

EXPLORATORY STUDIES ON MYCOBIOTA AROUND THE ROOTS OF INVASIVE PLANTS - CASE STUDY *Ailanthus altissima*

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Abstract

It is known that specific and common fungal species can synthesize hydrolytic enzymes (amylases, proteases, cellulases, lipases, pectinases, xylanases) and organic acids, thus causing changes in soil pH and reducing the rate of decomposition processes in the soil. Ailanthus altissima is an aggressive invasive tree in Romania. We aim to analyse if fungal communities from soil are altered by the presence of A. altissima; thus we conducted a field soil sampling in micro-habitats with different Ailanthus individuals' density and age. Mycological analysis assessed the fungal load of the samples and the species with the highest frequency. In the field, we also measured the Ailanthus tree DBH in all stands, recording trees' life stages, and their connection with the mycobiota's species diversity. Results showed mycobiota's biodiversity and its capacity to synthesize metabolites involved in soil decomposition. Analysis of the mycobiota around the roots of adults and root sprouts of A. altissima showed that the composition of the soil fungal community and the fungal activity require a longer invasion time to be affected.

Key words: *Ailanthus altissima*, around the roots, hydrolytic enzymes, soil mycobiota.

INTRODUCTION

Fungi are among the most biologically active and diverse groups of soil microorganisms. They play a crucial role in the decomposition of organic matter and the cycling of nutrients, thus are fundamental to ecosystem processes and plant growth, contributing to improved nutrient uptake and greater soil stability (Berendsen et al., 2012; Singh et al., 2025). Many fungal species - both specific (specialized) and common (ubiquitous) - secrete a variety of extracellular hydrolytic enzymes that break down complex organic molecules into simpler compounds for absorption such as: amylases (hydrolyze starch into simple sugars like glucose and maltose), proteases (degrade proteins into peptides and amino acids), cellulases (break down cellulose, a major structural polysaccharide in plant cell walls, into glucose units), lipases (catalyze the breakdown of fats and lipids into glycerol and fatty acids), pectinases (decompose pectin, a structural polysaccharide found in plant cell walls), and xylanases (degrade xylan, a hemicellulose component of plant biomass) (Dix & Webster,

1995; Gomoiu, 2009; Baldrian, 2014; De Beeck et al., 2021; Zuccarini et al., 2023).

These biochemical products are key to the fungi's ecological role, but they also influence the soil's physicochemical properties, including pH alterations and decomposition rates (Ritz & Young, 2004).

Through these enzymatic activities, fungi facilitate the initial stages of organic matter decomposition, initiating the release of nutrients essential for plant growth and microbial metabolism (Skujiniš & Burns, 1976; Idris, 2026).

In addition to hydrolytic enzymes, many fungal species also produce organic acids such as oxalic, citric, gluconic, and malic acids. These acids: lower the soil pH by releasing protons (H⁺) during metabolic reactions, solubilize metal cations (e.g., Ca²⁺, Mg²⁺, Fe³⁺) and nutrients bound in mineral lattices, making them more bioavailable, aid in the weathering of minerals and chelating of heavy metals, altering soil chemistry. However, the acidification of soil caused by fungal metabolism can also influence microbial community structure and overall soil biochemical balance (Liaud et al., 2014).

Plant invasion can influence litter decomposition, a key process in terrestrial nutrient cycling, through changes in fungal communities associated with both litter type and soil conditioning. Reduced fungal richness in soils conditioned by invasive plants alters decomposition dynamics, leading to differential breakdown of native and invasive litter. By modifying litter traits and reshaping soil fungal communities, invasive plants drive changes in decomposition processes, underscoring the need to consider litter inputs and soil fungi simultaneously when evaluating the impacts of plant invasion on ecosystem functioning (He et al., 2025).

Invasive plants frequently modify soil properties, producing legacy effects that alter soil conditions and, consequently, influence competition among native plant species. Fungal interactions enhance invasive plant success by improving nutrient acquisition, reducing pathogen pressure, and altering soil microbial communities to the disadvantage of native plants (Castro-Díez et al., 2019; Sun et al., 2026).

The development and architecture of plant root systems play a crucial role in shaping the diversity and composition of soil fungal communities, particularly those inhabiting the rhizosphere (the soil zone influenced by roots) (Peng et al., 2025; Martins et al., 2026).

