Metal Fluxes and Stresses in Terrestrial Ecosystems: synopsis towards holistic understanding

Rainer Matyssek[1], Rainer Schulin[2] and Madeleine S. Günthardt-Goerg[3]*

[1] Ecophysiology of Plants, Technische Universität München, Am Hochanger 13, D-85354 Freising-Weihenstephan/Germany. matyssek@wzw.tum.de
[2] Institute of Terrestrial Ecology ITÖ, ETH Zürich, Universitätstrasse 16, CH-8092 Zürich, Switzerland. schulin@env.ethz.ch
[3] Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland. madeleine.goerg@wsl.ch
* Corresponding author

Abstract
A synopsis is presented on the outcome of the multidisciplinary conference on "Metal Fluxes and Stresses in Terrestrial Ecosystems", held in Ascona/Switzerland, October 15–20, 2005. The synopsis pursues the rationale of a spatio-temporal scaling concept, as did the program structure of the conference, integrating mobility and availability of heavy metals (HMs) in soils, HM pathways through cell walls of root tips to aboveground plant parts, effect scaling between the cell and whole-plant level in relation to HM defense and evolutionary aspects, consequences of HM contamination in plant communities, and the applied aspect of phytoremediation. Major research needs were located regarding the quantification of HM fluxes and mass balances at the soil, whole-plant and system level, with particular attention to be directed to the interface between plants and the mycorrhizosphere. In scaling, relationships between HM bioavailability and life quality issues must be considered, implying an interdisciplinary view across biology, ecology, environmental chemistry, physics and medicine. HM contamination is crucial in "Global Change" scenarios, in terms of coupled biogeochemical cycling between the fluxes of carbon, water, metal and non-metal nutrients as well as HMs, and in relation to post-Kyoto policies. Only a mechanistic understanding of HM fluxes can provide a scientifically reliable basis for legislation, risk assessment and decision-making.

Keywords: heavy metals, trees, soils, mycorrhizosphere, scaling, bioavailability, phytoremediation, community level, defense, allocation, biogeochemistry

1 Introduction

Wrapping up the outcome of a scientific conference is a challenge, in particular, if the range of topics and concerns is as broad and complex as in the case of the multidisciplinary meeting on "Metal Fluxes and Stresses in Terrestrial Ecosystems", Centro Stefano Franscini, Monte Verità, Ascona, Switzerland, October 15–20, 2005 (Swiss Federal Institute for Forest, Snow and Landscape Research WSL 2005). This synopsis outlines the topics of the meeting and their interrelationships, critically discusses the outcome, and introduces into the papers of this and the subsequent issue of "Forest Snow and Landscape Research". Deriving a synopsis can profit, however, from the rationale of the programme structure of a conference. In the given case, a spatio-temporal scaling concept (Fig. 1; Sandermann and Matyssek 2004; Ehleringer and Field 1993), orienting at the structure of the research programme

'From Cell to Tree' (Swiss Federal Institute for Forest, Snow and Landscape Research WSL[1]), was chosen that started up from belowground processes (Sessions 1 and 2). The focus here was on the solubility and speciation of HMs in soils, including their "bioavailability" to plants, in particular trees, and the manifold interactions between root systems/mycorrhizae, microorganisms and abiotic factors in the soil. Session 3 highlighted the organ level of trees, in particular, the HM uptake through the cell walls of root tips and the subsequent translocation to other plant parts (Fig. 1). These aspects were pursued in Session 4 towards the whole-tree level ("From Cell to Tree"). This latter session bridged to Session 5, which focused on the role and potential of HM stress as an evolutionary factor for individual plant fitness, i.e. the trade-offs in "resource costs" between defence against HM stress, competitiveness relative to neighbouring plants and reproduction (Fig. 1; MATYSSEK *et al.* 2005). Session 6 addressed the system level, dealing with the issues of HM impacts on plant communities and ecosystems, including soil and groundwater contamination, HM deposition from the atmosphere and effects on food webs. Process scaling between the whole-plant and system level is important also in practical applications such as phytoremediation, which was the topic of Session 7. Proceeding from the "mycorrhizosphere" around tree roots (Sessions 1 and 2) towards the system level (Sessions 6 and 7), the workshop implicitly bridged also from short to long-term scales (Fig. 1; BALDOCCHI 1993).

