Article

How do Citrus Crops Cope with Aluminum Toxicity?

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World Agriculture faces daunting challenges in feeding the growing population today. Reduction in arable land extent due to numerous reasons threatens achievement of food and nutritional security. Under this back ground, agricultural use of acidic soils, which account for approximately 40 % of the world arable lands is of utmost important. However, due to aluminum (Al) toxicity and low available phosphorous (P) content, crop production in acidic soils is restricted. Citrus, in this context, gains worldwide recognition as a crop adapted to harsh environments. The present paper reviewed Al toxicity and possible toxicity alleviation tactics in citrus. As reported for many other crops, inhibition of root elongation, photosynthesis and growth is experienced in citrus also due to Al toxicity. Focusing at toxicity alleviation, interaction between boron (B) and Al as well as phosphorus and Al has been discussed intensively. Al toxicity in citrus could be alleviated by P through increasing immobilization of Al in roots and P level in shoots rather than through increasing organic acid secretion, which has been widely reported in other crops. Boron-induced changes in Al speciation and/or sub-cellular compartmentation has also been suggested in amelioration of root inhibition in citrus. Despite the species-dependent manner of response to Al toxicity, many commercially important citrus species can be grown successfully in acidic soils, provided toxicity alleviation Agro-biological tactics such as addition of phosphorous fertilizers are used properly.

Key words: Acidic soil, Aluminum toxicity, Citrus, Detoxification

Introduction

Aluminum toxicity in acidic soils Soil acidification, a process associated with leaching of basses, high oxidative biological activities which produce acids, high rainfall and low evaporation and some crop management practices etc. is recognized to be a major constraint in crop production, in particular, in the tropics and subtropics (López and Espinosa, 2000; Matsumoto, 2002; Ishitani et al., 2004). In agricultural lands, crop plants keep absorbing cations (such as K^+, Ca^{+2} and Mg^{+2}) releasing H^+ to maintain ionic balance in soil-plant environment. Addition of nitrogenous fertilizers may also releases H^+ through nitrification of ammonium (NH_4^+). Acid-soil syndrome is thus reported in acidic soils, which account for approximately 30% of the world's total land area.(Kochian et al., 2004; Chen et al., 2012) Furthermore, it has been estimated that over 40% of the world's potential arable lands are acidic. Crops grown in acidic soils can undergo several difficulties, including toxicity of aluminum (Al), hydrogen (H), and/or manganese (Mn), as well as potential nutrient deficiencies of magnesium (Mg) and calcium (Ca).

In terms of relative abundance, Al is the third element after oxygen and silicon and the most abundant metal in the earth's crust (Ma and Furukawa, 2003; Matsumoto and Motoda, 2012). It belongs to the non-essential category of metals, thus does not exert any known function in plant metabolism (Wang and Kao, 2004). However, the metal is considered to be the most widespread problem in acid soils, where land use for agricultural purposes was severely affected (Lilienfein et al., 2003). Depending on pH, Al exists in a number of different forms in the soil (Wang et al., 2006). Under acidic conditions, Al is solubilized into $[Al(H_2O)_6]^{3+}$, generally referred to as Al^{3+}, which is highly toxic to many plant species (Éva Darkó et al., 2004). Despite the fact that many plants find it difficult to withstand against the Al toxicity, it's most common forms i.e. oxides and aluminosilicates are harmless to plants (Ma and Furukawa, 2003; Wang and Kao, 2004).

Under Al-stress, sensitive plants display a number of toxicity symptoms depending on the species, variety and/or genotype. Inhibition of cell division in the root tip meristem by Al^{3+} is often reported for many species (Gunsé et al., 2003; Doncheva et al., 2005; Meda and Furlani, 2005). Increased rigidity of the double helix of DNA caused by accumulated Al^{3+} results in poor cell division in root tip meristem (Meriga et al., 2010). In fact, in many plants, inhibition of root elongation has been reported within a few minutes time even at micromolar concentrations of Al^{3+} (Matsumoto and Motoda, 2012). The growth of the plant is affected mainly due to poor uptake of moisture and nutrients by injured root tips (Samac and Tesfaye, 2003; Vitorello et al., 2005). In some cases, increased susceptibility to drought stress, lodging and nutrient deficiencies are also reported from affected plants (Sun et al., 2010).

