Chapter 3
Role of Arbuscular Mycorrhizal Fungi in Alleviation of Acidity Stress on Plant Growth

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Introduction

A large number of abiotic and biotic factors influence the establishment, health, and productivity of plants in both natural and agroecosystems. Among these, soil factors influence various plant processes to a greater extent since soil is the natural substrate for plants to anchor and take up nutrients and water. Around 30–40 % of the 1.44 billion ha arable land worldwide has suboptimal conditions for crop growth and thus has an adverse influence on agriculture (FAO 1992). Soil fertility is one of the major determinants for plant growth in both natural and agricultural ecosystems.

The adverse effects of soil fertility on plant growth and yield are mainly due to the deficiency of one or more essential nutrients necessary for plant growth. Factors such as acidity, alkalinity, salinity, erosion, and farming practices are the main causes for the decline in the availability of nutrients in the soil. Among the various factors that influence soil fertility, soil acidity is an important factor affecting plant growth worldwide (Iqbal 2012).

Soil pH is a highly sensitive factor, as it determines plant's survival, distribution, and its interactions with microorganisms, which are rather vital for the availability of essential nutrients and soil fertility (Marschner 1995). An increase in the H^+ ion concentration in the soil solution results in a decrease in soil pH, and soils with a pH < 5.5 or lower are categorized as acid soils. These soils occupy around 30 % (4 billion ha) of the world's total land area and 50 % of the world's cultivable lands (Von Uexküll and Mutert 1995; Baligar et al. 2001). Further, more than half of the world's acid soils (60 %) occur throughout the tropics and

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subtropics (Baligar and Fageria 1997; Fischer 1998). Therefore, acid soils affect crop yields in many 'hunger hot spots' of the world.

In natural ecosystems, soil acidity determines the availability of mineral nutrients such as phosphorus (P) and also determines the level and severity of phytotoxic elements such as aluminum (Al), manganese (Mn), and iron (Fe) (Kochian et al. 2004). When Al concentration increases in the soil solution in response to a reduction in pH, induction of reactive oxygen species and lipid peroxidation damage of root plasma membrane occur reducing root growth and plant's response to stress conditions (Yamamoto et al. 2001, 2002). Though Al ions present in acidic soils prevent the intrinsic toxicity of H^+, it can concurrently cause an extrinsic toxicity through calcium (Ca) and magnesium (Mg) deficiency (Kinraide et al. 2005).

Causes for Soil Acidity

Natural causes for acid soils include high rainfall, resulting in leaching of basic cations, acidic parental material, and decomposition of organic matter. Biological processes such as root and microbial respiration and uptake of cations such as ammonium (NH_4^+) also influence soil pH. Cultivation of legumes acidifies soils more as they take up more cations than anions compared to non-legumes. In addition to these above-mentioned natural causes, human activities, such as the extensive use of NH_4^+ fertilizers for crop production, industrial emission of nitrogen oxides and sulfur di-oxide resulting in acid rain and mining activities, all contribute to the acidification of soils.

Acid rain, an environmental hazard, is one of the primary reasons for soil acidification. Acid rain results in the leaching out of basic cations, reduces evaporation, releases bound Al into the soil solution, and increases the oxidative biological activities (Carver and Ownby 1995). During precipitation, water percolates through the soil particles washing away the basic cations from the soil, which are replaced by acidic cations such as Al^{3+}, Mn^{2+}, and H^+ ions (Sumner et al. 1991). However, the CO_2 containing water molecules entering the soil profile replaces the free salts quite rapidly in contrast to basic cations, which are replaced rather more slowly. This results in acidic soils under high rainfall regions (Brady 1990). Increased presence of SO_4^{2-} ions in rain water leads to the considerable eradication of H^+ and other cations from the soil profiles (Overrein et al. 1980). Biological oxidation of carbon (C), nitrogen (N), and sulfur (S) in the way of burning fossil fuels also results in acid rain.

Modern agriculture mainly focuses on higher yields with large inputs of synthetic fertilizers. However, the chemicals present in these fertilizers react with the soil mineral nutrients, resulting in changes in the soil pH. This indirectly affects plant growth and health. It has also been shown that the forms of N present or applied could influence soil pH (Marschner 1995). A significant correlation between soil pH and Al^{3+} was reported by Rout et al. (2001) in acidic soils in response to trim down the basic ions.

Results of Soil Acidity

Soil acidification leads to changes in the soil environment as well as in plant growth and metabolism, which can be summarized as follows:

1. Increase in the availability of Al, Mn, and H^+ ions in the soil solution (Kochian et al. 2004, 2005).
2. Reduction in the availability of essential nutrients such as P, N, Mg, Ca, molybdenum (Mo), and zinc (Zn) (Kochian et al. 2004).
3. Negative effects of Al and other ions on plant growth especially the root system resulting in reduced nutrient and water uptake (Barcelo and Poschenrieder 2002).
4. Defects in shoot growth and appearance of necrotic spots due to Mn toxicity (Schier and McQuattie 2000).
5. Changes in plant physiology, metabolic, and biochemical activities leading to mortality (Heijne et al. 1996; Kochian et al. 2005).
6. Accumulation of organic acids in the roots (Adams et al. 1999; Kinraide et al. 2005).
7. Changes in microbial populations and their activities, which are known to affect plant growth (Miller and Kissel 2010; Kaps and Kering 2011; Chen et al. 2012).

Influence of Soil Acidity on Al Availability and Toxicity

The third most ubiquitous element Al is a light metal comprising of 7 % of the earth's crust and usually represented in the form of oxides and aluminosilicates (Ma et al. 2001). In the soil solution, Al is present as $Al(OH)^{2+}$ and $Al(OH)_2^+$ at pH 4–5, Al^{3+} at pH 5.5–7, and $Al(OH)_4^-$ at pH 7–8 (Drabek et al. 2003). Nevertheless, soils differ in their potential to sustain it (Scancar and Milacic 2006). Forms of Al such as $AlSO_4^+$ and $Al(SO_4)_2^-$ or Al–F lack rhizotoxicity.

According to Kochian (1995), toxicity has been convincingly demonstrated only for Al_{13} and Al^{3+}. Consequently, when the soil pH drops to below 5.5, Al containing compounds tend to dissociate, resulting in the abundance of aluminum-hydroxy cations and Al^{3+} in soil solutions. In soils, the soluble forms of Al are present in two forms: monomeric in the form of Al^{3+}, Al–OH, Al–F, and Al–SO_4 (highly toxic) and acid-soluble Al in the form of polymer state (less toxic) (Xu and Ji 1998).

The Al^{3+} also forms mononuclear species that are more toxic in nature (Kochian 1995; Panda and Matsumoto 2007). Even at micromolar level, Al^{3+} ions can modify the morphology and physiology of plant roots as well as alter the activities of certain enzymes (Simon et al. 1994; Alvarez et al. 2012). Under acidic conditions, the complex forms of Al dissociate, resulting in the release of toxic form of Al as shown below:

$$Al\ (OH)_3 + 3H^+ \leftrightarrow Al^{3+} + 3H_2O$$

Aluminum toxicity is one of the key factors that are harmful for plant growth in acidic soils. Acid soils generally have high amounts of the mineral oxides, which readily inactivate or fix P by precipitation or forming complexes of Al and Mn oxide radicals, thus making it unavailable. The symptoms of Al toxicity in plants include inhibition of root growth, decline in the uptake of water and other essential nutrients (N, P, and Ca), and overall stunting of plant growth (Matsumoto 2000; Purcell et al. 2002; Fukrei et al. 2011). Formation of both primary and lateral roots is affected by high concentrations of Al in the soil solution, and even when the roots are formed, they are devoid of root hairs, thickened, brittle, and brown in color (Wang et al. 2006; Claudio et al. 2008; Gazey and Davies 2009; Bhalerao and Prabhu 2013). Aluminum is strongly adsorbed onto the plant root surface either by the exchange process or by formation of complexes.

