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# Arbuscular Mycorrhizae: Effect of Rhizosphere and Relation with Carbon Nutrition

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## Abstract

More than 90 % of terrestrial plants form symbiotic association with mycorrhizae which develop and promote cooperation belowground in rhizosphere. Mycorrhizal fungi produces spores in the soil and vegetative propagules in root fragments which respond to stimulation of root exudates in the rhizosphere. As a result, symbiotic relationship takes place where physiology and morphology of both participants rely on each other. Mycorrhizae are present in a range of horticultural, agricultural, forestry and other plant species. Along with mycorrhizae, other beneficial microbes also add in plant growth promotion, nutrient and uptake and stress tolerance either biotic or abiotic. The presence of bacteria in rhizosphere synchronizes with mycorrhizae termed as 'mycorrhizae helper bacteria' and increases plant growth by focusing on N and P in particular while micronutrients in general. Besides that, carbon has important structural and functional role in symbiotic association, because of mycorrhizal reliance on plants for food. Additionally, movement of C to the roots is an interesting area for exploration due to recent global focus on addressing climate change and carbon mitigation approaches particularly for sustainable agriculture. AM symbiosis can influence soil $CO_2$ emissions and soil in ecosystems dominated by mycorrhizal plants that

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contain 70 % more carbon per unit nitrogen than soil in ecosystems dominated by non-AM-associated plants. Absorption of $CO_2$ by mycorrhizae is contributing in climate change mitigation and translated as plant biomass production.

## 6.1 Introduction

The most widespread symbiotic association between microorganisms and plants is arbuscular mycorrhizal fungi (AMF), which is present in a range of horticultural, agricultural and forestry plants Marschner (2012). Different plant species are infected with indigenous AMF in their natural habitat (Ortas and Coskan 2016a). Mutualistic mycorrhizal fungi-root association has been known and being studied since 1885, when Frank for the first time gave the name *mycorrhiza* (*myco*, fungus; *rhiza*, root) to readily observable morphological complexes between fungi and tree roots. Mycorrhizal infection occurs in 83 % of dicotyledonous and 79 % of monocotyledonous plants (Trappe 1987).

According to Azcon-Aguilar and Barea (2015), beneficial microbes contribute in plant growth and increase nutrient uptake such as nitrogen and/or soluble phosphate. Understanding the mechanism of high N use efficiency by mycorrhizal/rhizobial plants and carbon allocation in a context of mutualistic system is critical for managing agricultural system for the ecosystem sustainability by microbial symbionts. Since there is significant effect of carbon on climate change and sustainability of agriculture, it is sound to explore the influence of beneficial organisms on carbon sequestration (Ortas et al. 2013). It has been suggested that soil microflora may have significant influence on the formation of mycorrhizal association. The results of Sutton and Sheppard (1976) showed that adding non-sterile soil leachate to a sterile soil increases biomass of AM hyphae.

Recently research groups on mycorrhiza have concentrated on the effect of mycorrhizal inoculum on nodulation, when both mycorrhizae and bacteria are inoculated together. It is an indication of additive and positive cooperation in between fungi and bacteria. Dual inoculation (of AMF and *Azotobacter*) had a synergetic effect on growth increase of the host plant. In rhizosphere, it is possible that some beneficial bacteria, such as symbiotic or free-living nitrogen fixer (Hamdia and Shaddad 2010), phosphate solubilizers and hormone producer organisms (Ratti et al. 2001), could develop cooperation with mycorrhizae. Besides that, very recently the role of mycorrhizae on $CO_2$ absorption is getting more attention because of continuously piling up of the atmospheric $CO_2$ concentration to affect climate. Since climate change is related with atmospheric $CO_2$, the role of mycorrhizae for plant growth promotion and biomass production through carbon absorption is significantly important.

## 6.2 Mycorrhizal Formation and Functions

Mycorrhizal fungi's characteristic structures are vesicles, arbuscules, hyphae (external and internal hyphae) and resting spores in the host root (Smith and Read 2008). One of the important structural features of mycorrhizae is hyphae which grow longitudinally between the cells of the root cortex. When fungal hyphae contact the root surface, penetration occurs through an aspersorium. After its development, fungus produces hyphae which penetrate between inner cortical cells (Berruti et al. 2013; Sieverding 1991; Smith and Read 2008). The AM root infection usually begins after hyphae extending from propagules (spores, hyphae and root fragments) penetrate into the host root from an entry point on root surface. The mycorrhizal fungi survive in the soil as resting spores, and when environmental conditions become favourable, they start to germinate. The spore formation is generally on the coarse external hyphae. These spores usually range from 50 to 600 μm (Sieverding 1991). Once infection is established, the developing fungi can produce inter- or intracellular vesicles (Rodriguez-Moran et al. 2015). Usually, vesicles are oval, round or lobe shaped and occur within or between cortical cells. They may contain lipid droplets which act as storage structures of fungus. Vesicle shape, wall structure content and their number can differ according to the fungal species forming mycorrhizae (Sieverding 1991; Smith and Read 2008). Arbuscules are intracellular, branched or tree-shaped structures of the symbiont and are formed by repeated branching. They are considered to function for the transfer of nutrients (Marschner 2012; Smith and Gianinazzipearson 1988).

The internal morphology of AMF can be easily observed on cleared and stained root samples under the microscope (Seok-Cho et al. 2007). The mycorrhizal fungus lives with host (plant partner) in a balanced close association. Mycorrhizal fungi can be seen in the soil as spores or as vegetative propagules in root fragments. Propagules of mycorrhizal fungi apparently respond to the stimulation of root exudate, and their hyphae and germ tubes grow and penetrate root epidermal cells. The colonization of the host tissue progresses, both internally and externally along the root surface. The formation depends on the association between host and fungi, the latter resulting in morphological and physiological changes which lead to the formation of different types of mycorrhizae. When mycorrhiza forms, symbiosis significantly changes the physiology and morphology of roots particularly and the whole plant generally (Bray et al. 2003; Wulf et al. 2003). In some plants such as onion and maize, there is a yellow pigmentation which accompanies root colonization. The physiological change is explained as the change has great impact on rhizospheric microorganisms, which alter permeability of the membranes. It is well understood that membrane permeability can alter the quantity and quality of root exudates and results in changed plant nutrient composition. The microbes in microsphere of mycorrhizal fungi may profoundly affect mycorrhizal functions, such as nutrient and water uptake. Moreover, mycorrhizospheric organisms and root exudates have significant influence on soil development as well. Mycorrhizal hyphae are normally supported by the host plants, but their biomass may be influenced by soil biotic and abiotic factors such as soil microorganisms.