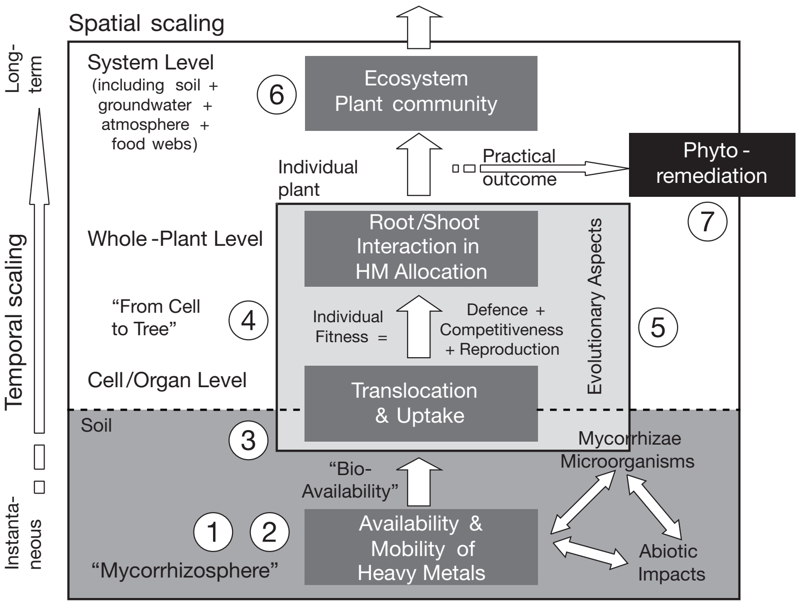

Fig. 1. Spatio-temporal scaling structure of the scientific programme of the conference "Metal Fluxes and Stresses in Terrestrial Ecosystems". Numbers denote sessions of the conference: 1 and 2 = Mobility and Availability of Heavy Metals (HMs) in Soils under Environmental Influences; 3 = Pathway through the cell wall of root tips to aboveground tree parts; 4 and 5 = From Cell to Tree, HM Defence and Evolutionary Aspects; 6 = Community consequences of HM contamination; 7 = Phytoremediation (see text for details).

[1] http://www.wsl.ch/forschung/forschungsunits/wald/waldentwicklung,
http://www.ito.ethz.ch/SoilProt/ZB/ ZBhome.html

The following account highlights the main outcomes of Sessions 1 through 7 and is based on the summaries prepared by the session leaders during the conference. The overall conclusions include perspectives and needs of further research on the impact of HMs on plants. We intend to view the synopsis of the conference within the larger context of plant and soil ecology rather than to provide a review-like overview on the range of HM action in plants and ecosystems.

2 Mobility and availability of HMs in soils under environmental influences

As a main conclusion of sessions 1 and 2, the need for long-term perspectives in risk assessment of HM effects was underlined, as requiring interdisciplinary and international cooperation. It was also felt that the spatial heterogeneity of forest sites deserves more attention. Interactions should be accounted for between long-term changes in HM reservoirs (including mobility and availability) and the variability in soil moisture and groundwater table. A "battery of tests" in HM analysis, requiring mandatory standardizations at the international scale, needs to be created that can be applied to soil samples under *in situ* conditions and related to detailed assessments of soil properties throughout depth profiles. The establishment of "timeless" methods (i.e. without need for future modification) may be considered a rewarding aim, but this will always be in conflict with the inevitable progress achieved in method development. Currently, improvements in sample storage and further development of statistical concepts are indispensable. The "flora and fauna perspective" in risk assessment is to be fostered, which demands for the elaboration of bioassays that can be compared and correlated with the outcome of the chemical assays. The development of bioassays using microorganisms and incorporating their interactions in the rhizosphere is of similar importance.

The primary aim is a mechanistic, process-based understanding of HM mobility and availability in soil. A distinction between the major land-use types (i.e. forests, grasslands, agricultural systems) is justified by the often dominating impact that land-use has on soil properties and processes. Such a differentiation must not distract, however, from searching for general underlying principles. In monitoring free metal concentrations, more attention should be given to the role of soil properties and climate influences. In doing so an ecosystem-related perspective can be developed, which highlights HM effects on plants, animals and microorganisms, in particular, those of the "mycorrhizosphere".