Influence of Soil Acidity on Mn Availability and Toxicity

Manganese is an essential micronutrient that plays a vital role in plant metabolism but toxic when present in excess. Manganese aids in the synthesis of chlorophyll and assimilation of nitrate and activates enzymes involved in the fat biosynthesis. Functional role of Mn involves the formation of riboflavin, ascorbic acid and leaf carotene. Normal or adequate level of Mn in plants is 30–500 mg/kg dry mass (Clarkson 1988), and deficiency occurs when the levels drop below 10–20 mg/kg dry mass (Marschner 1995). Manganese toxicity is an important factor limiting plant growth in acidic soils and especially in poorly drained soils (Horst 1988a, b; Delhaize et al. 2004). Manganese toxicity is possibly the second most important metal toxicity limiting crop production in acid soils next to Al (Foy et al. 1973; Sumner et al. 1991).

Manganese availability in the soil solutions is strongly dependent on soil pH. The availability of Mn increases in the soil as pH decreases. Soils tend to become deficient in Mn at pH 6.5 and toxic when the pH drops below 5.5 (Hue et al. 2001; Kochian et al. 2004; Ducic and Polle 2005). The Mn toxicity symptoms in plants include stunted growth and necrotic spots on shoots (Alam et al. 2000), but the physiological mechanisms for these symptoms are still elusive. Greenhouse experiments carried out to determine the adequate and toxic levels of Mn in five different crop species [rice (*Oryza sativa*), common bean (*Phaseolus vulgaris*), maize (*Zea mays*), soybean (*Glycine max*), and wheat (*Triticum aestivum*)] in an Oxisol indicated that 60–520 mg/kg of Mn was adequate for plant growth and 720–4,560 mg/kg of Mn was toxic to plant species (Fageria 2001).

Plants Tolerant to Acid Soils

Intense research has been carried out over the past two decades to identify, characterize, and understand the mechanisms adopted by plants to survive and thrive in acid soils. The results of these investigations reveal that three possible group of mechanisms appear to operate in plants to tolerate acidic conditions. These include the following: (1) exclusion of toxic ions such as Al and Mn from the root apex, (2) tolerance to toxic levels of Al and Mn through detoxification in the plant symplasm, and (3) enhanced efficiency in the uptake of limiting nutrients from acid soils (Kochian et al. 2004; Bhalerao and Prabhu 2013) (Fig. 3.1).

In the exclusion of toxic ion mechanism, roots tend to release organic acids such as maltate, citrate, and oxalate in response to the presence of metal ions in the soil solution (Hue et al. 1986; Adams et al. 1999; Kinraide et al. 2005; Iqbal 2012). These organic acids complex with the toxic ions in the rhizosphere and prevent their entry into roots. Therefore, tolerant crop genotypes such as wheat, maize, and sorghum (*Sorghum bicolor*) accumulate toxic ions several folds less in their tissues than the sensitive genotypes. Plants with internal detoxification mechanism complex toxic metal ions with organic acids (e.g., Al-oxalate) and store them in the vacuoles. Thus, plant like buck wheat can accumulate Al as high as 15,000 ppm in their leaves when grown on acid soils (Ma et al. 2001).

Phosphorus availability is one of the major constrains for plant growth in most of the tropical soils. Generally, the low availability of P in the soils is due to its low mobility, fixation into organic forms, and high adsorption to soil particles (Marschner 1995). In acid soils, P availability is limited due to its fixation with Al and Fe oxides on the clay particles (Kochian et al. 2004). Therefore, P is one of the major limiting factors for plant growth in acid soils. Nevertheless, plants have developed several morphological, physiological, and biochemical adaptations to acquire P from such acid soils. These include mechanisms for increased P mobilization and uptake, changes in root structure, and association with arbuscular mycorrhizal (AM) fungi.

Plant Mechanisms for P Mobilization in Acid-Stressed Soils

Exudation of organic acids is one of the most common mechanism plants adopt to mobilize P in acid soils. Phosphorus deficiency triggers the exudation of organic acids such as malate and citrate from the roots which dissociate bound P from mineral surfaces, solubilizes it from Al, Fe and Ca oxides and hydroxides through metal complexation. Such type of organic acid exudation also occurs in cluster roots, which are produced in response to P stress (Wasaki et al. 2003). There is also enhanced mobilization of sparingly available P through proton secretion (Yan et al. 2002; Gao et al. 2010; Yang et al. 2013). In addition, many plants exude phosphatases and RNAases under P stress. Plant phosphatase activity is not

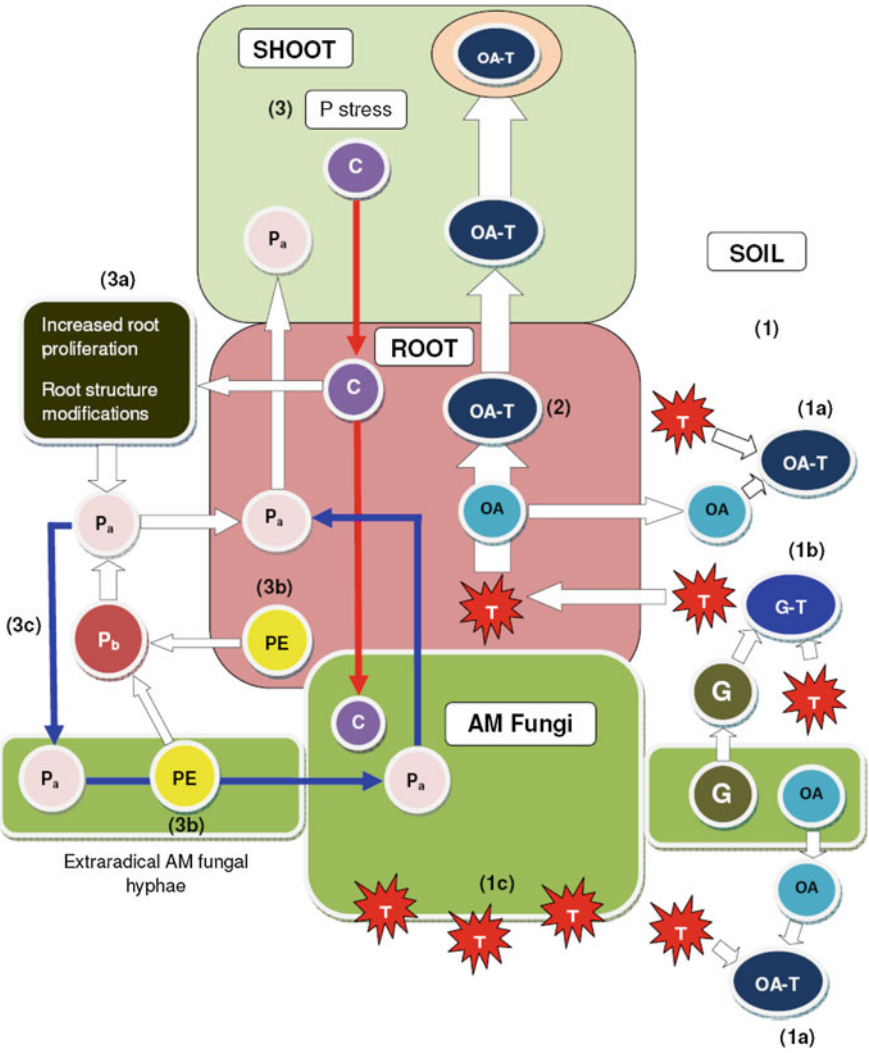

Fig. 3.1 Schematic presentation of the different mechanisms involved in plants acid tolerance. *1*. Exclusion of toxic ions, *1a*. organic acid (*OA*) complexation with toxic ions (*T*) to form *OA-T* complex, *1b*. binding of toxic ions with glomalin (*G*) of arbuscular mycorrhizal (*AM*) fungus forming a complex (*G-T*), and *1c*. binding of toxic ions to AM fungal structures; *2*. internal detoxification of toxic ions. Toxic ion complexation with organic acids (*OA-T*) and their storage in vacuoles; *3*. tolerance to phosphorus (*P*) stress: increased translocation of carbon (*C*) to roots, *3a*. changes in root structure and function, *3b*. phosphatases (*PE*) produced by roots and hyphae of AM fungi dissociates the bound P(P_b), and *3c*. uptake of available P(P_a) by AM fungal hyphae and their transfer to plant roots

constant, but may vary greatly across plant species and environmental conditions (Venterink 2011). These enzymes catalyze the hydrolysis of organic P, thereby enabling its uptake by roots. Furthermore, overexpression of transcription factor genes such as *OsPTF1*, *AtPHR1*, and *OsPHR2* enhances P uptake and accumulation under P-limiting conditions (Nilsson et al. 2007; Zhou et al. 2008). Likewise, plants with overexpression of the regulatory element miR399 tend to accumulate more P in plant parts under P-limiting conditions (Chiou et al. 2006; Lin et al. 2008; Gao et al. 2010).

