Modulation of Plant Micronutrient Uptake by Arbuscular Mycorrhizal Fungi

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Abstracts

Plants require light, water, and nutrients for better growth and reproduction. Arbuscular mycorrhizal (AM) fungi associate with root systems of most land plants and improve plant growth by enhancing the uptake of soil nutrients, including micronutrients. Contradictory influence of mycorrhizal plants in micronutrient uptake may be due to different edaphic conditions, which affect AM fungal root colonization and extraradical hyphal development. The micronutrient uptake of plants is influenced by different factors like availability of macronutrient like phosphorus (P) and micronutrients themselves in soil. AM fungal hyphal growth and root colonization are suppressed by high levels of micronutrients in soil. In soils the mobility of Cu, Zn, Mn, and Fe is low, and uptake by roots is restricted by low diffusion rates and root depletion zones created by plant roots. AM plants overcome this by exploring large volume of soil compared to roots and minimize the diffusion distance to enhance the availability of these immobile nutrients. Uptake of Cu and Zn or Mn and Fe is quite different. The uptake of Cu and Zn is affected by amount of plant and soil P levels, whereas the uptake of Mn and Fe is affected by indirect reduction of oxidation-reduction potential and availability of Mn and Fe in mycorrhizosphere. Under stress conditions, AM fungi help plants to increase their nutrient uptake, thereby imparting tolerance to prevailing stress. This is seen especially under saline conditions where AM fungal application limits the Na^+ and Ca^{2+} ion concentration in plants by enhancing Mg^{2+} uptake, thereby increasing chlorophyll concentration,

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photosynthetic efficiency, and plant growth. AM fungi are potential tool for improving plant health and rhizosphere for better uptake of micronutrients under various edaphic conditions.

14.1 Introduction

All plants in natural and seminatural ecosystems are colonized by AM fungi and form mycorrhizosphere in addition to rhizosphere (Johansson et al. 2004). Root and mycorrhizal fungi both influences the mycorrhizosphere region, whereas more particularly the term hyposphere refers to the region surrounding individual hyphae (Johansson et al. 2004). Soil microbes play a vital role on maintaining soil fertility and plant health (Gianinazzi and Schuepp 1994). Arbuscular mycorrhizal (AM) fungi are mutualistic symbiotic fungi, a major microbial population in soil, which influence the nutrient uptake and plant productivity (Johansson et al. 2004). Arbuscular mycorrhizal fungi are associated with more than 250,000 of plants worldwide (Smith and Read 1997). The formation of AM fungal symbiosis started with the penetration of host root cortical cells by AM fungi which form arbuscules (treelike), vesicles (saclike), arbusculate coils, and hyphal coils that interface with host cytoplasm (Fig. 14.1) (Smith and Read 1997).

These structures provide increased surface area for exchange of metabolites between plants and fungi. Arbuscular mycorrhizal fungi produce inter- and

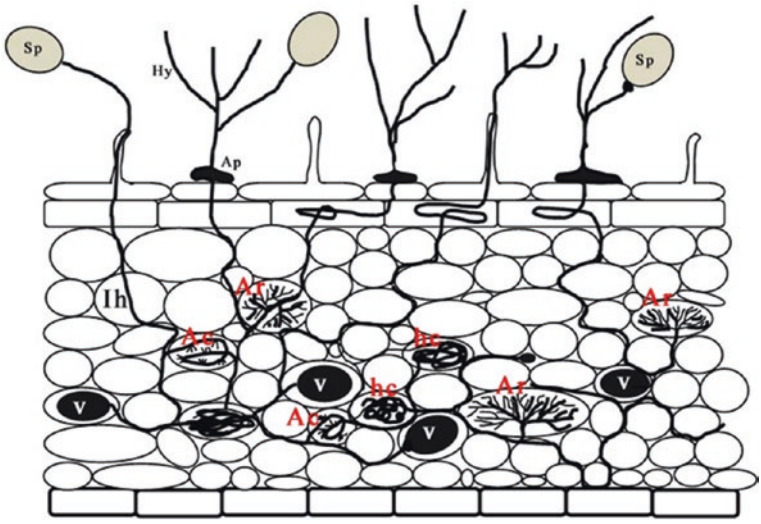

Fig. 14.1 Arbuscular mycorrhizal fungal interactions with host plant showing different functional structures. *Ap* arbuscular mycorrhizal fungal spore, *Hy* arbuscular mycorrhizal fungal hyphae, *Ap* appressorium, *V* vesicles, *Ar* arbuscules, *Ac* arbusculate coils, *Hc* hyphal coils, *Ih* intercellular hyphae

