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Review

Photosynthesis and photoprotective systems of plants in response to aluminum toxicity

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Aluminum (Al) toxicity is the major factor limiting plant growth in acidic soils, which comprise up to 70% of the world's potentially arable lands. Although, Al toxicity and tolerance in plant roots have been extensively studied during the past decades because inhibition of root growth is one of the earliest symptoms of Al injury and the most easily recognized symptom in solution culture, limited data are available on the effects of Al toxicity on leaf photosynthesis. In this paper we review the effects of Al on stomatal conductance, ultrastructure, pigments and light absorption, water relations, photochemistry, lipid peroxidation, photosynthetic enzymes, carbohydrates and their relations to the Al-induced photosynthesis inhibition in plant leaves. Al appears to preferentially impair thylakoids and photosynthetic electron transport chain in most plants. In addition to decreasing light absorption by lowering pigment concentration, both energy dissipation and antioxidant systems in Al-stressed leaves are enhanced to protect them from photo-oxidative damage under high light. The amelioration of brassinosteroids, boron (B), phosphorus (P) and mycorrhizas on the Al-induced decrease in CO_2 assimilation, as well as some aspects needed to be further studied are also discussed.

Key words: Aluminum toxicity, photosynthesis, photochemistry, photoprotective system.

INTRODUCTION

Aluminum (Al) is the most abundant metal and the third most abundant element in the earth's crust after oxygen and silicon, comprising approximately 7% of its mass (Foy et al., 1978). At mildly acidic or neutral soils, it occurs primarily as insoluble deposits and is essentially biologically inactive (Kochian et al., 2004). However, Al toxicity is one of the most deleterious factors for plant growth in acidic soils, which comprise up to 70% of the world's potentially arable lands (Von Uexküll and Mutert, 1995). Furthermore, the acidity of the soils is gradually increasing as a result of the environmental problems including some farming practices and acid rain. Soil pH significantly decreased from the 1980s to the 2000s in the major Chinese crop-production areas (Guo et al., 2010). During the past decades, significant progress has been made in our understanding of the mechanisms of Al toxicity and tolerance in plant roots because inhibition of root growth is one of the earliest symptoms of Al injury and the most easily recognized symptom in solution culture (Delhaize and Ryan, 1995) and some reviews addressed mainly on the topics have been published (Barceló and Poschenrider, 2002; Kochian et al., 2004; Ma, 2007; Panda and Matsumoto, 2007; Poschenrider et al., 2008; Ryan et al., 2001), but less is known about the effects of Al toxicity on leaves (Chen, 2006; Moustakas et al., 1997). Photosynthesis, which provides the ultimate carbon supply for plant growth and development, contains a series of multistep reactions requiring the accurate co-ordination of synthesis, maintenance and functional activity of its many

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components. Accumulating evidence shows that aluminum toxicity affects light absorption (Chen et al., 2005a), photosynthetic electron transport (Chen, 2006; Moustakas et al., 1996); gas exchange (Chen et al., 2005b; Hoddinott and Richter, 1987; Pereira et al., 2000; Jiang et al., 2008), photoprotective systems (Xiao et al., 2003a; Chen et al., 2005a; Ali et al., 2008); pigments (Chen et al., 2005a; Mihailoovic et al., 2008; Milivojević et al., 2000), ultrastructure (Moustakas et al., 1996; Konarska, 2010; Peixoto et al., 2002; Xiao et al., 2003b), carbohydrates (Chen et al., 2005b; Graham, 2002) and photosynthetic enzymes (Chen et al., 2005b) in plant leaves, the mechanisms of Al-induced decrease in CO_2 assimilation have not been fully understood yet (Chen, 2006). In this paper, we review recent progress that has been made in our understanding of the effects of Al toxicity on photosynthesis and photoprotective systems in plant leaves.

PHOTOSYNTHESIS

Considerable studies have showed that, aluminum inhibits CO_2 assimilation in many plant species including citrus (Chen et al. 2005b; Jiang et al., 2008; 2009a,b; Pereira et al., 2000), *Pinus massoniana* (Cao et al., 1992), longan (*Dimocarpus longan*, Xiao et al., 2005), sorghum (*Sorghum bicolor*; Ohki, 1986; Peixoto et al., 2002), tomato (*Lycopersicon esculentum,* Simon et al., 1994), wheat (*Triticum aestivum*, Ohki, 1986), beech (*Fagus sylvatica,* Ridolfi and Garrec, 2000) and maize (*Zea mays*) (Lidon et al., 1999). The magnitude of the decrease in CO_2 assimilation is influenced by plant species and cultivars. Pereira et al. (2000) investigated the effects of 0, 50, 100, 200 and 400 μM Al on CO_2 assimilation in four citrus rootstocks, 'Cravo' lemon (*Citrus limonia*), 'Volkamer' lemon (*Citrus volkameriana*), 'Cleopatra' tangerine (*Citrus reshni*) and 'Sunki' tangerine (*Citrus sunki*). The CO_2 assimilation was decreased by Al in all the rootstocks and the 'Cravo' lemon seedling was the most affected, with a decrease of 85% at 400 μM Al. Peixoto et al. (2002) reported that, the photosynthetic rate was affected by Al toxicity to a greater extent in Al-tolerant than in Al-sensitive sorghum cultivar.

STOMATAL CONDUCTANCE

Many studies have shown that Al-stressed leaves have higher or similar intercellular CO_2 concentration when compared with non-stressed control leaves, regardless of stomatal conductance is decreased by aluminum or not (Akaya and Takenaka, 2001; Chen et al., 2005b; Dong et al., 2008; Jiang et al., 2008; 2009a,b; Konrad et al., 2005; Peixoto et al., 2002; Pereira et al., 2000; Ridolfi and Garrec, 2000), meaning that, the decrease in CO_2 assimilation in response to Al is primarily by non-stomatal factors. However, Moustakas et al. (1996) suggested that stomatal closure is at least partially responsible for the Al-induced decreases in CO_2 assimilation in *Thinopyrum bessarabicum*, since the intercellular CO_2 concentration was lowered by 10%. Similar results have been reported in mung bean (*Vigna radiate*; Ali et al., 2008) and 'Mountain Pride' tomato (Simon et al., 1994).