One of the efficient strategies plants adopt to improve P uptake in the soils low in available P is to modify the architecture and morphology of their roots, thereby increasing the surface area of roots that are in contact with the soil. These could be achieved in several ways: (1) increasing the root:shoot ratio through modified allocation of carbon to the root system, (2) increased branching and production of thinner roots, (3) production of more profuse and long root hairs, and (4) formation of special type of roots such as cluster or proteoid roots (Niu et al. 2013).

Arbuscular Mycorrhizal Fungi

Another most common strategy plants adopt to uptake P from acid soils is to associate with the most common and widespread AM fungi. Belonging to Glomeromycota, AM fungi associate with roots of over 80 % of the wild and cultivated plant species (Selosse and Rousset 2011). Plants depend on AM fungi for the uptake of nutrients, especially P from nutrient-stressed soils, and the fungi in turn depend on plants for carbon (Smith and Read 2008).

Arbuscular mycorrhizal fungi contain two distinct phases: one within the roots (intraradical) that enables the transfer of nutrients taken up from the soil in exchange for carbon and another in the soil that is involved in nutrient exploration and reproduction. The extraradical fungal hyphae can be further distinguished into runner and absorptive hyphae. The runner hyphae grow externally to the root system and run between the root segments of single or multiple hosts. The main function of the runner hyphae is to initiate new colonization points (appressoria) on the root epidermis. The absorptive hyphae arising from the runner hyphae extend beyond the nutrient depletion zone and take up the inorganic minerals, especially P from the soil and translocate it to the host (Marschner 1991). Phosphorus is not easily accessible to plants in acidic soil due to its sparingly or insoluble nature. However, under such P-deficient conditions, mycorrhizal roots or AM fungal hyphae secrete phosphatase or phytase enzyme to solubilize insoluble P (Khalil et al. 1994; Tawaraya et al. 2006).

The AM fungi shield the root system of the host plant from the toxicity of Al and other ions under acidic conditions (Marschner 1995). It is well known that the effectiveness of AM fungal species in supporting P transfer to the host plant differs in response with the extent of colonization (Abbott and Robson 1981; Kittiworawat et al. 2010). Likewise, plant genotypes also exhibit variation in

tolerance to acidic conditions similar to AM fungal isolates (Sieverding 1991; Clark et al. 1999a, b). The AM fungal species tends to differ in their response to varying soil pH (Sano et al. 2002). Nevertheless, most investigations on the influence of soil acidity on AM fungi have focused on selecting suitable AM fungal species for growing plants in acidic soils (Cavallazzi et al. 2007).

Distribution of AM Fungal Spores and Phylotypes in Acid Soils

Though fewer or no spores have been found in acid soils with pH less than 5.5 (Wang et al. 1993), AM fungal spores have been found in acidic soils with pH as low as 2 (Cano et al. 2009). Distribution of certain AM fungal species appears to be strongly influenced by soil acidity. For example, spores of *Funneliformis mosseae* do not occur in soils with pH < 5.5 (Sieverding 1991). Although taxa of acidic soils mostly comprise species belonging to *Acaulospora* in soils with pH < 3.6–6.2 (Morton 1956; Oehl et al. 2006), spores of other taxa such as *Glomus* (Cano et al. 2009) and *Scutellospora* (Walker et al. 1998) have also been reported in low-pH soils with pH < 3.0. Further, spores of particular taxa could also occur in a wide range of acidic pH levels. For example, spores of *Glomus corymbiforme* have been reported to occur in acid soils, with pH ranging from 3.8 to 6.7 (Blaszkowski 1995).

A study on the distribution and abundance of AM fungi in Western Australian soils indicated that *Acaulospora* was the predominant fungus in low-pH soils or was the only species to be present in soils with pH < 5.0 (Nicolson and Schenck 1979). The influence of soil acidity on the restricted distribution and diversity of AM fungi do not always hold true. An assessment of AM fungal spore populations associated with sugar maple (*Acer saccharum*) in Eastern Canada showed that AM fungal species richness (number of spore morphotypes) and abundance were maximum in high acidic soils (pH 4.3) compared to moderate (pH 5.6–5.7) and low acidic soils (pH 6.0–6.3) (Moutoglis and Widden 1996).

An assessment of the community structure of AM fungi associated with *Miscanthus sinensis* in acid sulfate soils (pH 2.7–5.4) by An et al. (2008) suggested that soil pH could be the driving force for shaping up the community structure. In a later study, Higo et al. (2011) found that seven operational taxonomic units of AM fungal both from roots of *Wedelia* and from spores belonging to *Acaulospora*, *Glomus*, *Paraglomus*, and *Entrophospora* were reported in acid sulfate soils with a pH of 3.24 from Thailand.

Siqueira et al. (1990) showed that AM fungal spore production and species compositions were highly affected by changes in soil pH. As liming of acid soils favored the presence of *Claroideoglomus etunicatum*, *Rhizophagus diaphanus* and *Paraglomus occultum* originating from non-acidic soils predominated unlimed soils. Further, sporulation of *Gigaspora margarita* was abundant in unlimed soils,

but was rare in limed soils. A similar observation was noted by Coughlan et al. (2000) while examining the pH-induced changes in the diversity and sporulation of AM fungi associated with healthy and declining maple forests. While species such as *Rhizophagus clarus* and *Acaulospora* spp. sporulated in a wide range of soil pH from 4 to 7, certain species such as *Scutellospora calospora* sporulated only in soils with pH 5 or above.

Influence of Soil Acidity on AM Colonization

Many plants thrive at soil pH < 4 (Falkengren-Grerup 1994), and roots of these plants either lack or are minimally colonized by AM fungi (Higo et al. 2011). Arbuscular mycorrhizal fungal colonization has been observed in plants growing in soils with pH as low as 2.7 (Daft et al. 1975) and 3.5–3.9 (An et al. 2008). Studies by Clark et al. (1999a, b) have shown that root colonization of switchgrass (*Panicum virgatum*) by species of *Acaulospora*, *Claroideoglomus*, *Gigaspora*, *Glomus*, and *Rhizophagus* tended to decline with increasing soil acidity (Fig. 3.2). In contrast, root colonization in *M. sinensis* was maximum when raised on high acidic sulfate soils (up to 63 %, pH 3.5–3.9) compared to those raised under less acidic conditions (1.9 to 15.6 %, pH 5.4–6.1). However, the reduction in AM fungal colonization of root with increasing soil acidity has been reported in a number of species such as *Leucaena leucocephala* (Habte et al. 2011), *A. saccharum* (St Clair and Lynch 2005), barley (*Hordeum vulgare*) (Borie and Rubio 1999), *Clusia multiflora* (Cuenca et al. 2001), apple (*Malus prunifolia*)

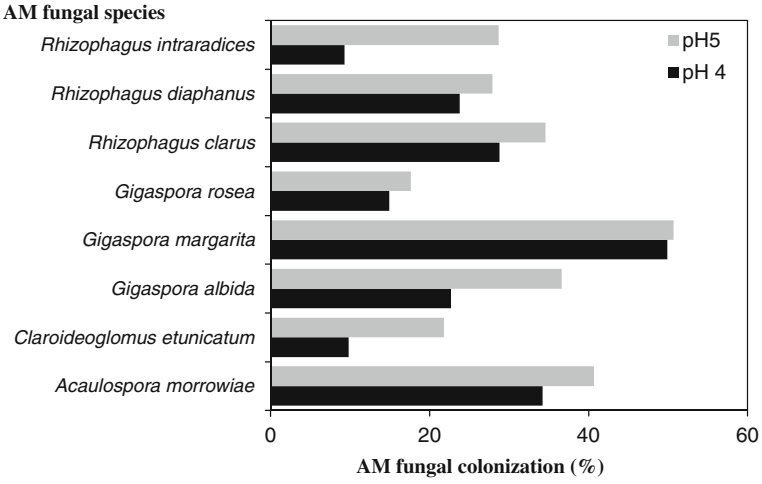

Fig. 3.2 Influence of soil acidity on the extent of root colonization by different arbuscular mycorrhizal (AM) fungi in switchgrass (data from Clark et al. 1999a)

(Cavallazzi et al. 2007), *Maianthemum bifolium, Glium odoratum, Mericurialis perennis*, *Stellaria memorum* (Postma et al. 2007), *Bupleurum falcatum, Cinidum officinale*, *Gentiana lutea* (Ueda et al. 1992), mung bean (*Phaseolus radiata*), and crotalaria (*Crotalaria mucronata*) (Lin et al. 2001).