## 6.3 Factors Affecting Mycorrhizal Association

Soil physical, chemical and biological factors affect mycorrhizal development. Water contents (Krishna et al. 2005), temperature (Zhang et al. 2016), light (Clark and St Clair 2011; Moratelli et al. 2007) soil type and their characteristics (Ortas and Coskan 2016b; Thougnon Islas et al. 2016) are illustrations of physical factors. Fitter et al. (2004) indicated that AM fungi respond directly to elevated soil temperature. Furthermore, examples of chemical factors are soil pH (Moon et al. 2016), phosphorus availability (da Silva et al. 2016), nitrogen forms (Smith and Read 2008), micronutrient levels (Hoffmann et al. 2009), salinity stress (Labidi et al. 2011; Ruiz-Lozano and Azcon 2000), organic matter content (Wang et al. 2015), excessive use of pesticides (Zocco et al. 2008), etc. Biological factors are based on host plant (Ocampo et al. 1980) interactions with other soil microorganisms such as pathogenic and competitive with other mycorrhizal fungi (Azcon-Aguilar and Barea 2015). These environmental conditions affect root colonization and fungal growth development in the cortex (Smith and Read 2008). It has been indicated that mean spore abundance was significantly different in cropped systems and soil management (Säle et al. 2015). Barea et al. (2011) and Burkle and Belote (2015) reported that disturbance of target semiarid ecosystem decreases density and diversity of mycorrhizal fungi population. In general, the sporulation of AMF is dependent on soil/plant nutrition, the ecophysiological status of hosts, climate, that is, previous precipitation and also sampling time.

Soil pH reflects the nutrient availability in soil through ion exchange process (Helgason and Fitter 2009). Varying soil pH can change species richness and community composition. For different mycorrhizal species, effect of soil pH on germination of mycorrhizal spores, hyphal growth from spores and hyphal growth from mycorrhizal roots may be different. Guo et al. (2012) have shown that soil medium with liming effect from pH 5.5 to 5.9 increased *G. mosseae* germination by 43–60 % with no further increase observed with addition of lime. The results of (Sivakumar 2013) showed positive correlation between the mycorrhizal spore abundance and soil pH moreover with root colonization. In general, soil with pH range 5.5–6.6, AMF is abundant (Sharma et al. 2009). Martensson et al. (2012) reported that the amount of AMF is very low in poor nutrient and drought-stressed habitat, and they also found that a high pH in the topsoil does not lead to higher AMF biomass.

The results of Alloush and Clark (2001) showed that mycorrhizal infection was strongly inhibited by Al and Mn. Similarly Lambais and Cardoso (1993) recorded that soil may have toxic concentration of Al and Mn to fungal growth, but it supported plant growth. It is believed that soil acidity is not an independent factor as pH itself may have little significant effect on spore germination and root colonization. Resting spores are thick-walled structures formed in the soil. Spore numbers are affected by several factors such as nutritional status of the host plant and soil moisture contents (Ortas and Coskan 2016a; Smith and Smith 2011; Smith and Read 2008).

The frequency of mycorrhizal infection is affected by nitrate ($NO_3^-$) and ammonium ($NH_4^+$) ions. According to Asghari and Cavagnaro (2012) and Valentine et al. (2002), the application of $NO_3^-$ or $NH_4^+$ resulted in higher level of mycorrhizal infection. Mycorrhizae formation was decreased at high level of $NH_4^+$-N (Wallenda et al. 1996). The application of increasing amount of $NO_3^-$ reduced the level of AM infection in lettuce roots when the root was inoculated with *G. mosseae* (Kohler et al. 2008). Wallenda et al. (1996) found that high $NO_3^-$ levels can result in the low mycorrhizal formation of conifer seedlings, but with $NH_4^+$ supply, fungi formed abundant mycorrhizae (Correa et al. 2006). The results of Irshad et al. (2002) showed $NO_3^-$ fertilizer is more inhibitory to AMF development than $NH_4^+$ fertilizer. Addition of $NO_3^-$-N to the soil decreases AMF infection (van Diepen et al. 2013) and infectivity of mycorrhizal propagules (Cornejo et al. 2007). $NH_4^+$-N application magnified considerable morphological changes and showed plasticity of *G. intraradices* (Bago et al. 2004). The mechanism responsible for nitrogen inhibition of AM formation is not fully understood.

## 6.4 Carbon Relation with Mycorrhizae

Soil microorganisms are dependent upon plants for supply of energy mainly carbon. By this way, population of organisms is indirectly dependent on plant photosynthesis. A figure of soil-fungi-plant and their relationship with plant carbon nutrition is presented in Figs. 6.1 and 6.2. The relationship between mycorrhizal fungus and the host plant is bidirectional (Fig. 6.1) where both sides derive benefits. The fungi obtain its required carbon directly from the roots, and at the same time fungi supply inorganic minerals, especially phosphorus (P) from the surrounding soil (Smith and

