



Title	Basic understanding of aluminum accumulator plants
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Citation	Eurasian Journal of Forest Research, 22, 59-62
Issue Date	2022
DOI	10.14943/EJFR.22.59
Doc URL	http://hdl.handle.net/2115/84960
Type	bulletin (article)
File Information	13) EJFR_Watanabe_final.pdf



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Basic understanding of aluminum accumulator plants

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Abstract

High concentration of aluminum (Al) ion solubilized in acid soils restrict plant growth. The mechanisms of plant adaptation to Al stress can be separated into Al exclusion and internal Al inactivation. In general, plant species that have developed mechanisms of the former type are called “Al excluders”, and those that have developed mechanisms of the latter type are called “Al accumulators”. Aluminium accumulators are widely distributed in acid soils, particularly in humid tropics. In addition to their geographical distribution, Al accumulators show a wide phylogenetic distribution in plant. Here I discussed physiological characteristics of Al accumulation among different Al accumulator species within various vascular plant taxa. Results from the literature suggested that variation of the Al detoxification and accumulation mechanisms in the tissue of Al accumulators seemed to be small in vascular plant.

Key words: acid soil, aluminum toxicity, aluminum accumulator plant, oxalate, silicon.

Introduction

Acid soils occupy approximately 30% of the world's ice-free land area (von Uexküll and Mutert 1995). It is well known that high Al ion concentration in soil solutions is the most important factor in restricting plant growth in acid soils. In non-acid soils, the naturally occurring Al forms are usually stable and non-toxic, but soluble Al ions become available in soil solutions when pH is below 5.5. In most plant species, the Al toxicity is a problem in roots. It has been reported that Al increases plasma membrane permeability by binding phospholipids (Matsumoto *et al.* 1992) and membrane proteins (Caldwell 1989), or by lipid peroxidation (Ikegawa *et al.* 2000). Al also increases cell wall rigidity (Wehr *et al.* 2004) by binding pectin (Horst *et al.* 2010) and hemicelluloses (Yang *et al.* 2011). Generally, the mechanisms of Al tolerance can be separated into Al exclusion and internal Al inactivation. Most plant species have developed the ability to exclude Al from roots as a method of adapting to acid soils (Kochian *et al.* 2015). The most well-known mechanism of Al exclusion is the exudation of organic acid anions from the root. Some organic acid anions can make stable complex with Al, resulting in Al inactivation in rhizosphere. The efficiency of Al-inactivation is dependent on the chelating ability of the secreted organic acid anions, which can be corresponded to their stability constants of Al-organic acid anion chelate. The major organic acids released from roots for Al detoxification (exclusion) are citrate (e.g. in maize (Pellet *et al.* 1995), *Cassia tora* (Ma *et al.* 1997), soybean (Yang *et al.* 2000), snapbean (Miyasaka *et al.* 1991), rye (Li *et al.* 2000), triticale (Ma *et al.* 2000)), malate (e.g. in wheat (Delhaize *et al.* 1993), rye (Li *et al.* 2000), triticale (Ma *et al.* 2000)) and oxalate (e.g. in buckwheat (Ma *et al.*

1997), taro (Ma and Miyasaka 1998)). It has been suggested that the exudation of organic acid anions is controlled by anion transporter. Some anion channel inhibitors inhibited oxalate secretion (and decreased the Al tolerance) in buckwheat (Zheng *et al.* 1998). Sasaki *et al.* (2004) isolated a novel gene, *ALMT1*, which encodes an Al-activated malate transporter in wheat. Homologues of wheat *ALMT1* were isolated in several plant species, such as *Arabidopsis thaliana* (Hoekenga *et al.* 2006) and *Brassica napus* (Ligaba *et al.* 2006).

