

Interaction of aluminium and drought stress on root growth and crop yield on acid soils

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Abstract

Background Aluminium (Al) toxicity and drought stress are two major constraints for crop production in the world, particularly in the tropics. The variation in rainfall distribution and longer dry spells in much of the tropics during the main growing period of crops are becoming increasingly important yield-limiting factors with the global climate change. As a result, crop genotypes that are tolerant of both drought and Al toxicity need to be developed.

Scope The present review mainly focuses on the interaction of Al and drought on root development, crop growth and yield on acid soils. It summarizes evidence from our own studies and other published/related work, and provides novel insights into the breeding for the adaptation to these combined abiotic stresses. The primary symptom of Al phytotoxicity is the inhibition of root growth. The impeded root system will restrict the roots for exploring the acid subsoil to

absorb water and nutrients which is particularly important under condition of low soil moisture in the surface soil under drought. Whereas drought primarily affects shoot growth, effects of phytotoxic Al on shoot growth are mostly secondary effects that are induced by Al affecting root growth and function, while under drought stress root growth may even be promoted. Much progress has recently been made in the understanding of the physiology and molecular biology of the interaction between Al toxicity and drought stress in common bean (*Phaseolus vulgaris* L.) in hydroponics and in an Al-toxic soil.

Conclusions Crops growing on acid soils yield less than their potential because of the poorly developed root system that limits nutrient and water uptake. Breeding for drought resistance must be combined with Al resistance, to assure that drought resistance is expressed adequately in crops grown on soils with acid Al-toxic subsoils.

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Keywords Aluminum toxicity · Cell-wall extension · Cell-wall porosity · Phytohormone · Root elongation · Soil acidity · Water relations

Introduction

Abiotic stresses such as drought, heat, soil acidity and soil salinity could cause extensive losses to global agricultural productivity and thereby impact food security, particularly in the developing countries. Resource-poor farmers are facing a range of challenges such as variability in weather patterns induced by global climate

change, soil acidity and low soil fertility due to nutrient depletion, and combinations of different abiotic stresses. It was shown that the response of plants to a combination of two different abiotic stresses is unique and cannot be directly extrapolated from the response of plants to each of the different stresses applied individually (Mittler 2006). A comparison made by Mittler (2006) of all major disasters between 1980 and 2004 in the United States caused production loss in excess of \$120 billion compared to \$20 billion loss caused by drought alone over the same period. Therefore, a combination of research approaches is urgently needed in order to understand the nature of multiple stress responses and to create avenues for developing plants that are resistant to multiple stresses yet maintaining high yields (Mittler and Blumwald 2010; Atkinson and Urwin 2012).

Soil acidity is one of the most important factors limiting crop production worldwide on approximately 30 % of the world's total land area and as much as 50 % of the world's potentially arable lands (von Uexküll and Mutert 1995). The tropics and subtropics account for 60 % of the acid soils in the world. In tropical areas about 43 % of soils are acidic comprising about 68 % of tropical America, 38 % of tropical Asia, and 27 % of tropical Africa. The factors that contribute to acid soil infertility and subsequent stunted plant growth on acid soils are complex. In acid mineral soils, a variety of individual chemical constraints and interactions among them limit plant growth. For example, in low pH soils, it is not usually hydrogen ion toxicity which affects plant growth but rather other toxicities, such as aluminium (Al) and manganese, and deficiencies of phosphorus, nitrogen, potassium, calcium, magnesium, and molybdenum (Rao et al. 1993). Aluminium toxicity is particularly severe at soil pH values of ≤ 5.0 (Foy 1974).

On many acid soils of the tropics, variability in rainfall distribution and longer dry spells during the main growing period of crops are becoming increasingly important yield-limiting factors (Beebe et al. 2011; Tang et al. 2001; Welcker et al. 2005) with the change in global climate. As a result, crop plants are needed that are tolerant of both drought and Al toxicity. In the common bean-growing regions of the Cerrados of Brazil, it is estimated that 80 % of the area is affected by intermittent drought stress. In the bean-growing acid soils of the Andean region (26 %) with its bimodal rainfall distribution, intermittent drought stress is also very common. In tropical

Africa soil acidity and Al toxicity are intense in several countries and under increasing population pressure, these acid soils are now additionally rapidly being brought into cultivation (Beebe et al. 2011; Wortmann et al. 1998). After the American continent, Asia has the second largest area of acid soils with interactions to seasonal drought in several countries (von Uexküll and Mutert 1995).

Since crop growth largely depends on the ability of roots to explore the soil and absorb water and nutrients, restriction of the development of the root system by Al will reduce crop yields if water and nutrients are limiting (Goldman et al. 1989; Kell 2011; Trachsel et al. 2010). The use of lime, phosphate fertilizers, organic matter and irrigation is highly productive particularly on acid soils, as practiced in the temperate climates of North America and Europe. However, liming is not an economically realistic alternative in regions with low potential yields because of unfavourable climatic conditions, and in many developing countries particularly in the tropics and subtropics, because the high cost is beyond the ability of low input resource-poor farmers. Also, the utilization of agrochemicals may have undesirable side effects which questions sustainability and threatens the environment (Miklas et al. 2006; Rao et al. 1993). On the other hand, even if liming can raise soil pH and overcome toxicity problems in the surface soil, the subsoil usually remains unaffected, since deep incorporation of lime is technically difficult and expensive. Therefore, studies on individual and combined stress factors of these two limitations are important to clarify the opportunities and constraints in breeding for adaptation to these soils. In this review we will summarize the knowledge on plant responses to Al toxicity and drought stress up to the molecular level, and we provide new perspectives into the breeding for the adaptation to these combined abiotic stresses.

Aluminium toxicity and root water-relations

It has been well recognized that Al can inhibit water uptake of roots and initiate drought stress (Tamás et al. 2006), mainly resulting from the modification of cell wall (CW) and plasma-membranes properties (Gunsé et al. 1997; Rengel 1996; Wagatsuma et al. 2005; Zhao et al. 1987). For sustained cell elongation and water uptake, CW loosening and synthesis of CW constitutes is required (Voesenek et al. 2003). Cell expansion requires

a driving force for water uptake by decreasing the turgor through CW stress relaxation produced by wall loosening (Schopfer 2006). Elongation of plant cells is controlled by the extensibility of CWs (McQueen-Mason and Rochange 1999). Several studies have revealed that the CW extensibility was reduced by Al (Barceló et al. 1996; Gunsé et al. 1997; Ma et al. 2004; Tabuchi and Matsumoto 2001). Gunsé et al. (1997) found that Al increased the hydraulic conductivity of an Al-resistant variety in maize (*Zea mays* L.) but decreased the hydraulic conductivity and CW extensibility of an Al-sensitive variety, suggesting that the influence of Al on the mechanical properties of the CW may play a prominent role in the Al-induced inhibition of root elongation. The rapid binding of Al in the root apoplast may reduce CW porosity and thus the mobility of higher molecular solutes. This has led to the hypothesis that Al may directly affect the root hydraulic conductivity (Kruger and Sucoff 1989; Maison and Bertsch 1997; Sivaguru et al. 2006). However, this has yet to be proven experimentally (George et al. 2012). Using artificial pectin membranes, Blamey et al. (1993) demonstrated that the binding of Al to pectin strongly reduced water permeability of the membranes. Recently, hemicellulose rather than pectins have been implicated in Al binding in CWs (Yang et al. 2011a). Further studies in *Arabidopsis thaliana* (L.) Heynh provided evidence that Al interacts specifically with xyloglucans (Zhu et al. 2012). The formation of an Al-xyloglucan complex in the CW inhibits wall loosening in the elongation zone of roots and thus contributes to inhibition of root elongation by Al. However, the role of xyloglucan-Al interaction in affecting water permeability of CWs needs to be explored.

Besides the CW, Al also rapidly affects the properties of the plasma membrane (Ishikawa and Wagatsuma 1998). Interaction of Al with membrane components modifies the membrane structural properties such as fluidity and permeability (Khan et al. 2009; Vierstra and Haug 1978; Wagatsuma et al. 2005). In the root cortical cells of Northern red oak (*Quercus rubra* L.), it was found that Al decreased the membrane permeability to water (Chen et al. 1991; Zhao et al. 1987). Water absorption into the root cells is also controlled by the water potential gradient which acts as the driving force for water uptake and build-up of turgor which is a prerequisite for cell extension. In Al-resistant wheat (*Triticum aestivum* L.) genotypes (Atlas 66 and ET8) the Al-induced increase of soluble sugars in the root cells can compensate for the net loss of osmotic

resulting from the release of malate and K^+ (Ryan et al. 1995), thus maintaining turgor and enabling the root cells to take up water and to maintain root elongation in presence of Al (Tabuchi et al. 2004).

Furthermore, gene expression analysis has revealed that Al suppressed the expression of the tonoplast aquaporins in rye (*Secale cereal* L.) (Milla et al. 2002) and induced the expression of the dehydrin gene *DHN4*, a well-known marker for water deficit in roots (Tamás et al. 2006).

