REVIEW OF LITERATURE

Mycorrhiza, the symbiosis between roots of vascular plants and fungi, have existed since the Devonian period and might have been essential for the evolution of land plants (Pirozynski and Malloch, 1975). Research on VAM association from the initial comprehensive description (Gallaud, 1905) entered a lag phase, until workers in the 1950’s demonstrated convincingly that VAM could enhance plant growth (Nicolson, 1967). During this period research was confined to reports on the range of plants forming mycorrhizal associations and the taxonomic position of the symbiotic fungi. However, these observations established that these associations were widespread. Janse (1896) undertook the first broad scale survey in Java, showing that great majority of tropical plants formed mycorrhiza. Stahl (1900) first categorized plant families into obligately, facultatively and non-mycorrhizal Gallaud (1905) differentiated VAM from orchid and ericoid mycorrhizas and described that arbuscule and vesicle structures are essential for the further understanding of mycorrhizal relationship. It is practically impossible to review all the voluminous literature available with regard to various aspects of VAM, hence in this review considerations are on (i) ecology, (ii) taxonomy and (iii) VAM fungal benefits to the hosts.

I. ECOLOGY

A. Distribution of VAM

Mycorrhizal ecologists by the early 1980’s believed that plants and their mycorrhizal status are relatively well known. Brundrett (1991) reviewed the mycorrhizal status of VAM plants in natural ecosystems. Since then several studies have appeared widening the knowledge of VAM fungi and their distribution in natural ecosystems. Koske et al.(1992) and Gemma et al.(1992), respectively have reported the mycorrhizal status of Hawaiian
angiosperms and pteridophytes. Ueda et al. (1992) found VAM association in 26 of the 33 species of medicinal plants they examined. Cooke et al. (1993) reported VAM in salt marsh grasses (*Distichlis spicata, Spartina patens*) growing in saturated soils. Mycorrhizal association in vascular epiphytes has been reported from Ethiopia (Michelsen, 1993). Rickerl et al. (1994) examined 8 wet-land species for VAM association and concluded that several wet-land plants develop substantial mycorrhizal infection in dry environment. Meney et al. (1993) detected VAM for the first time in two species of Cyperaceae (*Lepidosperma gracile, Tetraria capillaris*) and Restionaceae (*Alexgeorgea nitens, Lyginia barbata*) from natural habitats in south-west western Australia. The earlier investigations of mycorrhizal status of Indian plants are given below.

**The occurrence of VA-mycorrhizas in natural ecosystems in India**

<table>
<thead>
<tr>
<th>Ecosystem type</th>
<th>Vegetation surveyed</th>
<th>n*</th>
<th>Proportion of species with (VAM) and without (NM) mycorrhizae</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Subtropical evergreen forest</td>
<td>Trees</td>
<td>14</td>
<td>100% VAM</td>
<td>Sharma et al. (1984)</td>
</tr>
<tr>
<td>Ecosystem type</td>
<td>Vegetation surveyed</td>
<td>n*</td>
<td>Proportion of species with (VAM) and without (NM) mycorrhizae</td>
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<td>4. Edaphic vegetation</td>
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<tr>
<td>a) Tropical plains</td>
<td>Pteridophytes</td>
<td>737</td>
<td>50% VAM, 50% NM</td>
<td>Ragupathy and Mahadevan (1993)</td>
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<tr>
<td></td>
<td>Angiosperms:</td>
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<tr>
<td></td>
<td>herbs, shrubs &amp; trees</td>
<td></td>
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<tr>
<td>c) Red sandy loam soils</td>
<td>Grasses</td>
<td>21</td>
<td>100% VAM</td>
<td>Ammani et al. (1994)</td>
</tr>
<tr>
<td>d) Dry saline soils</td>
<td>Herbs, shrubs &amp; trees</td>
<td>54</td>
<td>56% VAM, 44% NM</td>
<td>Kannan and Lakshminarasimhan (1988) Janardhanan et al. (1994)</td>
</tr>
<tr>
<td>e) Dune vegetation</td>
<td>Herbs &amp; shrubs</td>
<td>79</td>
<td>70% VAM, 30% NM</td>
<td>Mohan and Natarajan (1988) Mohankumar et al. (1988)</td>
</tr>
<tr>
<td>f) Wet coastal vegetation</td>
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<tr>
<td>(i) Salt marshes</td>
<td>Herbs</td>
<td>4</td>
<td>100% VAM</td>
<td>Sengupta and Chaudhri (1990)</td>
</tr>
<tr>
<td>(ii) Mangroves</td>
<td>Herbs</td>
<td>25</td>
<td>100% NM</td>
<td>Mohankumar and Mahadeven (1986)</td>
</tr>
<tr>
<td>wetlands</td>
<td></td>
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</tbody>
</table>

\( n^* = \) Total number of species examined.

