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Poplar as a woody model for the phytomanagement of trace element contaminated soils

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Abstract

On a global scale, the effects of human activities, in particular changes in the way land is used and exploited and the resulting contamination, have had profound negative effects on biodiversity and ecosystem functioning. Consequently, restoring the marginal lands through the use of solutions inspired and supported by nature appears to be one of the European Union's main objectives. In this respect, eco-innovative phytotechnologies, such as phytoremediation, have become an important ecological engineering approach for the recovery of contaminated land. A relatively new area of phytoremediation is phytomanagement in which non-food crops with high biomass yields are used to reduce and control the risks associated with soil pollution, while enabling profitable and sustainable use of resources by extracting contaminants and recovering marketable biomass. Consequently, the best choice of plant species is crucial to the successful phytomanagement of contaminated sites. This meta-analysis highlights the importance of using fast-growing plants for phytomanagement purposes, focusing on woody species. Those from the Salicaceae family, which includes poplars (*Populus*), have attracted the most attention in recent decades. On the basis of this meta-analysis, poplars appear to be the best candidates for the remediation of metal-contaminated soils, particularly when combined with the most appropriate microbial consortia. Finally, we describe the molecular determinants of poplar involved in the management of trace elements (TE), as well as the valorisation processes that have been applied to poplar biomass from phytoremediation trials.

Key words: Nature based solutions, marginal lands, bioremediation, poplar microbiome, short rotation coppice, bioenergy

1 Nature Based Solution (NBS) for soil recovery

Soils are the keystone of healthy and vibrant ecosystems, providing physical, chemical, and biological substrates and functions necessary to support life. However, soils are under constant threat from pollution, creating a significant risk to human health and to terrestrial and aquatic ecosystems. There are an estimated 3 million contaminated sites in Europe with an average of registered sites of 3.69 sites / km² and those in need of urgent remediation are around 250 000. On this regard, it is well known that the existence of ~1,350,000 hectares of land in Europe deemed less favourable for conventional agriculture (Health and Environment). These soils are identified as “marginal lands”, which include contaminated and degraded soils. However, the total area of contaminated and degraded land is increasing due to anthropogenic activities, such as industrialization and mining activities. Indeed, in the last decades, mining and smelting operations have led to the contamination of many sites by potential toxic elements (TE), Quercia et al., 2006). Metal concentrations in the soils at these sites frequently reach toxic levels to both plants (Cobbett, 2003) and microorganisms (Dai et al., 2004), which reduce the diversity of microorganisms (Moffett et al., 2003). According to the data obtained from the EU commission, 60 to 70% of soils in the EU are currently unhealthy. In addition, a billion tonnes of soil are washed away every year due to erosion, which means that the remaining fertile top layer is disappearing quickly. Costs associated with soil degradation are estimated at over €50 billion per year. These lands cannot be used for food or feed production for health reasons but provide a large potential to produce biomass for material or energy use (Hullot et al., 2021).

On a global scale, the effects of human activities, particularly changes in the way a land is used and exploited (agriculture and forestry, exploitation of natural resources and industrial activities) and the resulting contamination, have had profound negative effects on biodiversity and ecosystem functioning. Between 1970 and 2008, global biodiversity declined by 30%, with no sign of slowing down. This is the fastest rate of decline ever seen. The total annual economic

cost of biodiversity loss and ecosystem degradation were estimated at between 2,400 and 4,500 billion dollars in 2008 (Biodiversity Lost and Ecosystem Degradation). Consequently, "halting the loss of biodiversity and the degradation of ecosystem services" remains one of the main objectives of the European Union (EU) (Biodiversity Strategies - Environment). At present, Europe's long-term policy is increasingly adopting a more systemic perspective, linking environment, health, and human well-being (Health and Environment). It is therefore necessary to find solutions inspired and supported by nature, simultaneously offering environmental, social, and economic benefits, and helping to build resilience (Nature Based Solution-Environment; Triest et al., 2016).

Eco-innovative phytotechnologies can remediate soil layers in contact with the roots and at the same time provide tree biomass (Bauddh et al., 2017), which can be used to provide high quality renewable raw materials for bio-energy production and fostering the bio-based economy and climate-change mitigation (Moreira et al., 2021). Phytoremediation, the use of plants to remove contaminants from the environment and in particular soils, has become an important approach in ecological engineering. However, contaminated lands are normally left fallow for a long period as there is a risk of bioaccumulation in food crops. A relatively new area of phytoremediation is phytomanagement in which non-food high biomass yielding crops are used to reduce and control risks arising from soil pollution, while making a profitable and sustainable use of resources possible by extracting contaminants and valorising marketable biomass. Considering the increasing demand of biomass and resulting potential land-use conflicts, the cultivation of industrial crops in contaminated soils offers great environmental benefits and new social and economic opportunities for primary producers, broader society and the entire bio-based value system. Phytomanagement is now widely applied worldwide for the remediation of soil contaminated by TE, within phytostabilisation (Simek et al., 2017; Burges et al., 2018) and phytoextraction scenarios (Sessitsch et al., 2013). Within this context, phytostabilisation

promotes the TE-stabilization by the decrease of their bioavailability in soil, often by combining the use of TE-excluding plants, soil amendments and/or microbial inoculants (assisted phytostabilisation) (Mench et al., 2010; Epelde et al., 2014; Kidd et al., 2015; Burges et al. 2016, 2017, 2018). However, phytoextraction refers to the accumulation of TE into harvestable plant tissues (Gomez et al., 2019).

Moreover, as mentioned above, rhizospheric microorganisms can actively participate in these phytoremediation processes and extend the application of phytoremediation (Thijs et al. 2016; Touceda-Gonzalez et al., 2017; Xue et al., 2018). It is well known that microorganisms play key roles within the ecosystems and in association with host organisms (Ciadamidaro et al., 2022). Plant microorganisms support different plant functions, e.g., water and nutrient absorption, or biotic and abiotic stress reduction (Hill et al., 2010; Li et al., 2013). The importance of biodiversity of soil microbial communities is increasingly recognized and considered as a major factor for human health both directly, by limiting the spread of potential pathogens (Berendsen et al., 2012), and indirectly, by contributing to processes that provide clean air, water, and healthy food. Therefore, the presence of microorganisms, such as ectomycorrhizal fungi and endophytes, could be extremely important in the amelioration of plant performance in a very stressful environment, such as soils contaminated with TE. For this reason, a proposed approach for the remediation of contaminated environment is based on phytoremediation techniques involving biological processes such as “plant-microbe” interactions (Kaur and Garg, 2018), through the inoculation of mycorrhizal strains, in order to improve the quantity and diversity of the fungi community and plant growth, and to foster the success of phytomanagement strategies.

Although phytomanagement strategies are well recognized for their capacities in the recovery of TE polluted sites, they present some limits and pitfalls associated to edaphoclimatic conditions. Potential edaphic constrains are principally physical such as compaction, reduced

water holding capacity and low aeration (Shrestha and Lal, 2011) and chemical properties such as pH, high TE concentrations, mixture of TE with other pollutants, low nutrient concentrations and OM contents (Kidd et al., 2015; Rogers et al., 2019). Among the climatic conditions that influence the success of the phytomanagement practices temperature and water chemistry directly affect the growth and the TE uptake of plants. Therefore, the best choice of plant species that tolerate all these conditions is crucial for the successful phytomanagement of contaminated sites, especially in the current scenario of climate change (Vangronsveld et al., 2009; Moreira et al., 2021).