Root-growth response of plants to aluminium toxicity and drought

Aluminium toxicity is the most important factor limiting plant growth on acid mineral soils (Carver and Ownby 1995; Foy 1984). A typical and most sensitive symptom of Al toxicity is a rapid (minutes) inhibition of root elongation (Delhaize and Ryan 1995; Horst et al. 1992), resulting in a reduced and damaged root system that limits uptake of nutrients and water (Kochian et al. 2004; Fig. 1). The root apex is the major perception site of Al toxicity (Ryan et al. 1993). In the root apical tissues, Sivaguru and Horst (1998) specified that the distal part of the transition zone (DTZ, 1–2 mm) is the most Al-sensitive apical root zone in maize. Application of Al to the DTZ but not the elongation zone (EZ) reduced cell elongation in the EZ to the same extent as application to the entire 10 mm root apex. Further evidence demonstrated that Al stress increased the accumulation of auxin in the root cap and root apical meristematic zone (MZ) (Kollmeier et al. 2000; Sun et al. 2010), while Al inhibited the basipetal transport of auxin (Hasenstein and Evans 1988; Kollmeier et al. 2000; Shen et al. 2008), supporting the proposal that the basipetal auxin signal transport was involved in the regulation of Al-stress signal transduction between the TZ and EZ (Fig. 1). The importance of the TZ as a main target of Al was also confirmed in common bean (*Phaseolus vulgaris* L.) by Rangel et al. (2007). However, in contrast to maize, in common bean both the transition zone (TZ, 1–2 mm) and elongation zone (EZ) are targets of Al injury.

Root elongation is also inhibited under water stress, but there are two main differences between Al and drought stress: (i) under drought stress shoot growth is much more affected than root growth (reviewed by Yamaguchi and Sharp 2010), whereas short and medium-term Al excess may strongly reduce root growth without affecting shoot growth (Kochian et al.

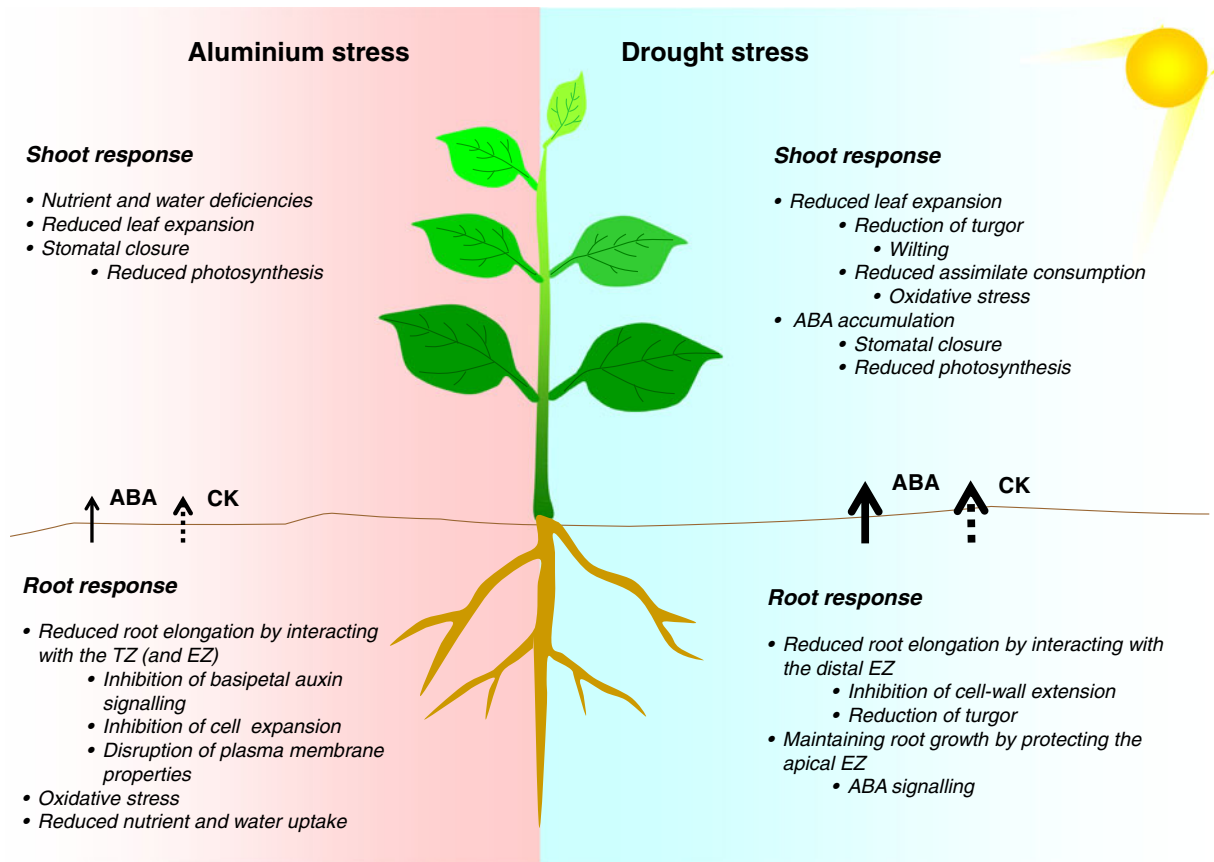


Fig. 1 Schematic representation of factors responsible for root and shoot-growth inhibition by Al toxicity (*left*) and drought stress (*right*). Short-term Al toxicity inhibits root elongation by interacting with the transition zone (TZ) and potentially the elongation zone (EZ) through the inhibition of basipetal auxin-signal transport, cell expansion and disruption of plasma membrane properties. Long-term Al stress causes oxidative stress and reduce nutrient and water uptake of roots, and subsequently results in nutrient and water deficiencies, reduction of leaf expansion, stomatal closure and reduced net photosynthesis of leaves. Drought stress inhibits root elongation by interacting

with the distal EZ through inhibition of cell-wall extension and reduction of turgor, while maintaining root growth by protecting the apical EZ through abscisic acid (ABA) signaling. In shoots drought stress reduces leaf expansion through the reduction of turgor and assimilate consumption leading to leaf wilting and oxidative stress, respectively, whereas the ABA accumulation causes stomatal closure and reduced net photosynthesis of leaves. ABA and cytokinin (CK) signalling might be involved in root to shoot communication under both Al and drought stress. Continuous and dashed arrows indicate enhanced or inhibited fluxes, their thickness the size of the flux

2004; Yang et al. 2009); (ii) Al toxicity reduces cell elongation along the entire elongation zone (Kollmeier et al. 2000), whereas under water deficit or osmotic stress cell elongation is inhibited only in the basal and central elongation zones (definition of zones according to Ishikawa and Evans 1993), but maintained toward the root apex (Sharp et al. 1988) in the distal and apical elongation zones (Shimazaki et al. 2005) (Fig. 1).

The maintenance of root elongation in the root apex is mainly achieved by three potential mechanisms: osmotic adjustment, modification of cell-wall extension and the accumulation of abscisic acid (ABA) (Sharp et

al. 2004; Yamaguchi and Sharp 2010; Fig. 1). The different response of root elongation under Al and drought stress appears of ecological advantage, because inhibition of root growth by Al in the Al-toxic subsoil allows the plants to more efficiently forage the more nutrient-rich surface soil for nutrients and water (Hairiah et al. 1995), while the maintenance of root growth under drought allows the roots to grow into the subsoil for better foraging of the subsoil for water and nutrients (Whitmore and Whalley 2009).

However, it has to be kept in mind that in soils particularly under field conditions, declining soil

moisture does not only induce water deficit in the roots but also increase the mechanical impedance of the soil which, additionally, strongly limits root growth (see comprehensive review by Bengough et al. 2011). There is only little information available on the interaction between mechanical impedance and Al toxicity on root growth. Foy et al. (1999) related the failure of Al-resistant crop genotypes to restricted root development in Al-toxic acid subsoil to its high bulk density. Horst et al. (1990) addressed this aspect and suggested, based on the comparison between hydroponically and sand-culture grown plants, that mechanical impedance alleviates Al toxicity by enhancing the release of high molecular weight root exudates (mucilage) protecting the root apex from Al injury (Horst et al. 1982).

