“BABEȘ-BOLYAI” UNIVERSITY
FACULTY OF BIOLOGY AND GEOLOGY
DOCTORAL SCHOOL OF INTEGRATIVE BIOLOGY

DOCTORAL THESIS

Summary

Scientific Supervisor:
Prof. Dr. Manuela BANCIU

PhD Student:
Dana Emanuela TIODAR
(married LUSHNYKOV)

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Understanding the Long-Term Effects of Mercury Contaminated Soils on the Diversity of Plants and Rhizosphere-Associated Microbiota

Scientific Supervisor:
Prof. Dr. Manuela BANCIU

PhD Student:
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Key words:

mercury, contamination, phytoremediation, microorganism-assisted phytoremediation, *Lotus tenuis*, *Diplotaxis muralis*, *Pseudomonas*, *Mesorhizobium*, *Streptomyces*

Summary:

Chapter I: General Introduction

Mercury (Hg) is a highly toxic heavy metal and a persistent environmental pollutant. It ranks 3rd on the ATSDR Substance Priority List due to its bioaccumulation and biomagnification properties (ATSDR, 2022). It is estimated that over 3000 sites globally are contaminated with Hg as a result of various industrial activities (Kocman et al., 2013). Moreover, Hg is toxic to plant life, disrupting cellular metabolism by binding to thiol groups in proteins, displacing essential cations in macromolecules like chlorophyll, and generating excessive amounts of reactive oxygen species (Natasha et al., 2020; Safari et al., 2019). However, several plant species have exhibited tolerance to Hg-contaminated soils that hinder growth for non-tolerant plants. Plant defense strategies include Hg immobilization by root exudates in the rhizosphere, limiting Hg uptake, root sequestration, restricting translocation to shoots, and chelating the mercuric ion using glutathione-based macromolecules, phytochelatines, which facilitate vacuole sequestration via ABC tonoplast transporters (Sun et al., 2021; Montiel-Rozas et al., 2016; Carrasco-Gil et al., 2013; J. Park et al., 2012). Plants employing these mechanisms form the basis of nature-based solutions of restoring contaminated sites.

This approach, known as phytoremediation, leverages tolerant plants to restore contaminated sites while preserving soil integrity and fertility, offering a cost-effective, eco-friendly alternative to engineering-based decontamination methods (Mench et al., 2009). Phytoremediation strategies vary based on plant capabilities: phytoextraction relies on metal-accumulating plants to uptake and translocate Hg to harvestable shoots, phytostabilization limits metal bioavailability by chelation, root immobilization and reduced translocation, and phytovolatilization enables plants to convert Hg^{2+} into volatile Hg^0 which is released into the atmosphere (Tiodar et al., 2021; Tangahu et al., 2011). The search for an efficient Hg (hyper)accumulator plant—one that translocates the highest amount of the absorbed Hg to shoots while sustaining high, stable biomass—remains ongoing. Investigating native vegetation in Hg-contaminated sites offers crucial insights into potential phytoremediation candidates, making studies that screen for Hg-accumulating species highly valuable.

Plant growth in soil is supported by soil nutrients and by the rhizosphere microbiota, which exchanges water and nutrients with the plant (Park et al., 2022; Rozmoš et al., 2022; Lehmann et al., 2020; Saccá et al., 2017). Many microorganisms are resilient to long-term Hg stress and have evolved mechanisms to resist and mitigate its toxic effects, thus aiding in soil decontamination (González et al., 2022; Chang et al., 2020; Agarwal et al., 2019). Common microbial metal resistance mechanisms include biosorption and intracellular chelation (Alcántara et al., 2017; Say et al., 2003), while fungi may also use Se-based Hg binding and vacuolar sequestration (Kavčič et al., 2019; Gueldry et al., 2003). A key bacterial resistance mechanism is encoded in the *mer* operon, which includes the *merA* gene coding for mercuric reductase (MerA), the enzyme needed for the reduction of Hg^{2+} to less toxic Hg^0 (Mathema, et al., 2011; Barkay et al., 1992). Fungi, often more resilient than bacteria, may employ Hg volatilization, although the exact pathways are not fully understood (Chang et al., 2020; Pietro-Souza et al., 2020), with some transcriptomic studies linking Hg volatilization to *merA* homologs and antioxidant responses (Chang et al., 2021). Microorganisms thus play a pivotal role in enhancing plant growth and detoxifying Hg in contaminated soils.

