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Acidic Soil Tolerance in Legume Crops: Mechanisms and Screening Methods: A Review

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Abstract

Legumes are a vital food source next to cereals. Legumes play an important role in the effective management of fertilizers and improve soil fertility, thereby sustaining agriculture. However, the productivity of legumes is significantly affected by acidic soils, which are re prevalent in many agricultural areas. Acidic soil tolerance in legume crops is a complex trait influenced by various mechanisms, including root adaptations, nutrient uptake efficiency, and tolerance to toxic elements. Understanding these mechanisms and developing effective screening methods are essential for breeding and selecting acid soil tolerant legume genotypes/varieties. This review paper provides an overview of the mechanisms associated with acidic soil tolerance in legume crops and examines the current screening methods used for identifying tolerant genotypes.

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Introduction

Legumes, which are an essential source of plant proteins and dietary fiber, are the most valued diet for humans after cereals. It plays a crucial role in global agriculture, providing essential nutrients, improving soil fertility, and contributing to sustainable cropping systems. The major food legumes consumed worldwide are pea (*Pisum sativum* L.), chickpea (*Cicer arietinum* L.), common bean (*Phaseolus vulgaris* L.), lentil (*Lens culinaris* Medik.), mung bean/green gram (*Vigna radiata* L.), urdbean/black gram (*Vigna mungo* L.), and cowpea (*Vigna unguiculata* (L.) Walp.), and the major oilseed legumes include peanut (*Arachis hypogaea* L.) and soybean (*Glycine max* L.) (Maphosa and Jideani, 2017). Due to their high nutritional value, legumes are ranked second after cereals. They are rich in protein (20–45%), carbohydrates (60%), dietary fiber (5–37%), and mineral matter (calcium, iron, potassium, phosphorus, copper, and zinc) with no cholesterol and low fat (Iqbal *et al.*, 2006). Legumes produce 5–7 times less greenhouse gases than other crops, allow carbon sequestration, improve soil fertility, and can be utilized in the form of green manure (Stagnari *et al.*, 2017). They are good for intercropping or relay inter cropping. However, legume productivity is severely constrained by Al toxicity.

Apart from other effects of Al toxicity, it also causes a fatal effect on legume/rhizobia symbiosis and ultimately on the nitrogen-fixation process. Al toxicity affects various stratagems of nitrogen fixation, either being root hair formation, rhizobial population, nitrogen metabolism, nitrogenase activity, or uptake of hydrogenases (Jaiswal *et al.*, 2018). Around 87% of the area under pulses is rainfed and predominantly restricted to marginal and submarginal soils, and abiotic stressors

are the key impediments to attaining the yield potential. Losses in pulses owing to biotic and abiotic stressors range from 30% to 100%, depending on the degree of the stress (Rana *et al.*, 2016). Due to the restricted availability of breeding lines/materials obtained from crossings between landraces and wild progenitors, grain legume breeding is time expensive and results in relatively poor yield gains when compared to cereal crops (Abdelrahman *et al.*, 2017).

Acid soils defined as soils with a pH of 5.5 or lower, are one of the most major challenges to agricultural production globally. Approximately 30% of the world's total land area consists of acid soils, and as much as 50% of the world's potentially arable lands are acidic (Von and Mutert, 1995). Alimunium, which constitutes approximately 7% of the Earth's mass, is easily released in water with the change of pH, thereby inhibiting plant growth, including root growth and its function (Kochian *et al.*, 2005) Al generally existing as Al(OH)3, which is insoluble in soils, dissolves in water as Al3+ under acidic conditions (pH < 4.5) and is released as Al(OH)4- under alkaline conditions. The Al3+ easily reacts with phosphoric acid and then it causes phosphorus deficiency on plants with the formation of insoluble aluminum phosphate in soils (Matsumoto, 200). Other harmful elements, such as Fe and Mn, also inhibit plant growth. Therefore, acid soils affect plant growth through indirect factors like dissolution of harmful elements, indicating that the understanding of the effect of acid soils on plant growth in terms of not only soil pH but also harmful elements is important for successful re-vegetation.