intracellular hyphae which are also connected with soils in rhizosphere regions beyond several centimeters away from the soil (Rhodes and Gerdemann 1975). The total surface areas of hyphae are higher in several orders of magnitude than that of roots which increase the nutrient uptake potentially. Moreover, AM fungal hyphae play an important role in soil stabilization through the formation of soil aggregates and mobilize the organically bound N from plant litter (Tisdall and Oades 1979; Hodge et al. 2001). Arbuscular mycorrhizal associations influence the mineral nutrient acquisition of colonized plants by various ways such as high spatial availability of nutrients and mobilization of sparingly available nutrients and protect the host plants against pathogens and abiotic stress (drought, salinity, metal toxicity, low temperature) (Marschner 1995). Arbuscular mycorrhizal (AM) fungi enhance plant growth by enhancing the absorption of N, P, K, Ca, S, Cu, Zn, Fe, and Mn through increase in the absorbing surface areas. AM fungal hyphae provide a greater absorptive root surface, capable of exploring greater volume of soil, thus limiting nutrients and water depletion zones (Clark and Zeto 1996). Plants colonized by AM fungi reduce toxicity of Al and Mn ions and pH of the rhizosphere, and these effects depend on edaphic and climatic conditions and compatibility between plant-fungus interactions. The mechanisms involved in better acquisition of Zn and Cu by colonized roots is thought to be similar to that of P (Lambert et al. 1979). In various reports, AM colonization in the concentration of potassium, calcium, magnesium (Lambert et al. 1979), iron (Liu et al. 2000), manganese (Eivazi and weir 1989; Lu and Miller 1989), and boron (Lu and Miller 1989) in plants was at various levels, low to low or unchanged compared to non-mycorrhizal plants.

Arbuscular mycorrhizal fungal colonization may alter the root morphology, which is responsible for high to low levels of nutrients uptake by plants. In addition to root morphology, rhizosphere microorganisms play a key role in nutrient uptake. The decrease or increase of the level of Mn to plant roots depends on the range and effectiveness of Mn-oxidizing and Mn-reducing microorganisms in the rhizosphere (Marschner 1988). Highly variable edaphic factors are crucial for inconsistent responses of mycorrhizal plants in micronutrient uptake, extraradical hyphal development and root colonization are influenced by soil conditions, and AM fungi in turn influence the uptake of these metals (Liu et al. 2000). In varied stress conditions like drought and salinity (Audet and Charest 2006), AM fungi improve the uptake of nutrients to enhance the survival of host plants. In wheat plants, both well-watered and water-stressed conditions aboveground mineral nutrient contents (P, Zn, Mn, Cu, and Fe) had been considerably high, compared to non-mycorrhizal plants. In saline conditions, high levels of Fe, Cu, and Zn concentration and total accumulation occurred in mycorrhizal host compared to non-mycorrhizal plants (Al-Karaki 2000).

14.2 Copper

Copper plays a vital role in photosynthetic and electron transport systems, activity of various oxidative enzymes, and pollen formation (Marschner 1995). Mycorrhizal peach seedlings show root copper concentration of 321% by inoculation of