Studies on the influence of soil acidity on root colonization by AM fungi also indicate the levels of total colonization, and root length with different AM fungal structures could vary with both the host and fungal genotypes. Root colonization of barley by *C. etunicatum* was found to be higher for the cultivar that was tolerant to Al (37.4 %) than for the cultivar that was sensitive to Al (26.9 %) raised on acidic soils (pH 5.15–5.70). Similarly, Habte et al. (2011) also showed that colonization of *L. leucocephala* roots by *G. aggregatum* varied with cultivars raised on acidic soils (pH 4.5).

Like the host genotypes, AM fungi also vary in their response in colonizing host roots under acidic conditions. For example, root colonization of switchgrass by different *Gigaspora* species (*G. albida, G. rosea,* and *G. margarita*) in acidic soils indicates differences in the extent of colonization (Clark et al. 1999a, b) (Fig. 3.2). Production of intraradical hyphae by *Rhizophagus* species and arbuscule production by *Gigaspora* species in switchgrass was found to be higher at low pH (Clark et al. 1999a) (Fig 3.3).

The influence of soil acidity on root colonization by AM fungi could be due to its effect on spore germination (Lambais and Cardoso 1989) and/or hyphal regrowth from mycorrhizal roots (Abbott and Robson 1985). However, the tendency of root colonization to increase with pH can be either due to the increase in the number of taxa involved in colonization or due to an enhanced ability of the associated taxa to colonize host roots (Yoshimura et al. 2013). The first possibility is supported by the observations of An et al. (2008) where the number of AM phylotypes detected in roots of *M. sinensis* increased with increasing soil pH. The second possibility is supported by a study by Clark (2002) who showed that five of the eight AM fungal species showed higher colonization levels in switchgrass with increasing soil pH.

Role of Soil pH on Extraradical Hyphae

The role of extraradical mycelium growing out from colonized roots in the symbiosis is well documented. In addition to initiating colonization of new roots, the extraradical mycelium acts as an extension of the root system in enhancing plants access to soil nutrients and water (Rohyadi 2008). Although the production of extraradical mycelium is an inherent characteristic of the fungi (Abbott and Robson 1985), it could be substantially influenced by soil conditions (Abbott and Robson 1981). In spite of their importance, studies on the effect of soil acidity on extraradical mycelium are limited. These limited studies suggest that the ability of AM fungi to form extraradical mycelium differs with substrate pH (Abbott and Robson 1985;

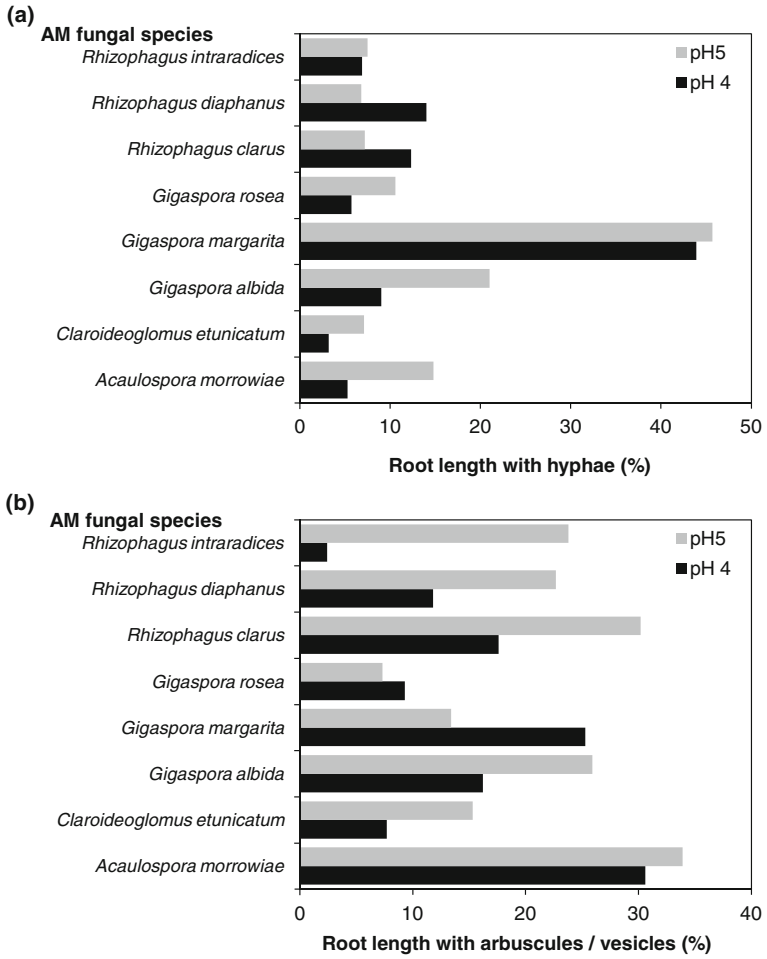

Fig. 3.3 Influence of soil acidity on root length containing hyphae **a** and arbuscules/vesicles **b** in switchgrass colonized by different arbuscular mycorrhizal (AM) fungi (data from Clark et al. 1999a)

Porter et al. 1987). van Aarle et al. (2002) tested the response of extraradical mycelia formation of two AM fungi, *S. calospora* and *Rhizophagus intraradices*, exposed to different acidic pH levels (4 and 5 or 6). The results of this study indicated that though both AM fungi were capable of forming extraradical mycelium at the higher pH, no detectable extraradical mycelium was detected for *R. intraradices* at lower pH.

Abbott and Robson (1985) showed that the spread of extraradical mycelium by a *Glomus* isolate was strongly inhibited at low soil pH, which was speculated to be caused by the aversion to the substrate (van Aarle et al. 2002). Similarly, extraradical mycelia formation by *G. margarita* originating from an acid soil was found

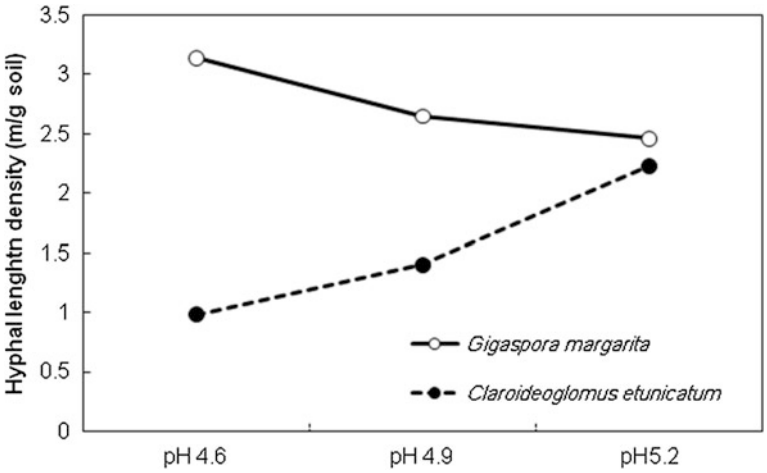

Fig. 3.4 Extraradical hyphal length density of *Gigaspora margarita* and *Claroideoglomus etunicatum* at different soil pH (data from Rohyadi 2008)

to be higher in low-pH conditions (4.6–5.6), whereas *C. etunicatum* also originating from an acid soil required a pH of 5.2 or higher for increased extraradical mycelia formation (Rohyadi 2008) (Fig. 3.4). These observations clearly suggest that the quantity of extraradical mycelium produced depends on specific pH ranges even for taxa originating from acid soils. In addition to these, host species could also influence the quantity of the extramatrical hyphae to certain extent as shown by Lin et al. (2001). Fungal species such as *Diversispora epigaea* and *Rhizophagus manihotis* produce more extraradical mycelium when associated with crotalaria than with mung bean (Fig. 3.5). The enzyme activities such as the alkaline