Ailanthus altissima, one of the most widespread invasive non-native species globally, thrives in temperate climates across various habitats, including urban areas, agricultural lands, semi-natural ecosystems, and wetlands (Fotiadis et al., 2011; Lazzaro et al., 2020; Liu et al., 2023; Marzioletti et al., 2025). Its invasion causes drastic changes in community composition, significantly reducing plant richness and diversity (Terzi et al., 2021).

The aggressive growth of *A. altissima* affects the regeneration of native species by altering nutrient cycling and producing toxic compounds (Lawrence et al., 1991; Brooks et al., 2021; Motti et al., 2021). A major advantage for *A. altissima* is its symbiotic relationship with arbuscular mycorrhizal fungi (AMF), which may be driven by resource availability (Badalamenti et al., 2015; 2018).

In contrast, *Ailanthus* negatively impacts seedling growth and ectomycorrhizal (ECM) fungal colonization of *Quercus rubra* (red oak), causing reduced root-to-shoot ratios, possibly

due to stress or inhibited root development induced by *Ailanthus* invasion (Bauman et al., 2013). This allelopathic effect may disrupt the beneficial symbiosis between red oak and ECM fungi.

Although invasive *A. altissima* and *Robinia pseudoacacia* co-occur and share similar growth and reproductive traits, they fulfill distinct ecological functions - *Ailanthus* exhibits allelopathy, while *Robinia* contributes to nitrogen fixation (Call & Nilsen, 2005; Gavrilidis et al., 2023; Miles et al., 2025).

A. altissima produces the allelochemical ailanthone in its roots and bark, which helps it outcompete other plants. Additionally, this compound acts as an anti-herbivore agent, deterring insects from feeding on its leaves (Sasnow, 2014).

Castellano and Gorchov (2012) reported that *Ailanthus altissima* selects for ectomycorrhizal (ECM) fungi that can tolerate allelopathic compounds present in the soil. The observed decrease in ECM root colonization may be a response to reduced carbon allocation to roots by the plant (Bauman et al., 2012).

Removal of *A. altissima* can lead to increased organic matter, soil moisture, and litter accumulation, which may facilitate the succession of ECM fungi and their host plants, thereby promoting long-term ecosystem restoration.

The high content of phenolic compounds in *Ailanthus* leaves, which possess antioxidant and antimicrobial properties, may explain the observed low fungal diversity in invaded soils (Cocîrlea et al., 2024 a, b; Zhao et al., 2005).

From a fungal perspective, some species show potential as biological control agents against *Ailanthus*. The fungus *Verticillium nonalfalfae* is a strong candidate due to its high host specificity, ability to infect new *Ailanthus* individuals through soil or connected roots, and long-term survivability in soil (Miles et al., 2025; Soler & Izquierdo, 2024; Hrabovský & Hladík, 2024). Additionally, Ding et al. (2006) demonstrated that *Fusarium oxysporum* f. sp. *perniciosum* causes wilt in *Ailanthus* in North America, indicating its potential as a control agent.

Small et al. (2010) described the allelopathic effects of *A. altissima* on tree and crop species, showing that these effects reduce crop yields not

only through plant-derived allelopathy but also by altering the biodiversity of soil microorganisms.

Sasnow (2014) emphasized the importance of microbiota - the community of microorganisms associated with plant rhizospheres and roots - in influencing plant health (Poli et al., 2016). This microbial community is shaped by both plant species and soil type. Specific members of the microbiota are either stimulated or suppressed by chemical exudates released into the rhizosphere, the soil region surrounding the roots (Berendsen et al., 2012).

This study aims to characterize the cultivable fungal community (mycobiota) associated with *Ailanthus altissima* and to elucidate the role of these fungi in soil organic matter decomposition through their production of hydrolytic enzymes. Specifically, we intend to compare the hydrolytic enzyme activities of fungal isolates obtained from the rhizosphere and root zones of *A. altissima* individuals at different developmental stages.