ULTRASTRUCTURE

As a result of thylakoid degradation, increasing aluminium concentration inhibits photosynthesis (Haug and Foy, 1984). Pettersson et al. (1985) reported that, both accumulation of cyanophycin granules and degradation of thylakoids were the most pronounced ultrastructural changes induced by Al in *Anabaena cylindrica*. Aluminum, at 10 uM, could result in severe injuries to chloroplast membranes of spinach (*Spinacia oleracea*; Hampp and Schnabl, 1975). Konarska (2010) reported that, the mesophyll cells from Al-stressed red pepper (*Capsicum annuum*) leaves contained; (a) enlarged chloroplasts having a disturbed lamellar system, filled with large starch grains and (b) rounded mitochondria characterized by the electron lighter matrix and the degradation of cristae. Xiao et al. (2003b) investigated the effects of Al toxicity on the ultrastructure of longan leaves. The damages to chloroplast were the most pronounced changes induced by aluminum. In Al-stressed leaves, chloroplast integrity was lost as shown by the disappearance of chloroplast membrane and the distortion of grana lamellae; plasma membrane was shrunk and detached from cell wall. Al-induced damages in longan leaves also included degradation of cell wall, a decrease in intercellular space and breakdown of tonoplast. Al toxicity also caused damages to mitochondrion membranes and resulted in a decrease in the number of cristae. Moustakas et al. (1996; 1997) reported that, 1 mM Al indirectly led to malformations in *Thinopyrum bessarabicum* chloroplasts, which displayed a distorted shape and distended size, as well as a decrease in photosystem II (PSII), photosynthetic electron transport rate due to chloroplast malformations. Pereira et al. (2000) suggested that, the Al-induced decrease in CO_2 assimilation in citrus is associated with structural damage to the thylakoids, as shown by a decrease in the ratio of variable fluorescence (F_v) to initial fluorescence (F_o). Similar results have been obtained for coffee (*Coffea Arabica*; Konrad et al., 2005) and sorghum (Peixoto et al., 2002). Al also altered wheat thylakoid function (Moustakas et al., 1995). Lidon et al. (1999) concluded that superoxide anion, singlet oxygen and H_2O_2 were not directly involved in the thylakoid degradation of maize and therefore, on photosynthesis inhibition. The possible decreased accumulation in superoxide anion and H_2O_2 might be associated with increased hydroxyl radical production through the Haber-Weiss cycle, which could be responsible for chloroplast acyl peroxidation and thus, for photosynthetic membrane degradation.

PIGMENTS AND LIGHT ABSORPTION

Aluminum-induced decrease in chlorophyll (Chl) concentration has been reported in many plant species, such as citrus (Chen et al., 2005a; Jiang et al., 2008; 2009a; 2009b), soybean (*Glycine max*; Milivojević et al., 2000; Ying and Liu, 2005), sorghum (Okhi, 1986; Peixoto et al., 2002), rice (*Oryza sativa*; Kuo and Kao, 2003); wheat (Okhi, 1986), longan (Xiao et al., 2005), beech (Ridolfi and Garrec, 2000) and barely (*Hordeum vulgare*; Abdalla, 2008). Pereira et al. (2006) showed that, Al resulted in a decrease in Chl synthesis by inhibiting the activity of δ-aminolevulinic acid (δ-ALA) dehydratase (EC 4.2.1.24) responsible for the formation of monopyrrole porphobilonogen, which is a part of the Chl molecule as well as the cytochromes. Mihailovic et al. (2008) found that Al decreased Chl in Al-sensitive maize inbred line (B-73), coincided with 5-ALA synthesis inhibition, chlorophyllase (Chlase, EC 3.1.1.14) activation and leaf deprivation of Fe and Mg. Although, the activity of Chlase in two Al-tolerant inbred lines (F-2 and L-2039) was increased by Al, the concentration of Chl was almost unaffected.

Our work showed that CO_2 assimilation in Al-stressed citrus leaves decreased to a greater extent than Chl concentration (Chen et al., 2005b; Jianag et al., 2008; 2009a,b), indicating that the decrease in Chl concentration in response to Al was probably not the primary factor limiting CO_2 assimilation. Similar results have been reported on beech (Ridolfi and Garrec, 2000). This was also supported by the results of Simon et al. (1994), who observed that Al decreased CO_2 assimilation in tomato, but had no effect on Chl level. However, Ohki (1986) observed in wheat and sorghum plants that increasing the concentration of Al in nutrient solution from 50 to 300 μM resulted in a proportional decrease in photosynthesis and Chl concentration. Peixoto et al. (2002) suggested that a combination of factors such as reduced pigment concentration, impaired PSII photochemistry and the distribution of enzymatic machinery accounted for the Al-induced decrease in CO_2 assimilation in sorghum.

There are mixed reports about the effects of Al on Chl a/b ratio. The ratio was increased by Al in 'Cleopatra' tangerine (Chen et al., 2005b) and in *Eucalyptus grandin* × *E. urophylla* (Yang et al., 1996), decreased in rice (Roy et al., 1988) and soybean (Ying and Liu, 2005) and unaffected in beech (Ridolfi and Garrec, 2000) and soybean (Milivojević et al., 2000). Peixoto et al. (2002) reported that, there was a greater decrease in Chl a than in Chl b of two sorghum under Al stress. The Al-induced decrease in Chl was initially more marked in the Al-tolerant cultivar. However, fourteen days after Al treatments, the Al-tolerant cultivar showed a relatively less decrease and a higher concentration of Chl than the Al-sensitive one. By contrast, the Al-induced loss in Chl b was always larger in the tolerant than in the sensitive cultivar. The Al-stressed, tolerant cultivar had a higher Chl a/b ratio. Recently, our studies with 'Sour pummelo' (*Citrus grandis*) showed that Chl a/b ratio remained unchanged or decreased in response to Al depending on the concentration of boron (B) and phosphorus (P) applied in the nutrient solutions (Jiang et al., 2008; 2009a,b).