Al alters plant functioning at very early stages. Toxic Al ions mostly target root tips and inhibit cell elongation and division in this zone. The latter results in root arresting supplemented by decreased water and nutrient uptake. Root tips become swollen and damaged. Sometimes, root lesions also occur. Plants have numerous Al-binding sites, which include cell walls, plasma membranes, cytoskeleton, and nucleus. Al expeditiously amasses in the plasma membrane and symplasm and affects various cellular processes (Panda *et al.*, 2009). It interacts with lipids inducing lipid peroxidation; causes an increase in reactive oxygen free radicals; disrupts cytoplasmic Ca2+ homeostasis; accumulates callose in the plasmodesmata; and disrupts cytoskeleton (Panda *et al.*, 2009). These changes ultimately affect several signalling cascades and processes operating inside the cell directly or indirectly. Al toxicity also causes accumulation of certain metabolites, induces behavioural changes in many enzymes, lowers P availability to plants, increases plant's susceptibility towards drought stress, and causes lodging (Arunakumara *et al.*, 2013).

Genetic diversity in Al tolerance among legume crops

The use of tolerant crop varieties is considered to be the best complement to non-genetic management option for combating Al-toxicity problem (Rao *et al.*, 1993). There are enormous variations in the tolerance of various legumes to Al stress. Plant height in pigeon pea was significantly reduced above 20 ppm Al, according to Narayanan and Sayamala (1989), whereas in soybean, Sapra *et al.*, (1982) realized that even 8 ppm Al was sufficient to reduce plant height. There was a drop in leaf number and size in pigeon pea only at very extreme concentrations of 40 and 60 ppm Al. Singh *et al.*, (2012) reported that root regrowth after hematoxylin staining, root and shoot lengths and their dry weights, and pods/plant reduced notably at 148 µm Al concentration. Dessureaux (1969) testified that at 20 ppm, leaf size was considerably condensed in alfalfa seedlings. The tap root length was considerably impeded at 40 ppm Al, although at 10 ppm, root length was stimulated. Klimashevskii *et al.*, (1970) noted in field pea plants that Al-tolerant cultivar exhibited only 32% diminution in growth at 11 mg Al3+/L; however, this concentration was totally injurious to Al-sensitive one. Root elongation was dwindled by approximately 50% under 9.3 mM AlCl3 mM/m3 in the rooting medium in the case of faba bean (Grauer and Horst, 1990). On the other hand, root elongation was wholly inhibited by 100mM/m3 AlCl3 in case of field pea (Matsumoto, 1991). The level of 20 ppm Al separated sensitive from tolerant chickpea genotypes via hematoxylin staining and root regrowth under short-term Al exposure (Singh *et al.*, 2011). However, at a level of 5 ppm Al3+, chickpea shoot dry weight was decreased by 70% in sensitive cultivars while intolerant cultivars decreased only by 27% (Rai, 1991). Al is mostly accumulated in the root apex of crop plants including Fabaceae. Al accumulation in these food legumes influences plant growth as well as yield. This inhibition of growth caused due to Al in lentil and mung bean cells was found to be well associated with the deposition of callose (Singh *et al.*, 2016).

Indications of Al toxicity in Legumes

Aluminum can quickly inhibit cell division, damage cell structure, diminish water as well as nutrient uptake, and hinder root elongation in leguminous plants (Arunakumara *et al.*, 2013). The influence of Al stress is

more prominent on roots. The most visible symptom of Al stress is root growth inhibition. The influenced roots become short, stubby, and lateral roots converting into peg-like or weaken to grow, and thus the entire root systems stop elongating and acquire brownish coloration as reported in pea plants (Singh and Choudhary, 2010). Shoot growth is often considered a secondary perceptible indication of Al noxiousness and often similar to deficits of phosphorus, calcium, magnesium, and iron (Foy, 1984). Generally, the plant canopy of Al-toxic plants surfaces as phosphorus becomes deficient. This imitates Al displacement of the plant's phosphorus metabolic process. Foliar symptoms resembling phosphorus deficiency have been reported in legumes like chlorosis in soybean (Foy *et al.,* 1973) and purple coloration in leaves and stems of lentil (Singh *et al.,* 2012). The inhibition of root elongation due to Al toxicity has been highly utilized as an attribute for the assessment of Al-tolerant cultivars in lentil (Singh *et al.,* 2021).