Thus, the exudation of organic acid anions is a key mechanism of Al tolerance in plant. However, it is also known that Al tolerance in plant cannot be explained only by the exudation of organic acid anions. When comparing Al tolerance and organic acid anion (citrate) exudation under Al stress in 7 different plant species, no correlation was observed between these two parameters (Wagatsuma *et al.* 2001). For example, rice has relatively higher tolerance to Al but does not exude significant amounts of organic acid anions from roots for Al tolerance (Wagatsuma *et al.* 2001). There are many reports studying Al tolerance mechanisms in rice. Watanabe and Okada (2005) suggested that the differences in Al tolerance between japonica (tolerant) and indica (sensitive) varieties can be explained by different electrochemical characteristics of root-tip cells. Ma *et al.* (2002) mapped quantitative trait loci (QTLs) for Al tolerance mapped in a population of 183 backcross inbred lines derived from a cross of Koshihikari (tolerant) and Kasalath (sensitive). In their study, three putative QTLs controlling Al tolerance were detected on chromosomes 1, 2 and 6. Khan *et al.* (2009) reported that the difference in lipid composition of plasma membrane could explain the difference in Al tolerance in rice. As explained above, many researchers are studying the mechanisms of Al tolerance in rice but

definite mechanism is still unclear.

Aluminum accumulator plants

Another important mechanism of Al tolerance is the internal Al tolerance. Generally, the most part of Al absorbed by roots cannot be transported to shoots. In some specific plant species adapted to acid soils, however, considerably large amounts of Al are transported and accumulated in shoots. Such plant species that highly develop the internal Al tolerance are often called “Al accumulators”, and are mostly woody plants. Such accumulator plants are also found in other toxic elements, including heavy metals (Memon and Schröder 2009), which may be a common adaptation mechanism of plants to toxic elements. Heavy metal accumulator plants have also been used in phytoremediation to remove toxic elements from the contaminated soil (Memon and Schröder 2009).

Then, how do Al accumulators resist such a high tissue concentration of Al? It has been shown in some accumulator species that organic or inorganic ligands form stable complexes with Al in the tissues, like in the rhizosphere of Al excluders exuding organic acid ligands from the roots. For example, *Melastoma malabathricum* (Figure 1), which is a woody plant growing in acid soils in Southeast Asia, accumulates more than 10,000 mg Al kg⁻¹ DW in the leaves as monomeric Al and Al-oxalate complexes (Watanabe *et al.* 1998). Similarly, the main Al-form in the leaves of *Hydrangea macrophylla* was reported to be an Al-citrate complex (Ma *et al.* 1997). Inorganic ligand for Al in tissues of Al accumulator species was also suggested. *Faremea marginata*, a woody species growing on mainly acid soils, is not only a strong Al accumulator, but also a Si accumulator. The form of Si in *F. marginata* is different from that in rice, a typical Si accumulator, and is likely to make complex with Al (Britez *et al.* 2002).

Why can they accumulate such high concentrations of Al in their tissues (shoots)? In strongly acid soils, rhizospheric Al activities are extremely high. In case of Al excluders, large amounts of organic acid anions, synthesized from photosynthate, are needed to inactivate rhizospheric Al in such soils, resulting in increase of carbon loss. Moreover, organic acid anions would diffuse in soil solution, and be decomposed by soil microorganisms. By contrast, Al accumulators can concentrate organic acid anions on inside plant. This is energetically-favored system to survive in strongly acid soils. Besides this, some Al accumulators utilize Al for their growth. Although *M. malabathricum* is a dominant species in some strongly acid soils with high concentration of both Al and iron (Fe) (e.g. acid sulfate soils), it is very sensitive to Fe toxicity. Fe is an essential micronutrient for plant, but excess Fe often induces an excess of reactive oxygen species. Watanabe *et al.* (2006) showed that Al absorption competitively decreases Fe absorption in *M. malabathricum*. This decrease of Fe accumulation allows *M. malabathricum* to distribute as a dominant plant species in strongly acidic soils.



Figure 1. *Melastoma malabathricum*.

Phylogenetic distribution of aluminum accumulator plants

Plant species with Al levels of at least 1000 mg kg⁻¹ in their leaves or shoots are defined as Al accumulators (Chenery 1948). The phylogenetic distribution of Al accumulator plants has been studied by several researchers. Jansen *et al.* (2002) comprehensively analyzed the data in the literature, and applied recent molecular phylogenies to evaluate the systematic and phylogenetic implications of the Al-hyperaccumulation characteristic. They found that Al accumulators are mainly eudicots, and are particularly common in basal, woody branches of fairly advanced groups, such as rosids and asterids, but the characteristic has probably been lost in more derived, herbaceous taxa (Jansen *et al.* 2002). Furthermore, Schmitt *et al.* (2017) showed that Al accumulators are also widely distributed in pteridophytes, and that Al hyperaccumulation is much more common in pteridophytes than in angiosperms.