Therefore, phytoremediation can be further enhanced through the use of microorganisms, especially when inoculation with compatible bioremediation species is performed in soils lacking natural microbial partners (Szada-Borzyszkowska et al., 2024). Although limited, some studies have shown success with microorganism-assisted phytoremediation under controlled conditions, particularly in pot experiments with inoculated plants (Sommer et al., 2025; Szada-Borzyszkowska et al., 2024; Guo et al., 2023; Putra et al., 2022; González-Chávez et al., 2019; Phanthavongsa et al., 2017). Phytoremediation trials for soil Hg decontamination have not yet been conducted in the field. However, insights into its potential effectiveness can be drawn from similar trials focused on the remediation of other heavy metals. For example, a mycorrhizal enhanced phytostabilization trial using poplar significantly reduced foliar Cu, Pb, Zn, and Cr concentrations when cultivated on a 1 ha field contaminated with 98 mg Cu kg^{-1}, 392 mg Pb kg^{-1}, 2067 mg Zn kg^{-1}, and 170 mg Cr kg^{-1} after a year and a half since the inoculation (Phanthavongsa et al., 2017). Similarly, a phytoextraction trial using the As hyperaccumulator, *Pteris vittata*, demonstrated enhanced shoot accumulation of As^{5+} following inoculation with a strain of *Pseudomonas vancouverensis* (Yang et al., 2020). Over 5 months in a field contaminated with 11 mg As kg^{-1}, the maximum shoot As concentration reached 19.56 mg kg^{-1}, likely due to the bacterial oxidation of As^{3+} into the more bioavailable As^{5+} form (Yang et al., 2020).

In conclusion, further research is essential to optimize microorganism-assisted phytoremediation for efficient soil decontamination. It is crucial to identify, characterize, and test additional Hg-tolerant plants and microbial partners to improve the effectiveness of this nature-based remediation approach.

Aim of the thesis

This thesis aims to identify plant-microorganism partnerships that can form a stable holobiont system for use in future attempts at remediating Hg-contaminated soils through microorganism-assisted phytoremediation. By studying the environmental conditions at a local contaminated site, this research seeks to understand the underlying plant behaviors influencing plant species distribution at the site and the extent of the stress that shaped adapted microbial communities in the field. This study focuses on assessing the impact of Hg contamination, identifying tolerant plant species, and analyzing the associated microbial communities of the most promising plants to deliver a blueprint for an effective in situ phytoremediation strategy.

To achieve this, three main objectives were defined:

(1) to assess the levels of Hg and other potentially toxic trace elements at the investigated historically contaminated site;

(2) to identify Hg-tolerant plant pioneers by conducting a plant populations distribution survey, determining their accumulation patterns, and linking their inherent traits to potential phytoremediation strategies such as phytostabilization or phytoextraction;

(3) to characterize the rhizosphere soil bacterial and fungal communities associated with the most promising plant species, particularly the legume *Lotus tenuis*, to determine key microbial taxa involved in Hg tolerance.

This research ultimately aims to inform the development of tailored microbial consortia to enhance phytoremediation efforts.

Chapter II: Plant Colonizers of a Mercury Contaminated Site: Trace Metals and Associated Rhizosphere Bacteria

A trace metal assessment was conducted at an Hg-contaminated site in Romania, revealing elevated levels of Hg, Pb, Cu, Zn, and Mn. Mercury posed the greatest environmental concern, with a median topsoil concentration of 962 mg kg^{-1} — exceeding the national intervention threshold by two orders of magnitude. The site's industrial legacy and background contamination constrained plant biodiversity, as a plant species survey identified low vegetation coverage dominated by herbs (*Diplotaxis muralis* and *Lotus tenuis*) and grasses (*Calamagrostis epigejos*).