The need for developing new methodologies is presently not regarded as critical for monitoring soil contamination, because interpretation may become too complex both for practical use and making policy. Rather, guidelines need to be established first. However, further methodological development remains important in promoting basic research (e.g. in view of the micro-spatial variability in the rhizosphere) and must not be impeded by the scope of legal regulations. Also, methodological progress ensures the option of revising such regulations, if necessary.

Up-scaling of HM fluxes and mass balances across spatio-temporal aggregation levels remains a primary task to be resolved. To this end, procedures need to adhere to the general scaling rules of experimental ecology (EHLERINGER and FIELD 1993; JARVIS 1993; SANDERMANN and MATYSSEK 2004). These rules dictate the degree of attainable spatio-temporal resolution dependent on the aggregation level (BALDOCCHI 1993). Scaling requires data for validation at each level of aggregation, and must exhaust the potential of analytical methodologies in HM risk assessment, including modeling. The potential of remote-sensing techniques, for example, still awaits a thorough evaluation with respect to diagnostics of HM injury to the vegetation. Awareness needs to be raised concerning the "life-span of data" (i.e. the time scale of their validity and representativeness). The importance of up-scaling needs to be balanced versus that of down-scaling (JARVIS 1993) – i.e. the challenge of understanding complexity must be weighted versus the necessity for simplification. Model complexity must be critically evaluated versus the complexity of the system that is to be covered by modelling.

3 Pathway through the cell wall of root tips to aboveground tree parts

"Bottle necks" in HM fluxes from soil to plant are governed by the balance between HM supply (including the role of litter) and uptake. This balance depends on both tree-external factors like the hydraulic resistance of the rhizosphere (which cannot be decoupled from HM mobility), as well as on internal mechanisms like plant-physiological transporters and barriers involved in HM uptake and translocation. More attention should be given to the role of ATPases and Cr/Pb affinities in membranes versus the passive uptake through the cell walls. In particular, the mucilage of the root apex and ectomycorrhizae should be highlighted in mediating HM influx into the tree. Within the root, aquaporins deserve closer examination for their potential involvement in HM uptake. In general, the significance of the symplastic versus apoplastic pathway for HM fluxes within the plant needs to be determined in more detail. The extent needs to be clarified to which the apoplast may serve as a particular sink in HM accumulation (similarly, e.g., as in the case of calcium oxalate in conifers; FINK 1991). It is unclear to which extent trees are able to block or control HM fluxes from the roots to the shoot. Conclusions drawn only from the assessment of HM levels ("HM concentration") in the shoot should be treated with caution. HM levels *per se* can be ambiguous as indicators of the actual HM uptake and partitioning. For example, the harvested biomass (in relation to rooting depth and soil density) needs to be accounted for (MERTENS *et al.* 2005). Reliability can be gained from cross-comparisons between HM level and pool size within the shoot, and the biomass production of the shoot.

To this end, a concept by TIMMER and MORROW (1984), originally introduced for analyzing fertilization effects in trees, may be adopted for unraveling the actual uptake of HMs and their interaction with biomass production (Fig. 2). The analysis is quantitative in relation to the initial status of plants or a control treatment. Figure 2 gives four examples of HM action, and how these are reflected by the relationships between HM pool size, mass-related HM level and biomass development (arrows A, B, C, D). Arrow A denotes HM 'dilution', as an increase in biomass is accompanied by an increased HM pool size but lowered HM level. Arrow B reflects 'balanced HM accumulation', as the HM level stays constant, while both biomass and HM pool size increase. Arrow C mirrors 'hyper-accumulation', as both HM pool size and level increase with an unchanged biomass. Arrow D indicates 'toxicity', as biomass development is retarded under HM stress (increased HM level), while the HM pool size remains unchanged. Using the rationale of Figure 2 for weighting HM uptake versus biomass production requires validation through experimentation. Given such validations, the concept can assess the "physiological significance" of altered HM levels in trees.