MATERIALS AND METHODS

Sample collection - field work

In December 2025, we developed a field trip in *Ailanthus altissima* dense stand outside

Bucharest (Bragadiru area) where the urban constant impact (air pollution, direct human impact, etc.) is lower and *A. altissima* individuals are in different age stages, meaning with different development of above-ground biomass and of the root system (rhizosphere = below-ground biomass) (Figures 1 and 2).

The soil is a mixture of different types of soils discharged here following the construction of the neighboring houses.

For characterizing the tree's age stage, we measured with a tape: the height and DBH (diameter at the breast level) for mature trees and 20 cm above ground level for low height and young stems.

Based on the idea that root system (architecture) development has a strong influence on fungal diversity (Peng et al., 2025; Martins et al., 2026), we collected soil samples from: a hill-like area where the roots of *A. altissima* could not reach the soil (control sample) (noted with number 1), near the trunk of an older trees where the roots are well developed as thickness and length (noted number 2), near the stem of single young shoot less developed (noted number 3, 5, 7 and 8), and groups of suckers originating from the roots: two young shoots (noted with number 4) or three young shoos (noted number 6) (Figure 3).



Figure 1. Location of *Ailanthus altissima* stand in the country and local areas



Figure 2. The above-ground architecture of the *Ailanthus altissima* individuals (left: old growth individual - sample 2, and group of 3 young individuals - sample 6)

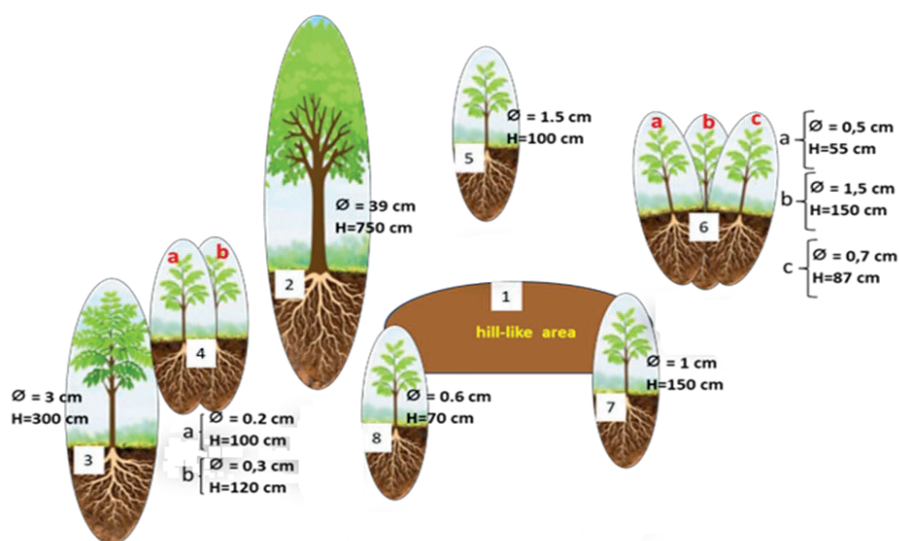


Figure 3. The location of the samples collection at the local area (Legend: H = height of the stem (trunk), Ø = diameter at DBH or 20 cm above ground for young individuals)

Isolation of fungi from the rhizosphere

In order to isolate fungi and estimate their cultivable fraction, soil samples were serially diluted (Sanders, 2012) and plated onto growth media containing yeast extract, glucose, chloramphenicol and agar (YGCA). The fungal load (CFU per g of dry weight) was calculated for the total mycobiota.

Morphological identification of each strain was achieved according to the relevant taxonomic keys (Kiffer & Morelet 1997).

Qualitative evaluation of hydrolase producing fungi

The ability of fungal strains to produce amylase, cellulase, lipase, protease, and xylanase was tested by agar plate-based assays (Ruginescu et al., 2020). The YGCA growth media containing, instead of glucose, one of the substrates of interest (i.e., starch, carboxymethyl cellulose - CMC, Tween 80, xylan and casein) were inoculated in triplicate with diluted soil samples and incubated at 28°C for 14 days.

The production of enzymes was indicated by clear zones around the colonies after flooding the plates with KI solution (amylase), Congo red solution (cellulase and xylanase), or 1N HCl (protease). Lipolytic activity was put in evidence by an opaque halo. The levels of enzyme activities (LEA) were evaluated using the formula LEA = diameter of the hydrolysis zone divided by the diameter of the microbial colonies (in millimeters).

