academicJournals

Vol. 10(2), pp. 12-18, March, 2015
DOI: 10.5897/BMBR2014-0234
Article Number: 1FFA2C251178
ISSN 1538-2273
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Biotechnology and Molecular Biology Reviews

Review

Correlating aluminium toxicity, heterosis and epigenetic mechanisms in maize yield improvement in acid soils

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Received 23 August, 2014; Accepted 24 February, 2015

Overuse of inorganic fertilizers have contributed to an increase in soil acidity in global arable land and consequently caused an increase in Aluminium ion ($Al^{3+)}$ toxicity and a reduction of crop yield of between 30-50% in developing countries. Studies show that Al^{3+} toxicity inhibits cell division in the root tip meristem in sensitive plants even at micromolar concentrations. Applications of lime, manure and compost are some of the most common methods used to overcome the impact of Al^{3+} toxicity. Other studies have identified natural variation for the multigenic Al^{3+} tolerance trait in many crop species and can be utilized in crop improvement. This review highlights a search for a clearer understanding of the molecular basis for Aluminium ion toxicity by correlating heterosis and epigenetic mechanisms like DNA Cytosine methylation in inbred and reciprocal maize hybrids crosses. Several recent studies indicated that the global differential gene expression regulated by epigenetic mechanisms between hybrids and parental inbred lines can potentially contribute to heterosis in maize.

Key words: Maize, heterosis, tolerance, epigenetics, aluminium ion toxicity.

INTRODUCTION

Aluminum ion (Al^{3+}) toxicity is one of the most critical factors that significantly limit crop yields on acid soils in about 50% of the arable land in the world (Kochian, 1995; Wood et al., 2000). The worldwide food insecurity problem caused by aluminium ion toxicity is only exceeded by drought stress in regard to abiotic limitation in crop production (von Uexku¨ll and Mutert, 1995). Aluminum metal (Al) has no effect on plant growth and function although it has been described as the most abundant metal on the earth crust comprising about 7% by mass of the earth's crust (Delhaize and Ryan, 1995). However, Al becomes soluble in acidic soils of pH less than 4.5 causing root growth and function inhibition, consequently reducing crop yields by about 10% in developing countries (Kinraide and Parker, 1989; Borrero, et al., 1995; Ma et al., 2001).

The ionic forms of Al^{3+} that are capable of crossing the plant membranes have been speculated to be mainly Al^{3+} and $AlOH^{2+}$ at pH below 4.5. The two are the products of $Al(OH)_3$ dissociation with the latter being known to be the most phytotoxic (Moore, 1974). The Al^{3+} toxicity has wide-ranging influences on plant growth and physiology especially at the seedling transition stage between the heterotrophic and autotrophic growth (Mona, 2008).

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Farmers have tried to battle this phenomenon via application of lime in order to raise the soil pH. This has resulted in ecological imbalance and pollution in farm lands, compelling scientists to venture into breeding crops which are tolerant to Al^{3+} in the pursuit of improving yield in major crops (Bennetzen and Hake, 2008). Hence, the problem of Al^{3+} in acid soils in the tropics is particularly complex and critical (Rao et al., 1993). However, intra-specific differences between maize inbred lines in response to Al^{3+} have provided clues to the understanding of the genetic basis of toxicity tolerance and aids in plant breeding for enhanced Al^{3+} tolerance (Tice et al., 1992).

