# Morphology and Physiology of Plants Growing on Highly Polluted Mining Wastes

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## Abstract

Biological methods have been described and suggested as a useful tool in studies on plant growth, development, and phytoremediation abilities in heavily polluted soil. Pot experiments are easier in practice, although field studies show a clearer picture of plant response to the stressors present in a polluted environment. Speciation (a form of toxic element), as well as mycorrhiza in the soil, play a role which is hard to overestimate. The enzymatic activity involved in this

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process will be discussed in this chapter. Plants used for recultivation should show a wide ecological tolerance to stressors. Plant resistance to trace elements (TE), induced systematic resistance (ISR), as well as root architecture alterations indicate a defence strategy in response to TE and possible TE accumulation in the tissue, with successful phytoremediation. Long-term exposure of plants to extremely high concentration levels of TE damages both their roots and functioning.

**Keywords**

Plant physiology · Polluted substrates · Root architecture · Trace elements · Wastes

## 7.1 Introduction

The level of environmental contamination with industrial debris (waste); not only its concentration but also the form (speciation) of the elements there, plays an important role. Physical and/or chemical methods are used in the reclamation of ecosystems through stabilization of elements in water and wind erosion. Biological methods—in the case of plants called phytoremediation—reduce the bioavailability and mobility of toxic elements. Pot experiments, which are easy to perform and flexible in correction, are often applied in such methods. Field studies, although much more difficult to modify, show real and well-documented plant responses to the stressors present in a polluted environment.

Although the following relationship appears to be obvious: the higher level of element concentration, the higher metal/metalloid uptake is observed in experimental plants; this is not always the case as there are several factors and soil properties that can influence phytoextraction. Microorganisms present in ecosystems play a particularly important role in this process. Enzymatic activity is a key parameter as it indicates the biological status (ecotoxicity) of the contaminated environment (waste). Increased enzymatic biosynthesis of phytochelatins is coupled with the heightened activity of the plant antioxidative system. Contaminating metal

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accumulation in the tissue is associated with unspecific plant response (pigment content, lipid peroxidation, or antioxidant activity).

Plant resistance to toxic elements takes the form of plant-fungi associations (mycorrhizal interactions), which lead to induced systematic resistance (ISR). Plant roots are in direct touch (contact) with all the nutrients and toxic components of an ecosystem and usually accumulate trace elements (TE). Their architecture alterations, influenced by the TE, is supported by mycorrhizal fungi in a defence strategy designed to cope with TE toxicity and the phytoremediation capability of plants. The above is accompanied by a cell wall (CW) and vacuole compartmentalization of TE. Binding TE with CWs, especially cross-linking by low-methyl esterified pectin's and enlargement of the CW capacity for sequestration, simultaneously increases the rigidity of the structure and therefore inhibits root elongation. Among the harmful effects of TE on root cell architecture, the most serious are alterations in the nucleus and nucleolus ultrastructure, while long-term plant exposure to extremely high concentrations of TE irreversibly damages root cells.

## 7.2 Plants Growing on Highly Polluted Substrates

Economic development promotes an increased demand for mineral raw materials, e.g. metal ores or coal extracted with the use of mining technologies. Highly contaminated industrial waste is becoming one of the most serious ecological problems worldwide, not only because of the high concentration of toxic elements but their diverse structure and considerable amount (Lottermoser 2010; Candeias et al. 2014; Behera and Prasad 2020). In 2014, the total amount of waste generated in the EU by all industrial activities and households was estimated to be 2503 million tonnes, the highest ever quantity recorded in the EU in the period 2004–2014. Over 64% of this amount of waste in 2014 was represented by mineral wastes from mining and extraction activities (EUROSTAT 2018). Nevertheless, there remain high concentrations of precious elements whose recovery from waste to pure form would be highly beneficial for industry (Aghaei et al. 2017). The concentrations of these elements are usually too high for the environment but too low for applied technologies to retrieve. The use of expensive technical methods for the thousands or millions of tons of waste deposited in settlers has long been an unrealistic idea. Conventional technologies used for reclamation of mining wastes are based on physical and chemical stabilization processes. Physical stabilization is targeted at a reduction of wind and water erosion; it consists of covering mine wastes with harmless materials, i.e. usually mining waste rocks, gravel, or topsoil collected from neighbouring areas. These remain provisional solutions and usually fail to produce long-lasting effects (Mohanty et al. 2010). Chemical reclamation consists of soil leaching/acid extraction and soil washing. The processes are usually based on the use of organic reagents for the removal of trace elements. They are considerably more efficient than physical methods and offer good results, especially in small objects with a high contamination level (Wang et al. 2017).

However, biological methods also seem to be a promising solution to mine waste remediation (Sangeeta and Maiti 2010; He and Kappler 2017). Particular attention has been paid in this area to phytoremediation (Wang et al. 2017). The goal of phytoremediation is to reduce the bioavailability and mobility of harmful pollutants from mining wastes, protect groundwaters, and prevent the spread of harmful substances into the consecutive elements of the food chain (Mohanty et al. 2010; Kuppusamy et al. 2016; Saha et al. 2017; Wang et al. 2017). Some plants have evolved several mechanisms for accumulation of excessive amounts of trace elements in tissues, even in extremely adverse conditions (Conesa et al. 2009; Mleczek et al. 2018). The knowledge of the application of phytoremediation techniques to neutralize contaminants originating from various mining wastes is still insufficient; therefore, further research is indispensable to find plant species that will be the most effective in solving the problem of different mining wastes (Mohanty et al. 2010). Studies on the possibility of the using plants for remediation of industrial wastes, including mining tailings were undertaken both as pot and field experiments.

### 7.2.1 Pot Experiments

Pot experiments using mining tailings offer the possibility to quickly modify the substrate (mixing, homogenization, enrichment) due to the low mass of used wastes. An example can be seen in the studies of Gupta and Sinha (2006), where different additions of tannery sludge were used in a pot experiment. Thanks to the relatively easy preparation of model systems, these studies indicated the optimal amount of tannery sludge (25%) for the practical use of phytoremediation by *Sesamum indicum* (L.). Too high a concentration of heavy metals and/or metalloids in wastes contribute to the death of plants and serious changes in their structure, which precludes their practical use (Krzesłowska et al. 2019; see also Sect. 7.6.2). It is worth emphasizing that such experiments have usually been limited to selected plant species such as *Pennisetum sinese* Roxb (Napier grass, HGN) as described by Ma et al. (2016a). The authors characterized the uptake of arsenic (As), cadmium (Cd), chromium (Cr), copper (Cu), manganese (Mn), lead (Pb), and zinc (Zn) in plants growing on tailing waste from Dabaoshan, Shaoguan (China) and showed that the efficiency of phytoextraction ranged from 12 to 26% with the highest content in total biomass of shoots and the highest concentration in fibrous roots. Such studies have highlighted the important role of a well-developed root system for further plant growth and heavy metal accumulation. In spite of the clear inhibition of *P. sinese* growth, its well-developed root system qualifies HGN as a suitable plant for effective phytoextraction of heavy metals from tailing wastes.

Studies on trees or shrubs and their use in phytoremediation (dendroremediation), owing to their extensive root system, have become more widespread and wide-ranging in recent years, yet the limitation imposed by the age and size of plants remains (Mleczek et al. 2017, 2019). Shi et al. (2017) analysed *Salix integra* growing on mine tailings from Hangzhou (China). This willow species was characterized by diverse tolerance and metal uptake with respect to the percentage of wastes in the mixed substrate. The results obtained in this study, like those—described in numerous other papers—have pointed to the potential of the plant in phytostabilization or phytoextraction of mine tailings. Unfortunately, the use of tree species that seem promising in practice in pot experiments is generally highly problematic and gives only part responses to numerous questions since the influence of environmental factors is limited (Budzyńska et al. 2017, 2021). Therefore, the best solution would appear to be to look (compare) for plants whose uptake of metals most efficient and then conduct field experiments, indicating at the same time differences in plant responses depending on their origin. An example of this approach can be found in the studies of Wang et al. 2007.

### 7.2.2 Field Experiments

Generally, field experiments with mine tailings do not allow us to implement such daring modifications of substrates as in pot experiments, but the information gained shows the real plant response to a polluted environment (García-Salgado et al. 2012). To date, these experiments have probably been conducted on each kind of polluted waste (Dudka et al. 1996; Yanqun et al. 2004; Ang et al. 2010; Fernández-Martínez et al. 2015). These mining wastes were characterized by different concentrations of toxic elements which greatly reduced plant growth and development (Dudka et al. 1996; Mleczek et al. 2017; Krzesłowska et al. 2019 see Sect. 7.6). Limitations in plant growth were rather more an effect of a possible nutrient imbalance than the phytotoxicity of metals, as described, e.g. by Dudka et al. (1996) who studied *Hordeum vulgare* L., *Poa pratensis* L., *Solanum tuberosum* L., and *Trifolium pratense* L. exposed to extremely high concentrations of Cd, Cu, Pb, and Zn (4000; 106; 3452 and 11,375 mg kg$^{-1}$, respectively). Mining wastes usually contain an extremely high concentration of toxic elements such as As (Santos-Jallath et al. 2012); mercury (Hg) (Fernández-Martínez et al. 2015), Pb (Freitas et al. 2004; Čudić et al. 2016), or antimony (Sb) (Okkenhaug et al. 2011). The high concentrations of these elements and their great quantity deposited in the environment have created a pressing need to select the most effective plants for phytoextraction of toxic elements (Anawar et al. 2011; García-Salgado et al. 2012). For this reason, numerous papers have focused on a comparison of several plant species growing on the same wastes (Zhao et al. 2014). However, only some of them have compared a wide range of plant species, e.g. Baroni et al. (2004) or Karimi et al. (2013) studies (64 and 49 species, respectively).

The most popular plants researched were trees and bushes (Madejón et al. 2005; Domínguez et al. 2008), but also grasses, mosses, native ferns or rushes (Craw et al. 2007; Čudić et al. 2016). Tree and bush species were especially interesting as regards their traits such as long life or an extensive root system capable of deep penetration into the waste (Pratas et al. 2005; Migeon et al. 2009). Moreover, trees are characterized by selective uptake of elements described, e.g. by Zhao et al. (2014), who studied 18 Chinese tree species. The authors showed that particular tree species are capable of *i*) effective phytoextraction of a single metal; *ii*) hyperaccumulation; or *iii*) multi-metal accumulation. There is a clear and interesting response of selected plants (also trees) growing on mining sludge. The majority of available literature data describes the following relationship: the greater the concentration of toxic metals in mining wastes the higher their concentration in plant organs (Martínez-Sánchez et al. 2011; Alagić et al. 2013; Karimi et al. 2013), however, the metals/metalloids uptake is not always dependent on its concentration in substrate (Baroni et al. 2004; Santos-Jallath et al. 2012).

The problem of mining waste decontamination is an effect of two distinct stress factors: the high concentration of toxic metals and high salinity. Additionally, mining wastes are often substrates with alkali pH, high salinity, a heavily concise structure (percentage participation of loam over 10), low content of bioavailable nutrients, and low water retention capacity (Ssenku et al. 2014; Kuppusamy et al. 2016). The significance of pH, waste chemistry, and the mechanism used by plants in these unfavourable conditions, for example, of *Betula* sp. and *Tilia* sp., was clearly described by Alagić et al. (2013). Tree species from highly polluted areas (Bor Region in Serbia—mining and metallurgy) were characterized by different mechanisms of As and Cd uptake: a high ability of assimilation through leaves in the case of *Tilia* sp. and clear transport from the soil for *Betula* sp. Similarly, Kalinovic et al. (2016) compared tree species (*Pinus nigra* Arn., *Sambucus nigra* L., and *T. grandifolia*) growing in areas polluted by emissions from a Cu smelter and by the tailing ponds of open pit mines. They found that rates of metal uptake were dependent on plant species and that element concentration differed in particular plants. However, conducting studies on extremely polluted wastes and interpretation of obtained results was in many cases, less effective concerning the analysis of total metal concentration only. To describe the real response of a plant, data on the concentration of bioavailable metal forms is necessary (Fernández-Martínez et al. 2015). This factor alone, especially in case of mining wastes highly contaminated with trace elements, can be crucial to plant survival, adaptation, and element uptake.

For this reason, low bioavailability was ‘increased’ by the addition of numerous additions, e.g. sewage sludge to combine waste into two different processes in one remedy technique (Forsberg and Ledin 2006). A high concentration of elements in mining wastes with a simultaneous high concentration of their bioavailable forms were, in the majority of studies, the cause of high phytoextraction of elements to plant roots or even to above-ground plant parts (Jung et al. 2002; Okkenhaug et al. 2011). A distinct relationship between As concentration in polluted substrate and plants was described by Martínez-Sánchez et al. (2011). It is necessary to state that despite the close correlation between the As concentration in the substrate and plant, the efficiency of As will depend on the plant species. A confirmation of this can be found in the results described by Chang et al. (2005) who analysed *Pteridium aquilinum* growing on areas polluted by two gold (Au) mines (Duckum mine and Myoungbong mine in the Republic of Korea). The high potential of the selected *Polypodiopsida Cronquist* species growing on highly polluted post-industrial wastes was also widely discussed (Visoottiviseth et al. 2002; Wang et al. 2007).

