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A review of hazardous elements tolerance in a metallophyte model species: *Erica andevalensis*

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ABSTRACT

As a result of mining activities large portions of land have been degraded. In this work, different tolerance/resistance mechanisms of *Erica andevalensis* Cabezudo y Rivera, which allow thriving and growing in soils from mine areas enriched with potentially toxic elements are reported. Different strategies were identified in *E. andevalensis* to tolerate high concentrations of metal(loid)s in soils through field and laboratory studies. The response of this species to high concentrations of hazardous elements varies according to the element. Experimental evidence for *E. andevalensis* adaptation to polluted soils/sediments and the role of other chemical elements (e.g. silicon) to enhance metal(loid)s tolerance is described. The species acts as an excluder for almost all elements and its tolerance to the harsh environments is due to complex mechanisms that include defense and avoidance.

1. Introduction

The establishment of cover vegetation by native species is relevant in land remediation projects especially under adverse soil conditions. Several human activities, like mining, are responsible of a great number of land degradation, and in many cases, soils and sediments in the neighborhood resulted contaminated with potentially hazardous elements (PHEs). In addition, these soils present adverse conditions for plant growth because of their low organic matter and unfavorable pH, lack of structure and frequently low water holding capacity. This is the case of soils developed on wastes from mining or impacted by acid mine drainage (AMD) in the Iberian Pyrite Belt (SW Iberian Peninsula, Spain and Portugal). The Iberian Pyrite Belt (IPB) is one of the largest sulfide deposits in the world (Tornos, 2006; Blasco et al., 2016). It is located in the South Portuguese Zone geological terrain, a major Variscan basement unit, and extends from Seville area (Andalusia region, Spain) to the Portuguese Atlantic coast (Marateca area, south of Lisbon) to a length of 250 km WNW–ESE direction (Matos and Martins, 2006; Relvas et al., 2006; Tornos, 2006). About 90 deposits of pyrite were identified in the IPB some abandoned and others still being exploitated. Mining activity in the IPB is known since the Calcolithic period related with pyrite gossans and copper veins structures. Later, in Roman times some mines were more intensively exploited but the increase in mining exploitation occurred especially in the 19th and 20th centuries when activity was greater environmental impact (Sáez et al., 1999; Matos and Martins, 2006; Relvas et al., 2006). At present, the environmental impacts observed in the abandoned mine areas are related to AMD generation, metal(loid)s dispersion, mine wastes management and unsafe mining infra-structures. The AMD occurrences are observed in several mine areas of the IPB, but the related environmental impacts in Portugal (e.g. São Domingos, Lousal, Aljustrel mine areas) are much smaller comparing with the Spanish IPB mines where intense AMD is observed (e.g. Riotinto, Tharsis, Aznalcollar and Sotiel mine areas) (Matos and Martins, 2006; Sarmiento, 2007; Abreu et al., 2010).

Under oxidizing conditions sulfides in mine wastes became instable generating AMD characterized by low pH, high concentrations of sulfate, iron and several potentially hazardous elements released during the sulfides oxidation processes (Abreu et al., 2010, Blasco et al., 2016). The AMD has contributed to the acidification and contamination of surface water and sediments along several kilometers of the water courses flowing in the mine areas (Quental et al., 2002; Olías et al., 2006; Hierro et al., 2012; Blasco et al., 2016). In some cases, edaphic endemic species are restricted to these specialized habitats (Kruckeberg and Rabinowitz, 1985), this occurs mainly in areas where edaphic conditions are particularly hostiles. Potentially hazardous elements disturb plant metabolism and physiological processes at different levels,

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and each plant species reacts with a different behavior according to the kind of metal(loid) and its concentration (Abreu et al., 2014a; Arenas-Lago et al., 2016; Palma et al., 2013; Santos et al., 2016). According to several authors (Macnair, 1993; Kruckeberg, 1986; Rajakaruna, 2004; Williamson and Balkwill, 2015), the high concentration of metal(loid)s in soils enriched with these potentially hazardous elements is a powerful selection factor for more-resistant plant genotypes. The effects of potentially toxic elements on plants depend on many factors such as plant species, the physical and chemical properties of the soil and the element. Such effects should cause the complete lack of vegetation or the development of a specific local flora of metal-tolerant species (Brooks, 1987; Macnair, 1987; Reeves and Baker, 1998, Whiting et al., 2004; O'Dell and Rajakaruna, 2011; Babst-Kostecka et al., 2016). Plants possess homeostatic mechanisms that are very important to ensure the survival since they allow the correct concentrations of essential elements in different cellular compartments and protect the damage from exposure to nonessential metal(loid) ions (Ernst et al., 1992; Clemens, 2001; Hall, 2002; Nagajyoti et al., 2010; Sinclair and Krämer, 2012; Alford et al., 2010). Metallophytes are plant species able to grow in metalliferous soils, as they have evolved a variety of mechanisms to cope with the excessively high internal metal(loid)s concentration via exclusion (preventing the entrance of contaminating elements in the harmful intracellular levels) or uptake and detoxification (Shaw, 1990; Hall, 2002; Baker et al., 2010; Krämer, 2010). These strategies are called exclusion (avoidance) and tolerance, respectively, and they may operate singly or in combination in PHEs detoxification (Gratão et al., 2005; Singh et al., 2016). Plants possess different avoiding strategies, which include fixation in mycorrhiza, plant cell walls, and root exudates sequestration. Mycorrhiza play an important role to exclude PHEs from the roots preventing them to reach the shoots (Bradley et al., 1982; Cairney and Meharg, 2003; Fomina et al., 2005; Vogel-Mikuš et al., 2006; Turnau et al., 2007; Ferrol et al., 2016). Tolerance mechanisms should involve the plasma membrane either by preventing the uptake of PHEs or through efflux mechanisms (Hall, 2002). Other mechanisms can also occur, such as chelation of PHEs by organic acids, amino acids (for review see Clemens, 2001) or peptides and their compartmentalization in organelles (keeping them away from metabolic processes) (Ernst et al., 1992; De, 2000; Hall, 2002; Reichman, 2002; Azzarello et al., 2012).

