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Mechanism of Toxicity and Tolerance in Plants Against Aluminum Stress

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Abstract

Aluminum (Al $^{3+}$) is rhizotoxic ions in the soil (mineral) acid. Al activities increases with increasing soil acidity, below pH 5.5 the solubility of Al $^{3+}$ cations will increase. High level of soluble can cause interference with metabolic processes and plant physiology. Cumulatively, the physiology of metabolic disorders and initially looked at the root system. The tip of the root and lateral roots become thickened and hair and roots become lower, causing a decrease in root length and root tissue enlargement thus inhibiting the growth of roots, the absorption of nutrients and water, will further lower the growth, production and productivity of crops. Although Al disrupt metabolism and suppress the growth of the plant, until a certain threshold of adverse effects in Al still be tolerated, depending on the type of plant and the level of activity of Al. Tolerance of crops to Al can be expressed through two mechanisms, namely: external tolerance mechanism and internal tolerance mechanism. The main difference between the two mechanisms is in the area of detoxification Al whether in symplast (internal) or apoplast (exclusion). The ability of plants to be able to adapt to drought stress Al, depends on the ability of plants to produce organic acid in an amount sufficient for eliminating the toxic influence of stress Al. Root exudates of plants capable of producing such an organic acid that plays an important role in adaptation strategies. The high production of organic acids is associated with the formation of specific enzymes, as a response to stress Al. Allegedly the sensitive strain, the synthesis of organic acids is not adequate to chelate Al

Keywords: Al stress, organic acids, soil acidity, tolerance mechanism

A. Introduction

Aluminum (Al^{3+}) is rhizotoxic ion that inhibits the growth and productivity of plants in acidic (mineral) soil (Huang J.W., Pellet D.M., Papernik L.A. & Kochian L.V., 1996). Indonesia has approximately 47.6 million hectares of Red-Yellow Podzolic soil (RYP) or 32.4 % of its total land area (Karama & Abdurrachman, 1993). Acidic (mineral) soil leads to major problems in plant growth, such as: (1) increasing concentration of H^+, toxicity of H^+; (2) increasing concentration of Al, toxicity of Al; (3) increasing concentration of Mn, toxicity of Mn; (4) decreasing concentration of macro nutrient (cation), deficiency of Ca^{2+}, Mg^{2+}, and K^+); (5) decreasing solubility of P and Mo (deficiency); and (6) inhibition in root growth and water absorption, nutrient deficiency, drought, and increase in nutrient leaching (Sopandie, 2013). Previous studies also found that the major obstacles in farming, particularly food crop farming, in acidic soil include harmful effect of Aluminum (Al) toxicity and low phosphorus availability (Otani & Ae, 1996; Fageria & Baligar, 1997; Schaffert R.E., Sorgo E.M.E, Alves V.M.C., Parentoni S.N. & Raghothama K.G., 2000) that could inhibit root growth as well as nutrient and water absorption, result in declining plant growth and production (Foy, 1983; Taylor, 1988; Sivaguru & Paliwal, 1993; Marschner, 1995; Ma, 2000; Sopandie D., Jusuf M. & Setyono T.D., 2000).

Activity of Al increases along with the increasing soil acidity, at pH below 5.5, solubility of Al^{3+} cation will increase (Marschner, 1995). Moreover, the absorption of P, Ca, Mg, and K was also found to significantly decrease at high concentration of Al (Matsumo H., Yamamoto Y. & Kasai M., 1992) and there was decrease in H^+-ATP-ase activity (Marschner, 1995). High solubility of Al might hinder metabolic and physiological processes in plants.

Cumulatively, this metabolic and physiological disruption is firstly found in root system (Picton S.J., Richards K.D. & Gardner R.C., 1991). Root tip and lateral roots become thickened and root hairs are suppressed (Wright, 1989) resulting in decreasing root length (Basu U, Good A.G., Aung T., Slaski J.J., Basu A., Briggs K.G. & Taylor G.J., 1999). Therefore, parameter of root length is mainly applied to assess plant resistance to Al toxicity (Delhaiz & Ryan, 1995). There are different responses in soybean genotype to aluminum stress. Bushamuka & Zobel (1998) compared the basal and apical root development of several maize and soybean varieties given lime and no-lime treatment. Sensitive varieties were found to suffer from disruption of root development, while tolerant varieties were not affected by the existence of Al. Sanzonowicz C., Smyth T.J. & Israil D.W. (1998), added that high saturated Al will inhibit lateral root elongation of soybean. Michelle R., Frederic G., David E.E. & Martin J.H. (2003), also applied the model of root growth to examine the resistance of *Picea abies* to Al toxicity. Inhibition in root growth has been reported many times such as in rice (Nasution & Suhartini, 1992), wheat (Delhaiz E., Craig S., Beaton C.D, Bennet R.J., Jagadish V.C., & Randall P.J., 1993), maize (Sivaguru M., Fransitisck B., Dieter V., Huber H.F. & Walter J.H., 1999), and soybean (Soepandi, *et al*., 2000).