G. mosseae and 178% by *G. versiforme*, whereas leaves show less than that of non-mycorrhizal plants, which implies that AM fungi play an important role in uptake instead of translocation (Wu et al. 2011). Arbuscular mycorrhizal fungal species shows different ranges of Cu uptake in different plant species. *G. etunicatum* and *G. mosseae* inoculated in wheat plant under well-watered and water-stressed conditions increased the shoot Cu concentrations (Al-Karaki et al. 2004). Spores of G. *etunicatum*, *G. macrocarpum*, and *Gigaspora margarita* inoculated in *Desmodium cinereum* showed increased Cu concentrations in root and shoot (Adiova et al. 2013). Tomato seedlings inoculated with *G. fasciculatum* and *G. intraradices* showed high tissue Cu concentration than non-inoculated tomato plants (Ramakrishnan and Selvakumar 2012). Arbuscular mycorrhizal fungal inoculation significantly increased the Cu concentrations in tea plants (Kahneh et al. 2006). In AM-inoculated cassava plants, the micronutrient uptake was high compared to non-inoculated plants. Most of the micronutrients were partitioned to roots, and Cu was consistently partitioned more to roots than shoots. This partition effect was due to AM fungal colonization, and the partitioning pattern could be attributed to the trace element toxicity. The level of micronutrient reduced to toxic, and the element could be diverted to the areas where it could be stored with less injury to plant. Copper is in toxic level, and roots are the sites of preferential when external supply is large (Simwambana and Ekanayake 2001). In AM-colonized citrus, stem and leaf accumulated 50 and 500% more Cu compared with non-mycorrhizal plants. But colonized citrus roots acquired 2–10 times more Cu compared with non-mycorrhizal plants. In maize, the concentration was 6 times higher in mycorrhizal roots; its concentration in shoots did not vary much between mycorrhizal and non-mycorrhizal treatments (Kothari et al. 1990). It is not clear whether the increased amount of Cu in roots of mycorrhizal plants is available to the plants, as it may be bound to fungal polyphosphate granules as has been shown for a Cu, Fe, and Mn by White and Brown (1979) or sequestered in fungal structures. In *Cicer arietinum*, increase in Cu uptake with P application may be due to increased root growth, which resulted in better exploration of soil volume. However, an antagonistic effect of Cu and P in rice was observed, where one of the nutrients were applied in large quantity (Tandon 2001). Higher rate of P application was found to have no influence on Cu concentration in red kidney beans, tomato, or sweet corn (Tandon 2001). This difference between genus and species of plants might be attributed to the genetic composition of plant species (Tandon 2001). Havlin et al. (2007) reported reduced uptake of Cu due to high rate of P application result in formation of copper phosphate, which is not readily available to plants. In calcareous soil, white clover with restricted rooting space, the delivery of Cu from the hyphal compartment ranged from 52 to 62% of the total uptake (Li et al. 1991). Increasing P supply to the hyphal compartment enhanced hyphal delivery of P and slightly depressed that of Cu with corresponding increase in the P in molar ration from 37 to 912 (25%). Thus, hyphal uptake and transport of P and Cu appear to be rather independent. In contrast, partitioning of Cu between roots and shoots was strongly affected by P. Phosphorus enhanced not only the content but also the concentration of Cu in the shoot dry matter indicating that the enhancement effect of P on Cu translocation was not exclusively regulated by

the shoot demand. These results also demonstrate that particularly with Cu the role of AM in uptake cannot properly be evaluated from only the shoot content or concentration. According to Liu et al. (2000), micronutrient and P level in soil significantly influence the uptake of Cu in maize. The micronutrient amount and P levels are not only factors which determine the uptake but also on which metal to be considered. The plants grown in low P regime have high extraradical hyphal growth and potentially explore large volume of soil and absorb large amount of micronutrients. Increased shoot P content in plants grown at high soil P levels can increase Cu sink size. This may stimulate uptake and translocation of Cu to plant shoots. Micronutrient uptake by plant roots are diffusion limited (Tisdale et al. 1993) and plants colonized by AM fungi uptake more metal nutrients via extraradical hyphae.

