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Review Paper

Harnessing the Potentials of Vesicular Arbuscular Mycorrhizal (VAM) Fungi to Plant Growth – A Review

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Abstract: *Mycorrhizae are symbiotic associations, formed between plants and soil fungi that play an essential role in sustainable crop production and soil fertility. Interest in Vesicular Arbuscular Mycorrhiza (VAM) fungi inocula propagation for agriculture is increasing due to their role in promotion of plant health, soil fertility, and soil aggregates stability in the developing economies. This review discusses the impact of VAM to plant growth, factors contributing to VAM utilization and associations to plant growth. The management and strategic applications of VAM to enhance growth of food crops most especially in Africa with an understanding of exploiting VAM benefits towards sustainable agricultural development is very important.*

Keywords: Mycorrhiza, Plant growth, VAM, Symbiosis, Nutrient uptake, Rhizosphere, Colonization.

1. Introduction

Poor land management and declining soil fertility often result in a negative feedback cycle characterized in part by an increase in soil-borne pests and diseases. Agricultural practices such as adding lime, inorganic fertilizers, and pesticides can change the physical and chemical nature of the soil environment, thereby altering the number of organisms and the ratio of different groups of organisms. Since plant health is intimately linked to soil health, managing the soil in ways that conserve and enhance the soil biota can improve crop yields and quality. A diverse soil community will not only help prevent losses due to soil-borne pests and diseases but also speed up decomposition of organic matter and toxic compounds, and improve nutrient cycling and soil structure. Microorganisms are the most abundant members of the soil biota. They include species responsible

for nutrient mineralization and cycling, antagonists (biological control agents against plant pests and diseases), species that produce substances capable of modifying plant growth, and species that form mutually beneficial (symbiotic) relationships with plant roots (SP-IPM, 2004). The most abundant members of the vast community of soil organisms that develops mutually beneficial relationships with plants roots and contributes majorly to plant growth are called mycorrhizal fungi. The most common and best known of these associations are the Vesicular Arbuscular Mycorrhizae (VAM) (Powell and Bagyuraj, 1984).

Vesicular Arbuscular Mycorrhizas are produced by aseptate mycelial fungi and are so-called because of the two characteristics structures-vesicles and arbuscules- found in roots with type of infection. They are by far the commonest of all mycorrhizas and are found in Bryophytes, Pteridophytes, Gymnosperms, excluding the Pinaceae which have sheating mycorrhizas, and in virtually all families of Angiosperms. They are of general occurrence in the Gramineae, Palmae, Rosaceae and Leguminosae, which all include many crop plants. Indeed most crop plants, including herbs, shrubs and some trees, possess this type of mycorrhiza. In the Angiosperms, apart from such families as Ericaceae and the Orchidaceae which have other types of mycorrhiza, the Chenopodiaceae, the Cruchidaceae, the Cyperaceae and the Resedaceae are odd exceptions in that most species from these families appear to be either non-mycorrhizal or at least only very sparsely infected. However, the striking fact is that the majority of all plants that are mycorrhizal have this type of infection. Associations resembling modern day VAM were present very early in the evolution of land plants. VAM may colonize the roots of a host plant roots either intracellular or extracellular, this filamentous network promotes bi-directional movement of nutrients where carbon flows to the fungus and inorganic nutrients move to the plant, thereby providing a critical linkage between the plant root and rhizosphere. VAM fungi help plants to capture nutrients such as phosphorus and micronuteints from the soil. It is believed that the development of the VAM symbiosis played a crucial role in the initial colonization of the land by plants and in evolution of the vascular plants (Brundrett, 2004). It has been said that it is quicker to list the plants that do not form mycorrhizae than those that do (Harley and Smith, 1983).

The mycorrhizal symbiosis is a key stone to the productivity and diversity of natural plant ecosystems (Jeffries *et al*., 2003). The symbiosis is a highly evolved mutualistic relationship found between fungi and plants, the most prevalent plant symbiosis known (Simon *et al*., 1993); and as a result VAM symbiosis is found in more than 80% of vascular plant families of today (Schüßler *et al*., 2001). The symbionts are formed by the majority of the vascular flowering plants and are found in ecosystems throughout the world. In general, the symbionts trade nutrients, and the arbuscular mycorrhizal (AM) fungus obtains carbon from the plant while providing the plant with an additional supply of phosphorus (as phosphate). While much research has focused on nutrient exchange, the VAM symbiosis is associated with a range of additional benefits for the plant including the acquisition of other mineral nutrients, such as nitrogen, phosphorus and resistance to a variety of stresses such as drought, soil/root borne pathogens, salts, heavy metals and soil stability. Consequently, the VAM symbiosis is of tremendous significance to life on this planet, in both natural and agricultural ecosystems (Smith and Read, 1997). The tremendous advances in research on mycorrhizal physiology and ecology over the past 40years have led to a greater understanding of the multiple roles of VAM in the ecosystem.

As a consequence, loss or perturbation of this relationship can have serious consequences in terms of plant community degradation, health or productivity. There are number of situations where manipulation or management of the mycorrhzal symbiosis is necessary to restore plant cover, improve plant health or increase plant productivity. These situations usually arise from anthropogenic sources, but natural events may also contribute (e.g volcanic activity, climate drift). Soils with an absence of appropriate mycorrhizal propagules can be found where subsurface soils are brought to surface (e.g. mine spoils, tunneling activities, volcanic depositions). In contrast, other soils may contain a mycorrhizal flora compatible with an established plant ecosystem, but may be subjected to a drastic change in plant community as a result of human intervention (e.g deforestation, shifting agriculture,

reforestation or revegetation). Likewise, plant growth can also be inhibited as a result of the accumulation of phytotoxic levels of heavy metals and organic xenobiotics (Jeffries and Barea, 2001).