Portable X-ray fluorescence spectroscopy confirmed substantial metal accumulation in plant tissues, particularly in roots. Redundancy analysis linked *L. tenuis* and *D. muralis* to Hg soil concentrations, highlighting their adaptability to extreme contamination. *Lotus tenuis* exhibited the highest Hg accumulation, with 10,869 mg kg^{-1} dry weight in roots and 1,070 mg kg^{-1} in shoots, followed by *D. muralis* (6,049 mg kg^{-1} in roots, 1,204 mg kg^{-1} in shoots). Given their accumulation patterns, both species can serve as bioindicators of Hg pollution. Moreover, their abundance and ability to establish on highly contaminated substrates suggest strong potential for phytostabilization in Hg-polluted brownfields.

To further characterize plant-microbe interactions, the rhizosphere prokaryotic communities associated with *D. muralis* were analyzed through rRNA amplicon sequencing and functional inference via PICRUSt2. *Pseudomonadota*, *Actinomycetota*, and *Acidobacteriota* were the most abundant phyla. Despite increasing Hg concentrations, bacterial alpha diversity remained stable, likely due to the widespread presence of the *merA* gene in 83% of the communities as was revealed by endpoint PCR on the total soil DNA samples. Notably, *merA*-positive communities exhibited an elevated abundance of inferred ABC transporters, suggesting additional metal resistance mechanisms. *Actinomycetota* was particularly enriched, displaying a 12-fold higher mean relative abundance in *merA*-positive communities compared to the community without *merA*.

Overall, rhizosphere trace metal concentrations accounted for 35% of the variance in plant distribution and metal accumulation patterns. The highest colonization and Hg immobilization potential was observed in *D. muralis* and *L. tenuis*, underscoring their suitability for phytoremediation strategies. Further identification of key bacterial taxa is needed to optimize microorganism-assisted remediation approaches.

Chapter III: Impact of Long-Term Mercury Contamination on the Rhizosphere Microbiota of *Lotus tenuis*: A Pathway to Resilience via Interkingdom Facilitation

Long-term Hg contamination exerts selective pressure on rhizosphere soil microbial communities, yet their compositional shifts and resilience mechanisms remain poorly understood. According to the stress gradient hypothesis, competitive interactions decline in favor of facilitative interactions as environmental stress intensifies. This study investigated bacterial and fungal communities associated with *Lotus tenuis* rhizosphere and bulk soils along an Hg contamination gradient (40–1,964 mg kg^{-1}) and compared them to control communities from an uncontaminated site to assess microbial responses to Hg stress.

High-throughput 16S rRNA amplicon sequencing revealed distinct community structures between contaminated and control soils. However, alpha diversity remained stable along the Hg gradient, suggesting microbial adaptation and stress resilience. *Mesorhizobium*, the nodulating symbiont of *L. tenuis*, was abundant across all conditions, while *Pseudomonas* was four times more prevalent in contaminated soils and twice as abundant in rhizosphere soils compared to bulk, indicating its Hg resistance and potential role as a non-rhizobial facilitator of nodulation. Functional screening of soil DNA for the *merA* gene revealed its absence in control soils but presence in 85% of Hg-contaminated rhizosphere samples, signifying bacterial adaptation through active detoxification. Fungal community shifts also reflected Hg stress adaptation. *Glomerales*, a key mycorrhizal order, exhibited a threefold increase in Hg-contaminated rhizosphere soils, underscoring its role in plant water and nutrient acquisition under extreme conditions.

Differential abundance analysis, using the ANCOM-BC2 algorithm, identified several bacterial taxa enriched in Hg-contaminated rhizosphere soils, including *Streptomyces*, a biocontrol agent with potential plant-growth promoting properties, *Allorhizobium-Neorhizobium-Pararhizobium-Rhizobium* and *Shinella*, two rhizobial plant-growth promoters, as well as *Nocardioides* and *Skermanella*, which may confer metal and aridity resistance, respectively. Among fungal taxa more abundant in Hg-contaminated rhizosphere soils were dark septate endophytes (*Darksidea* and *Acrocalymma paeoniae*), potentially enhancing plant stress tolerance, plant growth-promoting fungi (*Mortierella alpina* and *Chaetosphaeronema*), as well as pathogenic (*Aspergillus terreus* and *A. flavus*) and pathogen-suppressing (*Humicola* and

Vishniacozyma) species. Additionally, *Septoglomus*, *Dioszegia*, and *Articulospora* were associated with plants exhibiting the highest Hg shoot accumulation, highlighting potential fungal contributors to Hg uptake and tolerance.