In this review, we will highlight the importance of the selection of plant species for phytomanagement purposes, focusing on woody species, taking *Populus* trees as a model, and we will describe the poplar molecular determinants involved in the management of TE, as well as the valorisation processes that have been applied to poplar biomass from phytoremediation trials.

2 Tree-based phytomanagement strategies for TE contaminated soils

2.1 Selection of woody species

The efficiency of phytomanagement strategy is dependent on some specific factors related to TE bioavailability, site conditions, and plant characteristics. For instance, the bioavailability of the pollutants and root-microbial modifications of their solubility and chemical speciation in the rhizosphere play a key role in the phytoremediation systems (Wenzel, 2009). In the case of TE, plants might regulate their bioavailability by their root system. Directly or indirectly, root exudates modify the pH of the rhizospheric soil, which can increase element availability and affect cell membrane permeability (Jones et al., 2004; Neumann and Römheld, 1999) and, increasing or decreasing element uptake. Plant roots and root debris can also affect the bioavailability of cationic metals/metalloids via adsorption onto root surfaces or root-derived

biomolecules (Breckle and Kahle, 1992; Cathala and Salsac, 1975). Indeed, root activities has been widely documented in non-accumulating plants (Hinsinger and Courchesne, 2008) and accumulating plants (Kidd et al., 2009). As mentioned before, several factors related to site conditions could also influence the choice of adequate plants for phytomanagement purposes: i) type, concentration and location of TE; ii) physico-chemical soil properties; iii) water availability; iv) climatic conditions; and v) combined life cycles of pests and biological auxiliaries (O'Connor et al., 2019; Moreira et al., 2021).

Finally, the appropriateness of a certain plant for TE remediation is determined by various plant properties, such as: i) TE tolerance; ii) size, growth rate and rooting depth; iii) TE accumulation in above-ground plant parts; and iv) climatic adaptation and pest resistance (Kirkham, 2006; Pulford and Watson, 2003). In addition to the above-mentioned characteristics, the efficiency of remediation can be facilitated by genetic modification (e.g., overexpression of genes accountable for metal tolerance and uptake) or by increasing the bioavailability of metals in the growing media (Liu et al. 2020; Sarma et al. 2021; Trippe and Pilon-Smits 2021). Over the years, several studies have been carried out to optimize the method and to find the most suitable plants (Ciadamidaro et al., 2019). To make effective phytoremediation and the whole phytomanagement process economically sustainable, native plant species are the best candidates due to the limited risk of biological invasion and for their capacity to enhance local biodiversity and resilience to diseases (Burghardt et al., 2009; Dagenais et al., 2018). For these reasons, the best candidates can be found among woody species (Mohsin et al., 2019; Moreira et al., 2021; Nissim et al., 2023).

Nowadays, scarce information exists about plant performances for phytomanagement purposes under natural field conditions and most of the knowledge are related to herbaceous species (Marmioli et al., 2011). However, the use of fast-growing trees that are well adapted to different pedo-climatic conditions is an increasingly common practice in many regions of the

world and their use for environmental cleanup is increasing over time. Woody species constitute most of plant biomass in native Mediterranean forests and shrublands, and it has been estimated that around 3 trillion trees populate the planet (Crowther et al., 2015). They are important primary producers in local food webs, and they provide renewable energy and raw materials (Gomez et al., 2019). Woody species are perennial, long-lived organisms that play essential roles in ecological processes. Indeed, they are involved in biogeochemical cycles, climate regulation, soil conservation and habitat protection (Bonan, 2016; Trumbore et al., 2015). Their potential resides in large biomass production, extensive root systems, considerable tolerance to TE, and high accumulation of TE in the biomass (Pulford and Watson, 2003; Migeon et al., 2009). Different studies (Mertens et al., 2007; Evangelou et al., 2012) have already tested various trees, such as birch (*Betula pendula*), oak (*Quercus robur*), ash (*Fraxinus excelsior*) and maple (*Acer pseudoplatanus*) and demonstrated different behaviors and adaptation characteristics to TE contamination. In our previous study (Ciadamidaro et al., 2019), the growth performance and element accumulation of 38 tree species at three different marginal lands were measured, to identify the phytoremediation capacities of woody species never tested before.

The relevant impacts on afforestation of polluted site are that woody species tends to improve the physicochemical and biological properties of marginal lands, such as moisture, bioavailability of micro and macronutrients and biodiversity (Berhongaray et al., 2017; Wang et al., 2017; Wu et al., 2018). All these differences have had impacts on the outcome of phytomanagement strategies, and a careful selection of appropriate tree species/clones seems to be a pre-requisite for any field-based phytoremediation attempts (Pulford and Watson, 2003). Among woody species, the trees with rapid growth such as those of the Salicaceae family, which comprises willows (*Salix*) and poplars (*Populus*), have attracted most attention in the context of phytomanagement strategies (Chalot et al., 2020; Ciadamidaro et al., 2019; Isebrands

and Richardson, 2014; Marmioli et al. 2011). These are deciduous trees that lose all their leaves for part of the year and have been extensively tested for the phytoremediation TE contaminated sites (Dickinson, 2006; French et al., 2006; Meers et al., 2007; Ciadamidaro et al., 2014). Earlier papers showed beneficial effects on the metal accumulation potential of members of the Salicaceae family, out of which *Populus* is nowadays a thoroughly mapped genus (Marmioli et al., 2011).

2.2 Poplar-based phytomanagement

Poplar is a genus comprising around 22-45 species widely distributed over the northern hemisphere and planted in many parts of the world due to its high genetic diversity that makes it adaptable to other areas (Pandey et al., 2016). Nevertheless, poplars prefer temperate areas and moisty, well drained and aerated alluvial soils (Stanturf and van Oosten, 2014) with a pH ranged between 5 and 7 (Baker and Broadfoot, 1979). They are deciduous and fast-growing trees of the Salicaceae family (Eckenwalder, 1996) with high biomass production rate. *Populus* species is well known for its ability to stabilize the soil surface, reduce wind and water erosion of the soil and tolerate stressed conditions, such as salinity and dryness (Stanturf and van Oosten, 2014). In this regards, Chen and Polle (2010) observed very well adaptation of *P. euphratica* under salt stress by different physiological and molecular adaptation, such as changes in leaf morphology.