Peixoto et al. (2002) observed that the concentration of Car was decreased by Al to a greater extent in the Al-tolerant than in the Al-sensitive sorghum cultivar. The Al-induced loss in Car was also reported in longan (Xiao et al., 2005), soybean (Milivojević et al., 2000) and *Lens culinaris* (Azmat and Hasan, 2008). However, Abdalla (2008) found that 5 and 10 μM Al treatments for 30 days increased Car concentration in barley.

Since leaf light absorption did not decrease proportionally with decreasing Chl concentration (Chen and Cheng, 2003; Cheng et al., 2000), light absorption decreased to a lesser extent than Chl concentration in response to Al (Chen et al., 2005a,b). However, both Al-treated and control leaves showed very similar absorption spectra in the PAR (photosynthetically active radiation, approx. 400 to 700 nm) region except for a slight decrease in the Al-treated compared with control leaves (Figure 1).

WATER RELATIONS

Al interferes with leaf water relations. A study with mung bean showed that 1 and 10 mM Al treatments for 14 days decreased leaf relative water content (RWC) and water use efficiency (WUE = CO_2 assimilation/transpiration; Ali et al., 2008). Pereira et al. (2000) found that Al, at 100, 200, or 400 μM, decreased WUE in three of the evaluated four citrus rootstocks, due to an increase in transpiration and a decrease in CO_2 assimilation, while Al, at 50 μM, increased WUE, because Al increased CO_2 assimilation more than transpiration. In soybean, Al decreased both transpiration and WUE (Ying and Liu, 2005). Simon et al. (1994) observed that under 50 μM Al, WUE in one of the studied two tomato cultivars was increased by 56%, because Al decreased transpiration to a greater extent than CO_2 assimilation, whereas WUE in the other cultivar studied was not affected by Al, because Al reduced transpiration in proportion to the reduction of CO_2 assimilation. Our work showed that both leaf transpiration and WUE in 'Cleopatra' tangerine was decreased by 2 mM Al, whereas leaf RWC was unaffected (Chen et al., unpublished).

PHYTOCHEMISTRY

Al stress inhibited the Hill reaction in rice chloroplasts (Hao and Liu, 1989) and photosphorylation in the chloroplasts of both rice and longan (Hao and Liu, 1989; Xiao et

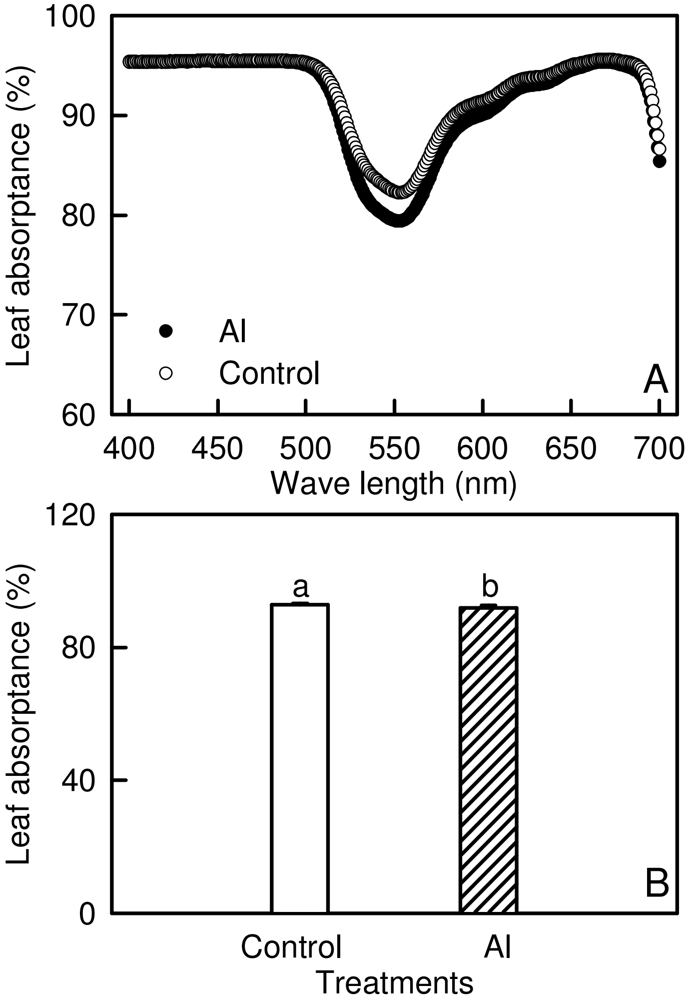

Figure 1. (A) Absorption spectra and mean absorption (B) in leaves from ‘Cleopatra’ tangerine (*Citrus reshni*) seedlings treated for 8 weeks with 0 (control) or 2 mM aluminum (Al). Each point in (A) represents mean (n = 5). Bars in (B) represent mean ± SE (n = 5). Different letters above the bars (B), indicate significant difference at $P < 0.05$ (Chen et al., unpublished; Chen et al., 2005a)

