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REVIEW

The role of arbuscular mycorrhizas in decreasing aluminium phytotoxicity in acidic soils: a review

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Abstract Soil acidity is an impediment to agricultural production on a significant portion of arable land worldwide. Low productivity of these soils is mainly due to nutrient limitation and the presence of high levels of aluminium (Al), which causes deleterious effects on plant physiology and growth. In response to acidic soil stress, plants have evolved various mechanisms to tolerate high concentrations of Al in the soil solution. These strategies for Al detoxification include mechanisms that reduce the activity of Al^{3+} and its toxicity, either externally through exudation of Al-chelating compounds such as organic acids into the rhizosphere or internally through the accumulation of Al–organic acid complexes sequestered within plant cells. Additionally, root colonization by symbiotic arbuscular mycorrhizal (AM) fungi increases plant resistance to acidity and phytotoxic levels of Al in the soil environment. In this review, the role of the AM symbiosis in increasing the Al resistance of plants in natural and agricultural ecosystems under phytotoxic conditions of Al is discussed. Mechanisms of Al resistance induced by AM fungi in host plants and variation in resistance among AM fungi that contribute to detoxifying Al in the rhizosphere environment are considered with respect to altering Al bioavailability.

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Introduction

Importance and origin of acidic soils

Soil acidity is one of the most important constraints to agricultural productivity worldwide, with acidic soils representing about 40 % of the total arable lands (Sumner and Noble 2003). Plant growth in acidic soils is limited by a set of conditions, including the excess of protons (H^+), aluminium (Al) and manganese (Mn) phytotoxicities, and deficiencies of essential nutrients, such as phosphorus (P), calcium (Ca), magnesium (Mg) and molybdenum (Mo) (Driscoll et al. 2001; Bolan et al. 2003; Fageria and Baligar 2008). Moreover, the limited agricultural productivity of acidic soils is due to diminished microbial activity as a consequence of the presence of high concentrations of deleterious chemical species of Al (Robert 1995; Fageria and Baligar 2003; Dahlgren et al. 2004).

Natural sources of soil acidity include the decomposition of organic matter, microbial respiration and plant absorption of cations, especially ammonium (NH_4^+), processes that have a direct impact on soil pH (Martens 2001; Tang and Rengel 2003). Erosion and leaching of basic cations, such as potassium (K^+), sodium (Na^+), calcium (Ca^{2+}) and magnesium (Mg^{2+}), also contribute to the acidification of soils, which is increased in areas with excessive rainfall. Furthermore, excessive addition of acidifying fertilizers, especially ammonium salts, and other agricultural practices are anthropogenic contributors to the acidification of soils (Bolan et al. 2003). Other human activities, including industrial emissions of sulphur dioxide (SO_2) and nitrogen oxides (NO_x) that generate acid precipitation and mining that generates acidity in soil/surface substrates, also acidify soils (Evangelou 1995; Driscoll et al. 2001; Frazer 2001; Norton and Veselý 2004; Clair and Hindar 2005). Thus, natural soil acidification is widespread and is exacerbated by human activity, which limits plant productivity in many regions around the world.

Aluminium forms in soil and phytotoxicity

Aluminium comprises approximately 8 % of the earth's crust, being the third most abundant element after oxygen and silicon (Ščančar and Milačič 2006). Most Al is present as oxides and aluminosilicates, which are solid amorphous or crystalline minerals that are not harmful to plant roots. However, many of these Al-containing minerals exhibit pH-dependent solubility, and the diverse ionic species of Al exhibit pH-dependent speciation that contributes to Al phytotoxicity in varying degrees. In acidic solutions (pH <5.0), Al exists as octahedron hexahydrate, $Al(H_2O)_6^{3+}$, which by convention is named Al^{3+}. When pH increases, Al^{3+} undergoes successive hydroxylations to form $Al(OH)^{2+}$, $Al(OH)_2^{+}$, $Al(OH)_3$ and $Al(OH)_4^{-}$ at pH 7–8 (Stumm and Morgan 1996). Acidic soils favour the solubilization of Al-containing minerals and generate the phytotoxic Al^{3+} ion, producing the main limiting factor for plant growth on such soils (Wagatsuma and Ezoe 1985; Pintro et al. 1998; Watanabe and Okada 2005). Aluminium toxicity to plants has been convincingly demonstrated only for Al^{3+} and the complex $AlO_4Al_{12}(OH)_{24}(H_2O)_{12}^{7+}$ (Al_{13}) (see Kochian et al. 2005). However, some experimental results also indicate the toxicity of hydroxylated Al compounds, mainly $Al(OH)^{2+}$ and $Al(OH)_2^{+}$ (Kinraide 1997). The Al^{3+} ion has a high affinity for oxyanions and various elements and compounds in the soil solution, such as organic acids, which modify Al availability and phytotoxicity.

Due to its importance in limiting agricultural and forest productivity, there have been numerous studies that describe the toxic effects of Al on plant root growth and physiology. The sites of these effects within the plant have been broadly reported to occur in the cell wall matrix of the root tip (Horst et al. 1999; Jones et al. 2006; Staß and Horst 2009), at the plasma membrane interface (Rengel and Zhang 2003; Ahn and Matsumoto 2006; Bose et al. 2010a), within the cytoplasm (Rengel et al. 1995; Jones et al. 1998; Rengel and Zhang 2003; Guo et al. 2007) and within subcellular compartments including the cytoskeleton (Vázquez et al. 1999; Blancaflor et al. 1998; Yamamoto et al. 2001). Many of the phytotoxic effects of Al induce broad-range secondary effects, such as disruption of signalling pathways and the production of reactive oxygen species (ROS). Together, these primary and secondary effects ultimately disrupt cell homeostasis and limit cell division, root elongation and the capacity of Al-sensitive plant genotypes to exploit water and nutrient reserves in the soil, reducing the health and productivity of crops and forests growing on acidic soils (Driscoll et al. 2001; Barceló and Poschenrieder 2002; Kochian et al. 2005; Ma 2007; St. Clair et al. 2008).

Aluminium tolerance mechanisms in higher plants

Plants markedly differ in their capacity to tolerate Al, and the mechanisms involved have been the focus of extensive research in the past 20 years (Delhaize and Ryan 1995; Ma et al. 2001; Ryan et al. 2001; Kochian et al. 2004, 2005). Aluminium-resistant plant species and/or genotypes within species have evolved mechanisms that detoxify Al and reduce its impact on cell physiology, allowing these species/genotypes to grow when exposed to Al in the environment. The mechanisms fall broadly into two categories that function within the rhizosphere to alter the chemical form and toxicity of Al in the environment and/or function within plant cells to reduce the negative effects of Al on plant metabolism (Delhaize and Ryan 1995; Jones et al. 1998; Ma et al. 2001; Barceló and Poschenrieder 2002; Kochian et al. 2004, 2005; Panda and Matsumoto 2007; Inostroza-Blancheteau et al. 2012).

Exudation of organic (carboxylic) acids from roots and the external detoxification of Al by chelation with these compounds are two of the most widely reported mechanisms used by plants to overcome Al stress (Delhaize et al. 1993; Li et al. 2000; Kollmeier et al. 2001; Piñeros et al. 2002; Shen et al. 2002; Zhao et al. 2003). Exudation of organic acids leads to the chelation of Al^{3+} in the rhizosphere and consequently reduces Al uptake by roots and its subsequent impacts on metabolism and growth. There is a close relationship between the alleviation of Al toxicity and the effectiveness of the different carboxylic anions produced by plant roots in forming stable Al complexes based on their stability constants ($\log K_s$), ranging between 7.4 and 12.3 for citrate, >6.1–7.3 for oxalate, >5.1–5.4 for malate and >3.2–4.6 for succinate, among other organic acid anions, with variations dependent on methods of measurement (Martel and Smith 1977; Charlet et al. 1984; Hue et al. 1986; Pawlowski 1998).

