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Review

Integrated strategies to overcome aluminum toxicity in tropical acid soils

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ABSTRACT

Aluminum (Al) toxicity is a major constraint to crop productivity in tropical acidic soils, which predominate in much of Indonesia and other humid regions. This review summarizes advances in understanding Al phytotoxicity, plant tolerance mechanisms, and agronomic, plant breeding, and molecular strategies to overcome Al stress. Plants exhibit two primary adaptation strategies: Al efflux from root tips, with organic acid exudation being crucial (mediated by the ALMT and MATE transporters), and internal detoxification through chelation, compartmentalization, production and activation of antioxidants, osmolytes accumulation, and hormonal regulation. Recent research emphasizes the role of Al receptors, signaling pathways, and regulatory genes such as Nramp and ABC transporters in enhancing Al tolerance. Agronomic strategies, including liming, exogenous compound applications, biostimulants, and beneficial microbes, complement molecular breeding and gene editing approaches such as CRISPR/Cas to develop acid-tolerant cultivars. The success of Brazil and China in conquering acidic soils is attributed to their ability to integrate genomics, physiology, and sustainable agronomic management in transforming acidic soils into productive agroecosystems. Continued collaboration and application of modern biotechnology tools will accelerate the development of crops resistant to Al toxicity, enabling sustainable agricultural productivity in tropical acidic soils.

Keywords: Al phytotoxicity; agronomy and crop improvement; research focus and strengths; tolerance mechanisms; ultisols

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INTRODUCTION

Although there are various definitions for acid soils, they generally refer to soils with a pH below 5.5 in the surface layer, which covers about 30% of the total land (Kochian et al., 2015; FAO, 2025), which are mainly located in humid climates. Acid soils, especially ultisols or oxisols with a pH<5, are widespread throughout the world. More than 50% of the world's agricultural land is classified as acidic soil, and about 60% of this acid soil is located in tropical and subtropical regions. The occurrence of soil acidity in tropical and subtropical regions is generally natural; however, anthropogenic factors can also contribute to soil acidity in these regions. (Pavlů et al., 2021). Anthropogenic factors that frequently cause soil acidification include the long-term use of large amounts of synthetic fertilizers, imbalances in soil nutrient cycles, accumulation of organic matter, excessive absorption, and leaching of base cations (Ofoe et al., 2023).

In Indonesia, acidic soils dominate the terrestrial landscape, covering more than half of the country's total land area. According to IAARD (The Indonesian Agency for Agricultural Research and Development, 2015), approximately 107.3 million hectares (56.1%) of the 191.1 million hectares of total national land area are acidic soils, consisting of podzolic, ultisol, oxisol, and spodosol soil types. Of this, an estimated 18.2 million hectares are suitable for food crop cultivation, primarily on slopes of less than 15% (IAARD, 2015). The most widespread distribution of acidic soils is in Sumatra, Kalimantan, and Papua.

Barriers to using acid soils in several tropical regions, such as Brazil, parts of the US, China, Thailand, and Malaysia, are generally similar and considered substantial. However, because these areas of acid soil are so vast, they are considered strategically important for utilization due to their significant potential for increasing food production. Various technical constraints must be overcome when managing acid mineral soils, particularly aluminum (Al) toxicity, low pH (<5.5), high phosphorus (P) fixation, low levels of exchangeable base cations and cation exchange capacity (CEC), toxic iron (Fe) and manganese (Mn) concentrations, high susceptibility to erosion, and low biotic element content (Marschner, 2012). Among these, Al toxicity is usually the most critical constraint to plant growth in acid soils. In addition, nutrient deficiencies—particularly of P, calcium (Ca), magnesium (Mg), nitrogen (N), and potassium (K)—are commonly observed.

In acid soils with a pH below 5.5, the cation exchange complex becomes increasingly saturated with Al, which tends to displace polyvalent cations such as Ca^{2+} and Mg^{2+}. In addition, Al is a strong binder of P and molybdenum (Mo) (Marschner, 2012; Sopandie et al., 2023). In mineral-rich acidic soils, Al toxicity remains a major growth-limiting factor. Aluminum is released from the soil in the form of $Al(OH)^{2+}$, $Al(OH)_2^+$, and $Al(OH)_3^+$, commonly referred to as Al^{3+}. In most major crops, Al ions rapidly inhibit root growth even at micromolar concentrations. The chemical interactions between Al and soil are complex, likely due to the diversity of organometallic and polynuclear complexes, as well as the coexistence of various ions in the soil matrix (Chauhan et al., 2021). Lowering soil pH below 5 increases the solubility of Al into monomeric forms ($Al(OH)^{2+}$, Al^{3+}, $Al(OH)_2^+$, and $Al(OH)_4^-$). Among these forms, the trivalent form (Al^{3+}) is the most detrimental to plant growth and productivity, as it triggers a series of Al-related toxicities in most plant species (Kochian et al., 2015; Silva et al., 2020).

Some countries that are considered successful in developing acidic soils sustainably are Brazil, China, and America. Brazil is the most successful country in developing acidic soils, supported by competent research activities and excellent government programs, with its acidic soils known as cerrados covering an area of 200 million ha (Cabral, 2021). The importance of acidic soil management for sustainable agriculture in Indonesia has become a necessity, where we must learn from countries that have successfully conquered acidic soils. This review outlines the general characteristics of acidic soils, aluminum (Al) toxicity, plant adaptation mechanisms to Al stress, and agronomic, breeding, and frontier approaches to overcoming soil acidity. It also highlights successful strategies implemented by several countries, with Brazil standing out as the most successful in managing acidic soils and transforming them into a foundation for national food security.