A high concentration of metals in wastes is not unequivocal with its effective transport to plants, as described by Craw et al. (2007) who studied two historic gold mining sites in north Westland (New Zealand) and the growth of diversified plant species with clear phytostabilization. Similar observations were also described by Fernández-Martínez et al. (2015), who showed that selected plant species can be considered as excluders only and by Santos-Jallath et al. (2012), who found a low correlation between As in soil and plants in spite of a high concentration of this metalloid in wastes of 183–14,660 mg $kg^{-1}$. The authors of the works conducted their studies mainly using plants naturally growing in situ but also plants cultivated in these areas (Domínguez et al. 2008; Álvarez-Ayuso et al. 2012; García-Salgado et al. 2012). An efficient phytoremediation strategy for plants cultivated on mining wastes was generally the result of the specific traits of a growing plant and the impact of environmental factors directly acting on this (Otones et al. 2011). Parraga-Aguado et al. (2014) analysed *P. halepensis* growing on a mine tailing disposal site in Spain observed the immobilization of Cd, Cu, Pb, and Sb in woody stems as well as the effective transport of As, Cd, Sb, Pb, and Zn to leaf litterfall with a possible return to the environment after the vegetation period.

## 7.3 Physicochemical Properties of Mining Wastes: Implication for Phytoextraction

Mining wastes usually include waste rocks, overburdens, slags, and tailings on land surfaces. Mine wasteland generally comprises a bare stripped area, loose soil piles, waste rock and overburdened surfaces, subsided land areas, tailings dams, and other land degraded by mining facilities, among which the tailings dams and waste rock surfaces often pose extremely stressful conditions for restoration (Li 2006; Gautam et al. 2016a). The largest amount of waste is generated by the mining and processing of coal, followed by non-ferrous and ferrous ores and industrial minerals. It is estimated that approximately 2–12 tonnes of overburden are removed with every tonne of metal extracted from ores (Mohanty et al. 2010). Storage of these wastes in heaps results in degradation of soils, contamination of water resources, pollution of air in adjacent areas, and a consequent reduction of biodiversity (Álvarez-Valero et al. 2008; Candeias et al. 2014; Ssenku et al. 2014; Saha et al. 2017). The high variability of the physicochemical properties of these wastes, as well as local hydrological, topographical, and meteorological conditions, contribute to a varied rate of release of various types of pollutants, including toxic trace elements. Therefore, detailed characterisation of these wastes is required to assess their potential toxicity and the possibility of further disposal thereof (Lottermoser 2010; Candeias et al. 2014; Cappuyns et al. 2014; Azarova et al. 2019).

Mining wastes contain numerous contaminants, e.g. salts, metalloids, metals, radionuclides, and others (Conesa et al. 2009; Lottermoser 2010; Ssenku et al. 2014; Kuppusamy et al. 2016), which are dispersed in the environment on a local and regional scale through the process of weathering or wind and water erosion (Conesa et al. 2009; Candeias et al. 2014). The content of Zn, Cu, Pb, nickel (Ni), Cd, and Cr in soils is usually in the range from 0.0001 to 0.065%, whereas iron (Fe) and Mn account for 10% and 0.002%, respectively (Kabata-Pendias 2004; Ernst 2006). Except for Fe, all elements present at a level higher than 0.1% become toxic to plants (Bothe and Słomka 2017). Macro and micronutrients, such as sodium (Na), potassium (K), calcium (Ca), magnesium (Mg), Fe, Zn, Mn, cobalt (Co), Cu, Ni, and molybdenum (Mo), are important for plant growth and development. However, their high concentrations in the mining waste substrate disturb physiological processes, causing abnormal plant development (Gautam et al. 2016a). The concentrations of As, Cd, Cu, Mn, Pb, and Zn are as low as 1 g $kg^{-1}$ in modern mining waste and can be higher than 50 g $kg^{-1}$ in historical wastes (Mendez and Maier 2008). A prerequisite for the application of phytoextraction techniques is the presence of trace elements in soluble and exchangeable fractions, which determines their bioavailability. Trace elements contained in mining wastes exhibit substantially higher bioavailability than those contained in non-contaminated soils (Ssenku et al. 2014). The mobility and bioavailability of trace elements in mining wastes depends on many physical and chemical properties, e.g. particle size distribution, structure, bulk density, water holding capacity, nutrient content, pH, salinity, and others (Sheoran et al. 2016; Jović et al. 2017; Kushwaha et al. 2018). Plants used in the phytoextraction process can influence the mobility and bioavailability of trace elements, thereby contributing to changes in the properties of the substrate. This is achieved by compounds secreted by plant roots such as organic acids, which induce changes in pH (Gerhardt et al. 2017). Therefore, prediction of the effectiveness of mining waste reclamation with phytoextraction techniques requires determination of the physicochemical properties of these wastes and their interactions (Sessitsch et al. 2013; Baldantoni et al. 2014; Sheoran et al. 2016).

The physical and chemical properties of mining wastes differ depending on their mineralogy, geochemistry, particle size in the extracted material, and moisture content. The basic sources of these materials are rocks, soil, and sediments from surface mining operations, especially from outcrops (Lottermoser 2010). Mining wastes are non-homogeneous geological materials that can consist of sedimentary, metamorphic, or magmatic rocks, soils, and loose sediments. The mineral composition of mining wastes is dominated by silica (70.43%), followed by $Al_2O_3$ (7.32%), $Na_2O$ (2.32%), $K_2O$ (0.08%), CaO (0.69%), FeO (2.14%), and $Fe_2O_3$ (2.8%) (Flores Badillo et al. 2015; Almeida et al. 2018). The mineral composition of mining wastes, e.g. calcite, plays an important role in controlling the level and potential bioavailability of trace elements in the environment (Kim et al. 2014).

Many mining wastes are characterized by unfavourable physical conditions, e.g. the absence of structure, tendency to crust, or low water retention capacity. As in the case of soil, the physical properties of mining wastes determine their usefulness in plant production and, hence, in the effectiveness of phytoremediation techniques. The physical properties of mining wastes are associated with their chemical composition and can significantly modify the availability of nutrients and the influence absorption of trace elements by the roots of plants used in phytoextraction (Almeida et al. 2018). The water holding capacity and availability for plants depend on the physical properties. The water content in the substrate significantly influences the efficiency of the phytoextraction process, as it determines, e.g. the bioavailability of contaminants. Low water capacity and/or low nutrient (phosphorus (P), nitrogen (N)) content increase the toxicity of trace elements in the substrate (Bothe and Słomka 2017). At higher humidity, plants take up more trace elements and produce a greater amount of biomass, which is directly reflected in a more efficient phytoextraction process (Dineshkumar et al. 2019). The water holding capacity of mining wastes is strictly dependent on their particle size distribution, which fundamentally determines the further management thereof and their impact on the environment. The particle size in these materials can vary depending on the parent rock, and their diameter usually represents that of the sand to clay fraction (Sun et al. 2018; Festin et al. 2019). The particle size may range from exceedingly fine (e.g., phosphate slimes, $<0.01$ mm) to very fine, e.g., most tailings that result from metal ore processing, typically $<0.1$ mm, to very coarse, e.g., typical blasted overburden, where the particle size exceeds many centimetres and a large part may have a size of the order of 1 m and greater. Very small particles of mining wastes can sometimes be transferred over long distances, thus contaminating large areas (Daemen and Akgün 2012; Gautam et al. 2016a). Larger fractions have no ability to accumulate organic matter and are poor in nutrients, devoid of structure, and vulnerable to crusting. They are also characterized by low water holding capacity (Rivera-Becerril et al. 2013). The high potential evapotranspiration and low water retention capacity of these fractions suggest that the water deficit limits the possibility of introducing plants, especially in arid regions (Sun et al. 2018). The finer fractions of these wastes usually exhibit greater water retention capacity, but water infiltration is often limited by the poor structural properties; hence, water often accumulates on the surface of these wastes (Hossner and Hons 1992; Sun et al. 2018). Finer fractions are also associated with the levels of toxic elements such as As, Pb, or Cd (Acosta et al. 2011; Silva et al. 2014). The predominance of fine fractions in these metals may lead to their excessive contents (Festin et al. 2019). Most mining wastes are characterized by high bulk density (Gautam et al. 2016a), often exceeding 1.6 g $cm^{-3}$ (Saha et al. 2017). Such a high density not only inhibits the development and growth of plant roots but also causes a reduction in general porosity and a deterioration of the air-water status of the substrate, which often determines the potential applicability of individual phytoextraction techniques. The most optimal system has a total porosity value of approximately 50%. Importantly, in the adverse air-water conditions of the substrate related to its high density and low porosity, plants may show nutrient deficiencies, even at an excess of elements in the substrate.

The reaction of mining wastes varies from very acidic to alkaline. The pH value depends on the content of carbonates, the potential release of acids by these wastes, and the parent rock (e.g. dolomites and limestones are alkaline) (Mendez and Maier 2008; Conesa et al. 2009; Rivera-Becerril et al. 2013; Cappuyns et al. 2014; Gautam et al. 2016a; Almeida et al. 2018; Festin et al. 2019). Extremely low or high pH values make mining wastes an unfavourable environment for the development of microorganisms and higher plants (Ssenku et al. 2014). The growth of most plants is hampered at soil $pH < 4$, which results from, e.g. reduced solubility and assimilation of essential nutrients by plants such as Ca and Mg (Dineshkumar et al. 2019). Additionally, low pH leads to the activation of $Al^{3+}$ ions, thus inducing their toxicity. At the substrate pH value of $<5.5$, this element is released from minerals containing aluminium (Al) oxides and hydroxides, which results in the generation of the $Al^{3+}$ ion. Plant roots are especially sensitive to the $Al^{3+}$ ion, which is highly toxic and often limits plant growth and development (Sun et al. 2018). At low pH, the solubility and biotoxicity of trace elements contained in mining wastes increases. The pH of the substrate influences not only bioavailability but also the accumulation of metal ions in roots. At lower pH, cationic forms of trace elements become more soluble, while anion forms are better soluble at higher pH values. Reduction in the pH value increases Zn, Mn, and Co absorption and diminishes, e.g. Ni uptake (Dineshkumar et al. 2019). In turn, in alkaline conditions, the absorption of nutrients is low as they are present as insoluble salts and cannot be taken up by plant roots. At pH $> 7$, the absorption of P is significantly reduced. At such an extreme reaction value it is impossible to achieve the expected effects of the phytoextraction process as most plants develop normally in the range of slightly acidic and neutral reactions; therefore, raising or reducing the pH value in such wastes to the range of 5.5–7.0 or 5.5–6.5 is crucial for the achievement of good results. The highest absorption of plant nutrients is observed at slightly acidic and neutral reactions; it is directly reflected in better plant growth and development as well as increased efficiency of the phytoextraction process (Ssenku et al. 2014).

The content of plant nutrients, in particular nitrogen, organic matter, and available phosphorus forms in mining wastes is an important determinant of the efficiency of the phytoextraction process (Rivera-Becerril et al. 2013; Ssenku et al. 2014; Almeida et al. 2018). Normal plant growth and development requires the presence of such elements as N, P, and K in the substrate. In comparison with non-contaminated soils, many mining wastes are characterized by lower levels of organic matter and available forms of essential plant nutrients (P, N, and K) (Ssenku et al. 2014).

A low N mineralization rate, low P availability and low content of organic matter are typical of mining wastes; hence, the efficiency of the phytoextraction process is low due to the poor nutritional status of plants. Management of such wastes should consist in the improvement of their condition, e.g. by application of exogenous sources of organic matter. Furthermore, some elements that play the role of micronutrients required for normal plant growth and development are often present in these wastes in unavailable forms or in inadequate proportions (Sun et al. 2018). To increase the efficiency of phytoextraction, it is necessary to identify thoroughly which nutrients are deficient and to apply additional fertilization with these components. At sufficient nutrient content, the adverse effect of abundant contaminants in mining wastes is neutralized. An example is Ca, which is not only required for normal plant growth but also neutralizes the excessive acidification of mining wastes. It has been emphasized that the pH and Ca content in the substrate are more important for normal plant growth and development than the total content of toxic trace elements contained therein (Sun et al. 2018).