The Al-activated efflux of organic acids, which is mediated by different systems in different plant species, is often specific for Al and may exhibit rapid or delayed kinetics (Ryan et al. 2001; Barceló and Poschenrieder 2002; Panda and Matsumoto 2007). Organic acid exudation in response to Al exposure has received considerable attention, and the underlying physiology and molecular biology are being elucidated (Wang et al. 2007; Liu et al. 2009; Maron et al. 2010). For example, the release of malate by Al-resistant *Triticum aestivum* genotypes reduced the accumulation of Al in Al-sensitive root tips and allowed root growth under Al exposure (Delhaize et al. 1993; Ryan et al. 1995). This response has been ascribed to the *Alt1* gene in *T. aestivum* that functions to rapidly release malate into the rhizosphere, chelating Al^{3+} and reducing its interactions with the cell wall, plasma membrane and subsequent uptake into the cell (Hoekenga et al. 2006). Similar systems have been identified for a variety of species, including *Zea mays* (Piñeros et al. 2002; Maron et al. 2010), *Hordeum vulgare* (Zhao et al. 2003; Wang et al. 2007) and *Arabidopsis thaliana* (Goodwin and Sutter 2009; Liu et al. 2009).

In addition to carboxylic acids, the exudation of diverse phenolic compounds may confer Al tolerance due to the ability of phenolic compounds to form stable complexes with the metal in the rhizosphere (Barceló and Poschenrieder 2002). Kidd et al. (2001) reported that, while Al exposure induced oxalate exudation in *Z. mays* varieties, patterns of production were not correlated with Al resistance and were modified by the composition of the rooting media. However, constitutive or induced Al resistance in these genotypes was associated with the exudation of catechol, catechin, quercitin and/or curcumin that quantitatively far exceeded the exudation of organic acids. The function of phenolic compounds as an Al tolerance mechanism is not well characterized, and their lesser affinity for Al^{3+} compared with organic acid anions, especially at acidic pH where H^+ and Al^{3+} ions would compete for binding sites within phenolic compounds, may reduce their efficacy to chelate Al^{3+} (Ofei-Manu et al. 2001).

As an alternative to these extracellular Al detoxification systems, an increase in the production of compounds that chelate Al intracellularly and reduce its interactions with plant metabolic processes has been proposed as an internal Al tolerance mechanism. Internal detoxification of Al is limited to Al-accumulating species, such as *Fagopyrum esculentum* (Ma et al. 2001) and *Hydrangea macrophylla* (Ma et al. 1997). In these species, the accumulation of Al to levels as high as 15,000 $\mu g\,g^{-1}$ was related to high intracellular concentrations of oxalate and citrate, respectively. Moreover, Klug and Horst (2010) noted that Al exposure of *F. esculentum* also led to the exudation of oxalate into root intracellular spaces and that Al resistance in this species may rely on both protection of the cell wall from Al binding and uptake and detoxification of Al internally. In addition, the up-regulation of ATP-binding cassette type transporters in many species exposed to Al suggests that there may be a broad-based expression of metabolic systems that compartmentalize metal complexes, in this case Al complexes, in the vacuole (Sasaki et al. 2002; Larsen et al. 2005; Zhen et al. 2007; Goodwin and Sutter 2009).

In addition to these reported mechanisms of Al resistance in plants, the vast majority of higher plants form associations with soil microorganisms that may synergistically promote or stimulate these mechanisms in the plant host or confer Al resistance to plant hosts through the operation of microbial-based systems. Among these microorganisms, arbuscular mycorrhizal (AM) fungi play a key role in fostering growth of most agricultural species and increase the productivity and environmental stress resistance of many ecologically and economically important tree species (Smith and Read 2008).

Arbuscular mycorrhiza and plant response to soil Al

The AM symbiosis is the oldest and most extensive plant–fungus association present in the world (Wang and Qiu 2006; Bonfante and Genre 2008), occurring in about 85 % of all the vascular plants in almost all terrestrial ecosystems (Öpik et al. 2006). As well as facilitating the acquisition of nutrients, especially P, from soil to host plants in exchange for fixed carbon (C) (Marmeisse et al. 2004; Cavagnaro 2008; Javaid 2009; Podila et al. 2009; Plassard and Dell 2010; Smith et al. 2011), the fungal symbionts play a crucial role in the alleviation of diverse abiotic stresses present in the soil environment (Jeffries et al. 2003; Evelin et al. 2009; Gamalero et al. 2009; Gianinazzi et al. 2010), including the presence of phytotoxic levels of Al (Rufyikiri et al. 2000; Yano and Takaki 2005; Klugh and Cumming 2007). AM fungi may increase the capacity of their host plants to withstand abiotic soil stresses through modulation of the edaphic environment and detoxification of harmful compounds in the mycorrhizosphere. Their production of low molecular weight exudates or glomalin and the biosorption of metals to fungal hyphae will modulate interactions between plants and soil Al (Barceló and Poschenrieder 2002; Janouskova et al. 2005; Borie et al. 2006; Gohre and Paszkowski 2006; Bedini et al. 2009; Podila et al. 2009; Zhang et al. 2009). In addition, increased host plant stress resistance may result from elevated uptake of P and other essential nutrients, changes in tissue metabolite concentrations and/or elevated activity of stress resistance pathways that are induced by the symbiosis (Tanaka and Yano 2005; Javot et al. 2007; Andrade et al. 2009; Abdel Latef and Chaoxing 2011; Karimi et al. 2011; Meier et al. 2012). These metabolic changes resulting from root colonization by AM fungi may serve to prime physiological systems against stress-induced perturbations to homeostasis and so contribute to conferred Al resistance in higher plants.

Contribution of the AM symbiosis to plant Al resistance

The majority of studies on Al resistance species have utilized non-mycorrhizal plants or species that do not form the symbiosis, e.g. *Arabidopsis thaliana*. The work on non-mycorrhizal plants clearly informs on the limits of adaptation to Al exposure in plants. However, there is a robust literature on the differences in physiology and environmental stress responses between non-mycorrhizal and mycorrhizal plants, and the ecological, physiological and molecular processes underlying these differences have the capacity to extend the limits of Al resistance in higher plants. The first studies of Al tolerance related with mycorrhizal associations were conducted in ectomycorrhiza and woody species (Denny and Wilkins 1987; Jones and Hutchinson 1988; Cumming and Weinstein 1990; Godbold et al. 1998). Ectomycorrhizal associations decrease Al toxicity in woody species by improving nutrient absorption, through Al accumulation in the fungal mycelia (Ahonen-Jonnarth et al. 2003; Moyer-Henry et al. 2005), and active organic acid production, especially oxalic acid (Griffiths et al. 1994; Malajczuk and Cromack 1982; Sun et al. 1999; Eldhuset et al. 2007).

Al binding to hyphae, exudates and glomalin in AM associations

The AM symbiosis benefits plants in acidic soils because of the increased access to limiting nutrients and the induction of general stress resistance metabolism in the host plants. It is prevalent in well-weathered tropical soils (Cardoso and Kuyper 2006), deciduous forests (Berliner and Torrey 1989; Yamato and Iwasaki 2002; Postma et al. 2007; Diehl et al. 2008) and in extremely acidic environments (Cumming and Ning 2003; Maki et al. 2008; Taheri and Bever 2010), the soils of which are dominated by Al.

The association of AM fungi with plant roots may extend the thresholds of Al resistance by extending or augmenting the resistance mechanisms of their host plants or by providing new Al-resistance mechanisms that serve to detoxify Al in the root environment. Limiting the interactions of the Al^{3+} ion with sensitive plant physiological and metabolic processes is a unifying mechanism of Al resistance (Delhaize and Ryan 1995; Ma et al. 2001; Ryan et al. 2001; Kochian et al. 2004, 2005).