The role of xylem/phloem interaction in tree-internal HM translocation and partitioning is another area with many open questions. In particular, the issue on how far HM exclusion from fruits and seeds depends on metal speciation and other factors is of paramount significance for food safety. In this context, bio-engineering may offer interesting perspectives to control metal allocation in crop and medicinal plants, however, such approaches must be thoroughly tested before they can be employed under realistic environmental conditions. Apart from that, the use of such approaches is contingent on public acceptance. Screening for existing genotypes and use of natural genetical resources remains an option that should, in particular, be fostered to unravel physiological traits associated with HM exclusion.

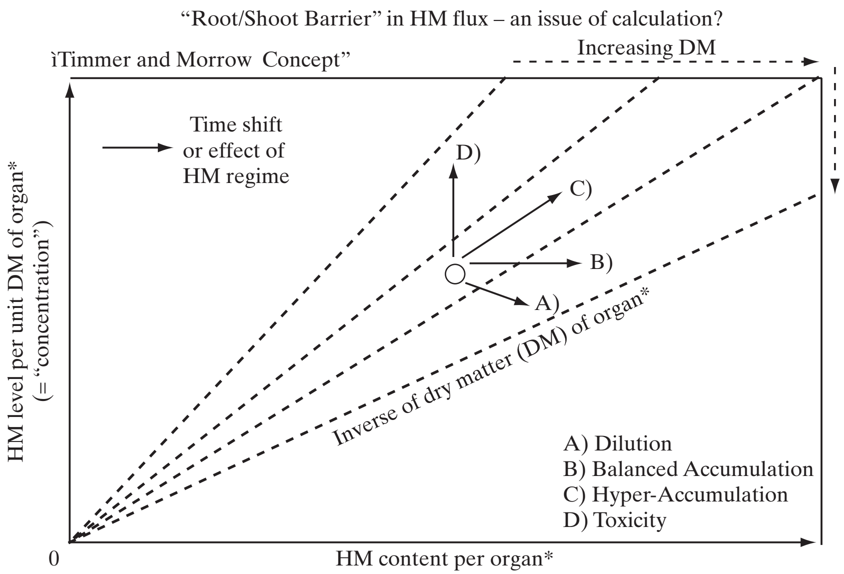

Fig. 2. Comparison between the biomass-related HM level in a plant organ (or the whole plant), the HM pool size within the organ (or whole plant), and the biomass of the organ (or whole plant) under consideration. Diagonals represent the inverse of the biomass, i.e. the slope of the depicted relationship between HM level and HM pool size, that is "DM^{-1}" resulting from the ratio "HM DM^{-1} versus HM" (DM = dry matter = biomass). Concept derived from TIMMER and MORROW (1994) and adapted to evaluate the relation between HM uptake and biomass development. Arrows point into the direction of four main effects starting from an initial stage (or control treatment; denoted by the open circle) to an advanced stage of development (the open circle represents an arbitrary starting point or control scenario). * Or whole plant.

4 From cell to tree, HM defence and evolutionary aspects

Plant reactions to HM stress involve avoidance, detoxification, defense and unspecific stress reactions (FINK 1999). Stress by redox-active HMs develops into toxicity, when mechanisms of HM defence become exhausted. When occurring as chelates (and being redox-inactive), HMs may interfere with metabolic processes and cause secondary effects. HM stress acts at different levels of tree-internal organization (at the cell symplast and apoplast, organ and, perhaps via perturbed resource allocation, the whole-plant level). The extent of HM toxicity in plants is process-dependent, which differs from the HM action in animals. In the foliage, the induction of "reactive oxygen species" (ROS) is crucial upon the uptake of redox-active HMs (DIETZ *et al.* 1999) and can contribute under HM stress to a hypersensitive response – similar to the rapid ("programmed") cell death observed during plant-pathogen interactions or under ozone stress (SANDERMANN 1996; KANGASJÄRVI *et al.* 2005). Accelerated cell senescence in and around the conducting tissues can already occur at moderate Zn and Cd concentrations (VOLLENWEIDER *et al.* 2006; ANDRÉ *et al.* 2006). Specific genes may be incited by HM stress, being aware that responses may differ between acute and chronic HM stress. Irrespective of potential HM specificity in gene response, whole-plant response to oxidative stress (regardless of the agent) at the biochemical and physiological level may obey general principles within the plant's metabolic redox regulation (SANDERMANN 2004). The extent of similarity across responses to different oxidative stressors requires, in mechanistic terms, a thorough experimental validation and represents a rewarding challenge of future research.