The selection of the most specific appropriate plant-fungus association for each specific environmental and ecological situation is one of the main challenges in current research on VAM. These situations are discussed in this review in context to their potential use for plant growth. The knowledge of the different factors influencing the diversity of VAM is essential in their use for sustainable agriculture. Thus, mycorrhizal technology becomes an important consideration in low-input, organic or soil-less agriculture. The desire to exploit VAM as a natural biofertlizers for the agricultural biotechnology industry was understandable, but it became clear that more knowledge was needed of the fungi themselves to allow commercial exploitation. Many inoculants companies have tried to commercialize the use of VAM with limited success. This has masked the importance of the symbiosis for normal plant growth and development in natural ecosystems where mycorrhizal plants dominate climax vegetation. The benefit of the symbiosis for nutrient uptake by plants in agro-ecosystems is important as the knowledge is applicable to human endeavors for ecosystem management, restoration and sustainability. In view of this, more complete understanding of how to manage vesicular arbuscular mycorrhizas for optimum plant growth, health and development is needed urgently as high-input plant production practices are challenged by a more sustainable biological production approaches.

2. The Interaction of VAM and Plant

2.1 Rhizosphere Ecology of VAM

Microbial activity in the rhizosphere is a major factor that determines the availability of nutrients to plants and has a significant influence on plant health and productivity. An understanding of the basic principles of rhizosphere microbial ecology, including the function and diversity of the microorganisms that reside there, is necessary before soil microbial technologies can be applied (Bolton *et al*., 1992). Recent research has shown that VAM fungi release a diffusional factor, known as the "MYC FACTOR" which activates the nodulation factor's inducible gene mtENOD11. This is the same gene involved in establishing symbiosis with the nitrogen-fixing bacteria, rhizobium (Kosuta *et al*., 2003). When rhizobium bacteria are present in the soil, mycorrhizal colonization can also increase the nodulations and symbiotic nitrogen fixation in mycorrhizal legumes (Hamel, 2005). The extent of arbuscular mycorrhizal colonization and species affects the bacterial population in the rhizosphere. Bacterial species differ in their abilities to compete for carbon compound root exudates. A change in the amount or composition of root exudates and fungal exudates due to the existing VAM mycorrhizal colonization determines the diversity and abundance of the bacterial community in the rhizosphere (Marschner and Timonen, 2004). The influence of VAM fungi on plant root and shoot, growth may also have indirect effect on the rhizosphere through the growth and degeneration of the hyphal network. There is also evidence that VAM fungi may play an important role on mediating the plant species specific effect on the bacterial composition of the rhizosphere (Marschner and Timonen, 2004)

2.2 Presymbiosis

The development of VAM fungi prior to root colonization, known as presymbiosis, consists of three stages: spore germination, hyphal growth, host recognition and appressorium formation (Nagahashi *et al*., 1996). Spores of the VAM fungi are thick walled multi-nucleate resting structures (Sbrana and Giovannetti, 2005). The germination of the spore does not depend on the plant as spores have been germinated under experimental conditions in the absence of plants both *in-vitro* and in soil. VAM fungal spores germinate given suitable conditions of the soil matrix, temperature, carbondioxide concentration, pH and phosphorus concentration (Sbrana and Giovannetti, 2005). The growth of VAM hyphae through the soil is controlled by host root exudates and the soil phosphorus concentration. Low phosphorus concentrations in the soil increased hyphal growth and branching as

well as induce plant exudation of compounds, which control hyphal branching intensity (Nagahashi *et al*., 1996; Tamasloukht, 2003). The branching of VAM fungal hyhae grown in 1mM phosphorus media is significantly reduced but the length of the germ tube and total hyphal growth was not affected. A concentration of 10mM phosphorus inhibited both hyphal growth and branching. This phosphorus concentration occurs in natural soil conditions and could thus contribute to reduced mycorrhizal colonization (Tamasloukht, 2003). Root exudates from VAM host plants grown in a liquid medium with and without phosphorus have been shown to effect hyphal growth. Pre-germinated surface-sterilized spores of *Gigaspora margarita* were grown in host plant exudates. The fungi grow in the exudates from roots starved of phosphorus had increased hyphal growth and produced tertiary branches compared to those grown in exudates from plants given adequate phosphorus.

When the growth promoting root exudates were added in low concentration, the VAM fungi produced scattered long branches (Tamasloukht, 2003). As the concentration of exudates was increased, the fungi produced more tightly clustered branches. At the highest concentration arbuscules, the VAM structures of phosphorus exchange were formed. This chemotaxic fungal response to the host plants exudates is thought to increase the efficacy of host root colonization in low phosphorus soils (Nagahashi *et al*., 1996). It is an adaption for fungi to efficiently explore the soil in search of a suitable plant host (Tamasloukht, 2003). Further evidence that VAM fungi exhibit host specific chemotaxis: spores of *Glomus mosseae* were separated from the roots of a host plants, non-host plants and dead host plant by a membrane only permeable to hyphae. In the treatment with the host plant, the fungi crossed the membrane and always emerged within 800um of the root, whereas in the treatments with non-host plants and dead plants, the hyphae did not cross the membrane to reach the roots (Gianinazzi-Pearson, 1996). This demonstrates that arbuscular mycorrhizal fungi have chemotaxic abilities, which enable hyphal growth toward the roots of a potential host plant. Molecular techniques have been used to further understand the signaling pathways, which occur between arbuscular mycorrhizae and the plant roots.