Under this background crop species which can grow on acidic soils gain increasing attention worldwide. In this context, *Citrus* spp. are widely recognized as hardy species, which can be cultivated successfully on acidic soils (Jiang et al., 2009a).

Citrus crops Citrus, a major group of fruit crops belong to family Rutaceae play a vital role in the achievement of nutritional security. These crops are primarily gained recognition as fruits, which are either eaten alone (sweet orange, tangerine, grapefruit, etc.) as fresh fruit, processed into juice, or added to dishes and beverages (lemon, lime, etc.). In addition to the food value, citrus crops possess medicinal value also, in particular, in traditional medicine (Manner et al., 2006). Out of many species coming under the common name of citrus, Table 1 summarizes several species which are of commercially important.

During last couple of decades, the global production of citrus has experienced an increasing growth. The continuous rise in citrus production is attributed to the increase in land extent under cultivation, change in consumer preference towards fresh and healthy food and rising income level of the consumers (UNCTAD, 2005). As of the latest records, global production and trade of citrus for 2011 has been forecasted at 51.4 million metric tons (MMT) and 3.8 MMT, respectively. Oranges constitute the bulk of the production, accounting for more than half of global citrus production, however, contribution of grapefruit, pommeloes, lemon and limes is also found to be significant (Table 2).

Effect of aluminum on citrus Pereira et al. (2003) investigated the effect Al on the growth of *Citrus limonia* Osbeck, *Citrus volkameriana* Hort. ex Tan, *Citrus reshni* Hort. ex Tan and *Citrus sunki* Hort. ex Tan in hydroponic culture and observed reduced growth of the shoot, leaf area ratio and leaf weight ratio under Al-stress. However, the relative growth rate (RGR) of all the rootstocks was found to be increased initially despite the presence of Al in the nutrient solution, which might be due to initial increase in net photosynthesis rate as reported by Pereira et al. (2000), who investigated gas exchange and chlorophyll fluorescence in four citrus rootstocks under Al-stress. Explaining the results, Pereira et al. (2003) further mentioned that Al could negatively affect the ability of plants to maintain and, or increase the existing dry matter due to Al-induced enhancement of potential respiratory component of the plant. According to Chen et al. (2005b), growth parameters such as leaf, stem and root fresh and dry mass of citrus plants (*Citrus reshni* Hort. Ex Tan)

Table 1. Citrus species, their common names and origin (extracted from Manner et al., 2006).

Species	Common name	Native origin
C. sinensis	Sweet orange	S. China, Indochina
C. reticulata	Mandarin	SE Asia
C. paradisi	Grapefruit	West Indies
C. mitis	Calamondin	China
C. medica	Citron	India
C. macroptera	Wild orange	Malaysia
C. limon	Lemon	SE Asia
C. hystrix	Kaffir lime	Malaysia
C. grandis	Pummelo	Malaysia
C. aurantium	Sour orange	S. China, Indochina
C. aurantifolia	Lime	Malesia

Table 2. Production of citrus in major producing countries in 2011/2012 (1000 metric tons).

Oranges	Grapefruit	Lemons and limes	Tangerines/Mandarins
Brazil (19053)	China (3000)	Mexico (1700)	China (15000)
United states (8140)	United states (1022)	EU-27 (1316)	EU-27 (3127)
China (6600)	South Africa (390)	Argentina (1200)	Japan (1015)
EU-27 (5521)	Mexico (300)	Turkey (850)	Turkey (875)
Mexico (3200)	Turkey (240)	United states (753)	Morocco (730)
Egypt (2350)	Israel (205)	South Africa (260)	Korea, South (645)
Turkey (1730)	Argentina (160)	Israel (61)	United states (635)
Other (4513)	Other (104)	Other (68)	Other (594)
Total (51107)	Total (5421)	Total (6208)	Total (22621)

Source: USDA 2012. Citrus world markets and trade. Foreign Agricultural Service.

showed marked reductions compared to control. Furthermore, it has been noticed that reductions in leaf and stem fresh and dry mass were greater than those of the root in response to Al. Confirming these findings, Jiang et al. (2008) reported a reduction in shoot dry mass in *Citrus grandis* (L.) seedlings irrigated for 5 months with nutrient solution containing different concentrations (0.2, 0.6 or 1.6mM) of Al. However, no significant decrease in root dry mass has been observed up to 0.6 mM Al in the nutrient solution. Similar results have been reported by Chen et al. (2009) with *Citrus grandis* (L.) seedlings irrigated with Al containing nutrition medium.

