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Aluminium Stress Tolerance in Legumes under Acidic Soils: Mechanisms and Methods – A Review

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ABSTRACT: Being one of the most abundant elements in earth's crust, Aluminium (Al) is ubiquitously present in the soil, mostly in unavailable forms at neutral or near neutral soil pH. However, under acidic soil conditions, when pH drops below 5, Al solubilizes into phytotoxic forms, adversely affecting root growth, vigor and productivity of plants, causing 25–80% yield reduction in cultivated crops. Legumes are an important component of human diet and an essential component of the ecosystem. Being highly sensitive to soil acidity, legumes are highly affected by Al toxicity, which is a major constraint for legumes production in acidic soils. Acidic soils predominate the tropical and subtropical regions of the world. In order to extend legume production in acidic soils, there arises a need to understand Al toxicity and develop suitable methods for combating Al toxicity stress. Thus, the present paper reviews Al toxicity-its nature and tolerance mechanisms, screening methods, genetics and breeding prospects in agricultural crops with special reference to legumes. Root growth inhibition is the first and most prominent indicator of Al toxicity, followed by several changes like altered cell division and DNA replication at root apex, severe oxidative stress, lipid peroxidation and callose accumulation at root tips. Among various mechanisms of Al toxicity tolerance, changes in rhizosphere pH and chelation of Al through exudation of organic acids are critical in combating the toxicity effects. Evaluation of plants under hydroponics culture based on root staining and root-regrowth parameters are the most preferred and reliable methods of screening. Improved technology-based phenotyping using seedling root architectural (SRA) traits are gaining importance pertaining to their higher precision and accuracy. Presence of wide range of genetic variability for Al tolerance has been revealed through various studies conducted in major legumes like *Phaseolus, Cicer, Lens* etc. Al tolerance loci have shown to be governed by both a simple (Lentil, pea, chickpea and pigeon pea) and complex (soybean) inheritance pattern, in a species dependent manner. QTLs specifying Al tolerance have been mapped in several crops including major legumes. Several important genes and pathways have been identified through various gene expression studies. In addition to genes like phosphoenolpyruvate carboxylase (PEPC), Citrate Synthase (CS), isocitrate dehydrogenase (ICDH), malate dehydrogenase (MDH) andion-transporters like voltage-dependent anion channel (VDAC), Al activated malate transporter (ALMT) and its homologues are the major genes found to be associated with malate/citrate mediated Al detoxification in legumes. This review will facilitate in further understanding the complex nature of Al toxicity tolerance in legumes and assist in development of varieties, suitable for acidic soil conditions through conventional breeding assisted by molecular and transgenic techniques.

Keywords: Al toxicity, legumes, root re-growth, organic acids, inheritance, mapping.

INTRODUCTION

Legumes particularly pulses are an essential component of human diet, contributing significant amounts of protein in addition to carbohydrates, and several vitamins and minerals. Through their unique property of fixing atmospheric nitrogenby the process of biological nitrogen fixation in symbiotic association with Rhizobium bacteria, legumes improve soil fertility and the functioning of ecosystems, thus also forming an important component of different cropping systems. With more than 78.3 million, ha of land planted to legumes, these species provide over 35% of the world's protein intake (Werner and Newton 2005). India is the largest producer of pulses in the world, with around 25% share in the global production, contributing around 19.3 million tonnes (ESI, 2015) but with a very low average productivity of 764 kg/ha (Pooniya *et al*. 2015). Acid soils, also known as ultisols or oxisols, classified by a pH of 5.5 or lower are widely distributed in the tropical and subtropical regions globally (Sade *et al*. 2016), also constituting about 16.7 % of the total geographical area of the Indian subcontinent (Maji *et al*. 2018). Deficiency of various nutrients and toxicity by metals like manganese (Mn), iron (Fe) and Al are prevalent in acid soils (Bose *et al*. 2015: Kochian *et al*. 2004; Gupta *et al*. 2013). Aluminium (Al), being one of the most abundant metals in the earth's crust is considered as the main abiotic stress causing 25–80% yield losses in crops cultivated on soils containing excessive aluminium (Singh *et al*., 2012). In acidic soils, when pH generally drops below 5, Al solubilizes into phytotoxic forms and causes root growth inhibition resulting in reduced vigour and productivity in crop plants. Thus, Al stress is one of the prime limitations of crop production in acidic soils.In fact, Al toxicity was in 67% of the world's acidic soils (Lin *et al*. 2012). Higher concentration of heavy metals like Al in soil reduces the activity of soil microorganisms, which simultaneously decreases the soil organic matter and leads to reduction in soil fertility (Yaman and Kumar, 2021). Legumes contribute significantly to the human diet, specially proving to be an important and cheap source of protein for the poor. Thus, there arises an increased need to identify new niches for legume production for increased food security while parallelly screening, understanding the mechanisms and finding new sources for Al stress tolerance in legumes, suitable for in Al-rich soils in order to bring more area under the production of legumes. This review elaborates Al toxicity – its nature and mechanisms as well as the breeding prospects with respect to legumes grown under acidic soils.