14.3 Zinc

Zinc is considered as a key element in maintaining cellular membrane integrity; acts as an essential enzyme metal constituent and functional, structural, or regulatory cofactor; and is associated with saccharine metabolism, photosynthesis, and protein synthesis in plants (Val et al. 1987), formation of pollen grains, and disease resistance potential (Marschner 1995). In addition, Zn plays a vital role in regulating gene expression and stress tolerance such as high solar radiation and temperature (Broadley et al. 2007). Arbuscular mycorrhizal fungi enhanced the uptake of Zn (Guo et al. 1996), although significantly smaller quantities compared to P. It is because Zn may not be as readily translocated from roots to shoots as P, since Zn distribution in roots and shoots is determined by soil P levels. But, Zn acquisition was decreased when P was increased in soil (Lambert and Weidensaul 1991), and enhanced acquisition of Zn occurred in high soil P levels (Raju et al. 1990). The increased Zn content was observed in various studies using different AM fungal species. *Plantago ovata* inoculated with *G. mosseae*, *Gigaspora margarita*, *Acaulospora morrawae*, and *G. deserticola* showed increased Zn concentrations (Mathur et al. 2006). Mycorrhizal-inoculated watermelon, cucumber, maize, cotton, horse bean, chick pea, and soybean showed high Zn concentration under non-fumigated conditions than fumigated conditions, because fumigation process eradicates the other beneficial organisms (Ortas 2012). Increased Zn concentrations were observed in alfalfa plants inoculated with *G. etunicatum*, *G. intraradices*, and *G. mosseae* under pot culture conditions (Zaefarian et al. 2011). Cucumber plants inoculated with *G. etunicatum*, *G. clarum*, and *G. caledonium* showed higher Zn tissue concentration than non-inoculated controls (Ortas 2010; Wang et al. 2008; Lee and George 2005). *Glomus versiforme*, *G. intraradices*, and *G. etunicatum* increased the uptake of Zn in apple root stocks in calcareous soils (Hosseini and Gharaghani 2015). In general view, the elements (Zn) with low mobility in the soil can be absorbed in higher levels by mycorrhizal plants (Yano-melo et al. 1999). The *Pistacia vera* inoculated with *G. mosseae* and *G. intraradices* showed higher Zn concentration than non-inoculated controls under greenhouse conditions (Bagheri et al. 2012). Inoculation of wheat with *G. mosseae* increased Zn uptake in wheat

tissues under calcareous soil conditions (Ghasemi-Fasaei et al. 2012). Higher Zn concentration (350%) was observed in *Euterpe oleracea* seedlings inoculated with mycorrhizal fungi *Scutellospora gilmorei*, *Acaulospora* sp., and *G. margarita* (Chu 1999). The higher uptake efficiency of Zn was observed in *Vitis vinifera* under pot experiment (Schreiner 2007). After P, Cu and Zn are second most important nutrients that are promoted by AM fungal colonization (Lee and George 2005). A comparative observation between mycorrhizal and non-mycorrhizal plants showed 32% higher Zn concentrations in roots (Lehmann et al. 2014). Extraradical hyphae contributed more in Zn uptake (Kothari et al. 1990), whereas in total zinc uptake, 48% is by fungal hyphae (Kothari et al. 1990). Extraradical hyphal growth of AM fungi has negative (Liu et al. 2000), positive (Seres et al. 2006), and neutral (Toler et al. 2005) impacts upon soil zinc additions. Decreased hyphal density of *G. intraradices* inoculated in maize plants with increasing soil Zn addition was observed (Liu et al. 2000). However, increased hyphal length density and intraradical colonization were found in soils added with zinc (Seres et al. 2006). The differences are likely due to complex interactions between edaphic and environmental conditions and difference in Zn addition. Moreover, plant and fungal identity is an important factor for responses of AM fungi to soil Zn addition. Increased Zn addition decreases the root colonization of AM fungi (Bi et al. 2003; Chen et al. 2004). This response results when at low toxic level, AM fungi improve Zn nutrition and at above toxic level, they protect plant tissues from Zn accumulation. The studies mostly focused on Zn effects on intraradical colonization have focused on Zn inputs in excess of this toxic level (Cavagnaro 2008). But few experiments on low level of Zn addition decreased AM fungal colonization in onion inoculated with *G. mosseae* (Gildon and Tinker 1983). The percentage of root length colonization was decreased from 74 to 47 to 0% over a range of Zn additions (0, 10, and 75 mg Zn/kg soil as $ZnSo_4$) and from 55 to 42 to 0% with Zn additions of 0, 10, 20, 40, and 75 mg Zn/kg soil. The reduction in colonization of sections of the root systems nor directly exposed to increased Zn (Gildon and Tinker 1983). In other studies, slight increase in colonization (40–46%) of white clover was observed in an unamended soil and high Zn addition treatment (400 mg/kg), and root biomass was similar in all treatments. Wild tobacco inoculated with *Glomus intraradices* increases colonization from 14 to 82% over a range of Zn addition (0–250 mg Zn/kg as $ZnSo_4$) (Audet and Charest 2006). In conclusion Zn does not necessarily result in a significant reduction in colonization, because AM fungal colonization was observed in plants growing in Zn-contaminated soils (Hildebrandt et al. 2006). These effects are due to selection of AM fungal species and for strains that can withstand high Zn concentrations. *Phaseolus vulgaris* colonized by *Glomus etunicatum* increased 24–92% with the addition of 5 mg/kg, whereas *G. mosseae* was not effective (88–90%) (Ortas and Akpinar 2006). These effects are provided by edaphic factors. A diverse range of responses of mycorrhizal colonization to Zn addition was reported by various authors (Vivas et al. 2006; Whitefield et al. 2004). Arbuscular mycorrhizal fungi and plant identity, edaphic factors, and other environmental conditions play an important role in modulating nutrient uptake and colonization responses in extraradical phase of colonization (Cavagnaro 2008). Arbuscular mycorrhizal fungi translocate the nutrients from