Poplar species, known as deep-rooted plants with high transpiration rates (Guerra et al., 2011), can effectively decrease the risk of contaminant leaching from surface water into groundwater (Bolan et al., 2011; Ciadamidaro et al., 2014), tolerates high TE concentrations and accumulates TE in its tissues without showing toxic effects (Dominguez et al., 2008). For all these reasons, this woody species has been extensively used for revegetation of land heavily contaminated with TE and so far for the use for phytoremediation purposes (Villette et al., 2019). However, poplar trees are extensively used for plantation under short-rotation coppice

(SRC) in many regions and they tolerate very high planting densities (Marmioli et al., 2011), which makes them more suitable for phytomanagement strategies (Fig. 1). Poplars are well known for their phytostabilisation capacities (Chandra et al., 2016), following the pattern observed for the other woody crops of retaining TE in roots (Shi et al., 2011; Baldantoni et al., 2014). Moreover, they presented the ability to accumulate preferentially Cd and Zn in their leaves (Migeon et al., 2009; Ciadamidaro et al., 2014, 2017, 2019), making them suitable for phytoextraction of these elements from contaminated soils (Robinson et al. 2009) and as biomonitors of soil contamination (Madejon et al., 2004). In previous studies we have indeed found high concentrations of Cd and Zn in leaves of *P. alba* (Ciadamidaro et al., 2014), *P. trichocarpa* x *P. maximowiczii* (Ciadamidaro et al., 2017) and *P. oxford* (Ciadamidaro et al., 2019) under field conditions.

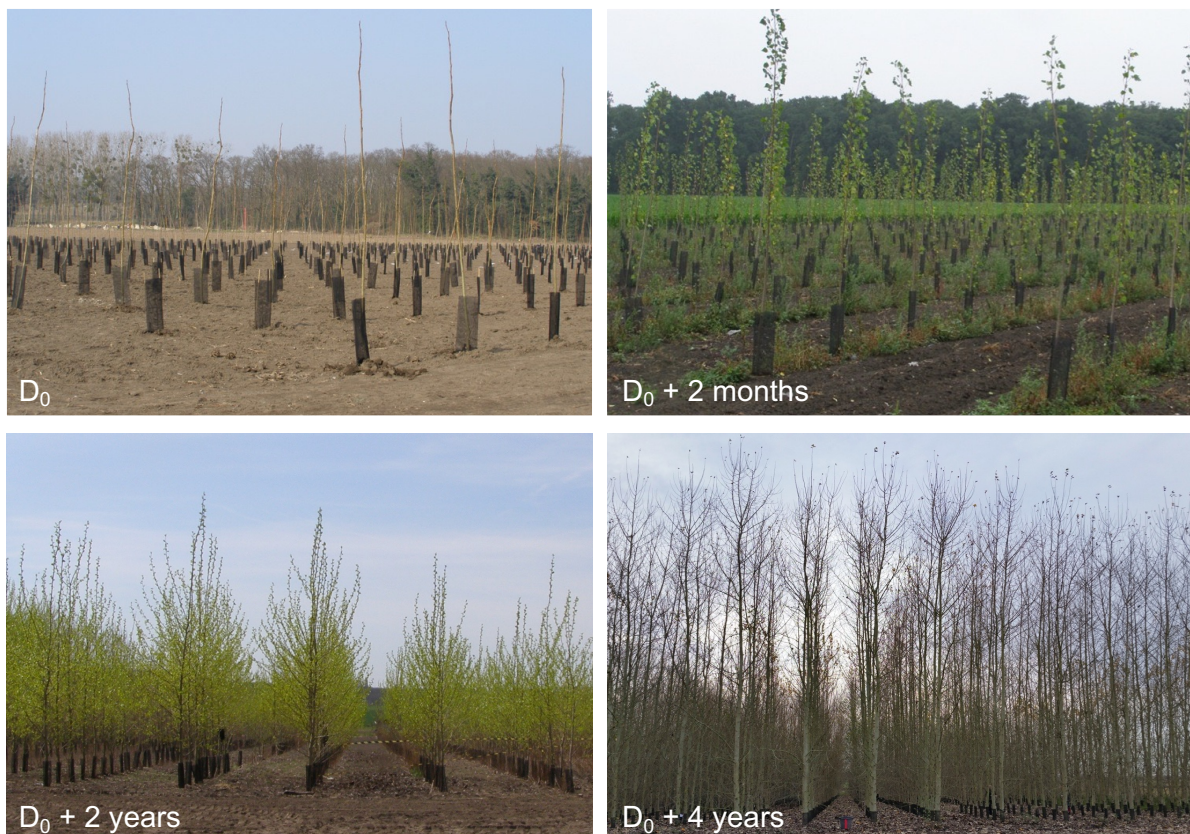


Figure 1. Views of a poplar plantation on a contaminated soil at different periods after plantation (D₀). Details are provided in Ciadamidaro et al. (2017).

Several studies indicated that some factors related to soil and plant characteristics might influence poplars capacities in tolerate and accumulate TE (Baldantoni et al., 2014). Soil pH is known for being one of the main parameters in driving TE availability, thus in the same way it might affect the intensity of TE accumulation in woody species, such as poplars. Different studies (Ciadamidaro et al., 2013; Migeon et al., 2012) found a negative correlation between soil pH and metal uptake. Hu et al. (2019) observed an increase of Ni accumulation related to a decrease in soil pH in the case of *Populus hopeiensis*. Other factor important in influencing accumulation in poplar species is the length of time that plants are exposed to TE. In previous research (Di Baccio et al., 2009), *Populus × canadensis Moench* exhibited a highly exposure time-dependent Zn accumulation, whereas Tózsér et al. (2017) demonstrated that the positive correlation between the time of exposure and tissue metal enrichment was non-significant after reaching certain concentrations.

Though poplars showed high capacities to tolerate and accumulate different TE at different concentrations (Assad et al., 2016; Thijs et al., 2018; Nissim et al., 2019, Yung et al., 2019), this ability seems to be strongly related to the type of poplar species, cultivars and hybrids (Migeon et al., 2009; Ruttens et al., 2011). According to this, Phanthavongsa et al. (2017) observed that poplars grown on highly contaminated soils accumulated excessive Cd and Zn in leaves compared with those planted on less contaminated soils, and the I-214 clone generally accumulated less PTEs than the Skado clone. In the same way, the study of Baldantoni et al. (2014) demonstrated that *P. alba* “AL22” showed higher Cu, Pb and Cd accumulation ability compared to the clone *P. nigra* “N12”, both growing in the same multi-contaminated soil. A larger experiment of Petrini et al. (2010) showed great variability in Cd accumulation at leaf level among 10 *Populus* clones.

Despite the large knowledge associated to poplar species in phytomanagement strategies, it remains a controversial issue related to their deciduous nature. The concern in the use of poplars for phytomanagement in the study area is related to the potential risk associated to the accumulation of TE concentrations in the topsoil due to litter fall and so on into the food chain. Research conducted by Pottier et al. (2015) showed an exponential increase of some TE concentrations in leaf, which could be reintroduced into the soil by the litter degradation. However, in contrast to these results, our previous study (Ciadamidaro et al., 2014) revealed that pseudo-total concentrations remained similar over time and the bioavailability of Cd and Zn in soils decreased under *P. alba* plantation. The chemical and biochemical properties of soil were not negatively affected by litter contamination, whereas natural processes appeared to be enhanced by the addition of organic matter content coming from the litter that influence soil pH.