Role of boron and phosphorous on aluminum toxicity
An investigation was conducted (Jiang et al., 2009b) with *Citrus grandis* L. seedlings to determine how boron alleviates Al-induced inhibition of root and shoot growth and results confirmed that inhibition of root and shoot growth is not due to Al-induced boron deficiency, but due to Al toxicity. Their findings on preventive measures of boron are in line with the results of Yu et al. (2009), who conducted a similar study with pea (*Pisum sativam*). According to Jiang et al. (2009b), boron induced changes in Al speciation and/or sub-cellular compartmentation would be the reason behind amelioration of root inhibition in citrus, which has previously stated by Corrales et al. (2008) also. However, Jiang et al. (2009b) further reported that boron induced amelioration of shoot growth and photosynthesis inhibition could be due to less Al accumulation in shoots.

In fact, the ability of boron in alleviation of Al toxicity has been reported for several other plants including apple (Wojcik, 2003) and wheat (Hossain et al., 2004). However, no ameliorative effects of boron on Al toxicity could be detected in maize (Wang et al., (2005), which is confirmed by Corrales et al. (2008) as they too have not observed any amelioration effect of boron on inhibition of root growth in maize.

Several possible mechanisms have been proposed in exploring the boron-induced alleviation of Al toxicity. Ruiz et al. (2006) assessed the Al toxicity in sunflower and suggested that boron- induced enhancement of glutathione (GSH) synthesis as the mechanism, through which boron ameliorate the Al toxicity. As observed previously (Yamamoto et al., 2001; Boscolo et al., 2003), increased concentration of GSH could minimize Al-induced oxidative stress in plants. Putting forward another mechanism for dicots, Stass et al. (2005) stated that boron could decrease in unmethylated pectin in cell walls of root tips discouraging Al binding to apoplastic compartments.

Phosphorus deficiency has been extensively discussed as a key factor attributed to poor crop performances in acidic soils. Inorganic phosphates in acidic soils are associated with iron (Fe) and Al compounds; whereas calcium (Ca) phosphates are predominant inorganic phosphate form in neutral or calcareous soils (Gyaneshwar et al., 2002). Unfavorable pH and high reactivity of Al and Fe in acidic soils decrease phosphorous availability as well as phosphatic fertilizer efficiency (Hao et al., 2002). Therefore, the majority of applied phosphatic fertilizers are readily fixed in soil and become unavailable to plants. In this context, it is presumed that sufficient P nutrition could guarantee the healthy growth of plants and improve resistance to other abiotic stresses including Al toxicity.

Several plant species have been employed in elucidating the interaction between added P and Al toxicity. Studies with soybean (Liao et al., 2006), rice (Nakagawa et al., 2003) and maize (Gaume et al., 2001) suggested that P

addition could alleviate Al toxicity. According to Chen et al. (2012), P-dependent alleviation of Al toxicity is based on two possible mechanisms. Al can be precipitated directly with P on the root surface, in root cell walls or within root cells or in the soil solution (Silva et al., 2001; Nakagawa et al., 2003; Zheng et al., 2005). As the other possible mechanism, external application of P could alleviate Al toxicity indirectly through improving the root morphology, which facilitates nutrient uptake or by secreting special root exudates (Liao et al., 2006).

Concluding their findings of the experiment conducted with *C. grandis,* Jiang et al. (2009a) reported that P could alleviate Al-induced inhibition of growth and photosynthesis through increasing Al immobilization in roots and P level in roots and shoots. Yang et al. (2011) too reported that Al toxicity in citrus (*C. grandis* and *C. sinensis*) could be alleviated by P through increasing immobilization of Al in roots and P level in seedlings rather than through increasing organic acid (OA) anion secretion.