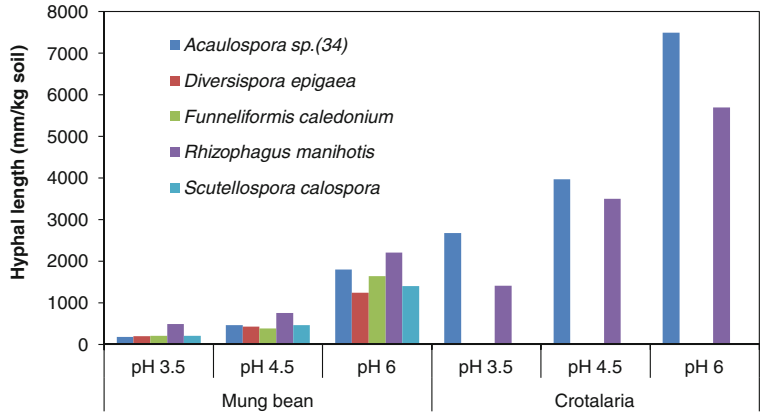

Fig. 3.5 Influence of soil acidity on extraradical hyphal length of different arbuscular mycorrhizal fungi in the rhizospheres of mung bean and crotalaria (data from Lin et al. 2001)

phosphatase and NADH-diaphorase activities in the external mycelium of AM fungi appear to be more sensitive to soil acidity (Vosatka et al. 1999; Malcova et al. 1999).

Effect of Soil Acidity on AM Spore Germination

Soil pH is one of the important soil factors that play a vital role in AM spore germination and presymbiotic hyphal growth. Most of the information on the influence of substrate acidity arises from the *in vitro* monoxenic cultures of AM fungi. A pH of 5.5 is usually maintained for standard monoxenic culture systems to maintain solubility and balance of the media components (Dalpé et al. 2005). However, the standard acidic pH maintained in monoxenic culture systems could affect the growth of certain AM fungal isolates. Maximum spore germination of *Acaulospora laevis* occurs between pH 4 and 5 and between pH 5 and 6 for *Racocetra coralloidea* and *Fuscutata heterogama* (Hepper 1984; Green et al. 1976).

The optimum pH for spore germination appears to be linked to the pH of the soil where the AM fungus originated. For example, the germination percentage of *A. laevis* spores originating from acidic soils tend to decline with increasing pH and the germination percentage drops to 10 % or less in neutral and alkaline soils (Hepper 1984).

Vosatka et al. (1999) tested the influence of simulated acid rain individually, or along with Al, amendment was on the germination of AM fungal spores belonging to *F. mosseae, Claroideoglomus claroideum,* and *Acaulospora tuberculata* associated with the rhizosphere of *Deschampsia flescuosa* seedlings (Vosatka et al. 1999). The results of this study suggested that *A. tuberculata* originating from high acidic soil exhibited greater tolerance to soil acidity than others.

Growth of AM Plants in Acid Soils

Compared with the amount of work done on the role of AM fungi on plant growth in non-acidic soils, less research has been done on acidic soils. The limited studies that have examined the role of AM fungi on plant growth in acidic soils have clearly revealed several benefits imparted by AM fungi on their associated host plants. In a greenhouse experiment, Heijne et al. (1996) determined the cause for the decline of two heathland herbs *Arnica montana* and *Hieracium pilosella* by growing them in the presence or absence of an AM fungus (*Rhizophagus fasciculatus*) on an extremely nutrient-poor sandy soil and irrigated with nutrient solutions with pH values ranging between 2.5 and 5.5. The results of the study showed that *A. montana* failed to survive and *H. pilosella* hardly grew in the absence of AM fungus, suggesting that AM symbiosis decreased the stress caused by soil acidity. Growth and mycorrhizal dependency of switchgrass varied with

AM fungal species and pH of the soil (Clark 2002) (Table 3.1). Shoot dry weights of switchgrass colonized by *G. margarita*, *G. albida*, and *C. etunicatum* were higher in low-pH soil than at a slightly higher-pH soil (Clark 2002) (Fig. 3.6).

Both shoot biomass and root biomass of *C. etunicatum*-colonized wheat plants were higher on an acid Andisol (pH 5.42) that was either unamended or amended with partly acidulated phosphate rock at the rate of 17, 43, or 86 kg/ha (Rubio et al. 2002). Nevertheless, *C. etunicatum* colonization was not effective in improving plant growth at any of these three levels when soluble P was added (Rubio et al. 2002). Grain and straw yield of wheat colonized by *R. intraradices* or two isolates of *F. mosseae* alone was higher in an acidic Alfisol (pH 5.2) soil treated with 50 and 75 % of recommended phosphorus pentoxide (P_2O_5) dose based on the targeted yield concept (Suri et al. 2011). Colonization of AM fungi along with increasing application rates of P_2O_5 resulted in consistent and significant improvements in straw and grain yields. All the three fungi along with 75 % P_2O_5 dose though produced acceptable yields; it was less than the yield at sole 100 % P_2O_5 dose (Suri et al. 2011).

Total biomass of broomsedge (*Andropogon virginatus*) colonized with isolates of *R. clarus*, *Acaulospora morrowiae*, and *R. heterogama* originating from acid or neutral soils was 2.3-, 2.0-, and 2.2-folds higher than the non-mycorrhizal plants when grown on sand culture and irrigated with nutrient solution at pH 4 (Kelly et al. 2005). The plant growth response was further amplified for *R. clarus* (12.89-folds) and *F. heterogama* (5.35-folds), but not for *A. morrowiae* when grown in sand culture containing 400 μm Al.

Shoot biomass of *L. leucocephala* cultivars (cv. K-8 and cv. K-636) colonized with *Glomus aggregatum* grown on Al-rich Oxisol and Mn-rich Vertisol acid soils increased with an increase in pH. Shoot biomass of mycorrhizal *L. leucocephala* cv. K-636 cultivar was higher than that of mycorrhizal cv. K-8 cultivar at pH 4.5 and 6.4, but was almost similar at the intermediate pH (Habte et al. 2011). Shoot and root dry mass of mung bean and crotalaria colonized by ten AM fungal species increased with increasing pH when grown on an acidic red soil. However, the growth response tends to vary with the AM fungi, host, as well as the growth period (Lin et al. 2001) (Fig. 3.7). Mycorrhizal dependency of both mung bean and crotalaria varied with soil acidity (Table 3.1). A reduction in shoot biomass was more prominent in crotalaria than for mung bean at pH 3.5. The increase in mycorrhizal dependency with increasing soil pH from 3.6 to 6.0 was more intense for crotalaria than mung bean (Table 3.1).