Tuomi *et al*. (2001) reported that exudates from potential host plant roots allow the VAM to undergo physiological changes, which allow it to colonize its host. VAM fungal genes required for the respiration of spore carbon compounds are triggered and turned on by host plant root exudates. In experiments, there was an increase in the transcription rate of 10 genes 0.5hour after exposure and an even greater rate after 1hour. A morphological growth response was observed 4 hours after exposure. The genes were isolated and found to be involved in mitochondrial activity and enzyme production. The fungal respiration rate was measured by Oxygen consumption rate and increased by 30% 3 hours after exposure to root exudates. This indicates that VAM spore mitochondrial activity is positively stimulated host plant root exudates. This may be part of a fungal regulatory mechanism that conserves spore energy for efficient growth and the hyphal branching upon receiving signals from a potential host plant. When arbuscular mycorrhizal fungal hyphae encounter the root of a host plant an appressorium (an infection structure) is formed on the root epidermis. The apressorium is the structure from which the hyphae can penetrate into the host's parenchyma cortex (Bolan, 1991). The formation of apressoria does not require not require chemical signals from the plant. VAM fungi could form apressoria on the cell walls of "ghost" cells in which the protoplast had been removed to eliminate signaling between the fungi and the plant host. However, the hyphae did not further penetrate the cells and grow in toward the root cortex, which indicates that signaling between symbionts is required for further growth once apressoria are formed (Nagahashi *et al*., 1996).

2.3 Plant-Nutrient Uptake

VAM are obligate symbionts. They have limited saprobic ability and are dependent on the plant for their carbon nutrition (Harley and Smith, 1983). VAM fungi take up the products of the plant host's photosynthesis as hexoses, fructose and sucrose. The transfer of carbon from the plant to the fungi may occur through the arbuscules or intraradical hyphae (Pfeffer *et al*., 1999). Secondary synthesis from the hexoses by VAM occurs in the intraradical mycelium. Inside the mycelium, hexose is

converted to trehalose and glycogen. Trehalose and glycogen are carbon storage forms which can be rapidly synthesized and degraded and may buffer the intracellular sugar concentrations (Pfeffer *et al.*, 1999). The intraradical hexose enters the oxidative pentose phosphate pathway, which produces pentose for nucleic acids. Lipid biosynthesis also occurs in the intraradical mycelium. Lipids are then stored or exported to extraradical hyphae where they may be stored or metabolized. The breakdown of lipids into hexoses, known as gluconeogenesis, occurs in the extraradical mycelium (Pfeffer *et al.*, 1999). Approximately 25% of the carbon translocated from the plant to the fungi is stored in the extraradical hyphae (Hamel, 2005). Up to 20% of the host plant's photosynthate carbon may be transferred to the VAM fungi (Pfeffer *et al.*, 1999). This represents a considerable carbon investment in mycorrhizal network by the host plant and contribution to the below ground organic carbon pool. An increase in the carbon supplied by the plant to the VAM fungi increases the uptake of phosphorus and the transfer of phosphorus from fungi to plant (Bucking and Shachar-Hill, 2005).

Phosphorus uptake and transfer is also lowered when the photosynthate supplied to the fungi is decreased. Species of VAM differ in their abilities to supply the plant with phosphorus (Smith *et al.*, 2003). In some cases arbuscular mycorrhizae are poor symbionts providing little phosphorus while taking relatively high amounts of carbon (Smith *et al.*, 2003). The benefit of mycorrhizae to plants is mainly attributed to increase uptake of nutrients, especially phosphorus. This increase in uptake may be due to increase surface area of soil contact, increased movement of nutrients into mycorrhizae, a modification of the root environment and increased storage (Bolan, 1991). Mycorrhizal can be much more efficient than plant roots at taking up phosphorus travels to the root or via diffusion and hyphae reduce the distance required for diffusion, thus increasing uptake. The rate of inflow of phosphorus into mycorrhizae can be up to six times that of the root hairs (Bolan, 1991). In some cases, the role of phosphorus uptake can be completely taken over by the mycorrhizal network and all the plant's phosphorus may be of hyphal origin (Smith *et al.*, 2003).

The significance of mycorrhizal symbiosis in the nutrition and well-being of the individual plant is well established. The most pronounced benefit for plant nutrient uptake through VAM have been described for nutrient which have limited mobility in the soil such as phosphorus. Evidences indicate that VAM colonized plants absorb and accumulate more phosphorus (P) compared to non-colonized plants when plants are grown in soils that are low in P (Smith and Read, 1997; Harrier and Watson, 2003; Azcon *et al.*, 2003). Smith and Read (1997) reported that influx of P in roots colonized by VAM could be 3 to 5 times higher than in non-colonized roots. Enhanced P uptakes through VAM have been observed in tuber crops such as cassava, potatoes, cocoyam and yam (Duffy and Cassells, 2000; Mulongoy *et al.*, 1998; Howeler, 1990). Not only the uptake of P is enhanced by VAM colonization of plant roots, the uptake of other macro and micronutrients like N, Ca, Mg, S, Cu, Fe, Zn and B have also been enhanced (Allen *et al.*, 2003; Hodge, 2003; Clark and Zeto, 2000; Marschner and Dell, 1994). Several studies have demonstrated the transport of inorganic Nitorgen (N) by VAM fungi (Johansen *et al.*, 1992; Hawkins *et al.*, 2000; Blanke *et al.*, 2005). Enhancements in the acquisition of K, Ca and Mg are often observed in VAM colonized plants grown on acidic soils than neutral or alkaline soils (Harrier and Watson, 2003). Zinc and Copper have been taken up by mycorrhiza in a deficient condition to increase plant yield (Gildon and Tinker, 1983; Kucey and Jarzen, 1987). Paradoxically, there is evidence that VAM can inhibit Zinc and Manganese (Mn) uptake at toxic concentration in soil thus reducing adverse effect on host (Dueck *et al.*, 1986).