Various mechanisms triggered the decline of root growth, nutrient deficiencies, and yield damages (Kochian, 1995). Under Al treatment, activities of various antioxidant enzymes like superoxide dismutase (SOD), ascorbate peroxidase (APX), and guaiacol peroxidase (GPX) also increased in legumes (Arunakumara *et al.,* 2013). Al stress caused an increase in callose and reactive oxygen species (ROS) production in the roots of lentil and mung bean (Singh *et al.,* 2016). Production of ROS promotes inhibition of root elongation triggered by Al (Wang *et al.,* 2019). Reports on Al toxicity in legumes reflecting species type, treatment levels, and duration, together with the effects on plants, are listed in Table 1.

Mechanisms of Al tolerance in legume crops

Several mechanisms contribute to acid soil tolerance in legume crops. These mechanisms can be classified into exclusion (apoplast) mechanism externally and tolerance (symplast) mechanism internally (Kochian, 1995). In respect of exclusion mechanism, secretion of organic acids and rise of rhizospheric pH supply Al tolerance in Fabaceae. Al exclusion from the root zone was found to be the chief mechanism in case of pea plants (Kichigina *et al.,* 2017). Detoxification of Al externally by the exudation of organic acids such as malate and citrate seems to be another mechanism for Al tolerance in food legumes (Miyasaka *et al.,* 1991; Yang *et al.,* 2000). Citrate and malate were released from roots of Al-tolerant cultivars and wild accession of lentil (Singh *et al.,* 2016) and soybean (Yang *et al.,* 2000). Miyasaka *et al.,* (1991) stated that Al-tolerant snap bean cultivar grown in the presence of Al secreted 70 times more citrate in the presence of Al, whereas Al-sensitive cultivar secreted it up to 10 times only. In internal tolerance mechanism, Al ions absorbed by cells are accumulated and chelating of Al takes place in the cytosol. This occurs with the help of organic acids, Al-binding proteins, localization of Al into the vacuole, and induction of protein synthesis that chelates Al in the symplast. Genetic factors play crucial role in determining the plant's ability to adapt to acidic conditions (Foy, 1998). Crop varieties with inherent acid tolerance traits, such as aluminum exclusion, aluminum detoxification, and organic acid secretion, exhibit better performance on acid soils. Physiological processes, including root development, nutrient uptake, pH regulation, and antioxidant defense systems, also play a significant role in acid soil tolerance (Singh, 2000).

Screening methods for acidic soil tolerance

Screening and selection of acidic soil tolerant legume genotypes are integral to breeding programs aimed at developing improved varieties. Various screening methods facilitate the identification of tolerant genotypes based on their performance under acidic soil conditions. The screening methods must be potent enough to distinguish the genotypes and constitute the focused production environment. The preliminary screening pursuits are typically accomplished on seedlings under commanded conditions with controlled Al treatment, and the prominence is provided to the phenotype tolerance to select tolerant genotypes.

Different screening methods have been used to evaluate Al tolerance: nutrient solution culture (Baier *et al.,* 1996), soil bioassays (Stolen and Andersen, 1978; Ring *et al.,* 1993), cell and tissue culture (Conner and Meredith, 1985) and field evaluations (Johnson *et al.,* 1997). Laboratory- and greenhouse-based techniques for screening for Al tolerance are widely used because they are quick, highly accurate, nondestructive, and can be applied at early developmental plant stages. Field-based techniques are more laborious (Carver and Ownby, 1995). Comparative studies of screening methods for tolerance towards Al toxicity have been conducted in pigeon pea (Choudhary *et al.,* 2011; Singh *et al.,* 2011), chickpea (Singh *et al.,* 2011), lentil (Singh *et al.,* 2012, 2016, 2021), mung bean (Singh *et al.,* 2015), urdbean (Singh *et al.,* 2015), pea (Singh *et al.,* 2007), and soybean (Villagarcia *et al.,* 2001) based on short- and long-term techniques.

Long-Term Screening Techniques

Soil Culture

Soil bioassays have a distinct advantage over nutrient solution culture when Al tolerance may be influenced by soil dependent external factors (Ring *et al.,* 1993). Evaluation of crop plants is usually conducted in Al toxic fields as this is the most direct screening method to measure agronomic traits and yield components. Selection on acidic soil is an intermediary phase earlier to field testing to assess genotypes under an environment closer to the field condition. The use of soil media has received less attention than solution media for Al tolerance evaluation, and relatively few examples of its use can be found in the literature. Overall parameters and traits associated with aluminum toxicity have been summarized in Fig. 1.

