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Review

Toxicity of aluminium on various levels of plant cells and organism: A review

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ABSTRACT

Industrial revolution brought prodigious encroachment on agricultural productivity but at apparent environmental costs. One of the major unfortunate consequences of industrialization is soil acidification. In acidic soils, aluminium (Al) is the primary limitation of crop productivity worldwide. Inception of soil acidification ($pH < 5$) brings solubilisation of toxic forms of Al into the soil solution, where already micromolar concentrations of it inhibit root growth and cause impairment of several other physiological and metabolic functions. Almost 50% of the total world's potentially arable land consists of acidic soils that cause Al toxicity hazard. The problem of Al toxicity has been further aggravated by the use of fertilizers and acid rains. This review provides the current updates of uptake mechanisms, accumulation and subcellular localization of Al in plants, as well as several aspects of Al functioning on various levels of plant organism.

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1. Introduction

Along with industrial and technological progress, all the countries in the world face major challenges in dealing with environmental problems arising from the pollution. Long latency period, the effect of cumulative and multitudinous subjection to multiple pernicious pollutants that might act synergistically, induce difficulties in unraveling associations between environmental pollution and health.

Unfortunately, the asinine discharges of such highly complex effluents from industrial sources which are composed of precarious components of varying quantity and quality lead to acute toxicity and immense acidification of soil. Soil acidification is a serious environmental problem of economic concern in recent years that limits crop productivity at commercial level (Von Uexküll and Mutert, 1995; Gupta et al., 2013). Decrease in soil pH may be deleterious in terms of escalating crop susceptibility to toxicity imposed by increased solubility of aluminium (Al) (Lin and Wu, 1994). Despite this, there are several other factors that may speed up the soil acidification like intensive agriculture, some impropriate farming practices, intensified leaching of basic cations such as Na^+, K^+, Ca^{2+}, Mg^{2+}, acidic rains, etc. (Krug and Frink, 1983; Guo et al., 2010).

Aluminium is the third most abundant and ubiquitously distributed metallic element in the earth crust comprising 7% of its mass after oxygen and silicon; however its specific, biological function is yet not known (Foy et al., 1978; Schmitt et al., 2016). Being the integral constituent of mineral soils, its presence could be easily notified in almost all forms of life (Poschenrieder, 2008). Aluminium is one of the integral components of mineral soil in which it is usually incorporated in the precipitated form as gibbsite or the harmless aluminosilicates form. The inception of soil acidification ($pH < 5.0$) initiate Al solubilisation to a limited extent that would led to the eventual release of phytotoxic form of Al, mainly as monomeric Al^{3+} which also formulates the mononuclear species such as $AlOH^{2+}$, $Al(OH)_2{}^+$, $Al(OH)_3$, and $Al(OH)_4$. However, among all forms of aluminium, Al^{3+} is considered as the most toxic one (Parker et al., 1989; Kochian 1995; Kinraide, 1997; Panda and Matsumoto, 2007; Vardar and Unal, 2007; Silva, 2012; Schmitt et al., 2016).

Aluminium toxicity in acidic soil is one of the major constraints for crop production worldwide (Ryan and Kochian, 1993; Kochian, 1995; Ma, 2000; Poschenrieder, 2008; Nunes-Nesi et al., 2014). Potential toxicity of Al could result from complex interactions of Al with apoplasmic (cell wall), plasma membrane, and symplasmic (cytosol) targets (Kochian et al., 2005). Several plant species are susceptible to the micromolar concentration of Al and the root growth inhibition is certainly the most easily recognizable trait of Al toxicity which can widely be marked as a measure of Al toxicity in plants (Čiamporová, 2002; Gupta et al., 2013; Schmitt et al., 2016). In fact, exploring root meristem as a plant bioassay scheme has been recommended for Al toxicity (Vardar and Unal, 2007; Silva, 2012; Gupta et al., 2013). Many plant species, whether naturally occurring in the field or experimentally grown, when subjected to prolonged Al exposure, undergo a series of physiological, cellular, molecular and morphological changes (Table 1). However, the meticulous mechanism responsible for Al toxicity is still not well known. As Al^{3+} poses the capacity of interaction with a number of intra- and extracellular components, variable mechanisms of Al^{3+} toxicity have been proposed such as cell wall modification, interruption of signaling pathways, disruption and depolarization of the plasma membrane, modified transport processes (Table 1) and Al^{3+} binding to the DNA (Tamas et al., 2004; Kochian et al., 2005; Ílleš et al., 2006).

