PLANT GENETIC APPROACHES FOR INCREASING CROP PRODUCTIVITY IN ALUMINIUM TOXIC ACID SOIL

Patiram, B. K. Sarma and K. R. Dhiman
ICAR Research Complex for NEH Region, Umroi Road, Umiam-793103, Meghalaya

ABSTRACT

The aluminium (Al) toxicity has been recognized as a major limiting factor of crop production on acid soils. In India, acid soil occupies 25 million ha of cultivated area having soil pH below 5.5, where the toxicity of Al and associated stress are the constraints to increase the productivity of crops. Many native plant species and cultivators exhibit genetic-based variability for Al sensivity that has allowed the plant breeders to develop resistant crops. The dynamics of Al in soils, phytotoxic Al in soils its toxic symptoms to plants, and mechanisms of tolerance are briefed. The review focuses on selection of plants genotypes by different methods and genetic improvement of Al-tolerance and future strategies to achieve higher crop productivity without liming acid soils Al-toxic soils.

INTRODUCTION

The challenges facing the population of acidic soils of the world for agricultural production to ensure the maintenance of soil productivity and social demands is the need of the good governance. The increasing human population and improvement of living standard requires to develop management practices and efficient utilization of resources. The mineral stress may be caused by nutritional deficiencies or toxicities, which are inherent to soil composition and often results into serious constraints for production and degradation of land. The Al toxicity has been recognised as a major limiting factor for crop productivity on acid soils, which accounts 12% of the world cultivated lands (UexHull and Mutert, 1995) and distribution of total world's acid soils are given in Figure 1. The factors that contribute to acid soil infertility and their effects on plant growth are complex (Kamprath and Foy, 1985). The mineral stress in soil is primarily related to nutrient deficiencies and toxicities of aluminium (Al) and manganese (Mn). In acid soils, specific mineral stress phenomenon are related to i) Deficiency of bases (Ca, Mg, K) and poor retention power of the bases released from the weathering of minerals and those applied as fertilizers or amendments, ii) Presence of the toxic constraints of Al and to a lesser extent Mn toxicity in many species, iii) High P fixation power of soil on the surfaces of highly active Al and Fe, rendering it unavailable to plants, iv) Deficiency of Mo, especially for growth of legumes, v) Reduction of soil biological activities, and vi) Fe and Mn toxicities to submerged rice.

Dynamics of Al in soil

Total soil content of Al ranges between 2.1% and 13.8% Al_2O_3 (McLean, 1976) predominantly as a part of the primary silicates and silica clays and in highly weathered soils as a crystalline gibbsite. The toxicity of Al can occur in soils when pH drops to levels low enough to cause the clay minerals structure to decompose (generally bellow pH 5.5, but particularly below 5.0). When this point is reached, some of the Al, formally a part of clay particles, migrates to cation exchange sites on clay surfaces and into the soil solutions. Most of the soils do not contain sufficient total Mn content to produce toxicity at pH bellow 5.0. On this basis of total area involved, Al toxicity is probably more important than Mn toxicity.

The soil solution Al^{3+} can be affected by the solubility of amorphus and crystalline Al minerals and by the solution concentration of ions contained in these Al compounds (Lindsay, 1979). The solution Al^{3+} may also be affected by soluble organic and inorganic anions, and by insoluble forms of organic matter and negatively charged clay minerals and oxides that form strong to weak complexes with Al and Al-hydroxyl ions (Hue et al., 1986, Thomas, 1988). The conceptual model that accounts for the process involved to control the Al^{3+} in soil solution is controlled by interaction between the eight processes as shown in Fig. 2 (Helyar et al., 1993). According to kinetic model in Fig. 2, the apparent solubility of aluminium oxides in the soil [$K_{sp(soil)} = (Al^{3+})/(H^+)^3$, increases

or decreases until :

$$r_2 = r_1 + (r_3 - r_4) + (r_5 - r_6) + (r_7 - r_8)$$

in which r_1 indicates the rate of dissolution of unsaturated minerals, r_2 is the rate of precipitation of saturated minerals, $(r_3 - r_4)$ is the net flow of Al to soil volume, $(r_5 - r_6)$ in the net rate release to the solution of surface complexed Al, and $(r_7 - r_8)$ is the net rate of decrease in capacity of the soil solution to contain Al without changing (Al^{3+}). The types and quantities on main minerals present in the soil and their saturation/desaturation status give additional indications which dissolution and formation process are likely to occur.

Phytotoxicity symptoms of Al

The prominent form of Al that is found in acidic soils is Al^{3+} and is highly toxic to plant roots (Kinraide, 1991). The toxicity of Al^{3+} results into poorly developed root system, which causes susceptibility to drought stress and nutrient deficiencies (Foy, 1988, Kochian, 1995). The Al toxicity produces a range of symptoms in the top plant - including small dark green leaves, stunted growth, delayed maturity, a purpling (which resembles P deficiency), wilting, and induced deficiencies of Ca (rolled leaves in barley and wheat and petiole collapse and chlorosis in soybean) (Foy et al., 1978). The deficiencies and toxicities may act independently or together to reduce plant growth (Clark, 1982). Al toxicity is particularly severe at soil pH values of 5.0 and below, but it cannot occur at high pH 5.5 in kaoliniatic (clay mineral) soils. In most cultivated crops, the symptoms of Al injury are first expressed by reduced root growth. Later the affected roots thicken and dont branch normally. The root tips disintegrate and turn brown, and adventious roots proliferate as long as crown is alive.