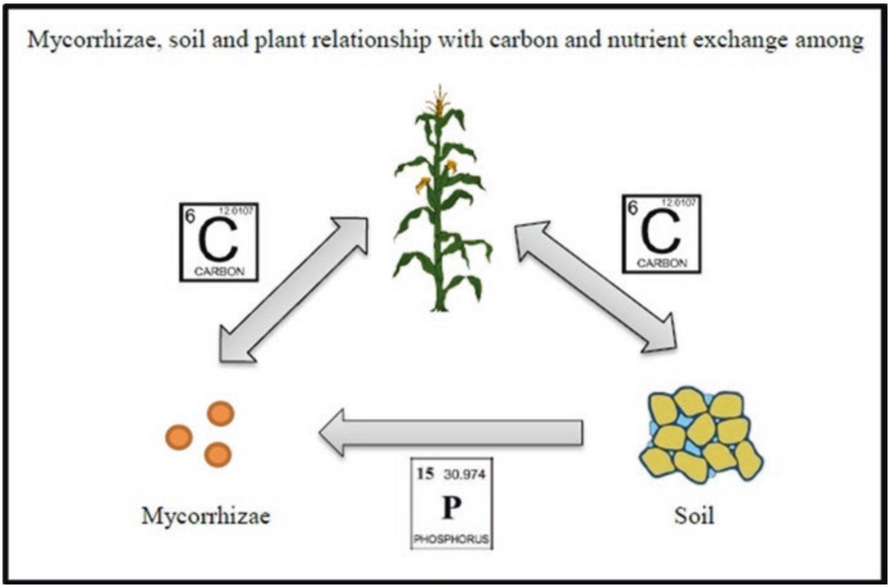

**Fig. 6.1** Relationship between mycorrhizae-soil and plant-carbon-nutrient exchange (Ortas 1994)

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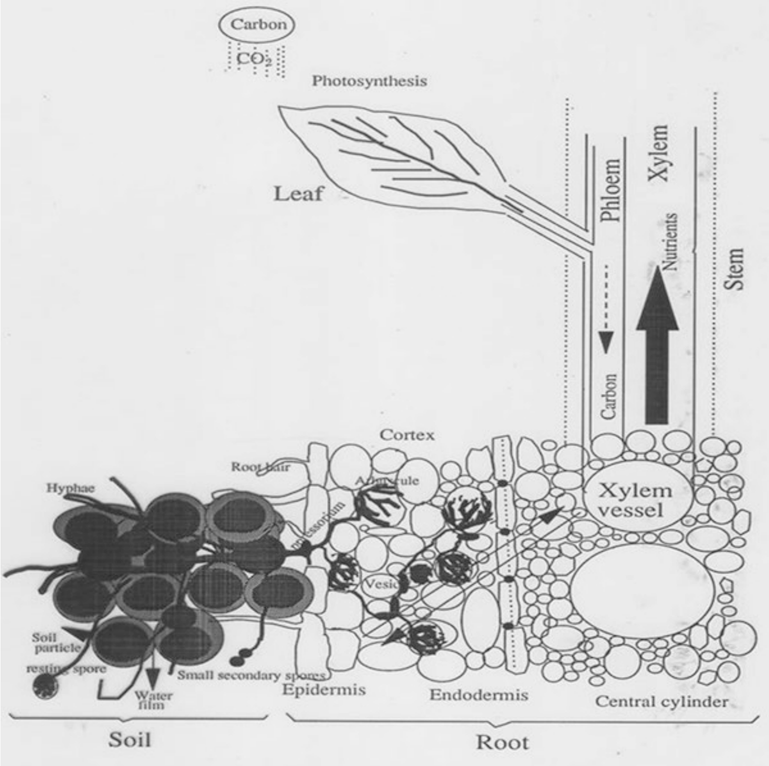

**Fig. 6.2** Nutrient transportation from soil to plant tissue and phloem transportation from leaves to mycorrhizal hyphae (Ortas 1994)

Read 2008). Carbon (C) and P are the key nutrients required for mycorrhizal development and functions. It is well understood that AMF are completely dependent on soluble carbohydrates produced by the host plant for carbon. This carbon demand can inhibit plant growth in stress conditions of low light intensity, high level of root colonization (Asensio et al. 2012) and low soil temperature. Mycorrhizal fungi, because of their unique carbon system, can efficiently combine soil mineralization and nutrient uptake by plant roots (Mellado-Vazquez et al. 2016).

In rhizosphere, soil bacteria and fungi generally immobilize mineral nutrients, as carbon is consumed, and thereby compete with plant for nutrients. A useful indicator of plant material supply to soil is net primary production. Living plant roots supply a tremendous amount of C to the soil which can potentially be used by microorganisms. The C utilization by mycorrhizae becomes important when competing with other soil microorganisms.

It is generally accepted that root exudes sufficient quantity of organic compounds to support microorganism population in rhizosphere and support growth of certain microorganisms derived by root exudate quality. In rhizosphere, C losses by plant roots in complex associations of root and soil microorganisms contribute both positively and negatively which determine plant efficiency. Roots in non-sterile media support a large population of microorganisms on external surface (the rhizoplane) and in rhizospheric soil. The population density of bacteria and partly fungi in the rhizosphere depends on the amount of exudate, mucilage and sloughed-off cells which are carbon based. In soil-grown wheat plants under non-sterile conditions during a period of 3 to 8 weeks, 20–40 % of traslocated C from shoot to root was lost as organic carbon (OC) into the rhizosphere.

It has been suggested that enhanced plant growth and C flow below ground could increase C storage in soils, and it could be the missing sink (Ford et al. 2012). Increased C flow to the soil can be directly via plant roots or indirectly via soil organisms, of which mycorrhizae could potentially be a very important element. Indeed, C allocation to mycorrhizal fungi is often around 10 % of total fixed C (C allocated to belowground fractions such as roots and mycorrhizal hyphae accounted for an average of 10 %, with 4.3 % allocated to mycorrhizal hyphae) (Tome et al. 2015) and has been estimated to be high as 20 %. Cheng et al. (1996) showed that carbon availability index (CAI) and water soluble organic carbon (WSOC) were inversely related to the relative distance from root surface, with several times higher concentration in the rhizoplane soils. It is widely known that carbon availability in the rhizosphere is much higher than bulk soil where AMF could be responsible for carbon sequestration (Ortas et al. 2013).

Most of the carbon is utilized fairly and rapidly by rhizospheric microorganisms. A large turnover of OC by microorganism’s activity in the rhizosphere has an important implication for both the carbon balance of plant and mineral nutrient relationships in the rhizosphere. At maturity, only a small fraction of the root-derived OC is retained in the root system.

Willis et al. (2013) indicated that the mechanisms involved in C transfer from plant to fungus are still not well understood. It has been estimated that mycorrhizal plants direct up to 20 % more photosynthate towards root system than non-mycorrhizal plants.