The effect of combined drought and Al stresses on root growth has hardly been addressed in the past. It has been postulated that a decrease in soil-water content during drought may increase the toxic Al concentration in the soil solution thus enhancing Al toxicity in plants (Schier and McQuattie 2000) which was confirmed by Yang et al. (2012) (Fig. 2). In Scots pine and Norway spruce, water deficit more strongly reduced the root elongation-rate and numbers of growing roots in a soil with pH 3.8 and high levels of Al than in a pH 5.9 soil and lower Al levels (Bartsch 1987). Krizek and Foy (1988a) and Krizek et al. (1988) observed that drought exacerbated the effects of Al toxicity in plants, and increasing the soil-moisture level reduced Al toxicity in barley (*Hordeum vulgare* L.) and sunflower (*Helianthus annuus* L.). Schier and McQuattie (2000)

found that at low soil moisture the growth of ectomycorrhizal pitch pine (*Pinus rigida* Mill.) seedlings was more inhibited by Al, and Al toxicity symptoms in roots were more severe. However, enhanced Al toxicity at low soil moisture was not in agreement with their results that drought stress reduced the Al concentration in leaves of sunflower (Krizek and Foy 1988b) and roots of ectomycorrhizal pitch pine (Schier and McQuattie 2000). Drought-induced lower Al accumulation in plants has been reported in Norway spruce seedlings (Slugeňová et al. 2011), leaves of evergreen Mediterranean oak (*Quercus ilex* L.) (Sardans and Peñuelas 2007) and in common bean (Yang et al. 2010). Using polyethylene glycol (PEG 6000) to simulate drought stress in hydroponics, Yang et al. (2010) found that PEG 6000 strongly blocked the Al accumulation in the root tips and consequently reduced the toxic Al-induced inhibition of root elongation in common bean. This PEG 6000-caused exclusion of Al from the root tips of common bean could not be explained by a decrease of cell-wall negativity determined by the concentration of cell-wall pectins and its degree of methylation (Eticha et al. 2005; Schmohl and Horst 2000; Yang et al. 2008), nor by enhanced citrate exudation from the root apex which has been shown to play a key role in Al exclusion and resistance in bean (Miyasaka et al. 1991; Yang et al. 2000; Rangel et al. 2010). Aluminium exclusion was mainly caused by the alteration of CW porosity resulting from PEG 6000-induced dehydration of the root apoplast (Yang et al. 2010).

It is important to note that PEG 6000 has been amply used as an ideal non-absorbed osmoticum to induce osmotic stress owing to its low penetration into the apoplastic and symplastic space because of its high molecular weight and size (Carpita et al. 1979; Hohl and Schopfer 1991), and thus it allows mimicking the response of plants to drought stress in hydroponic studies. It has been reported early in the 1960s that PEG can be used to modify the osmotic potential of nutrient solution in hydroponics and thus induce water deficit in a relatively controlled manner (Lagerwerff et al. 1961). Higher molecular weight ($MW \geq 6000$) of PEG solution mimic dry soil more closely than solutions of low-MW osmotica such as mannitol, sorbitol, inorganic salts or PEG of MW less than 6000, which infiltrate the CW and cause damages to the cell membrane (Fan and Blake 1997; Veslues et al. 1998). The consistency of the expression of 11 among 12 selected CW and osmotic stress-associated genes by PEG and

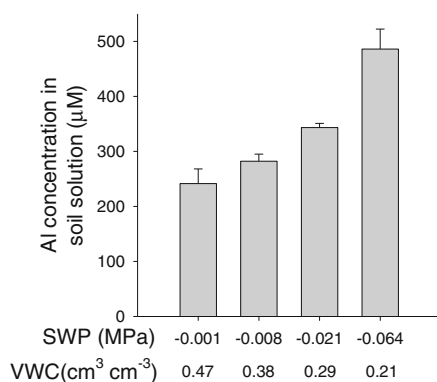


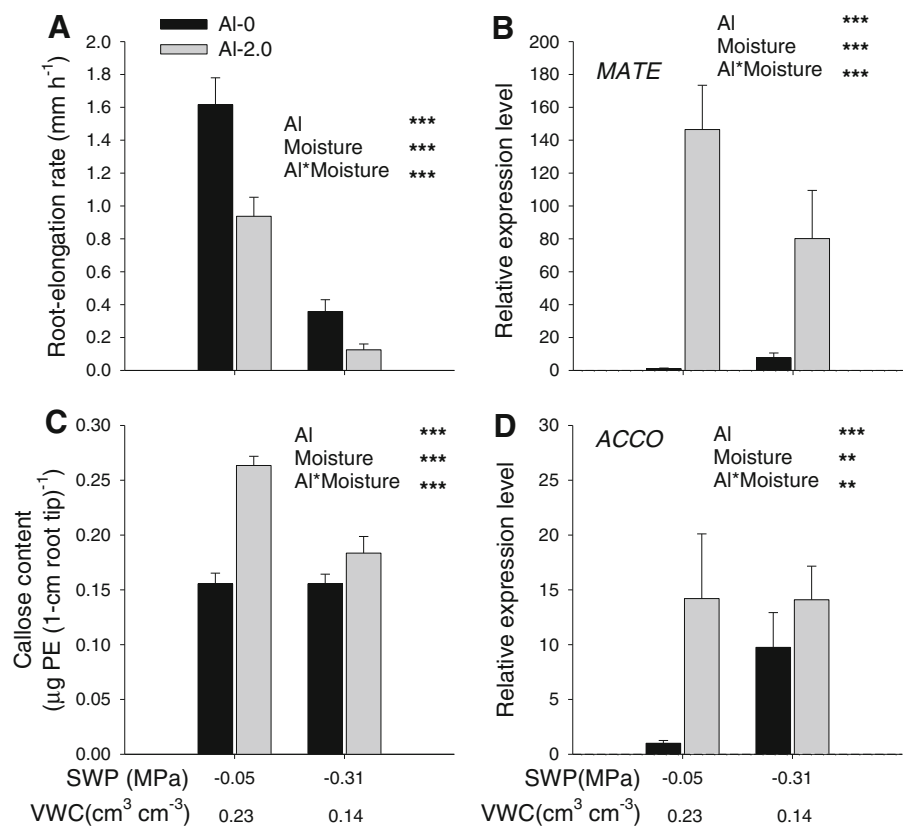
Fig. 2 Total soluble aluminium concentration in the soil solution under different levels of soil moisture. The soil solution from the incubated soil treated with 2 g $AlCl_3 \cdot 6H_2O$ was obtained by centrifugation. Bars represent means \pm SD, $n=3$. SWP: soil-water potential; VWC: volumetric water content. From Yang et al. (2012)

by drought in soil in root tips of common bean (Yang et al. 2011b; 2012) supports the use of PEG 6000 in hydroponics in determining short-term drought stress responses of root apices at the molecular level. However, it appears that the expression levels of most of genes changes more in root apices exposed to dry soil at a water potential of -0.31 MPa than at a water potential of -0.60 MPa in hydroponics. These great differences might result from the possibility to acclimate to osmotic stress (PEG 6000) in hydroponic culture, allowing sufficient water uptake to resume root elongation partly within 24 h, whereas in dried soil the adaptation to water deficit fails. This hypothesis can well explain the difference in the interactive effect of Al toxicity and drought stress between the two experimental approaches (PEG-simulated drought in hydroponics, Yang et al. 2010 and dried acidic soil, Yang et al. 2012); whereas PEG-simulated drought alleviated inhibition of root elongation by Al, low soil moisture enhanced root-growth inhibition in Al-toxic soil (Fig. 3a).

The PEG-induced inhibition of Al accumulation in the root tips of common bean (Yang et al. 2011c) was

consistent with PEG-suppressed Al-induced expression of the multidrug and toxin extrusion (MATE) family protein gene (Fig. 3b) confirming the PEG-induced alleviation of Al toxicity at the molecular level. Also, the reversion of another reliable Al-sensitive indicator (callose formation, Wissemeyer et al. 1987; Staß and Horst 2009) in the root tips by low soil moisture strongly supported this result under soil conditions (Fig. 3c; Yang et al. 2012). The Al-activated citrate transporter MATE has been suggested to be responsible for citrate exudation from the root tips and thus Al resistance in several plant species (Furukawa et al. 2007; Magalhaes et al. 2007; Maron et al. 2010; Yang et al. 2011b; Yokosho et al. 2011). In common bean, the expression of *MATE* is a prerequisite for citrate exudation, but the build-up of Al resistance in genotype Quimbaya in comparison to the Al-sensitive genotype VAX-1 is mainly dependent on the capacity to sustain the synthesis of citrate for the maintenance of the cytosolic citrate pool that enables continuous exudation (Eticha et al. 2010; Rangel et al. 2010). The *MATE* gene behaves as an Al sensor in common bean, independent of the Al resistance of the genotype (Eticha et al. 2010).