PLANT ALUMINIUM ION TOXICITY AVOIDANCE MECHANISMS

Plants avoid Al^{3+} toxicity by either an exclusion mechanism, which keeps the Al^{3+} from entering the roots or by immobilizing the Al^{3+} species which have already entered the roots. The basis of these mechanisms has been the focus of many researchers as reviewed by Kochian et al. (2004). Nevertheless, only the exclusion mechanism which involves the chelating of Al^{3+} by organic acids like citrate, malate and oxalate from the plants have been well documented (Maron et al., 2008). Exudation of organic acids by roots have been associated with the mechanism of Al^{3+} tolerance in plants (Sasaki et al., 2004) especially $citrate^{3-}$ ions in maize roots (Piñeros et al., 2007) but, it has been shown that in maize it is not necessarily correlated with it, implying that it is not the only mechanism involved in Al^{3+} tolerance in plants (Wenzl et al., 2001). Although the mechanism of the Al^{3+} induced growth inhibition is largely poorly understood and even controversial, the primary response of Al has been traced to be at the root apex (Sivaguru et al., 1999; Sivaguru and Horst, 1998). Later findings have revealed also the involvement of the cell wall, plasma membrane, and the cytoskeleton continuum (Miller et al., 1997) hence, necessitating a further investigation into the mechanisms. Studies on Al^{3+}-tolerant maize that secretes citrate in response to Al^{3+} treatment, found out that Al^{3+} activated an anion channel on the plasma membrane and that the Al^{3+}-activated anion channel is permeable to malate and citrate anions. The activation occurred more frequently in an Al^{3+}-tolerant genotype of maize than an Al^{3+}-sensitive genotype (Kollmeier et al., 2001).The mechanisms which underlie these differences remain largely unknown.

POSSIBLE ALUMINIUM TOXICITY, HETEROTIC AND EPIGENETIC MECHANISM MODELS

Morphologically maize exhibits a greater diversity of phenotypes than perhaps any other common grain crop (Kuleshov, 1933). The most significant and practical consequence of the huge maize genotype genetic diversity is the phenomenon of positive Heterosis. This is also referred to as hybrid vigor. Our results demonstrated and confirmed past results that there are differences in Al sensitivity between cultivars but also showed that low pH could be also influencing plants independently and at lower level. The influence of heterosis due to parent of origin also referred to as epigenetic imprinting was shown to be a significant factor to be considered in heterotic breeding, for example in our experiments, epigenetic imprinting of varieties denoted as inbred lines N9 and N6 showed differences of heterosis after screening for Al^{3+} and pH tolerance in reciprocal hybrids. The cross, N9 x N6 had 10.67 % response while its reciprocal N6 x N9 had a higher (14.29%) heterotic response but less was lower at low pH (Figure 1).

The molecular explanations of the above observations, involved the re-examination of the two models put forth by Ma et al. (2001), especially the pattern II as shown in Figure 2 and the influence of low pH and Al^{3+} toxicity on the cell membrane and in the cytosol can suggest possible mechanisms for Al^{3+} and low pH resistance, tolerance and its influence to heterotic mechanisms. The gene activation due to Al^{3+} toxicity which was at that time speculative could now possibly be explained in the light of stress regulators and epigenetic mechanisms (Chinnusamy and Zhu, 2009).

We found that Al^{3+} toxicity does not influence the activation or silencing of the Al genes directly but via immobilization of the movement of secondary and primary stress regulators in the cytosol. Al^{3+} entry in the cell cytoplasm has been shown to trigger reactive oxygen species (ROS), phytohormones and other secondary stress regulators which through cascade of events is suggested to trigger gene activation in tolerant plants but not in sensitive plants. The reason why Al^{3+} interferes with other ions like Ca^{2+} could be due to pH changes in and outside the cytosol. For example, studies have shown that Al was able to block Ca^{2+} channels at the plasma membrane of cultured tobacco cells (Jones et al., 1998). This mechanism is also being discussed in this paper, although some questions still abound. For example, is the exudation of citrate by Al^{3+} tolerant plants occurring for the purpose of keeping Al^{3+} out of the cell or is it taking place solely to remove the bound Al^{3+} organic acid complex? Furthermore, recent studies show that the level of citrate efflux is poorly correlated with the level of Al^{3+} resistance among a wide range of cultivars (Piñeros et al., 2007) which indicates that citrate efflux is not the main Al^{3+} resistance mechanism operating in maize (Piñeros et al., 2005).