However, as further ecosystem types are explored for VAM associations, surprises still appear (Allen, 1996). VAM association can also be found in unexpected plant groups and habitats. For example VAM has been found in aquatic trees (Khan, 1993), floating Typha mats (Stenlund and Charvat, 1994), parasitic plants (Palacios-Mayorga and Perez-Silva, 1993).
and in Proteaceae (Bellgard et al., 1994). Several workers have detected VAM infection in arboreal habitats (Janos, 1993), to a depth of 4 m in desert soils (Virginia et al., 1986) and 12-20 m in Amazonian forest soils (Nepstad et al., 1994) and in extreme environments like Antarctica (DeMars and Boerner, 1995) and deserts (Jacobson et al., 1993; Dhillion et al., 1995).

**B. Role of VAM association in natural ecosystems**

Mineral nutrients (especially P and N) appear to be the major constrain for plant growth in natural ecosystems (Brundrett, 1991). But plants have evolved strategies to ensure nutrient uptake and conservation through mycorrhization. Most plants in natural ecosystems are often less efficient in absorbing nutrients from soils than more opportunistic ruderal species which also have low nutritional requirements (Cardus, 1980; Chapin et al., 1986; Chapin, 1988). Plants in natural ecosystems are adapted to low nutrient levels and have less and slow growth rates which results in less demand for nutrients. These plants further conserve resources within long-lived shoot and root structures, efficiently reclaim minerals from senesceing tissues (Boerner, 1986; Chapin, 1988) and establish carefully regulated mycorrhizal associations (Brundrett and Kendrick 1990a).

Mycorrhizal infection occurs in seedlings germinating in natural plant community within a few days of radicle emergence (Read and Birch, 1988). A typical community of mycorrhizal plants is characterized by a high diversity of hosts, but a poverty of fungal species (Malloch et al., 1980). So different individuals of a species, ages or growth forms of plants are interconnected by one or more VAM fungi (Newman et al., 1992). This mycorrhizal hyphae networks could reduce plant nutrient competition and help subordinate species (such as seedlings shaded by canopy of mature plants) by interplant transfer of nutrient (Francis et al., 1986; Newman et al., 1992, 1994). Thus seedling of a given species is integrated into the enormous nutrient catchment
provided by the VAM fungal mycelium, facilitating their establishment. Further, Newman et al. (1992) demonstrated that nutrients could be transferred from dying roots to living plants through mycorrhizal links resulting in a preferential cycling of nutrients.

With the exception of extremely infertile parts, the natural climax communities of tropical biomes in warm climates are dominated by VAM plants (Brundrett, 1991). These include prairie (Miller, 1987), savannah (Newman et al., 1986), sub-tropical (Hogberg, 1986) and tropical (Janos, 1980a) forests. It is known that some species in nature fail to grow in the absence of VAM association and so are dependent on the association (Janos, 1980a). In some cases this is because of an ineffective coarse root system (Baylis, 1975). The presence of VAM propagules in most undisturbed natural ecosystems, ensure mycorrhization of these plants, thus facilitating the capture of nutrients and survivability of such species contributing to the maintenance of diversity (Read, 1993).

A few angiosperm families either rarely or do not form mycorrhizas. These include aquatic plants which normally grow in water-logged soils as well as halophytes (Tester et al., 1987). Mycotrophism is normally absent or rare in Cyperaceae and Juncaceae of monocots (Powell, 1975; Peat and Fitter, 1993). Among dicots Caryophyllaceae, Polygonaceae, Chenopodiaceae and Cruciferae usually lack mycorrhiza. In dicots, the loss of mycorrhiza is probably correlated with a weedy, herbaceous habit (Malloch et al., 1980).