Fig. 3 Root-elongation rate (a), callose content (b) and the expression of *MATE* (c) and *ACCO* (d) in the root tips (1 cm) of common bean genotype VAX 1 as affected by soil moisture and Al supply ($\text{g AlCl}_3 \cdot 6\text{H}_2\text{O kg}^{-1}$ soil). Two-day-old seedlings were grown in soil for 24 h. Bars represent means \pm SD, $n=12$ for (a), $n=4$ for (b), and $n=3$ for (c and d). qRT-PCR was performed using the β -tubulin gene as internal standard. For the ANOVA (two-way), **, and *** denote significance at $P < 0.01$, and $P < 0.001$, respectively. SWP: soil-water potential; VWC: volumetric water content. Compiled from Yang et al. (2012)



In addition, it has been speculated that the expression of the gene coding for 1-aminocyclopropane-1-carboxylic acid oxidase (ACCO) catalysing the last step of ethylene biosynthesis (Wang et al. 2002) contributes to the Al-induced inhibition of root elongation (Eticha et al. 2010; Sun et al. 2007). The high sensitivity of ACCO gene expression in response to Al in common bean was further verified by a significant correlation between ACCO expression, root elongation and Al concentration in the root tips (Yang et al. 2011b). However, different from the MATE gene, low soil-moisture stress also induced the expression of the ACCO gene in the root tips of bean and thus the expression remained high at Al and drought dual stresses (Fig. 3d; Yang et al. 2012).

The fact that in contrast to the hydroponic studies with PEG 6000, under soil conditions, combined drought and Al stresses aggravated the inhibition of root elongation beyond the effects of the individual stresses in an additive manner in common bean does not support the suggestion (Schier and McQuattie 2000) that low soil moisture-increased Al concentration in the soil solution (see Fig. 2) may enhance Al rhizotoxicity in plants. Circumstantial evidence rather indicated that the remaining Al in the root tips renders the root apex more drought-sensitive (Yang et al. 2012). Therefore, these results support the hypothesis that at low soil moisture in acid soils Al may prevent the acclimation of roots to drought and inhibit root growth into deeper soil layers thus restricting the acquisition of water from the subsoil. This hypothesis is supported by the results of Goldman et al. (1989) who found that soybean (*Glycine max* L.) plants grown in soil at combined Al and drought stress had lower levels of leaf relative water content, water potential, and lower transpiration rates than individual stress factors. Butare et al. (2011) also showed that in an acid Al-toxic soil, combined Al/drought stresses led to a more severe inhibition of root growth in *Phaseolus acutifolius* A. Gray and the Mesoamerican common bean genotypes. By analysis of the combined effect of short-term water-deficit stress and Al toxicity on citrate exudation from soybean roots, Nian et al. (2004) showed that the individual stress mainly impeded root growth, while combined stresses reduced both root and shoot growth. The Al-resistant genotype PI416937 exuded more citrate from roots than the Al-sensitive soybean genotype Young after 2 days of recovery from combined stresses.

Shoot-growth response of plants to aluminium toxicity and drought

In recent years, there has been a significant progress on our understanding of the shoot-growth responses of plants to aluminum toxicity and drought (Aftab et al. 2010; Beebe et al. 2009, 2010; Blum 2010; Chaves et al. 2003; Chen 2006; Manavalan et al. 2009; Okiyo et al. 2010; Wang et al. 2006; Zhang et al. 2007). The effect of Al and drought on shoot and root growth and the factors responsible for the inhibition of root and shoot growth owing to Al toxicity and drought stress are depicted in Fig. 1. There is a fundamental difference in the response of shoot growth to Al and drought: since in most plant species Al is not readily translocated from the roots to the shoots (Al excluders), Al effects on shoot growth are thus secondary effects induced by Al affecting root growth and function (George et al. 2012). In contrast, under drought stress the development of the root system is usually less inhibited than shoot growth, and may even be promoted (Sharp and Davies 1989; Sharp et al. 2004). For several crops such as maize, soybean, cotton (*Gossypium hirsutum* L.) and squash (*Cucurbita maxima* Duch.) the primary root maintains substantial elongation rates at water potentials lower than -1.5 MPa, whereas shoot growth is completely inhibited at much higher water potentials (Spollen et al. 1993).

Given the complexity of indirect factors possibly involved in Al-induced shoot growth inhibition it is not surprising that the described common responses of shoots to Al toxicity include: cellular and ultrastructural changes in leaves, increased rates of diffusion resistance, reduction of stomatal aperture, decreased photosynthetic activity, chlorosis and necrosis of leaves, decrease in total leaf number and size, and a decrease in shoot biomass (Mossor-Pietraszewska 2001). Al toxicity affects growth and gas exchange (Pereira et al. 2000; Simon et al. 1994a, b), carbohydrate content (Graham 2002), mineral nutrition (George et al. 2012; Lidon et al. 1999), organic acid metabolism (Watanabe and Osaki 2002) and nitrogen metabolism (Xiao 2002) of the shoot.

A primary response of plants to drought stress is the inhibition of shoot growth. The reduction in water availability from low soil moisture results in a complex response in shoot growth characterized by a decrease in the water potential of plant tissues, particularly in growing tissues, which leads to a variety of modifications in different plant processes (Blum 2010). These

include growth inhibition, accumulation of ABA and osmoprotecting solutes, stomatal closure, reduced transpiration and photosynthetic rates, induction of mechanisms of scavenging reactive oxygen species (ROS), and changes in the accumulation levels of proteins and mRNAs (Chaves et al. 2003; Manavalan et al. 2009; Rosales et al. 2012). Recent work on common bean shoot-growth responses to drought indicated that remobilization of photosynthates from vegetative shoot structures to pods, and from pod wall to grain is an important mechanism of retaining yield under drought (Beebe et al. 2010; Rao et al. 2009). If drought stress is not relieved, it leads to interrupted reproductive development, premature leaf senescence, wilting, desiccation and death (Neumann 2008). Decrease in leaf water potential during stress induces stomatal closure, leading to a reduction of CO₂ availability and consequently a decline in net photosynthetic rate and water-use efficiency (Bota et al. 2004; Chaves et al. 2003). The decline in net photosynthetic rate could lead to decrease in shoot growth rate and dry matter production (Lawlor and Tezara 2009). The inhibition of leaf growth and net photosynthetic rate under drought stress could allow diversion of essential solutes from growth requirements to stress-related house-keeping functions, such as osmotic adjustment that improves cell-water retention and turgor maintenance.

Signal molecules produced in the root in addition to water and nutrients are important mediators of shoot physiological processes. Root-to-shoot signalling is often considered to be important in regulating shoot growth and water use when soil conditions change (Dodd 2005). Hormones such as ABA and cytokinins (CKs) have been implicated in the root–shoot signaling, either acting in isolation or concomitantly (Chaves and Oliveira 2004; Davies et al. 2005; Schachtman and Goodger 2008; Wilkinson et al. 2012). ABA has been identified as one of the major chemical signals involved in stomatal functioning by the regulation of long-distance transport and modulation of ABA concentration at the guard cells (Chaves et al. 2003). However, increased CK concentration in xylem sap decreases stomatal sensitivity to ABA and promotes stomatal opening directly (Wilkinson and Davies 2002). Sivaguru et al. (2003) speculated that Al may interfere with ABA transport and signaling, and thus lead to the closure of stomata. The potential involvement of ABA and CK in root–shoot communications under Al and drought stresses are simplistically depicted in Fig. 1.

Understanding the interaction of aluminium/drought stresses on root growth

Cell-wall porosity

The plant cell-wall is a composite structure consisting of a cellulose–hemicellulose framework embedded within a matrix of pectins and proteins. This chemical structure determines its plastic and elastic properties allowing deformation in different directions (Carpita and Gibeaut 1993). Under water deficit the loss of water in the apoplast will result in a collapse of wall structure, and consequently reduction of wall porosity and polymer adhesion or cross-linking (Fig. 4; Moore et al. 2008b; Yang et al. 2011c).

The pores of the CW are the first barrier for mobile solutes such as ions, proteins, and water penetrating the wall (Brett and Waldron 1996), and plant cells interact with their environment through the porous network of the CW (Carpita et al. 1979). The pore size mainly depends on CW structure, hydrophobicity, CW chemical composition, and physical properties (Carpita et al. 1979; Chesson et al. 1997). According to Baron-Epel et al. (1988) the pore size of the CW is mainly controlled by the pectic matrix. Any change in the factors affecting the pectic matrix may change the porosity. For example, it was reported that low temperature decreased the pore size of the CW by modifying CW composition (Bauchot et al. 1999; Rajashekar and Lafta 1996). Boron can affect the pore size by influencing the borate ester cross-linked pectic network in the primary CW (Fleischer et al. 1999). Enhanced Al toxicity in boron-deficient plants could be related to the pore size of the CW (Horst et al. 2010). The pectic side chains may also control CW porosity as has been suggested by Brummel (2006). Water stress increased the formation of pectic side chains in a drought-tolerant cultivar of wheat (Leucci et al. 2008). Our finding of the PEG-induced reduction of CW pectin content in the root tips of common bean suggest that osmotic stress may interfere with the CW structure consequently resulting in the rearrangement of the wall polymers and thus affecting CW porosity (Yang et al. 2010). The reduced CW porosity resulting from the PEG-induced osmotic stress restricts the penetration of cations into the apoplast depending on the hydrated ionic radius: the higher the hydrated ionic radius, the lower was the ion accumulation in the root tips or ethanol-isolated CWs of root tips (Al³⁺>La³⁺>