nutrient depletion zones formed around the roots. Burkert and Robson (1994) elucidate that AM fungi take up Zn 40 mm apart from the root surface. In maize *G. intraradices* increase the uptake of both P and Zn of plants, and almost 9% of the added Zn was transported to the plants from a distance of 50 mm within 25 days (Jansa et al. 2003). The development of large mycelia network that can enhance the potential of AM fungi to locate and utilize heterogeneously distributed Zn in the soil would likely provide a competitive advantage to plants.

14.4 Manganese

Nutrient uptake by plants depends on availability of nutrients and effectiveness of root systems for absorption (Liu et al. 2000). Difference in manganese concentration between mycorrhizal and non-mycorrhizal plants was higher in roots than in shoots; this is due to mycorrhizal fungi altering the distribution of the nutrient (Arines et al. 1989). Mn acquisition was decreased in AM plant (Kothari et al. 1991). Mycorrhizal plants will uptake lower Mn which may be explained by the presence of some hyphal mechanism controlling microorganisms (Arines et al. 1989). Increased or decreased uptake of Mn has been shown to depend on the presence of Mn-oxidizing microorganisms or the accumulation of root-derived nutrients that increase the formation of complexes of the element (Merckx et al. 1983). Both chemical and microbial processes determine the chemical equilibrium between reduced and oxidized forms of Mn (Sparrow and Uren 1987). It is possible that AM fungi play an indirect role in the uptake of Mn and the effects depend on soil chemical and microbial characteristics (Arines et al. 1989). Soil pH and oxidation-reduction potential determine the Mn availability in soils. Higher Mn uptake has been observed in plants grown in acidic soil conditions, because Mn is more soluble in acidic than alkaline conditions (Habte and Soedarjo 1995). Arbuscular mycorrhizal fungi were found to reduce the number of Mn-reducing bacteria (Posta et al. 1994) or increase the number of Mn-oxidizing bacteria in the rhizosphere (Arines et al. 1992). Therefore, AM fungi indirectly reduce oxidation-reduction potential and Mn availability in mycorrhizosphere (Liu et al. 2000). Reduced forms of these elements are more available to plants (Marschner 1988). External hyphae are responsible for the effectiveness of mycorrhizal root absorption (Burkert and Robson 1994). Increased or decreased uptake of Mn may depend on which of the two functions prevails under given soil conditions (Liu et al. 2000). AM-colonized plants have low Mn levels compared to non-mycorrhizal plants under high micronutrient level. This is due to more reduced availability of Mn than increased absorption efficiency by AM fungi in high micronutrient level. Arbuscular mycorrhizal fungal hyphae contain polyphosphates which sequester Mn by polyphosphate granules and minimize transfer to roots of the mycorrhizal plants, and these are considered as filter mechanisms (Turnau et al. 1993). The enhancement or alleviation of Mn toxicity in mycorrhizal plants is not exclusively attributed to the AM fungal species, but may be the result of several interactions attributed to changes in host physiology, with reflection on the microbial community in the mycorrhizosphere (Filion et al. 1999) and on the biological

processes of Mn oxidation (Nealson et al. 1988) and reduction (Kothari et al. 1991). Nogueira and Cardoso (2003) reported that *Glycine max* associated with *G. etunicatum* and *G. intraradices* also presented higher P concentrations in the tissues, to support the higher Mn concentration in the tissues, suppressing the Mn toxicity symptoms. Bethlenfalvay and Farson (1989) observed that, although mycorrhizal plants presented greater Mn concentration, there were no toxicity symptoms. This might have occurred because of an increase of internal tolerance to Mn (Foy et al. 1978) by plants' better accumulation with P. The lower Mn concentration in mycorrhizal plant was proportional to increase the plant biomass (Nogueira and Cardoso 2003). A positive equilibrium between the oxidizing and reducing microorganisms for AM plants decreased Mn acquisition in plants (Clark and Zeto 2000). The root exudates and microbial population in rhizosphere regions are also important for low acquisition of Mn by plants (Posta et al. 1994).