HM tolerance depends on the plant's capacity of resource allocation into defence, whereas stress avoidance relies on the exclusion of HMs from uptake and/or on the ability to exclude MHs from metabolically vital processes in tissues and cells. In this latter respect, the role of cell walls and (ecto)-mycorrhizae as buffer against HM stress needs to be further clarified (Session 3). The resource demand of defence is only one component in whole-plant allocation and does internally compete with other metabolic needs, e.g. ensuring reproduction or sustaining competitiveness relative to neighbouring plants (MATYSSEK *et al.* 2005). Trade-offs between metabolic needs and related "opportunity costs" (STITT and SCHULZE 1994) occur while resources are being allocated, also including resource investments into defence against other stressors besides HMs (e.g. "cross-talking", "ecological costs": see HEIL and BALDWIN 2002). A conceptual model for guiding integrated research within a different context (e.g. effects of competition and pathogens under variable light, nutrient and CO_2/O_3 regimes; MATYSSEK *et al.* 2005) is adapted in Figure 3 in view of HM impact on trees.

Whole-tree performance under HM stress can thoroughly be understood only through unravelling the mechanisms that control allocation towards the resource needs for: 1) staying competitive (including reproduction), 2) sustaining defence (against the range of stressors) and 3) serving symbiontic relationships (plant-mycorrhizosphere interactions). These three major demands to be balanced by allocation make up the core of individual plant fitness (MATYSSEK *et al.* 2002, 2005). Such an integrated view is also needed to support research and provide conclusions on the evolutionary implications of HM stress. The concept of Figure 3 illustrates an ecophysiological perspective that may equally be adopted in relation to HM effects on plants.

Short and long-term studies on HM effects need to be conducted in a complementary way to clarify underlying mechanisms (Fig. 3, including primary and secondary stress effects at the molecular level), to assess their ecological significance under actual forest conditions – and to evaluate the consequences for allocation on a seasonal basis or even throughout the entire life span of trees. Whole-plant allometry which can be seen as the 3-dimensional expression of resource allocation may possess diagnostic potential regarding HM impact on trees. Moreover, the analysis of whole-tree allometry allows the distinction of HM-mediated effects on tree ontogeny (retarded growth) from regulatory readjustment in resource allocation at the whole-plant level (employing an approach similar to that demonstrated by KOZOVITS *et al.* 2005 in relation to CO_2/O_3 effects).

In the context of whole-tree resource allocation and allometry, particular emphasis should also be directed to the carbon source strength (photosynthetic performance) and stomatal regulation (water-use efficiency) under HM stress (HERMLE *et al.* 2006), the initiation and flushing of vegetative and reproductive buds as well as the extent and quality of reproduction and fructification. It is remarkable that there are apparently no HM hyperaccumulating tree species, although shrub species (which typically are pioneers) do exist with such traits. It may be worthwhile to explore whether pioneer tree species differ in HM accumulation from climax tree species.