EFFECTS OF ALUMINUM STRESS ON PLANTS

Al toxicity. Al toxicity in plants is a major constraint to crop productivity in acid soils worldwide (Chauhan et al., 2021; Kochian et al., 2015; Silva et al., 2020). Aluminum is a highly reactive element; Al toxicity will occur when it comes into contact with the cell wall, plasma membrane, and cytoplasm of apical root cells (Chauhan et al., 2021; Kochian et al., 2015). Kochian et al. (2015) illustrated the symplasmic and apoplasmic mechanisms of Al transport in higher plants, where Al can increase the production of ROS (reactive oxygen species) in various organelles, which causes oxidative damage (cellular Al toxicity). Al induces a series of Al-induced phytotoxic syndromes, including impaired root growth and development, decreased photosynthesis and plant growth, accumulation of reactive oxygen species (ROS), and damage to cellular and biochemical components. The adverse effects of Al^{3+} on plant growth and development have been well documented. Several researchers have reported Al^{3+} induced damage to plant cell components (Chauhan et al., 2021; Kochian et al., 2015; Ofoe et al., 2023; Szurman-Zubrzycka et al., 2019; Wei et al., 2021; Yamamoto, 2018; Zhang et al., 2019b) as described in Table 1.

Table 1. Aluminum (Al^{3+}) phytotoxicity, cellular damage, photosynthesis, and plant growth inhibition

Al^{3+} phytotoxicity	Symptoms and cellular damage
Oxidative stress and cellular damage	Al^{3+} induces oxidative stress and damages cellular components (nucleic acids, membrane lipids, proteins). ROS are produced in chloroplasts, mitochondria, or peroxisomes. Al^{3+} entering the cell disrupts membrane-bound organelles, including mitochondria, leading to cell injury. Al^{3+}-induced ROS trigger lipid peroxidation, accelerating membrane damage, protein degradation, and programmed cell death (Guo et al., 2018; Kochian et al., 2015;Ofoe et al., 2023; Yamamoto, 2018).
Cell wall damage	Al^{3+} binds strongly to the matrix of apoplastic pectin, thus altering the structural and mechanical properties of the cell wall, making it more rigid. The interaction of Al^{3+} with expansin reduces the mechanical extensibility of the cell wall (Chauhan et al., 2021).
Membrane damage	Al^{3+} binds to proteins and lipids, causing depolarization and reduced plasma membrane H^+-ATPase activity. This disturbs nutrient uptake, pH regulation, stomatal opening, and cell growth. It also inhibits Ca^{2+} and NH_4^+ uptake due to changes in membrane potential (Kochian et al., 2015; Wei et al., 2021; Zhang et al., 2017).
Nuclear and DNA damage	Al is affecting DNA and chromosome integrity, leading to DNA conformational changes, fragmentation, and chromatin degradation. Al^{3+} interferes with cell division and induces chromosomal abnormalities (Kochian et al., 2015; Szurman-Zubrzycka et al., 2019; Wei et al., 2021).
Disruption of signal transduction	Al toxicity inhibits signal transduction by interfering with Ca^{2+} signaling, intracellular pH, ROS generation, and stress-related hormones such as ABA, auxin, and ethylene (Li et al., 2025; Ranjan et al., 2021).
Disruption of the cytoskeleton	Al disrupts microtubule organization and polymerization, inhibiting root growth. It affects cytoskeletal dynamics directly or via altered Ca^{2+} signaling (Baranova et al., 2016; Ofoe et al., 2023).
Mitochondrial disruption	Al stress interferes with mitochondrial function through ROS overproduction, inhibition of electron transport and ATP synthesis, redox imbalance, and induction of programmed cell death (Yamamoto, 2018).
Chloroplast disruption	Al^{3+} inhibits photosystem II (PSII) electron transport, reducing oxygen evolution and chlorophyll fluorescence (Hasni et al., 2015).
Reduction in photosynthetic capacity	Al reduces chlorophyll content, fluorescence, net photosynthetic rate, stomatal conductance, and transpiration rate. (Cheng et al., 2020; Guo et al., 2018; Ofoe et al., 2023).
Inhibition of root growth and development	Al toxicity causes short, stubby roots due to inhibited elongation of primary and lateral roots (Buchanan et al., 2015; He et al., 2019; Hidayah et al., 2020; Sopandie et al., 2014; Zhang et al., 2019b). Root inhibition is related to auxin–cytokinin imbalance, where cytokinin accumulation in meristems suppresses cell division.
Reduction in water and nutrient uptake	Al triggers physiological drought and disrupts plasma membrane function, reducing nutrient transport mediated by H^+-ATPase. This affects uptake of K^+, NH_4^+, Mg^{2+}, and Ca^{2+} (Ofoe et al., 2023; Zhang et al., 2017).

PLANT TOLERANCE MECHANISMS TO ALUMINUM STRESS

There are wide differences among plant species in their tolerance to acidic soils with high Al content. The impact of Al^{3+} stress varies between species, even between varieties within the same species. These differences indicate the existence of different tolerance mechanisms in each plant in dealing with Al stress. Annual tuber plant species such as cassava are known to be highly tolerant to acidic soils, compared to sweet potatoes, tamarind, and taro/yam (Tanaka & Hayakawa, 1975). Other plant species that are highly tolerant include rice and buckwheat, while those that are tolerant include oats, soybeans, cowpeas, peanuts, and potatoes. Corn and wheat are considered medium-tolerant;

sorghum, barley, and onions are considered sensitive, while carrots, spinach, and celery are highly sensitive to Al stress (Tanaka & Hayakawa, 1975). Scientific evidence indicates that sorghum possesses moderate tolerance to aluminum (Al) toxicity and requires sufficient phosphorus (P) availability for optimal growth. Sopandie et al. (2014) and Sopandie et al. (2023) reported that sorghum exhibits moderate tolerance to aluminum (Al) stress. However, its growth is primarily constrained by phosphorus (P) deficiency, as evidenced by trials conducted on acidic soils in Jasinga, characterized by exchangeable Al levels ranging from 1.0 to 5.0 me 100 g^{-1}, a soil pH of approximately 4.0–4.3, and Al saturation between 25–30%.