What is Aluminium toxicity?

Al, the third most abundant element after oxygen and silicon is ubiquitously present in the soil of the planet. Belonging to the non-essential group of plant nutrients, Al has beneficial effects only on a limited number of plant species (Bojórquez-Quintal *et al*. 2017). Most of the Al remains unavailable at near neutral soil pH in the form of insoluble alumina silicates or oxides, which does not usually exposed to plants (Kochian *et al*. 2004). However, as the soil pH reduces towards higher levels of acidity, Al converts into phytotoxic forms in the soil solution adversely affecting the growth and development of plant systems. Al reacts differently in soil as compared to other soluble metals because of its smaller ionic radius and higher ionic charge. The total Al concentration as well as the speciation of Al in soil relies on the pH (Fig. 1) and the chemical environment of the solution (Kisnieriené and Lapeikaité 2015).

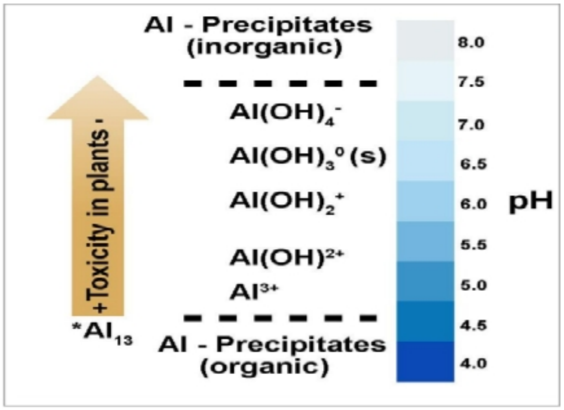

Fig. 1. Changes in the chemistry of Aluminium with change in soil pH (Bojórquez -Quintal *et al*. 2017).

How Al toxicity affect plants ?

Al toxicity affects plants in numerous ways, the most prominent effect being the prompt inhibition of root growth, occurring within hours or even minutes after exposure to Al^{3+} (Kochian *et al*., 2005), which is widely used as a biomarker to study Al toxicity. Studies on the root growth parameters i.e., cell division and elongation, revealed decreased mitotic activity when exposed to toxic concentration of Al in the root tips as observed in several species like wheat, maize and faba beans (Li *et al*. 2008; Frantzios *et al*., 2001). Further, observations revealed that Al induced change in cell division at the root apex and lateral roots resulted in increased cell wall rigidity by cross linking of pectins and reduced DNA replication by increasing rigidity of the double helix (Zhang *et al*., 2014; Eekhout *et al*., 2017). However, some other authors suggested that the primary mechanism resulting in inhibition of root growth is the inhibition of cell elongation (Ciamporova 2002; Zheng and Yang 2005).