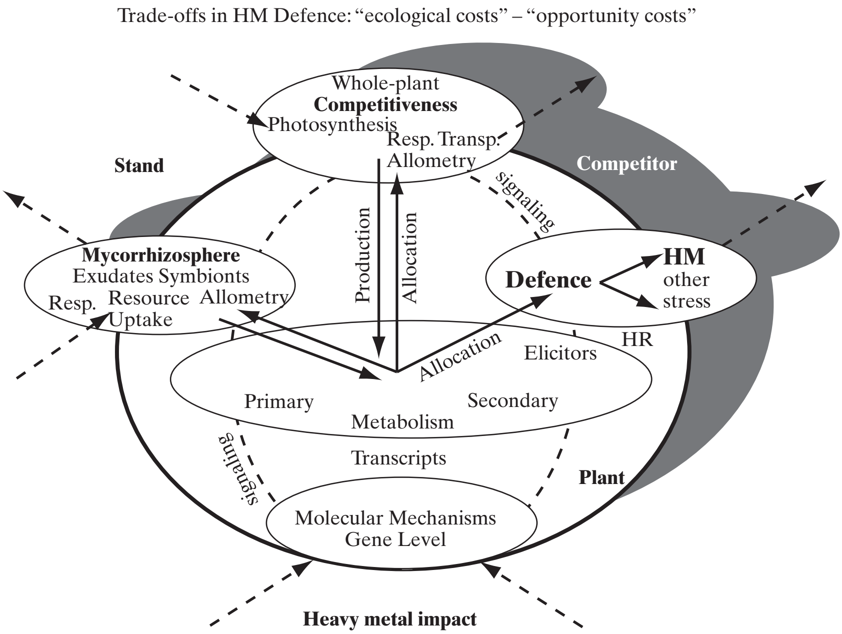

Fig. 3. Conceptual model. Arrows indicate major pathways in resource allocation between physiological demands within the plant and in exchange with the environment, as being under the control of environmental impact and molecular processes (see text for details; adapted from MATYSSEK *et al.* 2005 and SANDERMANN and MATYSSEK 2004).

5 Community consequences of HM contamination

The system level (plant community, ecosystem, landscape, global dimension) was the highest spatio-temporal scale covered by the conference. HMs were recognized as factors of "Global Change" scenarios. Attention needs to be directed to the extent to which changes in temperature and moisture regimes may affect the mobility and bioavailability of HMs in soils. If HM bioavailability is increased, potential constraints on the C sink strength of woody-plant systems may become a major concern in the context of the Kyoto Protocol and post-Kyoto policies. Particular relevancy may result for short-rotation agro-forestry (an important "Clean Development Mechanism" within the Kyoto Protocol), which accelerates resource turnover and, thereby, also promotes the turnover of HMs. Land-use changes that lead to erosion may promote HM release from (contaminated) soils and HM dispersal across ecosystems and the environment in general.

High degrees of "biodiversity" (understanding this term in the sense of an integral across the genetic inventory and the resource fluxes between the genotypes of a system) may favor high HM turnover. In particular, animals promote the mobility of HMs through ecosystem food webs. The challenge is to quantify HM effects on the resource fluxes between the genotypes and to learn about the buffering capacity and resilience of systems, as well as about the consequences for gene pools under HM stress.

Linking HM stress to issues of global concern is expected to boost the attractiveness of HM-related research for funding agencies. Basic research on "Global Change" scenarios, including the impacts of HM pollution, will foster the understanding of evolutionary "strategies" in trees of coping with HM stress (see Session 4). In this context, comparisons of tree performances are apparently useful between sites with naturally high HM levels and sites with anthropogenic HM contamination. Deficits exist in the quantitative understanding of the coupling between cycling of metal and non-metal nutrients and HMs in ecosystems. Such an understanding is important for the management for food webs and food quality, as some trace elements such as Cu and Zn are essential nutrients at low concentrations and are toxic at higher concentrations. In fact, Zn deficiency in human nutrition is a much greater health problem on a global scale than Zn toxicity. The development of methodologies by which such elements can be enriched to a defined degree in crop plants may thus become a viable strategy to deal with HM-contaminated soils. Similarly, phytotechnology has much potential for bio-mining soils and wastes in order to regain metals as raw materials for industrial productions (see comments on phytoremediation below). For some metals this may soon become important, as mineable deposits are increasingly exploited. It is interesting to notice that one third of the world stock in Cu accessible to human use is estimated to be present still in mineable ore deposits, one third to be bound in products, and one third to be dispersed in waste deposits, soils and sediments.

6 Phytoremediation

Phytoremediation represents the practical dimension that is derived from the basic knowledge on the HM action in plants along the spatio-temporal scaling levels (Fig. 1). In particular, the scaling step is of interest here between the plant individuum with its ability of HM accumulation (Fig. 2) and the plant cover with its effectiveness in extracting HMs from soils at the stand level (phytoextraction). One crucial aspect is the expected effectiveness of the chosen plant species, which is determined to a major extent at a given site by biomass production, organ/tissue HM concentration and the proper estimation of the time period of plant growth required. Not only are the climatic and edaphic conditions influential in the plant-based process, but also the time intervals of repeated coppicing of plant individuals and stands. Attention should be directed towards such soil properties that facilitate phytoremediation treatments. An argument in favour of phytoremediation is the fact that soil fertility will be restored and not destroyed as by hard engineering approaches. Finding clean fertile soil that can be used to replace excavated contaminated soil in sites designated for a "green" land-use is becoming more and more difficult. However, one has to be aware that each site is unique in its possibilities, limitations and monetary costs associated with the phytoremediation process.