Even though Al disrupts metabolism and suppresses plant growth, adverse effect of Al is still tolerated until certain threshold, depends plant types and the level of Al activity. Tolerant characteristic of plant to Al can be expressed hypothetically through two mechanisms, namely: Mechanism of external/exclusion tolerance and Mechanism of internal tolerance (Taylor, 1988; Kochian, 1995).

B. Methodology

1. *Aluminum Acidity and Nutrient Absorption*

In acidic soil with high mineral content, Al toxicity becomes the main limiting factor in plant growth. When investigating Al stress, difficulties related to processes occur in soil are often found due to its complexity. The forms of Al in soil are affected by pH. At pH < 4.0, soil is dominated by Al^{3+}, Aluminum hydroxide such as $Al(OH)^{+2}$ and $Al(OH)_2^+$ are formed at pH 4-5.5, while Al^{3+} content is ignored at pH > 5.5. However, result of study conducted by Ma Z. & Miyasaka S.C. (1998), proved that more than 95% of Al is in the form of Al^{3+} that is extremely toxic to plants at pH 4.3; pH < 4.5, 2007); pH < 5 (Kochian, 1995). Hence, Al^{3+} is the most toxic aluminum form to plants (Marschner, 1995; Kochian, 1995; Miyasaka S.C., Bute J.G., Howel R.K. & Foy C.D., 1991).

In both soil and plants, the monomer of Al cation may form bonds with: various organic and inorganic ligands, such as PO_4^{-3}, SO_4^{-2}, non-toxic F^-, organic acid, protein, and fat. Similar to other ions, Al is absorbed by plants either via diffusion or mass flow in free space that includes interspace in root tissue and dead tissue; cell wall, and xylem element. There is carboxylate group ($RCOO^-$) within this area that has function as cation exchanger. The primary cell wall is a tissue consists of cellulose and hemicellulose including pectin. In this tissue, pectin is formed by polygalacturonic acid, particularly in the middle lamella that functions as a place where cations (Al) are exchanged or rejected. Furthermore, casparian strip in endodermis will prevent the movement of Al to *stele*.

Normally, nutrient availability in acidic soil is low in amount. Moreover, plant ability to absorb nutrient is limited by high Al content. According to several studies, the absorption of P, Ca, Mg, and K by plants was found to significantly decrease in soil with high Al content, while Mn element is significantly absorbed. Deficiency of P is caused by the formation of Al-phosphate complex. Al directly interacts with P, both in soil solution and plant tissue, thus results in unavailable P for plants (Marschner, 1995; Takenaga, 1995). Similarly, the absorption of K element in roots is inhibited, while it increases in shoot. Increasing K absorption in shoot is possibly caused by the increasing role of K in maintaining ionic balance since K determines the osmotic potential in plants. In case of barley planted in media contained Al, it was found that Ca^{+2} and K^+ content was only a half of the initial amount compared to control (Matsumoto, *et al*., 1992). In *Fagus sylvatica*, the content of Ca, Mg, and Zn drastically decreased at the lowest Al concentration (0.1 mM $AlCl_3$) (Balsberg-Pahlson, 1990), due to competition between cations on binding site in root surface.

2. Aluminum Toxicity and Its Effect on Plants

Al toxicity is the major environmental stress that limits productivity in acidic soils. One of Al toxicity mechanisms involves the interaction between Al and ion transport system that has function in root plasma membrane. The role of this interaction between transport of Al/Ca^{2+} in Al toxicity mechanism has raised concern since Ca^{2+} plays important role in the regulation of several cellular processes in plant (Hepler & Wayne, 1985).

According to Marschner (1995), inhibition may occur in cell wall since Al replaces the position of Ca^{2+} in the middle lamella despite the essential role of Ca^{2+} in ion transport through plasma membrane as Ca^{2+} is the second messenger in H^+-ATP-ase activity with the help of calmodulin regulator protein. Replacement of Ca^{2+} bound to calmodulin will result in changes in enzyme activity. Later, Al and carboxyl group will form strong bond to prevent cell to grow bigger. Moreover, Al also interacts with bilayer lipid membrane of cell that may result in membrane structure damage since Ca^{2+} is replaced by Al^{3+} which eventually affects nutrient absorption. Furthermore, at the cellular level, Al ion affects permeability and transport activity of plasma membrane.