Al toxicity has been known to induce a series of reactions, involving disruptions in the cellular redox homeostasis, leading to severe oxidative stress (Zheng and Yang 2005; Yamamoto *et al*. 2001). The generation of Reactive Oxygen Species (ROS) can cause oxidation of various cellular components leading to cell death. In addition, binding of Al to cell membranes causes rigidification (Jones and Kochian 1997), initiating a radical chain of reactions by metal ions most importantly iron that accelerates the process of lipid peroxidation (Yamamoto *et al*. 2003). Lipid peroxidation as induced by Al, has been observed in several legumes like pea (Yamamoto *et al*. 2001), soybean (Cakmak and Horst1991), greengram (Panda *et al*. 2003), lentil (Singh *et al*. 2016) and chickpea (Choudhary and Sharma 2014).Yamamoto e*t al.* (2001) observed that callose production, lipid peroxidation and Al accumulation had comparable distribution on the surface of the root apex and accompanied by inhibition of root growth in Al treated pea seedlings. The defensive system of plants is equipped with various enzymatic antioxidants that works to detoxify the ROS. Detection of ROS in pea root apex two hours after exposure to Al stress, further increased with exposure time (Yamamato *et al*. 2003).

In plants, the apoplast of the peripheral cells of roots is the primary and major site of Al accumulation (Guo *et al*., 2004; Liu *et al*., 2008) from which it is translocated to other sites. In the apoplast, the major binding site seems to be the pectin matrix (Schmohl and Horst 2000) as increased levels of pectin in response to Al stress has been reported in sensitive genotypes by several studies (Horst *et al*., 1999; Liu *et al*., 2006). This binding can lead to altered cell characteristics and enzymatic reactions, leading to root growth inhibition (Schmohl and Horst 2000). In pea, it was also observed that lignin content increased in the root apes treated with Al in a time dependent manner. Lignin got concentrated at the epidermal and outer cortex regions, where morphological changes, including rupture were observed (Matsumoto and Motoda 2012).

Al induced stress has been known to result in several nutritional imbalances in different plant species. Phosphorus is an essential macro-element for the growth of legumes. Phosphorus is essential in plant metabolism, which plays an important role in many plant functions including energy storage and transfer, photosynthesis, transformation of sugars and starches, movement of nutrients in the plant and the transfer of genetic traits from one generation to another (Goud *et al.*, 2021). Aluminium toxicity leads to phosphorus (P) deficiency in plants due to its tendency to bind with P in a less available and insoluble form in soil and plant roots. Al-tolerant soybean genotypes expressed higher degree of Phosphorus efficiency (Liao *et al*., 2006; Liang *et al*., 2013). Al also interferes with the uptake of macronutrients like Ca and Mg and micronutrients like Mn and Zn as observed by higher uptake in tolerant genotypes in relation to sensitive ones (Mariano and Keltjens 2005; Silva *et al*., 2010).

Al induced Callose (1,3-b-d- glucan) formation in root tips as observed in several studies (Budikova and Durcekova 2004; Jones *et al*., 2006; Poschenrieder, 1995), is widely used as an excellent bioindicator for Al tolerance (Bhuja *et al*. 2004; Tahara *et al*. 2005; Meriga *et al*. 2003; Hirano, 2004). A negative correlation exists between root elongation and callose formation in response to Al exposure (Naggy *et al*., 2004), sensitive genotypes showing a tendency of higher callose accumulation internally (Silva *et al*., 2010; Silva *et al*. 2011). Such studies have suggested callose accumulation as a better and more sensitive indicator of Al tolerance than root inhibition (Tahara *et al.*, 2005).

Mechanisms of Al toxicity tolerance in plants. Plants have evolved various mechanisms of tolerance to counteract the toxic effects of Al which can be divided into two forms: 1. mechanisms of exclusion or resistance to Al (which avoids or reduces the entrance of Al to the cell) 2 mechanisms of internal tolerance (compartmentalization of Al in vacuoles or stabilization of Al in order to inhibit its toxicity).

MECHANISMS OF EXCLUSION

Alteration in the Rhizosphere pH

A small increase in the rhizosphere's pH can reduce the solubility, activity, toxicity and content of Al in plants through exclusion of the metal in the root apoplast (Yang *et al*. 2011). In Arabidopsis, alr-104 mutant which are Al-resistant and other such plant species use the H^+ and NH_4^+ influx and the efflux of OA in the root apex to increase the apoplastic pH in the presence of Al (Houman *et al*. 2009; Bose *et al*. 2010; Wang *et al*. 2015). Al mobility is known to decrease with increase in pH (Kochian 1995). In pea, the final solution pH under hydroponics correlated with Al tolerance of pea genotypes (Kichigina *et al*. 2017). Klimashevsky *et al*. (1972) reported similar results, where Al tolerant pea genotype Success had higher pH in the nutrient solution as compared to the Al sensitive genotype, Tulunsky Green.