The extensive hyphal networks produced by AM fungi have the capacity of directly binding Al (Joner et al. 2000; Gohre and Paszkowski 2006) or creating an expanded mycorrhizosphere in which Al is detoxified (Li et al. 1991; Tarafdar and Marschner 1994). Several studies have reported an increased Al resistance associated with elevated Al binding in root systems colonized by AM fungi. For example, when compared to non-mycorrhizal plants, concentrations of Al in roots of AM-colonized plants were 51 % greater for *Liriodendron tulipifera* colonized by *Glomus clarum* and *Glomus diaphanum* in sand culture (Lux and Cumming 2001), 210 % greater for *Ipomoea batatas* grown with *Gigaspora margarita* in an acidic soil (Yano and Takaki 2005) and 210 % greater in *Clusia multiflora*, a tropical woody species, inoculated with several *Acaulospora* species in soil (Cuenca et al. 2001). In these cases, Al may be bound extracellularly to AM fungal cell walls or be sequestered intracellularly in fungal vacuoles by polyphosphate granules (Toler et al. 2005; González-Guerrero et al. 2008; Zhang et al. 2009). Such Al immobilization and exclusion mechanisms active in the roots of AM-colonized plants may contribute to acquired stress resistance in the host plant.

Exudation of metal-binding compounds by mycorrhizal roots also plays a role in Al resistance facilitated by AM fungi. While there exists no direct evidence that novel Al-binding compounds are induced by AM fungi in host plants, several studies indicate that root exudation is maintained by under Al exposure by the association with the fungal symbionts. Strong effects of AM on Al phytotoxicity in the presence of free Al^{3+} concentrations have been reported in *L. tulipifera* as a result of differential organic acid exudation, notably citrate, between non-mycorrhizal plants and plants colonized by one of four AM symbionts, with greatest root exudation and Al resistance being associated with *Glomus clarum* colonization (Klugh and Cumming 2007). Altered exudation affected the activity of Al^{3+} in the root zone so that across different treatments, biomass and leaf P concentration were negatively correlated and leaf Al was positively correlated with free Al^{3+} in the root zone (Fig. 1). In *Andropogon virginicus*, a similar relationship was noted among six AM fungi and non-mycorrhizal treatments, with citrate again being the dominant organic acid that was produced under Al exposure (Klugh-Stewart and Cumming 2009).

The accumulation of Al in root tissues of mycorrhizal plants is not always associated with induced Al resistance or reduced Al levels in tissues of host plants, however. Several studies on *L. tulipifera* have indicated that AM either increased (Lux and Cumming 2001) or did not affect (Klugh-Stewart and Cumming 2009) Al accumulation in leaves and roots. In addition, Cumming and Ning (2003) noted that colonization by an acidophile AM fungal consortium reduced Al concentrations in roots, but not in leaves, of *Andropogon virginicus*. In these cases, the patterns of Al accumulation may reflect changes in the activity of Al^{3+} caused by plant and/or fungal exudates as well as functional characteristics of root systems that differ among host species. For example, increased translocation of Al to shoots may occur passively and at an elevated level when AM fungi stimulate exudation and the formation of Al complexes in the mycorrhizosphere that are subsequently more mobile within the plant root and more readily enter the xylem (Lux and Cumming 2001).

In addition to maintaining exudation by host roots under Al exposure, AM fungi also have the capacity to provide novel biochemical mechanisms that may confer Al resistance to their plant hosts. Glomalin is a component of hyphal and spore walls of AM fungi (Driver et al. 2005), and it quantitatively represents a significant fraction of the pool of soil protein due to its persistence and recalcitrance in

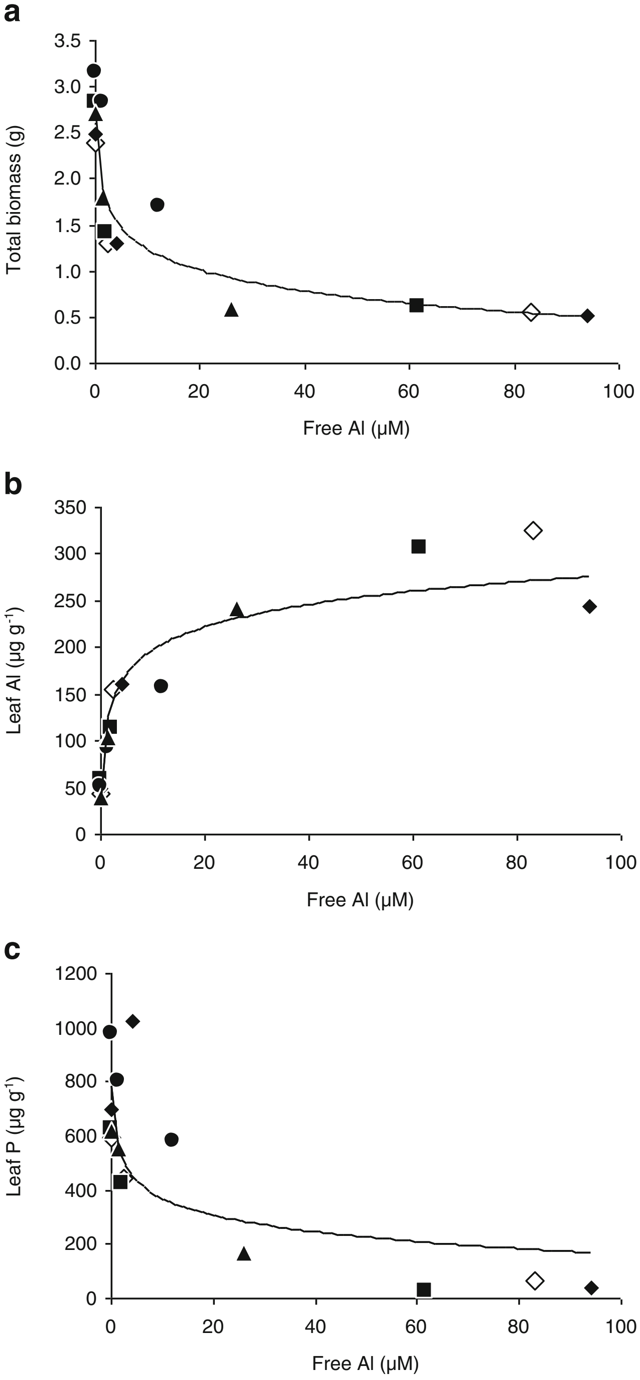

Fig. 1 Relationships between free Al (Al^{3+}) concentrations estimated in root zones and **a** plant biomass, **b** leaf aluminium (Al) concentration and **c** leaf phosphorus (P) concentration of non-mycorrhizal and mycorrhizal *L. tulipifera* in the presence of 0, 50 and 200 μM Al. *White diamond*, non-mycorrhizal; *black diamond*, *Acaulospora morrowiae*; *black square*, *Glomus claroideum*; *black circle*, *Glomus clarum*; and *black triangle*, *P. brasilianum* (reprinted from Klugh and Cumming 2007 with permission)

native soils (Wright and Upadhyaya 1996; Rillig and Mummey 2006; Bedini et al. 2007). Since glomalin has high cation exchange capacity and high affinity for polyvalent cations, it is of significance when considering AM fungal-induced metal resistance. In fact, there are reports that glomalin has the potential to immobilize high amounts of metals (Gonzalez-Chávez et al. 2004; Vodnik et al. 2008; Cornejo et al. 2008), and Etcheverría (2009) showed that glomalin-related soil protein (GRSP) has the capacity to sequester substantial quantities of Al (4.2 to 7.5 % by weight) in acidic soils of a temperate forest in southern Chile. Some studies indicate that GRSP production increases when AM fungi are subjected to adverse soil conditions (Vodnik et al. 2008; Cornejo et al. 2008), including acidic soils with elevated Al (Lovelock et al. 2004). Aguilera et al. (2011) have recently shown that GRSP can sequester Al within the glomalin molecule, which may provide a highly recalcitrant complex since some studies have indicated a high residence time of glomalin in soils (Rillig et al. 2001). The accumulation of this protein as an AM fungal response in soils with high Al content may represent an Al-binding mechanism that can be very important in the reduction of Al toxicity to mycorrhizal root systems. Thus, the capacity of some AM fungal species and ecotypes to maintain organic acid or glomalin exudation in the mycorrhizosphere in acidic soils may offer effective Al resistance mechanisms that reduce the concentration of free Al^{3+} in acidic soil solutions, so reducing directly Al phytotoxicity and facilitating root growth and exploration of the soil to support plant productivity.