RESULTS AND DISCUSSIONS

Abundance of Cultured Fungi

Soil fungal species decreased significantly when *A. altissima* was present as adult or suckers originate from the roots. The total fungal load for cultivable rhizospheric fungi ranged from $1,3 \times 10^4$ to 60 CFU dwt, with significant differences among the samples. The highest microbial densities were generally obtained on YGCA media (Tabel 1). Even so, the highest number of fungal CFU was found on the control sample represented by hilly-like area. In all the soil samples around the roots of *A. altissima*, the number of CFU was lower, which suggests the possible synthesis of some inhibitory compounds against fungi. The genera with the highest load in the rhizosphere were: *Aspergillus*, *Penicillium*, *Alternaria*, *Trichoderma*, *Chaetomium*, *Botrytis* and *Acremonium*.

Fungal colonies grew on all growth media with specific substrates for hydrolases, but in smaller numbers than on YGCA media. The lowest number of CFU was found in the media with hydrolase substrates for sample 8. Sample 6 contained the lowest number of CFU on the nutrient medium with CMC. Very few UFC were obtained on the nutrient medium with xylan (10) and for the other soil samples they were not identified. The lower number of CFU on the media with hydrolase substrates may be a consequence of the reduction of N total and the release of some inhibitory compounds by the roots of *A. altissima*. Medina-Villar et al. (2016) found that capability of *A. altissima* to decrease soil total N. It could be attributed to changes in the balance between N input and losses from the soil. Also, several properties, the composition of soil microbial communities and microbial activities need longer time since invasion to be altered.

Table 1. Abundance of Cultured Fungi on different growth media)

Sample code	CFU YGCA	CFU on starch nutrient	CFU on casein nutrient	CFU on CMC nutrient	CFU on Tween 80 nutrient	CFU on xylan nutrient
1	140000	13000	12000	1100	110	10
2	12000	100	10000	100	100	0
3	10000	100	12000	1200	100	0
4	13000	100	1400	110	110	0
5	1300	100	100	100	110	0
6	1200	100	100	10	100	0
7	1100	100	100	100	100	0
8	1100	80	75	80	60	0

Soil microbial communities in the field differ between invaded and non-invaded soil due to nitrate concentration and net nitrification rates in *A. altissima* soil. It was proved that the methanolic extracts of the leaves, of the barks and of the fruits have strong antimicrobial activity which can explain reducing the number of microorganisms in the soil where they reach (Caramelo et al., 2021; Zhao et al., 2005).

The fact that the lowest number of UFC was identified on the roots of *A. altissima* with a diameter of 6 cm is evidence that the release of inhibitory compounds begins immediately after the formation of roots. The time required for plant growth allows some fungi to adapt to the new conditions.

Production of Extracellular Hydrolytic Enzymes

The production of hydrolases by fungi was identified in all soil samples collected from MOVILA and from the rhizosphere of *A. altissima* specimens of different ages. Apparently, the percentage of hydrolase producing fungi is higher in the rhizosphere soil of *A. altissima*. The explanation lies in the fact that the number of CFU in the rhizosphere of the *A. altissima* samples was reduced compared to the control sample (hill-like area). Samples 4, 5 and 6 had higher amylase activity than the control, sample 1 comparable and samples 2, 3 and 7 lower than the control. Samples 1-6 had higher protease activity than the control and sample 7 had slightly reduced activity. Samples 1-4 and 6 had higher cellulase activity than the control, sample 7 had slightly reduced activity and in sample 5 this enzymatic activity was

absent. Samples 1, 2, 4 and 6 had higher lipase activity than the control, samples 3 and 5 had activity comparable to the control, and in sample 7 this activity was absent. Xylanase activity was present only in the control and absent in all other samples (Figure 4).

Most likely, the organic compounds present in the soil samples have a heterogeneous distribution as a result of the fact that the analyzed surface comes from the random deposits of waste from the neighboring households. As Fotiadis et al. (2011) mentioned, the spreading of *A. altissima* in urban areas is very intense, mainly in abandoned places (35.29%). The ability of the same species to grow and synthesize several types of hydrolases is the result of the versatility of the metabolism and the presence of enzyme inducers in the soil.