Modifications in Cell Wall Composition and Plasma Membrane Properties

The target site of Al toxicity and exclusion is the root cell wall, which is also the main binding site for Al(Horst *et al*. 2010; Yang *et al*. 2011; Kopittke *et al*. 2015; Liu *et al*. 2016). The pectin content in the cell wall and its degree of methylation is associated with the differences in resistance to Al (Eticha *et al*., 2005; Yang *et al*., 2011). Al exposure led to increased pectin methylesterase (PME) activity in the root tip of soybean seedlings (Cai *et al*., 2011) and increased accumulation of soluble de-esterified pectins in the root cap has been observed during the release of root border cells (RBCs) (Driouich *et al*., 2007) in response to Al toxicity. Plasma membrane's lipid composition plays an important role in Al-tolerance by creating a negative charge on the surface of the plasma membrane by the phospholipids and increasing the sensitivity to Al due to the metal's binding with the plasma membrane (Wagatsuma *et al*. 2015).

Release of Chelating Molecules. The most widely described Al exclusion mechanism is the exudation of organic acids from the root of plants (Kochian *et al*. 2015) in a species dependent manner (Brunner and Sperisen 2013; Schroeder *et al*. 2013). Plant roots secrete organic anions like malate, citrate and oxalate and chelates Al in a non-toxic Al-organic acid complex, which protects the root apex and promotes its growth. Being a component of the TCA cycle, malate and citrate are ubiquitous in all plant cells, while oxalate plays an important role in the regulation of Ca and metal detoxification (Brunner and Sperisen, 2013). In pea, acetate, pyruvate, citrate, pyroglutamate and succinate were exudated in response to Al stress and the root Al content was found to show negative correlation with pyroglutamate and the total organic acids exudated in response to Al (Kichigina *et al*. 2017). In soybean genotypes treated with Al, citrate and malate efflux increased in all genotypes initially, but only efflux of citrate in the Al tolerant genotypes was observed for an extended period along with lesser Al accumulation in the root tips as compared to the sensitive genotypes (Silva *et al*. 2001). Similarly, exudation of citrate was associated with increased tolerance to Al in chickpea genotypes (Sharma *et al*. 2015). In lentil, both malate and citrate exudation were significantly higher in the genotypes which were found to be resistant to Al toxicity, as compared to the sensitive ones and ILWL-15, a wild genotype of lentil showed the highest exudation of organic acids. Overall, the exudation of malic acid in the genotypes was relatively higher than citric acid exudation. The upregulation of genes involved in organic acid synthesis like citrate synthase (CS) and phosphoenolpyruvate carboxylase (PEPC)was believed to be responsible for conversion of different metabolites like oxaloacetate or phosphoenol pyruvate into malate or citrate (Singh *et al*., 2021). Thus, numerous studies conducted in different species of cultivable plants concludes that exudation of organic acids confers resistance to Al (Delhaize *et al*., 1993; Brunner and Sperisen 2013; Yang *et al*., 2013).

CAP Type Structures and Border Cells in the Radical Apex. Mucilage rich in polysaccharides, produced and exudated by the root cap and border cells of various plant species binds and detoxifies the metallic cations (Horst *et al*., 1982; Cai *et al*., 2013; Kumpf and Nowack 2015). In Al resistant genotypes of barley, bean, soybean and castor, the immobilization and detoxification of Al with the mucilage produced by the root cap and border cells leads to the exclusion of the metal (Miyasaka and Hawes 2001; Zhu *et al*., 2003; Cai *et al*., 2013; Alves Silva *et al*., 2014).