al., 2005). In ‘Cleopatra’ tangerine, Chen et al. (2005b) observed that photochemical quenching coefficient (qP) and photosynthetic electron transport rate through PSII were greatly decreased by Al. Similar results have been obtained for wheat (Moustakas et al., 1995) and *Thinopyrum bessarabicum* (Moustakas et al., 1996; 1997). Lidon et al. (1999) found that F_0 and maximum quantum yield of PSII (F_v/F_m) in maize remained unchanged, while photosynthetic capacity, electron transport rate through photosystem I (PSI) and the contents of cytochromes f and b563 decreased above the 9 mg L^{-1} Al treatment, suggesting that the Al-induced decrease in photosynthesis was associated with a reduction in photosynthetic electron transport rate through PSI. Recently, we investigated the Al-induced effects on PSII photochemistry in ‘Sour pummelo’ leaves assessed by the Chl a fluorescence (OJIP) transient (Jiang et al., 2008). Both control and Al-treated leaves showed a typical polyphasic rise in Chl fluorescence (Strasser et al., 1995). Al toxicity resulted in an increase in the heterogeneity of samples. OJIP transients from Al-treated leaves showed a large rise in the O-step and a large depression at the P-step (Figure 2). Al-treated leaves displayed positive ΔL-, ΔK-, ΔJ- and ΔI-bands around 150, 300 μs, 2 to 4 ms and 30 to 100 ms, respectively and decreased maximum amplitude of IP phase compared with controls (Figure 3). Al decreased total electron carriers per reaction center (RC; S_m), yields (F_v/F_m, quantum yield for electron transport at t = 0 (φ_{Eo}), quantum yield for the reduction of end acceptors of PSI per photon absorbed (φ_{Ro}), probability (at time 0) that a trapped exciton moves an electron into the electron transport chain beyond Q_A^- (ψ_{Eo}), efficiency with which an electron can move from the reduced intersystem electron acceptors to the PSI end electron acceptors (δ_{Ro}) and efficiency with which a trapped exciton can move an electron into the electron transport chain from Q_A^- to the PSI end electron acceptors (ρ_{Ro})) and fluxes (reduction of end acceptors at PSI electron acceptor side per RC at t = 0 (RE_o/RC) and reduction of end acceptors at PSI electron acceptor side per excited cross section (CS) at t = 0 (RE_o/CS_o)) and damaged all of the photochemical and non-photochemical reactions that we measured, as indicated by the decreases in performance index (PI_{abs}) and total performance index ($PI_{tot,abs}$). We concluded that, the impaired electron transport capacity accompanied by the lack of reducing equivalents were the main factor contributing to the decreased CO_2 assimilation in Al-stressed leaves.

LIPID PEROXIDATION

Evidence shows that Al decreases the rate of electron transport through PSI and PSII (Chen et al., 2005b; Lidon et al., 1999). This definitely causes the production of reactive oxygen species in chloroplasts, thus, inducing lipid peroxidation in chloroplasts. Lidon et al. (1999) reported that Al might inhibit the Mehler reactions and therefore, the reduction of nicotinamide adenine dinucleotide phosphate (NADP), which would affect the photosynthesis. Xiao et al. (2003a) showed that Al increased the permeability of plasma membranes, the generation of superoxide anion and the concentrations of H_2O_2 and malondialdehyde (MDA, an indicator of lipid peroxidation) in longan leaves. Sharma and Dubey (2007) reported Al, at 160 μM resulted in increased generation of superoxide anion and H_2O_2, and enhanced concentration of MDA in rice shoots, suggesting that Al toxicity was associated with the Al-induced oxidative stress. Kuo and Kao (2003) found that, the Al-induced increase in MDA concentration in detached rice leaves preceded the decreases of both Chl and protein concentrations, but Al did not increase H_2O_2 concentration. However, decreased CO_2 assimilation in Al-stressed ‘Cleopatra’ tangerine leaves could not be attributed to photo-oxidative damage,