Substrate salinity influences almost all aspects of plant development, including germination, vegetative growth, and reproductive development. It limits normal plant growth and development by its significant effect on water and nutrient uptake by plant roots. The salinity of mining wastes is associated with the excessive accumulation of sodium ions used in technological processes (Sun et al. 2018). The impact of excessive substrate salinity on plant development is mainly related to its influence on water and ion metabolism in plants, which is modified, and thus, normal development is affected. Substrate salinity significantly modifies ionic ratios $Na^+/Ca^{2+}$, $Na^+/K^+$, $Ca^{2+}/Mg^{2+}$, and $Cl^-/NO_3^-$, which leads to disturbances in the uptake of nutrients, in particular, $K^+$, $Ca^{2+}$, and $NO_3^-$, and plant growth inhibition (Bano and Fatima 2009). Sodium is a necessary element for normal plant growth and development and plays an important role in the maintenance of proper turgor in plant cells. However, its elevated concentration in the substrate exerts a toxic effect on plants. Increased uptake of $Na^+$ ions has an impact on the uptake of $K^+$; hence, plants may exhibit a deficiency of the former element as well. Substrate salinity exerts a significant effect on water availability for plants. At excessive salinity, the ability of plants to take up water from the substrate is impaired, which leads to osmotic stress and growth retardation (Munns 2002; Nouri et al. 2017). The direct impact of salt on plants can result in ionic stress, mainly caused by $Na^+$ and $Cl^-$ ions. Increasing concentrations of these ions in the plant organs causes leaf chlorosis, necrosis, and premature fall and can lead to the early death of individual organs and, consequently, entire plants. Moreover, salinity significantly determines the mobility of such elements as Pb, Cd, Zn, and Cu and the effectiveness of phytoextraction through competition with calcium for sorption sites, complexation with chlorides, complexation with sulphates, competition with Mg and/or Ca, etc. (Acosta et al. 2011; Filipović et al. 2018).

## 7.4 The Role of Microorganisms in the Disposal of Energy Waste (Furnace Waste)

The dynamic economic development of many countries, mainly in the second half of the twentieth century, resulted in the production of huge amounts of waste, which became a very serious problem in environmental protection. Waste is classified according to different criteria, depending on production (Rosik-Dulewska 2015). Industrial waste is a special group whose parameters strictly depend on the type of industry and production technology. In countries where the production of energy is based on coal or lignite, large amounts of energy waste are produced as a result of the combustion of ground coal. Non-combustible mineral parts in the form of dust are transported into smokestacks, where they are captured by filters and fly ash is formed. Apart from fly ash, coal combustion in boilers also generates slag. This waste falls to the bottom of the furnace or remains on the grate and then it is discharged outside. The vast majority of ash and slag hereinafter referred to as energy waste or furnace waste is collected in over ground landfills or in pits left after excavated minerals.

There are differences in the chemical composition of energy waste, depending on the type of coal burned, combustion technology, the type of transport to the landfill and storage method. Depending on the chemical composition of ashes and slags, they are classified into the following three types according to the so-called Oxide Module (OM):

$$\frac{SiO_2 + Al_2O_3}{CaO + MgO + Fe_2O_3}$$

- carbon silicate (OM $\leq$ 2.0),
- silicate (OM 2.1–5.9),
- aluminium silicate (OM $\geq$ 6.0).

Fresh energy waste is almost completely devoid of biological life due to its particularly unfavourable physicochemical properties. The following physical parameters are unfavourable: inadequate structure, low specific density, low bulk density, and high porosity. As far as the grain size is concerned, fresh energy waste usually has a sandy, or less frequently, a loamy structure. Therefore, it has a low capacity to retain water, which should be easily accessible, especially to plants and microorganisms. As far as the chemical parameters of energy waste are concerned, its high alkalinity (pH 8–12) is noteworthy. It results from the considerable content of alkali metal hydroxides, and a small amount of organic matter, i.e. available forms of N and P. Apart from that, the solubility of these ashes is also low—it generally ranges from about 2–10%. Energy waste usually contains trace amounts of organic xenobiotics, including polycyclic aromatic hydrocarbons (PAHs) and basic heavy metals (Cd, Cr, Cu, Ni, Pb, and Zn).

Energy waste is stored in landfills. As it generates high amounts of dust, it should undergo reclamation as soon as possible, which is very difficult and tedious. For successful land reclamation, it is first necessary to repair the chemism of energy waste by adequate NPK fertilization and by lowering its pH. It is also necessary to improve its physical properties – loosen or crush the waste mass and select adequate vegetation, depending on the plans to restore an agricultural or forest ecosystem in the future. Successful technical and biological reclamation initiates the transformation of these barren and almost ‘inanimate’ parent rocks into living forms, which are classified as technosols (WRB 2014).

A few years after successful reclamation organic matter available to microorganisms begins to accumulate in shallow surface levels, i.e. accumulation and humus levels because energy waste contains only small amounts (2–8%) of incompletely burnt pieces of coal (black carbon), which is a low-activity form in the soil environment (Gustafsson and Gschwend 1997; Zikeli et al. 2002, 2004; Strzyszcz 2004; Cornelissen and Gustafsson 2006). The investigations which were carried out 20 years after the initiation of land reclamation in a landfill with ashes and slag from a lignite-based power plant showed relatively small populations of basic groups of microorganisms, i.e. heterotrophic bacteria and bacteria of the *Azotobacter* sp. genus, actinobacteria, and moulds (Mocek-Płóciniak 2018).

Samples were collected from newly formed forest soils classified into the Technosols group, Spolic Technosols subgroup (WRB 2014). During the 4-year study (2012–2015) the counts of heterotrophic bacteria in the upper soil layers (0–15 cm) were fairly diversified and usually ranged from 10 to 90 $\times$ $10^5$ CFU $g^{-1}$ d.w. of soil. These values were several folds greater than the counts of these bacteria

**Table 7.1** Ranges of number and biomass of the most important soil organisms (Martyniuk 2017)

| Organisms | Number in 1 g | Biomass (kg ha$^{-1}$) |
|---|---|---|
| Bacteria | $10^7$–$10^9$ | 300–3000 |
| Actinobacteria | $10^6$–$10^8$ | 300–3000 |
| Moulds | $10^5$–$10^6$ | 500–5000 |
| Algae | $10^3$–$10^6$ | 10–1500 |
| Protozoa | $10^3$–$10^5$ | 5–200 |
| Nematodes | $10^1$–$10^2$ | 1–100 |
| Earthworms | 30–300 per m$^2$ | 10–1000 |

in the samples collected from a depth of 80–100 cm (usually 2–12 × $10^5$ CFU g$^{-1}$ dw of soil) (Mocek-Płóciniak 2018). The mean count of these bacteria in the samples amounted to about 22.54 × $10^5$ CFU g$^{-1}$ d.w. of soil. There were even smaller counts of bacteria of the *Azotobacter* sp. The count of these bacteria in the topsoil usually ranged from 10 to 30 CFU g$^{-1}$ dw of soil, whereas in the bottom levels (80–100 cm) it amounted to a few CFU g$^{-1}$ dw of soil. The average count of *Azotobacter* in the entire mass of ashes forming the technosols was 19.85 CFU g$^{-1}$ dw of soil. The count of actinobacteria in energy waste was also strongly diversified. In the consecutive years of the research, the count of these microorganisms did not always tend to decrease with the depth. The average count of actinobacteria in the whole research material (72 samples) was low, i.e. 13.19 × $10^5$ CFU g$^{-1}$ dw of soil. The samples collected from the landfill also contained small amounts of moulds which varied in individual years. The upper soil layers, especially at a depth of 0–5 cm, contained much more moulds (from about 1 to 170 × $10^5$ CFU g$^{-1}$ dw of soil) than the bottom levels at a depth of 80–100 cm (from 0 to 9.47 × $10^3$ CFU g$^{-1}$ dw of soil). The average count of moulds amounted to 26.15 × $10^3$ CFU g$^{-1}$ dw of soil. This was low in comparison with the count of these microorganisms in various soils formed from natural (postglacial) parent rocks (Table 7.1).

Enzymatic activity is another very important parameter illustrating the state of the biological environment of soils formed from industrial waste. It can be treated as a function of the activity of basic populations of the groups mentioned above of soil microorganisms and the root secretions of plants living on these soils. The activity of enzymes depends on their absolute amount, the size of the group of other reacting compounds than enzymes, and the catalytic efficiency (Murray et al. 1995). The catalytic efficiency in the emerging soil environment is affected by additional biotic and abiotic factors such as: the content of mineral and organic colloids, temperature, the properties and pH of water and air, the content and availability of biogenic elements as well as the count and species of microorganisms (Kobus 1995; Kucharski 1997). The value of enzyme activity reflects the in situ state. It is determined not only by the current soil conditions but also due to the accumulation of enzymes in the form of humus complexes, it is to a large extent determined by the history of events preceding the measurement, such as the climatic conditions and treatments applied to soil (Januszek 1999; Bielińska et al. 2016). The technosols formed from energy waste were considerably diversified not only in the count microorganisms but also in the content of the enzymes analysed in this study.

Dehydrogenase activity is an indicator of the intensity of the respiratory metabolism of soil microorganisms, mainly bacteria and actinobacteria (Praveen-Kumar and Tarafdar 2003). For this reason, dehydrogenase activity is regarded as a measure of the total microbial activity of soils and an index of ecotoxicity. During the studies (2012–2015) the dehydrogenase activity in the landfill soils was very low, i.e. 0.15–16.89 mg TPF $kg^{-1}$ d.w. of soil 24 $h^{-1}$ at a depth of 0–5 cm and 0.12–4.56 mg TPF $kg^{-1}$ d.w. of soil 24 $h^{-1}$ at a depth of 5–15 cm. The activity of these enzymes was almost unnoticeable at deeper levels (80–100 cm). This may have been caused by the supply of nutrients in the form of root secretions or the biomass of microorganisms (Yang et al. 2007; Futa 2017). The presence of carbon substrates induces and stimulates the biomass of enzymes by soil microorganisms (Renella et al. 2006; Fierer et al. 2003). The low dehydrogenase activity in the samples under analysis, which indicated the low overall microbial activity of the environment, was mostly related with the initial phase of the formation of biological balance (homeostasis) in the furnace waste soils and with the particular sensitivity of this group of intracellular enzymes to environmental factors (Januszek 1999; Bielińska et al. 2014).

Alkaline phosphatase—during the studies—exhibited the highest activity of all the enzymes analysed in the samples of technosols collected from the energy ash landfill. It was similar to the activity of this enzyme observed in soils formed from natural parent rocks. The alkaline phosphatase activity in most of the upper soil levels was more intense than at the lower levels. It was predictable due to the higher content of organic matter in the top soil levels, better air and water conditions and greater biomass of plant roots. In general, the higher alkaline phosphatase activity could also be attributed to low amounts of available forms of phosphorus at all levels of these soils (Kucharski et al. 2015). Urease is an enzyme that perfectly adapts to any environment, regardless of temperature, humidity, and pH. The only factor limiting urease activity is the availability of urea because the presence of this substrate is necessary for the synthesis of urease, which is an extracellular enzyme (Carbrera et al. 1994). The urease activity in the soils under study was low. This may have been the result of the nearly trace amount of easily available forms of N in this soil material. Proteases are a large group of enzymes due to the high diversity of proteins as substrates. They hydrolyse peptide bonds almost anywhere in the protein chain (Dahm and Rydlak 1997). The protease activity in energy waste forms was low. Bielińska and Futa (2009) observed a similar activity of this group of enzymes in other ash and slag substrates. It is noteworthy that there were significant correlations between the four enzymes in the technosols. However, the average activity of all the enzymes under analysis at a depth of 0–5 cm was significantly higher than at deeper levels.

To sum up, we can say that energy waste in the form of fly ash and furnace slags is a difficult parent material for the reclamation of gradually developing technosols. They are characterized by numerous unfavourable physicochemical, microbiological, and biochemical properties. The soil-forming processes, which were initiated by humans as the anthropogenic factor, are much slower here than in natural parent rocks. The period of more than 20 years of the formation of technosols proves that they have not yet achieved an optimal biological balance. This means that the composition of this microbiocenosis is not stable, and the count of microorganisms still varies. The enzymatic parameters also proved to be useful for the monitoring of the transformation of energy waste into soil. Although for many years the landfill has been remediated technically and biologically, as manifested by a beautiful oasis of plant and animal communities, so far neither explicit epipedons nor endopedons have appeared in the soil profile. Nor has biological life developed, which would be reflected by a stabile count of microorganisms and enzymatic activity. It seems that these processes must continue for a 50 years or more at least.

## 7.5 Physiological Aspects of Plant Survival on Heavily Polluted Sites

### 7.5.1 Plant Selection for Phytoremediation of Mine Tailings

Mine tailings, being waste disposal sites, pose a serious threat to surrounding ecosystems and local communities due to the considerable ease with which pollution can spread to the environment with wind and runoff water (Salas-Luévano et al. 2017). A recent approach to deal with contaminated mine tailings—having both environmental and social acceptance—is phytostabilization with tolerant plant species to create a permanent vegetation cover preventing the spread of the pollution via erosion, runoff, and percolation (Pulford and Watson 2003). The solidification of toxic elements (metals and metalloids) reduces their availability and enables sustainable revegetation of disturbed lands. The selection of pioneer plants for phytostabilization is crucial. However, it remains the subject of an on-going debate since there are no standard approaches for the management of multi-contaminated sites (Barbafieri et al. 2017). Recent studies have shown that selection of plants for recultivation of mine tailings should consider indigenous species with wide ecological tolerance instead of newly introduced exotic ones (Pratas et al. 2013; Kumar et al. 2017). Native species will most likely develop a fully functional ecosystem on degraded land by gradual alternation of the waste properties, mainly by improving organic carbon (C), N fixation, water storage, reduction of acidity and nutrient effluent, and also by improving the diversity of the soil microbiom (Shi et al. 2016; Demková et al. 2017a, b).