MECHANISMS OF INTERNAL TOLERANCE

Chelation mechanisms in the Cytosol. The chelation of Al with organic acid and the consequent sequestration into the vacuole is the mechanism behind internal detoxification of Al. Mostly, the plants that are tolerant to Al use organic acids for the sequestration of Al in the cytosol of the root cells followed by remobilization or translocation of Al toward the shoots. Oxalate, the predominant ligand in tea root cytosol, forms Al-oxalate compounds (Morita *et al*., 2004) and is translocated to the shoots in the form of Al-citrate or Al-malate (Morita *et al*. 2004, 2008). Buckwheat also shows similar mechanisms (Wang *et al*., 2015). In snapbean, Al stress leads to reduced concentration of citric, malonic, malic, glycolic, fumaric, and acetic acids in the roots with subsequent increase of the organic acid concentrations in stem exudates of Al sensitive plants than the Al tolerant cultivars. It indicated the higher Al-chelation potential of Al tolerant cultivars for Al detoxification (Lee and Foy, 1986) while in soybean; Al was internalized in cells of primary roots in the form of Al-citrate complexes (Silva *et al*., 2001).

Aluminium Transporters in the Plasma. Transport proteins are important for facilitating transportation through biological membranes. In plants, Al transportation through the vacuole tonoplast and plasma membrane has not been widely studied. Although, it was reported that the ABC transporters, transporters binding to ATP, AtABCI16/AtALS3, AtABCI17/AtSATR1/AtALS1 and OsALS1, and Nrat1 (Nramp Family) transporters are involved in the detoxification of Al in plants (Xia *et al*., 2010; Hwang *et al*., 2016). AtASL3, which is a type of ABC transporter located in the plasma membrane, which distributes Al inside the plant far from the root apex by transporting Al in direct or bound forms (Kang *et al*. 2011; Ryan *et al*., 2011). Although limited number of studies has been carried out in grain legumes, an Al-activated malate transporter (ALMT) has been reported to be associated with malate mediate Al detoxification in various legumes like *Medicago truncatula* (Chandran *et al*., 2008) and soybean (You *et al*., 2011; Liu *et al*., 2016). Similarly, MATE transporter involved in the transport of citrate or malate that facilitates the chelation of Al ions was identified in Chickpea (Zhang *et al*. 2020).

SCREENING METHODS FOR Al TOLERANCE

Genetic improvement of crops for Al toxicity tolerance has been aided by the availability of different screening methods, most of which are laboratory and greenhouse-based techniques suitable to be used in the early growth stages of plants. The experimental conditions used for screening germplasms need to be optimized. Field based techniques, although in use are more laborious, affected by a range of factors and difficult to screen.


(a) Screening lentil for Al tolerance under hydroponics.

(b) Root re-growth after Hematoxylin staining of lentil roots.

Fig. 2.

The most common screening method for Al tolerance is the nutrient solution culture under hydroponics (Fig. 2), which provides an easy non-destructive way to access plant root system while keeping various factors like treatment conditions, nutrient availability and pH under control, which are executed in laboratory or Greenhouse conditions (Carver and Ownby, 1995). Al tolerance is accessed mainly through staining roots exposed to Al using suitable dye like hematoxylin (Polle *et al*., 1978; Minella and Sorrells 1992; Bona *et al*., 1991; Tang *et al*. 2000) and eriochrome cyanine R (Anioł, 1995; Ma *et al*., 1997; Wang *et al*., 2006). The mechanism being the formation of coloured complexes between the dye and cations like Al (Kichigina *et al*., 2017). The other method involves the root length measurements and root re-growth/ elongation after exposure to toxic concentrations of Al, which is widely used as a biomarker to phenotype Al tolerance for genetic and molecular studies. It is also efficient to identify genotypes having superior alleles for Al tolerance (Hede *et al*., 2002).