Mycorrhizas increase the niche availability to a species. Perennial species that are normally or occasionally mycorrhizal occur in twice as many habitat types as infrequent perennials (Peat and Fitter, 1993). Under tropical conditions individuals of a given plant species are often widely spaced and infrequent. Plants in such a community belong to a continuum ranging from plants which consistently have mycorrhizas in almost all of their roots, to
those that never do. Miller (1987) have suggested that distribution of obligately mycorrhizal plants are likely to be where soil and nutrient levels are low and disturbance is minimal, while severe disturbance and high nutritional levels will favour non-mycorrhizal plants. In tropical (Janos 1980b) and deciduous (Rogers, 1982; Brundrett and Kendrick, 1988), forests and arid shrub/grass communities (Allen and Allen, 1984; Miller, 1987), the first colonizers of disturbance are often non-mycorrhizal or facultative species, while obligately mycorrhizal plants dominate over later stages. Annual species are often non-mycorrhizal (Trappe, 1987) possibly because they occur in disturbed habitats (Peat and Fitter, 1993). A small number of non-mycorrhizal species are able to persist in a mycorrhizal community, for example members of Cyperaceae. These species have a high degree of adaptability to spread by vegetative means (Francis and Read, 1994).

C. Factors influencing VAM fungi

a. Season: Seasonal changes in mycorrhizal infection and spore numbers have been recorded in deciduous forest (Brundrett and Kendrick, 1988; Mayer and Godoy, 1989; Brundrett and Abbott, 1994), grasslands (Gay et al., 1982; Sanders and Fitter, 1992a), salt marsh (Van Duin et al., 1990; Vardavakis, 1992; Lee and Koske, 1994a), tropical forests (Louis and Lim, 1987; Jha et al., 1992), arid and dry land (Allen, 1983; Meney et al., 1993) communities.

Large variations in VAM infection levels among seasons may occur because of rapid root growth or turnover of roots by plants during periods when soil moisture and temperature are favourable (Brundrett, 1991). Generally for plants with short-lived roots, the root length colonised by VAM fungi increase rapidly when roots grow and decrease when roots senesce (Land and Schonbeck, 1991). But these changes are gradual in many species
(especially perennial) because they have long-lived roots (Brundrett, 1991). The species with long-lived roots may function as keystone mutualist (Brundrett, 1991), benefiting all host plants by allowing VAM fungi to penetrate within them (Brundrett and Kendrick, 1990b).

Temporal variations in the periodicity of root growth and mycorrhizal activity occur in ecosystems which may be substantial enough to change the mycorrhizal status of plants (Brundrett, 1991). There were no significant variations in the mycorrhizal infection levels in the roots of many herbaceous plants in a deciduous forest community because only a fraction of their root systems were replaced each year (Brundrett and Kendrick 1988; 1990a). Seasonal changes in VAM activity are regulated by root phenology, since VAM associations are formed only in young roots and had a limited period of activity (Brundrett and Kendrick, 1990a). Mycorrhizal formation in the plants may be correlated with the environmental conditions prevailing, when plants produce new roots, as was observed in a temperate deciduous forest community (Brundrett and Kendrick, 1988). In this community, the root growth in most species was in summer (in warm soil) and were mycorrhizal, while those with root growth at spring or fall (in cold soils) had little or no mycorrhizas. Ietswaart et al. (1992) reported that VAM infection levels in three populations of Agrostis capillaris was lowest during winter and highest during summer and autumn. Similar observations were made by Mago and Mukerji (1994) in five species of Lamiaceae (Mentha viridis, Ocimum sanctum, O. basilicum, Salvia officinalis, Coleus variegatus).

Seasonal fluctuations in VAM spore numbers have been attributed to germination activities (Gemma and Koske, 1988a) soil micro- and macrofaunal activities (Rabatin and Stinner, 1988; McGee and Baczocha, 1994) and destruction of VAM spores by soil fungi and other parasites (Ross and Rottencutter, 1977; Lee and Koske, 1994b). The variations in VAM fungal
spores to initiate mycorrhization may also contribute to seasonal changes, as newly formed spores require a period of dormancy (Tommerup, 1983a; Gemma and Koske, 1988b). The spore numbers generally decline during periods of mycorrhizal formation and increases during periods of root senescence (Brundrett, 1991). Peak sporulation coincides with periods of fungal resource re-mobilization from senescenting roots (Gemma et al., 1989). This is supported by the observations where spore numbers are greatest when root activity is interrupted either by long dry season or at harvest in agricultural systems (Janos, 1980 b).

b. Climatic factors

(i) Rainfall and relative humidity: Very few ecological studies on VAM provide the effect of climatic factors on VAM fungi. Michelini et al. (1993) found significant relationship between VAM fungal infection and rainfall in Citrus. A reduction in the intensity and percentage of VAM fungal infection in three species of savannah grasses during dry season was noted by Newman et al. (1986) in Kenya. A similar drop in the infection levels of sugarcane was found in Barbados during the dry season (Chinnery et al., 1987). Braunberger et al. (1994) found that ‘false break’ (rain during summer) decreased mycorrhizal colonisation and proportion of root length colonised by VAM structures. Udayan et al. (1996) reported a positive relation between VAM fungal spore numbers and relative humidity in Acacia farnesiana, but a negative relationship in A. planiforms.