Uniqueness of the maize correlation of organic acids release and aluminium tolerance

Although the correlation between the release of organic acids and Al^{3+} tolerance has been shown in many plants including maize (Piñeros et al., 2002; Mariano and

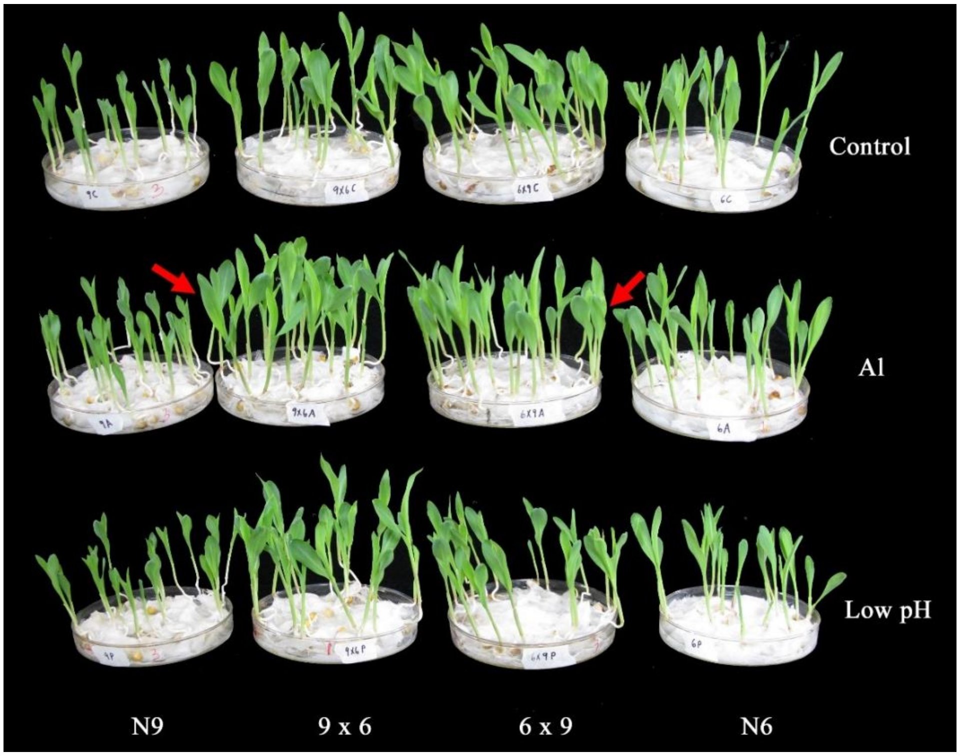

Figure 1. Intra heterotic screening using hybrids from Al sensitive inbred lines N9 and N6 and their reciprocal hybrids; shows that heterosis (red arrow) and a possibility of differences due to the genomic influences of the parent of origin (epigenetic imprinting).