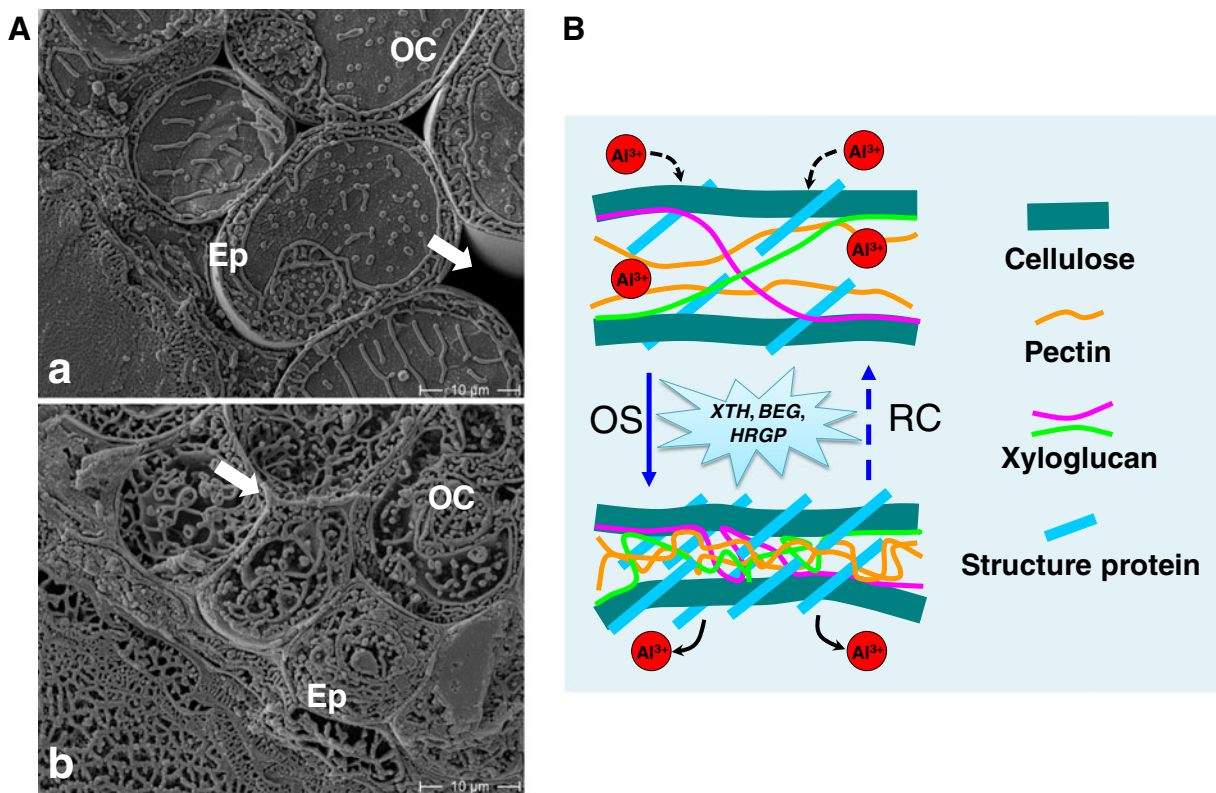


Fig. 4 **A** Freeze-fracture scanning electron micrographs of root-tip cross-sections (1–5 mm from the root apex) of common bean genotype VAX 1 grown for 4 h in the absence (*a*) or presence (*b*) of PEG (150 gL⁻¹ PEG 6000, -0.60 MPa osmotic potential, pH 4.5). Pictures show the epidermis (Ep) and one outer cortical cell layer (OC). Arrows indicate the presence (*a*) or absence (*b*) of intercellular spaces between the epidermis and the outer cortical cell layer. Scale bars=10 µm. **B** A model representing the effect of osmotic stress (OS) on the cell wall (CW) structure and Al

binding, and the possible role of CW modification-related genes or structure proteins in the OS-induced change in CW porosity and thus Al binding to the CW in common bean plants. The solid and dashed arrows indicate the recovery (RC) from osmotic stress, respectively. XTH: xyloglucan endotransglucosylase/hydrolases; BEG: beta-1,3-glucanase; HRGP: hydroxyprolin-rich glycoprotein. Based on Yang et al. (2010, 2011c)

Sr²⁺>Rb⁺) (Yang et al. 2010). Using freeze-fracture scanning electron microscopy (FSEM) Yang et al. (2010) showed that PEG 6000 but not PEG 1000 strongly reduced the intracellular spaces of the epidermis and the outer cortical cell layers in the root tips of common bean (Fig. 4a), indicating that PEG 6000 causes dehydration of the root apoplast more than PEG 1000 with its higher mobility in the apoplast owing to its smaller hydrodynamic radius (Kuga 1981; Yang et al. 2010).

Under water deficit the protection of plant cells from CW collapse and subsequent damage requires the maintenance of CW flexibility. Studies with resurrection plants have demonstrated that CW flexibility can be modified by a constitutively high content of pectin-associated arabinans (Moore et al. 2006,

2008a). Water is the most abundant component of the CW (approximately 75–80 % water) and decides on its pectic hydro-gel properties and thus viscoelastic nature (Cosgrove 1997). Loss of water from the CW matrix can seriously disrupt the polymer organization. The highly hydrophilic pectin can attract and sequester water and may behave as a lubricant between individual CW layers and thus avoid the CW collapse and damage from water loss. In addition, the hydrophilic protein dehydrin, which is supposed to be localized in the CW, may also play a role similar to pectin in preventing the CW from water deficit-caused mechanical fracture (Layton et al. 2010), maintaining the elastic extension (reversible stretching) properties and, consequently, the porosity of the CW. Also, CW structural proteins such as the hydroxyproline-rich

glycoprotein extensin, can cross-link with other polymers in the CW and thus affect CW porosity (Brett and Waldron 1996). A *HRGP* gene encoding hydroxyprolin-rich glycoprotein has been proposed to participate in the modification of CW porosity during PEG-induced osmotic stress in common bean (Fig. 4b; Yang et al. 2011c).

Loss of water from the CW matrix can bring the polymers into close proximity to each other, and thus cause polymer adhesion or cross-linking under water deficit (Moore et al. 2008b). Several CW-modifying proteins such as expansins, xyloglucan endotransglucosylase/hydrolases (XTHs), endoglucanases and pectin methylesterases (PMEs) play key roles in the modification of CW structure and thus porosity (recently reviewed by Sasidharan et al. 2011). In *Arabidopsis*, microarray analysis indicated that most of the CW-associated genes including genes encoding those above-mentioned CW-modifying proteins are down-regulated under water deficit (Bray 2004) supporting the results generated from transcriptome analysis of the drought (PEG stress)-subjected root apices of common bean by SuperSAGE (serial of analysis of gene expression) (Yang et al. 2011c). XTHs play key roles in modification of CW structure and extensibility through the cleavage and re-formation of bonds between xyloglucan chains (Bray 2004; Rose et al. 2002). The potential role of XTHs in the modification of CW porosity and Al binding to the CW during PEG-induced osmotic stress has been proposed by Yang et al. (2011c), who found that the expression of *XTH* genes was suppressed by PEG and rapidly reversed by removal of PEG stress, consistent with the change of Al accumulation in the root tips of common bean (Yang et al. 2010). In addition, the CW-loosening enzyme beta-1,3-glucanase (*BEG*) has been also predicted to be involved in the PEG-induced alteration of CW porosity (Yang et al. 2011c). Further studies are required to assess the role of those CW-modifying proteins in the alteration of CW porosity to verify the hypothesis forwarded in Fig. 4b.

Cell-wall extension

Plant CWs have the remarkable property of combining extreme tensile strength with extensibility, which plays principal roles in the control of growth and development of plants. A simplified model of the potential effects of drought and Al on cell-wall extension is shown in Fig. 5.

The progressive decrease of growth towards the basal region of root tips in the elongation zone under water deficit has been explained by reduced CW extensibility (Fan et al. 2006). Under Al stress, Al strongly binds to the negative charges provided by the carboxylic groups of galacturonic acids of the pectins (Blamey et al. 1990; Chang et al. 1999) and to hemicellulose (Yang et al. 2011a). There is little doubt that the high affinity of Al to the pectic matrix and hemicellulose will substantially affect the chemical and mechanical properties of the CW, and this Al-apoplast interaction has been proposed as the main cause of Al-induced inhibition of root elongation (Horst et al. 2010). Two possibilities have been suggested: i) Al rapidly and irreversibly displace Ca^{2+} at the site of Ca^{2+} -pectate cross-linkages, which plays a key role in controlling CW extensibility and thus cell elongation and development (Boyer 2009). The formation of cross-linkages by Al may rigidify the CW, thereby preventing wall loosening which is a prerequisite for cell elongation. ii) Strong binding of Al to the pectic matrix may prevent CW extension physically and/or physiologically by decreasing the effectiveness of CW-loosening enzymes (Wehr et al. 2004). In addition, Tabuchi and Matsumoto (2001) suggested that the Al-decreased mechanical extensibility of the CW in wheat roots could be attributed to an increase in ferulic and diferulic acids, which crosslink CW structural components and thus strengthen the CW (Brett and Waldron 1996). The water deficit-enhanced production of phenols in the root tips was made responsible for the progressive growth cessation towards the basal region in the elongation-zone of maize (Fan and Neumann 2004) and soybean roots (Yamaguchi et al. 2010).