Al resistance of AM plants—improved nutrient relations

The uptake of plant nutrients is critical to the maintenance of homeostasis and growth of plants under edaphic stress, and resistance to Al is often, but not always, reflected in limited perturbations to P, K, Ca and Mg acquisition as well as maintained concentrations of these elements in root and shoot tissues (Andrade et al. 2009).

The interaction between Al^{3+} and $H_2PO_4^-$ in the root zone can lead to the precipitation of $AlPO_4$, reducing the capacity of the plant to obtain P. AM fungi may permit plants to avoid such a stress. Numerous studies with a variety of plant hosts and AM symbionts have reported mycorrhizal protection of P acquisition in the presence of Al. Rufyikiri et al. (2000), using *Musa acuminata* colonized by *Glomus intraradices*, noted a positive effect of the AM symbiosis under Al exposure (78 and 180 μM) where shoot dry weight of mycorrhizal plants was greater than in non-mycorrhizal plants and the contribution of the AM fungus to water and nutrient uptake, including P, was particularly pronounced. These benefits were associated with a marked decrease in Al content in roots and shoots and a delay in the appearance of Al-induced leaf symptoms. In the case of *L. tulipifera*, a forest tree species especially sensitive to soil acidification and Al-induced P limitation, the maintenance by *Glomus clarum* of Pi acquisition under Al exposure (50, 100 and 200 μM) was critical in maintaining plant growth (Lux and Cumming 2001; Klugh and Cumming 2007). This strong link between AM-mediated Pi acquisition and Al toxicity tolerance may be related to the highly mycotrophic nature of this tree species. In contrast, Al had marginal effects on root and shoot P concentrations in *Andropogon virginicus* (Cumming and Ning 2003; Kelly et al. 2005), with shoot P often increasing under Al exposure. These effects were ascribed to growth dilution/concentration effects, where significant reductions in the growth of non-mycorrhizal plants without concomitant reductions in Pi uptake led to elevated tissue P concentrations.

The Al^{3+} ion, bound within the root apoplast, may also affect cation uptake by limiting the diffusion of Ca^{2+}, Mg^{2+} and other multivalent cations to the plasma membrane surface (Huang et al. 1992a, b; Kinraide et al. 2004; de Wit et al. 2010). Indeed, Ca and Mg limitation are classic Al toxicity symptoms in non-mycorrhizal plants (Foy et al. 1978). The AM symbiosis may alter these charge-based interactions within the plant root by the absorption of cations through fungal symbiont hyphae and their transfer to host plants (Ryan et al. 2003; Lee and George 2005; Ryan et al. 2007). In addition, AM fungi may alter reactions of Al^{3+} with the plant root cell wall through the production of metal-chelating compounds of fungal or host origin (Klugh and Cumming 2007; Cornejo et al. 2008). Borie and Rubio (1999), Rufyikiri et al. (2000) and Lux and Cumming (2001) all observed that AM fungi moderated Al-induced reductions in Ca and/or Mg concentrations in roots and shoots and that these changes were often associated with reductions in Al accumulation.

It is evident from the above reports that differences in the accumulation of nutrients in tissues may or may not be a good indicator of mycorrhizal benefits under Al exposure. Benefits may result from an increased C flux to and Al chelation in the mycorrhizosphere, or may reflect greater nutrient uptake effectiveness by AM fungi or changes in plant nutrient use efficiency resulting from the AM symbiosis (Smith and Read 2008). Differences in plant host, AM fungal species and Al exposure conditions will all influence the uptake by and translocation of nutrients within host plants, so that plant growth may be the best integrated response of the efficacy of the AM association in providing Al resistance.

Al resistance of AM plants—elevated host stress metabolism

Interactions between AM fungi and their hosts bring about a broad range of changes in plant metabolism, which may prime plant cells to cope with abiotic stresses in the root zone (Hohnjec et al. 2007; Goodwin and Sutter 2009). Changes in the regulation of antioxidant enzyme activities or the induction of specific stress-related systems following AM fungal colonization would contribute to host plant stress tolerance to unfavourable levels of soil Al by inducing metabolic stress resistance pathways that relieve the effects of Al on plant cell homeostasis (see Ouziad et al. 2005; Zhu et al. 2010; Abdel Latef and Chaoxing 2011). The induction in mycorrhizal plant tissues of metal transporters (Repetto et al. 2002; Ouziad et al. 2005), or antioxidant enzymes (Garg and Manchanda 2009), as well as the accumulation of secondary compounds and other metabolites (Peipp et al. 1997; Garg and Manchanda 2009), may all function to enhance plant resistance to Al. For example, Garg and Manchanda (2009) reported the elevated activities of superoxide dismutase, catalase and peroxidase in roots and leaves of *Cajanus cajan* colonized by *Glomus mosseae*, and these were associated with reduced lipid peroxidation in roots. Little information is available which directly links AM symbiosis and metabolic priming of host plants against Al stress. However, the impacts of Al on plants include increased oxidative stress (Naik et al. 2009; Hossain et al. 2011; Ma et al. 2012) so that the induction by AM fungal colonization of ROS enzymes or other compounds that would reduce the toxic effects of Al on metabolism could contribute to acquired Al resistance in mycorrhizal plants. Research in this area represents a vital avenue for continued investigation.

Variation in Al tolerance of AM fungal species and ecotypes

The benefit of Al tolerance that AM fungi may provide to plants is variable in terms of Al exclusion, nutrient acquisition or effects on plant growth (Borie and Rubio 1999; Kelly et al. 2005; Klugh-Stewart and Cumming 2009). This is a consequence of a substantial genetic variation among and within AM fungal species (Bever et al. 2001; Avio et al. 2009). Natural ecosystems contain native populations and communities of AM fungi that vary in their benefits to plants and in their response to the environment (van der Heijden et al. 1998; Clark et al. 1999; Bever et al. 2001). Changes in the soil environment may modify the fungal communities, so that those AM fungi able to adapt to the new environment may become more prevalent, and such changes may have implications for host plant performance in ecosystems (Bever et al. 2001; Taheri and Bever 2010). In general, AM fungi have been found in soils from pH 2.7 to 9.2, but different isolates of the same species vary in tolerance to acidity and most AM fungal isolates appear to be adapted to soil pH conditions close to those from which they were collected (Siqueira et al. 1984; Sylvia and Williams 1992; Bartolome-Esteban and Schenck 1994; Clark 1997). This has resulted from natural selection favouring the presence of better adapted AM fungal ecotypes in acidic soils and displacing from such environments those with lesser competitive ability (Ashen and Goff 2000).