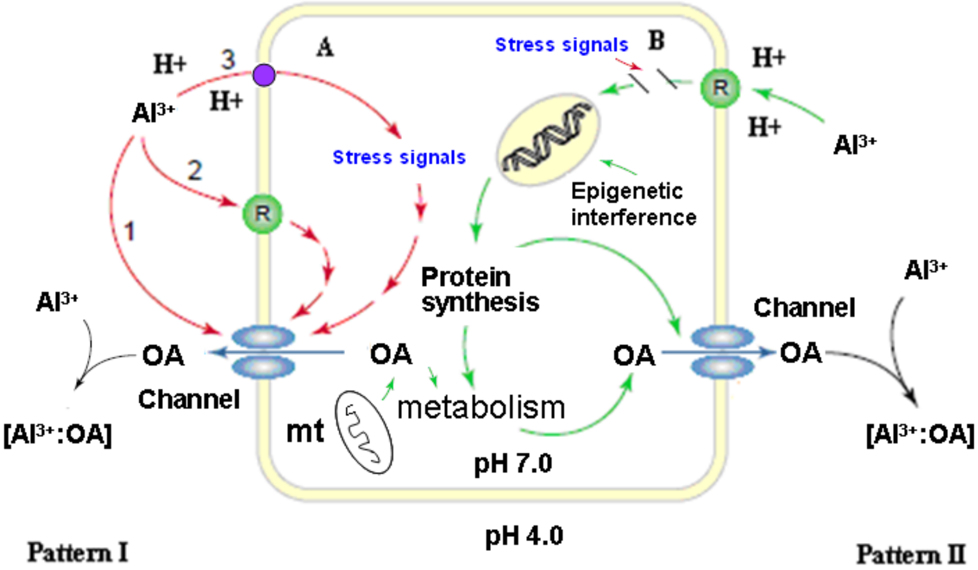

Figure 2. A Model showing Al^{3+} and low pH effects in the plant cell; Pattern I shows the three possible entry points for Al^{3+} and H^+ protons into a cell. Studies have shown some evidences of this pathway. It includes the exudation of organic acids which are coordinated from the mitochondria (mt). The pattern II has been speculative; hence an epigenetic influence is suggested to explain it together with the heterotic influence of Al^{3+} which is postulated as a byproduct of the two patterns both in the plasma membrane (**A**) and in the cytosol (**B**). The abbreviations R and OA represent the receptor and organic acid respectively (part of the diagram is adopted from Ma et al., 2001).

Keltjens, 2003), the case of maize has been isolated as being unique in that it is a more complex phenomenon which involves an array of genes alongside uncharacterized physiological mechanisms. The release of Al^{3+}-activated citrate was found not to be well correlated with Al^{3+} tolerance in maize (Piñeros et al., 2005). This suggested that there is likelihood of another tolerance mechanism which is operating in maize roots on top of the role played by the Al^{3+}-activated citrate in maize.

Some of the earlier postulated possibilities which have been put forth to explain this physiology include, a study which identified five different Al tolerance genomic regions in maize using quantitative trait locus (QTL) mapping (Ninamango-Cárdenas et al., 2003) and the description of Al tolerance as a quantitative trait which is subject to additive gene effects (Magnavaca et al., 1987; Pandey et al., 1994). Other studies on the nature of the stress which is induced by Al^{3+} toxicity have not been clear, although there are indications that an oxidative stress is induced in plant tissues exposed to these metal ions. Richards et al. (1998) and Mena et al. (2009) reported that reactive-oxygen species (ROS) can cause protein, lipid, and DNA damage in cells.

Epigenetic regulation of the maize repetitive genome

An understanding of the epigenetic regulation of the plant genome is an enormous endeavor especially for maize which contains abundant repetitive sequences (Eckardt, 2009). The revelation that epigenetic marks are influenced by environmental factors (Waterland and Jirtle, 2004) and consequently inherited transgenerationally (Rakyan et al., 2003), has boosted the investigation of how epigenetic variability can affect development and the overall phenotype of an organism.