Measurements of shoot and root growth in terms of length and total dry weight in long-term cultures provides a suitable method to differentiate Al-tolerant and sensitive genotypes. Growth response method, both short term (7 days) and long term (65 days) has been used in lentil where different parameters like seedling root length, shoot length and dry weight were estimated at the end of the growth period as a measure to evaluate the genotypes for Al tolerance (Singh *et al*., 2014). With advances in technology, seedling root architectural (SRA) traits are being analysed using root scanner (e.g., Epson Perfection V700, Long Beach, CA, USA) which improves phenotyping accuracy and precision while minimising human error (Singh *et al*. 2021). Various studies have suggested Callose accumulation in roots as an important indicator for detecting Al toxicity which is mediated by Al^{3+}exposure even under short-term period which is used to differentiate tolerant (less deposition) and sensitive genotypes in soybean and lentil (Wissemeier *et al*., 1987; Yang *et al*., 2000; Singh *et al*., 2018). Some of the widely used methods for screening Al tolerance in various legumes involves determination of ROS accumulation in cells using dihydroethidium (DHE) in pea (Kobayashi *et al*., 2004; Matsumato and Motada 2012), exudation of superoxide anion in chickpea (Sharma *et al*., 2015), estimation of enzymatic activities of SOD, APX, GPX and CAT in lentil (Singh *et al*., 2016), analysis of cell wall pectin in pea (Li *et al*., 2017), determination of lignin contentin pea (Matsumato and Motoda 2012), lipid peroxidation in soybean and chickpea (Zhang *et al*., 2007; Sharma *et al*., 2015), nutrient imbalances in pea (Kichigina *et al*., 2017) and Al induced exudation of organic acids in snapbean, soybean and pea (Lee and Foy 2008; Huang *et al*., 2017; Kichigina *et al*., 2017).

GENETICSOF Al TOLERANCE

Genetic variation and inheritance of Al tolerance loci. Availability of adequate genetic variability is a prerequisite for any crop improvement programme. Wide range of genetic variability has been detected for Al tolerance in various legumes from both cultivated and wild sources using different screening methods. In the genus *Phaseolus*, new genotypic sources from wild relatives like *Phaseolus coccineus* and Andean common bean genotypes were found to have outstanding performance in response to Al stress (Butare *et al*., 2011). Novel sources of Al toxicity were identified in wild *Cicer* germplasm (*Cicer reticulatum* and *Cicer echinospermum*) collected from Turkey (Vance *et al.,* 2021). Similarly, in lentil, large number of genotypes belonging to all the subspecies of the Genus *Lens* collected from all over the world, were screened through a combination of morphological, physiological, biochemical and molecular techniques. This study revealed presence of significant amount of genetic diversity among the genotypes, which led to the identification of several promising genotypes having high levels of Al toxicity tolerance (Singh *et al.,* 2016). In lentil, highly Al resistant genotypes and highly Al sensitive genotypes were identified from a collection of 440 lentil genotypes, that included landraces, wild accessions, breeding lines and exotic lines based on seedling root architectural (SRA) traits (Singh *et al*., 2021). Thus, the wild relatives of cultivated crops may provide a reservoir of high variability and important genes conferring resistance to Al stress which demands extensive exploration and evaluation programmes to identify these important resources.

Studies on the inheritance pattern of Al tolerance loci are important to design a suitable breeding programme for developing crops with Al tolerance or transferring the trait to other desirable genotypes through crossing programmes. Previous studies conducted in legumes has suggested Al tolerance to be a simply inherited trait (Singh *et al.,* 2018), controlled by one or few genes, whereas in cereals complex inheritance has been observed in case of rice (Ma *et al.*, 2002), wheat (Zhou *et al*., 2007) and maize (Guimaras *et al*., 2014). In chickpea, analysis of F_1, F_2, F_3 and backcross generations from parents contrasting for Al tolerance indicated dominance of Al tolerance over sensitivity, which fitted with typical 3:1 ratio in F_2 population, and the data from backcross and F_3 generations also confirmed Al tolerance to have monogenic dominant inheritance in chickpea (Singh *et al*., 2011). Similarly, in pea, a 3:1 segregation ratio of tolerance vs sensitivity obtained in F_2 and backcross generations suggested Al tolerance to be monogenic and dominant in inheritance (Singh and Choudhary 2009). Genetic studies conducted in pigeon pea for Al tolerance revealed 15:1 and 7:8:1 ratio in F_2 and F_3 generations respectively, which indicated Al tolerance to be under the influence of two dominant genes (Singh *et al*., 2011), while in lentil, presence of a single dominant gene with monogenic inheritance for Al tolerance loci was detected (Singh *et al*., 2014). Soybean shows a deviation from the simple inheritance, by showing a complex quantitative pattern of inheritance for Al tolerance loci involving polygenes. A study conducted by Qi *et al*. (2008) on mapping QTLs for Al tolerance revealed, Al tolerance to be under the control of two major genes (h2mg= 33.05%) and polygenes (h2pg= 52.73).