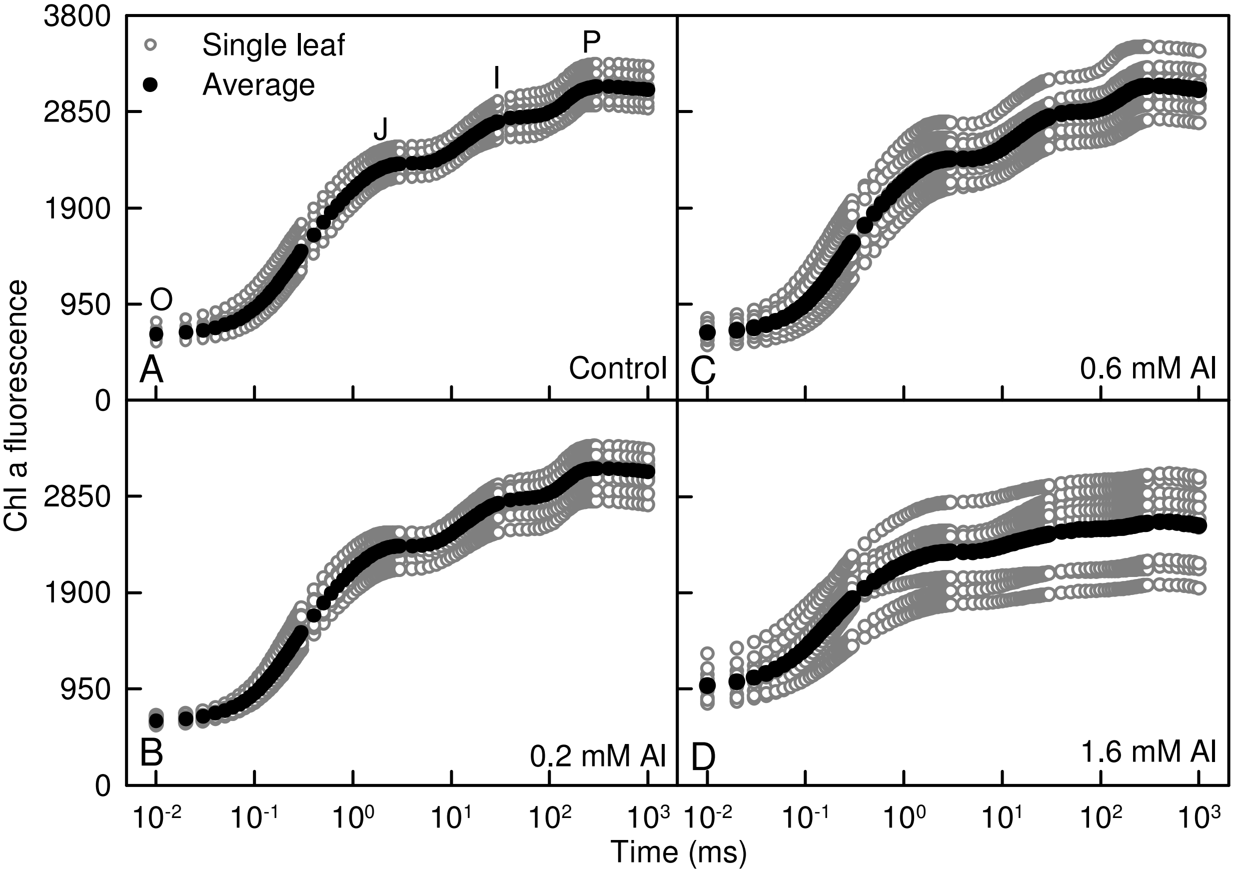

Figure 2. Effects of aluminum (Al) treatments on chlorophyll a (Chl a) fluorescence (OJIP) transient of dark-adapted citrus leaves from 'Sour pummelo' (*Citrus grandis*) seedlings treated for 5 months with 0 (control), 0.2, 0.6 or 1.6 mM Al plotted on a logarithmic time scale (0.01 to 1 s). The heterogeneity of the samples is increasing with increasing Al concentration (Jiang et al., 2008).

since Al had no effect on leaf MDA concentration (Chen et al., 2005a,b).

PHOTOSYNTHETIC ENZYMES

In 'Cleopatra' tangerine, Al stress either increased or had no effect on the activities of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco, EC 4.1.1.39), NADP-glyceraldehyde-3-phosphate dehydrogenase (GAPDH, EC 1.2.1.12), phosphoribulokinase (PRK, EC 2.7.1.19), stromal fructose-1,6-bisphosphatase (FBPase, EC 3.1.3.11), all involved in the Calvin cycle, depending on the basis (leaf area or protein) used to express enzymatic activity (Chen et al., 2005b). Three studies with 'Sour pummelo' showed that ribulose-1,5-bisphosphate carboxylase/oxygenase Rubisco activity remained unchanged or decreased to a lesser extent than CO_2 assimilation in response to Al depending on the concentrations of boron and phosporus applied in the nutrient solutions and that Al stress had no effect on Rubisco activation state (Jiang et al., 2008; 2009a,b). These results indicate that, the reduction in CO_2 assimilation in Al-stressed leaves cannot be attributed to a decrease in the activities of Calvin cycle enzymes. This agrees with the results of Hampp and Schnabl (1975), who observed that Al decreased CO_2 fixation, but had little effect on the activities of Rubisco and phosphoribulokinase (PRK) in spinach chloroplasts. However, the magnitude of the decrease in Rubisco activity was similar to or greater than that in CO_2 assimi-lation in response to Al in soybean (Dong et al., 2008). In longan, Xiao et al. (2005) found that, Al decreased leaf carboxylation efficiency (CE). Cao et al. (1992) reported that Al decreased ATP concentration and chloroplast GAPDH activity in *Pinus massoniana* needles.

CARBOHYDRATES

Simon et al. (1994) reported that, the accumulation of Al in the roots of tomato caused tissue damage, resulting in reduced sucrose utilization, probably causing an accumulation of leaf carbohydrates and feedback inhibition of