In the case of acidic soils and/or soils with elevated Al levels, variation can exist among ecotypes of potentially Al-tolerant AM fungi which is related to differences in sensitivity of life stage events, such as spore germination, germ tube growth, hyphal growth, root colonization and persistence. Data concerning fungal responses to soil acidity and Al are summarized in Table 1 and Fig. 2. In general, studies related to the effect of Al on spore germination and hyphal growth are limited, and results are variable (Table 1). For example, Lambais and Cardoso (1989) reported that germ tube growth in *Glomus macrocarpum*, *Gigaspora margarita* and *Scutellospora gilmorei* decreased in response to Al concentrations ranging from 0 to 130 μM Al in sand at pH 4.5. However, spore germination of *Gigaspora margarita* was not significantly influenced by Al, but it was deleterious in *Glomus macrocarpum* and *S. gilmorei*. *Glomus macrocarpum* was the most sensitive AM fungus assayed, with no spore germination or germ tube growth at 90 μM Al or higher levels (Lambais and Cardoso 1989). In another study assessing spore germination and germ tube growth, Bartolome-Esteban and Schenck (1994) found that *Gigaspora* species exhibited high Al tolerance, *Scutellospora* species were variably affected by high Al levels and isolates of *Acaulospora scrobiculata* were relatively sensitive to high Al, consistent with the findings of Lambais and Cardoso (1989). Recently, Klugh-Stewart and Cumming (2009) reported that spore germination rates of *Acaulospora morrowiae*, *Glomus etunicatum* and *Scutellospora heterogama* were unaffected by exposure to

Table 1 Arbuscular mycorrhizal fungal response to Al exposure. Data from: A) Lambais and Cardoso (1989 as reported in Clark 1997); B) Bartolome-Esteban and Schenck (1994); C) Klugh-Stewart and Cumming (2009)

A)		Aluminium concentration (μM)					
		0	40	130	0	40	130
		Spore germination (%)			Germ tube growth rating[a]		
Gigaspora margarita		81	76	78	3	2.3	2
Scutellospora gilmorei		70	38	31	2.5	1.8	1.3
Glomus macrocarpum		11	3	0	1.5	1	0
B)	INVAM	Aluminium saturation (%)					
	Designate	6	27	100	6	27	100
		Spore germination (%)			Hyphal growth (mm)		
Gigaspora albida	GABD 185	13	25	65	79	51	46
Gigaspora margarita	GMRG 444	70	55	66	210	185	197
Gigaspora gigantea	GGGT 109	92	93	67	138	225	304
Gigaspora gigantea	GGGT 663	40	19	18	215	240	166
Scutellospora heterogama	CHTG 139	35	41	40	97	104	80
Scutellospora pellusida	CPLC 288	75	80	75	31	20	16
Scutellospora calospora	CCLC 269	30	32	19	39	40	31
Scutellospora calospora	CCLC 348	56	46	54	45	40	28
Glomus manihot	LMNH 980	86	89	91	40	45	27
Glomus etunicatum	LETC 236	83	4	0	27	1	0
Glomus etunicatum	LETC 329	60	5	0	8	2	0
Glomus etunicatum	LETC 455	80	17	0	22	5	0
Glomus clarum	LCRL 551	36	26	3	18	4	2
Acaulospora scrobiculata	ASCB 456	14	4	14	1	1	1
C)	INVAM	Aluminium concentration (μM)					
	Designate	0		100	0		100
		Spore germination (%)			Hyphal growth (mm)		
Acaulospora morrowiae	WV107	45.4		50.9	22.7		12.7
Glomus claroideum	WV109E	25.3		6.8	10.1		6.4
Glomus clarum	WV234	71.7		44.4	80.2		47.4
Glomus etunicatum	VZ103A	33.5		29.6	18.7		9.6
Paraglomus brasilianum	BR105	39.4		16.9	24.5		8.2
Scutellospora heterogama	WV108	67.5		75.2	177.7		165.6

[a] Germ tube growth rating: 0 = no growth; 1 = 0–5 mm; 2 = 5–10 mm; 3 >10 mm

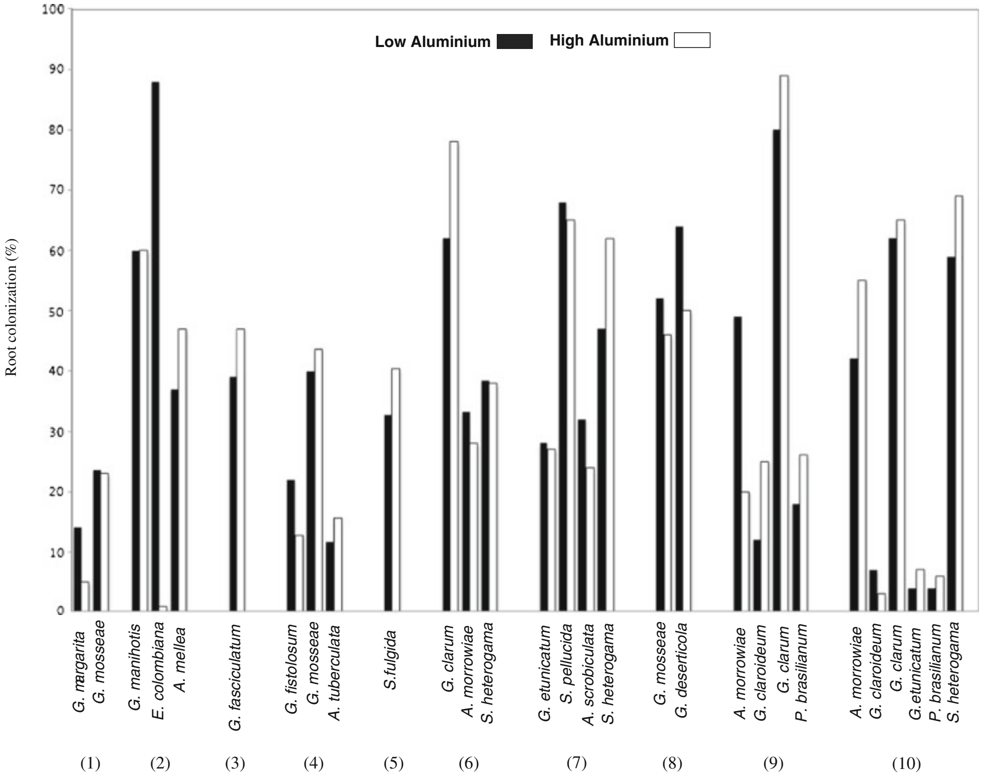

Fig. 2 Comparison of root colonization (in percent) by AM fungal ecotypes for plants grown under different low and high Al conditions. (*1*) *Z. mays* grown in an ultisol amended with 12 (low Al) or 0 meq $CaMgCO_3$ (100 g soil)$^{-1}$ (high Al) (Siqueira et al. 1984); (*2*) *Manihot esculenta* grown in an acid tropical soil and watered with solutions of pH 6.3 (low Al) or 3.9 (high Al) (Howeler et al. 1987); (*3*) *Hieracium pilosella* grown in a strongly weathered sandy soil and watered with nutrient solution with pH 5.5 (low Al) or 2.5 (high Al) (Heijne et al. 1996); (*4*) *Z. mays* was cultivated in sand-vermiculite and supplied with acid rain solution (low Al) or acid solution with 3 mM Al (high Al) (Vosátka et al. 1999); (*5*) *C. multiflora* grown in an ultisol and watered with distilled water (low Al) or acidified water at pH 3 (high Al) (Cuenca et al. 2001); (*6*) *Andropogon virginicus* exposed to 0 (low Al) or 400 μM Al (high Al) in sand culture (Kelly et al. 2005); (*7*) *Malus prunifolia* plants grown in limed soil (pH 6, low Al) or unlimed soil (pH 4, high Al) (Cavallazzi et al. 2007); (*8*) *Eucalyptus globulus* grown in sand/vermiculite/sepiolite substrate amended with 0 (low Al) or 600 mg Al kg^{-1} (high Al) (Arriagada et al. 2007); (*9*) *L. tulipifera* exposed to 0 (low Al) or 200 μM Al (high Al) in sand culture (Klugh and Cumming 2007); (*10*) *Andropogon virginicus* was exposed to 0 (low Al) or 100 μM Al (high Al) in sand culture (Klugh-Stewart and Cumming 2009)

100 μM Al, whereas germination was reduced in *Glomus clarum* and *Paraglomus brasilianum* and greatly inhibited in *Glomus claroideum*. However, hyphal length per spore suggested that germ tube growth and spore germination were differentially affected by Al exposure (Table 1). Such differences may reflect the variation in genotypes among spores within a single-species trap culture (Bever and Morton 1999) and subsequent selection and survival under imposed Al stress (Klugh-Stewart and Cumming 2009).