## 6.5 Mycorrhizae Affect Atmospheric $CO_2$ Absorption

Interaction between root and soil microorganisms controls nutrient availability and uptake by plants and influences soil greenhouse gas (GHG) emissions such as $CO_2$ and $N_2O$ (Jackson et al. 2008). This symbiosis increases the uptake of soil nutrients in exchange of photoassimilated carbon compounds (Fellbaum et al. 2012). Mycorrhizal fungi of chlorophyllous plants absorb C compounds from their host. The role of AM symbiosis for plant and soil GHG emissions might be particularly important in ecologically managed systems. Several studies have reported higher $CO_2$ emissions in mycorrhizal plants than non-mycorrhizal. The results of Heinemeyer et al. (2006) showed that concentration of $CO_2$ flux is highest in the mycorrhizal treatments. It has been previously suggested that AM symbiosis can influence soil $CO_2$ emission either due to direct respiration of the fungi or indirect impacts on heterotrophic microorganisms (Cavagnaro et al. 2008). On the other hand, Tome et al. (2016) reported that mycorrhizal contribution to soil respiration (11 ± 6 %) was of similar magnitude to the roots (12 ± 4 %). However, respiration of SOM and mycorrhizae significantly increased in late summer and autumn terms; this is related with priming effect of roots on SOM degradation or to a stimulation of mycorrhizal respiration. The organic matter has key role in soil ecosystems (Lejon et al. 2007), while limited information is available for SOM effects on AMF, though it is well acknowledged that growth of AMF can be both increase and decrease (Cavagnaro 2014; Ravnskov et al. 2006) by soil organic amendments.

Fitter et al. (2004) indicated that under field studies, variation in vegetation due to environmental changes may play enormous role in determining AMF community structure. Elevated $CO_2$ could stimulate mycorrhizal colonization, since plants are fixing more C, and its availability to the fungus is increased. According to hypothesis, more C could flow in the soil via mycorrhizal hyphae. The amount of C translocated below ground by AM fungal structures varies between 4 and 20 % of the total C fixed by the plant (Smith and Read 2008). Several researchers have examined mycorrhizal colonization in conditions of elevated $CO_2$, which might stimulate ectomycorrhizal colonization in various species (Langley et al. 2003), but the evidence for arbuscular mycorrhizae is less clear. The effect of mycorrhizal type on soil carbon is dependent on the effects of net primary production, temperature, precipitation and soil clay content. Hence, the effect of mycorrhizal type on soil carbon content holds at the global scale.

The impact of ectomycorrhizal fungi (EMF) on C turnover in forest soils has been considered limited. Rineau et al. (2012) indicated, using global data sets, that soil in ecosystems dominated by mycorrhizae-associated plants contains 70 % more C per unit nitrogen. Although some climatic models estimated that increased C storage in temperate forest soils is because of increased photosynthetic C allocation to roots and symbiotic fungi (Clemmensen et al. 2013; Drigo et al. 2010), there is still a room for exact degree of C storage estimation. Mycorrhizosphere activity may also stimulate decomposition of previously recalcitrant SOM (Cheng et al. 2012). The saprotrophic and EMF species produce a range of hydrolytic and oxidative enzymes with a potential effect to break down C-containing compounds such as OM and mobilize nutrients from SOM (Norby et al. 2010) Although photosynthates are likely the primary source of C used by EMF in ideal condition (Wolfe et al. 2012), many studies suggest that fungi may directly (Vaario et al. 2012) or indirectly (Rineau et al. 2012) access SOM-C pools.

## 6.6 Mycorrhizal Development Influenced by Rhizospheric Organisms and Nitrogen

It has been previously reported that effect of AMF on P uptake and plant growth was more in sterilized soil in comparison to non-sterilized soil. It has been hypothesized that more plant growth and P uptake may result from more N mineralization especially the mineral $NH_4^+$-N flush after soil irradiation. According to Ortas et al. (1996), (Ortas and Rowell (2000) and Ortas et al. (2004), the amount of $NH_4^+$-N

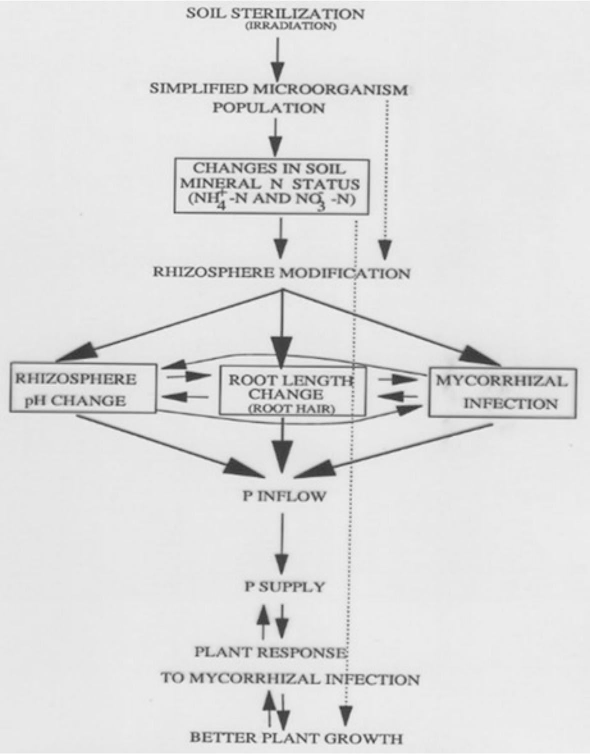

**Fig. 6.3** The effect of soil sterilization on nutrient dynamics and P uptake

should be taken into account for plant growth and P uptake (Fig. 6.3). Phosphorus uptake mechanisms are related with nitrogen effect on rhizosphere pH (Hinsinger 2001; Isaac et al. 2012; Rubio et al. 2012). Under partial sterile soil conditions, N mainly comes after dead organisms and organic matter degradation.

So far numerous pot experiments have been carried out in partially sterilized soil to eliminate the effects of indigenous mycorrhizae on self-introduced mycorrhizal inoculum. The results of inoculation experiments are generally positive, because unwanted growth response in sterilized soil is related to increased level of available N and in particular N mineralized from the soil microbial biomass (Ortaş and Harris 1996) along with elimination of nutrient competition with other microorganisms. The effect of sterilization on soil properties (Gebremikael et al. 2015) and nutrient dynamics has been widely studied (Ortas and Rowell 2004; Ortas et al. 2004; Ortaş and Harris 1996).