Although it is hard to locate the primary targets by determining the secondary effects so far, discernment of the target sites of the Al-toxicity is worthwhile for demonstrating the mechanisms through which Al exerts its detrimental effects on the root growth (Table 1). To conquer the toxicity inflicted by Al stress, the development of tolerant mechanism is the major aim of expertise and ingenuities of plant sciences (Kochian et al., 2005; Gupta et al., 2013).

Notably, the Al^{3+} toxicity has been marked as one of the major agronomic mishap and the most important topic of research, gaining perpetual attention day by day. The reason is that many crops are more or less susceptible in acidic soils, and the overall crop performance is highly influenced by toxic level of Al^{3+} (Vardar and Unal, 2007; Gupta et al., 2013). Though investigation of Al induced toxicity and tolerance mechanisms have still been preceded by number of laboratories around the world, the physiological and genetically based resistance mechanisms have gained much consideration in the recent years (Delhaize and Ryan, 1995; Marschner, 1995; Matsumoto, 2000; Silva, 2012; Gupta et al., 2013; Arenhart et al., 2016). Some investigations revealed that uptake of Al is restricted chiefly to the root system, where it agglomerated predominantly in the epidermis and the outer cortex (e.g. Jan, 1991; Ryan and Kochian, 1993; Kochian, 1995; Čiamporová, 2002; Schmitt et al., 2016) while others demonstrated its considerable accumulation in the shoot system as well (Kochian, 1995; Matsumoto et al., 2001).

To combat with the toxic effect of increased Al level in the environment plants have evolved several mechanisms including secretion of Al-chelating substances such as organic acids (OAs), mainly citrate, oxalate, and malate, also phosphate (Pi), and phenolic compounds from the roots (Barceló and Poschenrieder, 2002; Vardarand Ünal, 2007) (Fig. 5). Mostly, identified OAs were basically the deprotonated anions which were found at neutral pH in the cytosol but once get transported out through the root upon the onset of Al stress they would chelate the toxic Al^{3+} in the rhizosphere, and lead the formation of stable and non-toxic complexes (Table 1).It is the best documented mechanism employed by plant against Al stress (Yang et al., 2012; Brunner and Sperisen, 2013; Nunes-Nesi et al., 2014). Internal detoxification mostly includes forming of Al complexes with organic acids and its sequestration into vacuoles for maintaining low level of free Al in the plant cytosol (Hue et al., 1986; Baluška et al., 2003; Kinraide et al., 1994; Watanabe and Osaki, 2002). In this view, several genes that are known to have significant effect on Al tolerance were recognized (Delhaize et al., 2012; Fujii et al., 2012; Arenhart et al., 2013, 2014; Gupta et al., 2013; Ma et al., 2014).

Investigation of Al resistance mechanism is certainly important in plant in order to improve productivity on acidic soils. Nonetheless, the similar tolerance mechanisms have been reported in woody plants to avoid Al toxicity (Brunner and Sperisen, 2013). In addition, in wild herbs also the exudation of organic acids in response to increased concentration of Al has been also reported (Shivaguru et al., 2000). Additionally, in the cytoplasm Al ions also meet with some other kind of ligands with a wide range of binding affinities such as ATP, RNA, or sugar phosphate and phenolic compounds (Godbold and Jentschke, 1998). Further on the basis of several comparative studies some authors concluded that exudation of organic acids may not be the only mechanism of Al tolerance in higher plants (Bose et al., 2010). Therefore, it becomes immensely important to completely understand the resistant mechanisms adopted by species to cope with Al toxicity. Beside this, the tolerant genotypes should also be identified and grown on acidic soils in order to curb Al toxicity and to produce tolerant cultivar to increase crop production worldwide. This review explores our contemporary knowledge about Al functioning at the physiological and morphological level to enhance crop performance under the Al toxicity. Captivating documentation has been provided in the present literature pinning

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