Nutrient Solution Culture

Solution culture is the most common screening medium for Al tolerance which provides easy access to the root system, strict control over nutrient availability and pH, and non-destructive measurements of tolerance (Carver and Ownby, 1995). Solution culture technique is based on the inhibition of root growth under Al toxic conditions. In solution culture technique without staining, ratio of root growth in the presence of Al to its absence is determined. This technique is repeatable, non-destructive, rapid, cost effective, and independent of soil nutritional factors. Moreover, a huge quantity of plants can be accommodated in a brief period of time. However, it is not effective for the evaluation of Al tolerance in vegetatively propagated plants and at adult plant stages. Al toxicity also causes morphological damage to plant parts. Therefore, many root and shoot based morphological features are used for the evaluation of Al tolerance in legumes. These include traits like relative root elongation, root regrowth, root and shoot length and their dry weights, and root system architecture.

Sand Culture

Acidic soils with toxic amounts of exchangeable Al and sand assays have been exploited to detect tolerance in plants based on the growth of crop plants. However, results of sand assay were comparable with solution culture assay and more closely reflect Al tolerance in the field. However, the major demerit of this technique is that plants are exposed two times a day, firstly with an acidic Al solution and secondly to an acidic nutrient solution. In sand culture, Al and nutrients are supplied in solution form. This is because sand is nearly inert, and the dose of Al applied to plants can be controlled and replicated with precision. Previous results showed that sand culture provides more accurate results. In a study on pigeon pea, where the hydroponic and sand assays were compared for Al tolerance study, it was found that both the studies consistently differentiated tolerant and sensitive genotypes.

These two approaches interrelated well and were comparable over time and place (Choudhary *et al.*, 2011). In contrast, the results of sand culture were not well correlated with solution culture as per Villagarcia *et al.,* (2001). They observed that sand culture was required in ten times higher proportion to inhibit root elongation as compared to the hydroponic system. Grauer and Horst (1990) described a weak association among Al tolerance of 31 soybean genotypes in solution and sand culture. However, the precise basis for greater Al concentration in sand culture is still uncertain.

Root Growth method

The root growth method considers two Al tolerance parameters: root growth (RG) and a root tolerance index (RTI) (Baier *et al.*, 1995). The RG parameter is measured root growth under Al stress while RTI is root growth under Al stress compared to root growth without Al stress. A low-ionic-strength nutrient solution combined with a low Al concentration is used, as evidence suggests that Al tolerance studies should be conducted using solutions containing ionic strength and Al activity approximating soil composition. Relative root length is described as the ratio of the maximum root length under Al stress to that of the maximum root length under control condition. Long-term screening technique for Al tolerance using relative root length as an attribute in legumes is represented in Fig. 2. This type of screening strategy can be adopted under either hydroponic or sand assays.

Another major morphological character is root system architecture (RSA), which represents geometric organization of the discrete roots within a root system in the soil volume the root system occupies. Legumes have wide diversity of RSA among different species. Every type of RSA is supervised by a genetically regulated "post-embryonary root developmental program," which is multidimensional and allows phenotypic plasticity in reply towards stress including Al toxicity. RSA qualities

like anchorage, soil nutrient exploitation, and developmental plasticity have profound effects on yield, more specifically under stress conditions (Jung and McCouch, 2013). The development of nonintrusive techniques to actively study RSA may help in designing cultivars with optimum root systems for soils with Al toxicity (Rao *et al.*, 2016). Usually, hydroponics screening to denote RSA is preferred over the soil-based screening due to non-destructive approaches followed under hydroponic culture. Evaluation of root architecture at the seedling stage, i.e., seedling root architecture (SRA) under Al-stress conditions, has also helped to deduce Al tolerance within a large number of genotypes in one go. It also helps in the early detection of Al tolerance within the genotypes and allows breeders to develop Al-tolerant varieties (Singh *et al.*, 2021).

Short term staining techniques

Short-term screening techniques involve many staining and nonstaining methods for evaluation of Al toxicity tolerance.