3 Microbial-aided phytoremediation using poplar microbiome

As stated previously, the success of phytomanagement strategies depend on the capacity of plants to colonize stressed and degraded environments, and indirectly in their ability to interact with soil microorganisms. Microorganisms are ubiquitous across environments and play key roles within ecosystems and they could create mutualistic associations with host organisms (Ciadamidaro et al., 2022; Chalot and Puschenreiter, 2021). Indeed, plants are naturally associated with different bacteria and fungi, and both are known to assist their hosts with key functions and to improve plant growth and development (Coninx et al., 2017; Mercado-Blanco et al., 2018). It is extensively demonstrated that the combination of plant with microorganisms might enhance plant resistance to soil contamination and improve biomass production (Ciadamidaro et al., 2019; Phanthavongsa et al., 2017; Pogrzeba et al., 2017; Thijs et al., 2016). These associations are responsible of the increasing of the secretion of certain molecules, such as phytohormones, cytokinins and gibberellins, involved in different processes.

Plant-associated microorganisms may, *e.g.*, increase nutrient availability through the production of organic acids and siderophores (Álvarez-López et al., 2020), improve water and nutrient absorption, drive material cycles, and alleviate biotic and abiotic stresses (Li et al., 2013). Furthermore, a large range of woody species are known to select their microbial communities (Zhang et al., 2021) to improve plant resistance to stress (*e.g.*, through production of 1-aminocyclopropane-1-carboxylic acid deaminase), such as drought, insects, diseases, or TEs (Glick, 2014; Meyer et al., 2023).

During the last decades, the necessity of using different tree species in combination with microbial biotechnologies has been emphasized (Mench et al., 2010), as a method to improve the efficiency of phytomanagement strategies (Moreira et al., 2016). Salicaceae trees, particularly poplar, have been widely studied for their ability to create diverse microbial associations, including rhizospheric and endophytic interactions with microorganisms (Beckers et al., 2017; Ciadamidaro et al., 2022). It is now widely recognized that poplar is among the few cultivated trees that form strong symbiotic associations with microorganisms (Teste et al., 2020) and for this reason, the poplar microbiome has been well studied in phytomanagement contexts (Durand et al., 2017; Foulon et al., 2016; Schmidt et al., 2018; Vitali et al., 2019; Zappelini et al., 2015, Yung et al., 2021) (Table 1). Among these microorganisms, plant growth-promoting bacteria (PGPB) (Kong and Glick, 2017), and arbuscular mycorrhizal (AM) (Miransari, 2017), ectomycorrhizal (EM) (Gil-Martínez et al., 2018) fungi and Dark Septate Endophytes (DSE) (Deng and Cao, 2017), are major drivers of plant growth and tolerance to abiotic and biotic stress (Otero-Blanca et al., 2018).

PGPB promote soil bioremediation by direct or indirect mechanisms when in association with plants. Such mechanisms developed by PGPB include metal-protein complex formation, biotransformation, methylation, and demethylation (Tak et al., 2013). PGPB, *e.g.*, are

responsible of the production of the enzyme 1-aminocyclopropane-1-carboxylate deaminase (ACC-deaminase) that hydrolyses ACC into α -ketobutyrate and ammonia. This reaction induces the decrease of endogenous level of ethylene in plants, often provoked by TE excess (Glick, 2014). Therefore, PGPB could boost plant growth and development by the secretion of a variety of metabolites and hormones (Glick, 2012), by the increase of nutrients' bioavailability through mineral solubilisation (Ma et al., 2011), by nitrogen fixation (Kong and Glick, 2017), and by protection against pathogens (Glick, 2012). On this regard, in a study of Sharma et al. (2013), it has been proved that certain PGPB, the phosphate solubilizing bacteria (PSB), are able to solubilize P and favours its uptake by plant through acidification, exchange reactions and/or organic acid production. At the same time, recently (Guo et al., 2020) PGPB showed a capacity at decreasing TE availability in soil by the release of extracellular polymeric substances. These polymeric substances, indeed, might sequester TE by forming stable complexes.

Fungi are one of the most abundant components of the soil microbiota and their diversity is influenced by a variety of climatic and edaphic factors (Tedersoo et al., 2014). Mycorrhizal fungi are well known to form symbiotic associations with most (80%) terrestrial plants (Smith and Read, 2008). Previous study (Egidi et al., 2019) demonstrated that generalist Ascomycota dominates soils globally and that they have a significantly higher number of genes related to stress-tolerance and resource uptake. Poplars symbiotic fungi are well known for their essential roles in soil fertility, colonization, plant nutrition, and metal uptake (Smith and Read, 2010; van der Heijden et al., 2015). Several studies (Krpata et al., 2008; Regvar et al., 2010; Hryniewicz et al., 2012) exhibited recurrent association of AM and EC strains with different poplar clones, especially under stressful conditions, such as TE contamination. Bellion et al. (2006) found that the beneficial effects of this association is principally related to the capacities of EC to protect themselves and their hosts from TE pollution, e.g., by binding them into cell-wall components

or by sequestering large amounts of TE in vacuoles. Moreover, Ciccattelli et al. (2010) observed that *R. intradices* showed high capacity to improve plant biomass in highly stressful and nutrient-poor environments. For instance, in our recent studies, we underlined the capacities of EM and AM inoculation on poplar cultivars “Skado”, growing at a multi-contaminated site, in enhancing biomass production (Ciadamidaro et al., 2017) and reducing TE translocation in leaves (Phanthavongsa et al., 2017) (Table 1). In the past last years, special attention has been given to the use of inoculation of plants with microbial consortia, responsible of improving plant TE uptake and accumulation in phytoextraction techniques or limiting TE translocation from roots to shoots in phytostabilisation processes (Berthelot et al., 2016; Ma et al., 2019; Pepper et al., 2015). A proposed strategy for the remediation of stressed and degraded environments is based upon phytotechnologies involving the inoculation of microbial strains to improve the quantity and diversity of the microbial community.

Table 1. Impact of microbial inoculation on poplar growth and TE accumulation. Selected examples of field and greenhouse trials from the literature.

Experimental conditions	Poplar clones	Main features	Reference
Field trial Mixed (ECM + AM) inoculum	<i>Populus trichocarpa</i> x <i>P. maximowiczii</i> (Skado) <i>P. deltoides</i> x <i>P. nigra</i> I-214 (I-214)	Significant enhanced growth after 2, 4 and 7 years using a Slight decrease in TE content in leaves	Ciadamidaro et al., 2017 Phanthavongsa et al., 2017 Ciadamidaro et al., 2022
Field trial AM inoculum	<i>P. nigra</i> clone 62/154 <i>P. alba</i> clone 44/9	Mycorrhizal inoculation improved the efficiency of poplar on polluted soil.	Salehi et al., 2016
Greenhouse conditions Inoculation with 2 bacteria	<i>Populus deltoides</i> x (<i>Populus trichocarpa</i> x <i>Populus maximowiczii</i>) (Dender) <i>Populus deltoides</i> x (<i>Populus trichocarpa</i> x <i>Populus maximowiczii</i>) (Marke)	Bioaugmentation with both endophytes increased the shoot length of <i>Populus</i> ‘Marke’ Inoculation with <i>Methylobacterium</i> sp. reduced the bioaccumulation of Zn in ‘Marke’	Vannucchi et al., 2021
Greenhouse conditions	<i>Populus tremula</i> x <i>alba</i> INRA 717-1B4	Plant responses to DSEs varied from neutral to beneficial depending on the soil and the strain	Berthelot et al., 2017

Inoculation with 3 dark septate endophytes			
Greenhouse conditions with Pb contaminated agar medium Inoculation with 2 ECMF strain	<i>Populus × canescens</i>	Plants inoculated with the tolerant fungal strain grew better than the control plants	Szuba et al., 2017
Greenhouse conditions with TE contaminated soils Inoculation with 3 AM strain	<i>P. alba (clone AL35)</i>	Bioaugmentation with both endophytes increased the shoot length of Populus ‘Marke Inoculation with AM fungi increased Cu and Zn accumulation in poplar leaves. Mycorrhizal plants exhibited increased capacity for phytostabilization of HMs	Cicatelli et al., 2014

For all these reasons, understanding the interactions between poplar and microorganisms can be of particular socio-economically importance and many efforts have been made to characterize poplar microbiome (Cregger et al., 2018).