(ii) Light: Redhead (1975) postulated that day length may have an important role in VAM development which has been confirmed by other studies. Mycorrhizal development is greatly affected by light received by the shoot of the host plant. Low irradiation, short day length or shading can reduce the development of VAM. Reduced VAM colonisation under low light
Intensities has been reported in alfalfa (Daft and El-Giahmi, 1978), soybean (Bethlenfalvay and Pacovsky, 1983; Reinhard et al., 1994), clover (Tester et al., 1985) and onion (Pearson et al., 1991). Trent et al. (1988) found that grazing of winter wheat in the autumn appreciably decreased root length colonised per unit volume of soil. Daft and El-Giahmi (1978) demonstrated a marked reduction in VAM formation when pot grown grasses were defoliated. Under low photon irradiance, a decrease in growth of mycorrhizal plants may result (Bethlenfalvay et al., 1987, Smith and Gianinazizzi-Pearson, 1988), which has been ascribed to the carbon drain by the fungus. Development of arbuscules, the site of nutrient transport between the host and the fungus is affected by irradiance (Graham et al., 1982). In addition, Tester et al. (1986) observed that at early stages of mycorrhizal infection in Trifolium subterraneum, the number of entry points were reduced at low photon irradiance; however, no such reduction was noted by Smith and Gianinazizzi-Pearson (1990) in onion.

**(ii)** **Temperature**: Temperature has been shown to significantly influence VAM fungal colonisation and sporulation both under field and greenhouse conditions. High temperature generally results in greater colonisation and sporulation (Furlan and Fortin, 1973). Increased temperature decrease the lag phase of colonisation and Jarstfer and Sylvia (1993) noted decreased sporulation under high temperatures. Schenck and Schroder (1974) observed maximum arbuscule development in soybean near 30°C, but mycelial colonisation was greater between 28-34°C. Daniels and Trappe (1980) observed that the optimum temperature for germination of Glomus and Acaulospora species were around 20-25°C, whereas, Gigaspora had much higher optima. These studies indicate that increased soil temperature fastens the development of VAM.
The temperature effect may explain the slow development of infection in temperate soils (Black and Tinker, 1979) where soil temperatures are low compared to tropical soils. Since many species of VAM fungi are world-wide in distribution, it is possible that strains and species may be temperature adapted. Schenck et al. (1975) found that two isolates of *Gl. mosseae* from Florida germinated best at 34°C, whereas one from Washington had an optimum of 20°C. McGee et al. (1987) has shown that propagules of some isolates of VAM fungi can survive in dry soil temperatures up to 70°C and subsequently infect roots of ephemeral plants following rain.

Many studies have shown that isolates may differ in their optimum temperature, for germination, root colonisation and spore production (Graham et al., 1982; Tommerup, 1983b). Further, a single isolate may also exhibit different temperature optima for root colonisation and spore production (Schenck and Smith, 1982a). Nemec (1987) demonstrated that although an 1 hour treatment at 43°C and above reduced the infective ability of *Gl.intraradices* spores, the spores became completely non-viable only at temperatures of 60°C and above. Though, there have been a number of studies on the effect of temperature on the mycorrhizal formation (Furlan and Fortin, 1973; Hayman, 1974; Smith and Bowen, 1979), only a few have considered temperatures of 30°C and above. Smith and Roncadori (1986) showed that although optimum root growth response in cotton occurred at 30°C maximum root colonisation occurred at 36°C indicating a complex interactions between survival and germination of propagules and plant process such as root growth. Haugen and Smith (1992) demonstrated that *Gl.intraradices* infected cashew and mungbean at 30°C compared to 22°C or 38°C. Saito and Kato (1994) reported that the root length infected by soybean was little affected by low temperatures.
c. Edaphic factors

(i) Water: VAM colonisation has been found in plants over a wide range of soil water content like in xerophytes of arid regions (Khan, 1974; Mukerji and Kapoor, 1986), wet soils of marshes (Chaubal et al., 1982; Ragupathy et al., 1990; Rickerl et al., 1994), free floating (Bagyaraj et al., 1979) and submerged (Clayton and Bagyaraj, 1984) aquatic plants. Water-logging may inhibit mycorrhizal formation through lack of aeration as oxygen is necessary for fungal growth (Crawford, 1992). Further, under these conditions a complex array of toxic substances like H$_2$S, reduced Mn and organic acids are liberated, which may further inhibit VAM fungal spore germination and hyphal growth (Khalil et al., 1992). But, Le Tacon et al. (1983) observed that VAM fungal spore germination was little affected by oxygen tension until it was below 3 per cent.