The mechanisms involved in regulating CW extension capacity and hence root growth has been intensively investigated and frequently reviewed (Cosgrove 2005; Rose et al. 2004; Sharp et al. 2004; Wu and Cosgrove 2000). The extensibility of the CW is controlled by its structure as well as the activity of CW-modifying proteins such as expansins, XTHs and glucanases (Bray 2004; Wu and Cosgrove 2000). Under drought in Al-toxic acid soils and PEG-induced osmotic stress in hydroponics, the expression of both *XTHs* and *BEG* genes in the root tips of common bean were suppressed by both water deficit and Al stress leading to inhibition of root elongation (Yang et al. 2011c, 2012). Spatial pattern analysis of XTH by the detection of xyloglucan endotransglucosylase (*XET*) action in *Arabidopsis* and tobacco (*Nicotiana tabacum* L.) root

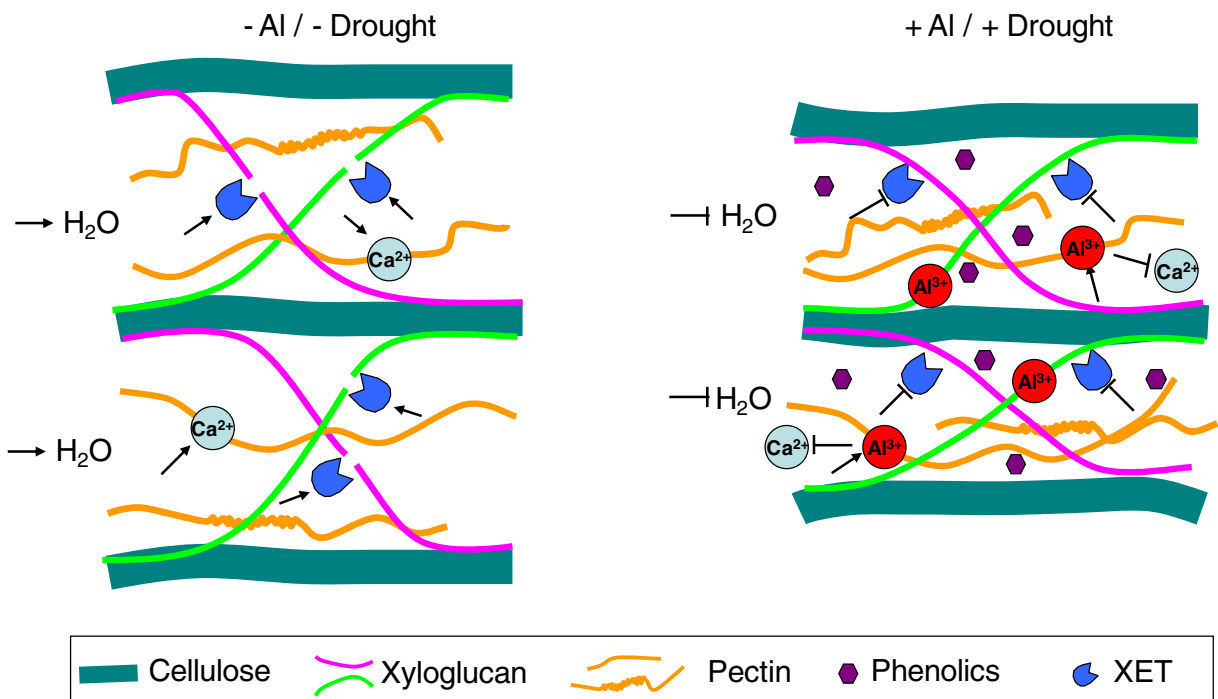


Fig. 5 A simplified model representing the effect of Al or drought stress on cell-wall extension. On the *left*, cell-wall extension without the stresses is shown: H₂O penetration into the cell wall and the symplast allows the build-up of osmotic pressure and high activity of the cell-wall modification-enzyme XET thus allowing cell-wall extension. On the *right*, the effect of drought or Al on cell-wall extension is shown: reduced

hydration of the cell wall and Al-inhibited XET activity, and strong binding of Al to pectins and xyloglucans reduce cell-wall extensibility. Al and drought-enhanced crosslinking of cell-wall structures by phenolics further reduce extensibility. XET: xyloglucan endotransglucosylase. Based on Yang et al. (2010, 2011c, 2012)

tips, showed that XTH in the cortex and epidermis of the elongation zone is primarily involved in wall loosening for root elongation (Vissenberg et al. 2000).

Phytohormone signal network

The growth and development of plants under environmental stresses is mediated by phytohormones such as ABA, auxin and CK, gibberellin (GA), ethylene and jasmonic acid (JA) (Wolters and Jürgens 2009). Based on the studies with common bean (Yang et al. 2012), the crosstalk between phytohormones in response to drought and combined drought/Al stresses affecting root growth is schematically shown in Fig. 6. Among the phytohormones, it is well known that ABA is produced under water-deficit conditions and plays an important role in the response of plants to drought. In the root tips, the accumulation of ABA increases towards the root apex (Saab et al. 1992) and is required for the maintenance of maize primary-root elongation

at low water potentials (Sharp 2002; Sharp et al. 2004; Yamaguchi and Sharp 2010). Zeaxanthin epoxidase (ZEP), 9-cis-epoxycarotenoid dioxygenase (NCED) and abscisic aldehyde oxidase (AAO) are the critical enzymes involved in the biosynthesis of ABA (Seo and Koshiba 2002). The expression of the genes encoding these enzymes is induced by drought in different plant species (Audran et al. 1998; Chernys and Zeevaart 2000; Iuchi et al. 2000; Qin and Zeevaart 1999; Seo et al. 2000; Seiler et al. 2011; Thompson et al. 2000; Yang et al. 2012) and is indicative of improved drought resistance (Iuchi et al. 2001; Qin and Zeevaart 2002).

Several hydroponic studies have shown that Al induces ABA production in the root tips of soybean (Hou et al. 2010; Shen et al. 2004) and barley (Kasai et al. 1993), which was supposed to regulate Al resistance mechanisms (Hou et al. 2010; Shen et al. 2004). However, growing common bean in an acid Al-toxic soil slightly but significantly reduced the ABA accumulation in the

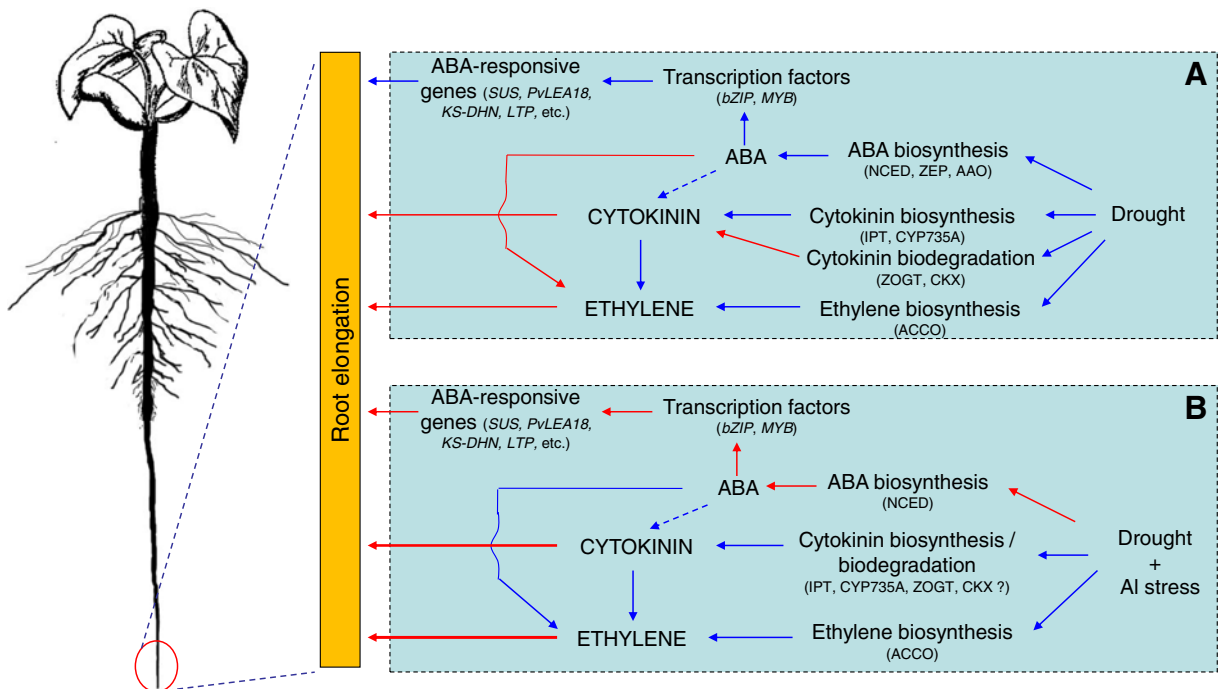


Fig. 6 Schematic representation of the potential regulatory mechanisms involved in acclimation to drought of root apices of common bean and how Al stress interferes with this acclimation. In **a**: Sole drought stress increase ABA, ethylene and cytokinin (CK) concentrations in root tips by the regulation of biosynthetic or degrading enzymes such as *NCED*, *ZEP*, *AAO* (ABA biosynthesis), *IPT*, *CYP735A*, *ZOGT*, *CKX* (CK biosynthesis and biodegradation) and *ACCO* (ethylene biosynthesis). The excess accumulation of CK and ethylene inhibit root elongation, whereas the drought-stimulated ABA accumulation maintains root elongation in the apical elongation zone by up-regulating the expression of ABA-dependent genes. The blue and red arrows indicate up- and down-regulated changes, respectively. In **b**: In comparison with the sole drought effect,