Role of nitric oxide on aluminum toxicity Gaseous free radical nitrous oxide (NO) is widely recognized to be involved in resistance mechanism of abiotic-stress in many plants (Hasanuzzaman et al., 2010; Marciano et al., 2010; Siddiqui et al., 2011). In fact, nitric oxide could mediate several physiological and biochemical functions in plants through its role as a signaling molecule (Besson-Bard et al., 2008). Even though enough research evidence on as to how nitric oxide minimize the abiotic stress is yet to receive, several authors reported that nitric oxide is involved in regulating plant's response to salinity (Song et al., 2009), water deficit (Neill et al., 2002) and to Al toxicity (Wang and Yang, 2005).

Al-induced inhibition of root growth was found to be prevented by nitric oxide in *Oryza sativa* (Marciano et al., 2010); *Hibiscus moscheutos* (Tian et al., 2007) *Cassia tora* (Wang and Yang, 2005), *Phaseolus vulgaris* (Wang et al., (2010) and *Citrus grandis* (Yang et al., 2012). Al-induced oxidative stress in roots was also reported to be minimized by nitric oxide in *Phaseolus vulgaris* (Wang et al., (2010) and *Cassia tora* (Wang and Yang, 2005), where the action of nitric oxide against root growth inhibition was found to be correlated with less Al accumulation in root apexes. According to Marciano et al. (2010), Al-induced inhibition of seed germination in *Oryza sativa* can also be prevented by nitric oxide.

Effect of aluminum on CO_2 assimilation It has been well documented that photosynthetic apparatus are also affected by the heavy metals toxicity. Heavy metals can interrupt different functions of photosynthesis either directly or indirectly. Light and dark reactions are directly affected by the heavy metals, while reductions in photosynthetic pigments and alteration of stomata function etc., can be considered as indirect effects (Mysliwa-Kurdziel et al., 2004). Though it has been reported previously that heavy metals are not involved in declining the activities of enzymes associated with Calvin cycle, there are enough evidence to say that metal-induced inhibition of enzymes involved in the Calvin cycle is highly responsible for reduced CO_2 assimilation (Romanowska, 2002), in particular, Rubisco and PEPcarboxylase (Mysliwa-Kurdziel et al., 2004). Inhibition of enzyme activities of the Calvin cycle and stomatal closure causing short supply of CO_2 are often reported (Seregin and Ivanov, 2001; Bertrand and Poirier, 2005; Linger et al., 2005). In addition, Barcelo and Poschenrieder (2004) reported that all most all the components of the photosynthetic apparatus, which include chlorophyll and carotenoid content, chloroplast membrane structure, light-harvesting and oxygen-evolving complexes, photosystems and constituents of the photosynthetic electron transport chain are influenced by heavy metals.

According to Chen et al. (2005a), in response to Al, CO_2 assimilation has decreased in Cleopatra tangerine (*Citrus reshni* Hort. Ex Tanaka) seedlings which confirmed previous report of Pereira et al. (2000) for four *Citrus* spp. rootstocks. They have further observed higher intercellular CO_2 concentration in Al-treated leaves than in control leaves, which is in agreement with both Pereira et al. (2000) and Peixoto et al. (2002), who too found higher intercellular CO_2 concentrations in Al-treated leaves than in control leaves. However, Al-induced stomatal conductance and intercellular CO_2 concentration appear to be dependent upon the species and/or cultivar, duration and Al concentration to which the plant is exposed.

Jiang et al. (2008) recognized Photosystem II (PSII) as the most sensitive photosynthetic apparatus to environmental stress, which is in line with Peixoto et al. (2002), who described the involvement of impaired PSII photochemistry to the reduction of Al-induced photosynthesis in sorghum. In fact, more or less similar comments were made by Chen et al. (2005b) in reporting their findings with citrus. According to them, Al-induced reduction in CO_2 assimilation is associated with a possible combination of factors, which

include reduced electron transport rate through PSII, increased closure of PSII RCs and increased photorespiration.