Erica andevalensis Cabezudoy Rivera (Fig. 1) is a perennial shrub up to 80 (− 1500) cm, with 4-verticillate 2–4 mm long linear-ovate leaves with strongly revolute entire margins and unicellular glandular hairs. Inflorescences umbellate with pink or sometimes white flowers of 4–7 mm flowering along the year. It is a vulnerable and endemic species of the Iberian Pyrite Belt (Cabezudo and Rivera, 1980), that colonizes mine tailings and the bank sediments of rivers such as the Tinto (Soldevilla et al., 1992; Asensi et al., 1999; García, 2006; Buján et al., 2007; Rodríguez et al., 2007; Monaci et al., 2011; Rufo et al., 2011) and Odiel (Trigueros Vera, 2011; Rufo et al., 2011) in Spain and São Domingos in Portugal (Abreu et al., 2008; Freitas et al., 2009; Anawar et al., 2011; Pérez-López et al., 2014; Durães et al., 2015). The species was classified as endangered by the Andalusian Regional Government (Aparício, 1999) and represents a good model organism to study the abiotic stress tolerance in extreme environments. The species can be found forming more or less isolated populations or can grow in association with *Erica australis* and a few other plant species (Aparício, 1999), but it seems to be the most tolerant to the extreme environmental conditions in the outskirts of Nerva and in the initial tract of the Tinto, where it forms a flourishing belt near the extremely acid mine drainage waters. The extraordinary capacity to adapt to extreme habitats has made two *Erica* species (*E. australis* L. and *E. andevalensis*) potentially useful plants for phytostabilization and to develop a self-sustaining vegetative cover on mine tailings and contaminated riverbank sediments (Abreu et al., 2008; Freitas et al., 2009; Monaci et al., 2011; Pérez-López et al., 2014). Understanding their survival strategies in these extreme environments provides unique challenges for its conservation. Plants that live in habitats characterized by harsh abiotic conditions, e.g. metal(loid)s excess, very low pH and nutritionally poor soils/sediments, provide a good example of how habitat-mediated divergent selection creates biological diversity. How these plants survive in this hostile environment? Why this species can be found only in these environments? What physiological mechanisms are employed by plants to maintain low intracellular PHEs levels? This work presents a review on the data concerning *Erica andevalensis* strategies to grow in metalliferous soils. It is a very convenient model plant species to study many aspects of metal(loid)s tolerance in extreme environments and to finally provide answers for the unresolved issues. This review summarizes: metal(loid)s tolerance mechanisms, metal compartmentalization after uptake, the role of Si in metal stress and defense mechanisms against metal(loid)s stress.

Fig. 1. *Erica andevalensis* growing close to the water in São Domingos (Portugal).

2. Metal(loid)s tolerance mechanisms and adaptation to mine soils

Different mechanisms of metal(loid)s tolerance are aimed at inactivating PTE that enter in the cytoplasm (e.g. Ernst et al., 1992). These may include a reduction of metal exposure by excretion of chelating substances, limiting accumulation in sensitive tissue or sequestration in tolerant organs, modified uptake systems at the plasmalemma or intracellular detoxification. A species may possess more than one tolerance mechanism (Shahid et al., 2017). Baker (1981) proposed two basic strategies for metal(loid)s tolerance in plants: (1) plants that concentrate PHEs in their aerial parts (*accumulators*) and consequently have detoxification mechanisms at cellular level, and (2) plants that maintain low metal(loid)s concentration in the leaves (*excluders*) due to the low translocation to shoots or through selective absorption by roots. Ericaceae family contains > 80 genera and about 2800 species, which display a cosmopolitan distribution even if they are better represented in South of Africa, North America, Himalaya and Southeast of Europe (Bayer, 1993) and includes pioneer species (Monni et al., 2000; Luteyn, 2002; Von Oheimb et al., 2009; Monaci et al., 2011; Abreu et al., 2014b). *Erica andevalensis*.

Ericaceae plants grow very well in mining areas of the Iberian Pyrite Belt (IPB). Mining activity in the IPB has generated a large volume of wastes and AMD, which are drained by the Tinto and Odiel rivers in Spain and São Domingos, Corona, Grândola and Água Forte streams in Portugal (Ruiz et al., 1998; Davis Jr et al., 2000; Abreu et al., 2010). In South Spain *E. andevalensis* may be found on Tinto and Odiel River banks as well as on mine tailings and acid soils (pH < 3.5) particularly