Our results are consistent with those obtained by Motard et al. (2015) revealing that increasing density of *A. altissima* is associated to lower soil microbial activity.

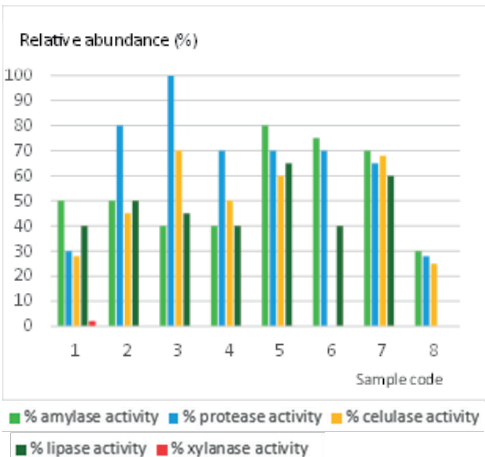


Figure 4. Relative abundances of microbial hydrolase producers recovered from the investigated site

Scavo et al. (2018) revealed that the decay/decomposition of plant materials (root system) releases a large quantity of allelochemicals into the soil with effect on microorganisms. If Hnini et al. (2024) consider that beneficial soil microorganisms, particularly Plant Growth-Promoting Rhizobacteria (PGPR) and Arbuscular Mycorrhizal Fungi (AMF), is a sustainable solution in general, it could be a new direction of our studies.

Many studies confirm that soil fungal communities and microbial activities do not require long invasion periods to be altered; significant shifts can occur in the short term (under 2-5 years) as invaders immediately modify soil pH, moisture, and nutrient availability (Bauman et al., 2013; Sasnow, 2014; Soler & Izquierdo, 2024; Miles et al., 2025).

CONCLUSIONS

The rhizosphere mycobiota of invasive *A. altissima* trees is significantly shaped by the density of the stands and the age of the individuals. Older stands often show increased soil nutrient pools (carbon and nitrogen) due to sustained leaf litter inputs and biological nitrogen fixation, which in turn alters fungal community structure.

This study provides a characterization of the cultivable mycobiota associated with *Ailanthus altissima*, highlighting the critical role of these fungi in soil organic matter decomposition through hydrolytic enzyme production. Our results demonstrate that fungal enzymatic activity is subject to spatial and temporal variations, influenced by both the root zone and the developmental stage of the host plant. These findings enhance our understanding of how invasive species alter nutrient cycling and soil health.

Future research should focus on integrating these culture - dependent results with metagenomic approaches to capture the full diversity of the non-cultivable fungal community. Additionally, further studies are needed to evaluate the long-term impact of these fungal-mediated processes on native plant re-establishment in post-invasion soils. Experimental trials utilizing the isolated fungal strains could also explore their potential in biotechnological applications or as indicators of soil ecosystem shifts during *A. altissima* expansion.

This research initiated the study of a sophisticated synergy between plant functional attributes and microbial activities in the rhizosphere of *Ailanthus altissima*, identifying the cultivable mycobiota associated with this invasive species as a key driver of soil organic matter decomposition, mediated by specialized hydrolytic enzyme production. We observed

that fungal enzymatic activities exhibit distinct spatial and temporal variations, which align with the broader ecological patterns identified in global meta-analyses regarding fine root biomass (RB) and functional trait dissimilarity. Our findings suggest that the success of *A. altissima* in invaded ecosystems is not only a result of its intrinsic traits - such as growth rate and stress tolerance - but also its ability to modulate belowground processes, i.e. the associated fungal communities facilitate nutrient cycling through enzymatic pathways. As these effects intensify with soil depth and developmental stages, the interplay between root architecture and microbial-mediated decomposition becomes a critical factor in ecosystem carbon sequestration and soil health. The isolated fungal strains and the root trait correlations established here provide a fundamental resource for future research. Integrating these findings with metagenomic approaches will be essential to fully decipher the mechanisms by which invasive - driven functional diversity alters the biogeochemical cycles of native habitats. Understanding spatial and temporal variations in fungal enzymatic activity is crucial for revealing their contribution to nutrient cycling and soil health in invaded ecosystems. The isolation and availability of our fungal cultures from both rhizosphere and roots will serve as valuable resources for further experimental evaluations of fungal-mediated decomposition processes in soils influenced by *A. altissima*.