The main aim of partial soil sterilization in mycorrhizal studies is to eliminate indigenous mycorrhizal spores and pathogenic microbial activity in the soil, but this procedure often alters the chemical and biological properties of the soil (Hassan et al. 2012). Under the greenhouse with sterile conditions, pathogen activities have been largely restricted, and plant growth especially root development was

**Fig. 6.4** The effect of mycorrhizal inoculation on the maize growth under fumigated and unfumigated field conditions (Ortas unpublished photo)

maximized. AMF have been shown to affect root growth, root exudate, nutrient absorption and host physiological response to environmental stresses (Folli-Pereira et al. 2012; Liu et al. 2015; ZhongQun et al. 2007). Increasing the AMF in soil, P nutrition for root growth also enhances and expands the absorptive capacity of the root system for water and nutrients which influence cellular processes in root (Smith and Read 2008; Tischer et al. 2015).

The main procedure so far adopted is elimination of indigenous fungi from soil than reinoculated under controlled conditions before their effects on plant growth can be assessed by comparing mycorrhizal and non-mycorrhizal plants. As expressed by Hetrick et al. (1988) and Miransari et al. (2009)), the effect of other soil microorganisms eliminated during soil sterilization on plant growth or mycorrhizal growth response is generally not considered. The contribution of AMF to plant growth in non-sterile soil may be different from sterile one. Nevertheless, it is extremely difficult to evaluate the contribution of AMF on plant growth in non-sterile soil. Under the fumigated soil conditions, reinoculation of mycorrhizae increased maize growth (Fig. 6.4).

With soil sterilization, soil organisms are killed and organic matter mineralization releases sufficient nutrients such as $NH_4^+$-N and $NO_3^-$-N. Partial soil sterilization can result in four–tenfold increase in $NH_4^+$-N level (Ortaş and Harris 1996; Tanaka et al. 2003). The contribution of soil partial sterilization to nutrient release may be explained as follows:

**Table 6.1** Literature on the effect of partial sterilization on mineral nitrogen release from organic compounds and soil microorganisms

| $NH_4^+$–N | $NO_3^-$-N | References |
|---|---|---|
| ND | $NO_3^-$-N | Bowen and Cawse (1964) |
| $NH_4^+$-N↑ | ND | Salonius et al. (1967) |
| $NH_4^+$-N↑ | $NO_3^-$-N↓ | Rovira and Bowen (1969) |
| $NH_4^+$-N↑ | $NO_3^-$-N↓ | Singh and Kanehiro (1970) |
| $NH_4^+$-N↑ | ND | Jenkinson et al. (1972) |
| $NH_4^+$-N↑ | ND | Arunachalam et al. (1974) |
| $NH_4^+$-N↑ | ND | Stribley et al. (1975) |
| $NH_4^+$-N↑ | $NO_3^-$-N | Jakobsen and Andersen (1982) |
| $NH_4^+$-N↑ | $NO_3^-$-N | Ramsay and Bawden (1983) |
| $NH_4^+$-N↑ | $NO_3^-$-N | Taufiaul and Habtem (1985) |
| $NH_4^+$-N↑ | $NO_3^-$-N | Speir et al. (1986) |
| $NH_4^+$-N↑ | ND | Griffiths (1987) |
| $NH_4^+$-N↑ | $NO_3^-$-N↓ | Kitt et al. (1988) |
| $NH_4^+$-N↑ | $NO_3^-$-N↓ | Thompson (1990) |
| $NH_4^+$-N↑ | $NO_3^-$-N↑ | Magnavacca and Sanchez (2003) |
| $NH_4^+$-N↑ | $NO_3^-$-N↑ | Xiao et al. (2010) |
| $NH_4^+$-N↑ | $NO_3^-$-N↓ | Gebremikael et al. (2015) |
| $NH_4^+$-N↓ | $NO_3^-$-N↑ | Buchan et al. (2012, 2013) |

↑ = Increase, ↓ = Decrease, ND = No Data

1. Some extractable nutrients come from decomposition or breakdown of organic matter present in soil as a direct result of irradiation treatment.
2. Several enzymes, including the urease (which produces ammonia as a decomposition product), are released after irradiation.
3. Some nitrogen is released from dead organisms (Ortaş and Harris 1996), and other nutrients are possibly released after the death of soil microorganisms (such as bacteria, fungi and actinomycetes).

Partial soil sterilization generally stimulates subsequent plant growth which is associated with an increased net mineralization of $NH_4^+$-N (Tanaka et al. 2003). The effects of partial soil sterilization on N-release reported in the literature are shown in Table 6.1.

The fertility of sterilized soil may be different than non-sterilized soil (Ortas 2003). According to Malkomes and Dietze (1998), partial soil sterilization drastically reduces the microbial population of soil with total eradication of certain microorganism groups. It is well known that N is one of the essential macronutrients and is required by plants in considerably large amount than P. According to Clemmensen et al. (2008) and (Tahovska et al. (2013) in different climates and neutral to slightly acid soils, the primary form of N available to plants is $NH_4^+$-N. The supply of nitrogen can influence rate of plant growth. Plant species differ in the form and amount of inorganic N uptake and its metabolism in roots (Azcon-Aguilar and Barea 2015). N supply to the host plant root influences, either directly or indirectly, susceptibility of the roots to infection, which can be influenced by rhizosphere pH change (Turnbull et al. 1995). Since N forms alter rhizospheric soil pH, two different N forms $NH_4^+$ and $NO_3^-$ may affect mycorrhizal development in different ways as well (Ortas et al. 1996; Ortas et al. 2004).

It is widely accepted that plants can increase P uptake by chemically modifying the rhizosphere (Conversa et al. 2013; Marschner 2012; Ortas 1997). The main mechanism that has been suggested is pH alteration through excretion of $H^+$ and $OH^-/HCO_3^-$. pH is a major factor influencing the soil solution concentration of many plant nutrients, and plant-induced variation in pH affects the availability of many nutrients (Gao et al. 2012; Nietfeld and Prenzel 2015; Ortas and Rowell 2000; Valentinuzzi et al. 2015). The pH changes surrounding environment and infected roots, thereby affecting P availability. The intensity of AM root colonization, host plant P uptake and growth response to AM has been reported to be pH dependent (Baar et al. 2011; Zhu et al. 2007).