Inhibition by Al on Ca^{2+} influx into plant cells quickly occurs and is reversible as Al blocks Ca^{2+} channel on the surface of outer membrane of root cell plasma membrane or through Al transport into cell via Ca^{2+} channel. This Ca^{2+} influx blocking by Al starts the phenomenon commonly appears due to Al toxicity (Huang, *et al.*, 1996). The biochemistry mechanism of phytotoxicity proposed in the last review assumed that Al is not only required to enter the cell, but it has to be active inside cell.

There have been many reports of studies that mentioned root plant as the target tissue of Al toxicity. Root tip is the main target of Al toxicity and the decreasing in root length can be detected in just several minutes after the addition of Al. The first one is interference on root cap (calyptra) that modulates Al signal and has function as the detector of gravity and mechanical resistance. In turn, there will be decrease in mucigel secretion of root cap where the cells play role as the source of endogenous growth regulator. The next phenomenon is the inhibition of root growth that includes shortening and enlargement of root tissue, water loss, and the absence of healthy lateral roots (Delhaize & Ryan, 1995; Sopandie, 1999; Sopandie, *et al*., 2000; Sopandie, 2013). The effect of Al toxicity on root tip is seemingly caused by cell division disturbance. First, cells become binucleate (cells have two nuclei) and if Al penetrates to the nucleus, it will be deposited due to compound that contains P thus hindering enzyme activity that controls cell wall polysaccharides deposition. Besides, Al strand in pectin will also harden the cell wall. Canges in growth pattern will disrupt the absorption and transport of essential nutrients such as Ca, Mg, P, and K (Marschner, 1995; Takenaga, 1995).

As mentioned by Ma (2000), Al concentration of 20 μM was found to inhibit maize root elongation up to 70%, yet this problem can be solved through the addition of silicic acid. Based on the result of this study, concentration of toxic Al^{3+} significantly decreased with the addition of silicic acid. In fact, the addition of higher amount of silicic acid successfully decreased the concentration of Al^{3+}. The decreasing Al^{3+} was parallel with the declining level of root elongation. It is expectedly due to the complex formation of Al and silicic acid. This study also reported that the complex of Al-Si was dissolved in water. Silicon (Si) is the second most abundant element found in Earth's crust. Normally, Si is found together with Al in soil solution in the form of monosilicic acid. The mechanism responsible for this decreasing Al toxicity by silicic acid is probably caused by include solution effect, declining Al activity outside plants, and effects in cytoplasm as well as enzyme activity.

3. *Mechanism of plant tolerance To aluminum stress*

Plants that are tolerant to Aluminum toxicity have the ability to suppress the adverse effect of that Al toxicity. The criteria for plant tolerant to aluminum include: (1) roots are able to continuously grow and no damage is found in root tip; (2) plant could produce less acidic condition in root area; (3) translocation of Al ion to the upper part of plant is low since most of it is stored in roots; (4) due to certain mechanism, Al ion cannot inhibit the absorption of Ca, Mg, and K; and (5) plants are able to neutralize the effect of Al ion thus absorption and translocation of P is not disrupted. However, the mechanism of plant tolerance to Al toxicity is not similar in every plant. In fact, it is different in every cultivar of a species (Kochian, 1995). This variance indicates different mechanisms of tolerance in every plant to respond to Al stress.

The mechanism of tolerance to Al is more determined by the ability of plant root to prevent Al to enter cell membrane by secreting organic acids.

Mechanisms of plant tolerance to Al stress can be classified into two mechanisms, namely: External/exclusion tolerance mechanism and Internal tolerance mechanism (Taylor, 1988; Kochian, 1995). The main difference between the two mechanisms is regarding Al detoxification area, whether it is in symplast (internal) or apoplast (exclusion). The first mechanism (external mechanism or rejection) is a system of tolerance created by plant by preventing Al not to enter symplast through: (a) Al immobilization in cell wall, (b) selective permeability of plasma membrane, (c) pH barrier in rhizosphere, (d) exudation of ligands that chelate Al such as exudation of organic acids, (e) exudation of P, and (f) Al efflux. Moreover, the second mechanism; a mechanism that generates plant to have tolerant ability to accumulate Al in cells (internal tolerance mechanism) that is in the form of: (a) Al chelating by organic acid in cytosol, (b) Al compartmentation in vacuole (Matsumoto, 1991), (c) specific protein that is able to bind Al, (d) isozyme that is resistant to Al, and (e) induction of specific protein synthesis in plasma membrane that will decrease Al absorption and increase Al efflux (Taylor, 1988). According to Ryand P.R., Delhaize E. & Randall P.J. (1995), considering the possibility of tolerance mechanism to Al, it was expected that the mechanism of tolerance to Al is more determined by the ability of plant root to prevent Al to enter cell membrane by secreting organic acids.