Across many studies of AM development in plants exposed to Al, there is a tendency for fungal colonization to be unaffected or increase of host roots, although some fungal species/isolates do exhibit reductions in colonization in response to Al in the environment (Fig. 2). Increased root colonization by AM fungi could influence C release into the rhizosphere, increasing the availability of organic acids and other C substrates. In the study by Klugh-Stewart and Cumming (2009), Al did not affect mycorrhizal colonization of *Andropogon virginicus*, which suggests that Al does not inhibit the formation of the symbiosis by Al-resistant or Al-sensitive AM fungi (Fig. 2). However, growth and protection of *Andropogon virginicus* from Al among AM fungal species was not associated with any of the AM fungal resistance traits, suggesting that selection of Al resistance may occur at the spore germination and hyphal growth stages but that the Al resistance mechanisms in AM fungi may not be extrapolated to the life stage in host plants (Cuenca et al. 2001; Klugh-Stewart and Cumming 2009).

Variation in AM fungal Al resistance—root colonization and plant performance

The maintenance of plant growth under exposure to Al may be the best indicator of AM fungal resistance to Al in soils. In Fig. 3, data are presented from 13 studies involving different AM fungi and where Al was a controlled variable. Analysis of these data indicates that there are significantly different plant growth benefits (fold increases) from AM depending on both the Al level (*F* 179; $p<0.001$) and the AM fungal ecotype (*F*

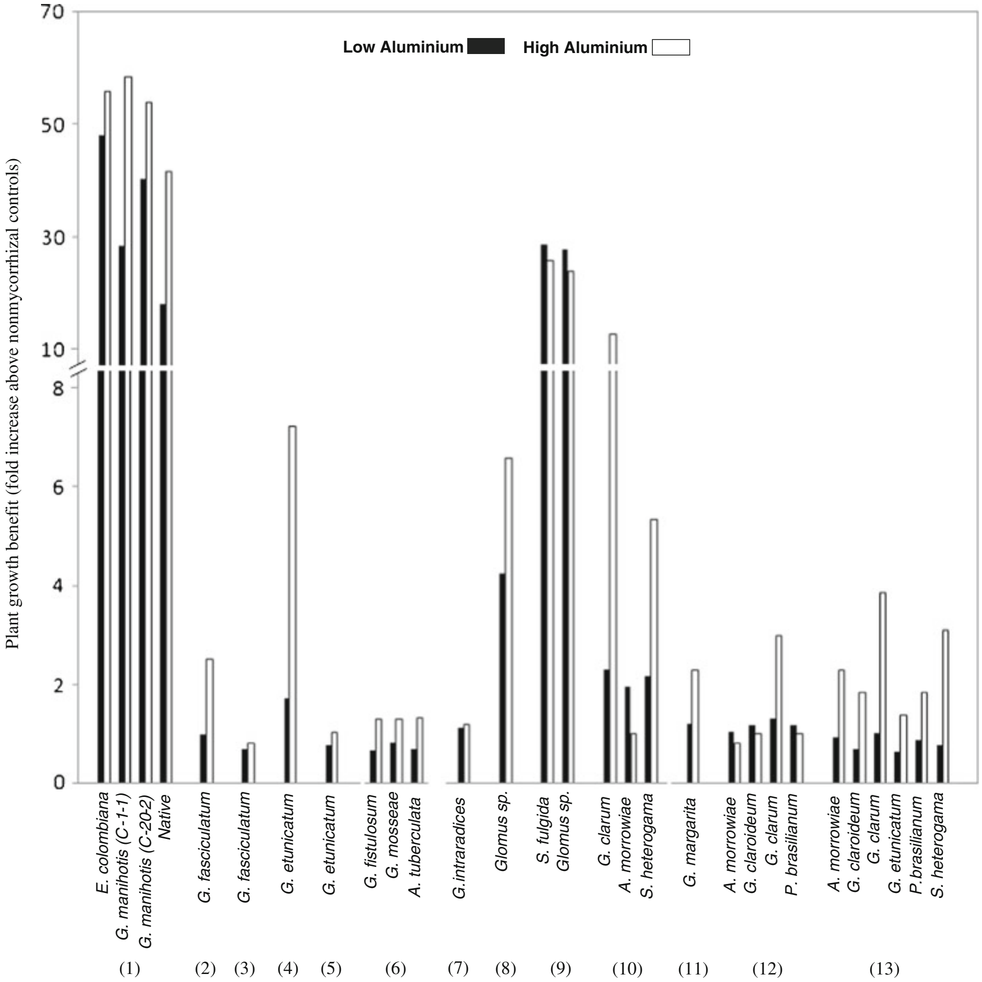

Fig. 3 Comparison of plant growth benefit (fold increase above nonmycorrhizal controls) from AM fungal ecotypes for plants grown under different low and high Al conditions. (*1*) *Manihot esculenta* grown in an acid tropical soil limed to pH 5.3 (low Al) or 3.9 (high Al) (Sieverding 1991 as reported in Clark 1997); (*2*) *Hieracium pilosella* and (*3*) *Deschampsia flexuosa* grown in a strongly weathered sandy soil and watered with nutrient solution with pH 5.5 (low Al) or 2.5 (high Al) (Heijne et al. 1996); (*4*) Al-tolerant *H. vulgare* and (*5*) Al-sensitive *H. vulgare* grown in an acidic andisol that was limed (pH 5.3, low Al) or unlimed (pH 4.6, high Al) (Borie and Rubio 1999); (*6*) *Z. mays* cultivated in sand-vermiculite and supplied with acid rain solution (low Al) or acid rain solution with 3 mM Al (high Al) (Vosátka et al. 1999); (*7*) *M. acuminata* plants grown in sand culture with 0 (low Al) or 180 μM Al (high Al) (Rufyikiri et al. 2000); (*8*) *L. tulipifera* exposed to 0 (low Al) or 200 μM Al (high Al) in sand culture (Lux and Cumming 2001); (*9*) *C. multiflora* grown in an ultisol and watered with distilled water (low Al) or acidified water at pH 3 (high Al) (Cuenca et al. 2001); (*10*) *Andropogon virginicus* exposed to 0 (low Al) or 400 μM Al (high Al) in sand culture (Kelly et al. 2005); (*11*) *I. batatas* plants cultivated in an acidic silty loam soil that was limed (pH 5.2, low Al) and unlimed (pH 4.2, high Al) (Yano and Takaki 2005); (*12*) *L. tulipifera* exposed to 0 (low Al) or 200 μM Al (high Al) in sand culture (Klugh and Cumming 2007); (*13*) *Andropogon virginicus* exposed to 0 (low Al) or 100 μM Al (high Al) in sand culture (Klugh-Stewart and Cumming 2009)

1,384; $p<0.001$). Moreover, the positive effect on plant growth under Al exposure depends on the Al-by-AM fungal species interaction (F 9,529; $p<0.001$), reflecting the fungal species-specific dependence of induced Al resistance.