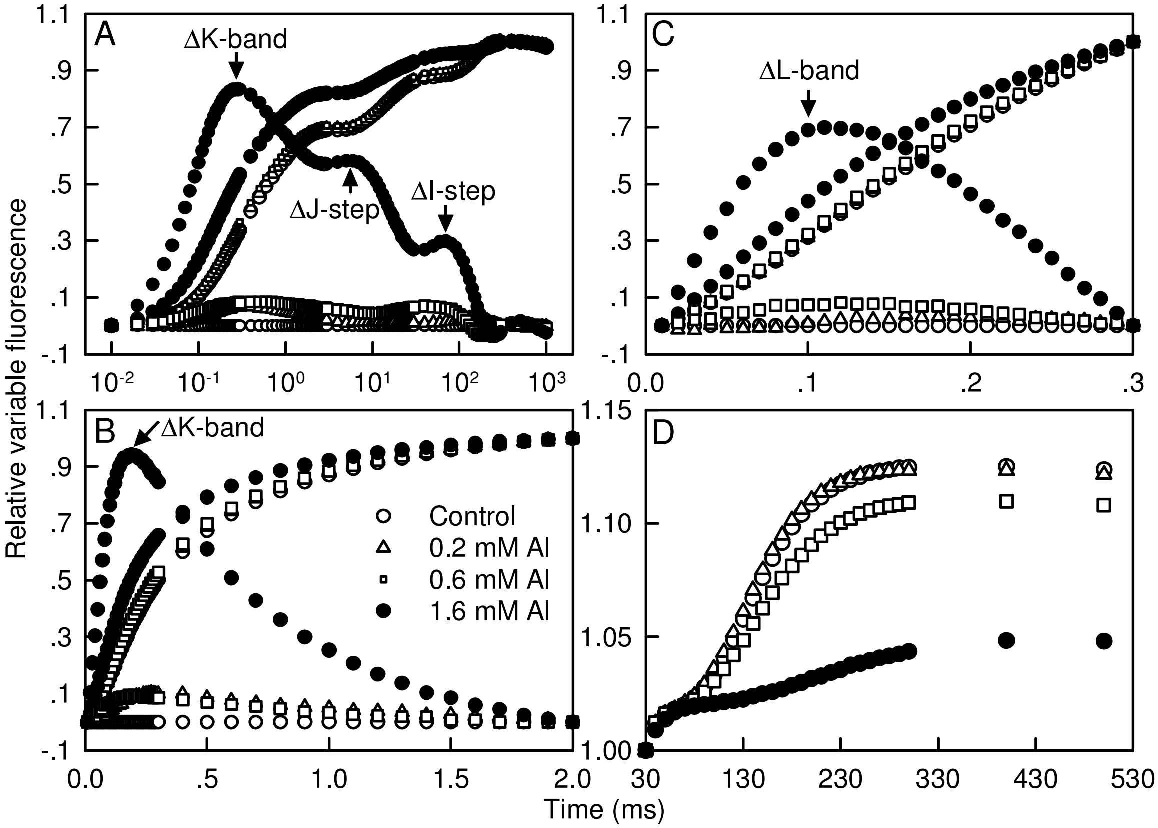

Figure 3. Mean chlorophyll a (Chl a) fluorescence kinetics (F_t) expressed as the kinetics of relative variable fluorescence: (A) between F_0 and F_m: V_t, $(F_t - F_0)/(F_m - F_0)$; (B) between F_0 and F_J; W_t, $(F_t - F_0)/(F_J - F_0)$; (C) between F_0 and $F_{300\mu s}$; $(F_t - F_0)/(F_{300\mu s} - F_o)$; (D) between F_0 and F_I: $(F_t - F_0)/(F_I - F_0)$ in dark-adapted leaves from 'Sour pummelo' (*Citrus grandis*) seedlings treated for 5 months with 0 (control), 0.2, 0.6 or 1.6 mM aluminum (Al). In each of the plots (A), (B) and (C), the differences of the four samples to the reference sample of non-stressed control seedlings are plotted with an amplication of 5, 6.5 and 6, respectively. The ΔK and ΔL bands are clearly revealed in the plots (B) and (C), respectively. The IP phase normalized on the F_0 to F_I phase = $(F_t - F_0)/(F_I - F_0) - 1$ (Jiang et al., 2008).

photosynthesis. Unfortunately, carbohydrates were not determined in this study. However, 2 mM Al treatment for 8 weeks had no effect on area-based concentrations of glucose, fructose, sucrose, starch and total non-structural carbohydrates (TNC) in 'Cleopatea' tangerine leaves, but the demand for carbohydrates was decreased in Al-stressed leaves. The Al-induced decreases in both the use of carbohydrates for growth and the translocation of carbohydrates from the leaves might explain why carbohydrate concentration was little affected despite a severe impairment of CO_2 assimilation in leaves (Chen et al., 2005b). Graham (2002) showed that, 1 mM Al treatment for 8 weeks increased sucrose concentration, decreased glucose, sorbitol and total soluble carbohydrate concentrations and had no effect on fructose, starch and TNC concentrations in peach (*Prunus persica*) leaves. Wan (2007) observed that, total soluble sugar, reducing sugar and sucrose concentrations in longan leaves was increased by Al concentration up to 0.37 mM, then decreased with increasing Al concentration, while CO_2 assimilation always decreased with increasing Al concentration (Xiao et al., 2005). In barely, 10 μM Al obviously decreased the concentrations of reducing sugars, starch and total sugar, but had little effect on sucrose level (Abdalla, 2008). These results indicate that, feedback inhibition by carbohydrate accumulation does not contribute to the Al-induced decrease in CO_2 assimilation.

PHOTOPROTECTIVE SYSTEMS

Chen et al. (2005a,b) observed that, Al-stressed 'Cleopatra' tangerine leaves only used a smaller fraction of the absorbed light in electron transport, since CO_2 assimilation decreased to a greater degree than leaf Chl concentration or leaf light absorption in response to aluminum. As a result, more excess excitation energy existed in Al-stressed leaves when compared with controls under high photon flux at midday. It has been suggested that, excess absorbed light can be harmlessly dissipated as heat through xanthophyll cycle-dependent hermal energy dissipation in the antenna pigment complexes of PSII (Demmig-Adams and Adams, 1996; Niyogi et al., 1998). This is supported by previous results that Al increased non-photochemical quenching (NPQ) in coffee leaves (Konrad et al., 2005) and coefficient of non-photochemical quenching (qN) in *Thinopyrum bessarabicum* leaves (Moustakas et al., 1996). But the xanthophyll cycle-dependent thermal energy dissipation might be not the main way to dissipate excess excitation energy in Al-stressed 'Cleopatra' tangerine leaves, since thermal dissipation of excitation energy, measured as NPQ, was slightly decreased by Al (Chen et al., 2005a). However, dissipated energy (dissipated energy flux per CS at t = 0 (DI_o/CS_o), quantum yield at t = 0 for energy dissipation (φ_{Do}) and dissipated energy flux per RC at t = 0 (DI_o/RC)) was higher in Al-stressed (Sour pummelo' leaves) than in controls (Jiang et al., 2008; 2009a,b). An alternative route for energy dissipation and consumption of photosynthetic electrons is directly in the water to water cycle or indirectly in the photorespiration (Asada, 1999). As expected, the activities of enzymes such as superoxide dismutase (SOD, EC 1.15.1.1), ascorbate peroxidase (APX, EC 1.11.1.11), monodehydroascorbate reductase (MDAR, EC 1.6.5.4), dehydroascorbate reductase (DHAR, EC 1.8.5.1) and glutathione reductase (GR, EC 1.6.4.2) and the concentrations of antioxidant metabolites like ascorbate (AsA), dehydroascorbate (DAsA), reduced glutathione (GSH) and oxidized glutathione (GSSG)) involved in water to water cycle, the activity of catalase (CAT, EC 1.11.1.16, an enzyme involved in scavenging the bulk H_2O_2 generated by photorespiration) (Chen et al., 2005a) and the activity of Rubisco in 'Cleopatra' tangerine, were increased by aluminum (Chen et al., 2005b). Similarly, exposure to Al generally increased the activities of catalase, ascorbate peroxidase (APX) and guaiacol peroxidase (GPX, EC 1.11.1.7) in *Populus tremuloides* and *Populus trichocarpa* leaves (Naik et al., 2009). Al, at 160 µM, increased the activities of SOD, total and cytosolic APX, MDAR, DHAR and GR and the concentration of DAsA, decreased the activities of CAT and choloroplastic APX, the concentrations of AsA and total ascorbate (AsA + DAsA) and the ratio of AsA to DAsA, but had no effect on the concentrations of GSH, GSSG and total glutathione (GSSG + GSH) and the ratio of GSH to GSSG in rice shoots, suggesting that SOD, PGX and cytosolic APX played a key role in combating oxidative damage (Sharma and Dubey, 2007). In detached rice leaves, Al increased the activities of APX, CAT and GPX, but decreased that of SOD. In longan, Al-treated leaves had higher or similar protein-based activities of GPX, APX and GR and fresh weight-based GSH concentration depending on Al concentration applied, but decreased catalase activity and ascorbic acid concentration; leaf superoxide dismutase activity was increased by 0.185, 0.370 and 0.740 mM Al, but decreased by 1.110 and 1.850 mM Al (Xiao et al., 2003a). In another study, Xiao et al. (2005) showed that Al increased the activity of glycolate oxidase (GO, EC 1.1.3.15; a key enzyme involved in photorespiration) in longan leaves. Closure of PSII RCs will result in formation of reactive oxygen species. The up-regulation of enzymatic and non-enzymatic antioxidants agreed with the increased requirement for scavenging reactive oxygen species in Al-stressed leaves due to increased closure of PSII RCs, as indicated by decreased qP (Chen et al., 2005a,b). Although, superoxide anion and H_2O_2 generations increased in Al-stressed 'Cleotapra' tangerine leaves, Al had no effect on leaf MDA concentration (Chen et al., 2005a). It was concluded that, the up-regulation of antioxidant systems provided considerable protection to Al-stressed leaves against photo-oxidative damage.