4 Molecular processes for the management of TE

Cobalt, copper, iron, manganese, nickel, and zinc are essential trace elements (TE) in cellular processes in plants, as they act as key cofactors for many enzymes, are components of transcription factors and other proteins, and are essential for the functions of mitochondria and chloroplasts. However, when present in elevated concentrations, along with non-essential metals such as cadmium, lead, and mercury, essential TE can become very toxic, as they can cause oxidative damage or compete with other essential ions. A network of uptake, exclusion, chelation, trafficking and storage mechanisms ensures that TE homeostasis is maintained at cellular level. Plants use sequestration, exclusion, and chelation strategies to detoxify TE (Angulo-Bejarano et al., 2021, Seregin and Kozhvnikova, 2023). Several poplar genes have been deciphered over the last 15 years, with an acceleration in poplar research since the publication of the genome in 2006 (Tuskan et al., 2006). Below is an overview of the mechanisms described.

4.1 Uptake and internal transport of metals

Genome-wide analysis of TE transporters was undertaken following the publication of the poplar genome (Tuskan et al., 2006; Migeon et al., 2010; Li et al., 2015). Seventy-three full-length TE transporter genes were reported in the *Populus* genome, which was the largest number of TE transporters genes identified in any single species to date. Several recent papers have highlighted features of a number of these genes (Table 2). Several gene families indeed include transporter genes involved in TE uptake and sequestration, such as the *CDF* family for Zn, Fe/Zn or Mn (Montanini et al., 2007; Peiter et al., 2007) and the *NRAMP* family for Mn and Fe (Pottier et al., 2015).

Zn. Zinc is an essential element for plant growth and development and is involved in a range of physiological processes. Poplar growth and development are highly sensitive to environmental Zn at early developmental stages but relatively resilient at later developmental stages and Zn homeostasis is maintained primarily in roots and leaves where active metabolism is occurring. Interestingly, the poplar clone *P. deltoides*, clone Lux showed increased uptake and accumulation of Zn in shoot without significant reduction in growth makes this an interesting candidate for the phytoremediation of Zn-polluted sites (Stoláriková-Vaculíková et al., 2015). One of the first Zn transporter to be fully characterized was a member of the so-called *CDF* family, named *PtdMTP1* (Blaudez et al., 2003). Its heterologous expression in relevant yeast mutants conferred resistance specifically to Zn, possibly because of sequestration into the vacuole. A *HMA* protein was latter demonstrated to be involved in Zn (Adam et al. 2011). Overexpression of *PtHMA4* result in doubling of Zn accumulation in leaf tissues in an overexpressed *PtPCS1* line, whereas *HMA4* was down regulated in response to excess Zn. Two members of the ZIP family were found to be related to Zn transport in poplar (Adams et al., 2012). *PtZNT1* was expressed in roots and was thought to control Zn entry into root cells. *PtZIP1.2* was found to be expressed in poplar stem tissue and was up-regulated under adequate

Zn and was down-regulated under Zn excess. The coordinated activity of the two genes may ensure a maintenance of Zn cellular concentrations.

Cadmium. Cadmium is a highly toxic TE for most living organisms. Due to anthropogenic activities, Cd pollution has become a serious problem worldwide. In a recent study, *Populus cathayana*, a dioecious species, was found to display sexual dimorphism in Cd tolerance (Li et al., 2022). When sufficient Zn was made available, male poplars exhibited elevated Cd accumulation, low root-to-shoot translocation, elevated antioxidant defence abilities, and an increased photosynthetic rate, while female poplars were much less responsive to Cd stress than males. Being a non-essential metal, Cd is often taken up by proteins involved in the transport of divalent cations of essential metal into the roots of plants. In a study by Rome et al (2016), Cd was sought to induce the expression of a few transporter genes such as members of the *IRT1*, *NRAMP* and *OPT3* families. The role of *NRAMP1* in Cd transport was recently confirmed in *Populus canescens* (Yu et al., 2022). In another study, a novel ABC transporter gene named *PtoABCG36* was cloned (Wang et al 2019). Overexpressing *PtoABCG36* in yeast and in *Arabidopsis* enhanced Cd tolerance by decreasing Cd content in plants, indicating that *PtoABCG36* may function as a cadmium exclusion pump under Cd stress in plants (Table 2).

Copper. Cu is a redox-active transition metal essential for plant growth and development. Its reversible oxidation-reduction features make Cu very valuable as a cofactor in several metalloproteins. At equilibrium, the Cu ion plays a key role in plant growth and development, including in poplar (Zhang et al., 2015). The *PtCOPT* family was made of 7 highly similar members, all of them having tissue-specific expression patterns. Some of the *PtCOPT* were induced by several nutrients, including Cu. The authors emphasizes that *PtCOPTs* may play key roles in balancing the concentrations of Cu with another nutrient in *P. trichocarpa*. A study also highlighted the role of miRNA in Cu deprivation (Ravet et al., 2011).

Manganese. Mn is the second most prevalent transition metal, after iron, in the Earth's crust and an essential micronutrient for all organisms, including plants. Photosynthetic organisms have an additional specific requirement for Mn (Mn) for light energy conversion and water-splitting. This metal is an essential constituent of the mitochondrial manganese superoxide dismutase. Two recent papers have dealt with Mn transport in poplar. The first published in 2020 (Gao et al 2020) described three genes that showed some ability to transport Mn. The expressions of *PtrMTP8.1*, *PtrMTP9* and *PtrMTP10.4* in the $\Delta pmr1$ mutant yeast alleviated its sensitivity to Mn. In a recent paper (Pottier et al. 2022), the authors demonstrated that the poplar genome contained two paralogues of *NRAMP* that encode functional metal transporters, and which functions *in planta* have however diverged. *NRAMP3.2* bear the same function in TE retrieval from the vacuole as its ortholog in *Arabidopsis AtNRAMP3.2* and *AtNRAMP4*, whereas the *NRAMP3.1* gene displays a distinct subcellular localization as well as a distinct function. The authors suggested that *Potri NRAMP3.1* could be involved in Mn distribution in poplar aerial organs.