Anderson et al. (1984) and Ebbers et al. (1987) reported changes in predominance of VAM fungal species across a soil moisture gradient site, which had a much greater influence on plant populations. In addition a correlation between water content and spore numbers existed across a natural soil moisture gradient in the field (Anderson et al., 1984). Khalil and Loynachan (1994) reported a higher VAM fungal spore populations in poorly drained soils compared to well-drained and moderately drained soils. Water has been shown to affect VAM fungal sporulation. However, little information is available on water availability and VAM fungal sporulation relationship, especially under field conditions. Non-saturated and non-stressed water conditions are best for spore production both in high- and low-P conditions (Nelsen and Safir, 1982). Evidences from aeroponic and hydroponic cultures have demonstrated the benefits of a well watered and aerated rhizosphere for the production of several Glomus spp. (Sylvia and Hubbell, 1986). Water activity was found to be the important determinant of VAM fungal spore...
germination in vitro (Douds and Schenck, 1991). Saif et al. (1975) reported that Gigaspora spp. were only prevalent in soils that remained at ca. 50-60 per cent water holding capacity.

In natural ecosystems rain may stimulate germination of indigenous mycorrhizal fungi (Wilson, 1984). In regions characterized by hot dry summer and cool winter growing season plants die during summer and re-establish with onset of winter rains. However rains during summer results in a decrease of mycorrhizal propagules (Braunberger et al., 1994). The infectivity of germinated spores tend to decrease after a storage in dry soil (Tommerup, 1984; Muginer and Mosse, 1987; Douds and Schenck, 1991). Tommerup (1987) indicated that spores of VAM fungi can probably survive for at least 20 years in dry soils, but only for 2 years in moist soils. Similarly, mycorrhizal roots remained viable for 6 months when stored in dry conditions (Tommerup and Abbott, 1981) but lost viability in moist soils (Tommerup, 1983a). Spores of Scutellospora spp. collected from semi arid soils were not infective after a wetting and drying cycle (McGee, 1989). In perennial ecosystems with seasonally dry climates, the loss of infectivity has been reported during dry season. In contrast, the extraradical mycelia of Scu.calospora (Jasper et al., 1993) and hyphae in dried root fragments are reported to remain infective through summer (Tommerup and Abbott, 1981) and initiate activity during a false break. The soils of south-western Australia are known to dry to an equivalent metric potential in excess of -35 MPa and these dry conditions may last for 6 months before the next rain commences (Jasper et al., 1989a). McGee et al. (1987) observed the survival of VAM propagules in an Australian soil reaching 70°C during summer Jasper et al. (1989a) demonstrated that the external hyphae of A.laevis remained highly infective in soils which had a metric potential of -21 MPa. Jha et al. (1992) reported a positive relation between soil moisture and root infection levels but a negative relationship
between soil moisture and spore numbers. Al-Agely and Reeves (1995) reported a negative relation between soil moisture content and mycorrhizal inoculum potential in a sand dune ecosystem.

(ii) pH: The importance of soil pH has been felt and studied by several authors, but these authors have dealt the effect of pH as one of the factors in a wider study (Abbott and Robson, 1991). Studies on soil pH can be subdivided into effects on spore germinations (Daniels and Trappe, 1980), spore production (Kruckelmann, 1975; Read et al., 1976) and effects on plant growth and nutrients uptake (Lambert and Cole, 1980). It is difficult to evaluate the effect of pH under field conditions since many chemical properties of the soil vary with changes in pH. In spite of the fact that no general correlation has been found between soil pH and VAM fungi, it is well known that soil pHs favour particular VAM fungal species. Natural soils of the world cover a pH range of 2.8 to >10 (Bass Becking et al., 1960). Spores of Gl.mosseae and Gl.margarita have not been found in soils with pH <5.5 and Entrophospora colombiana have not been found in natural soils with pH >5.5 (Mosse, 1972; 1973a; Sieverding, 1989). In contrast species like A.scrobiculata, A.morrowiae, A.spinosa, A.myriocarpa, Gl.aggregateum and Scu.persica were observed over a wide range of soil pH 3.8-8.0 (Sieverding, 1989).