Hematoxylin Staining Method

The hematoxylin staining method is an extremely powerful tool for observing tolerance without laborious quantitative measurements. The hematoxylin dye forms complexes with tissue Al that has been immobilized as AlPO 4 by phosphate on or immediately below the root surface (Ownby, 1993). There are several variations of the hematoxylin method. Polle *et al.*, (1978) used the hematoxylin-staining pattern of root tips as an indicator of Al tolerance. As the intensity of staining increases, reflecting a higher level of Al uptake, the level of tolerance decreases. Another procedure using hematoxylin, the modifed-pulse method, evaluates Al tolerance based on the ability of Al tolerant seedlings to continue root growth after a short pulse treatment with high Al concentrations (Aniol, 1984). Aluminum sensitive seedlings do not show root re-growth because their apical meristem has been damaged. This method can be applied to determine Al tolerance through either measuring root regrowth (Gallego and Benito, 1997) or evaluating seedlings on a 1 to 3 scale (tolerant, medium tolerant, and susceptible) based on their ability to present root regrowth (Riede and Anderson, 1996).

Hematoxylin staining is also employed as a means of measuring root regrowth (RRG). Singh *et al.*, (2012) reported that hematoxylin with tailored pulse technique assesses Al tolerance on the basis of the capability of Al-tolerant seedlings to maintain root growth after a brief pulse treatment with high Al concentration in lentil. Al-sensitive seedlings did not show RRG because their apical meristem was damaged, whereas tolerant genotypes showed continued root growth. Singh *et al.*, (2012) examined variation of Al tolerance in lentil and found that RRG after staining had significant correlation with root and shoot length, dry weight of roots and shoots, and pods/plant. Later, Singh *et al.*, (2016) also evaluated Al resistance in 285 wild and cultivated lentil genotypes in a nutrient solution by measuring RRG after hematoxylin staining of root apices. On the basis of this parameter, they were able to distinguish genotypes into different groups.

Genotypes that had mean primary RRG <0.5 cm were categorized as Al sensitive. On the other hand, genotypes with mean primary RRG significantly >1.0 cm were counted as resistant. Seedlings exhibiting intermediate RRG (0.50–1.00 cm) were considered as moderately resistant. They also found that RRG was correlated with seed yield under Al toxic field conditions. Screening techniques involving the use of staining dyes are represented in Fig. 3.

Root Regrowth Without Staining

Root regrowth without staining has been used as an indispensable morphological marker for testing Al tolerance in plants. Choudhary and Singh (2011) efficiently screened 32 genotypes of pigeon pea under Al toxic conditions using RRG as parameter. This screening method has also been used in chickpea (Singh *et al.*, 2011) and pea (Singh and Choudhary, 2010) (Fig. 2 c, d).

Callose Deposition

The higher the Al-induced injury to the root, the higher is the Al-induced callose deposition. Due to higher affinity of aniline blue dye with callose, higher accumulation of callose can be denoted by the level of fluorescence due to Al-morin complex (Singh *et al.*, 2015). Callose synthesis was found to be positively associated with internal Al concentration and negatively associated with root elongation rate in the case of bean cultivars under Al toxic condition (Massot *et al.*, 1999). Singh *et al.*, (2021) exhibited that callose formation is induced by Al as a mark of injury, markedly in the root apex. Singh *et al.*, (2018) have mapped Al resistance loci in lentil using RRG after hematoxylin staining and callose accumulation as markers. Al stress also triggered callose production in the root tips of alfalfa (An *et al.*, 2020).

Table.1 Aluminum toxicity tolerance studies in different legume crops

Legume crops	Al treatment level	Duration of treatment	Major finding	Tolerant genotype	Reference
Soybean	2 and 5 µM	3 days	Reduced tap root elongation	PI4117021, PI416937, and Biloxi	Villagarcia *et al*., 2001
Mung bean	74and 185 µM	48 hour	Al inhibited root elongation rate and root regrowth and augmented build up of Al, callose, H2O2, and lipid peroxidation. It triggered antioxidant response in the tolerant genotype	Pusa-672	Singh *et al.*, 2015
Lentil	74, 148, 222 and 296 µM	24hour to 65 days	Al depressed root growth and shoot growth and pods/plant	L-7903, L-4602 and ILL-6002	Singh *et al.*, 2015
Chick pea	5, 10 and 20 pmm Al	24-48 hour	Al depressed root regrowth and increased root staining	ICC14880 and IPC92-39	Singh *et al.*, 2011
Pea	10, 20, 30, and 40ppm Al	24 hour to 24 days	Al stress reduced relative root growth and increased root staining	PC-5511-1-2	Singh *et al.*, 2007
Pigeon pea	2 and 5 µM	24-48 hour	Al reduced root regrowth and increases staining	IPA7-10 and T-7	Singh *et al.*, 2011
Urdbean	74 and 185 µM	48 hour	Al treatment increased callos and ROS production and triggered antioxidant activities	Mash-114	Singh *et al.*, 2015