Mechanism of Al toxicity

The most widely accepted measure of Al toxicity symptoms is the inhibition of root growth. The root apex (root cap, meristem, and elongated zone) accumulates more Al and attracts greater physiological damage than the mature root tissues (Delhaize and Ryan, 1995). Several mechanisms have been proposed to explain how Al disrupts cellular function, disruption of mineral nutrition and metabolisim, which has been reviewed (Taylor, 1988, Kochian, 1995, Delhaize and Ryan, 1995). Bennet and Breen (1987, 1991) suggested that the root cap is a site perception of Al injury, based on anatomical studies of maize root and suggested that Al might inhibit root growth indirectly *via* a single-response pathway involving the root cap, hormones, and secondary messengers. McQuattie and Schier (1990) examined the red spruce seedling to Al injury in nutrient solution and examination of root tips and 5-10 mm segments from the tips, revealed numerous cellular changes in Al-stress roots; premature vacuolation, accumulation of phenolic-like material, loss of cells from peripheral cell layers, formation of intercellular spaces, increased disruption of cellular membranes and degeneration of the cytoplasm. Marschner (1991) described the possible inhibitory effects of Al on root growth; inhibition of cell division and elongation, replacement of Ca^{2+} and Mg^{2+} from the middle lamella, replacement of Ca_{2+} from the plasma membrane to cystosol through influx, and subsequently callose formation in root cap and rhizomal cells. The callose (1,3-beta-Dglucose) formation is the rapid and sensitive marker of Al-induced injury (Zhang et al., 1994). In plant roots Al accumulates mainly in the cells located in the apical elongation zone and inhibit cell elongation rapidly. Yamamoto et al. (2002) reported Al enhanced reactive oxygen species (ROS), which leads to respiration inhibition. ATP depletion and inhibition of cell growth/elongation.

Phytotoxic forms of aluminium

The soil exchangeable Al has proved to be a poor indicator of Al-toxic soils and efforts to correlate some measure of plant growth (root length, yield, dry weight, etc.) with components of soil solution are often hindered by the lack of understanding and awareness of Al specification (Delhaize and Ryan, 1995, Kochian, 1995). The knowledge of Al specification in or around the rhizosphere is of primary importance for Al toxicity caused by its interaction in the apoplasm. However, if Al toxicity is the result of symptomatic Al interaction, it might be necessary to know which Al species transported across the root-cell plasma membrane (PM) as well as which Al species is causing toxicity within the symplasm (Kochian, 1995).

The soil solution soluble Al can exist in many different ionic forms. Al hydrolyzes to Ca^{3+}, dominates below pH 5, whereas the $Al(OH)^{2+}$ and $Al(OH)^{+}$ species form as the soil pH increases. At near-neutral pH the soil phase gibbsite $[Al(OH)_3]$ occurs, whereas aluminium $[Al(OH)_4^{-}]$ dominates in alkaline conditions. Monomeric Al will form low molecular weight complexes with a number of ligands, such as organic acids, proteins, lipids,

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PO_4^{-3-}, SO_4^{2-}, and F^-. Attempts have been made recently to demonstrate the toxicity of individual Al species in solution. It is difficult to draw the conclusion, which Al monomer is the major phytotoxic species, and nearly all the monomeric Al species listed above have been considered toxic in one study or another (Kinraide, 1991). Kinraide et al. (1992) have developed a model based on modified Guoy-Chapman-Stern analysis electrostatic interactions between Al^{3+}, other cations, and the negatively charged cell surface. This model was used on the assumption that the negatively charges surface membrane surface would generate a strong attractive force for trivalent cation such as Al^{3+} and other cations had the ability to reduce the negative surface charge of plasma membrane than with the activity of Al^{3+} in bulk solution. This model indicated the important role of negatively charged root-cell surface in toxicities not only Al^{3+}, but also to other potentially toxic cations and anions.

Mechanism of tolerance

The observation on plant adaptation have shown species of plant have a much wider range of adaptation than others (Wright, 1989). Many plant species and cultivars show an inherited tolerance to Al stress, and these species and cultivars have become important resources for investigating Al toxicity and tolerance. Differential uptake of Al into root could account for differences in tolerance between genotypes. However, conflicting results have been reported. Apparent resistance of plants to adverse soil conditions is generally caused by avoidance mechanism rather than a tolerance. Avoidance mechanisms for toxic ions within the root or within the cell wall of roots (Turner and Gregory, 1967). The internal resistance mechanisms include chelting of Al in cystosol with organic acids or acidic polypeptides, compartmentation of Al in the valuole, induction of protein synthesis, synthesis of Al-resistant isoenzymes, and synthesis if specific of Al-binding proteins (Taylor 1988, Taylor 1991). However, the information on the above at the molecular level is limited. Aniol (1984) suggested that plants could develop Al tolerance through the synthesis of proteins that bind or sequester Al and render it innocuous within the symplast. As Al tolerence is determined by potentially many genes, the task of identifying specific proteins that might confer Al tolerance is difficult. An understanding of genomic affinities helps to formulate effective breeding programme designed to transfer desirable genes from wild relatives or primitive varieties of crop plants into otherwise superior cultivars. Rice shows the highest tolerance to Al toxicity among small-grain cereal crops, however, the mechanisms and genetics responsible for its high Al tolerance are not yet well understood. Slaski (1990) observed that Al tolerant cereal species had more total NAD kinase activity than Al-sensitive cereal species. Cruz-Ortega and Ownby (1993) had suggested that root experiencing Al stress were more susceptible to other toxic metals and pathogen. As a defence response, cell may thus synthesize PR protein such as TAL-18. Callose and probably MLPs have been reported for function in binding heavy metals (Horst, 1991. Snowden and Gardner, 1993). Basu et al. (1994) identified the RMP51 (51-kDe protein) as the criteria of Al tolerance 'protein'. Carber and Owenby (1995) opined that some of the properties of a novel inducible Al tolerance' protein would include : i) Consistantly high concentrations in tolerant lines and induced levels or absence in sensitive line; ii) co-segregation with tolerant phenotypes when tolerant and Al sensitive cultivars are crossed; iii) relatively specific to Al toxicity; and iv) physiological role that is consistent with proposed mechanism for metal tolerance (e.g. protein involved in production or secretion of chelating ligands or one that is part of an Al efflux pump or some other exclusion process).