Resistance to Al stress refers to the capacity of plants to sustain satisfactory growth and yield under conditions of Al stress. As illustrated in Figure 1 (Kochian et al., 2015), plant resistance to Al operates through two principal mechanisms: (a) the Al exclusion mechanism, defined as the plant’s ability to prevent Al from entering the root apex via either the apoplastic or symplastic pathway; and (b) the Al tolerance mechanism, whereby Al that enters the plant is subsequently detoxified and compartmentalized.

External mechanisms (Al exclusion)

Organic Acid Exudation. Organic acid exudation represents the most prominent strategy for Al excretion from root tips into the rhizosphere, with organic acids serving a fundamental role in this process (Buchanan et al., 2015; Kochian et al., 2015; Ofoe et al., 2023). Numerous studies have demonstrated that adaptation of soybean, corn, wheat, sorghum, taro, buckwheat, and various other species to Al toxicity is primarily mediated by the external secretion of organic acids capable of chelating Al, as outlined by Sopandie (2024). Among these, citric acid exhibits the strongest chelation capacity against Al, followed by oxalic acid and succinic acid (Ma et al., 2001). Compelling evidence indicates that malic acid exudation from wheat roots and citric acid exudation from maize roots are triggered by the activation of anion channels in the plasma membrane (Kochian et al., 2015).

Figure 1 illustrates the mechanism by which organic acids bind aluminum (Al), forming stable complexes that make Al non-toxic within the cells of Al-tolerant plants. It also compares this mechanism with that observed in Al-sensitive species (Kochian et al., 2015). In tolerant plants, Al is chelated by carboxylate groups (Al–COOH), resulting in its inactivation. These complexes are subsequently translocated into the vacuole via the tonoplast membrane, facilitating Al detoxification (Al compartmentation). In contrast, sensitive plants lack the ability to form Al–COOH complexes, leaving Al in its active form, which can disrupt cell division and inhibit ion channel function, ultimately impairing nutrient transport within plant cells. Our previous research on soybeans indicated that citric and malic acids contributed significantly to the adaptation of soybeans to Al toxicity in tolerant soybean Yellow Biloxi (Kasim et al., 2001; Sopandie, 2024).

As mentioned by Kochian et al. (2015) and Liu et al. (2023), organic acid (OA) exudation is recognized as a central strategy for aluminum (Al) tolerance in plants. In response to Al stress, many species release negatively charged organic molecules into the rhizosphere, where they chelate Al ions and prevent their uptake by root tissues (Kochian et al., 2015). Buchanan et al. (2015) pointed out that among the most frequently secreted compounds are citric, malic, and oxalic acids, with citrate and malate being predominant across various species. In contrast, oxalate release appears to be species-specific, having been reported primarily in buckwheat (*Fagopyrum esculentum*) and taro (*Colocasia esculenta*). To elucidate the genetic basis of this mechanism, researchers have employed Al-tolerant genotypes to identify transporter genes responsible for OA efflux. One such gene, *TaALMT1*, encodes an Al^{3+}-activated channel in the plasma membrane that facilitates malate release in wheat (*Triticum aestivum*). This channel operates independently of the *MATE* family, which mediates citrate transport, suggesting that Al resistance in wheat and sorghum may have arisen through distinct evolutionary pathways despite converging on similar physiological outcomes. Recent studies indicate that certain members of the *ALMT* and *MATE* gene families may not be directly associated with aluminum tolerance, but instead contribute to other physiological roles within the plant system (Sasaki et al., 2016). In addition, some species also exude secondary metabolites such as benzoxazinoids and phenolic compounds, which may play complementary roles in stress mitigation (Zhao et al., 2019). Ma et al. (2020) showed that alfalfa grown in nutrient solution at pH 4.5 and Al concentration up to 100 µM produced more free proline than control plants. While phosphate exudation appears to have limited impact on Al resistance in wheat, external supplementation of phosphate has been shown to enhance Al tolerance in sorghum under stress conditions (Lestari et al., 2017).

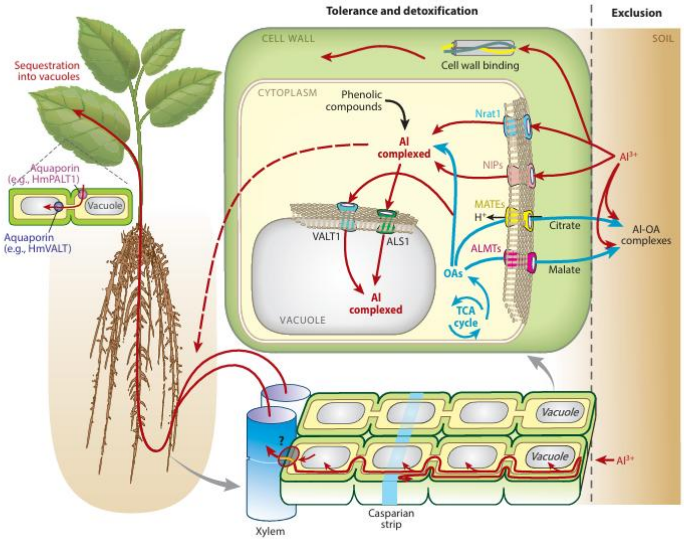

Figure 1. General model describing the mechanisms of Al resistance (Al exclusion and Al tolerance/detoxification) in plants against aluminum stress (Kochian et al., 2015)

Internal mechanisms

Some Al-accumulating plant species do not exhibit toxicity symptoms even when cultivated in soils with high aluminum concentrations. As noted by Yan et al. (2021), Al hyperaccumulators such as citrus are known to possess internal mechanisms for detoxifying aluminum. These internal strategies may involve chelation and redistribution of Al within the cytoplasm, synthesis of stress-related proteins triggered by Al exposure, activation of Al-resistant defense pathways, or stimulation of hormonal responses that confer Al tolerance (Yan et al., 2021). In addition, Ofoe et al. (2023) described that internal detoxification processes encompass modifications to the cell wall, intracellular detoxification and compartmentalization, accumulation of osmolytes, enhanced antioxidant production and activity, as well as hormonal regulation in response to Al-induced stress.