Fig.1 Summary of different parameters and screening techniques used for the evaluation of Al tolerance

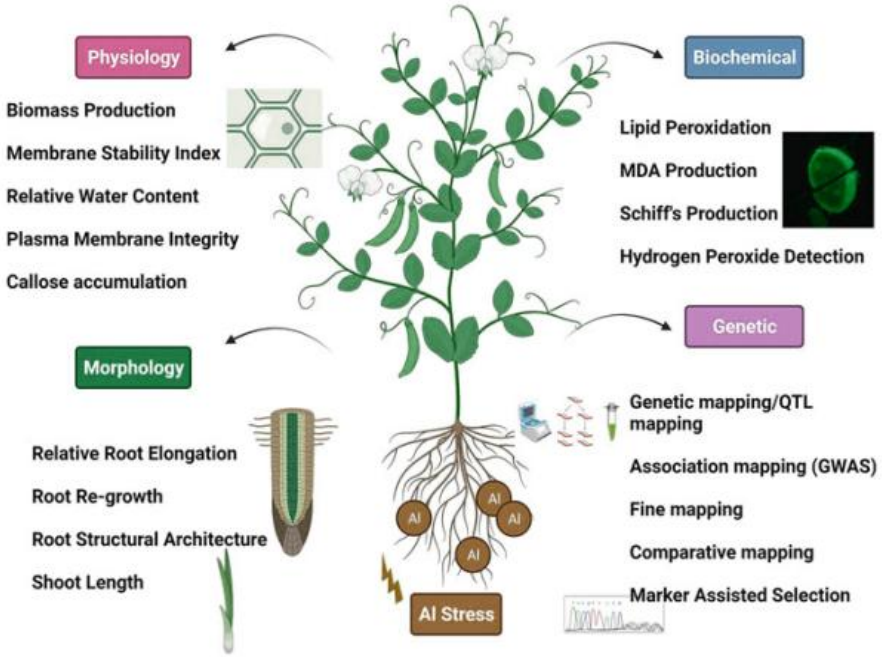


Fig.2 Long-term screening technique for Al tolerance using relative root length. (a, b) Change in relative root lengths of chickpea genotypes, (c, d) relative root length as parameter to differentiate Al tolerant and sensitive genotypes of pea under hydroponic and sand condition

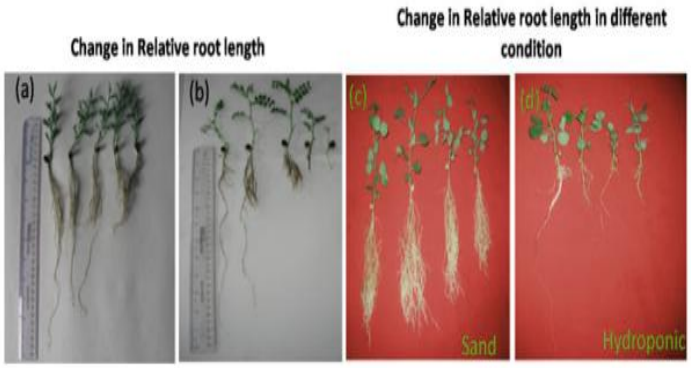
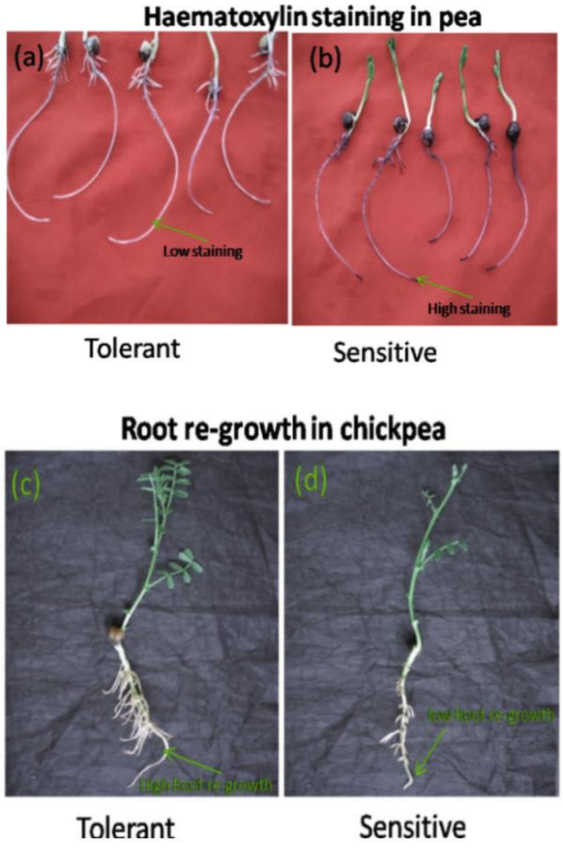