Plant dry weight of micropropagated apple rootstocks colonized by *C. etunicatum*, *S. pellucida*, *A. scrobiculata*, or *F. heterogama* was higher than non-mycorrhizal rootstocks when grown on acid soils with a pH of 4.0 or altered to pH 5.0 or 6.0 by adding $CaCO_3$ (Cavallazzi et al. 2007). However, root dry weights of apple rootstocks colonized by *F. heterogama* and *A. scrobiculata* were slightly less than the non-mycorrhizal rootstocks. The R/S ratios of mycorrhizal rootstocks were less than the non-mycorrhizal rootstocks. Mycorrhizal dependency of apple rootstocks colonized by *C. etunicatum* and *S. pellucida* was generally higher compared to those colonized by *A. scrobiculata* and *F. heterogama*

Table 3.1 Influence of soil acidity on mycorrhizal dependency[a] in different hosts

		pH 3.5	**pH 4.5**	**pH 6.0**
Mung bean (Lin et al. 2001)	*Acaulospora* sp. 34	−1.67	62.50	200.00
	Acaulospora sp. 53	1.67	−37.50	70.00
	Diversispora epigaea	0.00	−12.50	0.00
	Funneliformis caledonius	0.00	50.00	160.00
	Funneliformis mosseae	−3.33	75.00	90.00
	Fuscutata heterogama	−3.33	0.00	60.00
	Gigaspora sp.47	5.00	25.00	−10.00
	Rhizophagus manihotis 38	6.67	100.00	180.00
	Rhizophagus manihotis 49	0.00	25.00	30.00
	Scutellospora calospora	0.00	0.00	0.00
		pH 3.5	**pH 4.5**	**pH 6.0**
Crotalaria (Lin et al. 2001)	*Acaulospora* sp. 34	415.38	1946.67	1331.58
	Acaulospora sp. 53	23.08	53.33	178.95
	Diversispora epigaea	−15.38	33.33	252.63
	Funneliformis caledonius	−30.77	153.33	226.32
	Funneliformis mosseae	−15.38	120.00	421.05
	Fuscutata heterogama	69.23	106.67	52.63
	Gigaspora sp.47	−15.38	146.67	315.79
	Rhizophagus manihotis 38	69.23	346.67	794.74
	Rhizophagus manihotis 49	−30.77	40.00	236.84
	Scutellospora calospora	−38.46	33.33	78.95
		pH 4.6	**pH 4.9**	**pH 5.2**
Cowpea (Rohyadi 2008)	*Claroideoglomus etunicatum*	13	14	47
	Gigaspora margarita	81	65	53
		pH 4	**pH 5**	
Switchgrass (Clark 2002)	*Acaulospora morrowiae*	2075.00	2112.50	
	Claroideoglomus etunicatum	1743.75	3475.00	
	Gigaspora albida	518.75	1712.50	
	Gigaspora margarita	1856.25	3181.25	
	Gigaspora rosea	12.50	6.25	
	Rhizophagus clarus	4443.75	3018.75	
	Rhizophagus diaphanus	3731.25	3531.25	
	Rhizophagus intraradices	−25.00	1087.50	
		pH 5.15	**pH 5.7**	
Barley 'Carmen' (Borie and Rubio 1999)	*Claroideoglomus etunicatum*	719	98	
		pH 5.15	**pH 5.7**	
Barley 'teffi' (Borie and Rubio 1999)	*Claroideoglomus etunicatum*	6.67	−17.6	
		pH 4.48		
Chickpea (Alloush et al. 2000)	*Rhizophagus clarus*	18.39		
		pH 5.2		
Wheat (Suri et al. 2011)	*Funneliformis mosseae* (IARI)	15.39		
	Funneliformis mosseae (Local)	13.40		
	Rhizophagus intraradices (TERI)	14.02		

[a] Calculated from the cited studies according to Plenchette et al. (1983)

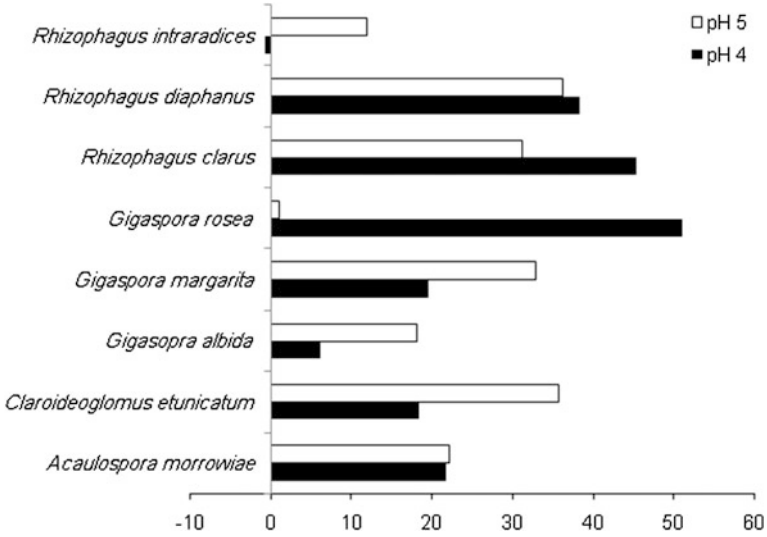

Fig. 3.6 Influence of soil acidity on shoot dry weight of switchgrass colonized by different arbuscular mycorrhizal fungi (calculated from Clark 2002)

(Cavallazzi et al. 2007). As the mycorrhizal dependency of apple rootstocks colonized by *C. etunicatum* and *S. pellucida* increased with an increase in soil pH from 4 to 6, a decline in mycorrhizal dependency was evident for rootstocks colonized by *A. scrobiculata* and *F. heterogama*.

Clusia multiflora seedlings inoculated with AM fungal inocula originating from acid or neutral soils accumulated more shoot and root masses and had increased root lengths than non-mycorrhizal seedlings grown on an acid humic Ultisol at pH 4.2 and irrigated with acidified water of pH 3, 4, and 5 (Cuenca et al. 2001). The shoot/root ratio of mycorrhizal seedlings was higher than that of non-mycorrhizal seedlings irrespective of pH levels and origin of AM inocula (Cuenca et al. 2001).

Sweet potato (*Ipomoea batatus*) plants colonized by *G. margarita* and raised on an acidic soil that was either unlimed (pH 4.2) or limed (pH 5.2) had significantly higher plant biomass than non-mycorrhizal plants at pH 4.2 and not at pH 5.2 (Yano and Takaki 2005). Shoot biomass of cowpea (*Vigna unguiculata*) colonized by *G. margarita* was higher than those colonized by *C. etunicatum* when grown on an acidic Podozole (pH 4.9) (Rohyadi 2008). As the AM fungal benefit on plant growth declined from 81 to 39 % with an increase in pH from 4.6 to 5.2 for plants colonized by *G. margarita*, it increased from 13 to 33 % for plants colonized by *C. etunicatum*. Such an inverse pattern was also evident for mycorrhizal dependency of cowpea plants colonized by *G. margarita* and *C. etunicatum* (Table 3.1).

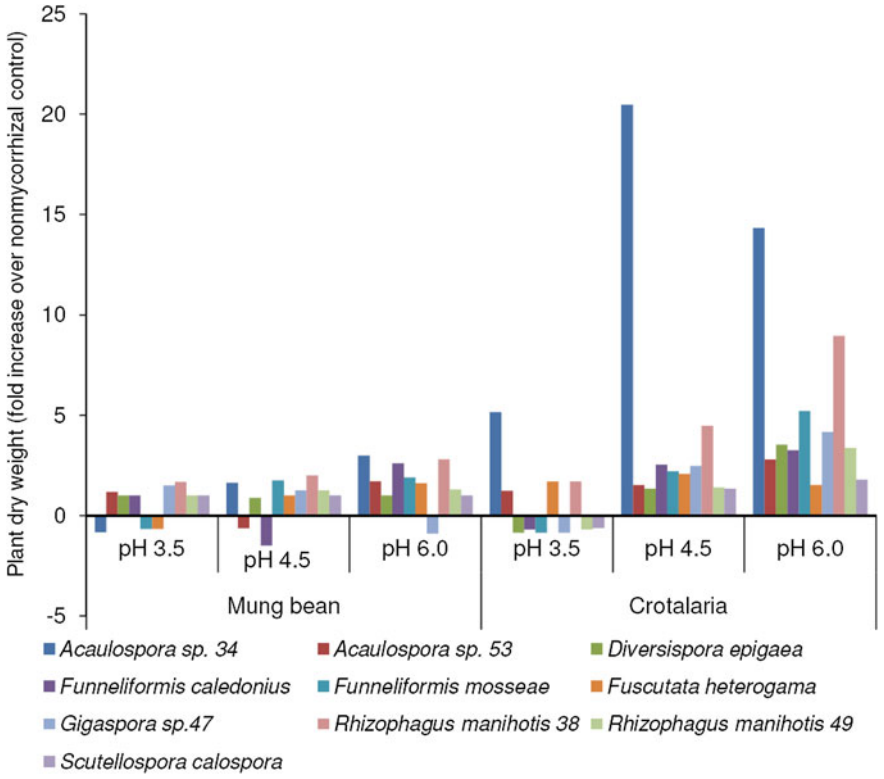

Fig. 3.7 Influence of soil acidity on growth of mung bean and crotalaria colonized by different arbuscular mycorrhizal fungi after 45 days of growth (calculated from Lin et al. 2001)

An investigation on the role of *C. etunicatum* on growth of barley cultivars that were either tolerant or sensitive to Al on an unlimed (pH 5.15) or limed (pH 5.70) Andisol indicated that the growth benefit of *C. etunicatum* association was more pronounced in Al-tolerant ('Carmen') than in Al-sensitive ('Steffi') barley cultivar (Borie and Rubio 1999).