Much of current evident pointed the major role of certain acids secreted from plant roots in response to Al treatment that can form complexes with Al^{3+} to protect plant roots (Ma, 2002, Ryan et al., 2001) in the cystosol or at the root-soil interface. The different organic acid anions secreted from the roots of tolerant cultivars of different crops are given in Table 1.

Ma et al. (2001) identified the two pattern of organic acid secretion from plant root (Fig. 3)

- In Pattern I, Al activates an anion channel on the plasma membrane permeable to organic acid anions. This stimulation could occur in one of the three ways : (i) Al^{3+} interacts directly with the channel protein to trigger its opening; (ii) Al^{3+} interacts with a specific receptor R on the membrane surface or with the membrane itself to initiate secondary messenger cascade that then activates the channel; (iii) Al^{3+} enters the cytoplasm and activates the channel directly, or indirectly *via* secondary messenger.

- In Pattern II, Al interacts with the cell; encode proteins involved with metabolism of organic acids or their transport across the plasma membrane. Organic anions form a stable complexes with Al, thereby Al^{3+} detoxify in the rhizosphere.

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The release of organic acids is quick in Pattern I and gets delayed for several hours in Pattern II after the addition of Al in nutrient solution. The Al-activated efflux from maize, trigger both a rapid efflux of citrate as well as a delayed release and induction of noval protein is not required for quick secretion (Ma, 2002), whereas for second type of secretion, protein induction is required (Ma et. al., 2001). The high rate of organic acid excertion involves several reactions, such as an increase in organic acid synthesis (Taktia et al., 1999) and a superior ability for organic acid transport at the plasma membrane (Ryan et al., 1995). Number of genes relating to an increase in organic acid synthesis was isolated, thereafter introduced into several plant species (de la Fuente et al., 1997., Koyama et al., 2000., Tesfaye et al., 2001). These transgenic plants showed enhanced organic acid excretion from the roots and in turn could improve Al tolerance.

MANAGEMENT APPROACH TO AMEND THE Al-TOXIC ACID SOILS

The problem of mineral stress may be reduced by changing the minerals in the soils and by modifying the genotype of the plants, so they can be better cope with the mineral stress environment that actually exists. The former approach is to raise the soil pH by liming or other liming amendments to eliminate the toxicity of Al in acid soils and to provide the better soil environment for plant roots growth. It is believed that an understanding of the farmers' resource management system in indispensable to implement sustainable resource management concepts. In our country, the farmers of the acid soil region are almost not accustomed to use the lime to ameliorate the acidic soils for increasing the productivity from the economic point of view to raise the soil pH to 5.5 by liming (Patiram and Prasad, 1991).

Most of the farmers from generations have developed the agricultural system of crops production, in which either crops can survive without liming or raising the soil pH by burning of biomass (shifting agriculture in north eastern region and some parts in other region) to get temporaty relief from Al toxicity. Most of the root, tuber, and plantation crops survive well on acidic soils and taken as cash crops on acid soils of the country. Upland crops (cereals, pulses, oilseeds, vegetables, etc.) do not yield well on acid soils having pH below 5.5 without liming. On these respects, sufficient research work have already been done. However, as stated erlier most of the farmers of acidic uplands are reluctant to use lime as an amendment for acidic soils. Under such situations, the improvement of agricultural crops will be a rewarding activity for plant breeders to overcome this problem to a great-extent by modifying the genotype of the plants adapted to Al-toxic acid soil mineral stress environment and could be promising alternative or supplement to liming and other agronomic practices (Foy, 1988., Spain, 1976).

Screening techniques

Traditionally, selection for Al tolerance has relied upon cell and tissue culture, solution culture, soil bioassays, or field evaluation (Caver and Ownby, 1995). The non-destructive laboratory and greenhouse-based techniques are widely employed with rapidity and high degree of accuracy in the early developmental stages. Field screening techniques are more laborious and do not have same reputation of success, but are very critically needed to complete the transition from Al tolerance to acid soil tolerance. Because of complexities, and difficulties involved in controlling and measuring complex soil properties, much of the work with Al tolerance has been conducted either in green house or by use of nutrient solution techniques.

Cell and tissue culture : Both can serve at least two functions in a breeding programme. Callus assays may be developed to survey preexisting variability for Al tolerance (Parrot and Burton, 1990) or selection pressure can be applied in cell culture to recover Al-tolerant cells. Low pH (<4.5) inhibits cell growth even in the absence of Al and also agar solidification. The solidification has been overcome with addition of solidifying agent to the callus growth medium (Parrot and Burton, 1990) and use of sponges soaked in a liquid medium to support callus (Meredith et al., 1988). The tissue culture can play the significant role in true selection of Al tolerant and not tolerant to other nutrients to the low cultured medium.