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REFERENCES

- Badalamenti, E., & La Mantia, T. (2015). Arbuscular mycorrhizal fungi positively affect growth of *Ailanthus altissima* (Mill.) Swingle seedlings and show a strong association with this invasive species in Mediterranean woodlands. *The Journal of the Torrey Botanical Society*, 142(2), 127-139.
- Badalamenti, E., Ciolfi, M., Lauteri, M., Quatrini, P., & Mantia, T.L. (2018). Effects of Arbuscular Mycorrhizal Fungi on the Vegetative Vigor of *Ailanthus altissima* (Mill.) Swingle Seedlings under Sustained Pot Limitation. *Forests*, 9(7), 409.
- Baldrian, P. (2014). Distribution of extracellular enzymes in soils: spatial heterogeneity and determining factors at various scales. *Soil Science Society of America Journal*, 78(1), 11-18.
- Bauman, J.M., Keiffer, C. H., & Hiremath, S. (2012). Facilitation of American chestnut (*Castanea dentata*) seedling establishment by *Pinus virginiana* in mine restoration. *International Journal of Ecology*, 2012(1), 257326.
- Bauman, J., Byrne, C., & Hiremath, S. (2013). *Ailanthus altissima* (Tree-of-Heaven) interferes with beneficial symbionts with negative impacts on oak regeneration. *Journal of the American Society of Mining and Reclamation*, 2(1), 1.
- Berendsen, R.L., Pieterse, C.M., & Bakker, P.A. (2012). The rhizosphere microbiome and plant health. *Trends in plant science*, 17(8), 478-486.
- Brooks, R.K., Barney, J.N., & Salom, S.M. (2021). The invasive tree, *Ailanthus altissima*, impacts understory nativity, not seedbank nativity. *Forest Ecology and Management*, 489, 119025.
- Call, L.J., & Nilsen, E.T. (2005). Analysis of interactions between the invasive tree-of-heaven (*Ailanthus altissima*) and the native black locust (*Robinia pseudoacacia*). *Plant Ecology*, 176(2), 275-285.
- Caramelo, D., Pedro, S.I., Marques, H., Simão, A. Y., Rosado, T., Barroca, C., & Gallardo, E. (2021). Insights into the bioactivities and chemical analysis of *Ailanthus altissima* (Mill.) Swingle. *Applied Sciences*, 11(23), 11331.
- Castellano, S.M., & Gorchov, D.L. (2012). Reduced ectomycorrhizae on oak near invasive garlic mustard. *Northeastern Naturalist*, 19(1), 1-24.
- Castro-Díez, P., Vaz, A.S., Silva, J.S., Van Loo, M., Alonso, A., Aponte, C., & Godoy, O. (2019). Global effects of non-native tree species on multiple ecosystem services. *Biological Reviews*, 94(4), 1477-1501.
- Cocîrlea, M.D., Simionescu, N., Petrovici, A.R., Silion, M., Biondi, B., Lastella, L., & Oancea, S. (2024a). In vitro screening of ecotoxic and cytotoxic activities of *Ailanthus altissima* leaf extract against target and non-target plant and animal cells. *International Journal of Molecular Sciences*, 25(11), 5653.
- Cocîrlea, M.D., Soare, A., Petrovici, A.R., Silion, M., Călin, T., & Oancea, S. (2024b). Phenolic composition and bioactivities of invasive *Ailanthus altissima* (Mill.) swingle leaf extracts obtained by two-step sequential extraction. *Antioxidants*, 13(7), 824.
- De Beeck, M.O., Persson, P., & Tunlid, A. (2021). Fungal extracellular polymeric substance matrices—highly specialized microenvironments that allow fungi to control soil organic matter decomposition reactions. *Soil Biology and Biochemistry*, 159, 108304.
- Ding, J., Wu, Y., Zheng, H., Fu, W., Reardon, R., & Liu, M. (2006). Assessing potential biological control of the invasive plant, tree-of-heaven, *Ailanthus altissima*.