additional Al exposure leads to an aggravated inhibition of root elongation by the suppression of ABA-dependent drought-induced gene regulation and by further promoting CK and related ethylene synthesis. The blue and red arrows in **b** indicate the enhanced and inhibited changes in comparison with the sole drought-induced changes in **a**, their thickness represents the magnitude of the changes. *IPT*, adenosinephosphate isopentenyl-transferase; *CYP735A*, cytochrome P450 monooxygenase 735A; *CKX*, CK oxidase/dehydrogenase; *ZOGT*, zeatin-O-glucosyltransferase; *ACCO*, 1-aminocyclopropane-1-carboxylic acid oxidase; *ZEP*, zeaxanthin epoxidase; *NCED*, 9-cis-epoxycarotenoid dioxygenase; *AAO*, abscisic aldehyde oxidase. Based on Yang et al. (2012)

root tips and had no effect on the expression of genes involved in ABA biosynthesis (Yang et al. 2012). In spite of this, under combined Al and drought-stress conditions Al suppressed the drought-stimulated ABA production as well as the expression of the *NCED* gene in the root tips. Therefore, the suppression of ABA production in the root tips by Al reduced the drought resistance of the roots. The critical role of ABA in drought resistance depends on its involvement in the regulation of drought-induced genes (Bray 1997, 2002). The transcription factors *bZIP* and *MYB* are responsible for the down-stream regulation of ABA-dependent genes (Shinozaki and Yamaguchi-Shinozaki 1997, 2007). The consistency of the expression of *bZIP*, *MYB*, and ABA-dependent genes such as *SUS* (sucrose

synthase), *PvLEA18* (late embryogenesis abundant protein), *KS-DHN* (KS-type dehydrin) and *LTP* (lipid-transfer protein) (Brocard-Gifford et al. 2004; Hundertmark and Hinch 2008; Orellana et al. 2010) with the change of ABA accumulation and the expression of *NCED* in the root tips of common bean under Al and drought stress, suggest that the Al toxicity-enhanced drought sensitivity of the root apex is due to the impact of the gene regulatory network involved in ABA signal transduction (Yang et al. 2012).

In addition to ABA, ethylene is implicated in the inhibition of root elongation (Le et al. 2001). The results by Yang et al. (2012) indicated that the Al-aggravated drought-induced inhibition of root elongation in common bean may partly be due to an

enhanced expression of the ethylene biosynthesis gene *ACC* (see Fig. 3d) and thus ethylene production in root tips.

The interplay of phytohormones plays a crucial role in the regulation of root growth and has been widely studied. For example, several studies have demonstrated that ethylene regulates root growth mainly through effects on auxin biosynthesis and transport-dependent auxin distribution (Růžička et al. 2007; Stepanova et al. 2007; Swarup et al. 2007; Sun et al. 2010). The CK-auxin interaction is fundamental in controlling root development (reviewed by Moubayidin et al. 2009). It is well known that CKs may also strongly inhibit root growth (Werner et al. 2001). Under water-deficit conditions, ABA can suppress ethylene production, and the maintenance of root elongation requires increased ABA levels to prevent excess ethylene production (LeNoble et al. 2004; Sharp et al. 2000; Spollen et al. 2000; Sharp 2002). Ding et al. (2008) found that ABA could suppress CK activation of cell division in the roots of *Medicago truncatula* Gaertn.. Takei et al. (2004) observed that ABA treatment highly reduced the expression of the CK biosynthesis genes *CYP735A1* and *CYP735A2* in the roots of *Arabidopsis*. Cytokinin stimulated ethylene biosynthesis (Chae et al. 2003) and ethylene mediated the CK-induced inhibition of root elongation as observed in pea (*Pisum sativum* L.) (Bertell and Eliasson 1992), *Arabidopsis* (Cary et al. 1995; Růžička et al. 2009) and common bean (Massot et al. 2002). However, the analysis of the IAA content in the root tips of common bean under Al and drought stress conditions by Yang et al. (2012) did not support an involvement of the auxin-dependent regulatory signaling network in the Al-drought interaction on root growth. The reason for the aggravation of the inhibition of root elongation by drought through Al (Yang et al. 2012) may partly be due to reduced ABA levels, promoted CK production (Fig. 7) and subsequently stimulated synthesis of ethylene in the root tips of common bean as depicted in Fig. 6.

Interaction of aluminium-drought stresses on crop yield

Crop yield is the result of a multitude of developmental, physiological and biochemical processes and their interactions at any level of plant organization and any level of biological scale that are under genetic control.

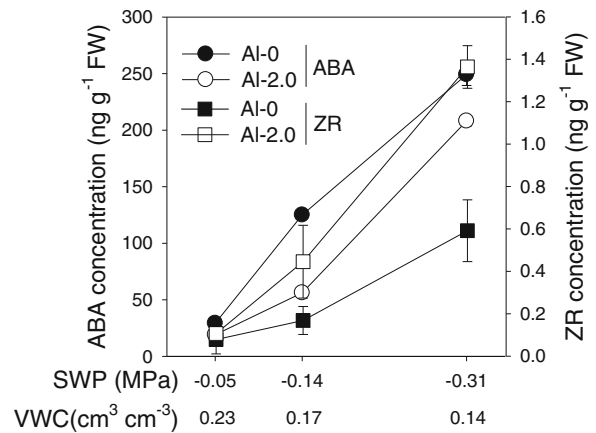


Fig. 7 Abscisic acid (ABA) and zeatin riboside (ZR) concentrations in the 1-cm root tips of common bean genotype VAX-1 as affected by soil moisture and Al supply ($\text{g AlCl}_3 \cdot 6\text{H}_2\text{O kg}^{-1}$ soil). Two-day-old seedlings were grown in soil for 24 h. Bars represent means \pm SD, $n=3$. SWP: soil-water potential; VWC: volumetric water content. Compiled from Yang et al. (2012)

The sum total is integrated toward a final effect on yield (Blum 2010). Knowledge on the interaction of Al-drought stresses on crop yield is limited. The most direct method of evaluating the interaction of Al and drought stresses is by measuring economic yield (grain or forage) under field conditions. Field evaluation for soil acidity and Al toxicity is normally conducted in two duplicate tests: one in an unamended, naturally acid plot, and the other in a lime-amended plot. The data are reported as the ratio of grain or forage yield in the unamended plot to that in the lime-amended plot to adjust for differences in yield potential without soil-acidity stress. This methodology was used by a number of researchers to screen crop and forage germplasm for their adaptation to acid soils (Baier et al. 1995; Carver and Ownby 1995; Johnson et al. 1997; Marschner 1995; Rao et al. 1993, 1998, 2004, 2011; Rao 2001; Tang et al. 2003c; The et al. 2001). Field studies conducted on an acid soil in Cameroon by The et al. (2001, 2006, 2012) indicated that yield of the soil acidity-tolerant maize cultivar ATP-SR-Y was up to 60 % higher than that of the soil acidity-sensitive cultivar Tuxpeno-Sequia. Among the maize germplasm tested, there was a large variability in grain yield on non-corrected acid as well as on corrected non-acid soil. One of the phenotypic plant characteristics that best correlated with the adaptation of the genotypes to soil acidity was seminal root length (The et al. 2001).