Solution culture : Nutrient solution techniques are considerably more precise as compared to field screening, because the important variables can be controlled. The main demerits are that relatively large volume of distilled water is needed and pH changes in the solutions change both the solubility and form of Al. The most common criteria used to measure Al toxicity are to compare either root length or root weight of Al-affected plants with control plants grown in absence of Al. However, root length and root weight, measurement are required to be made in individual plants which is quite time consuming. It can become a serious limitation to a breeder selecting

for Al-tolerance progeny in a large segregation. Konzak et al. (1976) developed two simplified methods to grow seedlings for Al-tolerance, plastic holder plus filter paper and placing seeds at the top of double paper towel in a "Rag Doll" fashion.

The heamatoxylin staining method is the good method for screening Al tolerance in solution culture (Polle et al., 1978). The Heamatoxylin dye binds to tissue Al immobilized by extracellular phosphate on or immediately below the root surface (Ownby, 1993).

Soil bioassay : Soil media offer the distinct advantage over nutrient solution media for screening genotypes to varying levels of Al stress and now attention are given on this aspect. Foy (1976) discussed the conditions necessary to screen plants especially for Al or Mn tolerance. Mitigating effect of other nutrients or organic matter must be considered properly matching a certain soil with breeding objective. Screening in soils representative of the targeted production area where Al is yield limiting, would provide a critical immediate step in selection of tolerant genotype-after primary screening in nutrient solutions and before tedious and costly screening under natural field condition.

Field screening : The ultimate and directly integrated measurement of tolerance is to screen the cultivars under field condition for economic yield. The general procedure is to conduct duplicate tests in natural acidic soil and lime-amended block to allow the direct measurement of tolerance and stress to be overcome by amendment. The inherent spatial variability of field for pH or plant nutrients (e.g., P), which influence Al stress severity, can result to biasness for the interpretation of field trials (Ball et al., 1993). Such type of variability may also lead to an inefficient analysis by use of a covariance or nearest-neighbour method.

Breeding approach : The simple breeding method for improving acid soil Al tolerance is to back cross genes with relatively large effects from locally untapped parents to adapted suceptible parents. The tolerance expression can be first hand received from the rapid solution culture bioassay. Al tolerance genes are easily tracked through consecutive backcross (BC) generations by haematoxylin staining.

GENETIC IMPROVEMENT FOR Al TOLERANCE

The development of plants depends on the interaction of the genotype with the environment (Lewis, 1976). yp = ge. Where yp = phenotype (yield and quality of the products for which plants were grown), g = genotype (genetic potential), and e = environment (including soil, weather, pests, cultural practices, growth relators, etc.)

The deficiencies of N, P, K, Ca, Mg, and other plant nutrients are common in acid soils. For these stress conditions, plant tolerance depends upon high productivity of crops per unit availability of soil nutrients, greater feeding power/solubilizing mechanism for the deficient nutrients at the plant root surface, and/or root system which is more extensive or otherwise capable of utilizing nutrients which exists at very low soil solution levels. Such type of several crops should be developed to avoid mechanisms to Al toxicity and tolerance mechanism to nutrient stress. The problem of soil acidity stress may be reduced by the application of amendments. Different genetic system may operate in seedlings *vs.* adult plant or at different levels of Al stress. The observations on plant adaptation have shown some species of plants have a much wider range of adaptation than others (Wright, 1989). Many plant species and cultivars show an inheritable tolerance to Al stress, and these species and cultivars have become important resources for investigating Al toxicity and tolerance. Utilizing this genetic variability in plant breeding and selection programmes, plants can be developed with resistance to many adverse acidic soil conditions. This is an important strategy for crop improvement in Al toxic acidic soils is to select for cultivars with increased Al tolerance.

Dilley et al. (1975) gave the stress on the three major research imperatives for environmental stress.

- Manipulate crops or their environments in ways which avoid or reduce stress injury and increase productivity;

- Exploit genetic potential for developing new varieties of crops resistance to environment stress; and

- Elucidate the basic principles of stress injury and resistance in plants and evaluate the scope and nature of stress damage to crops.

Jenning (1974) suggested that plant breeder would select future varieties under natural condition. The weaker plant varieties die and surviving plants continue to develop through cross pollination or mutation that lead certain environmentally adaptive characteristics. In acid soils, such adaptation includes tolerance to high levels of Al and manganese and capability to grow normally nutrient-poor conditions. Observations on plant adaptation have shown that some species of plants may have wider range of adaptation than others. Utilizing this genetic variability in plant breeding and selection programmes, plants can be developed with tolerance to many advarse acid soil conditions. Among the small grains, barley is the most Al-sensitive species, while rye (*Secale cereale* L.) appears to possess highest degree of Al tolerance (Foy, 1983). Genotypic variation to Al tolerance also exist within species (DeSousa, 1988, Foy et al., 1965, Lafever et al., 1977, Reid et al., 1969). Neeman (1960) was probably the first to report varital differences in wheat and attributed them to Al toxicity. Foy et al. (1965) also observed a wide range of response to wheat and barley varieties of diverse origin on two Al toxic soils. It was also found that varieties developed on acid, Al toxic soils, usually had greater tolerance than those developed on soil which were non-toxic. Rincon and Gonzales (1992) showed that Al-sensitive wheat cultivars accumulated more Al in its root apices (2 mm terminus of root) than Al-tolerant cultivars.