4. *Exudation of Organic Acids*

One of secondary metabolites is the production of low-molecular-weight organic acid compounds. The synthesis of various organic acids from plant roots as a response to Al stress is the characteristic of plant species that is able to adapt to acidic mineral soil. The role of organic acid in chelating Al in vascular plants has been frequently reported, such as by Pellet D.M., Grunes D.L. & Kochian L.V. (1995) and Zheng S.J., Ma J.F. & Matsumoto H. (1998). Root cell and all existing components will inhibit the adverse effect of Al on root elongation as well as the absorption of nutrient and water, while outside the plant root, organic acid will chelate Al thus plant will be tolerant to Al stress (Ma, 2000). Organic acid synthesized by plants that are tolerant to Al stress can be in the form of accumulation or exudate, either by accumulating it in symplast or exuding it to rhizosphere. The types of organic acid that are detected in plants experiencing Al stress include: citric acid, isocitric acid, fumaric acid, malic acid (Pellet, *et al*., 1995; Otani & Ae, 1996; Sopandie, 1999), and oxalic acid (Ma & Miyasaka, 1998; Zheng, *et al*., 1998; Swasti & Rozen, 2007). Several types of plant are able to secrete more than one type of organic acid from root tip. Indirectly, organic acid help increasing P availability by chelating Al (Marschner, 1995), thus P that is supposedly bound to Al can be made available to plants.

Result of study conducted by Swasti & Rozen (2007), showed that treatment of Al stress has stimulated the synthesis of oxalate acid. This organic acid synthesis confirms the mechanism of internal Al chelating by those organic acids in plant roots. The synthesis of organic acid due to accumulation process shows internal tolerance mechanism to prevent adverse effect of Al. As mentioned by Kochian (1995), and Ma (2000) regarding the tolerant plant. The mechanism can occur internally, that is by accumulating organic acid in root tissue. Study conducted by Sopandie (1999); Kasim (2001), proved that Al in nutrient solution successfully stimulated the synthesis of citric acid and malic acid in root tip of soybean plant grown in nutrient culture medium. Several tolerant genotypes of soybean showed increasing accumulation of citric acid and malic acid of 2-5 times higher than those of sensitive species. This high production of organic acids is related to the formation of specific enzymes as a response to Al stress (Pellet, *et al*., 1995; Sopandie, 1999).

Organic acid plays role in Al inclusion through its release from roots and Al detoxification in symplast in which the organic acid could chelate Al and reduce or prevent plant from the effect of toxicity at a cellular level (Pellet *et al*., 1995). Taylor (1991); Kochian (1995); and Ma (2000), reported that there is certain mechanism in tolerant plant to prevent Al to enter plants, namely the external tolerance mechanism. Ma (2000), mentioned that the external mechanism of Al chelating occurs through organic acid exudation to rhizosphere to form Al-organic acid complex. Internally, there is Al inhibition by the components of root cell such as cell wall, plasma membrane, DNA, and enzyme. If the components of root cell cannot inhibit the toxic effect of Al, there will be disruption of root elongation as well as absorption of nutrient and water.

The ability of plant to adapt to Al stress condition really depends on its ability to produce sufficient amount of organic acid to eliminate toxic effect of Al stress (Swasti & Rozen, 2007). Plant root is able to produce exudates like organic acid that plays important role in adaptation strategy (Ma & Miyasaka, 1998; Zheng, *et al*., 1998; Ma, 2000), it is expected that organic acid synthesis in sensitive strains is not adequate to chelate Al.

C. Conclusion

Although Al disrupts metabolism and suppresses plant growth, until certain threshold, the adverse effect of Al is still tolerated, depends on the types of plant and the level of Al activity. The level of Al toxicity depends on the activity of Al^{3+} ion in the media. If Al^{3+} is in the form of chelated ion, it is less toxic to plant growth compared to ionic Al such as Al^{3+}. The mechanism of tolerance to Al is more determined by the ability of plant root to prevent Al to enter cell membrane by secreting organic acids. Synthesis of various organic acid from plant roots as a response to Al stress is a characteristic of plant species that is able to adapt to acidic mineral soil. The role of organic acid in chelating Al in vascular plants is performed through process will inhibit the adverse effect of Al on root elongation as well as the absorption of nutrient and water, while outside the plant root, organic acid will chelate Al thus plant will be tolerant to Al stress. Organic acid synthesized by plants that are tolerant to Al stress can be in the form of accumulation or exudate, either by accumulating it in symplast or exuding it to rhizosphere. The types of organic acid that are detected in plants experiencing Al stress include: citric acid, isocitric acid, fumaric acid, malic acid, and oxalic acid. The ability of plant to adapt to Al stress condition really depends on its ability to produce sufficient amount of organic acid to eliminate toxic effect of Al stress. Plant root is able to produce exudates like organic acid that plays important role in adaptation strategy.

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