Mechanisms of aluminum tolerance in citrus   As of numerous reports available in the literature on this topic, a considerable number of studies with Al-sensitive and Al-resistant species/cultivars have been conducted and based on the findings, it could be suggested that Al toxicity and the mechanisms attributed to Al-resistance are extremely complex phenomena (Matsumoto, 2000; Ciamporová, 2002; Éva Darkó et al., 2004). Out of the several possible mechanisms, exclusion is widely accepted as the key contributor in preventing/minimizing Al toxicity in plant species (Delhaize et al., 2007; Garzon et al., 2011). As reported by many authors, exclusion is expected to occur as a result of one or combination of following processes; exudation of chelating ligands, formation of pH barrier at the rhizosphere or at root apoplast, cell wall immobilization, selective permeability of the plasma membrane and Al efflux (Éva Darkó et al., 2004; Wang et al., 2006; Delhaize et al., 2007; Tolra et al., 2009).

Al-induced secretion of organic acid as chelating agents has been shown to be the dominant detoxification mechanism for many plant species (Kochin et al 2004; Poschenrieder et al., 2005; Ma 2007; Maron et al., 2010). Though secretion patterns, temperature sensitivity, response to inhibitors, dose response to Al etc., depend on the species of concern (Ma 2007; Dong et al., 2008), citrate, malate, and oxalate are reported to be exudated at the rhizosphere and the apoplast of many plant species (Ryan et al., 2001; Poschenrieder et al., 2005). In some plants, secretion of organic acids commences immediately after the exposure of the plant to Al, thus induction of genes is not expected (Ma, 2007). However, there are plants, where Al-induced expression of genes and synthesis of proteins involved in metabolism are needed to initiate secretion of organic acids (Ma et al., 2001).

Among the other mechanisms, rise of pH at the soil solution has been reported, because, rising pH could reduce the Al solubility permitting the formation of less-toxic Al species such as Al-hydroxides and Al-phosphates etc., (Wang et al., 2006). Exudation of organic acids from roots is also encouraged by elevated pH at rhizosphere. However, Garzon et al. (2011) elaborating their findings of the experiment carried out with two maize varieties reported that neither rhizosphere pH changes nor Al-tolerance were clearly related to Al-induced changes in exudation of organic acids into the rhizosphere. Formation of stable complex with ionic Al is known for some of these organic acids, thus, can prevent binding of Al^{3+} with extra- and intracellular substances of the root (Li et al., 2000). Chelation of Al^{3+} by other forms of ligands in the cytosol (Ma et al., 2001), Al compartmentation in the vacuole, etc. and several other possible Al^{3+} protective mechanisms are also found in the literature (Éva Darkó et al., 2004).

With regard to citrus, Yang et al. (2011) reported that *C. sinensis* roots secrete more malate and citrate than *C. grandis* in response to Al toxicity, however, Al-induced secretion of malate and citrate decreased with increasing P supply. According to them, involvement of P in alleviating Al toxicity through increasing immobilization of Al in roots is much stronger than toxicity reduction through increasing organic acid anion secretion. Furthermore, the higher Al-tolerance observed in *C. sinensis* may be due to secretion of organic acids and precipitation of Al by P in roots. Chen et al. (2009) also observed Al-induced secretion of malate and citrate in *C. grandis*. They reported that concentrations of malate and citrate were less affected by the interaction of P and Al in roots compared to leaves. According to their findings, concentrations of both organic acids were higher in shoots with Al than without Al; whereas in roots, both were lower with Al than without Al. Therefore decreased concentrations of malate and citrate in roots in response to Al could be due to Al-induced exudation of organic acids under P.

Conclusion

Crop production in acidic soils is restricted mainly due to Al toxicity and low available P content. Citrus by nature is adapted to hardy environments, thus is widely grown in tropical and subtropical areas, where acidic soils are predominately used in Agriculture. However, the degree of adaptation to acidic soils is greatly dependent upon Al-resistance, ability to acquire P and other nutrients. As elaborated above, though sensitive to Al toxicity, the ability of citrus to withstand against adverse impacts of Al toxicity through several mechanisms is impressive. Adoption of experimentally proved agro-biological technologies such as use of phosphorous and/or boron in alleviating Al toxicity is thus encouraged ensuring sustainable citrus production in acidic soils.

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