These findings deepen our understanding of rhizosphere microbial resilience under chronic Hg exposure and provide potential microbial candidates for microorganism-assisted phytoremediation strategies.

Chapter IV: General conclusions and originality of the results

IV.1. Conclusions

Globally, soil degradation is an escalating issue driven by unsustainable industrial and agricultural practices, leading to biodiversity loss and increased risks to food security, water quality, and climate regulation. Among soil pollutants, mercury is particularly hazardous due to its persistence, toxicity, and biomagnification potential, necessitating urgent remediation strategies. Phytoremediation, which utilizes plants to stabilize and detoxify contaminants, represents a promising approach, particularly when combined with Hg-resistant rhizosphere microbiota that enhance plant survival and metal sequestration.

This thesis aimed to identify effective phytoremediation strategies for an Hg-contaminated site by following three main objectives: (1) assessing soil pollution levels, (2) identifying Hg-tolerant plant species, (3) and characterizing their associated microbial communities.

The site assessment revealed Hg as the primary contaminant, with rhizosphere soil concentrations exceeding national safety thresholds by two orders of magnitude. Vegetation at the site was sparse, yet *Diplotaxis muralis* and *Lotus tenuis* emerged as key species, with *L. tenuis* accumulating the highest Hg concentrations in both roots (10,869 mg kg^{-1} DW) and shoots (1,070 mg kg^{-1} DW). Microbial community analysis of *D. muralis* rhizosphere indicated stable alpha diversity across the Hg gradient, likely due to the widespread presence of the *merA* gene, suggesting long-term microbial adaptation. Dominant bacterial phyla included *Pseudomonadota*, *Actinomycetota*, and *Acidobacteriota*, with *L. tenuis* and *D. muralis* showing strong phytostabilization potential by immobilizing Hg at the root level (**Chapter II**).

Further investigation into the *L. tenuis* rhizosphere revealed microbial community shifts in response to Hg exposure compared to non-contaminated control soils. The species' ability to establish nitrogen-fixing symbioses positioned it as a valuable pioneer plant in Hg-polluted environments. Despite the Hg gradient (40–1976 mg kg^{-1}), alpha diversity remained stable, supporting the hypothesis that long-term contamination selects for a resilient microbial community. Consistent with the stress-gradient hypothesis, microbial interactions likely transitioned toward mutual facilitation, favoring species diversity and functional stability. Differential abundance analysis identified key potentially Hg-resistant bacteria enriched in the Hg-contaminated rhizosphere soil (*Streptomyces*, *Allorhizobium-Neorhizobium-Pararhizobium-Rhizobium* sp., *Shinella* sp., *Nocardioides*) and fungi (*Darksidea* sp., *Mortierella alpine*, *Vishniacozyma* sp.), which could contribute to plant health and stress mitigation in Hg-contaminated environments (**Chapter III**).

This research underscores the combined role of plant tolerance and rhizosphere microbial resilience in Hg-contaminated soils, forming a foundation for microorganism-assisted phytoremediation strategies. The identification of functionally valuable microbial taxa associated with Hg-tolerant plants provides a critical resource for future remediation efforts. These findings highlight the potential for developing bioaugmentation approaches using locally adapted microbes to enhance native plant establishment and metal stabilization, paving the way for more effective phytoremediation applications in Hg-contaminated sites.

IV.2. Originality

This thesis presents novel contributions to the field of phytoremediation by identifying promising Hg-tolerant plant species and plant-associated microorganisms. It is the first comprehensive characterization of the flora and rhizosphere microbial communities associated with the most promising native plant species at the Hg-contaminated site of the former Turda Chemical Plant in Romania, providing a taxonomic profile of bacterial and fungal communities associated with two plant species.