Daft et al. (1975) reported considerable VAM infection in plants growing in a mine spoil of pH 2. Sparling and Tinker (1978) found no obvious effect of pH on mycorrhizal infection in three grassland sites at pH 4.9, 5.9 and 6.2. Previous studies indicate some evidence for differences in adaptation of strains and species of VAM fungi to soil pH. Lambert and Cole (1980) reported that an isolate of Gi.gigantea failed to infect at low pH and six isolates of Gl.tenue differed in their ability to form mycorrhizas at low pH. One report (Janardhanan et al., 1994) in literature exists on the occurrence of typical
VAM at alkaline pH extreme (10.5) which occurs in natural soils of saline regions where upward movement of water precipitate mineral salts.

Peat and Fitter (1993) indicated that mycorrhizal dependent plant species occur at higher maximum pHs than infrequently mycorrhizal species. This reflects availability of plant nutrients: P, Fe, Mn, Zn, Cu and Co availabilities are reduced in soils with a high soil pH (Brady, 1990). Typically mycorrhizal plant species, therefore, might be at an advantage over rarely mycorrhizal species in such habitats. Alternatively VAM fungi might offer protection against toxicities in high pH soils, possibly from elements such as Mo.

Laboratory studies indicate a good germination of VAM spore requires a pH range of 6 to 7, although there are cases of germinating at pH 5 and below as well as at pH 8 and above (Siqueira et al., 1982). The pH optima for spore germination may probably differ with each VAM species and to environments to which each is indigenous. For example Gl. mosseae common in alkaline soils (Gerdemann and Trappe, 1974) germinated well on water or soil extract agar at pH 6 to 9. Similarly Gi. coralloidea (=Scu.coralloidea) and Gi. heterogama (=Scu. heterogama) from more acidic Florida soils germinated best at pH 4 to 6 (Green et al., 1976). The distribution of fine endophyte to pH 4.5 and coarse endophyte at pH 7.5 has been reported by Wang et al. (1985, 1993). It has been established that spore germination is pH sensitive, but different species have very different pH optima (Robson and Abbott, 1989). Greater than 40 per cent germination of Gl. epigaeum spores was found over a pH range of 4.8 to 8, the optimum being 7 (Daniels and Trappe, 1980). The effect of soil acidity on VAM fungi is almost exclusively due to metals such as Al, Fe and Mn in soil solution (Russel, 1973; Robson and Abbott, 1989). Hepper and Smith (1976) showed that VAM fungal spore germination on agar is sensitive to metals such as Mn, Cu and Zn, whose activities in soil solution is dependent of pH.
(iii) **Nutrients**: Phosphorus: A little quantitative relationship exists between the extent of mycorrhizal colonisation and the concentrations of soil P. Sites with large amounts of soil P may have high levels of infection and/or large spore numbers. In contrast sites with small amount of P may have low levels of infection or spore numbers (Hayman, 1978; Gianinazzi-Person et al., 1980; Jeffries et al., 1988). Positive (Jha et al., 1992; Udaian et al., 1996) and negative (Bolgiano et al., 1983; Boerner, 1986; Morita and Konishi, 1989) relations have been found between the amount of extractable soil P and VAM fungal infection.

Application of P to the soil often adversely affect root colonisation by VAM fungi through inhibition of spore germination (Miranda and Harris 1994), depressing the development of arbuscules, vesicles, internal and external hyphae and penetration points (Menge et al., 1978; Schwab et al., 1983a; Abbott et al., 1984; Thompson et al., 1986; Miranda and Harris, 1994; Suriyapperuma and Koske, 1995) and sporulation (Menge et al., 1978; Nelsen et al., 1981). However, VAM fungi vary in their sensitivity to soil P (Trouvelot et al., 1987; Lamar and Davey, 1988). Sanders (1975) proposed two possibilities to explain these inhibitions i.e., either soil P may have a direct inhibitory effect on external hyphal growth or there may be an indirect effect associated with the P status of the plants.