2.4 Host Range Specificity and Plant Responsiveness

The specificity, host range and degree of colonization of mycorrhizal fungi are difficult to analyze in the field due to the complexity of interactions between the fungi within a root and within the system. There is no clear evidence that arbuscular mycorrhizal fungi exhibit specificity for colonization of potential VAM host plant species as do fungal pathogens for their host plants (Smith and Read, 2002). This may be due to the opposite selective pressure involved. In parasitic relations the host plant benefits from mutations, which prevent colonization whereas in symbiotic relationship the plant benefits from mutation that allow for colonization by VAM (Smith and Read, 2002). Juan *et al.*

(2006) in their molecular study of VAM reported that there were no clear patterns of host specificity, as the most common glomalean sequence groups were present in both plant species. The PCR-DGGE approach used in their study can only characterize the VAM community in terms of presence or absence, and this may mask quantitative differences in colonization of different plant species by particular VAM taxa. No information is available about the relative abundance of different fungal taxa in the plant roots. However, plant species differ in the extent and dependence on colonization by certain VAM fungi and some plants may be facultative mycotrophs while others may be obligate mycotrophs (Smith and Read, 2002). The ability of the same VAM fungi to colonize many species of plants has ecological implications. Plants of different species can be linked underground to a common mycelial network. One plant may provde the photosynthate carbon for the establishment of the mycelial network, which another plant of a different species can utilize for mineral uptake. This implies that arbuscular mycorrhizae are able to balance below ground intra- and interspecific plant interactions (Smith and Read, 2002). Host-plant preferences of VAM has been reported to occur between different VAM taxa (Helgason *et al*., 2002; Vandenkoornhuyse *et al.,* 2002, 2003; Gollotte *et al*., 2004), and root architecture has been hypothesized to be related to the presence of VAM species with potential different functions (Newsham *et al*., 1995).

Mycorrhizal dependency and plant responsiveness to mycorrhiza are terms commonly used in mycorrhizal research with a variety of meaning (Menge *et al*., 1978; Habte and Manjunath, 1991; Janos, 1988; Plenchette *et al*., 1983; Baon *et al*., 1993; Smith *et al.,* 2003). Mycorrhizal dependency was first defined by Gerdamann (1975) as the degree to which a plant is dependent on the mycorrhizal condition to produce its maximum growth or yield at a given level of soil fertility. Different numerical expression has been used for mycorrhizal dependency has been expressed as the difference in the shoot dry weigth between mycorrhizal and non-mycorrhizal plants (Habte and Manjunath, 1991; Plenchete *et al*., 1983; Smith *et al*., 2003) or as a percentage of the shoot dry weigth of non-mycorrhizal plants (Baon *et al.,* 1993; Gange and Ayres, 1999). Janos (2007) defined mycorrhizal dependency as the lowest level of phosphorus availability at which plants can grow without mycorrhizas. The definition represents plant responsiveness to mycorrhizas, which means the difference in growth between plants with and without mycorrhizas at any designated level of phosphorus availability. When expressed relative to the growth of plants with mycorrhizas (Habte and Manjunath, 1991; Plenchette *et al*., 1983; Smith *et al*, 2003), it reflects the proportional growth improvement attributable to mycorrhizas (Janos, 2007). It is calculated from a logistic equation fitted to the phosphorus response curve of plants without mycorrhizas. This definition differs from conventional usage, which fails to distinguish dependency from responsiveness. Plant responsiveness to VAM fungi colonization can be influenced by soil type, availability of soil P, effectiveness of mycorrhizal species and many other variables. Plant responsiveness to VAM can vary greatly from one plant species to another and even between cultivars or ecotypes within a single species (Hetrick *et al*., 1992). It is therefore useful to determine whether or not a plant derives or nor benefits from VAM symbiosis and to know how to manage it accordingly (Plenchete *et al*., 1983).

2.5 VAM Associations

Mycorrhizal associations produced by Glomeromycota fungi are known as arbuscular mycorrhizas (AM) or vesicular-arbuscular mycorrhizas (formerly also endomycorrhizas, or endotrophic mycorrhizas) and are abbreviated as VAM (Schüßler *et al*., 2001). There is disagreement about whether arbuscular mycorrhizas or vesicular-arbuscular mycorrhizas is the most appropriate name to, because some fungi do not produce vesicles, but arbuscles are not consistently used to identify associations (i.e. they are absent in myco-heterotrophs and older roots). These associations involve primitive fungi in the Glomeromycota and a wide diversity of plants. The presence of arbuscles in a root is used to designate plants with VAM. However, these structures are ephemeral and may be absent from field-collected roots. Once inside the parenchyma the fungi forms highly branched structures for nutrient exchange with the plant called "arbuscles" (Bolan, 1991). These are the distinguishing structures of arbusclar mycorrhizal fungus. Arbuscles are the sites of exchange for phosphorus, carbon, water and other nutrients (Sbrana and Giovannetti, 2005). Consequently, hyphal

colonization alone is often used to identify VAM associations, but hyhae and vesicles of VAM fungi will also occupy non-host. Hyphal coils or longitudinal hyphae, but not arbuscles, may be seen in roots collected from the field (Brundrett and Kendrick, 1990). Consequently, determining if older roots had VAM may require prior knowledge of that plant species. This knowledge includes root phenology information and prior observations of the same or closely related species.