Fig.3 Short-term screening technique for Al tolerance (a, b) using hematoxylin staining and (c, d) root regrowth



Fluorescence Staining Methods

Use of fluorescence dyes such as aniline blue, morin, and fluorescein diacetate (FDA) to differentiate Al-tolerant genotypes from sensitive ones has been testified in many legumes (Singh *et al.*, 2016). These dyes can be used to detect callose deposition, Al-induced H2O2 production, and presence and estimation of Al contents in roots and shoots.

Detection of Al-Induced H2O2 Level

Level of DCF-DA fluorescence depicts the level of Al-induced injury caused due to production of H2O2.

Higher injury corresponds to higher damage due to Al ion, while lower fluoresce depicts less Al-induced injury to the roots. Evans blue (0.025%, w/v) is used for localizing the loss of plasma membrane integrity (Yamamoto *et al.,* 2001). Hydrogen peroxide- and H2O2-generated apoplast diamine oxidase (DAO) activities were received chemically via transmission electron microscopy in pea (Sujkowska-Rybkowska and Borucki, 2014). They found the participation of DAO in the production of a huge quantity of H2O2 in the nodule apoplast under Al toxicity. Hydrogen peroxide production was visualized in lentil roots by DCF-DA, which produced green fluorescence (Singh *et al.,* 2016).

The DCF-DA fluorescence in the root tips of control plants was insignificant, while it amplified significantly under Al stress. The level of H2O2 was found to be increased in both the resistant and sensitive genotypes although low signals were observed in resistant breeding lines while intense green fluorescence was observed in the root's tips of sensitive cultivars. H2O2 was determined in both roots and shoots by the method of Sagisaka (1976) in the case of black gram. The H2O2 content was observed to increase progressively in all the treated samples with the rising period of stress and concentration of Al3+ (Awasthi *et al.,* 2017). Under Al stress, H2O2 production was found to be more in *Vigna radiata* than in *V. mungo* and *V. umbellate*.

Challenge and future perspectives

Although significant progress has been made in understanding the mechanisms and screening methods for acid soil tolerance in legume crops, several challenges remain. The genetic basis of acid soil tolerance is a complex and involves multiple genes and alleles. Unrevealing these genetic factors requires further research, including genomics and transcriptomics studies. The QTLs controlling Al tolerance-related traits could be immediately deployed in breeding schemes through marker-assisted selection. Equally important will be to invest on legume germplasm collection programs for improving Al tolerance. Molecular breeding based on "omics" has better advantage and renders different opportunities over conventional breeding. These techniques can be used for screening a large, diversified germplasm in a limited time and space resulting in an early and precise detection of candidate gene(s). Application of machine learning (ML) in quantitative trait locus (QTL) mining and artificial intelligence can further help in determining the genetic determinants of Al tolerance in pulses.

Additionally, validation of screening methods across different legume species and genotypes is necessary to ensure their effectiveness and reliability. Participatory research and field trials involving farmers are crucial for selecting acid soil tolerant genotypes based on their agronomic performance and acceptability. Furthermore, promoting the adoption of acid soil tolerant legume varieties among farmers through extension services and capacity building programs is essential for achieving sustainable agriculture in acid soil areas.

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