The selection of appropriate species may be achieved via different experimental setups, such as (1) investigations on specimens collected from mine tailings showing high tolerance to the pollution (Boojar and Goodarzi 2007; Barbafieri et al. 2017; Abreu et al. 2012; Pistelli et al. 2017); (2) cultivation of native plant species under controlled conditions using waste material as a substrate (da Silva et al. 2018); (3) in situ cultivation of plant species naturally occurring at mine tailings.

### 7.5.2 Physiological Determinants of Plant Tolerance to Mining Waste Materials

Metal ion toxicity triggers physiological and developmental changes that lead to adaptation and defence reactions in the plant. However, non-essential and excess of essential metals also cause irreversible damage. Heavy metal ions present in the soil can be taken up alongside nutrients with water and incorporated into plant tissues. Plants have to continuously maintain physiological concentrations of both essential and non-essential metal ions to achieve ionic homeostasis. Moreover, this homeostasis must be maintained in a cell-tissue and organ-specific manner (Sharma and Agrawal 2005; Hu et al. 2013). Plants growing in certain areas are exposed to high localized concentrations of metal ions. When exposed to excess metals, the vast majority of plant species adopt an excluder strategy which involves avoidance of exposure, minimizing their uptake, and intracellular sequestering in the cell wall and vacuoles to prevent their harmful effects in cells (DalCorso et al. 2013; Hossain and Komatsu 2013). Reduced growth is one of the most common physiological consequences of heavy metal exposure in plants (Hu et al. 2013; Tamás et al. 2008). Metal ions can have devastating effects on basic metabolism, transport processes, membranes, and cellular structure. There are reports about metal induced disturbances in the structural and physiological integrity of leaves which impact the rates of photosynthesis and respiration, and consequently energy provision. Heavy metal toxicity also affects the ability to take up water and nutrients and transport processes between various organs (Ying et al. 2010; Barceló and Poschenrieder 2004). Major changes in the functioning of the organs will affect developmental processes such as flowering, embryogenesis, and seed formation. Exposure to toxic metal ions or high concentrations of non-toxic ions, therefore, triggers stress reactions and necessitates adaptation at all levels: physiological, structural, and molecular (Gautam et al. 2016b; Tamás et al. 2008; Hall 2002; Hirayama and Shinozaki 2010).

The mechanisms of metal tolerance exhibited by some plant species are a unique and very interesting feature of plants in stress condition. Besides exclusion strategies, they include the extracellular chelation of metal ions, the restriction of ions in the apoplast, and the detoxification and compartmentalization of metal ions inside the plant tissues (Hossain and Komatsu 2013; Dickinson et al. 1991; Hall 2002). The most advanced strategies used by plants are based on hypertolerance and the hyperaccumulation of metal ions without any negative effects on growth and yield (DalCorso et al. 2013; Dickinson et al. 1991; Van der Ent et al. 2013). It has been observed that a high concentration of metal in hyperaccumulators may secondarily protect them against herbivores and pathogens (Boyd 2012; Cabot et al. 2013). Hyperaccumulators are a small number of plant species that grow on naturally or anthropogenically metal-contaminated soils and possess the ability to accumulate and tolerate extraordinarily high metal concentrations in above-ground tissues (e.g., $>1\%$ Zn, 0.1% Ni or 0.01% Cd in leaf DM) (Baker et al. 2000). These species are classified as either absolute metallophytes (occurring only on metalliferous soils) or pseudometallophytes (present at both metalliferous and non-metalliferous sites).

Tolerant species are favoured by natural selection in contaminated environments due to their ability to survive or else to competitively exclude non-tolerant plants.

Plant roots are the organs that are directly exposed to the heavy metal content of contaminated soils. The availability of metals to plants is strongly dependent on the chemical and physiological conditions in the rhizosphere. The availability of metal ions for plant roots increases in slightly acidic conditions and decreases in alkaline soils (McGrath et al. 1988). Acidic conditions may significantly reduce plant growth by the secretion of different root exudates like organic acids, peptides, amino acids; plant enzymes can increase the pH of the rhizosphere and counteract this effect (Pavlovkin et al. 2009). This mechanism greatly increases the extent of metal ion precipitation and complexation in the vicinity of the roots and thereby helps to reduce the impact of heavy metal toxicity (Reichman 2002). The ability of plants to buffer the rhizosphere is dependent on the type of soil and level of organic matter content, the availability of phosphorus, nitrogen, and iron. All of these factors have significant effects on the accessibility and uptake of zinc, cadmium, and other heavy metal ions (Dickinson et al. 1991; Hirayama and Shinozaki 2010; Broadley et al. 2007). Strategies for modifying an acidic rhizosphere are particularly important for soil rich in Al and Zn. Aluminium is an important growth-limiting factor in acidic soils (Horst et al. 2010). Aluminium binds primarily to cell surface components such as mucilage. In the cell walls of rhizodermal cells, Al interacts mainly with pectins and hemicellulose (Gautam et al. 2016a, b; Schmohl and Horst 2000). In the presence of silicon (Si) and boron (B), Al is mostly bound in the cell wall matrix and thus halted in an extracellular space that limits Al-induced changes. The cell wall, therefore, represents an important physical and physiological barrier against the symplastic entry of metal ions, moreover the properties of the cell wall help to determine the anatomical characteristics of the root in terms of its growth rate (see Sect. 7.6.3). The plasma membranes of the root cells are the first physiological barriers to the entrance of heavy metals into the symplast. The metal ions affect the plasma membrane like induction of lipid peroxidation in the plasma membrane and the loss of highly mobile essential ions, leading to serious ion imbalances in the cytoplasm (Horst et al. 2010). However, a significant part of the metal is bound at the plasma membrane interface, and it has been suggested that this could be one of the factors responsible for metal tolerance. Iwasaki et al. (1990) showed that 60% of Cu in the roots of both *Lolium multiflorum* (Italian ryegrass) and *T. pratense* was bound by the cell wall and plasma membrane. Additionally, in *Minuartia verna ssp. hercynica* growing on heavy metal-contaminated medieval mine dumps, high concentrations of Fe, Cu, Zn, and Pb have been found associated with cell walls and membranes. In comparison, no accumulation of heavy metal was detected in the cytoplasm suggesting a determined use of exclusion by the metal adapted subspecies (Liptáková et al. 2013). When some of the heavy metal (HM) ions overcome biophysical barriers and enter the cytoplasm, it triggers the initiation of several cellular defence mechanisms to nullify and attenuate their toxic effects. The primary strategy includes biosynthesis of diverse cellular biomolecules which play the role of ligands and chelators such as low-molecular-weight protein, nicotianamine, putrescine, spermine, mugineic acids, organic acids, glutathione, phytochelatins, and metallothioneins or cellular exudates such as flavonoid and phenolic compounds, protons, heat shock proteins, and specific amino acids, such as proline and histidine, and hormones such as salicylic acid, jasmonic acid, and ethylene (Hossain and Komatsu 2013; Hall 2002; Broadley et al. 2007; Boyd 2012). With an elevated level of metal ions, the balance of cellular redox systems is disturbed, which leads to the increased induction of reactive oxygen species (ROS) (Boyd 2012). To mitigate the harmful effects of free radicals an antioxidant defence mechanism is activated in cells, composed of enzymatic antioxidants like superoxide dismutase (SOD), catalase, (CAT), ascorbate peroxidase (APX), guaiacol peroxidase (GPX), and glutathione reductase (GR) and non-enzymatic antioxidants such as ascorbate (AsA), glutathione (GSH), carotenoids, alkaloids, tocopherols, proline, and phenolic compounds (flavonoids, tannins, and lignin) that act as the scavengers of free radicals (Pavlovkin et al. 2009; Boyd 2012; Sharma and Agrawal 2005). Some of the biological molecules involved in cellular metal detoxification can be multifunctional and have antiradical, chelating, or antioxidant roles. Exploitation and upregulation of any of these mechanisms and biomolecules may depend on plant species, the level of their metal tolerance (Hall 2002; Cabot et al. 2013), plant growth stage, and metal type. One of the molecules that performs a key function in response to metal stress is glutathione. Glutathione (GSH), a sulphur-containing tripeptide, is considered to be the most important cellular antioxidant involved in cellular defence (Sharma and Agrawal 2005) and functions directly as a free radical scavenger. Glutathione levels in plants are known to change under metal stress due to the role of GSH as an antioxidant, metal-ligand, and also the precursor for the biosynthesis of phytochelatins (PCs) (Barałkiewicz et al. 2009). Phytochelatins are short-chain thiol-rich repetitions of peptides of low-molecular-weight synthesized by the enzyme phytochelatin synthase (PCS) with the general structure of (γ-glutamyl-cysteinyl) -glycine that have a high affinity to bind to HMs (Barałkiewicz et al. 2009). Phytochelatins, as a key player in processes of metal homeostasis and detoxification, have been identified in organisms from yeast and fungi to many different species of animals (Rodrigo et al. 2016; Emamverdian et al. 2015). PCs are reported to have been used as biomarkers for the early detection of HM stress in plants (Emamverdian et al. 2015). In the cytosol, PCs bind HM, and metal-phytochelatin complexes are actively transported to the vacuole, the transport is probably mediated by an Mg ATP-dependent carrier or an ATP-binding cassette (ABC) transporter (Manara 2012). It has been shown that Cd significantly enhances the synthesis of phytochelatins (PCS) in plants. However, Sun et al. (2010) reported that the variation in phytochelatin production in the roots and shoots of two Cd-treated species, viz., *Rorippa globosa* and *R. islandica* might be used as a biomarker for Cd hyperaccumulation, and the synthesis of PCS may be related to an increase in the uptake of Cd ions into the cytoplasm. However, the authors suggest that PC biosynthesis is not the primary mechanism for Cd tolerance. Similarly, the uptake and accumulation of Cd have influenced the biosynthesis of PCs in *Brassica napus,* and in the shoot, the concentration of PC3 and PC4 was higher than the PC2 irrespective of the quantity of Cd uptake (Selvam and Wong 2008). This result suggests that in the detoxification of Cd, higher molecular weight thiol complexes are involved in the shoot. PCs types and chain lengths show variation among plant species as well as HM types. In legumes, it is reported that PCs with longer chains bind more strongly to Pb in comparison to shorter PCs (Sharma and Dietz 2006). Phytochelatins, along with other stress resistance factors can form a synergistic defence in plants under HM stress which, in turn, can strengthen plant's resistance to metal. Chen et al. (2008) demonstrated that the increased enzymatic biosynthesis of PCs coupled with the heightened activity of the antioxidative system in *B. chinensis* L. led to effective detoxification of Cd. But there is no conclusive study to show whether the number of chains can have any impact on the effectiveness of the PC or of the role of PCs in metal tolerance.

Beside PCs in the plant cell metallothioneins (MTs) are also present; they are a group of low molecular mass, cysteine-rich, metal-binding proteins (Sharma and Dietz 2006). It has been suggested that metallothioneins may have a role in trace metal metabolism and cell homeostasis rather than metal tolerance per se.

Different plant parts, species, and metals appear to elicit different responses and possibly more than one response. However, there are certain mechanisms which appear to hold promise as being more widespread than others. There are reports suggesting that plants tolerant to Zn, Fe, or Al exclude organic acids. Plants tolerant to Cd, and possibly Zn, synthesize phytochelatins although it is not clear whether this is a tolerance mechanism or a transport system to sequester metals away in vacuoles. High cellular concentrations of organic acids may have a role in metal tolerance, especially as the complexing agent in vacuoles.

Only scattered studies have been conducted to determine the physiological background of elevated tolerance of pioneer plants naturally inhabiting heavily polluted sites such as mine tailings. Among them selected species of grasses, perennial plants, shrubs, and arboreal plants can be pronominally found, indicating their ability to survive under stressed conditions such as high salinity and extremely elevated concentrations of metal/loids. Along with their accumulation abilities, plants collected at contaminated sites are most often analysed for unspecific responses such as pigment content, lipid peroxidation using the TBARS assay, total antioxidant activity using a DPPH radical, total phenolic compounds, total glutathione, free amino acids, proline accumulation, and the activity of antioxidative enzymes such as SOD, GPX, and CAT. Despite highly adverse growing conditions, for the majority of investigated species, a physiological shift to an oxidative stress state was barely observed. As reported, pioneer species collected at former mining sites or mine tailings did not suffer any significant oxidation of membrane lipids or enhanced activation of antioxidant systems in comparison to plants of the same species derived from ecologically clean areas (Pistelli et al. 2017) or other sites with different pollution levels (Boojar and Goodarzi 2007; da Silva et al. 2018). This indicates the existence of highly effective mechanisms developed in pioneer species enabling intense accumulation of heavy metals in selected organs without the induction of oxidative stress.