Efficiency of AM Fungi in Ameliorating Al Toxicity

The AM fungal association can modify the interaction between plant and soil and also protect the host plant under stress environments such as heavy metals (Smith and Read 2008; Muthukumar and Bagyaraj 2010). The presence of high concentrations of Al^{3+} in the soil is deleterious to the survival and activity of the microorganisms (Rohyadi 2006). The uptake of Al by roots and its translocation within plants are greatly reduced by AM fungal association. The production of

exudates by the extraradical mycelium results in the chelation of heavy metals in the mycorrhizosphere (Tonin et al. 2001; Hall 2002).

Mycorrhizal tulip-poplar (*Liriodendron tulipifera*) seedlings had higher concentrations of P in their leaves and higher biomass in contrast with the non-mycorrhizal plants when raised on substrates amended with various concentrations of Al (Lux and Cumming 2001). Kelly et al. (2005) inoculated broomsedge with five isolates of three AM fungal species (*R. clarus*, *A. morrowiae*, and *F. heterogama*) in substrates amended with 400 μm Al. The results of this study indicated that *R. clarus* was more resistant to Al toxicity (22.4–92.7 %) and growth inhibition, followed by *F. heterogama* and *A. morrowiae* (Kelly et al. 2005). Rohyadi et al. (2004) also showed that plant growth especially the shoot and root dry weights of cowpea plants inoculated with *G. margarita* was higher compared to plants inoculated with *C. etunicatum* at different soil acidic levels (4.4, 4.9, and 5.2).

However, the resistivity for Al appears to be much higher for AM fungal isolates originating from Al-rich soils compared to those from non-contaminated soils. For instance, *C. multiflora* seedlings inoculated with natural inoculum of AM fungi originating from acidic as well as neutral soils and watered with acidic solution indicated that seedlings inoculated with AM fungal inoculum originating from acidic soil accumulated less Al and root growth was normal compared to seedlings inoculated with AM fungal inoculum from neutral soil (Cuenca et al. 2001). In general, the abundance of vesicles in the roots colonized by AM fungi originating from non-acidic soil indirectly indicates that the plants are under some sort of stress as vesicle production tends to peak under stress conditions (Cooke et al. 1993). Though several factors are shown to affect AM fungi under low pH, the crucial or dominant ones are still elusive.

Aluminum toxicity affects root architecture as mentioned earlier, which affects nutrient and water uptake (Foy et al. 1978). Compared to roots, the extraradical mycelium of AM fungi can spread beyond the nutrient depletion zone surrounding the root and take up low mobile nutrients like P from the soil and translocate it to the host (Smith et al. 2000). The extraradical hyphae of AM fungi can spread up to 10 cm from the root surface (Jakobsen et al. 1992), and the smaller diameter of the fungal hyphae than roots (Bolan 1991) increases the surface area for absorption by fourfold. This favors the efficient uptake of P and other soil nutrients by the mycorrhizal roots in nutrient-stressed soils.

Like plants, AM fungi also possess certain defense mechanisms to protect themselves against various stress conditions. There is enough evidence to believe that exudation of organic acids by AM fungal hyphae (Plassard and Fransson 2009) especially the citrate, malate, and acetate (Tawaraya et al. 2006; Toljander et al. 2007) could ameliorate the Al toxicity. Therefore, AM fungi-colonized roots are well protected from the deleterious effects of the metal toxicities (Clark and Zeto 1996; Maddox and Soileau 1991) through extensive hyphal network and root exudates.

In addition, root colonization by AM fungi could also influence the release of carbon by plant roots into the rhizosphere, increasing the availability of organic

acids and other substrates (Seguel et al. 2013). For example, Klugh and Cumming (2007) showed altered concentrations of organic acids in the root zones of AM tulip-poplar raised on sand culture and irrigated with a nutrient solution of pH 4.0. In addition, the organic acid production by AM plants was independent of the degree of colonization. A similar observation was also made in a later study by Klugh-Stewart and Cumming (2009) for AM broomsedge. The fungal hyphae bind the toxic metals like Al extracellularly to the cell walls or sequestrate intracellularly in vacuoles by phosphate granules (Toler et al. 2005; González-Guerrero et al. 2008; Zhang et al. 2009).

Certain studies indicate that AM fungi could also sequester Al in their vesicles and auxiliary cells (Yang and Goulart 1997; Cuenca et al. 2001). Investigations by Yano and Takaki (2005) and Cuenca et al. (2001) showed that sweet potato and *C. multiflora* could accumulate >200 % of the normal Al concentration in their roots without exhibiting any toxic symptoms when colonized by *G. margarita* and *Acaulospora* species, respectively. Likewise, a 51 % increase in tissue Al level was noted in the roots of tulip-poplar inoculated with *R. clarus* and *R. diaphanus*.

In addition, the production of glomalin, which is an abundant glycoprotein in the soil, is produced by the hyphal wall of AM fungi (Treseder and Turner 2007). The glomalin deposited in the soil when the hyphae senescence is reported to sequester toxic minerals considerably. Etcheverría (2009) showed that glomalin-related protein (GRSP) could bind around 4.2–7.5 % of Al in acidic soils of a temperate forest in southern Chile. The production of GRSP has been shown to be directly proportional to the adverse soil conditions, especially low pH (Vodnik et al. 2008; Cornejo et al. 2008). These mechanisms significantly reduce the deleterious effects of Al and improve the functionality of plants. Altogether, AM fungi play a vital role in ameliorating the effects of Al stress by various detoxifying mechanisms.

Efficiency of AM Fungi in Ameliorating Mn Toxicity

The concentration of Mn in shoots and roots of mycorrhizal plants is often lower than that in non-mycorrhizal plants (Kothari et al. 1991; Nogueira and Cardoso 2000; Nogueira et al. 2004). Similar concentrations of Mn have been reported in shoots (1.02 and 1.04 mg/g) and roots (0.38 and 0.33 mg/g) of non-mycorrhizal and mycorrhizal (*G. margarita*) sweet potato grown on an acid soil (pH 4.2) (Yano and Takaki 2005). Likewise, Mn toxicity was less severe in mycorrhizal plants than in non-mycorrhizal soybean plants in spite of similar concentrations of Mn in these plants (Bethlenfalvay and Franson 1989).

Habte et al. (2011) speculated that AM fungal colonization in *L. leucocephala* cultivars (cv. K-636 and cv. K-8) was low in Mn-rich acid Oxisol soil at pH 4.5 because of the high similarity in the reactivity of the host and the fungi to Mn toxicity. The tolerance of *L. leucocephala* seedlings to acid toxicity in Mn-rich Oxisol varied with the pretransplant mycorrhizal status of the seedlings. Tolerance level of *L. leucocephala* cv.K-636 that was less tolerant than cv. K-8 in Mn-rich

Oxisol improved when the seeds were mycorrhized prior to transplantation. Nogueira et al. (2002) also reported that soybean inoculated with *C. etunicatum* under different levels of Mn (0, 5, 10, 20, and 40 mg/kg) exhibited better growth and less Mn toxicity symptoms (callose deposition).