Cell wall modification. The cell walls of root tissues can act as a physical barrier, limiting the entry of Al into the cells. However, these walls can also be sites of Al interaction because they are rich in carboxylic compounds—such as pectin, cellulose, and hemicellulose—which have a strong binding affinity for Al ions (Wu et al., 2022). In Arabidopsis root cell walls, hemicellulose has a higher affinity than pectin, making it a primary target for Al. According to Wang et al. (2015) and Yan et al. (2018), enhancing Al tolerance requires modifications to the cell wall composition.

Cytoplasmic Al chelation by organic acids or polypeptides. Internal Al detoxification in some Al-tolerant plants is mediated by an intracellular Al chelation system and the compartmentalization of Al-OA (Al-organic acids) complexes within the vacuole. Al-tolerant plant species such as *Hydrangea, Melastoma malabathricum*, buckwheat, and black tea (*Camellia sinensis*) can detoxify and accumulate relatively high levels of Al in their leaf tissues without exhibiting Al toxicity (Wang et al., 2015; Bojórquez-Quintal et al., 2017). In the leaves, Al citrate is converted to Al oxalate and compartmentalized into the vacuole (Wang et al., 2015). According to Fu et al. (2020), in tea plants, Al can form non-toxic complexes with catechins in the leaves (Fu et al., 2020).

Al-induced stress protein production. Al stress in plants triggers the production of specific stress-related proteins that play a role in detoxification, antioxidant defense, cell wall repair, and signal transduction. Examples include proteins involved in antioxidant activity, glutathione metabolism, and proteins involved in callose degradation to mitigate cell wall damage caused by Al toxicity (Sun et al., 2020; Niedzielaa, 2022). Research by Sopandie et al. (2003) showed that Al-tolerant soybean was able to synthesize a specific 79.8 kD protein in root tips when exposed to Al stress. This membrane protein is suspected to play a role in facilitating a decrease in Al influx or increasing Al exclusion from the cytoplasm, thereby protecting plants from Al toxicity.

Transporters for internal Al tolerance. Transporters involved in internal Al tolerance in plants include ABC transporters, which sequester Al into the vacuole by transporting UDP-glucose to modify the cell wall, and the Nramp transporter *Nrat1,* which imports trivalent Al ions into root cells for subsequent detoxification. The Aluminum-activated Malate Transporter (ALMT) family, a family of MATE transporters, also plays a crucial role by transporting organic acids such as malate for external chelation, but may also be involved in internal mechanisms such as vacuolar sequestration (Huang et al., 2024; Kochian et al., 2015; Ofoe et al., 2023). In rice, the *OsNrat1* gene—classified as a member of the natural resistance-associated macrophage protein (Nramp) family—codes for a plasma membrane transporter that facilitates aluminum (Al) uptake and plays a role in Al tolerance (Li et al., 2014). Meanwhile, ALS1 (Aluminum Sensitive 1), an ABC-type transporter located in the tonoplast, is crucial for transporting Al into the vacuole, thereby supporting internal detoxification processes in species such as rice, Arabidopsis, and buckwheat.

AGRONOMIC STRATEGIES TO INCREASE PLANT TOLERANCE TO ALUMINUM TOXICITY

Application of nutrients and other compounds. Over the past few years, many researchers have explored several strategies to reduce Al toxicity in plants. Several materials have been used, including nutrients (B, Si, Ca, Mg, NH_4, SO_4) and plant growth regulators (salicylic acid, auxin, putrescine), and others, which have been shown to have significant positive effects in mitigating Al toxicity (Table 2; Rahman & Upadhyaya 2021).

Application of exogenous compounds. Our studies have shown that the application of citric acid and pure peat water can increase aluminum (Al) tolerance in oil palm seedlings (Hidayah et al., 2020). Under 400 μM Al, the application of citric acid at 25 ppm and 50 ppm, and peat water at 200 ppm and 300 ppm, significantly increased root length, root dry weight, photosynthesis rate, chlorophyll and carotenoid content, CAT (catalase) and APX (ascorbate peroxidase) activities, while reducing MDA levels. The beneficial effects of these compounds have also been observed in mature oil palm plants. A subsequent study (Hidayah et al., 2024) on 9-year-old oil palms showed that basal application of salicylic acid, citric acid, Ca^{2+}, B, and Cu around the root zone effectively suppressed Al toxicity and led to increased bunch production (Table 3). Fruit yield improvement that occurred under this treatment was closely linked to enhanced physiological performance. It is worth noting that the 17th leaf of a 9-year-old oil palm tree exhibited lower MDA levels, elevated photosynthetic activity, and increased enzymatic antioxidant responses, including CAT and APX (Table 3). These physiological shifts suggest that the applied exogenous compounds effectively triggered signaling pathways that mitigate reactive oxygen species (ROS), thereby strengthening the plants' resilience to aluminum-induced stress.