Notably, *Diplotaxis muralis* and *Lotus tenuis* were identified as pioneer, autochthonous, Hg-tolerant species with strong phytostabilization potential, thriving on heavily contaminated soils and accumulating significant Hg levels in their roots. The rhizosphere microbiota of both plants exhibited adaptive resistance mechanisms, suggesting a role in mitigating Hg contamination through microbial detoxification pathways.

This research also highlights the complexity of microbial inter-kingdom interactions that facilitate plant survival in Hg-contaminated environments. The study examined microbial resilience across a broad Hg concentration gradient, revealing key Hg-responsive taxa that likely contribute to long-term ecosystem stability. Unlike previous studies, which often focused on narrower contamination gradients and fewer samples, this research provides a large-scale perspective on microbial adaptation. Furthermore, specific bacterial and fungal taxa, identified at the genus and species levels, were linked to extreme Hg contamination, offering a valuable foundation for developing optimized microbial consortia for microorganism-assisted phytoremediation.

Overall, this thesis delivers applicable insights into in situ remediation strategies by proposing a plant-microbe holobiont approach, integrating Hg-tolerant plant species with functionally beneficial bacterial and fungal partners for enhanced phytoremediation efficiency.

IV.3. Perspectives

This thesis establishes a foundation for future research on *D. muralis*- and *L. tenuis*-centered Hg phytoremediation trials. Greenhouse experiments should assess the plants' tolerance to a range of Hg soil concentrations using either contaminated field soil or Hg-spiked substrates. Additionally, soil inoculation trials should evaluate the bioremediation potential of key bacterial and fungal taxa, both individually and in consortia, to formulate the most effective microorganism-assisted phytoremediation strategy. Field trials at the Hg-contaminated site will be necessary to quantify phytostabilization efficiency by measuring Hg immobilization in roots and bioaccumulation potential.

Further investigations should focus on isolating and characterizing the identified microorganisms to confirm their plant growth-promoting properties and Hg resistance in vitro. Genomic and transcriptomic analyses of highly tolerant strains could reveal cellular mechanisms underlying microbial adaptation to Hg stress. Alternatively, metagenomics and metatranscriptomics could be applied to field samples to uncover functional pathways used by microbial communities in response to chronic Hg contamination.

On a fundamental level, understanding plant Hg uptake and tolerance mechanisms is crucial, as key genetic determinants regulating Hg accumulation in plant tissues remain unknown. Identifying these molecular pathways could pave the way for genetic engineering approaches to enhance Hg accumulation in potential (hyper)accumulator species or develop safer crops for cultivation in Hg-contaminated soils.

In conclusion, this research provides a launching point for two major research avenues: fundamental studies exploring plant and microbial Hg tolerance mechanisms and applied research advancing Hg soil remediation strategies using plant-microbe interactions.

Disemination of the Results

List of publications included as chapters

Chapter I

Tiodar[†], E. D., Văcar[†], C. L., & Podar, D. (2021). Phytoremediation and microorganisms-assisted phytoremediation of mercury-contaminated soils: challenges and perspectives. *International Journal of Environmental Research and Public Health*, *18*(5), 2435. https://doi.org/10.3390/ijerph18052435, **IF** 4.614 (2021).

(†)These authors share equal contribution.

Chapter II

Tiodar, E. D., Chiriac, C. M., Pošćić, F., Văcar, C. L., Balázs, Z. R., Coman, C., Weindorf, D. C., Banciu, M., Krämer, U., Podar, D. (2024). Plant colonizers of a mercury contaminated site: trace metals and associated rhizosphere bacteria. *Plant and Soil*, 502(1), 373–396. https://doi.org/10.1007/s11104-024-06552-7, **IF** 4.9 (2022).

Chapter III

Tiodar, E. D., Văcar, C. L., Grimm, M. C., Ganea, I. V., Balázs, Z. R., Abrudan, A. M., Timár, C., Tanțău, I., Banciu, M., Angel, R., Podar, D. (2025). Impact of Long-Term Mercury Contamination on the Rhizosphere Microbiota of *Lotus tenuis*: A Pathway to Resilience via Interkingdom Facilitation. *bioRxiv*. https://doi.org/10.1101/2025.04.07.647525

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