Earlier studies on the influence of AM in acid soils suggested that colonization by AM fungi generally enhanced the uptake of Mn^{2+} by host plants (Mederios et al. 1994; Clark and Zeto 1996; Clark et al. 1999b; Lux and Cumming 2001). Nogueira and Cardoso (2003) investigated the effectiveness of three AM fungi (*Glomus macrocarpum, C. etunicatum,* and *R. intraradices*) on soybean in two different soils (sandy and clay). The results of this study showed that soybean plants had lower Mn content and biomass in sandy soil compared to clayey soil. Nevertheless, plants inoculated with *C. etunicatum* and *R. intraradices*, and *G. macrocarpum* exhibited Mn toxicity symptoms and had reduced biomass in clayey soil indicating the soil-type influence on Mn toxicity.

Most of the studies on the role of AM fungi on plant nutrient uptake in acid soils indicate an enhanced Mn uptake by AM plants. Nevertheless, the influence of AM fungi on Mn uptake by plants in acid soils could be time dependent as shown by Nogueria et al. (2007) where soybean plants colonized by *C. etunicatum* or *G. macrocarpum* had higher concentrations of Mn during initial stages of growth and lower concentrations during later phase of plant growth. There are also studies indicating that AM fungi reduce the amount of Mn entering the roots by suppressing the activity of Mn oxidizing and reducing bacteria in the rhizosphere at pH 5.7 or higher (Bethlenfalvay and Franson 1989; Kothari et al. 1991; Nogueria et al. 2007).

AM Fungal Amelioration of Plant P Deficiency

In contrast to an increment in the concentrations of Al and Mn in the soil, there is a simultaneous decline in the availability of essential nutrients such as P, K, and Mo (Fageria et al. 1990). Depletion of these essential mineral nutrients inversely affects the plant growth, leading to reduction in crop production. As already mentioned, P fixation and availability depend mainly on soil pH (Hsu 1964). Minimal availability of P is one of the common and well-known limiting factors for plant growth and development in soils with a pH range of 2–4 (Bowden et al. 1980; Nian et al. 2003).

The worldwide distribution and causes for P-limiting soils have recently been discussed in detail by Lynch and Brown (2008). In acid soils, P exists in the form of insoluble mineral complexes such as Al–P and Fe–P and therefore is not available for uptake by plants (Sample et al. 1980). Complexolysis is a process in which the complexing agents such as the exudated organic acids liberate minerals from their complex insoluble forms through organic acidolysis, and complex and chelate formations (Courty et al. 2010). These processes are most suited for the solubilization of P adsorbed to Al or Fe oxyhydroxides.

The development of extensive hyphal network in the soil ameliorates the effects of extremely low pH through improved uptake of P. Smith et al. (2000) showed

that about 80 % of the total P acquired by AM *Medicago truncatula* were provided by the extraradical mycelium of the fungi associated with those plants. The functions of the fungal hyphae radiating out from the colonized roots are more important in acid soils as the development and proliferation of roots are severely affected in soils with low pH.

Rohyadi (2008) observed an increase in P uptake in maize colonized by *G. margarita* under acidic conditions and suggested that the enhanced P levels in AM maize tissues could be due to the greater exploration of soil by the AM fungal hyphae. This suggestion is supported by the observation where the P-uptake response of cowpea plants colonized with *G. margarita* was 104 and 46 % higher compared to plants colonized with *C. etunicatum* at pH 4.6 and 4.9. Similarly, the amount of P uptake per unit root length of *G. margarita*- and *C. etunicatum*-colonized cowpea plants were 75–144 % and 41–88 % higher compared to non-mycorrhizal plants.

Toro et al. (1998) stated that AM fungi not only had the access, but also could reach to the unexploited sources of P in deficient soils. The enhanced growth of maize colonized by *C. etunicatum, Glomus diaphanum,* and *R. intraradices* in spite of the low number of arbuscules in the roots in an acidic soil (pH 4.2–4.5) was attributed to the hyphal network in the soil reaching for the sparingly available P sources (Clark and Zeto 1996).

In a later study, Clark (2002) showed that the P inflow rates per unit root length of mycorrhizal switchgrass were around 18-fold higher compared to non-mycorrhizal plants when grown on soil with pH 4. However, the inflow rates declined to half when the plants were raised on a slightly higher pH of 5. The effectiveness of AM fungi on stress amelioration under acidic conditions could be attributed to the proliferation of external hyphae rather than colonization (Rohyadi 2008).

The AM fungi associated root system are highly efficient than non-mycorrhizal root systems as they could use various forms of phosphate such as inorganic and organic P sources (Tarafdar and Marschner 1994; Ravnskov et al. 1999), which are limited in acid soils. Colonization of switchgrass by four different AM fungal isolates (*R. intraradices* WV894, *R. clarus* WV751, *C. etunicatum* WV579A, and *Acaulospora mellea* BR152A) in five acid soils (Lily, Porters, Tatum, Rayne, and Pacolet) resulted in varied extractable plant P pools (Clark et al. 2005). These differences in P pools were attributed to the varied uptake of P by different AM plants, similar to the observations made by Graw (1979), Saif (1987) and da Silva et al. (1994).

Role of AM Fungi in the Uptake of Other Nutrients

Plants growing on acidic soils also have limited access to several essential mineral nutrients other than P such as Ca, Mg, potassium (K), copper (Cu), and zinc (Zn). Low levels of ions migrate to the exchange sites in the rhizospheric region under acidic conditions, rendering it less available for the plants (Sumner et al. 1991). These nutrient limitations are often compensated by extended extraradical hyphal

network of AM fungi. Enhanced acquisition of several mineral nutrients (including Zn and Cu) was reported in maize in response to colonization by *C. etunicatum, G. diaphanum,* and *R. intraradices* in acidic soils with a pH of 4.2–4.5 (Clark and Zeto 1996).

Alloush and Clark (2001) demonstrated a better uptake and translocation of Ca, Mg, and K by *R. clarus* in maize when grown on soils with a pH 4.7. A similar increase in K, Ca, and Mg uptake was also reported for maize plants in acidic soils (Liu et al., 2000). Siqueira et al. (1990) also reported higher concentrations of Ca in the tissues of *Brachiaria* grass (*Brachiaria decumbens*) colonized by AM fungal assemblage with taxa originating from different acidity compared with non-mycorrhizal plants when grown on soils with pH 4.5.

Certain studies in contrast to the above-mentioned observations have reported the lack of plant benefit from AM fungi in acid soils. Sweet potato plants colonized by *G. margarita* failed to improve the uptake of P, K, Ca, and Mg when grown on soils with pH ranging from 4.2 to 5.2 (Yano and Takaki 2005). A similar observation was made in wheat colonized by species of *Funneliformis* and *Rhizophagus* failed to improve plant N, P, K, Fe, Mn, Zn, and Cu concentrations when grown on an acid Alfisol (Suri et al. 2011).

Conclusions and Future Considerations

Acidic syndrome is a major factor that limits crop production worldwide. Research over the past two decades has contributed immensely to our understanding on the various adaptations plants have evolved to ameliorate the effects of soil acidity. Conventional agricultural practices involve the application of lime, gypsum, and P fertilizer to improve crop growth and yield in acid soils. These amendments though achieved the desired target to certain extent, high input costs, and depleting reserves of raw materials, and their unavailability restricts their widespread and long-term use.

Breeding plant genotypes that are tolerant to acidic soils or genotypes with high nutrient use efficiency may be one possible solution. Nevertheless, available evidence indicates the potential role of AM symbiosis in improving plant growth in acidic soils. Further, studies examining the role of AM fungi on plant growth and yield in acidic soils have been conducted under controlled conditions with a limited number of fungal isolates. Results of such studies though help to elaborate our understanding on AM symbiosis in acid soils; it could substantially differ under field conditions.

Furthermore, there are clear indications that continuous culture of AM fungal genotypes originating from acid soils under normal soil conditions would result in the loss of the acquired characters. Therefore, standardization of culture conditions is essential to retain the acquired characters and exploit these fungi as bioinoculants. An alternative strategy to exploit the symbiosis for the maximum benefit in acid soils would be to understand and manipulate the factors that influence AM symbiosis.

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