Major modifications are required in the plant host cell to accommodate the arbuscules. The vacuoles shrink and other cellular organelles proliferate. The plant cell cytoskeleton is reorganized around the arbuscules. There are two other types of hyphae, which originate from the colonized host plant root. Once colonization has occurred, short-lived runner hyphae grow from the plant root into the soil. These are the hyphae that take up phosphorus and micronutrients, which are conferred to the plant. VAM fungal hyphae have a high surface to volume ratio making their absorptive ability greater than that of plant roots (Boswell *et al*., 1998). VAM hyphae are also finer than roots and can enter into pores of the soil that are inaccessible to roots (Brundrett, 2004). Detail examinations of plants in natural ecosystems often show consistent differences between host plants in both the intensity and consistency of mycorrhiza formation (proportion of root system involved). These observations have shown that species generally either have consistently high levels of mycorrhizas, low, or variable levels of mycorrhizas, or are not mycorrhizal (Brundrett and Kendrick, 1988). Plants belonging to these categories are designated as obligatorily mycorrhizal, facultatively mycorrhizal, or nonmycorrhizal. Plants with facultative mycorrhizas consistently have low levels of colonization (i.e under 25% of root length) (Brundrett and Kendrick, 1988).

3. Factors Contributing to Utilization of VAM by Plants

Climatic and edaphic factors such as temperature, rainfall, light, atmospheric CO_2, soil pH, moisture content, fertility level and density of inoculums have significant influence on VAM and root colonization (Singh, 2005; Miller and Jackson, 1998; Li and Zhao, 2005). The influence of climatic and soil factors vary with plant species and can be positive or negative (Muthukumar and Udaiyan, 2002).

3.1 Climatic Factors

The effects of climatic factors on VAM root colonization and diversity are complex. In the relationship between light, temperature, rainfall, atmospheric CO_2 and VAM colonization, positive (Li and Zhao, 2005; Braunberger, 1994; Singh, 2005) as well as negative correlation (Mutuhukumar and Udaiyan, 2002; Saif, 1981) have been observed. It is generally considered that of light were positively correlated with mycorrhizal colonization (Koide and Mosse, 2004), and higher light levels can enhance the efficiency of photosynthesis, which can contribute more carbon compounds to VAM growth. Light duration and intensity increased VAM colonization and spore density of most plant species (Ferguson and Menge, 1982; Singh and Tyagi, 1989; Wang, 1987). Elevated CO_2 was reported to increase VAM colonization and spore density of some plants (Morgan *et al*., 1994; Staddon *et al.,* 1998, 1999; Staddon, 1998; Klironomos, 1998) but did not translate into increased yield of most crops. Although VAM colonization has been found in plant at temperature as low as $5^{o}C$, a temperature range of 18-$40^{o}C$ with the optimum for most fungal-host species near $30^{o}C$ are usually observed (Entry *et al*., 2002; Smith and Read, 1997). The influence of temperature on arbuscular mycorrhizal plants appears related to the exact fungal-host species combination, the development stage of the plant, temperature controlling fungal germination, photosynthesis and carbon flow to roots (Entry *et al.,* 2002). Spores of VAM fungi differ in their optimum germination temperatures (Matusubara and Harada, 1996). *Glomus intraradices*, *G. clarum*, *G. microaggregatum*, were reported in the most adapted to the hot and arid environment of China (Li and Zhao, 2005).

3.2 Soil Factors

Soil condition is also an important factor in the extent of VAM root colonization and diversity. Soil pH, moisture, nutrient status and texture have shown correlation with VAM root colonization and diversity (Klinomoros *et al.*, 2001; Miller and Jackson, 1998). Soil pH influences VAM fungal species composition, colonization and effectiveness (Van Aarle *et al.*, 2002; Hayman and Tavares, 1985). It has been reported that spore germination, hyphal elongation and infection with VAM fungi are suppressed on acidic or alkaline agar or soil (Daniel and Trappe, 1980; Van Aarle *et al.*, 2002). On the contrary, Ulhamm (2006) and Siquiera *et al.* (1984) reported no significant correlation between colonization, spore density and spore pH. The response of arbuscular mycorrhizas to soil pH seems to be dependent primarily on the fungal species (Hayman and Tavares, 1985). In China, *Glomus sp.* appears to dominate in alkaline and neutral soils while Acaulospora sporulate more abundantly in acid soils (Zhang *et al.*, 1998b; Gai *et al.*, 2006).

Indication for probable influence of soil organic matter (SOM) on the VAM species diversity and root colonization has been found. Covacevich (2007) reported the frequency of occurrence of *G. mosseae* decreased with increasing organic matter content while *G. sinousum* and *G. taiwanese* were found only when SOM was less than 1.5%. Miller and Jackson (1998) reported inverse correlation between VAM colonization and soil organic matter. Soil fertility status most especially P availability have significant influences on VAM. Root colonization, spore production, hyphal growth and response of plants to VAM inoculation are reduced by abundance of P in soil (Abbot and Robson, 1991; Bethlenfalvay, 1992; Covacevich, 2007). However, the magnitude of the effect of P strongly dependent on the host plant dependency on mycorrhiza (Plenchette, 1983) and other environmental factors (Smith and Read, 1997). Information on the influence of the high content of other mineral nutrient on VAM in soil is rarely available but abundance of N has been reported to have no effect on VAM colonization of plant (Covacevich, 2007). The rate of infection of VAM fungi in plants is strongly influenced by amount of spore propagules (Giovanetti, 1985; Mohammed *et al.,* 2004; Lekberg and Koide, 2005). Low numbers of propagules in field soils may result in low level of colonization (Smith and Read, 1997). Factors such as soil P content, presence of plant root and crop species influence the density of spores in an environment (Kurhl and Phleger, 1996; Troeh and Loynachan, 2003). Isobe *et al.* (2007) reported that soil P content correlate with spore density.