Table 2. Several applications of nutrients and other substances for the mitigation of aluminum toxicity in various plants

Applied substance	Plant	Mitigation mechanism
Boron	*Citrus trifoliata*	Limits Al entry into the symplast by reducing Al immobilization.
	Pisum sativum	Restricts Al binding to the cell wall, reduces tissue damage in roots and shoots, and prevents chlorophyll content reduction.
Magnesium	*Glycine max*	Regulates the synthesis and exudation of citric acid
	Triticum aestivum	Reduces Al-induced Mg deficiency.
Silicate	*Sorghum bicolor*	Forms Si–Al complexes to reduce Al binding to cell walls.
Sulfur	*Citrus grandis*	Reduces Al transport from roots to shoots and enhances citrate secretion by roots.
Calcium	*Glycine max*	Reduces Al toxicity in roots.
Ammonium	*Oryza sativa*	Competition with Al at binding sites, and changing the pH
Salicylic acid	*Oryza sativa*	Suppresses Al uptake.
Auxin	*Triticum aestivum*	Reduces Al accumulation at root tips.
	Glycine max	Stimulates citrate exudation and increases PM H^+-ATPase activity.
Putrescine	*Oryza sativa*	Suppresses cell wall polysaccharide biosynthesis and reduces ethylene emission.
Biochar	*Populus sp.*	Alters soil pH.
Melatonin	*Glycine max*	Enhances the exudation of organic acid anions and antioxidant enzyme activity.

Note: Source: Rahman & Upadhyaya, 2021

Table 3. Effect of exogenous compounds on the number of normal bunches, average bunch weight, productivity, and physiological performance of oil palm aged 9 years

Exogenous compounds treatments (ppm)	Number of normal bunches	Average bunch weight (kg)	Productivity (kg tree^{-1})	Photo-synthesis rate [μmol m^{-2} s^{-1}]	CAT activity [U (mg protein)$^{-1}$]	APX activity [U (mg protein)$^{-1}$]	MDA content [nmol (mg protein)$^{-1}$]
Control	9.7c	11.2b	108.1c	8.81c	6.74c	0.00715d	58.20a
Ca 50	11.0b	11.2b	122.8bc	7.82c	8.34b	0.01546c	44.92a
Ca 50 + Salicylic acid 50	14.0a	12.0a	164.5a	21.62b	12.87ab	0.03661a	24.70b
Ca 50 + Salicylic acid 50 + citric acid 50	13.0a	12.0a	155.4a	32.80a	27.46a	0.0246b	20.11b
Ca 50 + Salicylic acid 50 + citric acid 50 + B 50	13.4a	11.9a	155.3a	24.25b	24.56a	0.02529b	23.25b
Ca 50 + Salicylic acid 50 + citric acid 50 + B 50 + Cu 50	13.4a	11.9a	158.6a	21.50b	26.9a	0.03342ab	12.74c

Note: Numbers followed by the same letters in the same column are not significantly different based on DMRT at the level α = 5%; Ca = $CaCl_2$. (Source: modified from Hidayah et al., 2024)

In a separate investigation, Sopandie et al. (2024) reported that oil palm cultivated on ultisol soils with high aluminum saturation (approximately 83%) exhibited markedly low bunch productivity. This decline was primarily attributed to a high rate of bunch rejection and a reduced oil yield, which fell below 19%. Under such stress conditions, the application of exogenous compounds to developing fruits post-anthesis proved beneficial. Treatments involving calcium (Ca^{2+}), naphthaleneacetic acid (NAA), and 1-methylcyclopropene (1-MCP) - applied individually or in combination- enhanced fruit development and oil yield, although they did not significantly affect bunch number, bunch weight, or fruit set. The most notable increase in oil content per unit dry mesocarp was observed with the combined application of 100 ppm 1-MCP, 50 ppm Ca^{2+}, and 200 ppm NAA (Table 4). For maximizing oil yield per bunch, promising results were also obtained from the combinations of 100 ppm 1-MCP + 200 ppm NAA, 50 ppm Ca^{2+} + 200 ppm NAA, and the single treatment of 50 ppm Ca^{2+} (Sopandie et al., 2024).

Application of ameliorants (lime, manure). Soil acidity in ultisols, which is common in several tropical countries, must be reclaimed with lime combined with various integrated soil management interventions, thereby significantly increasing crop yields and enhancing the resilience of tropical agroecosystems. However, many studies related to the use of lime and other ameliorants on acidic soils often provide varying conclusions, with large quantities of lime and ameliorant requirements, thus constraining its application (Sopandie, 2024). Therefore, a calibration experiment is needed by combining NPK fertilizer as a base fertilizer, lime ameliorant, and manure in the same experiment.

Table 4. Effect of exogenous compounds on fruit to bunch and oil content

Treatments	Oil ratio in mesocarp		Fruit to bunch (FB) (%)	Oil to bunch (OB) (%)
	ODM (%)	OWM (%)		
M0C0N0	75.83f	50.61f	51.67bc	21.65c
M0C0N200	80.04bc	56.80cd	48.67bc	24.74bc
M0C50N0	79.05bcd	57.37bcd	65.67a	33.96a
M0C50N200	79.21bc	56.99cd	66.33a	33.90a
M100C0N0	80.54ab	60.50a	56.67b	30.16ab
M100C0N200	78.16cde	59.32ab	65.33a	34.73a
M100C50N0	79.38bc	56.78cd	49.00bc	22.74ab
M100C50N200	82.00a	57.23cd	55.33b	28.51ab
M200C0N0	78.78bcd	55.91d	65.67a	30.10ab
M200C0N200	78.80bcd	57.87bcd	52.67bc	26.86ab
M200C50N0	78.02cde	58.33bc	41.00c	21.61c
M200C50N200	80.69ab	57.71bcd	48.33bc	24.99bc
M300C0N0	77.25ef	56.30cd	51.67bc	25.42bc
M300C0N200	78.32cde	57.11cd	55.67b	27.89bc
M300C50N0	77.47ef	53.91e	45.00c	21.59bc
M300C50N200	79.30bc	56.99cd	59.67ab	30.54ab

Note: Numbers followed by the same letters in the same column are not significantly different based on DMRT at the level α=5%; ODM= Oil to dry mesocarp; OWM= oil to wet mesocarp. Note: 1-MCP (M0=0 ppm, M100=100 ppm, M200=200 ppm, and M300=300 ppm), CaCl2 (C0 =0 ppm and C50= 50 ppm), and NAA (N0= 0 ppm and N200 = 200 ppm). (Source: Sopandie et al., 2024)