Several other studies have used a host plant with several AM fungal ecotypes and assessed different responses reflecting Al resistance. Cavallazzi et al. (2007) showed that mycorrhizal colonization of apple plants was significantly influenced by acidophile selected fungal isolates of *Glomus etunicatum*, *Scutellospora pellucida*, *S. heterogama* and *Acaulospora scrobiculata* in soils varying in pH (4.0, 5.0, 6.0) and Al availability (2.7, 0.3 and 0 cmolckg^{-1}). Under the highest Al level, plants colonized by S. *heterogama* had the greatest leaf P concentration and the lowest leaf Al concentration, whereas plants inoculated with *Acaulospora scrobicalata* exhibited reductions in AM colonization, the lowest biomass and tissue P content and the highest tissue Al content (Cavallazzi et al. 2007). In studies with *L. tulipifera* and *Andropogon virginicus*, Klugh and Cumming (2007) and Klugh-Stewart and Cumming (2009) observed different benefits of AM fungal ecotypes to Al in diverse host plants. Moreover, an early AM colonization can be an important factor in Al tolerance for agricultural plants cropped in acid soils (Seguel et al. 2012). In general, their results suggest that

Al tolerance in host plants depends on the adaptability of the AM fungi to edaphic conditions, including high Al levels, and the physiological specificity of the host plant with a particular AM fungal ecotype, which may explain why, in some cases, the same fungal ecotype gives different responses in association with different plant species.

In a study utilizing several ecotypic isolates of three AM fungi and *Andropogon virginicus* at different Al levels, Kelly et al. (2005) found that *Glomus clarum* isolates provided the greatest resistance to toxic levels of Al (400 μM), *S. heterogama* isolates showed intermediate benefits for plant growth and plants colonized by *Acaulospora morrowiae* isolates were the least Al resistant (Kelly et al. 2005) (Fig. 3). Across these fungal species and ecotypes, Al resistance measured as plant biomass was positively correlated with root colonization and negatively correlated with the accumulation of Al in leaf tissue. However, there was no association between plant Al Tolerance Index (biomass with Al/biomass without Al) and pH at the site of fungal isolation, suggesting that broad patterns of Al resistance behaviour in AM fungal isolates for *Andropogon virginicus* may override ecotypic variation in Al resistance within AM fungal species or that Al resistance as a trait is not stable (see "Stability of Al resistance in AM fungi").

Variation in AM fungal Al resistance—AM mechanisms of Al resistance

Differences in Al absorption and translocation by host plants associated with different AM fungal ecotypes under high Al levels may reflect underlying mechanisms of Al resistance

Table 2 Accumulation of Al in plants exposed to low and high Al levels with and without AM fungi. Some values extrapolated from figures in each reference

Plant	AM treatment	Shoot Al (mg/kg)		Root Al (mg/kg)		Reference
		Low Al	High Al	Low Al	High Al	
Hordeum vulgare (Al tol.)	*G. etunicatum*	145	296			Borie and Rubio (1999)
	Nonmycorrhizal	246	405			
Hordeum vulgare (Al sens.)	*G. etunicatum*	147	312			
	Nonmycorrhizal	307	252			
Musa acuminata	*G. intraradices*	200	700	5,500	5,750	Rufyikiri et al. (2000)
	Nonmycorrhizal	300	1,500	7,000	8,500	
Liriodendron tulipifera	*Glomus* spp.	180	423	800	930	Lux and Cumming (2001)
	Nonmycorrhizal	140	180	500	610	
Clusia multiflora	*S. fulgida*	125	160	12,000	12,500	Cuenca et al. (2001)
	Glomus spp.	100	95	9,000	20,000	
	Nonmycorrhizal	220	200	20,000	17,500	
Andropogon virginicus	*G. clarum*	10.9	43.2	342	1,868	Kelly et al. (2005)
	A. morrowiae	9.9	165.2	416	3,089	
	S. heterogama	12.5	93.3	334	2,494	
	Nonmycorrhizal	15.0	225.4	583	2,721	
Ipomoea batatas	*G. margarita*	240	360	4,780	4,690	Yano and Takaki (2005)
	Nonmycorrhizal	370	480	5,340	2,230	
Malus prunifolia	*G. etunicatum*	1.6	5.2			Cavallazzi et al. 2007
	S. pellusida	3.1	5.4			
	A. scrobiculata	2.4	7.6			
	S. heterogama	3.3	3.2			
	Nonmycorrhizal	7.1	4.0			
Liriodendron tulipifera	*A. morrowiae*	45	240			Klugh and Cumming (2007)
	G. claroideum	50	300			
	G. clarum	43	155			
	P. brasilianum	30	235			
	Nonmycorrhizal	40	330			
Andropogon virginicus	*A. morrowiae*	25	75			Klugh-Stewart and Cumming (2009)
	G. claroideum	15	63			
	G. clarum	18	70			
	G. etunicatum	14	72			
	P. brasilianum	15	91			
	S. heterogama	10	73			
	Nonmycorrhizal	14	70			

that vary according to the fungal symbiont. The biosorption and sequestration of Al in the mycelium (Joner et al. 2000) and changes in the chemical speciation of Al (Lux and Cumming 2001; Cumming and Ning 2003), which implies the production of root exudates (Klugh and Cumming 2007; Klugh-Stewart and Cumming 2009), are mechanisms that may vary among different AM fungal species and ecotypes and may confer Al tolerance to plant plants.

In the studies noted above, a limitation of the absorption and translocation of Al to host plant shoots is often the variable associated with AM-mediated Al resistance. This reduction is often associated with elevated P acquisition, suggesting that AM fungal species or ecotypes conferring Al resistance alter the chemistry of the mycorrhizosphere, as already discussed. As indicated in Fig. 1, the growth of *L. tulipifera* with several fungal symbionts could be related to the concentration of Al^{3+} in the root zone, which also influenced the accumulation of Al in plant tissues (Table 2). A similar pattern has been noted for *Andropogon virginicus* (Klugh-Stewart and Cumming 2009), with patterns of resistance consistent across multiple ecotypes within AM fungal species (Kelly et al. 2005). These broad patterns suggest that the stimulated flux of C, primarily as citrate, into the mycorrhizosphere may be a major mechanism of Al resistance in AM plants, just as it functions in numerous non-mycorrhizal plant species.

Stability of Al resistance in AM fungi

An additional factor that should be considered when assessing metal resistance of AM fungi is their origin and culture conditions. Many isolates used in studies on the role of AM fungi in host metal resistance, whether focusing on growth, physiology or molecular responses, utilize inocula generated from common soil trap cultures (Morton et al. 1993). Factors influencing the community composition and genetic makeup of AM fungi in a trap culture include the host plant species, seasonality of collection and abiotic factors in the trap environment, including substrate chemistry. When assessing metal resistance and extrapolating from cultured AM fungi, consideration should be made of potential changes in the genetic make-up of the AM fungal isolates in culture. Bever and Morton (1999) noted that considerable heritable variation for spore shape was maintained in cultures of *S. pellucida* in trap cultures. In an analogous fashion, trap cultures may enrich variation over time in field-collected, metal-resistant AM ectotypes because the selection pressure for metal resistance is removed and nuclei that do not carry metal-resistant genes may proliferate. Such a process was suggested by Kelly et al. (2005) to exist for three AM fungal species that did not exhibit clear patterns of Al resistance in relation to the pH of the sites of their original collection. Similarly, Malcová et al. (2003) and Sudová et al. (2007) noted that metal-free culture of metal-resistant *Glomus* ecotypes reduced their resistance to metals compared to the same lines maintained under metal exposure. Clearly, care must be taken when culturing metal-selected isolates for long-term studies of metal resistance in AM fungi.