The epigenome has been found to be most prone to dysregulation during early development because it is during this time that an organism's DNA synthetic rate is at its highest peak, and accordingly, substantial epigenetic reprogramming may also take place during this period, which is required for future proper cell and tissue development. The organism at this period is also characterized to have a high vulnerability to environmental stresses and hence it is at this transition stage before full autotrophic life that is predicted to be most suitable for identifying metastable epialleles. These epialleles can be variably expressed in genetically identical individuals due to epigenetic modifications caused by the stresses and are most likely established during early development (Dana et al., 2007). Environmental stresses can cause epigenetic changes to occur at higher frequencies in crop plants causing generation of phenotypic variations that are not correlated with genetic variation (Lukens and Zhan, 2007). Any disturbance of the intrinsic DNA methylation patterns in plants may lead to numerous interlinked functional and phenotypic abnormalities or adaptive opportunities (Kakutani, 2002; Rapp and Wendel, 2005). Normal plant metabolic and physiological processes can be altered during stress or disease related conditions and these changes are mainly determined by temporal changes in gene expressions that are mediators of altered cellular properties (Jiang et al., 2000). These temporal changes are hereby hypothesized as being linked to heterosis or being epigenetic in maize. The screening of inbred lines and their reciprocal hybrids (He et al., 2013) in Al^{3+} toxicity to determine; the genes or gene families involved in Al^{3+} stress and heterosis; the level of heterosis in Al^{3+} toxicity and at low pH and the subsequent analysis of cytosine DNA methylation levels in maize can contribute in identifying the mechanism which underlies the molecular basis of Al^{3+} toxicity in maize and also in correlating it to maize heterosis from an epigenetic aspect. The current situation in this field shown that some genes are differentially regulated due to Al^{3+} stress among different plant species (Ezaki et al., 1996; Hamel et al., 1998; Mao et al., 2004); although several genes are related to general stress responses which are not to particularly related Al^{3+} tolerance (Kochian et al., 2004). We tried to elucidate the Al^{3+} triggered genes by separating the low pH stress and from Al^{3+} toxicity and by using a standardized Al^{3+} sensitive maize plant to screen inbred lines and their reciprocal hybrids in the two treatments alongside the differential use of endogenous enzymes to cut and analyze the CCGG sites using the methylation-sensitive amplified polymorphisms (MSAP) (Kimatu et al., 2013). One of the main genes we found was CSLD2 (CELLULOSE-SYNTHASE LIKE D2). The Genetrees in Figure 3 represents the evolutionary history of the CSLD2 gene families as generated by using the longest protein from the gene Orthology/Paralogy prediction method pipeline at Ensembl. It shows the likely phylogenetic tree with internal nodes revealing duplication or speciation events.

This finding can extend the current understanding of epigenetic and transcriptional regulation by Al^{3+} stress in maize from heterotic and epigenetic aspects and may form the basis for more intensive and extensive genomic investigation for crop improvement in Al^{3+} toxicity prone acid soils. Interestingly, DNA methylation changes in hybrids had been correlated with the altered expression of a subset of the genes (Shen et al., 2012).

The epigenetic mechanisms and their influence in crop development

More studies on tolerance and genetic control mechanisms are needed for the development of tolerant varieties (Abate et al., 2013), for example no variety of commercial maize and sorghum has been breed which is Al^{3+} tolerant in Kenya although several studies have come up with some guidelines of what to expect, (Kisinyo et al., 2014). Epigenetic mechanisms have been studied