It has been reported that Al toxicity restricts the yield of many crops particularly in regions with acid subsoils throughout the world (Sumner et al. 1986). Aluminium toxicity decreases drought resistance and the use of subsoil nutrients (Wang et al. 2006). Deleterious effects of subsoil soil-acidity on crop yield will thus be influenced by the extent to which a plant depends on the subsoil for supply of water and nutrients, especially when the topsoil dries out (Jozefaciuk and Szatanik-Kloc 2001; Stodart et al. 2007; Tang et al. 2001, 2003a, b). Sorghum (*Sorghum bicolor* (L.) Moench) growing on acid soils yields less than its potential because of the poorly developed roots that cause reduced nutrient and water uptake (Meda and Furlani 2005; Bernel and Clark 1998). During the rainy season the soil moisture in the topsoil can sufficiently sustain shoot growth, while in the dry season the low rainfall will force the roots to explore deeper subsoil for water. The growth of roots grown in the acidic subsoil will then subsequently suffer from Al toxicity and the Al-impeded root growth will further restrict the exploitation of deeper subsoil for water.

Similar to acid soil stress, yield under drought stress with reference to yield under non-stressed conditions, has normally been employed as the primary phenotypic selection criterion in improving drought resistance in crops (Blum 2010). Farmers frequently request early maturing cultivars in environments where the growing season is limited by water availability. However, early maturity also has disadvantages including limited yield potential. Recent breeding efforts for improving drought resistance in common bean resulted in small seeded Mesoamerican lines (coded as SER and SEN) with up to 36 % greater yield per day in unfavorable environments (Beebe et al. 2008). The lesson learned from this work was that shoot biomass and yield should be selected for while retaining the ability to partition greater proportion of photosynthates from vegetative plant structures to grain (Rao et al. 2009; Beebe 2012).

Crop-yield improvement-strategies for adaption to combined aluminium toxicity and drought stress

Crop yield improvement for adaptation to acid soils with seasonal drought stress at the molecular and physiological level is very complex and challenging.

The simplest approach to breeding for adaptation to combined Al toxicity and drought stress is to select for grain or forage yield which are the integrating traits, and to carry out the selection in a managed stress environment. A possible breeding strategy for developing crops for superior adaptation to combined stress conditions of soil acidity and drought could involve screening germplasm under well watered and drought-stressed conditions on an acid soil and make selections based on superior performance (yield) under both conditions. It is widely recognized by breeders and agronomists that field screening is highly variable and complex. Thus there is a need to select for secondary phenotypic traits for both Al and drought resistance which can be easily identified using screening methods at laboratory, greenhouse and field level. These phenotypic traits should be linked to molecular genotypic traits. Significant progress in crop improvement can be achieved by the use of screening methods where the stresses are carefully managed and by choosing parents of crosses with desirable shoot and root traits for genetic recombination to improve yield under individual and combined stress factors (Beebe et al. 2008, 2009).

A number of shoot and root traits contribute to improved drought adaptation (Blum 2010). The root traits maximise water uptake and the shoot traits optimise the use of absorbed water for producing grain during drought stress. In sorghum, the panicle weight of the first filial generation (F1) of hybridisation between inbred P1 (drought-tolerant) and P2 (Al-resistant) was greater than either P1 or P2 under both stress and non-stress conditions, suggesting that multiple stress resistance can increase sorghum productivity (Okiyo et al. 2010). Using different bean species, Butare et al. (2011) found that Al partially ameliorated the negative effects of water stress in Al-resistant *Phaseolus coccineus* L. genotypes. This response was strongly in contrast with Al-sensitive *Phaseolus acutifolius* and the Mesoamerican common bean genotypes, where combined stress led to a more severe inhibition of root development. These observations were consistent with the results obtained by Yang et al. (2012). Thus, it appears promising to use interspecific crosses with *Phaseolus coccineus* to improve combined drought and Al resistance of common bean (Butare et al. 2012).

Both Al toxicity and water stress should be considered in breeding for better adaptation to acid soils.

Amelioration of these constraints in the topsoil can be achieved by liming, fertilization and irrigation. For example, in eastern regions of the Western Australian wheat belt, Porter and Wilson (1984) found that the application of lime to the acidic subsurface soil layers increased wheat yields by 69 % and 175 % at two sites. Using the computer model APSIM (Agricultural Production Systems Simulator), Tang et al. (2003a) concluded that liming and nitrogen application increased yields of wheat in all rainfall zones, but the yield increments were much greater in the high than the low rainfall zones, and that improved yields were correlated with increased rooting depth and associated decreased nitrate-N leaching. Doss and Lund (1975) reported that the reductions in the yield of cotton resulting from shallow root systems on acid sub-soils can be overcome by frequent irrigation of the surface soil, but rooting depth and pattern were not affected by irrigation. The management of plant nutrients is very helpful to alleviate the adverse effects of drought (Waraich et al. 2011). However, the soil amendments are neither economic options for poor farmers nor effective strategies for alleviating the subsoil acidity stress. Tang et al. (2003a, b, c) have found that the yield benefits arising from growing Al-resistant wheat were greater than those from ameliorating soil acidity by liming. Therefore, screening of crop germplasm and developing appropriate varieties with high resistance against combined Al toxicity and drought could lead to higher and more stable crop yields, particularly in the smallholder farms of the tropics (Beebe et al. 2009; Beebe 2012).

In two near-isogenic wheat genotypes differing in Al resistance, Tang et al. (2001) found that the Al-resistant genotype ET8 can produce more than five times the root length of Al-sensitive genotype ES8 in the acidic subsoil. The genotypic variation in growth and yield of wheat grown under subsoil acidity results from the difference in root proliferation into the subsoil and hence in the exploitation of water and nutrients in the acidic subsoil layer (Tang et al. 2002). The genotypic variation in response to liming appears to result from the difference in the sensitivity of root proliferation to low pH and high Al (Tang et al. 2003b). Wasson et al. (2012) proposed that wheat varieties with a deeper root system, a redistribution of branch root density from the surface to depth, and with greater radial hydraulic conductivity at depth would have higher yields in those rainfed systems where crops rely on soil moisture from deeper

layers for grain filling. The evaluation of the trait and development of selection processes for root-system traits (deep, highly branched roots) combining laboratory and field phenotypic screening in a breeding programme have been thoroughly reviewed by these authors.

Therefore, deep rooting is particularly important for the improvement of yield in the breeding for adaptation to Al toxicity and drought stress (Sponchiado et al. 1989). Combining functional genomics with traditional breeding (Ishitani et al. 2004; Manavalan et al. 2009; Mir et al. 2012) will contribute greatly to bridging the gap between phenotype and genotype in the context of breeding for complex traits such as adaptation to abiotic stresses.

Conclusions and future perspectives

Drought can be exacerbated by subsoil Al toxicity, which reduces root elongation and restricts the plant roots to explore the acidic subsoil to absorb water, and thus diminishes the ability to avoid drought stress. Little is known about the interaction of Al toxicity and low soil moisture stress at the root-tip level. In common bean, drought/osmotic stress reduced Al uptake and Al toxicity. However, Al toxicity enhanced the drought-induced inhibition of root elongation. The physiological and molecular evidence suggests that the reason for this Al-aggravated drought sensitivity of root apices is a disturbance of the gene regulatory network involved in ABA signal transduction and cross-talk with other phytohormones such as CKs and ethylene that are necessary for maintaining root growth under drought. These suggestions need to be substantiated through further studies in the future focusing on the following aspects: i) Understanding the role of genes related to CW modification in the interaction of Al toxicity and drought stress; ii) Clarification of the cross-talk of phytohormones in the Al-regulated drought-inhibited root elongation necessary to better understand the internal regulatory mechanism of root growth under individual and combined stresses using reverse genetic approaches; iii) Comparative analysis of the relationship between Al toxicity and drought stress in monocots and dicots which appears attractive given the different structural components of the CW.

Effects of Al on shoot growth are mostly secondary effects that are induced by Al affecting root growth and function, while under drought stress root growth may even be promoted. There is limited knowledge on

the interaction of Al and drought stresses on crop yield. Present knowledge suggests that Al toxicity decreases drought resistance primarily by reducing the use of subsoil water and nutrients, and crops yield less under combined stresses.

Breeding for drought resistance must be combined with resistance to Al, to assure that drought resistance is expressed adequately in crops grown on soils with acid Al-toxic subsoils. A possible breeding strategy could involve screening germplasm under well watered and drought-stressed conditions on an acid soil and make selections based on superior performance (yield) under both conditions. Since field screening is highly variable and complex secondary phenotypic traits for both Al and drought resistance which can be easily identified using screening methods at laboratory, greenhouse and field level need to be linked to molecular genotypic traits.

An integrated improvement of resistance against both stress factors is likely to be more productive than considering them in isolation. It appears necessary to identify molecular markers QTLs (quantitative trait loci) for adaptation to combined Al and drought stresses with focus on genes controlling root growth increasing the efficiency of traditional breeding approaches. The challenge is to identify QTLs of major effects that are independent of the particular genetic background and clone the genes in the QTL. The ability of next generation sequencing and advanced metabolic profiling to co-sequence or co-screen a large number of F2 or RILs coupled with statistical linkage analysis could improve the efficiency of molecular breeding for improved adaptation to combined stresses of Al and drought.

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