Plant tissue P has often been considered as an important factor for controlling VAM infection (Menge et al., 1978; Sylvia and Neal, 1990) and others have extended this conclusion to changes in root membrane permeability and to the availability and quantity of root exudates (Ratnayake et al., 1978; Graham et al., 1981; Schwab et al., 1983b; Thomson et al., 1986). Bolan et al. (1984), however reported that increasing soil P gradually from a severely deficient condition could increase mycorrhizal infection, before the expected decrease occurred as soil P became sufficient. This increase in VAM
infection due to small amounts of P application suggests that mycorrhization may to certain extent depend on soil P and not totally on plant P (Graham et al., 1981). Sanders and Fitter (1992b), however, have found no relationship between plant P and VAM infection in grassland species. Johnson et al. (1991) found that the negative relation between VAM infectivity and total P became insignificant when P was held constant and suggested that soil pH and P interact in their effect on mycorrhization. Mycorrhizal infection and VAM structures had a significant negative relationship with soil P in cut grassland following long term slurry application (Christie and Kilpatrick, 1992). However, Sylvia and Neal (1990) reported that root colonisation by VAM fungi was not affected when plants were deficient in N, but when N was sufficient P addition suppressed root colonisation. But the response of VAM fungal infection and spore numbers to soil P can vary with host species (Muthukumar et al., 1994b).

Nitrogen: In many ecosystems nitrogen limits plant growth and plants require large amounts of this nutrient for their growth (Azcon, 1994). There have been a few studies on the effects of N on VAM fungi compared to P. Studies indicate that N suppresses root colonisation (Mosse and Phillips, 1971; Menge, 1984). Hepper (1983) demonstrated that increased application of NO$_3^-$ increased the levels of root colonisation in lettuce. In contrast, Chambers et al. (1980) reported that both NH$_4^+$ and NO$_3^-$ depressed VAM formation and suggested the effect to a drop in rhizosphere pH. Thompson (1986) found that pH modifications by nitrogen sources influenced mycorrhization. Azizah and Habte (1989) found that root colonisation of Leucaena by Gl. aggregatum was enhanced by NH$_4$NO$_3$ application. Sylvia and Neal (1990) suggested that plant N-stress, like P-stress promotes mycorrhization. Although N-deficiency can reduce the exudation of amino-acids (Bowen, 1969; Russell, 1979), this may not significantly influence mycorrhizal formation and needs further
examinations. In addition these authors observed that increasing soil P did not suppress VAM colonisation in N deficient plants, but P addition suppressed colonisation in N sufficient plants (Sylvia and Neal, 1990). Jha et al. (1992) found that soil N was positively related to VAM infection and negatively to spore numbers. Like P, the effect of soil-N on VAM fungal colonisation and spore numbers can vary with plant species (Muthukumar et al., 1994b; Udaiyan et al., 1996).

Other nutrients: The role of other nutrients on root colonisation and spore abundance of VAM fungi is little known compared to P and N. Potassium (K) has been reported to have no effect on VAM fungi (Daniels and Trappe, 1980). But Ebbers et al. (1987) reported significantly positive correlation between spore abundance and available soil K in priaire drop seed (Sporobolus heterolepis). Zahka et al. (1995) indicated that concentrations of soil K was a key predictor for variations observed in colonisation levels and for the occurrence of arbuscules in the root cortical cells. Micronutrients like Cu, Zn and Mn are reported to inhibit VAM fungi at concentrations under in vitro conditions (Hepper, 1979; Gildon and Tinker, 1983). Christie and kilpatrick (1992) found a negative relation between soil Zn concentration and VAM fungal infection levels and suggested a combined effect of Zn-pH leading to this inhibition. In contrast, McIlveen and Cole (1978), reported the stimulatory effect of Zn on spore germination at low concentrations. Sreenivasa and Bagyaraj (1988) reported that the sub-optimal levels of Zn, Cu and Mn could enhance root colonisation and sporulation of Gl. fasiculatum associated with Rhodes grass (Chloris gayana).

(iv) Organic matter: Soil organic matter has been reported to influence VAM fungi. Read (1991) related changes in vegetation and mycorrhizas on both altitudinal and latitudinal gradient to soil organic matter. His scheme shows that as one progress from tropical to temperate regions, one moves
from soils which are mainly inorganic (due to rapid decomposition and rapid nutrient cycling), through soils of increasing organic matter (due to low decomposition rates). Vegetation changes from herbaceous through deciduous, mixed and coniferous forests to ericaceous vegetation. Similarly mycorrhizal types changes from VA mycorrhiza through ecto- to ericaceous mycorrhizas.