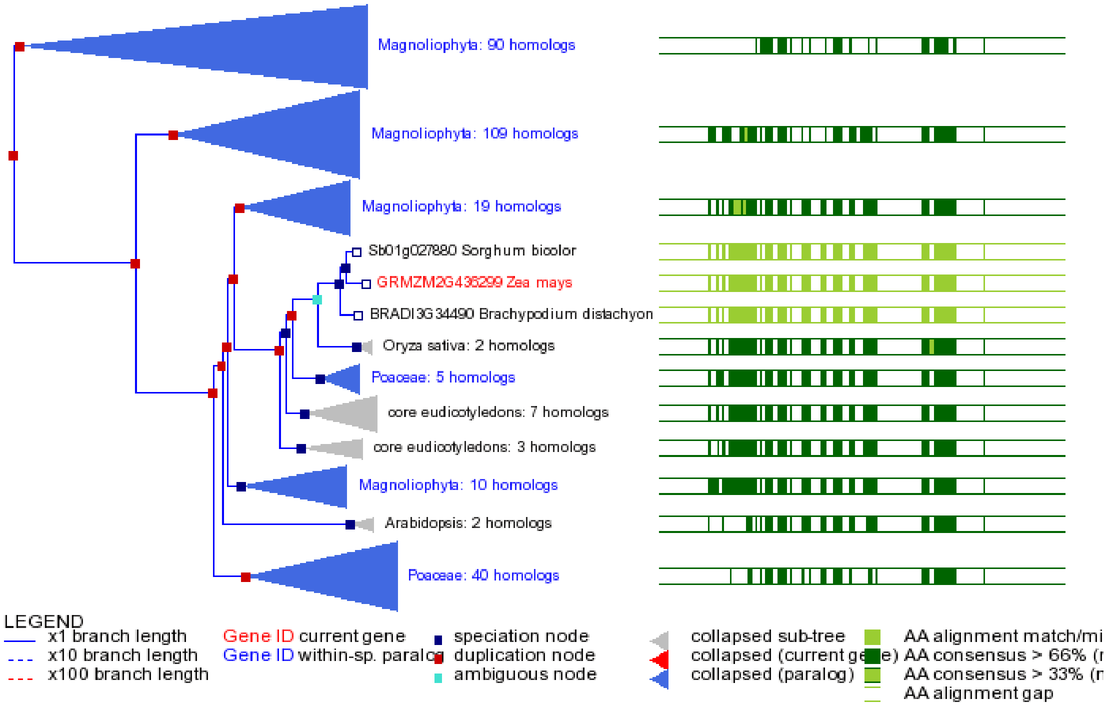

Figure 3. Gene Tree of the CSLD2; the CSLD2 is shown in red. The red squares represent duplications nodes; blue squares represent speciation nodes, giving rise to paralogues, orthologues, or between-species paralogues. Another class of node, ambiguous, is shown as a lighter blue square. The Taxonomy IDs refers to the NCBI Taxonomy Browser indexes. The green bars show the multiple alignments of the peptides while white bars show the alignment gaps.

to show that they have a significant influence in crop development, for example DNA cytosine methylation variation in flax (Fieldes et al., 2005)˙ It is interesting to note that the few studies which have been done show that crop genomes which are agriculturally superior avoid cytosine methylation as compared to those which are sensitive to methylation (Duvick and Cassman, 1999). However, low maize yields which correlated with high degree of methylation were observed in Central Iowa, United States (Lukens and Zhan, 2007).

Epigenetic selection of the new density-tolerant maize hybrids (Tani et al., 2005), in a separate study showed that the proportion of genes that are additively expressed was higher compared to a density sensitive hybrid (Guo et al., 2006). DNA methylation plays a vital role in tuning gene expression in response to environmental stimuli. This role of DNA methylation as an epigenetic mark contributes to epiallelic diversity and modulation of gene regulation. Hence such differences in DNA methylation within and between genotypes need further studies which can contribute to heritable trait differences for selection during abiotic crop improvement programs. Because trait differences which are caused by methylation have also been observed within natural populations (Cubas et al., 1999). Recent studies by Schmitz et al. (2013), who studied the level, pattern and origin of epigenomic variation in *A. thaliana* by characterizing the genomes, methylomes and transcriptomes of wild populations of *A. thaliana*, proposed that, though single CG methylation polymorphisms do not have a genetic basis in this species, genetic variation does affect RNA-directed DNA methylation (RdDM) which occurs at differentially methylated regions. Thousands of methylation quantitative trait loci were identified in these regions. Therefore, there is evidence that RdDM-targeted genes might have chosen the transposon silencing mechanism to preserve their silenced condition in vegetative tissues and trans-generationally, and ensure appropriate expression vital for germ-line and seed development. Hence, we should be careful not to attribute all epigenetic changes to a single factor like aluminium ion toxicity although the extent and inheritability of such variations can be of significant importance in future crop breeding programs. There are strong suggestions that other processes that effect epigenetic changes like the siRNA-mediated transcriptional gene silencing pathway and other non-coding repeats are functionally interlinked and hence further mutant involving studies are needed to unfolding these mechanisms (Xiong et al., 1999; Alleman et al., 2006). Furthermore, epigenetic marker-assisted breeding strategies can be applied to select for agronomical desirable epigenetic quantitative traits in crops (Zhang and Hsieh, 2013).

Conflict of interests

The author(s) did not declare any conflict of interest.

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