The local acidification around mycorrhizal-infected roots may be very important for P uptake. It was suggested that application of N and possibly P resulted in mycorrhizae making a significant contribution to the plant's P status. As mentioned above, because of utilization of $NH_4^+$-N by hyphae of mycorrhizal plants, this may have further consequences in the rhizosphere pH. Recent studies of Cely et al. (2016), Feitosa de Souza et al. (2016), Hall and Bell (2015), Zhou et al. (2016) and Zong et al. 2015) showed better understanding to the effect of mycorrhizal infection on P uptake. However, additional study, especially the effect of $NH_4^+$-N supply on P uptake with and without AMF, is required. It is also necessary to understand the relationship between P uptake and rhizosphere pH change (caused by $NH_4^+$-N) with VA inoculation an area which has received little attention in the past (Ortas 2012a). Gahoonia and Nielsen (2004) indicated that manipulation of rhizosphere pH through agronomic measures such as application of $NH_4^+$ or $NO_3^-$ fertilizers may be more practical than breeding approaches.

## 6.7 Mycorrhizal Importance in Rhizospheric Soil

AMF are the largest symbiotic associations between plants and fungi which make significant contribution on physical, chemical and biological aspects of soil quality through AM fungal hyphae extending into the rhizosphere and thereby improving the absorption of nutrients especially P and micronutrients (Karandashov and Bucher 2005; Ortas 2003; Smith and Read 2008). Burkle and Belote (2015) results showed that the relationship between productivity and diversity varied among pioneer treatments and mycorrhizal amendments. This means that soil and crop management is related to the existence of mycorrhizae (Almaca and Ortas 2010; Ortas and Coskan 2016a). The establishment of mycorrhizae causes changes in the physiology of host plants. Like other soil microorganisms, AMF act as ecosystem engineers on roots and surface of the plants.

**Fig. 6.5** Aggregate formation by the plant roots and AM mycelium (Ortaş 2008)

## 6.8 Mycorrhizae Effect on Soil Development Related with C Fixation

In an ecosystem, mycorrhizae actually play an important role across the rhizosphere and provide an organic link between the root and bulk soil. Moreover, mycorrhizae have significant effect on soil development. Aggregates encapsulate SOC and reduce rate of decomposition. Similarly, plant roots and AMF hyphae provide physical protection to soil C against microbial decomposers through aggregation (Leifheit et al. 2015; Ortas et al. 2013). AMF play a contributory effect on soil aggregate formation (Fig. 6.5) because of the symbiosis which significantly changes the root functioning (Espeland et al. 2013). The AMF symbiosis may also influence soil biogeochemical processes and GHG emissions through change in soil physical properties such as soil water holding capacity (Cavagnaro et al. 2006). Organic compounds and AMF hyphae are important in binding soil into macroaggregates and microaggregates (Singh et al. 2009). Thus, depletion of SOM and the degradation of soil structure can adversely affect soil fertility and crop productivity. Soil aggregation is one of the important soil characteristics that mediates many soil chemical, physical and biological properties and improves soil quality and sustainability (Ortas et al. 2013).

Graf and Frei (2013) reported that EMF increase water stable aggregates (WSA) along with promotion of plant growth. Therefore, mycorrhiza has a significant impact on soil resilience which is also an important component of soil quality. Several studies have reported that soil biology, especially mycorrhizal fungi, significantly influences soil fertility and soil quality.

## 6.9 Mycorrhizal Application for Plant Growth and Nutrient Acquisition

AMF influence soil functions such as C, N and P cycling to support plant growth and nutrition in the agro-ecosystem. Colonization by AMF ameliorates abiotic plant stress by enhancing plant nutrient uptake and delivering drought tolerance (Lehmann et al. 2014). The symbiosis influences plant water relation and drought resistance (Augé et al. 2015). AMF play a significant role in the establishment of plants in different environments by assisting in nutrient uptake enhancement along with stress tolerance such as drought and salt stress and even protecting them against soil pathogens (Azcon-Aguilar and Barea 2015).

There are good studies which explain that mycorrhizal plant has enhanced capability of plant root in acquiring nutrients from soil, particularly when the nutrient is poorly soluble and present in low concentration (Abrahao et al. 2014; Teste et al. 2014). For a given dry weight, mycorrhizal plants usually have higher P concentration in plant tissue than non-mycorrhizal plants (Zhang et al. 2014). Several crop plants absorb more P from low P soils when infected with AM fungi (Ortas 2003; Ortas et al. 2001). It has been found that mycorrhizal-infected roots can utilize rock P, whereas non-mycorrhizal roots cannot (Chinnusamy et al. 2006). How mycorrhizal plants obtain more P from soil than non-mycorrhizal plants is not yet fully understood. Several mechanisms have been proposed to define the AM effect on improving the absorption of available phosphate. Miranda et al. (2016) evaluated the effect of mycorrhizae and phosphorus (P) on forage peanut and reported that the seedlings grown in pots and fertilized with P, the extent of the response was higher for those inoculated with AMF. Moreover, Ortas et al. (2013) showed different mycorrhizal species significantly inoculated different plant roots and observed root colonization and P uptake. The species *G. clarum* was more efficient under conditions of low P availability for citrus seedlings (Ortas 2015).

Mycorrhizae may induce both quantitative and qualitative changes in plant P utilization (Smith and Read 2008). The amount of acid phosphatase present in AM hyphae (Cavagnaro 2014) and increased phosphatase activity of root surface as a result of infection (Guo et al. 2016) may liberate inorganic P from organic P sources, making P available for uptake. Alford et al. (2010) suggested that the roots of mycorrhizal plants may alter the rhizosphere chemistry by changing soil pH and produce exudates such as organic acids which may increase the availability of phosphorus by liberating phosphate ions in the soil (Rajkumar et al. 2012). There is still a wide research gap in understanding mechanism involved for increased P availability in the soil by mycorrhizal-infected roots. The low dry weight increment of experimentally inoculated plants in same conditions may be mycorrhizal, and all make greater demands on their host for carbon than the naturally released into the soil.