14.5 Ferrous

Arbuscular mycorrhizal fungi altered (increase or decrease) the Fe acquisition (Clark and Zeto 1996; Caris et al. 1998). Mycorrhizal-colonized plants grown under low pH uptake higher Fe content compared to AM plants grown in higher pH (Medeiros et al. 1993). Moreover, mycorrhizal plants grown in alkaline soil showed increased Fe uptake than those plants grown in acidic conditions (Clark and Zeto 1996). Reduced Fe is more available to plants (Marschner 1998). Arbuscular mycorrhizal fungi increase or decrease the uptake of Fe which may depend on the oxidation-reduction potential and effectiveness of root systems for absorption, of which these two functions prevail under given soil conditions (Liu et al. 2000). Under conditions of low nutrient level, AM fungal hyphae enhanced uptake of Fe by improved scavenging of this element. Mycorrhizal-inoculated maize grown in Fe-deficient soils showed improved Fe uptake (Clark and Zeto 1996). In mycorrhizal maize and soybean (Pacovsky et al. 1986) plants, the shoot Fe concentrations were low (Kothari et al. 1990). In general iron acquisition has been related with the presence of root exudates such as phytosiderophores (Marschner and Romheld 1994) and organic acids like citric, oxalic, and phenolics in mycorrhizosphere regions (Marschner 1998). In addition AM fungal species, host plant, and edaphic and various stress conditions determine the iron acquisition (Al-Karaki et al. 1998; Caris et al. 1998).

14.6 Arbuscular Mycorrhizal Fungal Hyphae in Nutrient Uptake

The mobility of micronutrients in soil is very much low, and AM fungal hyphae aid in the uptake of more micronutrients, which gives more absorptive area compared to root alone and minimizes the distance of diffusion, thereby enhancing the absorption by immobile micronutrients (Jakobsen et al. 1992). In soils contained high

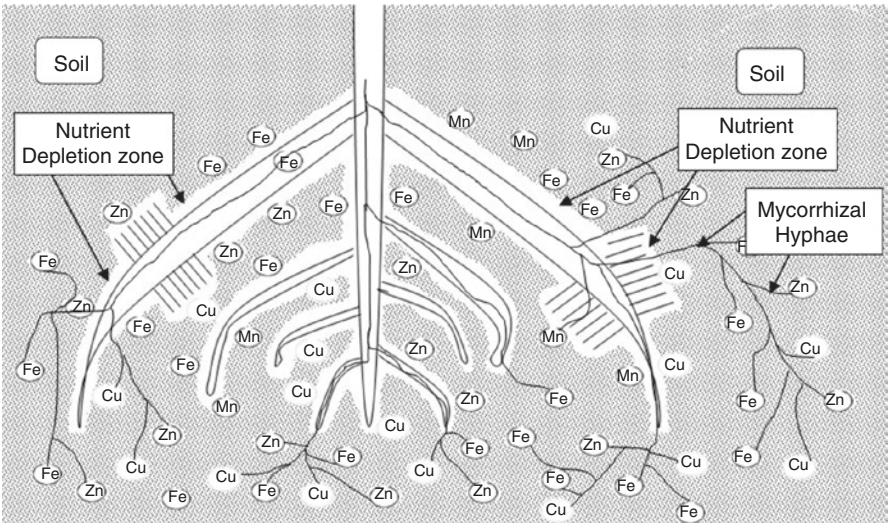

Fig. 14.2 Micronutrient absorption strategy of arbuscular mycorrhizal fungi through extraradical fungal hyphae in rhizosphere regions

density of extraradical hyphae which had higher absorption surface and metal diffusion distance will be low (Fig. 14.2). Therefore, AM plants effectively absorb the low-mobility metal nutrients (Burkert and Robson 1994). Arbuscular mycorrhizal fungal hyphae are more efficient in nutrient absorption than non-colonized roots. The higher uptake of mycorrhizal plants is due to fungal hyphae, and mycorrhizal plants should have a hyphal surface area at least equal to the total root surface area of non-mycorrhizal plants. In maize plants, hyphal surface area is 19% of the root surface area of non-mycorrhizal plants (Kothari et al. 1990), which shows P absorption efficiency per unit surface area basis of hyphae is at least five times higher than roots.