Molecular mapping of Al tolerance gene : Traditionally, selection of plant cultivars for Al tolerance has relied upon field evaluations, soil bioassay, or solution culture methods (Carber and Ownby, 1995). Stoolmaker (1974) first attempted to roughly locate genes for acid soil tolerance in wheat by comparing the response of diploid, tetraploid and hexaploid species relative to their genome constitution. The various hexaploid genotypes (AABBDD) had the highest degree of tolerance. The importance of the D genome for acid soil tolerance was demonstrated by increasing sensitivity of a tetraploid derivative lacking D genome from 'Canthetch', a hexaploid cultivator and tolerance recovered by addition of D genome from several sources. Even greater tolerance is provided by R genome from rye (*Secale cereale* L.). The genome can be ranked in decreasing order of tolence R>D>A>B. To understand the genetic control of Al tolerance to determine the homology of Al tolerance genes, molecular mapping has been initiated in different crops (Tang et al., 2000, Rhue et al., 1978, Bianchi et al., 2000)

Al is conditioned by the Alt 1 gene in wheat cv Carazinho (Delhaize et al., 1993) and two or more genes Atlas 66 (Brezonsky, 1992). In wheat major Al tolerance gene have also been mapped to the long arm of chromosom 4D (Luo and Dvorak, 1999; Reide and Anderson, 1996), and the loss of this same chromosome arm resulted in the elimination of Al tolerance (Anitol and Gustafson, 1984). The inheritance of Al in barley has been reported to be controlled by a single gene and also mopnogenic shifted from dominant to recessive as Al concentration increased (Minella and Sorrells, 1992), indicated Al tolerance is a gene dosage-dependent trait. The trisomic analysis of barley also revealed that Al tolerance is also located on chromosome 4H (Minella and Sorrells, 1997). From these studies, the possibility emerged that orthologus loci might play a role in determining Al tolerance variation in wheat and barley (Tang et al., 2000) Rhue et al. (1978) reported the single dominant gene for Al tolerance in maize; however, Khan and Mcneilly (2000) indicated the involvement of a multiple allelic series for Al tolerance.

The markers identified can find their broadest utility if they can be successfully converted to a PCR-based format. In this case, marker assisted A tolerance section may be conducted more rapidly than other available methods incuding haematoxyin staining, particularly if PCR-based markers are to be used for other traits as well (Tang et al., 2000). The identification of Single Nucleotide Polymorphisms (SNPs) from a broad range of organisms, including crops is the rapid and low cost method as moecular markers-assisted plant breeding. Single Nucleotide Primer Extension (SnuPE) assays are used to genotype SNPs from minimum amount of plant leaf tissue at the seedling stage. The SNPs identified by cDNA sequences (cNSNPs), and promoter region SNP (pSNPs), can directly affect gene function and are 'perfect molecuar markers'; there is no chance of recombination between the marker and the gene of interest (Paris et al., 2001)

FUTURE STRATEGIES TO INCREASE THE PRODUCTIVITY
OF CROPS IN Al-TOXIC ACID SOIS OF INDIA

The genetic improvement of crops to increase their productivity in acid soils of our country, occupying the cultivated area of 25 m ha below the soi pH 5.5, where the toxicity of Al is the major constraints. Such type of problematic soils are mainly concentrated in north eastern region and western ghats with sporadic distribution

in Jharkhand, Himachal Pradesh, Orrisa, West Bengal, Chatisgarh, etc. Moreover, in our country farmers are not accustomed to use the lime for ameliorating the acid soils to increase the productivity of crops other than rice, tuber and rhizomatus crops. Under such situations, the genetic improvement of crops (cereals, pulses and oilseeds) is justified where application of lime is out of question. This can be done in a systematic way to overcome the Al toxicity on acidic soils through breeding of tolerant crops as follows :

- Efforts should be made to test or characterize tolerance limit of existing cultivars before breeding begins. The experience of other countries (Australia, America) can be utilized.

- What limit of tolerance are available with our own stock of crop varieties and this tolerance can be improved ?

- Objectives must define research and development needs in screening and breeding in relation to needs of the farmers and researchers.

- Assay techniques to be adopted for screening should be precise with available methodologies and be capable of handling large numbers of germplasm.

- In field, where screening to be taken, the soil stress must be identified and characterized and sites must represent the characteristics of the region concerned with least spatial variation for better transfer of information from one site to other.

- We must also decide the part of the test area be limited to fertilizer or organic agriculture to suit the economic condition of the farmers.

- For the success of screening and breeding for Al tolerance, a wide network of linked research and development programmes should be taken in different zones of the acidic soils of India to identify the problems and to asses the best approaches to solve the problem. In this regard, the role of regional and international centres would be identified for tolerant strains or sources of germplasm to make germplasm stocks available.

- Generally plant breeders are accustomed to working individually, or in a multidisciplinary team, primarily with other biologists. Therefore, a well-integrated, multidisciplinary team of plant breeders, soil scientists, and plant physiologists should be considered at planning stages so as to look at the problem in totality. The all team members should consider in setting goals, defining objectives, making critical decisions, and evaluating progress.