QTLs and gene expression associated with Al tolerance. Presence of high amount of genetic variability for Al tolerance suggests that different plant species evolved special mechanisms to survive Al toxicity. Various studies conducted in order to understand the nature of genetic control of Al stress tolerance led to discovery of several genes homologous to glutathione-S-transferase (GST) and phenylalanine ammonia lyase (PAL genes) in tobacco (Ezaki *et al.*, 1995), Sali3-2 and Sali5-4 in soybean (Rhagland and Soliman 1997), ZmaI in maize (Menossi *et al*., 1999), Mtn29 pEARLI8 and pEARLI1, pEARLI2, pEARLI4, and pEARLI5 in *Arabidopsis thaliana* (Richards *et al*., 1998) and phosphatidylserine synthase in wheat (Delhaize *et al*., 1999) which were upregulated during Al phytotoxicity. In soybean, five QTLs belonging to different linkage groups mostly derived from Al tolerant plant PI416937 conditioning root extension under high Al stress conditions were identified using RFLP markers (Bianchi-Hall *et al*., 2000), while Wang *et al*. (2019) identified five QTLs explaining 39.65% of Relative root elongation (RRE) and apical Al content (AAC) using RAD sequencing. Many workers used gene expression studies and identified Al tolerance genes in soybean that includes phosphoenol pyruvate carboxylase (PEPC), homolog of translationally controlled tumour proteins (TCTPs), inosine-5’¢-monophosphate dehydrogenases (IMPDHs) (Ermolayev *et al*., 2003), aluminum-induced 3-2 (Sali3- 2), aluminum-induced 5-4a (Sali 4-5a) (Ragland and Solimon 1997) and Cys2His2 and ADR6 transcription activators (Duressa *et al*., 2010).

An Al activated malate transporter (ALMT) has been found to be associated with malate mediated Al detoxification in various legumes like *Medicago truncatula* (Chandran *et al.,* 2009), soybean (You *et al*. 2011, Liu *et al*., 2016). Similarly, 56 annotated MATE transporter genes involved in the transport of citrate or malate that facilitates the chelation of Al ions were reported through genome wide studies in the *Cicer* genome (Zhang *et al*. 2020). In diploid Alfalfa, four RFLP markers were found to be associated with Al tolerance (Sledge *et al*., 2002). Additionally, three putative QTLs on linkage groups LGI, LGII and LG III were identified using EST-SSR based markers and a candidate gene associated with malate release was mapped near one of the QTLs on LGI (Narasimhamoorthy *et al*., 2007). In polyploid Alfalfa, QTLs for Al tolerance were identified on linkage groups (LG1, LG4, and LG7 explaining 20.8, 15.2, and 21.7% of the variation respectively, using interval mapping. In common bean, QTL analysis using SNPs identified 8 QTLs explaining 7.6 to 14.7% of Al resistance and a candidate gene encoding a malate transporter was mapped within QTL RL7.1 on chromosome Pv07 (Njobvu *et al.,* 2020). Similarly, 2 major QTLs, one for fluorescent signals associated with callose accumulation and another for root re-growth under Al toxicity stress were identified explaining 52% and 11% of phenotypic variation respectively, were identified in lentil (Singh *et al*., 2018). Expression studies conducted in lentil to understand the differential exclusion mechanism responsible for Al tolerance through exudation of organic acids revealed upregulation of Citrate Synthase (CS) and phosphoenol pyruvate carboxylase (PEPC), while down regulation of isocitrate dehydrogenase (ICDH) and malate dehydrogenase (MDH) was observed in the tolerant genotypes. Further upregulation of ion-transporters like ALMT-1, MATE-a,b,c and voltage-dependent anion channel (VDAC)was observed in resistant genotypes, which suggests their involvement in extrusion of citrate and malate from the exposed roots. Down regulation or reduced expression of these genes was observed in the sensitive genotypes (Singh *et al*., 2021). The QTLs and candidate genes identified through these studies will facilitatein developing suitable Al tolerant cultivars in legumes through marker assisted breeding programmes.