14.7 Difference Between Mycorrhizal and Non-mycorrhizal Plants

Arbuscular mycorrhizal fungal colonization changes host plant morphology. Fungal hyphae provide efficient surface with subsequent transfer to the host, capacity of the mycorrhizal or hyphae to utilize micro- and macronutrients not available to non-mycorrhizal roots, and increased viability of mycorrhizal roots than non-mycorrhizal. Non-mycorrhizal plant and mycorrhizal plants are compared in growth and nutrient uptake in various pot experiments using sterile soils. When compared to non-AM plants, AM plants acquire more phosphate (P) from the rhizosphere and attain better growth. In so many cases, the uptake of other elements also differs between mycorrhizal and non-mycorrhizal plants. However, it is impossible to determine the direct effect of AM fungi to plant micronutrient uptake by simply comparing the uptake of

non-mycorrhizal plants from the nutrient uptake of mycorrhizal plants. Arbuscular mycorrhizal fungi contribute directly or indirectly to plant growth. Many of these are related to better P uptake of mycorrhizal plants from low P soils, leading to greater shoot growth and root length, in particular, are less increased (Gnekow and Marschner 1989). Soil with adequate P levels morphology of shoot and root differed between AM and non-AM plants. Approximately 40% of the total root length was reduced in non-mycorrhizal maize plants when compared to mycorrhizal inoculated maize plants approximately 40%, in the presence or absence of mycorrhiza. AM-colonized or uncolonized plants differ in so many aspects, and the difference in the micronutrient content of plants does not necessarily reflect (George et al. 1992).

14.8 Impact of Micronutrient by AM and Non-AM Plants

Mycorrhizal and non-mycorrhizal plant comparison is problematic, but most of the current studies regarding AM fungal effects on plant micronutrient uptake are determined from such comparisons. In AM plants, concentration and total content of Zn and Cu are increased (Sharma et al. 1994). This becomes especially clear, and fertilization with additional P is needed when compared to mycorrhizal and non-mycorrhizal plants, to achieve similar P uptake in both treatments (Pacovsky and Fuller 1988). Arbuscular mycorrhizal fungal colonization does not influence the micronutrient uptake in few studies (George et al. 1992). Plant species and cultivar, fungal species, soil pH, soil physical conditions, soil temperature, soil P availability, and the levels of nutrient supply all influence the mycorrhizal effect on micronutrient uptake (Kilham and Firestone 1983; Liu et al. 2000). The broad generalizations are not possible for plants colonized by AM fungi. Direct or indirect effects of mycorrhizal colonization and more detailed investigations are required for the uptake of extraradical hyphae in order to determine the changes in micronutrient uptake resulting from mycorrhizal colonization (George et al. 1992).

14.9 Implications for AM Functioning in Nutrient Uptake

The amount of AM fungi which is active in nutrient transfer does not necessarily depend on the length of root colonized by AM fungi (Smith and Gianinazzi-Pearson 1990). Only during periods of high P demand do AM fungi contribute to the necessary rate of uptake (Sanders and Fitter 1992). The plants are in the stage of flowering and seed production which have highest rates of photosynthesis and respiration which needs high P demand. This is when AM fungi are more effectively involved in nutrient uptake (Sanders and Fitter 1992). *Phaseolus lanceolata* and *Rumex acetosa* showed highly irregular patterns of nutrient uptake which cannot be attributed to a specific period in the growth season (Sanders and Fitter 1992). From this it is impossible to determine exact periods of nutrient uptake from soil, because plant nutrient content was measured in shoots only, whereas in pot experiment, number of plants and replication were limited, so roots were used for mycorrhizal

assessment. It is possible that the timing of nutrient uptake into the roots could occur sometime before the transfer to the shoots. This creates more complexity in detecting a relationship between colonization levels and nutrient uptake (Sanders and Fitter 1992).