Iron. The redox properties of iron make it an essential element for practically all life (Connorton et al., 2017). Plant chloroplasts are particularly rich in iron–sulphur (FeS) proteins such as Photosystem I, ferredoxins and a range of metabolic enzymes. Two genes belonging to the iron-regulated transporter (*IRT*) were characterized from two *Populus tremula* lines, an iron chlorosis resistant and a susceptible line. These two genes were strongly up-regulated under Fe deficiency (Huang and Dai 2015). A yeast complementation test revealed that both *PtIRT1* and *PtIRT3* genes were able restore the Fe uptake capacity under the iron uptake-deficiency condition.

Mercury. Hg is a non-essential metal that may be incorporated into leaf tissues. When grown on Hg contaminated soils, Hg entry into poplar leaves was demonstrated to occur exclusively through an atmospheric pathway (Assad et al 2016). In a recent study, *PtABCC1*

was shown to play a key role in enhancing tolerance and accumulation to Hg in poplar, which provides a promising way for phytoremediation of Hg contamination (Sun et al., 2018). However molecular mechanisms involved in Hg entry into eukaryotic cells remains unknown. Our recent set of data suggest that poplar leaves may be a pertinent indicator of Hg contamination in the atmosphere for any Hg content in soil, particularly by using dendrochemistry to record historical Hg emissions from past industrial activities. (Maillard et al., 2016).

Aluminium. Aluminium is widespread in the Earth's crust and its availability to plants increases with decreasing pH of the soil. The toxicity of Al may drastically reduce plant growth in acidic soils, where $\text{pH} < 5.5$, Al being present as the most toxic trivalent cation Al^{3+} . The mechanisms for plant adaptation to Al toxicity have been reviewed (Kochian et al., 2015; Ofoe et al., 2023). However, poplar cuttings from *in vitro* culture were characterized with a reduced sensitivity to the toxic aluminium ions, both in vitro and in a soil from a polluted area (Bojarczuk, 2004). The Al-inducible MATE gene *PtrMATE1* was recently isolated from *P. trichocarpa* (Li et al., 2017). *PtrMATE1* was not directly involved in Al transport per se but contribute to Al poplar cell detoxification by external complexation through the extrusion of citrate.

Table 2. Selected genes of transporters isolated and/or characterized from poplar cultivars involved in TE uptake and chelation.

Genes and gene families	Poplar cultivar	Metal transported	Reference
ZIP			
<i>PtZNT1</i> <i>PtZIP1.2</i>	<i>Populus trichocarpa</i>	Zn	Adams et al., 2012
P-type ATPase (HMA)			
<i>PtHMA4</i>	<i>Populus trichocarpa</i>	Zn	Adams et al., 2011 De Oliveira et al., 2018
COPT			
7 genes	<i>Populus trichocarpa</i>	Cu	Zhang et al., 2015

NRAMP			
<i>PcNRAMP1</i>	<i>Populus × canescens</i>	Cd	Yu et al., 2022
<i>PtNRAMP3.1</i>	<i>Populus trichocarpa</i>	Mn	Pottier et al., 2022
<i>PtNRAMP3.2</i>	<i>Populus alba</i> 'Villafranca' clone		
<i>PaNRAMP1.3</i>	<i>Populus alba</i> 'Villafranca' clone	Mn	Romè et al., 2016 Vannucchi et al., 2020
CDF			
<i>PtMTP1</i>	<i>Populus trichocarpa</i>	Zn, Co	Blaudez et al., 2003
Various <i>MTP</i>	<i>Populus trichocarpa</i>	Zn, Fe/Zn or Mn	Montanini et al., 2007 Peiter et al., 2007
<i>PtrMTP8.1</i> , <i>PtrMTP9</i> and <i>PtrMTP10.4</i>	<i>Populus trichocarpa</i>	Mn	Gao et al., 2020
ABC (ATP-binding cassette)			
<i>PtABCG36</i>	<i>Populus tomentosa</i>	Cd	Wang et al., 2019
<i>PtABCC1</i>	<i>Populus trichocarpa</i>	Hg	Sun et al., 2018
MATE			
<i>PtrMATE1</i> <i>PtrMATE2</i>	<i>Populus trichocarpa</i>	Al	Li et al., 2017
IRT			
<i>PtIRT1</i> , <i>PtIRT3</i>	<i>Populus tremula</i>	Fe	Huang and Dai, 2015
<i>PaIRT1</i>	<i>Populus alba</i> 'Villafranca' clone	Cd	Romè et al., 2016
Glutathione related			
<i>PtPCS1</i>	<i>Populus trichocarpa</i>	Zn	Adams et al., 2011 Filiz et al., 2019
γ -ECS	<i>Populus tremula</i> x <i>P. alba</i>		Koprikova et al., 2002 He et al., 2015
<i>PaPCS1</i>	<i>Populus alba</i> L. 'AL35'	Zn and Cu	Pallara et al., 2013
Metallothionein related			
	<i>Populus alba</i> L., cv. Villafranca WT and 10ECA and 46ECA clones	Zn and Cu	Turchi et al., 2012
<i>PtdMT1a</i> , <i>PtdMT1b</i> , <i>PtdMT2a</i> , <i>PtdMT2b</i> , <i>PtdMT3a</i> , <i>PtdMT3b</i>	<i>Populus trichocarpa</i> × <i>P. deltoides</i> cv. Beaupré	Zn and Cu	Kohler et al., 2004
<i>PaMT1</i> , <i>PaMT2</i> <i>PaMT3</i>	<i>Populus alba</i> L., cv. Villafranca	Zn and Cu	Castiglione et al., 2007

4.2 Glutathione and phytochelatin related pathways

Thiol compounds have metal-binding activity that is involved in cytosolic buffering, vacuolar sequestration, and long-distance transport in the phloem (Clemens, 2019). Our current understanding on thiols as TE ligand derived from mutant phenotypes and indirect biochemical

evidence. In poplar only few thiol-based mechanisms have been described, that may contribute to TE homeostasis in cells (Table 2).

Zn. In addition to several transport proteins involved in Zn homeostasis, the phytochelatin synthase (PCS) was detected in the poplar genome (Adams et al. 2011). The *PtPCS1* transcript level in poplar is modulated to allow Zn entering under plant deficiency, while being inhibited under excess. The two genes were further addressed in 2 different clusters, subgroup A1 including the sequences of both Arabidopsis PCSs and poplar (Potri.014G195800.1) whereas subgroup A2 had poplar (Potri.014G195900.1) and other plant sequences (Filiz et al., 2019).

Cd. In many organisms, γ -glutamylcysteine synthetase (γ -ECS) involved in the biosynthesis pathway of glutathione (GSH), is also a key enzyme as precursor of phytochelatin (PCs). In an early study, a bacterial gene for GSH synthesis was overexpressed in poplar and cadmium accumulation was followed in hydroponics (Koprikova et al., 2002). Poplar lines over-expressing the so-called glutamylcysteine synthetase (γ -ECS) enzyme accumulated significantly more Cd in root tissue. The same research group later published two additional papers in which the role of γ -ECS in Cd tolerance in poplar was confirmed (Ivanova et al., 2011, He et al., 2015).