Phylogenetic variation of aluminum forms in the tissue of aluminum accumulator species

Aluminium forms in the tissue of Al accumulator plants have been reported in various studies (Figure 2). It has been reported that oxalate is the most common ligand for a part of Al in the tissue of Al accumulator species in various clades of angiosperms (Ma *et al.* 1997; Maejima *et al.* 2014; Morita *et al.* 2006; Watanabe *et al.* 1998), whereas a high concentration of non-chelated monomeric Al was also detected in the leaves of woody eudicots (Maejima *et al.* 2014; Watanabe *et al.* 1998). Oxalate has often been regarded as an end product that is not further metabolized or only slowly metabolized. Whereas various functions of oxalate have been suggested, the most common function is the regulation of Ca levels and protection against herbivory by forming Ca oxalate crystals (Franceschi and Nakata, 2005). Moreover, oxalate itself is toxic in a soluble form. Therefore, from the other perspective, it is possible that excess oxalate is detoxified by binding with Ca in plant. Detoxification of Al by oxalate in plant might be derived from Ca oxalate crystal formation. Furthermore, as another ligand for Al, silicon (Si) was also suggested to contribute in some Al accumulator species (Britez *et al.*

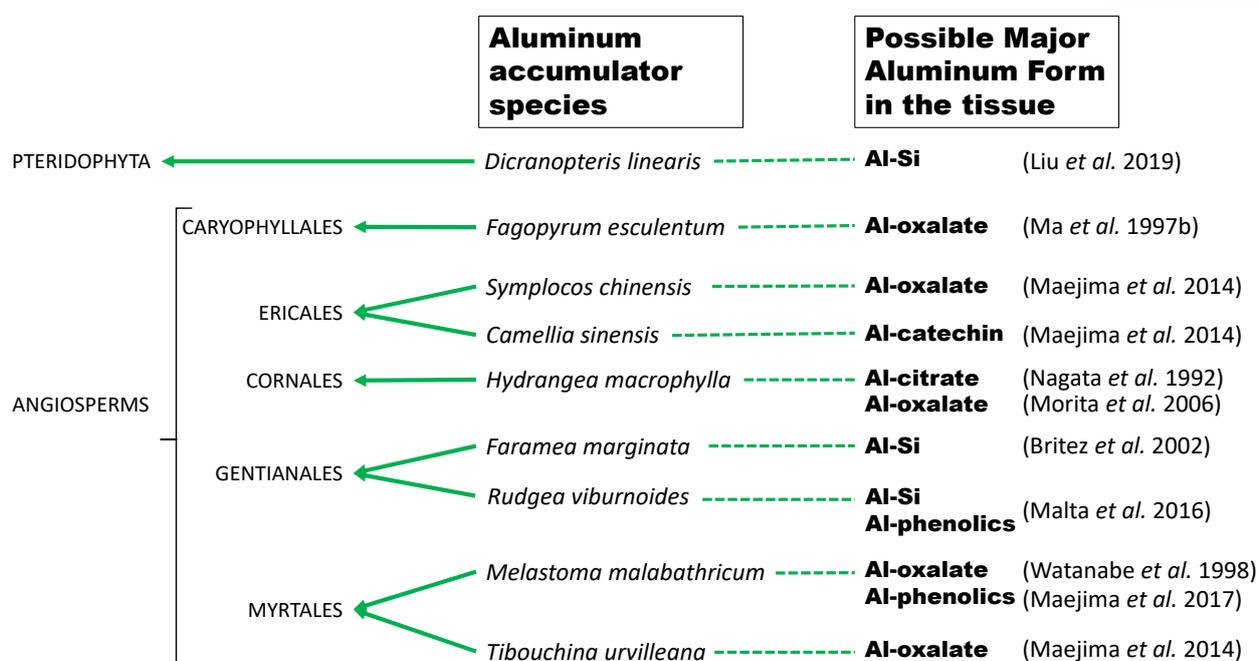


Figure 2. Possible major aluminum forms in the tissue of aluminum accumulator plants.

2002; Malta *et al.* 2016), including *Dicranopteris linearis*, a fern (Liu *et al.* 2019). These results imply that internal Al detoxification mechanisms by making Al-oxalate or Al-Si complexes in plant tissue may be very primitive and common in vascular plants.

Acknowledgments

I would like to express my appreciation to JSPS for supporting Bilateral Joint Seminar.

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