Table 5. Effects of combination fertilizer and ameliorant on the production of soybean grown at acid soil ultisol Jasinga Bogor

Combination of NPK fertilizer, dolomite, and manure	Soybean yield (tons ha^{-1})	
	Rainy season	Dry season
P0: Control	1.18 c	1.32 c
P1: (½ recommended dose NPK) + (dolomite ¼ x Exc. Al^{3+}) ha^{-1}	2.15 b	2.17 b
P2: (½ recommended dose NPK) + (dolomite ¼ x Exc. Al^{3+}) + (1.25 tons of manure) ha^{-1}	2.16 b	2.51 ab
P3: (½ recommended dose NPK)+ (dolomite ¼ x Exc. Al^{3+}) + (2.5 tons of manure) ha^{-1}	2.17 b	2.46 ab
P4: (recommended dose NPK) + (dolomite ¼ x Exc. Al^{3+})+ (2.5 tons of manure) ha^{-1}	2.91 ab	2.53 ab
P5: (recommended dose NPK) + (dolomite ½ x Exc. Al^{3+}) ha^{-1}	2.96 ab	2.50 ab
P6: (recommended dose NPK) + (dolomite 1 x Exc. Al^{3+}) ha^{-1}	3.36 a	2.77 a

Note: Numbers followed by the same letter in the same column are not significantly different in the DMRT test at the 5% level. The recommended dose of NPK was (75 kg Urea, 150 kg SP-36, and 100 kg KCl) ha^{-1}; dolomite dosage for Al neutralization was 3.94 tons ha^{-1}; Soybean varieties Tanggamus and Anjasmoro (both tolerant to Al) were used. (Source: modified from Hasibuan et al., 2018).

In the previous study, a calibration experiment conducted by Hasibuan et al. (2018) evaluated the combined application of ameliorants, NPK fertilizers, and organic manure to identify the most effective treatment for soybean cultivation on ultisols (mild to moderate acidity stress; pH 4.60; exchangeable Al: 1.97 me 100 g^{-1}; Al saturation 11.30%; Table 5). Their findings showed that treatment P5—which consisted of the standard NPK recommendations (75 kg Urea, 150 kg SP-36, and 100 kg KCl) supplemented with dolomite at half the rate of exchangeable Al—was able to increase soybean yields more than twofold compared to the control (Table 5). The highest yield was recorded under treatment P6, which applied the full NPK recommendation along with dolomite at a 1:1 ratio to exchangeable Al, consistent across both rainy and dry seasons. Interestingly, this yield was statistically comparable to that of treatment P4, which combined the same NPK dosage with dolomite at ¼ × exchangeable Al and 2.5 tons ha^{-1} of manure. Tanggamus and Anjasmoro soybean varieties gave the same response to all treatments; the production of these two varieties was not significantly different, indicating that these two soybean varieties are tolerant to Al stress.

These results suggest that soybean cultivation on moderately acidic soils requires, at a minimum, dolomite at ¼ × exchangeable Al, 2.5 tons ha^{-1} of manure, and the full recommended NPK dose. Under resource-limited conditions, acceptable yields (>2.0 tons ha^{-1}) may still be achieved using half the NPK recommendation, dolomite at ¼ × exchangeable Al, and 1.25 tons ha^{-1} of manure. Treatments P4, P5, and P6 demonstrated that supplementing NPK fertilizer with dolomite and manure effectively raised soil pH from 4.6 to a range of 4.9–5.8, reduced Al^{3+} solubility from 1.75 to 0–0.52 me 100 g^{-1}, and lowered Al saturation from 11.30% to 0–3.65%. These improvements were accompanied by a marked increase in phosphorus availability (from 4.83 ppm to 5.10–11.10 ppm) and base saturation (from 70.3% to 75–100%) (Hasibuan et al., 2018).

Increasing Al tolerance through association with microbes (microbe-associated Al tolerance). Microorganisms possess remarkable adaptations that enable them to survive under extreme environmental conditions. Their role in alleviating both biotic and abiotic stress in plants is well recognized, particularly in enhancing plant growth and resilience under adverse conditions (Rahman & Upadhyaya, 2021; Wei et al., 2021). Several studies have highlighted the contribution of mycorrhizal fungi to aluminum (Al) tolerance in different plant species. For instance, *Bacillus* spp. has been shown to mitigate Al toxicity in maize, while *Glomus* sp. contributes similarly in banana cultivation. The ectomycorrhizal fungus *Pisolithus* enhances Al tolerance in *Eucalyptus* by sequestering Al within fungal tissues and improving the host's nutrient uptake. Likewise, inoculation with *Gigaspora margarita* has been found to alleviate Al-induced stress symptoms in the roots of sweet potato (*Ipomoea batatas*). Despite these promising findings, the underlying mechanisms remain only partially understood. Wei et al. (2021) summarized several PGPRs that are useful in increasing plant tolerance to Al, as explained in Table 6.

CROP IMPROVEMENT FOR ALUMINUM STRESS TOLERANCE

Crop improvement for aluminum stress tolerance includes selecting and crossing superior varieties, using efficient breeding methods to identify tolerance genes, and utilizing genetic variation in local varieties or germplasm. Another approach is genetic engineering to introduce Al resistance genes (Chauhan et al., 2021). A more common approach is plant improvement through conventional breeding, which involves screening for tolerant plants through phenotypic testing and measuring root growth responses (Ofoe et al., 2023; Chauhan et al., 2021). Al tolerance improvement focuses more on improving root adaptation to Al stress. However, the genetic regulation of aluminum tolerance involves numerous genes, reflecting its multigenic character. Therefore, in order to improve it, a special approach is needed, such as character dissection into supporting components that are closely related to tolerance characters, taking into consideration two main things: (1) these character components have diversity in the breeding population, and (2) this diversity is genetically controlled and can be inherited. It is known that the secretion of citric acid and/or malic acid from root tips is closely related to the diversity of plant tolerance to Al toxicity. These differences in tolerance diversity occur in cereal crops such as rice, triticale, corn, sorghum, barley, wheat, rye, and millet, as well as legumes such as soybeans and alfalfa.