An integrated model for induced Al resistance by AM fungi

The colonization of roots by AM fungi facilitates Pi acquisition and leads to broad changes in gene and protein expression in host roots. Together these changes could contribute to Al resistance in host plants. As has been discussed in earlier sections, induced Al resistance varies with the AM fungal species or isolate, and it is possible that these also affect the underlying changes in host metabolism

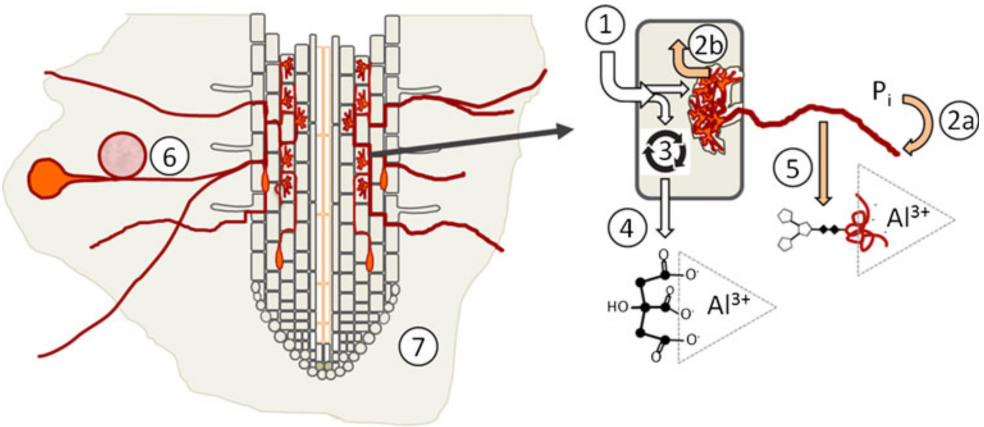

Fig. 4 Hypothetical model for Al resistance induced by AM fungi in higher plants. (*1*) Colonization increases sink demand and the influx of fixed C to root cells; (*2a*) AM fungi enhance Pi uptake and (*2b*) transfer to the host, which overcomes potential P limitation resulting from Al in the rhizosphere; (*3*) colonization stimulates C processing in roots through glycolysis and the citric acid cycle, increasing the availability of organic acids and other C substrates for exudation; (*4*) exudation of organic acids chelates Al^{3+} in the rhizosphere; (*5*) the production of glomalin by AM fungi sequesters Al^{3+} over long time frames; (*6*) accumulation of Al in AM fungal structures such as spores and hyphae. Altogether, these changes in root metabolism and exudation lead to (*7*) an enlarged mycorrhizosphere in which Al is chelated and sequestered

resulting from root colonization. Increased demand for C resulting from the symbiotic association (Wright et al. 1998; Kaschuk et al. 2009) is accompanied by increased processing of photosynthate through glycolysis and the tricarboxylic acid (TCA) cycle in host roots (Fig. 4, steps 1 and 3). For example, Recorbet et al. (2010) noted that several proteins in these cycles, including enolase and malate dehydrogenase, were more highly expressed in *Medicago truncatula* roots colonized by *Glomus mosseae* and *Glomus intraradices* than in nonmycorrhizal roots. Similar patterns have been observed in roots of *Populus tremuloides* (Desai 2012) and *Oryza sativa* (Campos-Soriano et al. 2010) colonized by *Glomus intraradices*. Increased processing of C through the TCA would additionally provide substrate for organic acid exudation (Fig. 4, step 4). The utilization of photosynthate by the fungal symbionts for hyphal growth will ensure symbiotic Pi acquisition by the host plant under conditions of Al exposure, which in turn contributes to the maintenance of photosynthesis and C supply to the symbiotic root system (Fig. 4, step 2). In addition, glomalin produced by AM fungi will sequester Al^{3+} over long time frames (Fig. 4, step 5) and this, together with Al accumulation in fungal structures (Fig. 4, step 6), could provide an important Al tolerance mechanism according Aguilera et al. (2011). Altogether, changes in C processing and organic acid exudation from root tissues, Pi acquisition via fungal hyphae and production of glomalin can contribute to the chelation, sequestration and detoxification of Al^{3+} in the mycorrhizosphere.

Conclusions and future prospects

Soil acidity is a major limitation to agricultural production throughout the world and one of the major causes of Al stress situations. The AM symbiosis has great potential to increase plant growth by mediating soil solution chemistry at the root–soil interface, improving nutrient acquisition and altering plant stress responses, some or all of which positively contribute to plant performance in acidic soils. Mechanisms that alter Al^{3+} bioavailability in the mycorrhizosphere, which will influence Al impacts on nutrient uptake, may underlie Al tolerance of plants associated with Al-resistant AM fungi. Current data suggest that the biosorption of Al to hyphae and probably glomalin, as well as sustained organic acid exudation from roots of plants colonized by Al-resistant AM fungi, are at the basis of Al resistance mechanisms conferred by the AM symbiosis that are not yet fully understood. Continued research is needed to understand the roles played by AM fungi in increasing the Al resistance in crops and trees growing in acidic soils where Al is the principal limiting factor.

In agronomic systems, it is a common practice to apply amendments, such as lime, gypsum and phosphate fertilizer, to enhance the quality and quantity of agricultural production on acidic soils. However, limited reserves of raw material (rock phosphate) are increasing input prices of phosphate fertilizers, and sustained inputs of these materials are not feasible, especially in developing economies. For agricultural systems on acidic soils, one possible solution is the use of genotypes of Al-tolerant crop species and/or genotypes with high P use efficiency when available. Thus, it is possible to reduce fertilizer inputs, especially on marginal soils or where the process of P fixation is very intense, as in acid or allophanic soils. Within the same context, the exploitation of AM fungal ecotypes adapted to high soil levels of Al and their management or enhancement, by inoculation with native fungi, may provide significant increase to agricultural production on acidic soils. The use of diverse AM fungal species adapted to Al in soils as biofertilizers should be considered as part of integrated crop management, which is projected to be an important avenue to improve crop yields through better nutrient supply and may be especially important for agriculture on acidic soils with phytotoxic Al levels.

The use of AM fungal inoculants can, in general, be feasible in certain types of production systems where crops are confined to a reduced surface area, such as nurseries, horticultural or ornamental systems established in acidic soils with high Al^{3+} levels. In such cases, the cost related to the application of inoculants would represent a marginal fraction of all production costs, and the development of AM fungal inoculants could be a viable alternative for improving the quality, yields and sanitary status of production. The use of inoculants might also be beneficially utilized under conditions where native soils/ecosystems have been severely disrupted, such as reclamation projects following strip mining or in the installation of ornamental plants and trees in urban settings where soils have been stockpiled or soil substrates created as part of these activities. Several studies have also demonstrated the high impact of different agricultural practices on the diversity, density and functionality of AM propagules. In these cases, the alignment of management inputs and activities with the goal of maintaining a diverse and functionally beneficial AM fungal community may foster sustainable agronomic production. Thus, the correct choice of agronomic management to be implemented in acidic soils, particularly when extensive crops are established, represents a way to increase the positive effects of AM fungi without requiring elevated inoculations.

In summary, ongoing and future research on AM symbioses and acidic soils with high Al levels should be extended to include:

- Further characterization of AM fungal contributions to host plant Al resistance, including the role of fungal-specific exudates in detoxifying Al^{3+} in the mycorrhizosphere and broad-scale changes in metabolism induced by AM fungi that may prime host plants to cope with perturbations in homeostasis resulting from Al exposure

- Characterization of Al resistance of natural AM fungal communities and selection of the most feasible ecotypes to be adopted as biofertilizers based on parameters including high native resistance to Al^{3+} and high ability to produce significant amounts of hyphae and glomalin
- Development of adequate and easily performable molecular tools to monitor the persistence and seasonal cycles of AM fungal isolates used as inoculants in colonizing roots of host plants
- Analysis, at the local scale, of the effects of different agronomic practices on the functionality of native AM fungal communities, particularly when annual extensive crops are used in rotation, and the selection of agronomic practices to improve the diversity and functionality of indigenous AM fungi where the use of inoculants cannot be implemented due to technical and economic limitations

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