In contrast to NPQ, the percentage of antheraxanthin (A) + zeaxanthin (Z) in the xanthophyll cycle pool (violaxanthin (V) + A + Z) or A + Z concentration on a leaf Chl basis at both predawn and midday was higher in Al-treated than in control 'Cleopatra' tangerine leaves. At midday, the percentage of A + Z in the xanthophyll cycle pool or A + Z concentration on a leaf Chl basis increased, especially in Al-treated leaves, but A + Z accounted for less than 40% of the total xanthophyll cycle pool even in Al-treated leaves, with the balance in V. The increase in the conversion rate of V to A and Z in Al-treated leaves might help to quench the $^1O_2$, whose production might increase in Al-treated leaves under high light due to increased closure of PSII (Chen et al., 2005a,b). NPQ is thought to depend on the accumulation of de-epoxidation products (A + Z) of the xanthophyll cycle pool, but under Al stress, the changes in NPQ in 'Cleopatra' tangerine leaves did not correspond to the changes in the percentage of A + Z in the xanthophyll cycle pool (Chen et al., 2005a). Similar results have been obtained in *Chlamydomonas reinhardtii* (Förster et al., 2001) and sorghum (Cousins et al., 2002). This suggests that, NPQ development in Al-treated 'Cleopatra' tangerine leaves may be impaired and/or A + Z had functions other than involvement in thermal energy dissipation. The mechanisms underlying these phenomena need to be addressed in future research.

AMELIORATION OF ALUMINUM-INDUCED PHOTOSYNTHESIS INHIBITION

Brassinosteroids

Dong et al. (2008) reported that, both 24-epibrassinosteroid (EBR) and long-effective brassinosteroid (coded as TS303) alleviated the Al-induced decrease in CO_2 assimilation by increasing Chl concentration, F_v/F_m, stomatal conductance, carbonic anhydrase (EC 4.2.1.1) activity, Rubisco concentration and activity in soybean. Ali et al. (2008) observed that, both 24-epibrassinolide (EBL) and 28-homobrassinolide (HBL) alleviated the Al-induced decreases in carbonic anhydrase activity, RWC, WUE, Chl concentration, stomatal conductance, intercellular CO_2 concentration and CO_2 assimilation in leaves and plant growth and further enhanced the Al-induced increases in the activities of SOD, CAT and PGX in leaves and the concentrations of proline in roots and leaves of mung bean. Therefore, it was concluded that the elevated levels of proline and antioxidant systems were at least partially responsible for the amelioration of Al toxicity in mung bean seedlings.

Boron

Studies showed that, boron (B) alleviated Al toxicity in squash (*Cucurbita pepo*) (LeNoble et al., 1996), common bean (*Phaseolus vulgaris*) (Stass et al., 2007), cucumber (*Cucumis sativus*), maize (Corrales et al., 2008), pea (*Pisum sativum*) (Yu et al., 2009) and 'Sour pummelo' (Jiang et al., 2009b). However, limited data are available on the ameliorative effects of B on the Al-induced photosynthesis inhibition. Yu et al. (2009) reported that B alleviated the chlorosis-symptoms of Al toxicity and prevented the decrease in Chl concentration after prolonged exposure to Al stress, which was accompanied by a lower Al level in pea shoots. Recently, our work (Jiang et al., 2009b) showed that, B alleviated the Al-induced decreases in CO_2 assimilation, stomatal condutance, Chl concentration, F_v/F_m, maximum amplitude of IP phase and $PI_{tot,abs}$ and increases in F_o, K-band, relative variable fluorescence at J- and I-steps in 'Sour pummelo' leaves. Generally, the ameliorative effect of B on all these parameters mentioned was 25 µM B >10 µM B ≥ 50 µM B > 2.5 µM B. Corrales et al. (2008) reported that, Al increased the concentration of GSH in roots of maize plants growing with adequate B supply, but not in those growing in excess B, which in turn caused extensive cell damage in the root tips of maize plants even in the absence of Al. Our results showed that, at the absence of Al stress, 50 µM B slightly decreased the root dry weight of 'Sour pummelo' seedlings, meaning that these plants received excess B. This would explain why the ameliorative effect of 50 µM B was lower than that of 25 µM B, because +Al roots, stems and leaves displayed higher or similar B concentration. These results indicate that, the B-induced amelioration of photosynthesis inhibition and photoinhibitory damage occurring at both donor and acceptor sides of PSII is probably caused by less accumulation of Al in leaves (Jiang et al., 2009b).