Table 6. Effects of several PGPR on plant tolerance to Al^{3+} toxicity

Strain	Function	Target plant	Mechanism of Al^{3+} toxicity reduction
Bacillus sp. PSB16	Produces organic acids (OA) and polysaccharides	*Oryza sativa*	Chelates Al, increases solution pH, and promotes rice growth
Bacillus toyonensis Bt04	Produces auxin and cytokinin	*Zea mays*	Reduces Al accumulation in young maize roots, promotes maize growth, and enhances root development
Pseudomonas plecoglossicida Pp20	Produces ACC deaminase and IAA	*Zea mays*	Increases root length and dry root mass
Pantoea agglomerans CAH6	Produces siderophore	*Vigna radiata*	Reduces Al uptake
Rhizobium panacihumi DCY116T	Produces IAA	*Panax ginseng*	Enhances proline, phenolic, and sugar content, and induces expression of ROS-scavenging related genes
Stenotrophomonas maltophilia Sb16	Produces OA and polysaccharides	*Oryza sativa*	Chelates Al, increases solution pH, and promotes rice growth
Enterobacter sp. RJAL6	Releases oxalate, citrate, succinate, and siderophore	*Lolium perenne*	Promotes ryegrass growth by forming Al-siderophore complexes

Note: Source: Wei et al., 2021

Advances in molecular biology have played an essential role in improving crop performance on acidic soils such as Ultisols, particularly by enhancing aluminum (Al) tolerance and phosphorus (P) uptake efficiency. In Brazil, a key breakthrough was the identification of the *SbMATE* gene in sorghum, which encodes a transporter responsible for citrate efflux—an essential mechanism for detoxifying Al ions in the rhizosphere (Magalhaes et al., 2007; Table 7). This mechanism involves chelation of Al by citrate, reducing its phytotoxicity. Complementary findings in wheat and other cereals revealed the involvement of the ALMT gene family, which facilitates malate exudation as another organic acid-based detoxification strategy (Ma et al., 2001). Both *MATE* and *ALMT* transporters are membrane-bound proteins that contribute to Al resistance by enabling the release of organic acids from root cells, thus mitigating aluminum stress in acid soils and supporting the development of tolerant cultivars.

In China, rice has become a model crop for acid soil research. The discovery of *STAR1/STAR2* (Sensitive to Aluminum Rhizotoxicity) genes, encoding an ABC transporter that modifies cell wall properties to reduce Al binding, provided a breakthrough in understanding rice Al tolerance (Huang et al., 2009; Table 7). Further genomic studies and marker-assisted selection have accelerated the release of rice varieties with higher productivity on acidic soils (Li et al., 2014). These advances demonstrate that molecular genetics complements agronomy and plant breeding by providing specific gene targets (e.g., *ALMT, MATE, STAR1/STAR2*) and functional markers for breeding programs. Such integration has accelerated the release of acid-tolerant cultivars, thereby supporting the long-term productivity of Ultisols.

Genetic engineering and gene editing (such as *CRISPR/Cas9*) (Li et al., 2022) can improve aluminum (Al) tolerance in plants by introducing genes such as *ALMT* and *MATE* (Fang et al., 2024), which encode organic acid transporters for chelating and detoxifying Al, or genes such as *ALS3* (which encodes an ABC transporter) involved in internal Al detoxification. The *ALS1* and *ALS3* genes, for example, have been shown to enhance Al tolerance in *Arabidopsis thaliana*. This approach helps plants overcome the growth retardation and severe yield losses caused by Al toxicity in acidic soils, both through detoxification of external Al in the soil and internal sequestration within cells (Li et al., 2022; Zhang et al., 2019a).

RESEARCH EXCELLENCE IN UTILIZING ACID ULTISOL SOILS IN VARIOUS COUNTRIES

Research related to the utilization of acid ultisol soils has been quite well developed in several tropical countries, such as Brazil, China, and the United States. Brazil has the most advanced position following the establishment of EMBRAPA(*Empresa Brasileira de Pesquisa Agropecuária*). EMBRAPA is the Brazilian Agricultural Research Corporation, a public institution that develops research, innovation, and technological solutions for agriculture and livestock in Brazil. Founded in 1973, EMBRAPA has a pivotal role in establishing the technological foundation of Brazilian tropical agriculture and also has an extensive international collaboration network.

Cabral (2021) underlined EMBRAPA's key contribution to transforming the acidic soils of the Cerrado into productive farmland. Located in central-western Brazil, the Cerrado is a tropical savanna that has undergone major agricultural development since the 1970s. This transformation has positioned the region as a major global supplier of food. The expansion of soybean cultivation and pasture systems reflects the success of Brazil's agricultural modernization. EMBRAPA's achievements stem from scientific innovations, particularly the breeding of soybean varieties suited to acidic soil conditions. EMBRAPA has integrated liming, phosphorus fertilization, and crop rotation with advanced breeding programs, resulting in soybean and corn varieties that thrive in acidic soils. Their molecular breakthroughs, such as the discovery of *SbMATE* in sorghum and *ZmMATE1* in corn, have positioned Brazil as a global leader in aluminum (Al) tolerance research (Magalhaes et al., 2007; Table 7). Through modern plant breeding, Brazil has developed crop varieties suited to tropical conditions and tolerant to the seasonal climate of the Cerrados. Soybean, originally a temperate crop, has successfully adapted to the tropics. Over four decades, Brazil's grain production has increased sixfold, while the area under cultivation has increased only 1.6-fold. This represents a significant increase in productivity. In addition to food crops, the Cerrados is also an important area for livestock production, such as beef cattle and dairy (Cabral, 2021).