4.3 Metallothionein related pathways

An important role in detoxification and homeostasis of intracellular metals is played by metallothioneins (MT), which are metal binding proteins composed of a ubiquitous family of low-molecular weight proteins containing Cys-rich domains at the amino and carboxy-terminal regions.

Zn and Cu. In an earlier study, six metallothionein-related genes were identified in the *P. trichocarpa* \times *P. deltoides* cv. Beaupré poplar genome, where they form a multigene family. The six different *MT* transcripts were detected constitutively in poplar tissues. However, in poplar roots, only treatment with Zn had a stimulating effect on type 1 and type 2 *MT* gene

expression (Kohler et al., 2004). Similarly, 3 *MT* genes were characterized in *P. alba* L., cv. Villafranca (Castiglione et al., 2007). The results obtained showed that in the white poplar *PaMT1* and *PaMT3* gene expression in leaves was greatly stimulated by elevated concentrations of Zn, the different *MT* genes responding in an organ- specific manner. To expand knowledge on the role exerted by metallothionein in TE tolerance in poplar, the performance of the non-transformed clone Villafranca (NT) and the selected high performing clone AL22 was compared monitoring TE translocation and accumulation in roots and leaves and several stress indicators (antioxidant defenses) in the presence of excess concentrations of Zn and Cu (Turchi et al., 2012). The authors concluded that metallothionein could play a role in ROS scavenging leading to enhanced TE tolerance and increased Zn and Cu sequestration in root and leaf. The same group of researchers later confirmed the role of metallothionein by expressing a metallothionein gene from *Pisum sativum* in white poplar (*Populus alba* L., cv 'Villafranca'). Higher tolerance to Cu of the *PsMT* expressing poplar lines was measured, as well as lower reactive oxygen species (Balestrazzi et al., 2009).

5 Coppicing management and valorization of the biomass

5.1 General considerations

The production of biomass by dedicated poplar-based forestry was studied by AFOCEL and INRA from the 1980s onwards in France, comparing short rotation coppice (SRC, planting density of 1,000 to 2,000 stems/ha, rotation of 7 to 10 years.) and very short rotation coppice (VSCR, planting density of 5,000 to 10,000 stems/ha, rotation of 2 to 4 years) systems (Berthelot and Gavaland, 2007). SRCs for paper production were developed over a few hundred hectares at the initiative of several pulp mills. More recently, over the last ten years or so, there has been renewed interest in lignocellulosic biomass because of national and European policy decisions aimed at increasing the share of renewable energies in the energy mix. Numerous

research projects have sought to characterize the value of energy crops for agriculture and forestry (Bastien et al., 2015). Among woody species, poplar has several major advantages, such as rapid growth, a good ability to sprout, good adaptation to French soil and climate conditions, ease of propagation and a high level of genetic improvement (clonal varieties). However, the inclusion of this type of dedicated perennial crop on farms raises the question of the silviculture practices: planting density, length of rotation, type of harvest. Results, obtained on sites well adapted to poplar and for several cultivars, clearly indicate that SRC systems produce more woody biomass per hectare than vSRC systems, over a period of 6 to 8 years (Table 3). Other factors also seem to favor SRCs, such as better biomass quality (lower proportion of bark) and lower export of mineral elements (Berthelot et al., 2010), as well as lower installation costs (de Morogues et al., 2011). Poplar vSRC may still be of interest in specific situations, such as plantations intended for purification or phytoremediation, irrigated systems, where their production will be strongly stimulated by water inputs, or under power lines where the maximum tolerated tree height is low.

5.2 (v) SRC for phytoremediation

For the feasibility of the phytoextraction, the use of (very) SRC crops have been fostered within recent years, combining phytoremediation with the production of valuable biomass on the contaminated land (Padoan et al., 2020). Fast-growing plants belonging to the *Populus* genera were the most studied as woody crops and metal accumulators, have been shown to be highly productive (Castiglione et al., 2009; Ruttens et al., 2011; Ciadamidaro et al., 2019; Chalot et al., 2020) (Table 3). The pioneering research on poplar SRC was held by a group in Belgium in the early 2000 (Table 3). The objectives of this work were to study the clonal variation in vertical distribution of TE within a tree and to quantify the phytoextraction potential of six poplar clones in a SRC culture on a moderately contaminated soil (Laureysens et al.,

2004, Laureysens et al., 2005). Al, Cd and Zn were found to be most efficiently taken up and were primarily accumulated in leaves and bark.

In a project that aimed at exploring the potential of poplar for phytoremediation (Chalot et al., 2020), large field trials of several hectares were implemented to produce enough biomass for further valorisation and estimate productivity at a realistic scale. Field trials were based on the utilization of a large panel of poplar cultivars, planted on SRC and vSRC schemes. In the culture conditions cultivars can be divided into three classes of production i) High potential (Dvina, I-214, Triplo and Skado), greater than 9 t DM / ha / year, ii) Average potential (Lena, Koster, Muur, Vesten, Trichobel and Bakan) between 4 and 8 t DM / ha / year and iii) Low potential (Dorskamp, Flevo and Fritzi Pauley) less than 3 t DM ha / year. However, it is important to compare these data with those of other trials of poplar in France. These comparisons reveal that at equal ages, the most productive cultivars produce as much biomass as other cultivars grown on other conditions in France, in non-polluted site. This indicates the great potential of poplar biomass production in phytoremediation.

Table 3. Some examples of coppicing schemes for poplar in the context of phytoremediation at field scale. Np, not provided.

# of poplar clones tested	Coppicing scheme	Range of poplar yields	Reference
4	SRC 20,000 cuttings per ha	3.5-8.1 odt/ha/year (depending on clone and year)	Nissim et al., 2022
2	SRC 2,500 cuttings per ha	1.7-38.5 odt/ha/year (depending on clone and sampling year)	Ciadamidaro et al., 2022 Ciadamidaro et al., 2017
14	SRC 2,500 cuttings per ha	3-9 odt/ha/year depending on poplar clone and site	Chalot et al., 2020
2	np	1-3 odt/ha/year (depending on clone and season)	Kubatova et al., 2018, 2022
6	vSRC 15,000 cuttings per ha	2-5 odt/ha/year depending on poplar clone	Michels et al., 2016
2	vSRC 13,330 cuttings per ha	4-6 odt/ha/year depending on poplar clone and site	French et al., 2006
6	vSRC 10,000 cuttings per ha	2-3.8 odt/ha/year depending on poplar clone	Laureysens et al., 2005

13	vSRC 10,000 cuttings per ha	4-18 odt/ha/year depending on poplar clone	Laureysens et al., 2004
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5.3 Economical valorisation of poplar biomasses

Several industrial processes have been explored for the valorisation of poplar-borne woody biomasses. These include combustion (Monedero et al., 2017), pyrolysis (Roy & Dias, 2017), bioethanol (Jung et al., 2013; Guo et al., 2014; Morales-Vera et al., 2022) and pulp production (Wu et al., 2014). Within the past decade, some of these industrial processes have been verified with phytoremediation-borne poplar biomass, allowing to assess the suitability of the poplar biomasses and describing related-operational problems due to the presence of pollutants in the treated biomass. Phytoextraction leads to metal-enriched plant biomass whereas (aided) phytostabilisation leads mostly to plants with TE concentrations in the range of physiological levels.