Plants may not only be used for the extraction of soil-contaminating metals, but also to prevent the uncontrolled migration and dispersal of the contaminants from the site. The prevention of soil erosion through the establishment of a HM-tolerant plant cover is one important function plants can be used for in such a scheme of phytostabilisation. Long time periods required for phytoremediation are usually accepted by populations of HM-contaminated regions, as long as economic restrictions are prevented.

The use of non-food oil crops for biofuel production is another option to make phytoremediation more economic. Concerns about the HM contamination of biofuel and coppiced wood grown on contaminated soil, regarding HM release into the atmosphere upon fuel and wood burning, can easily be dealt with by available air-filtering technology. HM concentrations in biofuels and wood produced on metal-contaminated sites are not higher than in many incinerated wastes. Phytoremediation is also an option to treat wastewater and contaminated groundwater under certain conditions.

There is a clear need for site (e.g. mine, brownfield or former agricultural land), region (economic needs) and climate-dependent guidelines on HM flux management, where phytoremediation and phytostabilization are treatment options. Using models should be fostered as a basis of decision-making with respect to the evaluation of technologies for the treatment of HM-contaminated sites. A major problem of phytoextraction is the long period of time usually required with the current state of the technology for reaching the remediation goal, as well as the large degree of uncertainty in the estimation of these time spans. Clearly, further research is needed on the time scales required for the effective use of phytoremediation capacities. The availability of remediation techniques must not be used, however, as an excuse to reduce efforts to minimize HM emissions.

7 Conclusions and research needs

Although considerable knowledge exists about HM impacts on trees and induced stress responses, information deficits prevail about the mechanistic understanding of HM effects in trees and ecosystems. Major research needs are a more detailed and precise analysis and quantification of HM fluxes and mass balances at the soil, whole-plant and system level (stand, ecosystem, landscape, regional and global scale). The interaction of HM fluxes with the resource fluxes intrinsic to biodiversity requires particular attention in this context. One focal point is the interface between plants and the mycorrhizosphere, as the soil-to-plant passage of HMs is critical for food webs and groundwater quality, as well as for the effectiveness of phytoremediation and the application of evolutionary principles to the breeding of remediation plants.

Spatio-temporal scaling concepts are required that can guide mechanistic research towards a holistic understanding of HM effects, as indicated in the programme structure of the conference and the synopsis presented here. Consistencies need to be evaluated across neighbouring scaling levels (BALDOCCHI 1993) through experimental validation and modelling, applying up- and down-scaling approaches in a complementary way (JARVIS 1993). Although the monetary budget often dictates a preference for modelling, it must not be overlooked that the latter cannot replace experimental databases (for model development, parameterisation and validation). New methodologies need to be elaborated, in particular for data assessment at highly aggregated spatial and long-term scales. In scaling, also the relation between heavy metal bioavailability and life quality issues should be taken into consideration (e.g. environmental quality, food safety). This requires a holistic multidisciplinary view including biology, ecology, environmental chemistry and physics as well as medicine. HM contamination must be considered an important factor in "Global Change" scenarios, not only with respect to the Kyoto Protocol and post-Kyoto policies, but also in view of the coupled biogeochemical cycling of metal and non-metal nutrients and HMs, and their links with the global water and carbon cycles. Only a sound mechanistic understanding of HM fluxes can provide a scientifically reliable basis for legislation, risk assessment and decision-making relating to HM pollution of the environment.

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8 References

André, O.; Vollenweider, P.; Günthardt-Goerg, M.S, 2006: Foliage response to heavy metal contamination in Sycamore Maple (*Acer pseudoplatanus* L.). For. Snow Landsc. Res. (submitted).

Baldocchi, D.D., 1993: Scaling water vapor and carbon dioxide exchange from leaves to a canopy: Rules and tools. In: Ehleringer, J.R.; Field, C.B. (eds) Scaling Physiological Processes, Leaf to Globe. San Diego, Academic Press. 77–114.