- Organic acids are to be implicated in Al-tolerance mechanisms for a range of plant species; a logical approach is to manipulate organic acid biosynthesis or catabolism. Many of the genes encoding key enzymes in organic acid metabolism have been cloned.

REFERENCES

Anitol, A. 1984. *Plant Physiol* 76:551-555.
Anitol, A. 1990. *Plant Soil* 123:223-227.
Anitol, A. and Gustafson, J.P. 1984. *Can. J. Genet. Cytol.* 26:701-705.
Ball, S.T., Mulla, D.J. and Konzak, C.F. 1993. *Crop Sci.* 33:931-935.
Basu, U., Basu, A. and Taylor, G.J. 1994 *Plant Physiol.* 104:1007-1013.
Bennet, R.J., Breen, C.M. and Fey, M.V. 1987. *Environ.l Exp. Botany* 27:91-104.
Bennet, R.J., Breen, C.M. 1991. *Plant Soil* 134:153-166.
Berozonski, W.A. 1992. Genome 35:689-693.
Bianchi-Hall, C.M., Carter T.F. Jr., Rufty, T.W., Arellano, C., Boerma, H.R., Ashley, D.A. and Burton, J.W. 1998. *Crop Sci.* 38:513-522.
Carber, R.F. and Ownby, J.D. 1995. *Adv. Agron.* 54:117-173.
Clark, R.B. 1982. Plant response to mineral element toxicity and deficiency. In "Breeding Plants for Less Favorable Environment" (eds. Christiansen, M.N. and Lewis, C.F.), pp 71-142. John Wiley & Sons, New York.
Crutz-Ortega, R. and Ownby, J.D. 1993. *Plant Physiol.* 89:211-219.

de la Fuente, J.M., Crutz-Ortega, R., Ramirez-Rodriguez, V., Cabreta-Ponce, J.L. and Herreta-Estrella, L. 1997. *Science* 276:1566-1568.

Delhaize, E., Ryan, P.R. and Randal, P.J. 1993. *Plant Physiol.* 103:695-702.

Delhaize, E. and Ryan, P.R. 1995. *Plant Physiol.* 107:315-321.

DeSousa, C.N.A. 1998. *Plant Breed.* 117:217-221.

Dilley, C.D., Heggestad, H.E., Powers, W.L. and Weiser, C.J. 1975. Environmental stress in : Crop Productivity-Research Imperatives (ed. Brown, A.W.A., Byerly, T.C., Gibbs, M. and San Pietro, A.), pp 309-355. Charles F. Kettering Foundation, Yellow Spring, Ohio, USA.

Foy, C.D., Armiger, W.H., Briggle, J.W. and Reid, D.A. 1965. *Agron. J.* 57:413-417.

Foy, C.D., Lafever, H.N., Schwartz, J.W. and Fleming, A.L. 1974. *Agron. J.* 66:751-758.

Foy, C.D. 1976. General principles involved in screening plants for aluminium and manganese. In "Plant Adaptation to Mineral Stress in Problem Soils" (eds. Wright, M.J. and Ferrari, S.A.), p. 255.267. Cornell University, Ithica.

Foy, C.D., Chaney, R.L. and White, M.C. 1978. *Annual Review of Plant Physiol.* 29:511-566.

Foy, C.D. 1983. *Iowa State J. Res.* 57:355-391.

Foy, C.D. 1988. *Commun. Soil Sci. Plant Anal.* 19:959-1093.

Helyar, K.R., Conyers, M.K. and Munns, D.N. 1993. *J. Soil Sci.* 44:317-333.

Horst, W.J., Asher, C.J., Szulkiewiew, P. and Wissemeier, A.H. 1991. Short term response of soyabean roots to aluminium. In "Plant-Soil Interactions at Low pH' (eds. Wright, R.J. Baligar, B.C. and Murrmann, R.P.), pp. 733-739. Kulwer Academic Publisheds, Dorddrecht, The netherlands.

Hue, N.V., Graddock, G.R. and Adams, F. 1986. *Soil Sc. Soc. Am. J.* 50:28-34.

Jennings, P.R. 1974. Science 186:1085-1088.

Kamprath, E.J. and Foy, C.D. 1985. Lime-fertilizer-plant interactions in soils. In " Fertilizer Technology and Use" (eds. Engelstad, O.P.), pp. 91-151. Soil Science Society of America, Madison, Wisconsin.

Kinraide, T.B. 1991. *Plant Soil* 134:167-178.

Kinrade, T.B., Ryan, P.R. and Kochian, L. 1992. *Plant Physiol.* 99:1461-1468.

Khan, A.A. and McNeilly, T. 2000. *J. Genet. Plant Breed.* 54:245-249.

Kochian, L.V. 1995. *Annu. Rev. Plant Physiol. Plant Mol. Bio.* 46:237-260.

Konzak, C.F., Polle, E. and Kittrick, J.A. 1976. Screening of several crops for aluminium tolerance. In "Plant Adaptation to Mineral Stress in Problem Soils" (eds. Wright, M.J. and Ferrari, S.A.), p. 311.328. Cornell University, Ithica.

Koyama, H., Kawamura, A., Kihara, T., Takita, E. and Shibata, D. 2000. *Plant Cell Physiol.* 41:1030-1037.

Lafever, H.N., Campbell, I.G. and Foy, C.D. 1977. *Agron. J.* 69:563-568.

Lewis, C.F. 1976. Genetic potential for solving problems of soil mineral stress : Over view and evaluation, In "Plant Adaptation to Mineral Stress in Problem Soils" (eds. Wright, M.J. and Ferrari, S.A.), p. 107.109. Cornell University, Ithica.