- Biocontrol science and technology*, 16(6), 547-566.
- Dix, N.J., & Webster, J. (1995). Fungi of soil and rhizosphere. In *Fungal ecology* (pp. 172-202). Dordrecht: Springer Netherlands.
- Fotiadis, G., Kyriazopoulos, A.P., & Fraggakis, I. (2011). The behaviour of *Ailanthus altissima* weed and its effects on natural ecosystems. *Journal of Environmental Biology*, 32(6), 801.
- Gavriliadis, A.A., Grădinaru, S.R., Onete, M., Breuste, J., & Ioja, C. (2023). The influence of vacant land presence on proliferation of invasive alien plant species: the case of *Ailanthus altissima* (Mill.) Swingle Var. *Altissima*. In Breuste J., Artmann M., Ioja C., Qureshi S. (Eds.), *Making Green Cities: Concepts, Challenges and Practice*, 2nd Edition (pp. 279-295). Cham: Springer International Publishing.
- Gomoiu I, 2009, Long-term fungal survival in various environmental conditions, in Enache M., Dumitru L. (Eds.) *Stress adaptation: survival condition and/or biodiversity factor*, 95-104.
- He, Y., Fan, F., Zhang, Y., Jia, B., Siemann, E., & Lu, X. (2025). Plant invasion affects litter decomposition differently in native and invasive plant conditioned soils. *Plant and Soil*, 512(1), 333-346.
- Hnini, M., Rabeh, K., & Oubohssaine, M. (2024). Interactions between beneficial soil microorganisms (PGPR and AMF) and host plants for environmental restoration: A systematic review. *Plant Stress*, 11, 100391.
- Hrabovský, M., & Hladík, M. (2024). Control of invasive *Ailanthus altissima* in the Danube floodplain forests in Bratislava using chemical and biological agents. *Forest Ecology and Management*, 569, 122225.
- Idris, A. (2026). Enzymes of importance to rhizosphere processes. *Microbial Enzymes*, 343-359.
- Kiffer, E., & Morelet, M. (1997). Les deutéromycètes: Classification et clés d'identification générique. INRA Editions, Paris, France.
- Lawrence, J. G., Colwell, A., & Sexton, O.J. (1991). The ecological impact of allelopathy in *Ailanthus altissima* (Simaroubaceae). *American journal of Botany*, 78(7), 948-958.
- Lazzaro, L., Bolpagni, R., Buffa, G., Gentili, R., Lonati, M., Stinca, A., & Lastrucci, L. (2020). Impact of invasive alien plants on native plant communities and Natura 2000 habitats: State of the art, gap analysis and perspectives in Italy. *Journal of Environmental Management*, 274, 111140.
- Liaud, N., Giniés, C., Navarro, D., Fabre, N., Crapart, S., Gimbert, I.H., ... & Sigoillot, J.C. (2014). Exploring fungal biodiversity: organic acid production by 66 strains of filamentous fungi. *Fungal Biology and Biotechnology*, 1(1), 1.
- Liu, D., Semenchuk, P., Essl, F., Lenzner, B., Moser, D., Blackburn, T.M., & Dullinger, S. (2023). The impact of land use on non-native species incidence and number in local assemblages worldwide. *Nature Communications*, 14(1), 2090.
- Martins, S., Brito, C., Baltazar, M., Dinis, L.T., & Pereira, S. (2026). Exploring the Role of Root Exudates in Shaping Plant–Soil–Microbe Interactions to Support Agroecosystem Resilience. *Horticulturae*, 12(1), 90.
- Marzalletti, F., Lozano, V., Große-Stoltenberg, A., Carranza, M.L., Innangi, M., La Bella, G., & Brundu, G. (2025). Assessing eco-physiological patterns of *Ailanthus altissima* (Mill.) Swingle and differences with native vegetation using Copernicus satellite data on a Mediterranean Island. *Ecological Informatics*, 87, 103080.
- Medina-Villar, S., Rodríguez-Echeverría, S., Lorenzo, P., Alonso, A., Pérez-Corona, E., & Castro-Díez, P. (2016). Impacts of the alien trees *Ailanthus altissima* (Mill.) Swingle and *Robinia pseudoacacia* L. on soil nutrients and microbial communities. *Soil Biology and Biochemistry*, 96, 65-73.
- Miles, H.H., Salom, S., Shively, T.J., Bielski, J.T., McAvoy, T.J., & Fearer, C.J. (2025). A review of potential biological controls for *Ailanthus altissima*. *Annals of the Entomological Society of America*, 118(2), 101-109.
- Motard, E., Dusz, S., Geslin, B., Akpa-Vinceslas, M., Hignard, C., Babiari, O., & Michel-Salzat, A. (2015). How invasion by *Ailanthus altissima* transforms forest and litter communities in a temperate forest ecosystem. *Biological Invasions*, 17(6), 1817-1832.
- Motti, R., Zotti, M., Bonanomi, G., Cozzolino, A., Stinca, A., & Migliozi, A. (2021). Climatic and anthropogenic factors affect *Ailanthus altissima* invasion in a Mediterranean region. *Plant Ecology*, 222(12), 1347-1359.
- Peng, S., Zhang, Y., & Chen, H.Y. (2025). Plant functional trait dissimilarity drives plant mixture effects on fine root biomass and trait variations. *New Phytologist*, 249(2), 764-776.
- Poli, A., Lazzari, A., Prigione, V., Voyron, S., Spadaro, D., & Varese, G.C. (2016). Influence of plant genotype on the cultivable fungi associated to tomato rhizosphere and roots in different soils. *Fungal Biology*, 120(6-7), 862-872.
- Ritz, K., & Young, I.M. (2004). Interactions between soil structure and fungi. *Mycologist*, 18(2), 52-59.
- Ruginescu, R., Gomoiu, I., Popescu, O., Cojoc, R., Neagu, S., Lucaci, I., & Enache, M. (2020). Bioprospecting for novel halophilic and halotolerant sources of hydrolytic enzymes in brackish, saline and hypersaline lakes of Romania. *Microorganisms*, 8(12), 1903.
- Sanders, E.R. (2012). Aseptic laboratory techniques: plating methods. *Journal of Visualized Experiments (JoVE)*, (63), e3064.
- Sasnow, S. (2014). Examination of the soil bacteria responsible for the decomposition of ailanthone, an inhibitory chemical in *Ailanthus altissima*. *DePaul Discoveries*, 1(1), 10.
- Scavo, A., Restuccia, A., & Mauromicale, G. (2018). Allelopathy: principles and basic aspects for agroecosystem control. In *Sustainable agriculture reviews 28: ecology for agriculture* (pp. 47-101). Cham: Springer International Publishing.
- Singh, M., Chauhan, A., & Singh, P.K. (2025). Impacts of invasive plant species on arbuscular mycorrhizal fungi: consequences for ecosystem functions and plant communities. *International Journal of Environmental Studies*, 1-17.
- Skujiņš, J., & Burns, R.G. (1976). Extracellular enzymes in soil. *CRC critical reviews in microbiology*, 4(4), 383-421.