Development of Al tolerant varieties through breeding and biotechnology. The best alternative for combating Al-toxicity problem is the use of tolerant varieties of crops rather than the usage of various traditional methods like liming. For development of Al-tolerant crop varieties, mostly cultivars growing in highly acidic soils of the world are selected and developed as potent varieties (Hede *et al*., 2001; Stodart *et al*., 2007; Caniato *et al*., 2011). Natural selection and adaptation or selection by early agriculturalists in these regions being the most likely reasons for such associations (Stodart *et al*., 2007; Caniato *et al*., 2011). Another method of creating and increasing genetic variability for Al-tolerance is through mutation treatment. Identifying quantitative trait loci (QTLs) that confers tolerance to Al is another important aspect in development of Al tolerant varieties. Such QTLs have been identified in many legumes as already discussed. Molecular markers associated with these QTLs will be helpful in developing Al tolerant varieties through various marker-assisted breeding programmes.

The production of transgenic varieties having tolerance to Al is considered as an important constituent of crop management strategies to increase crop production in acidic soils, also protecting forests around strongly acidified industrial regions (Roy *et al*., 2011). Varieties tolerant to Al have been derived from somaclonal variation under in-vitro condition (Foy *et al*., 1993; Duncan *et al*., 1995; Jan *et al*., 1997; Sibov *et al*., 1999). It shows the usefulness of in-vitro techniques for identification of tolerant somaclonal variants as well as genetic engineering methods for obtaining genotypes with enhanced aluminium tolerance (Samac and Tesfaye 2003; Singh *et al*., 2011). Following the first cloning of the TaALMT1 gene, a malate transporter activated by Al (TaALMT1) in wheat (Sasaki *et al*., 2004), it was transferred successfully into an Al-sensitive barley cultivar, providing Al resistance (Delhaize *et al.,* 2004); however, its use in conferring Al resistance in Al-sensitive wheat cultivars remains unknown. The success of this experiment shows the potential of using transgenic techniques for developing transgenic Al stress resistant varieties in future. Over expression of genes controlling the biosynthetic pathways of the enzymes involved in biosynthesis of organic acids like malate, citrate etc. in transgenic plants may help in developing varieties tolerant to Al toxicity stress through the tools of biotechnology.

CONCLUSION AND FUTURE SCOPE

Al toxicity is one of the prime limitations of crop production in acidic soils, especially at pH below 5.0 where Al becomes phytotoxic and inhibits plant root growth. In addition to its adverse effect in the plant root system, Al also leads to disruptions in cellular redox homeostasis, oxidative stress, increased ROS production, lipid peroxidation and nutrient imbalances. Al induced accumulation of callose in the root tips and inhibition of root growth are used as important biomarkers for screening Al tolerance in plants cultured under hydroponics. Plants have evolved numerous mechanisms to tolerate Al toxicity stress, most importantly the secretion of organic acids like malate, citrate, oxalate etc., which chelates the Al ions externally in the rhizosphere, or internally in the cytosol of the plants, thus preventing its toxic effects on the plants. High level of genetic variability has been observed for Al tolerance in legumes and QTLs identified for Al tolerance in major legumes may assist in developing efficient Al tolerant varieties suitable to be grown in acidic soils through marker assisted improvement programmes. Expression studies have identified various stress related genes to be upregulated during Al stress conditions and in addition to several others ALMT, an Al induced malate transporter has been reported to mediate Al detoxification in legumes. These genes may be transferred to related species or from wild to cultivated ones through transgenics technology for development of Al resistant varieties. Since relatively less research has been conducted in legumes with respect to Al stress tolerance as compared to cereals, extensive studies need to be done to identify new sources of variation. In addition, understanding the inheritance of Al tolerance loci in depth and identification of the genes and pathways involved so that efficient breeding methods assisted with biotechnological tools may facilitate the development of suitable Al tolerant/resistant cultivars of legumes in near future.

Conflict of Interest. None.

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