3.3 Agriculture, Tillage and Phosphorus Fertilizer

Many modern agronomic practices are distruptive to mycorrhizal symbiosis. There is great potential for low input agriculture to manage the system in a way that promotes mycorrhizal symbiosis. Conventional agriculture practices, such as tillage, heavy fertilizers and fungicides, poor crop rotations and selection for plants which survive these conditions, hinder the ability of plants to form symbiosis with arbuscular mycorrhizal fungi. Most agricultural crops can perform better and are more productive when well colonized by VAM fungi. VAM symbiosis increases the phosphorus and micronutrient uptake and growth of their plant host (George *et al.*, 1992). Management of VAM fungi is very important for organic and low agriculture systems where soil phosphorus is generally low, although all agroecosystems can benefit by promoting arbuscular mycorrhizae establishment. Some crops that are poor at seeking out nutrients in the soil are very dependent on VAM fungi for phosphorus uptake. Heavy usage of phosphorus fertilizer can inhibit mycorrhizal colonization and growth. As the soil's phosphorus levels available to the plants increases, the amount of phosphorus also increases in the plant's tissues and carbon drain on the plant by the VAM fungi symbiosis become non-beneficial to the plant (Grant *et al.*, 2005). A decrease in mycorrhizal colonization due to high soil phosphorus levels can lead to plant deficiencies in other micronutrients that have mycorrhizal mediated uptake such as copper (Timmer and Leyden, 1980). For example flax, which has poor chemotaxic ability, is highly dependent on VAM mediated phosphorus uptake at low and intermediate soil phosphorus concentrations (Thingstrup *et al.*, 1998). Proper management of VAM fungi in the agroecosystems can improve the quality of the soil and the productivity of the land.

Agricultural practices such as reduced tillage, low phosphorus fertilizer usage and perennialized cropping systems promote functional mycorrhizal symbiosis.

Tillage reduces the incoculation potential of the soil and the efficacy of mycorrhizaes by disrupting the extraradical hyphal network (Miller *et al*. 1995; McGonigle and Miller, 1999; Mozafar *et al*. 2000). By breaking apart the soil macro structure the hyphal network is rendered non-infective (Miller *et al*., 1995; McGonigle and Miller, 1999). The distruption of the hyphal network decreases the absorptive abilities of the mycorrhizae because the surface area spanned by the hyhae is greatly reduced. This in turn lowers the phosphorus input to the plants which are connected to the hyphal network (McGonigle and Miller, 1999). In reduced tillage system heavy phosphorus fertilizer input may not be required as compared to heavy tillage systems. This is due to the increase in mycorrhizal network which allows mycorrhizae to provide the plant with sufficient phosphorus (Miller *et al*., 1995).

3.4 Perennialized Cropping Systems

Cover crops are grown in the fall, winter and spring, covering the soil during periods when it would commonly be left without a cover of growing plants. Mycorrhizal cover crops can be used to improve the mycorrhizal inoculums potential and hyphal network (Kabir and Koide, 2000; Boswell *et al*., 1998; Sorensen *et al*., 2005). Since VAM fungi are biotrophic, they are dependent on plants for their hyphal networks. Growing a cover crop extends the time for VAM growth into the autum, winter and spring. Promotion of hyphal growth creates a more extensive hyphal network. The mycorrhizal colonization increase found in cover crops systems may be largely attributed to an increase in the extraradical hyphal network which can be colonize the roots of the new crop (Boswell *et al*., 1998). The extraradical mycelia are able to survive the winter providing rapid spring colonization and early season symbiosis (McGonigle and Miller, 1999). This early symbiosis of plants to tap into the well established hyphal network and be supplied with adequate phosphorus nutrition during early growth which greatly improves the crop yield.

3.5 Soil Quality

Restoration of native VAM fungi increases the success of ecological restoration project and the rapidity of soil recovery (Jeffries *et al*., 2003). There is evidence that this enhancement of soil aggregate stability is due to the production of a soil protein known as glomalin. Glomalin related soil proteins (GRSP) have been identified using a monoclonal antibody (Mab32B11) raised against crushed VAM fungi spores. It is defined by its extraction conditions and reaction with the antibody Mab32B11. There is other circumstancial evidence that glomalin is of VAM fungal origin. When VAM fungi are eliminated from soil through incubation of soil without host plants the concentration of GRSP declines. A similar decline in GRSP has also been observed in incubated soils from forested, afforested and agricultural land and grasslands treated with fungicide (Rilling *et al*., 2003). Glomalin is hypothesized to improve soil aggregate water stability and decrease soil erosion. A strong correlation has been found between GRSP and soil aggregate water stability in a wide variety of soils where organic material is the main binding agent, although the mechanism is not known. The protein glomalin has not yet been isolated and described, and the links between glomalin, GRSP and arbuscular mycorrhizal fungi is not yet clear (Riling, 2004).