Table 7. Research focus and strengths of several countries in the utilization of acidic ultisol soils for various crops

Country	Agronomy focus	Breeding & germplasm	Physiology insights	Molecular/gene discovery	Key references
Brazil (±200 million ha; Cerrado, Amazon)	Liming, phosphate fertilization, crop rotation (*Embrapa*)	Acid-tolerant soybean & maize widely adopted	Root Al tolerance, P-use efficiency	*SbMATE* (sorghum citrate efflux), *ZmMATE1* (maize), *ALMT1*	Cabral (2021); Magalhaes et al. (2007)
USA (Southeast; Alabama, Georgia, Mississippi; Southern Red Soils)	Soil conservation, cover crops, cotton–maize–peanut rotation	Cotton, maize, peanut with moderate tolerance	Legume N_2 fixation, nutrient uptake under low pH	*ALMT1* homologs, QTL for Al tolerance in maize/soybean	Cheng et al. (2025); Kochian et al., (2015)
China (South) (Guangdong, Guangxi, Hunan, Fujian)	Liming, organic–inorganic fertilization, rice–legume rotations	Rice, maize, citrus, tea acid-tolerant varieties	Root adaptation in rice, P efficiency	*STAR1*/*STAR2*, *NRAT1*, QTL for Al tolerance	Huang et al., (2009); Li et al., (2014); Zhu & Shen (2024)
Indonesia (±45 million ha; Sumatra, Kalimantan, Sulawesi)	Fertilization (P, dolomite, biochar), maize–soybean & sorghum; application of exogenous compound for oil palm	Local soybean, sorghum & maize lines screened for acid tolerance; application of exogenous compounds on oil palm	Nutrient uptake and crop adaptation studies	*GmALMT*, *GmMATE* homologs (soybean); early QTL mapping in maize/rice	Effendi & Sudarsono (2015); Hidayah et al., (2024); Sopandie et al., (2014; 2024)

Country	Agronomy focus	Breeding & germplasm	Physiology insights	Molecular/gene discovery	Key references
Malaysia (Peninsular Malaysia, Sabah, Sarawak)	Oil palm & rubber agronomy, fertilization, liming, drainage	Clonal selection in oil palm & rubber	Oil palm physiology under Al/P stress	Genomics for oil palm nutrient & stress adaptation	Mahmud & Chong, (2022); Pupathy & Sundian (2022)
Thailand (Southern and Northeastern Thailand)	Soil & water management for rice/rubber	Rice breeding with IRRI collaboration	Root tolerance to Fe/Al toxicity	Pup1 locus (OsPSTOL1) introgression into rice	Gamuyao et al., (2012)

In the United States, the focus is on conservation agriculture, cover cropping, crop rotation, and microbial association in the Southeast, with soybeans, corn, cotton, and peanuts as the main crops (Cheng et al., 2025). Molecular research has advanced through QTL mapping and the identification of ALMT1 homologs in cereals, which has strengthened breeding programs for acid tolerance (Kochian et al., 2015; Table 7). China has combined intensive agronomic research with robust molecular discoveries. Rice has become a model species for acid soil tolerance, with the identification of *STAR1/STAR2* and *NRAT1* (Huang et al., 2009; Li et al., 2014; Zhu & Shen, 2024), which confer resistance to Al toxicity. These molecular insights, combined with large-scale breeding and fertilizer trials, have resulted in the release of acid-tolerant rice and corn cultivars (Table 7).

In Indonesia, research primarily focuses on agronomic practices such as liming, phosphorus fertilization, and organic amendments for corn-soybean systems. Local germplasm screening has supported breeding, while molecular studies in soybean (GmALMT, GmMATE homologs) and QTL mapping in maize are important but emerging areas of research (Effendi & Sudarsono, 2015) (Table 7). Malaysia has emphasized agronomy and breeding for perennial crops such as oil palm and rubber, with significant advances in fertilization and liming, as well as an improvement of the water management system (Mahmud & Chong, 2022; Pupathy & Sundian, 2022). Molecular research focuses on genomic resources for oil palm nutrient efficiency and stress adaptation, although this remains less integrated than for perennial crops. Meanwhile, Thailand has concentrated on rice cultivation in acidic soils, often in collaboration with IRRI. Physiological studies of root adaptation have been complemented by the introgression of the *Pup1* locus (OsPSTOL1), which improves phosphorus uptake efficiency in acidic soils with low P levels (Gamuyao et al., 2012). Overall, these findings suggest that while Brazil and China are excellent in integrating agronomy, breeding, physiology, and molecular genetics, other countries such as Indonesia, Malaysia, and Thailand are developing their strengths in crop-specific systems. The convergence of agronomic management with molecular discoveries provides a strong foundation for the sustainable use of ultisols in tropical and subtropical regions.

CONCLUSIONS

Aluminum toxicity continues to limit crop productivity on tropical acid soils, including those in Indonesia. Plants have evolved adaptive responses, such as root-level exclusion and internal detoxification, supported by membrane-bound receptors and signaling pathways that regulate key transporter genes (e.g., *ALMT, MATE, Nramp, ABC*). Current research trends highlight integrated strategies—molecular breeding, genome editing, and context-specific agronomic practices. While liming and chemical amendments remain useful, their cost restricts adoption by smallholders. Biostimulants and beneficial microbes offer promising, low-input alternatives for improving crop performance.

Going forward, the challenge is not only to identify new tolerance genes but also to decipher the regulatory systems that govern plant responses to Al stress. Advances in omics and precision breeding are opening up new possibilities for developing cultivars tolerant to acid soils. International collaboration, particularly with institutions like EMBRAPA in Brazil, will be important in accelerating Indonesia's efforts to utilize its abundant acid soil resources for sustainable agriculture.

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