelium; V1, bacteria, V2, mineral P and N; V3, organic P and N; V4, plants (a, belowground; c, aboveground parts), V5, micronutrients and toxic substances, V6, soil fungi or micro-invertebrates.

**Tables**

**Table 13.1** Reviews and chapters relevant for the biogeochemical role of AMF (use of AMF in agriculture and organic farming not included).

Topic	Review or chapter
<i>Basic issues</i>	
Species, individuals, populations and communities, hyphal networks of AMF	Taylor et al. (2000), Glass et al. (2004), Rosendahl (2008), Young (2009)
Evolutionary ecology of AMF, selection	Cairney (2000), Mehard and Cairney (2000), Helgason and Fitter (2009), Hartman et al. (2009)
Succession of AMF	Hart et al. (2001), Piotrowski and Rillig (2008)
<i>Interaction with other environmental objects</i>	
Interactions with bacteria	Boer et al. (2005), Bonfante and Anca (2009)
Interactions with rocks and minerals	Hoffland et al. (2004), Gadd (2007, 2010), Rosling et al. (2009), Martino and Perotto (2010)
Influence on aboveground consumers	Moore et al. (2003), Gehring and Bennet (2009), Koricheva et al. (2009)
Interaction with genetically modified plants	Liu (2010)
Use of AMF for induced phytoextraction of metals	Lebeau et al. (2008, 2011)
<i>Effects on ecological processes</i>	
Processes and functions of AMF in ecosystems	Allen et al. (2003), Rillig (2004), Simard and Durall (2004), Goltapeh et al. (2008), Garg and Chandel (2011)
Role of AMF in water circulation	Auge (2001), Allen (2007, 2009, 2010)
Role of AMF in phosphorous cycling	Jansa et al. (2011)
Effect of AMF on plant root systems	Berta et al. (2002), Hodge et al. (2009)
Effect of AMF on soil structure, glomalin	Rillig and Mammey (2006), Treseder and Turner (2007)
<i>Scale and modelling</i>	
Scale of AMF, heterogeneity in space, and modeling	Miller and Kling (2000), Johnson et al. (2006), Chaudary et al. (2008), Wolfe et al. (2009), Johnson (2010)
<i>Biogeochemistry of trace elements, ecotoxicology, management of contaminated sites</i>	
Effects of metals on AMF	Pawlowska and Charvat (2004), Gadd (2005)
Effect of AMF on translocation of metals from soil to plants	Audet and Charest (2007a, 2007b, 2008)
Effect of AMF on improving trace elements deficiency	Cavagnaro (2008)
Effect of AMF on heavy metal tolerance of plants, use in phytoremediation	McGrath et al. (2001), Khan (2005, 2006), Hullebusch et al. (2005), Gohre and Paskovski (2006), Hildrebrandt et al. (2007), Mathur et al. (2007), Giasson et al. (2008), Gamalero et al. (2009), Khan et al. (2009), Wenzel (2009), Smith et al. (2010), Vamerali et al. (2010), Turnau et al. (2010)
Effect of AMF on organic pollutants, use in phytoremediation	Leyval et al. (2002), Brar et al. 2006, Joner and Leyval (2009)

**Table 13.2** Examples of direct roles of AMF and organic matter observable at micro scales and of indirect roles observable at scales ranging from pot to soil column (lysimeter) and to field plot (adapted from Neagoe et al. 2011).

Soil layer	Roles	Direct role by immobilization metals	Direct role by mobilization of metals	Direct role by supporting the mobilization or immobilization of metals	Indirect roles
Soil layer relevant for plants	AMF	Biosorption, intracellular accumulation	chemoorganotrophic leaching, bioweathering	Organic matter decomposition, organic acid and glomalin production	Transfer of metals to plants, and to lower soil layers
	Organic matter	Immobilization in litter, immobilization in soil aggregates, chelates in fine pores	Organochemical weathering, soluble chelates, organocolloids, free enzymatic degradation of immobile organic carbon	Energy source for microorganisms, buffering of soil solution	

**Table 13.3** Experimental approach at three scales for the study of AMF roles in metal mobility (adapted from Iordache et al. 2012).

Name of the system and usual scales	Environmental complex system studied at these scales	Patterns studied / control variables	Reference for detailed methodology
Pot $10^{-2}$ m <sup>2</sup>	Soil + plants + AMF	Exploration by root, bioaccumulation / organic carbon, other microorganisms, level and spatial structure of amendments	Neagoe et al. (2004), Iordache et al. (2004), Stancu et al. (2010)
Lysimeter $10^{-1}$ - $10^0$ m <sup>2</sup>	Soil + plants + AMF + small scale hydro-system	Same as in pots + leaching, internal redistribution, net outputs / same as in pots + soil structure, hydraulic conductivity, humidity, redox potential in soil profile	Neagoe et al. (2006), Iordache et al. (2006), Visan et al. (2008), Neagoe et al. (2009), Nicoara et al. (2010)
Plot $4 \times 10^0$ - $10^2$ m <sup>2</sup>	Soil + plants + AMF + other organisms	Same as in pots + heterogeneity in space, margin effects, other effects due to external entities (natural seed bank, consumers) / same as in pots + variables for external entities.	Neagoe et al. (2005, 2010)