Dietz, K.-J.; Baier, M.; Krämer, U., 1999: Free Radicals and reactive oxygen species as mediators of heavy metal toxicity in plants. In: Prasad, M.N.V.; Hagemeyer, J. (eds) Heavy metal stress in plants. Berlin, Springer. 73–97.

Ehleringer, J.R.; Field, C.B., 1993: Scaling Physiological Processes, Leaf to Globe. San Diego, Academic Press. 388 pp.

Fink, S., 1991: Unusual patterns in the distribution of calcium oxalate in spruce needles and their possible relationships to the impact of pollutants. New Phytol. 119: 41–51.

Fink, S., 1999: Pathological and regenerative plant anatomy. Encyclopedia of plant anatomy Vol. XIV/6. Berlin, Stuttgart, Gebrüder Bornträger. 1095 pp.

Heil, M.; Baldwin, I.T., 2002: Fitness costs of induced resistance: emerging experimental support for a slippery concept. Trends Plant Sci. 7: 61–67.

Hermle, S.; Günthardt-Goerg, M.S.; Schulin, R., 2006: Effects of metal-contaminated soil on the performance of young trees growing in model ecosystems under field conditions. Environ. Pollut. 144, 2: 703–714.

Jarvis, P.G., 1993: Prospects of bottom-up models. In: Ehleringer J.R.; Field C.B. (eds) Scaling physiological processes, Leaf to Globe. San Diego, Academic Press. 117–126.

Kangasjärvi, J.; Jaspers, P.; Kollist, H., 2005: Signalling and cell death in ozone-exposed plants. Plant Cell Environ. 28: 1021–1036.

Kozovits, A.R.; Matyssek, R.; Blaschke, H.; Göttlein, A.; Grams, T.E.E., 2005: Competition increasingly dominates the responsiveness of juvenile beech and spruce to elevated CO_2 and/or O_3 concentrations throughout two subsequent growing seasons. Glob. Chang. Biol. 11: 1387–1401.

Matyssek, R.; Schnyder, H.; Elstner, E.-F.; Munch, J.-C.; Pretzsch, H.; Sandermann, H., 2002: Growth and parasite defence in plants: the balance between resource sequestration and retention. Plant Biol. 4: 133–136.

Matyssek, R.; Agerer, R.; Ernst, D.; Munch, J.-C.; Osswald, W.; Pretzsch, H.; Priesack, E.; Schnyder, H.; Treutter, D., 2005: The plant's capacity in regulating resource demand. Plant Biol. 7: 560–580.

Mertens, J.; Luyssaert, S.; Verheyen, K., 2005: Use and abuse of trace metal concentrations in plant tissue for biomonitoring and phytoextraction. Environ. Pollut. 138: 1–4.

Sandermann, H. Jr., 1996: Ozone and plant health. Annu. Rev. Phytopathol. 34: 347–366.

Sandermann, H. Jr., 2004: Molecular ecotoxicology of plants. Trends Plant Sci. 9: 406–413.

Sandermann, H.; Matyssek, R., 2004: Scaling up from molecular to ecological processes. In: Sandermann, H. (ed) Molecular Ecotoxicology of Plants. Ecol. Stud. 170: 207–226.

Stitt, M.; Schulze, E.-D., 1994: Plant growth, storage and resource allocation: from flux control in metabolic chain to the whole-plant level. In: Schulze, E.-D. (ed) Flux control in biological systems: from enzymes to populations and ecosystems. San Diego, Academic Press. 57–118.

Swiss Federal Institute for Forest, Snow and Landscape Research WSL (ed) 2005: Metal fluxes and stresses in terrestrial ecosystems. Abstracts. Birmensdorf, Swiss Federal Research Institute WSL. 112 pp.

Timmer, V.R.; Morrow, L.D., 1984: Predicting fertilizer growth response and nutrient status of jack pine by foliar diagnosis. In: Stone, E.L. (ed) Forest Soils and Treatment Impacts: Sixth North American Forest Soil Conference. Knoxville, USA, University of Tennessee. 335–351.

Vollenweider, P.; Cosio, C.; Günthardt-Goerg, M.S.; Keller, K., 2006: Localization and effects of phyto-extracted cadmium in leaves of tolerant willows (*Salix viminalis* L.) II. Microlocalisation and cellular effects of cadmium. Environ. Exp. Bot. 58: 25–40.

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