- Small, C.J., White, D.C., & Hargbol, B. (2010). Allelopathic influences of the invasive *Ailanthus altissima* on a native and a non-native herb1, 2. *The Journal of the Torrey Botanical Society*, 137(4), 366-372.
- Soler, J., & Izquierdo, J. (2024). The invasive *Ailanthus altissima*: A biology, ecology, and control review. *Plants*, 13(7), 931.
- Sun, J., Pan, L., Akbar, R., He, F., & Girkin, N. (2026). Playing dirty: How soil legacies shape invasive plant dominance and community dynamics. *Applied Soil Ecology*, 218, 106670.
- Terzi, M., Fontaneto, D., & Casella, F. (2021). Effects of *Ailanthus altissima* invasion and removal on high-biodiversity Mediterranean grasslands. *Environmental Management*, 68(6), 914-927.
- Zhao, C.C., Shao, J.H., Li, X., Xu, J., & Zhang, P. (2005). Antimicrobial constituents from fruits of *Ailanthus altissima* SWINGLE. *Archives of pharmacal research*, 28(10), 1147-1151.
- Zuccarini, P., Sardans, J., Asensio, L., & Peñuelas, J. (2023). Altered activities of extracellular soil enzymes by the interacting global environmental changes. *Global Change Biology*, 29(8), 2067-2091.