Li, X.F., Ma, J.F. and Matsumoto, H. 2000. *Plant Physiol.* 123:1537-1543.

Lindsay, W.L. 1979. Chemical Equlibria in Soils. Wiley, New York.

Luo, M.C. and Dvork, J. 1996. *Euphytica* 91:31-35.

Ma. J.F., Zheng, S.J., Hiradate, S. and Matsumoto, H. 1997a. *Plant Cell Physiol.* 38:1019-1025.

Ma. J.F., Zheng, S.J., Hiradate, S. and Matsumoto, H. 1997b. *Nature* 390:569-570.

Ma, J.F. 2000. *Cell Physiol.* 41:383-390.

Ma, J.F., Ryan, P.R. and Delhaize, E. 2001. *Trends Plant Sci.* 6:273-278.

Ma, Z. and Miyakasha, S.C. 1998. *Plant Physiol.* 118:861-865.

Marschner, H. 1991. *Plant Soil* 134:1-20.

McLean, E.O. 1976. *Commun. Soil Sci. Plant Anal.* 7:619-636.

McQuattie, C.J. and Schier, G.A. 1990. *Can. J. Forest Res.* 20:1479-1497.

Meredith, C.P., Connor, A.J. and Schettini, T.M. 1988. *Iowa State J. Res.* 62:523-535.

Minella, E. and Sorrells, M.E. 1997. *Crop Sci.* 32:593-598.

Minella, E. and Sorrells, M.E. 1997. *Plant Breed.* 116:465-569.

Miyasaka, S.C., Bute, J.G., Howell, R.K. and Foy, C.D. 1991. *Plant Physiol.* 96:737-743.

Nennan, M. 1960. *Plant Soil* 12:324-328.

Ownby, J.D. 1993. *Physiol. Plant* 87:371-380.

Parrot, W.A. and Bouton, J.H. 1990. *Crop Sci.* 30:378-380.

Paris, M., Lance, R. and Jones. M.G.K. 2001. Proceed. 10th Austr. Barley Techn. Symp. (2001):1-6.

Patiram and Prasad, R.N. 1991. *Trop. Agric.* (Trinidad) 68:284-288.

Pellet, D.M., Grunes, D.L. and Kochian, L.V. 1995 *Planta* 196:788-795.

Reid, D.A., Jones, J.D., Armiger, W.H., Foy, C.D., Koch, E.J. and Starling, T.M. 1969. *Agron. J.* 61:218-222.

Reid, C.R. and Anderson, J.A. 1996. *Crop Sci.* 36:905-909.

Rincon, M. and Gonzales, R.A. 1992. *Plant Physiol.* 99:1021-1028.

Rhue, R.D., Grogan, C.O., Stockmeyer, E.W. and Everett, S.H. L. 1978. *Crop Sci.* 18:1063-1067.

Ryan, P.R., Delhaize, E. and Randal, P. 1995. *Planta* 196:103-110.

Ryan, P.R., Delhaize, E. and Jones, D.L. 2001. *Annu. Rev. Plant Physiol. Plant Mo. Bio.* 52:527-560.

Slaski, J.J. 1990. *J. Plant Physiol.* 136:40-44.

Snowden, K.C. and Gardner, R.C. 1993. *Plant Physiol.* 103:855-861.

Spain, J.M. 1976. Field studies on tolerance of plant species and cultivars to soil conditions. In "Plant Adaptation to Mineral Stress in Problem Soils" (eds. Wright, M.J. and Ferrari, S.A.), p. 213.222. Cornell University, Ithica.

Taylor, G.J. 1988. The physiology of aluminium tolerance. In "Metal Ions in Biological Systems" (eds. Sigel, H. and Sigel A.), pp. 165-198. Marcel Dekker Inc., New York.

Takita, E., Koyama, H. and Hara, T. 1999. *Top. Plant Biochem. Physio.* 10:57-93.

Tang, Y., Sorrells, M.E., Kochian, L.V. and Garvin, D.F. 2000. *Crop Sci.* 40:778-782.

Tesfaye, M., Temple, S.J., Allan, D.L., Vance, C.P. and Samac, D.A. 2001. *Plant Physiol.* 127:1836-1944.

Thomas, G.W. 1988. *Commun. Soil Sci. Plant Anal.* 19:833-856.

Turner, R.G. and Gregory, R.P.G. 1967. The use of radioisotopes to investigate heavy metal tolerance in plants. In "Isotopes in Plant Nutrition and Physiology", pp. 493-509. Proceedings of the Sytmposium (Vienna, 1966). International Atomic Energy Agency, Vienna.

UexKull, Von and Mutert, E. 1995. Global extent, development and economic impact of acid soils. In "Plant Soil Interactions at Low pH : Principles and Management" (ed. Dare, R.A.), pp. 5-9. Kulwer Academic Publishers, Dorddrecht, The Netherlands.

Yamamoto, Y., Kobayashi, Y., Devi, S.R., Rikshi, S. and Matsumoto, H. 2002. *Plant Physiol.* 110:1019-1025.

Yang, Z.M., Ma, J.F. and Takata, S. 2001. *Plant Physiol.* 110:1019-1025.

Zhang, G., Hoddinot, J. and Taylor, G.J. 1994. *J. Plant Physiol.* 144:229-234.