4. Exploiting the Benefits of VAM to Plant Growth

Jeffries *et al*. (2003) review on "The contribution of arbuscular mycorrhizal fungi (AMF) in sustainable maintenance of plant health and soil fertility. Though, special attention was paid to plant health but not to plant growth which is obviously known that there are many biological and environmental factors that affects plant growth of which plant health is just one of them. This aspect of this review focused more on benefit of VAM to plant growth. There are wealth of published reports which now provide quite indisputable evidence that infection of plant roots by VAM fungi increase

phosphate uptake, especially under conditions of low phosphate availability. This review cited special examples. Hayman and Mosse (1971) found that in some phosphate deficient soils they obtained up to a 20-fold increase in shoot mass of non-mycorrhizal onions merely by adding phosphate in the order of 1 ton superphosphate acre^{-1} (2.5Mg 10^4 m^{-2}). Comparable increases in shoot mass were obtained by growing mycorrhizal onions in the same soil but without the added phosphate. It appears, as with sheating mycorrhizas, that the host obtains maximum benefit when the mineral nutrient regime is least favorable for growth. Most attention has been paid to the effect of VAM on crop plants such as apples, maize, onions and tomatoes but one of the earliest reports was of their effect on plants of the mixed rain forests of New Zealand (Baylis, 1959, 1967). Much more recently attention has been paid to their role in other natural or semi-natural ecosystems, such as grasslands in the Pennines, Yussock grassland in New Zealand, lowland tropical rainforest trees in Costa Rica and in man-made habitats such as plant communities establishing on coal tip spoils in Pennsylvania and Scotland. VAM associations have been of significant help to crop production and soil fertility as reported by many researchers across different agroecological zones in many countries. Olsen *et al.* (1999), Cordier *et al.* (1996) and Kahiluoto and Vestberg, 1998) worked individually on increase plant nutrients (Phosphorus and Nitrogen) extending the volume of soil accessible to plants. Dodd *et al.* (1990) reported how VAM associations greatly increase the efficacy of N-fixation by *Rhizobium*. Root colonization by VAM fungi is a unique area that has justified the potential of VAM as bioprotectant and as biofertlizer providing protection to plants from parasitic fungi and nematodes and also increase plant growth and yield (Cordier *et al.*, 1998; Morin *et al.*, 1999; Odebode *et al.*, 2001; Killani, 2010). There are difficulties to completely interpret the reported work on the non-nutritional benefit and relationship of VAM to changes in water relations, phytohormones levels, carbon assimilation (Brundrett, 1991; Smith and Read, 1997). Though, Andrade *et al.* (1998) documented the importance of the soil mycelium of mycorrhizal fungal in the formation of water-stable soil aggregates. Mycorrhizal benefits enhance the growth form changes to root architecture, vascular tissue e. t. c coupled with greater yield, nutrient accumulation, and/ or reproductive success (Stanley *et al.*, 1993; Miller *et al.*, 1997; Osonubi *et al.*, 1999). The roles in mechanical aggregation have been questioned (Degens *et al.*, 1994), but secretions such as glomalin may be more important (Wright and Upadhyaya, 1998). The significant amounts of carbon transfer through fungus mycelia connecting different plant species has been measured (Simard *et al.*, 1997). This could reduce completion between plants and contribute to the stability and diversity of ecosystems. Soil hyphae are likely to have an important role in nutrient cycling by helping to prevent losses from the system, especially at times when roots are inactive (Lussenhop and Fogel, 1999). Hyphae are conduits that may transport carbon from plant roots to other soil organisms involved in nutrient cycling processes. Thus, cooperating with other members of the decomposition soil food-web is very important for uptake of nutrients.

The stimulation of microorganisms by the plant root system has now attracted attention. Microbial activity has been found to be an important factor influencing metal solubility and an immobilizer of soil metals due to precipitation of sulphides and hydrated ferric oxides or by exudation of polysaccharides (Lodenius and Autio, 1989; Ernst 1996). Organic functional groups on the surface of bacterial cell walls play an important role in adsorption of metals from the solution (Fein *et al.* 1997). Under other conditions Pb, Zn and Cu may be mobilized from the carbonates and oxides by microbial activity (Bloomfield, 1981). Biological methods to remove pollutants have mainly employed bacteria and saprobic fungi, while the role of mycorrhizal fungi has been almost completely neglected. A well-developed mycorrhhizal symbiosis may enhance the survival of plants in polluted areas by better nutrient acquisition, water relations, pathogenic resistance, phytohormone production, contribution to soil aggregation, amelioration of soil structure, and thus improved success of all kind of bio and phytoremediation. The use of mycorrhizal parameters as an indicator of changes occurring during soil restoration and a tool for biomonitoring of soil quality has already been addressed by Lovera and Cuenca (1996), Haselwandter (1997) and Jacquot *et al.* (2000). Levels of colonization of grasses in polluted field soils have been shown to correlate with heavy metal contamination (Mikanova *et al.* 2001). Plants such as *Plantago lanceolata* might be of special value for biomonitoring (Orlowska *et al.* 2002). This species is strongly mycorrhhizal, suitable for use in growth chambers and greenhouses where it easily forms mycorrhizal associations and can be vegetatively propagated (Wu and

Antonovics, 1975), facilitating the avoidance of genetic variability in response to toxic susbstances. In addition it is widespread and tolerant to a broad range of soil types and pollutants (Wu and Antonovics, 1976; Baromi *et al*. 2000). The potential of VAM fungi to increased tolerance to adverse environmental conditions (e.g heavy metal pollutants) have been reported by Joner and Leyval (1987) and Cuenca and Lovera (1992). Increased tolerance to drought (Cuenca and Lovera, 1992), increased tolerance to salts (Joner and Leyval, 1996) and reduce transplant shock (Sylvia *et al*., 1993) were as well reported.