Phosphorus

Phosphorus (P) deficiency is considered to be the key cause of growth reduction in Al-stressed plants (Quartin et al., 2001). Evidence has shown that, P application can alleviate Al toxicity in plants, such as 'Sour pummelo' (Jiang et al., 2009a), rice (Nakagawa et al., 2003), sorghum (Tan and Keltjens, 1990a,b) and *Lespedeza bicolor* (Sun et al., 2008), but little information is available on the ameliorative effects of P on the Al-induced photosynthesis inhibition. Recently, we (Jiang et al., 2009a) investigated the amelioration of P on the Al-induced inhibition of growth and photosynthesis in 'Sour pummelo' seedlings. Under Al stress, P increased root Al and root, stem and leaf P, but decreased stem and leaf Al. P alleviated the Al-induced decreases in leaf CO_2 assimilation, Rubisco activity, Chl concentration, F_v/F_m, maximum amplitude of IP phase and $PI_{tot,abs}$, and increases in leaf F_0, relative variable fluorescence at K- and I-steps. We concluded that, P alleviated the Al-induced inhibition of growth and impairment of the whole photosynthetic electron transport chain from PSII donor side up to the reduction of end acceptors of PSI, thus, preventing photosynthesis inhibition through increasing Al immobilization in roots and P level in roots, stems and shoots.

Mycorrhizas

Mycorrhizal fungi have been demonstrated to alleviate Al toxicity in their host plants (Andrade et al., 2009; Arriagada et al., 2007; Borie and Rubio, 1999; Cuenca et al., 2001; Cumming and Weinstein, 1990; Hentschel et al., 1993; Jentschke and Godbold, 2000; Schier and McQuattie, 1995; 1996). However, reports concerning the ameliorative effects of mycorrhizal fungi on the Al-induced photosynthesis inhibition are not always identical. In eastern white pine (*Pinus strobes*), chlorosis and tip necrosis were more pronounced in non-mycorrhizal than in mycorrhizal seedlings 12 weeks after exposure to Al (Schier and McQuattie, 1995). In pitch pine (*Pinus rigida*), no large differences in photosynthesis were observed between nonmycorrhizal and mycorrhizal seedlings, but the whole plant rates were clearly higher in mycorrhizal seedlings since shoot dry weight were 50% greater in this treatment than in nonmycorrhizal seedlings (Cumming and Weinstein, 1990). In Norway spruce (*Picea abies*), 5 weeks after exposure to 800 µM Al, Chl concentration in seedlings colonized with *Paxillus involutus* decreased to a lesser extent than in non-mycorrhizal seedlings; 10 weeks after exposure to Al, both non-mycorrhizal and mycorrhizal seedlings displayed similar decreases in Chl and photosynthesis (Hentschel et al., 1993). Similar results have been obtained in Norway spruce inoculated with *Lactarius rufus* (Jentschke et al., 1991). It was concluded that, differences in physiological responses to Al between mycorrhizal and non-mycorrhizal Norway spruce seedlings might be reduced in the long term due to impaired mineral nutrient uptake.

CONCLUSION

Physiological and biochemical studies have shown a decrease in photosynthesis owing to Al stress; however, many questions remain unanswered. Aluminum appears to preferentially impair thylakoids and photosynthetic electron transport chain in most plants, but the mechanisms involved have yet to be identified. Stomatal and non-stomatal limitation of photosynthesis is still the subject of debate. The mechanisms of Al affecting stomatal conductance need to be further studied. It is still unclear that the impact of Al on photosynthesis is direct or indirect. Why does Al inhibit photosynthetic enzymes in some species, but not in others? The xanthophyll cycle-dependent thermal dissipation of excess absorbed light in the antenna pigment complexes of PSII is a major process in plant photoprotection under stress conditions, but the thermal dissipation of excitation energy in Al-stressed 'Cleopatra' tangerine leaves, measured as NPQ, was slightly decreased by Al. In addition, the Al-induced changes in NPQ do not correspond to the changes in the percentage of A + Z in the xanthophyll cycle pool. The mechanisms underlying these phenomena need to be addressed in future research. Brassinosteroids, B, P and mycorrhizas can alleviate Al-induced decrease in CO_2 assimilation; however, the mechanisms involved are not fully understood. Al stress is present not only in acidic soils but also in alkaline ones; however, phytotoxic effects of Al on photosynthesis have been demonstrated mainly for Al under acid conditions, very limited data are available on the effects of Al at alkaline condition on photosynthesis and photoprotective systems in plant leaves (Moustakas et al., 1996; 1997). In addition to Al toxicity, most acidic soils include toxic levels of manganese (Mn) and iron (Fe), as well as deficiencies of some essential elements, with P being another major factor limiting plant growth in acidic soils (Kochian et al., 2004); however, very limited data are available on the effects of Al interactions with Mn, Fe or other elements on photosynthesis. There are few studies on Al-induced changes in gene expression, protein synthesis and metabolites involved in photosynthesis. Current techniques such as genomics, transcriptomics and proteomics offer the opportunity to understand the molecular mechanisms, as well as physiological and biochemical mechanisms involved in photosynthetic responses of plants to Al, which will be useful in improving plant Al-tolerance by genetic engineering and breeding.

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Abbreviations

Chl, Chlorophyll; **Chlase,** chlorophyllase; **PSI,** photosystem I; **PSII,** photosystem II; **GAPDH,** glyceraldehyde-3-phosphate dehydrogenase; **MDA,** malondialdehyde; **Rubisco,** ribulose-1,5-bisphosphate carboxylase/oxygenase; **PRK,** phosphoribulokinase; **CE,** carboxylation efficiency; **TNC,** total non-structural carbohydrates; **SOD,** superoxide dismutase; **APX,** ascorbate peroxidase; **MDAR,** monodehydroascorbate reductase; **DHAR,** dehydroascorbate reductase; **GR,** glutathione reductase; **AsA,** ascorbate; **DAsA,** dehydroascorbate; **GSH,** reduced glutathione; **GSSG,** oxidized glutathione; **CAT,** catalase; **GPX,** guaiacol peroxidase; **GO,** glycolate oxidase; **A,** antheraxanthin; **Z,** zeaxanthin; **V,** violaxanthin.

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