## 6.10 Soil P Influenced by Mycorrhizal Association

In agricultural and horticultural ecosystems, mycorrhizal colonization has been frequently observed less associated with high rates of P application (Elbon and Whalen 2015). The symbiosis of plant with AMF increases its efficiency in absorbing nutrients from the soil solution, especially the nutrients of low mobility such as phosphorus (Brito et al. 2013), which makes it possible to use phosphate fertilizers of low solubility in seedling production (Silva et al. 2016). Khade et al. (2010)

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hypothesized that the infection is affected by P status of the plant rather than soil P levels. Graham et al. (1981) provided evidence that the roots of sorghum produce less root exudates in high P soils and hypothesized that colonization was affected by high soil P levels. It has been concluded that a large amount of P uptake can be explained by the increased surface area of hyphae alone (Sharif and Claassen 2011). In such case, plants have several mechanisms to employ for more P uptake, such as acidification of rhizosphere (Zahra et al. 2015) and excretion of organic acids (Palomo et al. 2006). Mobilization and solubilization of P are the principal chemical (soil pH change) and biological causes of increased nitrogen availability (Isaac et al. 2012). The soil organisms are also involved in mobilization of phosphate. Plant roots infected with AMF are known to have a higher phosphorus (P) absorption ability compared to non-mycorrhizal plants in P-deficient soils (Conversa et al. 2013; Smith and Smith 2011). Large inputs of soluble P, associated, for example, with application of superphosphate, can decrease mycorrhizal advantages by inhibiting the growth and activity of the vegetative mycelium (Greenhalgh et al. 1994). According to Feitosa de Souza et al. (2016), infection is affected by soil P as well as plant P concentration. As plants vary in their ability to absorb P and mycorrhizal fungi vary in their response to soil P, each plant-soil-AM symbiont system must be evaluated separately.

The soil P concentration is usually critical in mycorrhizal infection. Soil P must be sufficient for host plant growth and colonization of mycorrhizae. Very high and very low phosphorus levels may reduce mycorrhizal infection/colonization (Goncalves de Oliveira et al. 2015; Lirio Rondina et al. 2014). It is well established that infection by mycorrhizal fungi is significantly reduced at high soil P levels (Balzergue et al. 2013). The level of P in the plant has also been shown to influence the establishment of mycorrhizae with high levels inhibiting colonization; moreover it depends upon the root system (Yang et al. 2015). Ortas (2012a) showed that addition of P decreased AM infection in wheat under field conditions. The high concentration of soluble phosphate decreases AMF percentage (Table 6.2). Ortas (2012a) reported that with increasing P levels, mycorrhizal colonization significantly reduces. In *G. mosseae*-inoculated plants, when plant received no P fertilizer, root colonization was 90.8 % and with P treatment root colonization was 57.1 % (Table 6.2). Controlled plant roots had 3–10 % of colonization, but *G. etunicatum*-inoculated plants had 41–72 % and *G. mosseae*-inoculated plants had 30–75 % root colonization. Therefore, mycorrhizae formation, response to added P, host nutrient requirement and mycorrhizae responsiveness are all interrelated.

The results of mycorrhizal research have strongly suggested that infection does not change the size of labile pool, but the hyphae extend beyond P depletion zone and provide a well-distributed surface for absorbing phosphorus (Sharif and Claassen 2011). Rubio et al. (2012) demonstrated a field and greenhouse experiments and showed that different plant species have different effects on rhizosphere P depletion which is related with plant P demand. Plants uptake P from the soil solution at a much faster rate than they can diffuse to the root surface. Consequently, a P depletion zone develops around the absorbing organs (mycorrhizal hyphae or roots) of the plants (Marschner 2012).

**Table 6.2** Effect of P, Zn and mycorrhizal inoculation on maize plant root infection (Ortas 2012a)

| Mycorrhizal species | Treatments | | Root infection (%) | |
|---|---|---|---|---|
| ***Control*** | P0 | | 2.0 | ±1.00 |
| | P1 | **Zn0** | 2.3 | ±2.50 |
| | P2 | | 2.7 | ±3.10 |
| | P0 | | 2.0 | ±2.00 |
| | P1 | **Zn1** | 3.0 | ±3.00 |
| | P2 | | 3.0 | ±2.60 |
| ***G. etunicatum*** | P0 | | 93.7 | ±2.90 |
| | P1 | **Zn0** | 87.9 | ±2.20 |
| | P2 | | 66.7 | ±13.6 |
| | P0 | | 89.1 | ±5.20 |
| | P1 | **Zn1** | 78.0 | ±11.4 |
| | P2 | | 70.4 | ±9.40 |
| ***G. mosseae*** | P0 | | 90.8 | ±3.40 |
| | P1 | **Zn0** | 91.4 | ±3.50 |
| | P2 | | 57.1 | ±35.4 |
| | P0 | | 82.4 | ±15.2 |
| | P1 | **Zn1** | 79.7 | ±7.10 |
| | P2 | | 79.8 | ±9.40 |

Since the diffusion of P in soil is very slow, P absorption capacity of roots does not have great effect on rate of uptake. When plant roots are not able to absorb sufficient P for adequate growth, then plants employ other physiological variables of root on P absorption by increasing the amount of P available to diffuse the root surface interpreted (Isaac et al. 2012). The direct effect of soluble P on fungi metabolism, mainly by regulating enzymatic activities, is related to phosphate transfer to the host and has been recently discussed. Carrasco et al. (2011) showed higher levels of acid phosphate activity in the root and rhizosphere infected by *G. mosseae* and *G. geosporum* compared with control. Although increased phosphatase activity has been demonstrated in several mycorrhizal symbioses, plant roots and other microorganisms can also produce acid phosphatase. In this case, it is difficult to interpret contribution of mycorrhizae.