Other studies have attempted to determine the potential of native non-pioneer species for revegetation of disturbed areas characterized by multi-metal pollution. A recent study by Drzewiecka et al. (2019) revealed a diversified uptake of elements by the common tree species *Acer platanoides* and *T. cordata* accompanied by a species-specific pattern of physiological reaction to cultivation in mining sludge characterized by high salinity, pH, TOC and highly elevated concentrations of trace elements, including arsenic. Both species were assigned as metal excluders due to their low bioconcentration and translocation abilities for the majority of detected elements. Among several secondary metabolites investigated in photosynthetic tissue, biosynthesis of glutathione and low-molecular-weight organic acids, both showing chelating abilities towards metal ions, was greatly reduced. However, salicylic acid accumulation appeared to serve a critical role in the tolerance mechanisms of *A. platanoides,* determining lower retardation of foliar growth compared to plants cultivated in unpolluted soil than *T. cordata*.

### 7.5.3 Influence of Arbuscular Mycorrhiza on Plant Condition During Phytoremediation

According to Smith and Smith (2012), in natural environments, a non-mycorrhizal condition should be considered as abnormal for the majority of plant species. Consequently, experiments aimed at evaluating plant resistance to toxic elements (including survival rate, biomass production, and phytoextraction efficiency) or the physiological mechanisms underlying the elevated tolerance of some species should consider the effect of plant–fungi associations. Among mycorrhizal interactions of plants, arbuscular mycorrhiza (AM) with Glomeromycota with the largest genus *Glomus* is the most abundant symbiosis for vascular land plants and epiphytes. In general, Glomeromycota form a close and highly beneficial symbiosis with the roots of 70–90% of land plant species (Smith and Read 2008; Prasad et al. 2017). As reported by Okiobé et al. (2015), root colonization with Arbuscular Mycorrhizal Fungi (AMF) can increase the yield of plants from 50 to 200%, mainly via a facilitated influx of water, P and N to plant roots, as well as other mineral nutrients elevating plant nutritional status. Compared to sterile plants, mycorrhizal associations may lead to an increase of up to 80% of P, 60% of Cu, 25% of N, 25% of Zn, and 10% of K uptake (Soares and Siqueira 2008). In exchange, plants transfer some of their soluble carbohydrates to the fungus mycelium to be utilized as carbon sources in order to maintain the mycorrhizal symbiosis (Bonfante and Genre 2010).

AMF spores and mycelium are extremely resistant to high concentrations of heavy metals. Up to 40% AM fungal colonization of plant roots was reported for plants growing in multi-metal polluted soils despite high levels of Cd and Pb concentrations (1220 and 895 mg $kg^{-1}$, respectively) (Weissenhorn et al. 1994). As recently assumed by Schneider et al. (2016), arbuscular mycorrhiza is highly beneficial in fungi-assisted phytoremediation by influencing both the availability of metals for plants and the overall plant condition. AMF action is based on heavy metal dilution in plant tissue based on increased plant growth, reduced uptake by precipitation or metal chelation in the rhizosphere, and as a result of metal retention and immobilization in fungal structures, with a consequent reduction of their translocation to shoots (Schneider et al. 2016). Model studies have confirmed the efficient metal-binding capacities of *Glomus* mycelium towards Zn with concentrations exceeding 1200 and 600 mg kg$^{-1}$ for *G. mosseae* and *G. versiforme*, respectively (Chen et al. 2001). Furthermore, symbiotic plant/fungus interactions lead to the phenomenon of induced systemic resistance (ISR). Previous or simultaneous colonization of roots enhances plant ability to fight biotic challenges, i.e. to cope with necrotizing pathogens or parasites (Burketova et al. 2015). Combined systemic acquired resistance (SAR) and ISR lead to an overproduction of plant hormones and signalling compounds, such as salicylic, jasmonic acids, and ethylene, resulting in the induction of pathogenesis-related (PR) proteins, phytoalexins, and intensified cell wall lignification (Choudhary et al. 2008; see Sect. 7.6.2). As a consequence, AMF colonization of plant roots may elicit a significant reduction in the incidence or severity of various diseases on a diversity of plant hosts also employed in phytoremediation processes. Considering the sustainable ecosystem created during revegetation of disturbed lands, management of the rhizosphere microbiome, including fostering of indigenous AMF communities or root inoculation with AMF enhances nutrient uptake, improves plant health, pest resistance, and drought tolerance (Bender et al. 2016; Varma et al. 2017a, b, c). Recent studies have confirmed the critical role of symbiotic fungi in phytoremediation strategies using enhanced species diversity (legume tree species co-cultured with grasses and N-fixing herbs) based on the reduction of nutrient loss, elevated availability of dissolved organics and mineral nutrients, and soil erosion resistance (Yang et al. 2016).

## 7.6 Alterations in Root Architecture as an Indicator of Plant Ability to Cope with Toxic Trace Elements

Plant roots are in direct contact with many elements, including toxic trace elements (TE) present in the contaminated substrate and are generally the main plant organs which accumulate TE (Baker 1981; Verbelen et al. 2006). The exception to this rule are hyperaccumulating plants (see also Sect. 7.5.2)—species, often endemic to naturally mineralized soils, which accumulate high concentrations of metals and metalloids in their above-ground tissues without developing any toxicity symptoms (Baker 1981; Baker et al. 2000; Suman et al. 2018; Ashraf et al. 2019). Moreover, plant roots, due to their relatively simple and predictable structural organization and developmental zonation, are considered to be an ideal model system to study the various responses of plants to TE (Verbelen et al. 2006). Structural alterations in plant roots are often well visible and relatively easy to estimate. Therefore, these traits could be useful as indicator symptoms for the assessment of the plant ability to cope with stress conditions. They could be beneficial in the selection of examined plant species for reclamation of TE contaminated soils or as bioindicators for the scale of pollution (Schneider et al. 2013; Pita-Barbosa et al. 2015; Krzesłowska et al. 2019).

This chapter includes a short characterization of root architectural alterations in response to TE, such as trace metals (Pb, Cd, Cu, Zn, Al) and metalloids (As). We selected the most common alterations in root architecture at the different levels of root organization that have been previously described for several vascular plant species: morphological, anatomical, and cellular modifications, considered as the symptoms of a plant defence strategy and abnormalities caused by TE which lead to deleterious effects.

We excluded from this chapter alterations of root architecture in hyperaccumulating plants, which are able to accumulate large amounts of TE in their aerial parts in general with no effect on yield as compared to agronomic crops or non-accumulator plants species which belong predominantly to the genera *Alyssum* and *Brassicaceae* (Baker et al. 2000; Prasad and Freitas 2003; Verbruggen et al. 2009; Suman et al. 2018; Ashraf et al. 2019) including such species as *Pteris vittata,* a hyperaccumulator of As (Ma et al. 2001; Danh et al. 2014), *Arabidopsis halleri*, a hyperaccumulator of Cd and Zn (Verbruggen et al. 2013; Schvartzman et al. 2018), *Sedum alfredii,* a hyperaccumulator of Cd (Zhou and Qiu 2005) and several *Noccaea* (*Thlaspi)* species which are hyperaccumulators, e.g. *N. caerulescence* Cd, Pb, Ni, *N. goesingense* Ni and Zn, *N. ochroleucum* Ni and Zn*, N. rotundifolium* Ni, Pb, Zn (Baker et al. 2000; Prasad and Freitas 2003). Moreover, most hyperaccumulators are not considered as suitable plant species for phytoremediation, in particular, phytoextraction, because of their small biomass (Suman et al. 2018; Ashraf et al. 2019).

### 7.6.1 Morphological Alterations in Root Architecture

Uptake and accumulation of TE by plant roots result in the occurrence of a range of alterations. On the one hand, they include modifications considered as symptoms of plant resistance strategy to TE, on the other hand, the deleterious effects of TE toxicity.

Plants are sessile organisms, and in general, they use two main strategies to cope with TE: exclusion and accumulation (by either sequestration or compartmentalization) (Baker 1981; Viehweger 2014). The alterations in root morphology are predominantly involved in the exclusion strategy, which protects plant roots from TE influx. One of the most common is an increase of root exudate secretion and formation of a mucilage barrier limiting the entry of TE into the root. It has been demonstrated that exclusion is the main defence strategy of plants to cope with Al (Barceló and Poschenrieder 2002; Cai et al. 2013) but it also functions in response to other TE, such as Pb, Cd, Cu (Morel et al. 1986; Seregin and Kozhevnikova 2008; Colzi et al. 2015). Root exudates predominantly contain organic acids (e.g. Barceló and Poschenrieder 2002), and/or polysaccharides such as pectins (Seregin and Kozhevnikova 2008; Yang et al. 2008; Cai et al. 2013)—components able to bind and immobilize TE ions (Barceló and Poschenrieder 2002; Seregin and Kozhevnikova 2008; Yang et al. 2008; Cai et al. 2013). Hence, the mucilage layer which appears on the root surface, in particular in root apex regions, protects the root from an influx of TE ions (Barceló and Poschenrieder 2002; Seregin and Kozhevnikova 2008; Cai et al. 2013; Colzi et al. 2015). The increase of the amount of mucilage, detectable even by light microscopy, has been demonstrated, e.g. in response to Al in *Pachyrhizus ahipa* (Poschenrieder et al. 2008), *Oryza sativa* (Cai et al. 2011), tolerant populations of *Glycine max* (Cai et al. 2013), and *Camelia sinensis* (Li et al. 2017) as well as in response to Cu in tolerant populations of *Silene paradoxa* (Colzi et al. 2015). It is worth emphasizing that binding TE by root exudates within the rhizosphere is considered to be one of the main defence strategies for TE, thanks to which many plant species belonging to so-called excluders or metallophytes (Baker 1981), are able to grow on highly TE polluted substrate, e.g. mine tailings (Baker 1981; Seregin and Kozhevnikova 2008; Colzi et al. 2015).

Other modifications considered as symptoms of a defence strategy visible in the root morphology is an increase in the number of living root border cells (RBC; cells of the root cap that have undergone cellular separation but are still attached to the root via a soluble polysaccharide matrix; Driouich et al. 2007). It was found that in *Vigna unguiculata* 'Red Caloona' exposed to As, RCB were separated from the root tip as layers (Kopittke et al. 2012). It was suggested that RCB possibly contributes to the plant's ability to withstand an excess of TE in two main ways: (1) accumulating high levels of TE and (2) secretion of mucilage where TE can be bound and retained (Cai et al. 2011, 2013; Kopittke et al. 2012). Both processes resulted in the limitation of TE entrance into the root (Cai et al. 2011, 2013). Such a mechanism has been demonstrated in several other plant species coping with TE, e.g. in *S. armeria* growing on Cu polluted mine tailings (Llugany et al. 2003), in *O. sativa* and *Glycine max*, exposed to Al (Cai et al. 2011, 2013) and in *Vigna unguiculata* 'Red Caloona' exposed to As (Kopittke et al. 2012).

Another morphological alteration regarded as a symptom of plant defence against TE is the appearance of Fe plaque on the root surface. This response was predominantly observed in rice exposed to As(V) and As(III) (Farooq et al. 2016). The release of $O_2$ into the rhizosphere of waterlogged soils (anaerobic conditions) can result in the formation of an Fe-rich plaque (ferrihydrite) surrounding the root system, with the concomitant oxidation of As(III) to As(V), which then adsorbs strongly to the Fe plaque (Farooq et al. 2016; Kopittke et al. 2017). The experiments with rice showed that Fe plaques adsorb both As(III) and As(V), minimizing As uptake by roots and consequently its toxic effects on root anatomy and subsequent As translocation to shoots (Deng et al. 2010).

An interesting morphological alteration of the root also considered as a symptom of plant defence strategy against TE was the increase of lateral root length. This occurred under field conditions where extension of lateral roots into less toxic surface soil was an adaptative growth response which can avoid TE toxicity (Poschenrieder et al. 2008).

To sum up, most alterations in the root morphological architecture are evidently to restrict the amount of TE entry into the root. It is worth noting that both a marked decrease of TE influx into the root, and a beneficial influence for plant adaptation to areas polluted with TE, can result from cooperation with symbiotic organisms, such as symbiotic bacteria, mycorrhizal (see also Sect. 7.5.3), and endophytic fungi (Rajkumar et al. 2012; Cabral et al. 2015; Ma et al. 2016b; Mishra et al. 2017; Domka et al. 2019). For example, mycorrhizal and endophytic fungi can play a role as a barrier, effectively immobilizing TE and reducing their uptake by host plants via binding metal ions to hyphal CWs and sequestration in vacuoles (Rajkumar et al. 2012; Cabral et al. 2015) as well as by the secretion of extracellular metal-chelating molecules, such as glycoprotein glomalin produced by arbuscular mycorrhizal fungi (Cabral et al. 2015; Sharma et al. 2017; Domka et al. 2019) or organic acids, siderophores, exopolysaccharides, and phenolic compounds produced by fungal endophytes and other mycorrhizal fungi (Mishra et al. 2017; Domka et al. 2019). The alterations caused by TE in the relationship of symbiotic organisms with plant roots and subsequently the alterations in plant root architecture, as well as the role of symbiotic organisms in the defence strategy of plants to cope with TE toxicity and their beneficial role in phytoremediation capability of plants is a very broad topic, widely studied and reviewed (Rajkumar et al. 2012; Cabral et al. 2015; Ma et al. 2016b; Mishra et al. 2017) and would require an entirely separate chapter.