5. Strategic and Sustainable Management of VAM for Plant Growth

Sustainable management and production of VAM for plant growth is currently facing challenges such as high plastic response of roots to the edaphic environment, sustainable agronomic efficiency in a changing environment, linking greenhouse and field data, limited availability to use of VAM inocula and heterogeneous soil environment. Nevertheless field-based studies have shown increases in early growth and development of crops even in unsterilized soil when inoculated with effective VAM populations, particularly in the tropics e.g latin America. Dodd *et al*. (1990) and Sieverding (1991) performed over 50 field trials inoculating responsive cassava varieties with effective VAM in acid soils of varying fertility and obtained an average of a 20-25% increase in tuber yields (3 tonnes per hectare) a greater stability in production year-on-year. The usefulness of this approach was demonstrated for small farm holdings in Latin America, which comprise the majority of farms in these countries if not the biggest agricultural area.

The use of effective VAM populations to increase early growth and development of sorghum in an oxisol in Colombian savanna system when fertliser with rock phosphate. Other areas where inoculation would be the obvious management option include Horticulture where micropropagation is becoming more common to produce clonal outplanting material. *Postvitro* inoculation of seedlings would be desirable prior to outplanting in field or greenhouse since the plants can easily be raised with an effective mycorrhiza with minimum inoculums input. The benefit of reducing fertilizer inputs to optimize conditions for the VAM has been noted for strawberry where different VAM stimulated either increased stolon production or earlier flowering (Williams *et al*., 1992). This was done by using slow-release fertilizer sources. The expense, however, involved in inoculums production will only be justified, in today's economic climate, for high value agricultural or horticultural crops where there are extra benefits to better plant growth like improved plant fitness or tolerance of biotic or abiotic stresses.

The merits of maintaining high levels of both indigeneous inoculums and biodiversity of VAM, by adopting appropriate soil management practices over inoculation, has been debated in many recent reviews (Bethlenfalvay and Lindermann, 1992). In the growing season in the Colombian Llanos improved the subsequent growth of the forage and crop legumes *Stylosanthes capitata* and cowpea respectively compared with converted savanna. This was correlated with greater early colonization due to increased levels of VAM inoculums surviving the dry season and by populations of VAM different to that found in the direct savanna sown plots (Dodd *et al*., 1990a). There have been a few other novel approaches to the study and testing of methodologies to manipulate VAM in the field in recent times. The recent use of molecular probes, however, has enabled gene sequences of rDNA from root samples in natural and adjacent arable field in the United Kingdom (UK) to be compared. This showed that there was a marked decrease in sequence diversity detected in roots of crops compared with roots of plants in the natural ecosystems (Helgason *et al*., 1998). As further screening of the sequence diversity of VAM colonizing roots is correlated more precisely with those from specific species then it should become easier to identify those VAM functioning in different plants at any one time. The spinoff will be an ability to manipulate VAM for the production system once effective functional assemblages of VAM have been identified.

In natural ecosystems or low-tillage agriculture, young seedlings can germinate and effectively 'plug' into an already established 'motorway' of hyphae of VAM, which permeates the soil and links

different, plant species. The lack of host specificity is the secret to the success of VAM in mixed plant communities. The benefit to plants in natural plant communities is perhaps that less carbon from the plant photosynthate is needed by VAM following colonization since it is plugged into a pre-established mycelium. In contrast, crops in agricultural systems are frequently sown into tilled soil where this mycelium has been completely disrupted. There is a conflict of interest in the idea of maximizing plant production against an aim of maintaining a high biodiversity of VAM in soils. The latter maybe a necessity in natural ecosystems or restoration of degraded natural habitats but selection for efficient populations of VAM compatible with the aim of maximizing yield of certain crops may require a different management approach in ecosystems.

Graham *et al*. (1997) reported that modern agricultural practices, such as high levels of fertilizer and pesticide inputs and long-term monocultures, have proven adverse effects on the diversity of soil microbiota, which are at odds with the use of VAM. The answer may ultimately lie in the use of both intensive and extensive agro-systems alongside each other to provide both basic food requirements and supply an increasing market for sustainable-produced crops. It is becoming clear that sustainable production practices, e.g crop rotations with legumes, would benefit the survival of inoculums of VAM for subsequent mycorrhizal crops. One potential weakness is that both systems are using varieties (genotypes) of crops bred for high inputs. This is a selection process driven by conventional plant production, and the varieties may not be suitable for optimal production under organic or other sustainable systems. There are examples of where modern lines of plants in commercial production appear to be less susceptible to colonization by VAM as a result of breeding e.g wheat (Hetrick *et al*., 1992). Other work has shown that the inbred lines of *Zea mays* L. with resistance to fungal pathogens were less able to form mycorrhizas compared with disease susceptible lines (Toth *et al*., 1990). The relationship, however, between reduced colonization and nutrient uptake ability of VAM is uncertain and maybe uncoupled genetically. However, there is evidence for increased root fibrosity to compensate for the reduced role of VAM. These traits will operate fine under high input agricultural production, but can the same varieties produce high yields under reduced input systems? This may need a change in emphasis in plant breeding in the future to screen for optimal functioning of VAM under normal nutrient and environmental stresses if sustainable production is to become more widespread.

Conclusion

Harnessing natural biodiversity such as VAM is a biotechnological approach which counter balances the current negative image of genetically modified organisms in conventional production systems. Therefore, the benefits of the symbiosis for nutrient uptake by plants in restoration, management and sustainability in agro-ecosystem is very important but a more complete understanding of how to manage VAM for optimum plant growth and development is urgently needed.

Acknowledgement

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