## 6.11 Effect of Mycorrhizal Infection on Nitrogen Uptake

The effect of N form and P rate application on total dry matter production on harvesting varied with mycorrhizal inoculation. Hoeksema et al. (2010) reported in a meta-analysis work that N-fertilization is an important predictor of plant response to mycorrhizal inoculation. AMF inoculation enhanced differences between N sources (Ortas and Rowell 2004). Sorghum plants infected with mycorrhizae had nearly three times more shoot dry matter yield than non-inoculated control plants

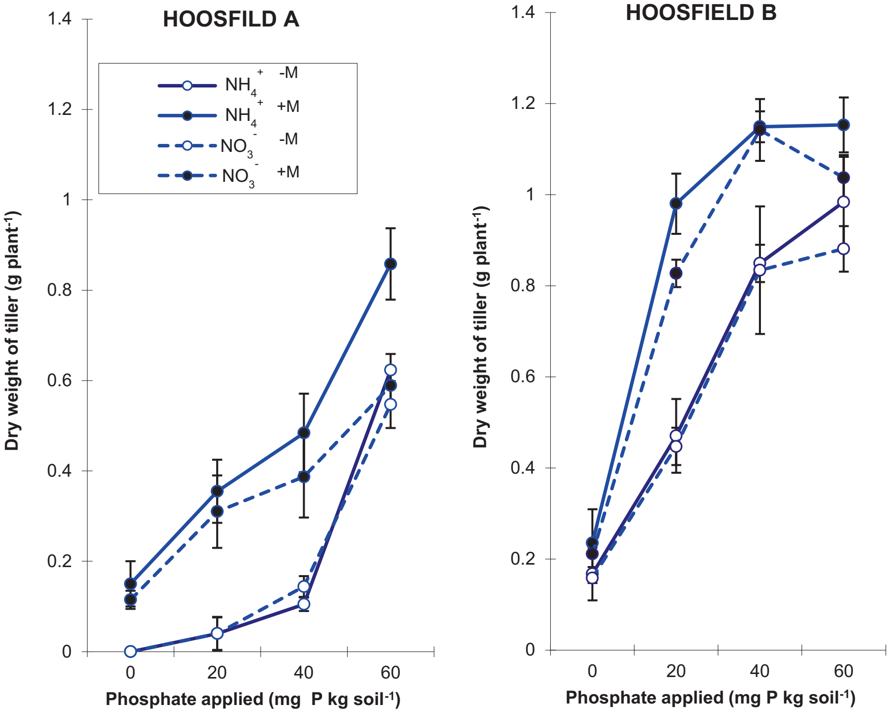

**Fig. 6.6** Effect of nitrogen form, phosphate rate and AMF inoculum on dry weight of sorghum shoot at 40 days (+M AMF inoculum used, −M no inoculum) (Ortas et al. 1996)

(Fig. 6.6). Mycorrhizal inoculation with increased P application significantly enhanced tiller dry weight production (Ortas et al. 1996).

When the N source was $(NH_4)_2SO_4$, the specific absorption rate of N by mycorrhizal roots (nitrogen absorbed per g of root) was higher than that of non-mycorrhizal roots (Smith 1980). Similar results have been reported by Ortas et al. (1996) when soil was sterilized, as a result of more mineral $NH_4^+$-N, and the specific absorption rate of N was higher. Moreover, ectomycorrhizal and ericoid mycorrhizal fungi generally appear to prefer $NH_4^+$-N to $NO_3^-$-N (Kosola et al. 2007; Kranabetter and MacKenzie 2010). Lundeberg (1970) has shown that most of the 27 ectotrophic mycorrhizal fungi grew better with $NH_4^+$-N than $NO_3$-N.

According to Azcon-Aguilar and Barea (2015), mycorrhizal infection stimulated growth of $NH_4^+$-N-fed plants more than that of $NO_3^-$-N. Increasing availability of P by the rate of N fixation was related to AM fungus infection with dual application of mycorrhizal fungi and rhizobium. Barea et al. (1987) by using $^{15}N$ technique showed that both $NH_4^+$-N and $NO_3^-$-N forms of N can be absorbed by AM hyphae and that growth enhancement of legumes by AM can be attributed to both enhanced N fixation as well as improved N uptake from the soil, especially with the $NH_4^+$-N forms (Tome et al. 2015). The release of $NH_4^+$ from nodules to the soil was immediately absorbed by the surrounding AM hyphae. N uptake by AMF has been reported to take place in the following situations:

1. Mycorrhizal fungi increase plant-absorbed $NO_3^-$-N and $NH_4^+$-N from the growing substrate (Ortas et al. 1996).
2. Mycorrhizal fungi assimilate $NH_4^+$-N via glutamine syntheses, and this would have a significant influence on the function of external hyphae (Johansen et al. 1996).
3. Fungi directly uptake $NH_4^+$-N through the hyphae (Marschner and Dell 1994; Perez-Tienda et al. 2014). According to Javaid (2009) $NH_4^+$-N can be taken up by plant roots because it is relatively immobile compared to $NO_3^-$-N in soil.
4. Mycorrhizal fungi increase N inflow of plant roots. N inflow was considerably increased when supplied as $(NH_4)_2SO_4$ (Ortas 1994).

## 6.12 Micronutrient Uptake Significantly Affected by Mycorrhizae

Since mycorrhizal hyphae can exploit more efficiently large volumes of soil, in the presence of AM symbiosis, more nutrients are taken up and transported specifically. In addition to P, AMF enhance the acquisition of other nutrients such as sulphur and potassium (K) (Ortas 2003) and immobile micronutrients, particularly Zn and Cu (Li and Christie 2001; Ortas 2012a). When P and Zn contents of leaves were compared with the recommended levels, entire P status of mycorrhizal plants was observed above the normal level, regardless of AM fungi. Watts-Williams et al. (2015) reported that up to 24 % of Zn in shoots of the AM plants was delivered via the AM pathway in soil with Zn concentration. In addition, non-mycorrhizal plants apparently suffered from Zn deficiency according to leaf analysis, whereas Zn status of inoculated plants was around an acceptable level. *G. intraradices* appeared to be more effective than *G. mosseae* in terms of Zn concentration of leaves. Wu and Zou (2009) and Ortas (2012b) showed that sole AMF inoculation significantly increased total dry weight, leaf P, K, Ca, Mg, Fe, Cu and Mn contents and root P, K, Ca, Fe, Cu and Zn contents of the seedlings, compared to the non-AMF control. The result of Balliu et al. (2015) indicates that AM fungi may increase the uptake of Fe to host plant.

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