In addition to modifications considered as symptoms of resistance strategies, morphological alterations in root architecture may also have harmful effects. One of the most common is the reduction of root length (Čiamporová 2002; Poschenrieder et al. 2008; Lux et al. 2015; Fahr et al. 2013), usually the result of the inhibition of both root elongation because of less turgor, higher rigidity of cell walls (see Sect. 7.6.3) and mitotic activity of meristematic cells (Samardakiewicz et al. 2009; Fahr et al. 2013; Gzyl et al. 2015). It is worth noting that together with a decrease of root length, a decrease of root biomass was often observed. For example, in soybean seedlings, the deleterious effect of As was even more evident in the root biomass than in the total root length for all As treatments compared to control plants, even for the lowest As concentration tested (25 µM; Armendariz et al. 2016). A reduction of root biomass was also detected in four tree species *A. platanoides*, *A. pseudoplatanus*, *T. cordata,* and *Ulmus laevis* growing on mining sludge containing extremely high levels of TE, e.g. As, Cd, Cu, Pb, Zn (Mleczek et al. 2017).

An obvious morphological alteration in response to TE is a change in the root colour. In contrast to the whitish colour of roots in plants not treated with TE (Fig. 7.1A), those of plants exposed to TE become brownish, e.g. roots of *Cajanus cajan* in response to As or even dark brown, lime trees growing on mining sludge (Fig.7.1B; Krzesłowska et al. 2019). Moreover, the shape of the taproot and lateral roots are often irregular in response to most TE such as Al (Čiamporová 2002), As (Pita-Barbosa et al. 2015), Cd, and Zn (Sofo et al. 2017) and to many TE present in mining sludge (Fig. 7.1B; Krzesłowska et al. 2019). Furthermore, in many plant species, lateral roots become markedly shorter and thicker. This trait, together with the reduction of the tap root length, and the increase of its thickness, results in the formation of a stunted root system, observed in many plant species, e.g. in wheat and maize exposed to Al (Čiamporová 2002; Doncheva et al. 2005), several plant species exposed to Pb (Fahr et al. 2013), in *C. cajan* (Pita-Barbosa et al. 2015) and soybean (Armendariz et al. 2016) exposed to As, as well as and in Arabidopsis exposed to Cd,

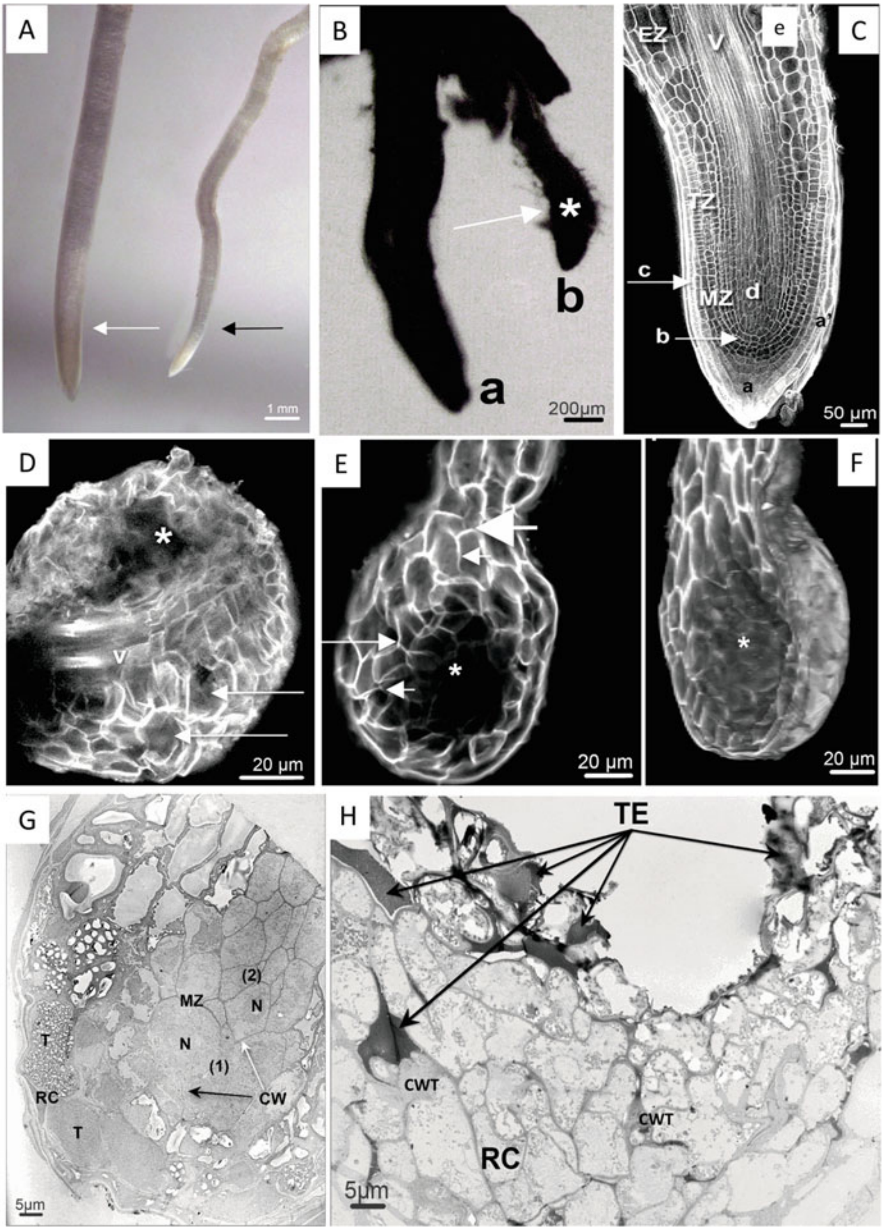

**Fig. 7.1** *Tilia cordata* (**A**) Typical morphology of roots, in particular root apex, in control. Light grey—young root (black arrow), older light brown (white arrow). (**B**) Plants exposed to mining sludge extremely contaminated with, e.g. As, Cd, Cu, Cd, and Zn. Two root apices (**a** and **b**), characterized by irregular thickness, almost black probably because of the deposited TE. Root apex '**b**' markedly swollen (asterisk) at some distance from the tip. The root hair zone is located close to the root tip (white arrow). (**C**) Control—typical root architecture, all root apex zones and tissues are easy to distinguish (clearing technique). (**D**–**F**) The architecture of the root apex in the tree exposed to mining sludge—markedly but unevenly swollen. (**D**–**E**) Optical sections of cleared roots demonstrating (1) various thickness and shape, (2) the diversity of the arrangement of cells,

Zn (Sofo et al. 2017), and Cu (Lequeux et al. 2010). Lime trees exhibit similar root systems when growing on mining sludge (Krzesłowska et al. 2019).

Well visible alterations in root morphology also concern root hairs. In toxic concentrations of Al, root hair growth is reduced or ceases (Čiamporová 2002). Similar reactions have been found in *A. thaliana* exposed to Cd (Fan et al. 2011) and Pb (Krzesłowska et al. 2016) as well as in poplar treated with Pb (Krzesłowska et al. 2016). In addition, cell wall thickenings (CWT) form at the tip of root hairs (Fan et al. 2011; Krzesłowska et al. 2016; see Sect. 7.6.3). Because of the reduction of root apex zones (see Sect. 7.6.2) the root hair zone is often located abnormally close to the root tip, e.g. in *A. thaliana* exposed to Cd and Zn (Sofo et al. 2017) or in lime tree roots growing on mining sludge (Fig. 7.1B; Krzesłowska et al. 2019).

The highest concentration of TE is detected usually within the root apex. This has been demonstrated for most examined TE, such as Al (Garzón et al. 2011), As (Kopittke et al. 2012), Cd (Lux et al. 2015), Cu (Lequeux et al. 2010), and Pb (Rabęda et al. 2015). This could explain why serious morphological malformations are observed in this region, such as swollen tips detected, e.g. in response to Al in maize (Doncheva et al. 2005) and barley (Zelinová et al. 2011) as well as in the lime trees growing on mining sludge (Fig. 7.1B–G; Krzesłowska et al. 2019), curved tips in response, e.g. to Cd (Lux et al. 2015) and As (Pita-Barbosa et al. 2015). Moreover, in the root apex, a reduction or complete absence of the root cap has often been observed, e.g. in response to As (Pita-Barbosa et al. 2015) and a mixture of TE in mining sludge (Krzesłowska et al. 2019).

### 7.6.2 Alterations in Root Anatomy

Similar to morphological alterations, modifications in root anatomy can be divided into (1) defence strategy symptoms and (2) deleterious effects of TE.

Defence strategies in root anatomy mainly concern the formation of efficient barriers for fast, apoplastic radial movement of TE within the root. This mechanism protects plants from TE influx into the vascular tissues and their transport into the

**Fig. 7.1** (continued) (3) diversity of cell sizes and shapes. Many cells in the external layers are strongly enlarged, surrounded by abnormally thick CWs (white arrows). Vascular tissues (v)—abnormally close to the root tip (**D**) and empty space (asterisk) (**E**). (**F**) The micrographs from 3D reconstruction illustrating the uniformly swollen shape of the root apex and the size of the internal space lacking any tissues and cells. (**G**, **H**) Different ultrastructure of the root apices, (**G**) root apex showing strong reduction of the root cap (RC) and the meristematic zone (MZ). Cells in these two regions vary in CW thickness (1) thin CWs and (2) thickened CWs. (H) Root apex where only several layers of root cap cells are preserved and the interior is empty. Numerous CW thickenings (CWT) and TE deposits, different in size and shape (arrows) are visible). Abbreviations: meristematic zone (MZ), transition zone (TZ), elongation zone (EZ), **a**—root cap, **a′**—lateral root cap, **b**—meristem, **c**—protoderm, **d**—ground meristem, **e**—cortex, and **v**—vascular tissues. (Krzesłowska et al. 2019—with permission) stem and leaves (Seregin and Kozhevnikova 2008; Lux et al. 2011). Therefore, one of the most important alterations in plant root anatomy is the acceleration of endodermis maturation. Such a reaction was observed in several plant species exposed mainly to Cd and Pb (Seregin and Kozhevnikova 2008; Lux et al. 2011). Interestingly, acceleration of maturation has also been recently demonstrated for the exodermis (hypodermis), in maize exposed to Cd (Liška et al. 2016). Maturation of exo—and endodermis is associated with the appearance of suberin and lignin within their CWs (Esau 1977). The occurrence of suberin and lignin makes the CWs impermeable to aqueous solutions and consequently for the transport of both essential elements (Esau 1977) and TE (Seregin and Kozhevnikova 2008; Krzesłowska 2011; Lux et al. 2011). Therefore, mature exodermis and endodermis function as real barriers limiting radial, especially apoplastic, transport of TE within the root (Lux et al. 2011; Kopittke et al. 2012; Liška et al. 2016). However, it is worth noting that the endodermis layer is still permeable for water solution and many elements via symplastic transport (Esau 1977; Seregin and Kozhevnikova 2008).

Importantly, accelerated maturation, in response to TE, results in the formation of suberized endodermis closer to the root apex, as demonstrated in several plant species in response to Cd, e.g. *A. thaliana*, *S. dioica*, *Karwinskia humboldtiana, Cucurbita pepo* (Lux et al. 2011). A similar reaction also concerns the exodermis (Liška et al. 2016). Hence, accelerated maturation of both cell layers, exo- and endodermis, in plant roots exposed to TE leads to the appearance of both barrier tissues closer to the root apex than in roots of plants not exposed to TE. This extends the area of the root where the radial transport of TE is markedly limited, including normally unprotected regions close to the root apex.

The barrier role of the endodermis was commonly demonstrated for Pb transport in many plant species, e.g. in *Raphanus sativus* (Lane and Martin 1977), *Allium cepa* (Wierzbicka 1987), poplar (Książek and Woźny 1990), the aquatic plant *Lemna minor* (Kocjan et al. 1996). Moreover, such a function was clearly demonstrated for As (V) and As (III) transport in *Vigna unguiculata* 'Red Caloona' by using synchrotron-based X-ray fluorescence techniques (Kopittke et al. 2012). Hence, the limitation of radial apoplastic transport is a widespread defence strategy of plants against TE.