5.3.1 Combustion and the fate of metal during the industrial process

The search for an increasing exploitation of renewable energy sources and a reduction of greenhouse gas emissions-GHG emissions in the production of heat and electricity, has advanced the development of bioenergies. Biomass production for bioenergy purposes needs the use of very fertile soils, which however may compete with food crops and eventually lead to the exploitation and conversion of arable lands. The use of phytoremediation-borne biomasses may thus represent an alternative and considered as an advantageous resource. In a pioneering work, we investigated the fate of TE from poplar wood during the conversion process of biomass to heat that allows for an efficient separation of the various ash fractions. The phytoremediation wood was harvested from a TE-contaminated agricultural site planted with a high-density poplar stand (Chalot et al., 2012). During the combustion process, Cd, Pb, and Zn were significantly recovered in the ash fraction of the filter, thus complying with all regulatory thresholds. It was calculated that 70 g of Cd may ended up into 140 kg of ashes (Fig.

2). It is true that we were only displacing the problem, but immobilizing Cd and other TE in ash will drastically limit their environmental impact.

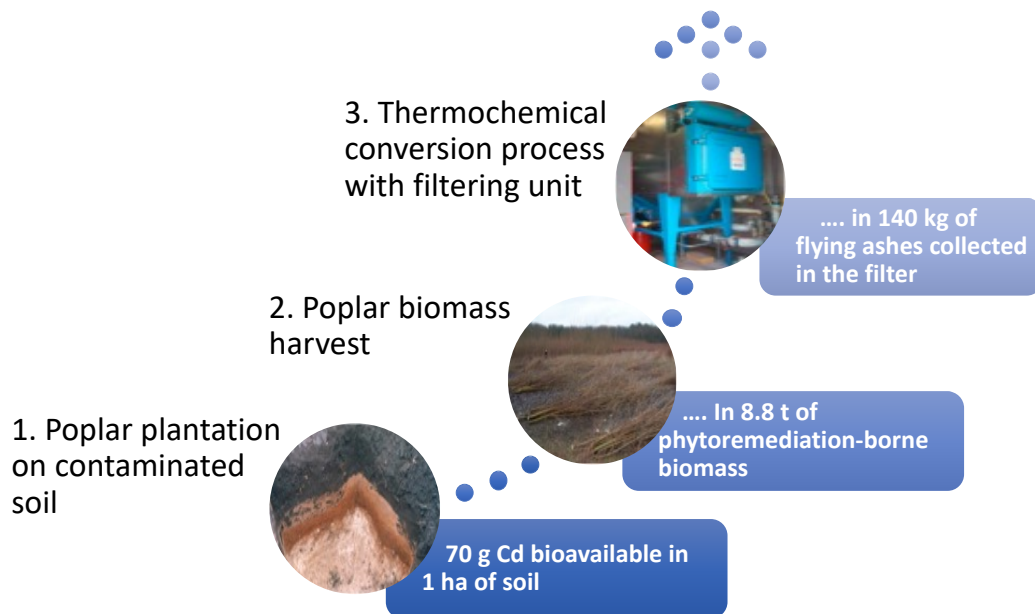


Figure 2. Fate of cadmium from soil to the final by-product during the thermochemical conversion process of poplar biomass (data from Chalot et al., 2012).

5.3.2 Torrefaction and pyrolysis of TE enriched poplar biomass

In a recent study, torrefaction (at 290°C) and pyrolysis (at 450 and 800 °C) assays were carried out at a pilot scale with TE-enriched poplars from a contaminated soil to follow the fate of TE in the various end-products (Bert et al., 2017). It was evidenced that metals contained in TE-enriched poplar biomass did not hinder the process by modifying the yield of end-products. However, TE were recovered in the various by-products, depending on the temperature. At 450 °C, TE were recovered in biochar, in bio-oil and further in gases. Zn, Pb and Cd were mostly recovered in gases, which became the second TE recovery compartment. It was concluded that by-passing potential TE limitations and control TE emissions, end-products should be treated or upgraded to allow the use of TE-enriched biomass as feedstock. However, in this study, it was found that chlorine content of the initial biomass was a key factor to take

into account when biomasses have to be processed, volatile metal chloride complexes being formed at process temperatures. The knowledge of biomass composition would help to predict volatilization.

5.3.3 Gasification of TE enriched poplar biomass

In recent assays, the fluidized-bed gasification of phytoremediation-borne poplar biomass was analysed. Poplars were originated from an area contaminated by polychlorinated biphenyls (PCBs) and TE (Ancona et al, 2019, Gallucci et al., 2022). To this end, the quality of the biomass (assessment of contaminant content) was evaluated, and particular attention was paid to the trapping of potential contaminants (TE and PCBs) in the ash during the gasification process and to any additional catalytic activity due to the presence of metals. The authors concluded that, although energy from biomass produced on a contaminated site is currently regarded as waste and incurs disposal costs, poplar biomass grown on multi-contaminated soil can be used for energy purposes without any impact on the environment.

6 Conclusions and perspectives

On contaminated lands, the application of phytoremediation with woody crops at field scale is a great challenge that aims at controlling and reducing the environmental impact of those sites while developing economic opportunities. Based on the results of this meta-analysis, we found poplars to be relevant candidates for the remediation of metal-contaminated soils; however, metal uptake preferences of the genus should be considered to achieve the most efficient remediation capacities. The implementation of large field trials is a key stage to provide theoretical and technical knowledge in poplar-based phytomanagement strategies. Regarding this purpose, feedback from field study is scarce. Most large-scale studies realized so far pointed out the complexity of environmental processes that are not considered in greenhouse

experiments. These poplar biomasses may enter valorisation pathways if (i) TE do not disturb the functioning and the performance of the processes, (ii) if the TE transfer is controlled and impacts on the environment are prevented, and (iii) if such plant use complies with current regulation. The balance between costs and benefits will help to select the best valorisation option.

Traditional physiological and genetic studies of metal homeostasis are being enhanced by genomics and metabolomics approaches. These breakthrough approaches are being developed in different research projects to initiate the next generation of bioremediation technologies. The strategy would be to increase metal accumulation in a synthetic biology approach combining the expression of several key genes (coding for metal transporters of the ZIP, NRAMP, HMA and MTP families as depicted in Table 2) in the same plant under the control of tissue-specific promoters to drive uptake at the root epidermis, root-to-shoot transfer in the vasculature and metal sequestration in the wood. Metal sequestration could be targeted to shoots rather than to leaves using wood specific promoters, for examples pointing out the role of, *e.g.*, non-coding RNAs as part of regulatory module that includes the MATE transporter and that may control Pb²⁺ tolerance, uptake, and plant growth in *Populus tomentosa* (Chen et al., 2022). The role of miRNA as part of a regulatory network that play pivotal roles in sulfur-mediated Cd accumulation and detoxification in Cd-exposed poplars was recently highlighted in *Populus deltoides* (Shi et al., 2020). In addition to well-known transport and sequestration proteins, these regulatory networks underlying the physiological responses of poplar to metal exposure deserve attention.

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