14.10 Consequence in Mycorrhizosphere

AM fungal colonization not only modulates the morphophysiology of the host root, and colonization also changes the conditions in mycorrhizosphere (Linderman 1992). There is a considerable difference of root exudation between AM-colonized and non-colonized root (Schwab et al. 1983). Root exudations are energy sources for microorganisms in rhizosphere (George et al. 1992). The suitable example is plant Mn uptake; when compared to non-AM plants, either decreased or increased concentration was observed in AM plants (Liu et al. 2000). The mechanisms responsible for this contrasting behavior are different root exudations of AM fungal-colonized roots and a lower number of Mn-reducing bacteria in mycorrhizosphere, so Mn uptake (Kothari et al. 1991), when the Mn-oxidizing bacterial population will be high in the mycorrhizosphere which causes to less soil Mn availability (Arines et al. 1992). In addition exudation of Mn-chelating exudates may be decreased in AM-colonized plants (Bethlenfalvay and Farson 1989). Decreased root exudation reduced the population of siderophore producing bacteria, thereby reducing their role in plant Fe supply (Crowley et al. 1992). Alternatively fungal siderospheres could compete with the plant for soil Fe, or fungi could decrease direct plant Fe uptake by degradation of plant-borne Fe (III) chelators as bacteria (Crowley et al. 1992).

14.11 Effect of Nutrient Uptake by AM Fungi in Saline Soils

Arbuscular mycorrhizal fungi alleviate salt stress, shown to promote plant growth and tolerate salinity by employing a variety of mechanisms, one of which is enhancing nutrient acquisition (Al-Karaki and Al-Raddad 1997). Arbuscular mycorrhizal colonization strongly affects Ca^{2+} concentration in plant. In lettuce, Ca^{2+} uptake was increased; roots are colonized by AM fungi (Cantrell and Linderman 2001). Yanomelo et al. (2003) reported high Ca^{2+} concentration in mycorrhizal than in non-mycorrhizal banana plants. High Ca^{2+} has a beneficial effect on toxic effects of NaCl by facilitating higher K^+/Na^+ selectively leading to salt adaptation (Cramer et al. 1985; Rabie and Almadini 2005). Jarstfer et al. (1998) reported that AM fungal colonization and sporulation are enhanced by Ca^{2+} ions. But in *Acacia auriculiformis*, when compared to mycorrhizal and non-mycorrhizal, there are no changes in the concentration of Ca^{2+} in shoot tissues. This indicates that AM fungi may not be so important to the nutrients moving to plant roots by mass flow as compared with nutrients moving by diffusion (Tinker 1975); when compared to P, Ca^{2+} is not translocated to onion roots through mycorrhizal hyphae as readily and effectively (Rhode

and Gerdemann 1978). In addition AM fungal inoculation depressed the Ca:P ratio by increased production of oxalate in the mycorrhizosphere, which is able to scavenge Ca^{2+} from the solution (Azcon and Barea 1992). Arbuscular mycorrhizal fungi improving Mg^{2+} can support a higher chlorophyll concentration (Giri et al. 2003). This suggests that salt interferes less with chlorophyll synthesis when compared to non-mycorrhizal plants (Giri and Mukerji 2004). Improved plant growth by increasingly chlorophyll concentration is due to effective uptake of Mg^{2+} ions by AM fungi.

Conclusion

In minimum micronutrient levels, mycorrhizal plant acquires increased quantities of micronutrient either by direct uptake from the soil by extraradical hyphae and translocate to the plant or by mycorrhizal effects on root and mycorrhizosphere effects. Although AM fungi are ubiquitous in agricultural and natural forests, predictions about mycorrhizal effects on plant microelement balance are not possible. The influence of AM fungi depends on the specific element, soil conditions, and plant and fungal type. In agronomic practices, fertilization of crops by chemical fertilizers is cost-effective and causes various problems in soil conditions and quality of agricultural products. In large scale manipulation of AM fungi will be useful for framers by decreasing fertilization cost. Including micronutrient uptake, AM fungi play a multifunctional role, protecting the crops from metal toxicity, various stress conditions (e.g., drought, salinity, etc.), and pathogens and uptake of other macronutrients like P, N, and K. Through AM fungal technology, crop plants attain benefit, and world plant production can be improved through enhanced nutrient uptake especially micronutrient.

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