Cells with lignified cell walls play similar roles to that of the exo- and endodermis. It was observed that in maize exposed to Cd, the lignification was accelerated and concerned protoxylem cells and xylem parenchyma cells (Lux et al. 2015). An increase of lignification was also observed in tobacco exposed to Cd (Siemianowski et al. 2014) as well as in *Arabidopsis* (Lequeux et al. 2010) and tolerant populations of the metallophyte *S. paradoxa* (Colzi et al. 2015) treated with Cu. In addition, it was demonstrated that xylem elements occurred closer to the root apex, similarly to the accelerated maturation of the endodermis and exodermis described above. For instance, in pine trees exposed to Cd, premature xylogenesis was observed as well as in roots of barley (Lux et al. 2015) and soybean (Gzyl et al. 2015) exposed to the same metal. The occurrence of lignified vascular tissues abnormally close to the root tip was also detected in *T. cordata* growing on mining sludge (Fig. 7.1D; Krzesłowska et al. 2019). As mentioned above, lignified CWs—similarly to CWs containing suberin—are not permeable to water solutions transporting TE and thus form a barrier for radial toxic TE movement and their entry into the vascular tissues (Lequeux et al. 2010; Lux et al. 2015; Colzi et al. 2015).

Taking all these facts into consideration it can be concluded that alterations in root anatomical architecture involving higher suberification and lignification of root CWs as well as their occurrence closer to the root apex in plants exposed to TE, are the symptoms of plant defence strategies against TE (Seregin and Kozhevnikova 2008; Lux et al. 2015).

However, besides the symptoms of defence strategy, many other alterations, signs of the detrimental effects of TE toxicity, have been demonstrated in root anatomy architecture. Some of them relate to alterations in root morphology. The reduction of root length and the occurrence of swollen or curved tips were probably the result of the marked reduction of root apex zones. This predominantly concerned the reduction of the elongation zone (EZ), as observed in plants exposed to Al (Čiamporová 2002) and in *C. cajan* treated with As (Pita-Barbosa et al. 2015), but also the reduction of the meristematic zone (MZ) and the transition zone (TZ) (Fig. 7.1D, G), as in lime trees growing on mining sludge extremely contaminated with As, Cd, Cu, Pb (Krzesłowska et al. 2019). Together with TZ and MZ reduction, an irregular arrangement of the cells building the root apex tissues and a large diversity of disorders in their size and shape, e.g. the occurrence of many abnormally large cells, were well visible (Fig. 7.1D–H). The alterations in lime trees were analysed using confocal laser scanning microscopy combined with a clearing technique (Krzesłowska et al. 2019). Since plant tissues are not transparent, application of the clearing technique allowed the imaging of the whole root apex by confocal fluorescence microscopy and its subsequent 3D reconstruction (Timmers 2016). Thanks to this technique it was also possible to demonstrate one of the most dramatic disorders in root anatomy which occurred in lime trees growing on mining sludge, i.e. a lack of internal tissues in the root apex (Fig. 7.1E, F; Krzesłowska et al. 2019). Interestingly the external cell layers of the root apex, mainly root cap (if it was present) and ground meristem in such root apices were preserved (Fig. 7.1E, F, H; Krzesłowska et al. 2019).

In many plant species, the main abnormalities caused by TE were observed predominantly in the rhizodermis and cortex. For example, disintegration of cortical cells, a reduction of the cortex area, broken, collapsed cells, and larger intercellular spaces in this tissue occurred in many plant species, e.g. in response to Al (Čiamporová 2002), in willow and poplar exposed to Cd (Lux et al. 2015) as well as in response to As in *C. cajan* (Pita-Barbosa et al. 2015), several species of *Brassicaceae* (de Freitas-Silva et al. 2016) and in soybean (Armendariz et al. 2016).

Toxic effects of TE on root anatomy architecture were also visible in vascular tissues. For example, the secondary xylem vessel elements were reduced in diameter in plants exposed to As, such as *C. cajan* (Pita-Barbosa et al. 2015) and several species of *Brassicaceae* (de Freitas-Silva et al. 2016).

Serious alterations in root anatomy also concerned the lateral root zone. For example, in *C. cajan* treated with As the division orientation of phellogen and cambium cells and disintegration of the parenchyma cells adjacent to lateral roots were observed (Pita-Barbosa et al. 2015). Moreover, e.g. in response to both As and Cd, the primordia of lateral roots often did not develop and were retained within the cortex (Pita-Barbosa et al. 2015; Fattorini et al. 2017). In experiments examining maize root response to Cd applied only from one side of the root, it was demonstrated that primordia of the lateral roots developed only on the side which was not exposed to Cd. Thus Cd inhibited lateral root development (Lux et al. 2015).

### 7.6.3 Alterations in Root Architecture at the Cellular Level

Since the beginning of the research into plant cell reactions to TE, many alterations in cell ultrastructure have been described. It is a very broad topic widely studied and reviewed (Čiamporová 2002; Horst et al. 2010; Krzesłowska 2011; Lux et al. 2015; Fahr et al. 2013; Parrotta et al. 2015; Horiunova et al. 2016). Therefore, in this chapter, we have decided to focus mainly on the alterations in root cell architecture which can be considered as symptoms of defence strategies to TE such as CW remodelling, an increase of vacuolization and activity of vesicular transport. The most common detrimental effects of TE, modifying root architecture at the cellular level, are briefly described.

As alterations in morphology and anatomy were involved in exclusion strategies—many modifications in root structure at the cellular level are predominantly involved in compartmentalization strategies. Two cell compartments play a key role in compartmentalization: the cell wall and vacuole. These two compartments sequester TE ions protecting more sensitive sites in the protoplast from their toxicity (Krzesłowska 2011; Ovečka and Takáč 2014). The occurrence of TE, such as Pb, Cu, Cd, Al, within the CW has been reported since the earliest studies of plant cell reactions to these elements (e.g. Malone et al. 1974; Woźny et al. 1982; Wierzbicka 1998; Neumann and zur Nieden 2001; Sousa et al. 2008; Małecka et al. 2008; Krzesłowska 2011) and also recently (e.g. Colzi et al. 2012, 2015; Parrotta et al. 2015; Krzesłowska et al. 2016; Li et al. 2017; Krzesłowska et al. 2019).

Plant CWs accumulate large amounts of TE because this compartment is abundant in components able to bind divalent and trivalent metal cations, such as pectins, cellulose, hemicellulose, proteins (Krzesłowska 2011), and organic acids (Kopittke et al. 2017). However, pectins in particular play a crucial role in the binding and immobilization of TE within CW, especially low-methylesterified pectins (up to 40%), which are cross-linked by TE ions (Krzesłowska 2011; Inoue et al. 2013; Rabęda et al. 2015). Interestingly, alterations in root structure at the cellular level concerning plant CW are involved mainly in the increase of CW capacity for TE sequestration (Krzesłowska 2011; Le Gall et al. 2015). Because the CW capacity for TE binding and sequestration depends mainly on the amount of low-methylesterified pectins (Krzesłowska 2011; Inoue et al. 2013; Rabęda et al. 2015)—as expected—the level of this pectin fraction often increased in response to many TE (Krzesłowska 2011). The increase of low-methylesterified pectin levels has been clearly demonstrated in recent years, e.g. in wheat (Sun et al. 2016) and *Camellia sinensis*

(Li et al. 2017) exposed to Al, in sensitive populations of *S. paradoxa* in response to Cu (Colzi et al. 2012) as well as in Douglas fir trees treated with Cd (Astier et al. 2014).

Augmentation of CW capacity for TE sequestration also leads to the increase of CW thickness—one of the most widespread alterations observed at the cellular level in many plant species, e.g. in response to Al (Čiamporová 2002; Horst et al. 2010), As (Schneider et al. 2013; Armendariz et al. 2016), Cu (Colzi et al. 2015) or in plants growing on mining sludge containing a mixture of TE (Probst et al. 2009; Krzesłowska et al. 2019).

Furthermore, besides the general increase of the CW thickness local CW thickenings were also observed in roots of plants exposed to TE, in particular, Pb (Krzesłowska 2011; Le Gall et al. 2015). It is worth emphasizing that generally CW thickenings were characterized by high levels of low-methylesterified pectins and the occurrence of callose, which physically limit TE movement. It was detected that CW thickenings accumulated large amounts of TE. Hence, the formation of local CW thickenings also increased low-methylesterified pectin levels and the apoplast capacity for TE accumulation in plant roots (Krzesłowska 2011). Recent results have demonstrated, moreover, that formation of local CW thickenings is a widespread defence strategy of plants to cope with TE. Such alterations of CWs occurred in the root apices of poplar and Arabidopsis in response to Pb (Krzesłowska et al. 2016) and in lime trees exposed to a mixture of TE (e.g. As, Pb, Cd, Cu, and Zn) present in mining sludge (Fig. 7.1H; Krzesłowska et al. 2019). Furthermore, CW thickenings abundant in low-methylesterified pectins, accumulating high levels of Pb were also found in the apical zone of tip growing root hairs in Arabidopsis and poplar (Krzesłowska et al. 2016). Similar reactions were demonstrated for the root hair tips of Arabidopsis exposed to Cd (Fan et al. 2011). Hence, alterations in root structure at the cellular level concerning the formation of local CW thickenings, detected in diverse plant species and cell types differing in the type of growth, anisotropic (diffuse) and tip growing cells, demonstrated that this alteration in root architecture can be considered as a really widespread defence strategy of plants for coping with TE.

On the other hand, it should be remembered that binding TE within CWs, especially cross-linking by low-methylesterified pectins, and the enlargement of CW capacity for TE sequestration simultaneously increases the rigidity of this structure and therefore inhibits root elongation (Krzesłowska 2011). Thus, the increase of low-methylesterified pectin levels is a symptom of the defence strategy characteristic for plants which are not constitutively adapted to elevated amounts of TE in the substrate, e.g., in response to Al (Eticha et al. 2005; Amenós et al. 2009; Tolrà et al. 2009) or Cu (Colzi et al. 2012), Cd (Meyer et al. 2015) because in metallophytes, such as tolerant populations of *S. paradoxa,* rather a decrease of low-methylesterified pectins level was observed in their CWs (Colzi et al. 2012).

As mentioned above (see Sect. 7.6.2), remodelling of root CWs also includes the appearance of lignin and suberin that results in impermeable barrier formation for water solutions transporting TE. Such CWs also restrict the entrance of TE into the protoplast. The barrier role of CW for TE penetration is also underlined by callose deposition, known as a component impermeable to TE which protects the PM and protoplast from TM penetration or at least limits the amount of TE that is able to enter the interior of the cell. Callose is quickly synthetized in response to TE, as demonstrated mainly in response to Al and Pb (Krzesłowska 2011). However, the callose barrier is often not sufficient, and TE can penetrate the protoplasts, was demonstrated, e.g. for *Lemna minor* exposed to Pb (Samardakiewicz et al. 2012).

The alterations in root architecture at the cellular level also involve the increase of cell vacuolization, e.g. in *Arabidopsis* (Fan et al. 2011; Lux et al. 2015) and soybean (Gzyl et al. 2015) exposed to Cd, in *Arabidopsis* exposed to Pb (Fig. 7.2B; Krzesłowska and Neumann, unpublished data) as well as in *A. sativum* treated with Pb (Jiang and Liu 2010) and Cu (Colzi et al. 2015). Similar to the increase of CW capacity for TE sequestration, higher vacuolization of cells, predominantly meristematic cells, in plant roots exposed to TE, can also be considered as a defence strategy against TE. Vacuoles, besides CW, are the crucial plant cell compartment for TE sequestration (Verbruggen et al. 2009; Lux et al. 2015). High accumulation of TE in vacuoles was found for most TE. However, some TE are preferentially accumulated in these organelles, e.g. As(III) and Cd (Verbruggen et al. 2009; Farooq et al. 2016). As(III) and Cd ions are bound in the cytosol with glutathione or phytochelatins and these complexes are translocated via the tonoplast into the vacuole (Verbruggen et al. 2009; Farooq et al. 2016). However, the vacuole is also an important plant cell compartment for the accumulation of other TE, such as Pb (Samardakiewicz and Woźny 2000; Jiang and Liu 2010; Glińska and Gapińska 2013), Al (Poschenrieder et al. 2008), and Cu (Lequeux et al. 2010).