Zheng, S.J., Ma, J.F. and Matsumoto, H. 1998. *Plant Physiol.* 103:209-214.

Zheng, S.J., Ma, J.F. and Matsumoto, H. 1998. *Plant Physiol.* 117:745-751.

Table 1. Organic acid exudation from different plant roots.

Plants/Crops	Organic acid release	Reference
Wheat (*Triticum aestivum*)	Malate	Delhaoze et al. (1993)
Snapbean (*Phaseolus vulgaris*)	Citrate	Miyasaka et al. (1991)
Maize (*Zea mays*)	Citrate	Pellet et al. (1995)
Cassia tora	Citrate	Ma et al. (1997)
Soybean (*Glycine max*)	Citrate	Yang et al. (2001)
Buckwheat (*Fagopyrum esculentum*)	Qxalate	Ma et al. (1997)
Taro (*Colocasia esculenta*)	Oxalate	Ma & Miyasaka (1998)
Rapseed (*Brassica napus*)	Malate and citrate	Ma (2000), Zheng et al. (1998)
Oat (*Avea sativa*)	Malate and citrate	and Li et al. (2000)
Radish (*Raphamus sativus*)	Malate and citrate	
Rye (*Secale cereale*)	Malate and citrate	
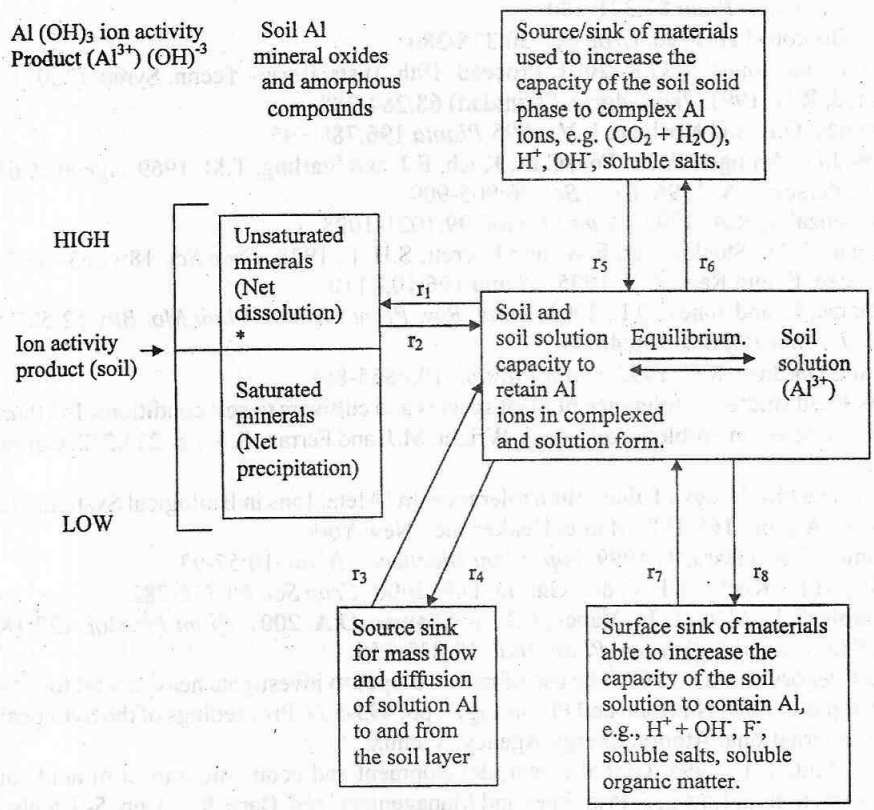
Fig. 2. Conceptual model of the rate processes and soil Al forms involved in controlling (Al^{3+}) in soil solution (Adopted from Helyar et al., 1993)
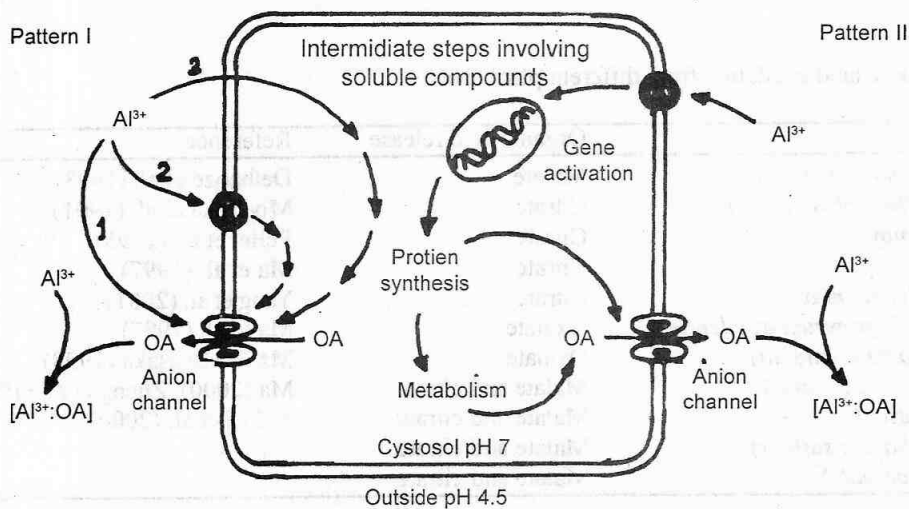

Fig. 2. Conceptual model for the aluminium (Al)-stimulated secretion of organic acid anions from plant roots (Adopted from Ma et al., 2001)