Besides high protoplast vacuolization, the alterations of root architecture at the cellular level exposed to TE include a noticeably higher number of vesicles indicating more intensive vesicular transport. For example, in *A. thaliana* exposed to Pb evidently more vesicles occurred in root apex cells (Fig. 7.2B) in comparison to the control (Fig. 7.2A; Krzesłowska and Neumann, unpublished data). Interestingly, the cargo of many vesicles were large Pb deposits, evidenced by X-ray microanalysis (Fig. 7.2C–C″; Krzesłowska and Neumann unpublished data). Pb deposits were located in the vesicle lumen and/or within membranes surrounding the vesicles (Fig. 7.2C; Krzesłowska and Neumann, unpublished data). Interestingly, many vesicles carrying Pb deposits were located in the vicinity of CWs accumulating Pb, in particular near CW junctions (Fig. 7.2C; Krzesłowska and Neumann unpublished data)—the regions of CWs where the highest Pb accumulation was detected (Rabęda et al. 2015). Furthermore, in *A. thaliana* and poplar roots, many vesicles containing Pb deposits were also visible in the vicinity of CW thickenings (Krzesłowska, unpublished data). It is generally known that TE, in particular, Pb, have been commonly detected within structures of the endomembrane system such as plasma membrane invaginations, vesicles, Golgi apparatus, the trans-Golgi network (TGN), the endoplasmic reticulum (ER) and vacuoles (Krzesłowska 2011). Hence, TE, already present within the endomembrane system, can be easily removed from the protoplast by the secretion pathway and sequestered in the CW and their thickenings (e.g. Malone et al. 1974; Woźny et al. 1982; Wierzbicka et al. 2007; Meyers et al. 2009; Krzesłowska et al. 2010). Therefore, a higher number of

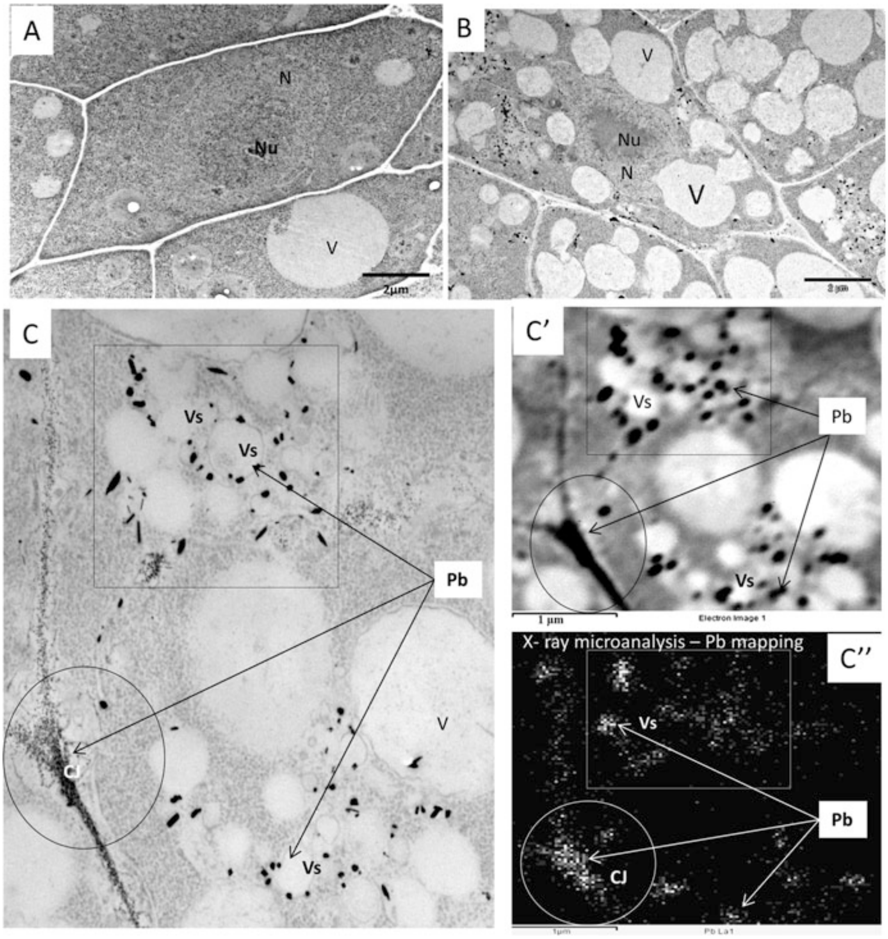

**Fig. 7.2** Ultrastructure of *Arabidopsis thaliana* (L.) root apex (micrographs comes from JEM 1400 (JEOL Co., Japan). Pb identity and distribution mapping was confirmed by EDS X-ray microanalysis using transmission electron microscope JEM 1400 (JEOL Co., Japan)JEM1400 JEOL Co., Japan, equipped with a—Energy Dispersive X-ray Spectroscopy (EDS, INCA Energy TEM, Oxford Instruments, Great Britain). (**A**) Control cells surrounded by thin CWs. Nucleus (N) with nucleolus (Nu) located in the centre of the cell—typical for meristematic cells. (**B**–**C**″) Root apex cells of plants exposed to Pb (1 mM; 4 h). (**B**) Meristematic cells containing high number of relatively small vacuoles (V). Nucleus (N) with nucleolus (Nu) located in the centre of the cell typical for meristematic cells. (**C**) Cell showing high numbers of transport vesicles (Vs). Numerous electron dense Pb deposits (black arrows) located both on the membranes surrounding the Vs as well as in the Vs lumen. Vesicles located in the vicinity of CWs and CW junctions (CJ) both contain many Pb deposits. (**C**′) Detail of the boxed area in (**C**) used for the determination of Pb distribution by EDS—X-ray microanalysis. (**C**″) Mapping of Pb distribution examined by EDS X-ray microanalysis (eclipse and rectangular on the micrographs **C**, **C**′, and **C**″ include the same regions of interest; **C**′ and **C**″ comes from Energy Dispersive X-ray Spectroscopy (INCA Energy TEM, Oxford Instruments, Great Britain—therefore squeezed in comparison to **C**)

vesicles transporting TE can be considered as a symptom of the defence strategy involved in TE removal from the protoplast and their sequestration in CW and CW thickenings.

Among the harmful effects of TE on root cell architecture the most serious ones concern alterations in nucleus and nucleolus ultrastructure, e.g. Pb caused an increase of chromatin condensation in *Lemna minor* root apices (Samardakiewicz and Woźny 2005) Cr, Cd, and Pb caused formation of binucleate cells, micronuclei, 'budding' nuclei and nucleoli partly outside nuclei in *A. cepa* roots (Glińska et al. 2007). Moreover, TE, such as Pb, Cd, commonly caused inhibition of mitotic activity including a marked decrease in the number of dividing cells, e.g. in *Lemna minor* (Samardakiewicz and Woźny 2005), *Pisum sativum* (Fusconi et al. 2006), *A. cepa* (Wierzbicka 1988; Glińska et al. 2007) and even an absence of dividing cells as in the root apex of *T. cordata* exposed to mining sludge (Krzesłowska—unpublished data). Moreover, many alterations in the mitosis process were detected—including prolongation of prophase and metaphases, reduction of metaphase and anaphase and disorders of chromosomes, such as: c-metaphases, sticky and lagging chromosomes, chromosome bridges, induced, e.g. in the presence of Pb and Cd (Wierzbicka 1988; Samardakiewicz and Woźny 2005; Fusconi et al. 2006; Glińska et al. 2007; Samardakiewicz et al. 2009; Jiang et al. 2014; Gzyl et al. 2015).

One of the main targets of TE is actin and tubulin cytoskeleton where severe alterations in the arrangement have often been observed (Fusconi et al. 2007; Amenós et al. 2009; Samardakiewicz et al. 2009; Liu et al. 2009; Gzyl et al. 2015; Horiunova et al. 2016). The most harmful effects of TE on the cytoskeleton were observed in the root transition zone, concerning both microfilaments (Amenós et al. 2009) and microtubules (Samardakiewicz et al. 2009). For example, Al caused an assembly of dense but disorganized actin filaments at the cross walls and depolymerization of F-actin just beneath the plasma membrane in a sensitive variety of *Zea mays* (Amenós et al. 2009). It is worth emphasizing that disorders of F-actin in this zone, where meristematic cells exit the division phase and prepare for filamentous actin (F-actin)-dependent rapid cell elongation (Verbelen et al. 2006), besides increasing cell wall stiffness, resulting from binding TE ions mainly to low-methylesterified pectins described above, could be one of the most important reasons for the inhibition of root elongation caused by TE (Amenós et al. 2009; Horiunova et al. 2016).

Trace elements also affect microtubules, both cortical microtubules and microtubules involved in nucleus and cell division. It was demonstrated that TE could alter the 3-dimentional (3D) orientation of cortical microtubules and their dynamic instability (alteration of polymerization and depolymerization process). Moreover, it was demonstrated for soybean roots that Cd affected also the microtubule of the preprophase band and phragmoplast, e.g. disorders of microtubule array and their depolymerization (Gzyl et al. 2015; Horiunova et al. 2016) resulted in the formation of an incomplete cell plate and subsequently incomplete cell walls (Samardakiewicz et al. 2009; Krzesłowska et al. 2019). During mitosis TE, in particular, Pb, caused disorders of the mitotic spindle, often similar to colchicine

(Samardakiewicz et al. 2009). It is likely that most of the disorders in nucleus division described above are the result of alterations in the mitotic spindle caused by TE (Liu et al. 2009; Gzyl et al. 2015; Horiunova et al. 2016).

Root plastids seem to be a primary target of TE excess. Unfortunately, there are almost no data about the effect of TE deficiency or excess on nongreen plastids. The detailed review of Barceló and Poschenrieder (2006) came to the conclusion that except for Cd (decreased starch content and reduced internal membrane system in root plastids), no visible ultrastructural damage is observed in the organelles of the roots, but the metals rather disturb the polar zonation of the organelles within the cells. Changes in the amyloplasts and their arrangement in root columella cells may directly influence root gravitropism and growth direction and seem to be associated with, for example, Al stress-induced root growth defects.

Moreover, ultrastructural and morphological damage after Pb treatment was observed in the root meristematic cells of *A. sativum* during a long exposure (48–72 h), revealing mitochondrial swelling and loss of cristae. Plasmolysis occurred in some cells (Jiang and Liu 2010).

In general, extremely high concentrations of TE and long-term plant exposure could lead to complete damage of root cell protoplasts (e.g. Fig. 7.1H; Jiang and Liu 2010; Schneider et al. 2013; Armendariz et al. 2016; Krzesłowska et al. 2019) (Table 7.2).

## 7.7 Conclusions

The effectiveness of phytoextraction techniques in the remediation of mining wastes is mainly influenced by their physical and chemical properties. A prerequisite for the application of the phytoextraction process is at least low solubility of trace element ions, which determines their bioavailability. The solubility of elements is mainly influenced by pH (high in acidic conditions, while the elements are immobilisedin alkaline conditions). Mining wastes are an extreme environment for the development of most plants due to poor physical conditions, e.g. insufficient/excessive humidity, high salinity, extreme pH values, low content of available nutrient forms, low organic matter content, low biological activity, etc. Therefore, prior to the application of phytoremediation techniques, additional enrichment of mining wastes should be considered, e.g. with exogenous sources of organic matter. Otherwise, the phytoextraction process may not yield satisfactory results in such an extremely difficult environment for the life of most plants.

Microorganisms present in the ecosystem, inoculation of plants with microorganisms resistant to TE as well as the introduction of such microorganisms to the ecosystems enriched with TE can increase plant phytoremediation potential. Symbiotic microorganisms together with plant defence strategies such as the increase of enzymatic activity, e.g. involved in the antioxidative system, accompanied by TE compartmentalization by a cell wall and vacuole play an important role in plant resistance to TE stress.

**Table 7.2** Alterations in root architecture—at the morphological, anatomical, and cellular level of organization

| Morphological alterations | Anatomical alterations | Cellular alterations |
|---|---|---|
| Modifications considered as defence strategy symptoms | | |
| Higher number of border cells accumulating TE | Suberized and lignified endodermis located close to the root tip | Increase of CW thickness |
| Increased amount of mucilage immobilizing TE on root apex surface | Increase and/or acceleration of root cell lignification including cortex, endodermis, xylem | Formation of local CW thickenings abundant in low-methylesterified pectins binding TE |
| Increase of Fe plaque thickness absorbing As | | Increase of vesicular transport activity |
| More numerous and longer lateral roots | | Higher vacuolization of protoplast |
| Disorders by TE | | |
| Reduction of root length and root biomass | Reduction of root apex zones | Malformation of nucleus structure and shape |
| Brownish or even dark brown colour of the root apex and/or the whole root | Lack of root cap | Inhibition of mitotic activity, mitotic process disorders and alterations of chromosomes (chromosome bridges, c-metaphases, sticky chromosomes) |
| Root apex, swollen, curved | Disorders in rhizodermis and cortex tissue arrangement, occurrence of abnormal size and shape of cells, occurrence of cells with destroyed protoplasts | Alterations in microtubule and actin cytoskeleton arrangement |
| Root hairs developed closer to the root tip | Primordia of lateral roots retained in the cortex | Depolymerization of microtubules and F-actin |
| Increase in the length of the lateral root zone | | Disturbance of the polar zonation of amyloplasts, within the cells, swelling of mitochondria and reduction of mitochondria cristae |
| Short lateral roots or lack of them | | Plasmolysis and destruction or lack of protoplasts |

The nature and the scale of alterations in plant root architecture, the organ which is in direct contact with TE in the substrate, could be considered/ used as the markers/indicators of plant phytoremediation ability in certain environment. However, we have to accept that long-time exposure of plants to extremely high concentration levels of TE, exceeding a certain dose of the stress factor—results in severe damages of root structure, their functions and the consequence death of plants.

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