There are relatively few data to support the speculation that organic matter added to the soil encourages mycorrhizal development (Hayman, 1987; Abbott and Robson, 1991). The abundance of *Glomus* spores in organic matter fragments has been noted in sand dunes of Scotland (Nicolson, 1959) and near Lake Huron (Koske *et al.*, 1975). The extensive proliferation of VAM fungal hyphae in association with organic matter suggest that chemical exudates released from organic matter may stimulate mycorrhization (Hepper and Warner, 1983; St. John *et al.*, 1983). VAM colonisation levels are higher in organic farms compared to conventional farms (Lengnick and King, 1986; Bokhorst, 1989; Werner *et al.*, 1990; Ryan *et al.*, 1994). Harinikumar and Bagyaraj (1988) reported varied response of VAM fungi to different organic matter amendments at similar rates. These authors further noted an enhanced VAM infection and propagule levels in maize and soybean cultivated in maize straw or *Pongamia* leaf, but not in paddy straw amended soils.

As the addition of fresh organic matter at appropriate amounts to acid soils protect VAM symbiosis and plants sensitive to Al-toxicity (Soedarjo and Habte, 1993), higher amounts could decrease VAM fungal effectiveness and benefits (Brechelt, 1987; 1989). Similarly Christie and Kilpatrick (1992) reported a marked decrease in VAM infection with increased application of both pig and cow slurries. A study by Joner and Jackobsen (1995) with $^{32}$P labelled organic matter indicated that mycorrhizal plants utilized P from organic matter more efficiently than non-mycorrhizal plants. Veeraswamy
et al. (1993) reported that soil amendment with both straw and urea enhanced VAM root colonisation to greater extent than their individual amendments.

Soil types tend to influence the effect of organic manures on VAM fungi. Application of farmyard manure (FYM) at the rate of 0.5 to 1.0% (W/W) to a vertisol had no effect on VAM infection levels in sorghum, chickpea, pigeon pea, sunflower, safflower, pearls millet and green gram both under greenhouse and field conditions (Wani and Lee, 1995). But Harinikumar and Bagyaraj (1989) reported increased mycorrhization of crops in response to FYM application in a red sandy loam oxisol. Kruckelmann (1975) found that the decrease in VAM fungal spore numbers in response to FYM was more pronounced in loamy sand soil compared to silty clay loam.

Other agronomic practices like mulching and crop rotation are known to influence VAM fungal-organic matter interactions. Studies at an alfisol site in ICRISAT have shown that mulching with paddy straw or FYM in minimum tilled or deep tilled plots had no effect on VAM fungal spore populations (Wani and Lee, 1995). In contrast mulching of sandy soils with barely straw increased VAM fungal spore numbers by 2.4 times (Lee and Wani, 1991). However, Jockobsen and Jensen (1981) reported a reduction in VAM fungal infection and plant growth due to mulching with barley straw. Nappi et al. (1980) observed a significant reduction in VAM fungal spore densities in all layers of surface mulched soils than in weeded soils, since the amount of organic matter are likely to be greater in mulched than in weeded soils. Baltruschat and Dehne (1988) observed that the inhibitory effect of green manures on VAM fungal inoculum potential was more pronounced in continuous monoculture than in crop rotation.

d. Biological factors

(i) Host plant: The presence of a host plant is a prerequisite for VAM
fungal colonisation and subsequent sporulation. Members of non-mycorrhizal families such as Chenopodiaceae, Cruciferae (Jagpal and Mukerji, 1988) and Amaranthaceae (Neeraj et al., 1991), became minimally colonised by VAM fungi, particularly when grown in the presence of a host plant (Ocampo et al., 1980). The results on the influence of non-host plants on the infection levels of mycorrhizal plants are contradictory. The presence of non-mycorrhizal plants reduced infection in mycorrhizal plants (Iqbal and Qureshi, 1976) possibly because of toxic non-host exudates (Glenn, 1982). Ocampo et al. (1980) in contrast detected an enhanced levels of infection in the mycorrhizal host plant when grown in the presence of non-mycorrhizal plants. The proliferation of VAM hyphae on the root surfaces of non host species (Ocampo et al., 1980) suggest that the non-host roots does not release any toxic factors in the surrounding soil. The passive colonisation of non-mycorrhizal hosts by VAM fungi (Giovannetti et al., 1994) increase the survivability of VAM fungi in the absence of host roots.

Although VAM fungi have an extremely wide host range, the existence of host preference has been suggested by many researchers (Mosse, 1975; Bagyaraj et al., 1988; Tewari et al., 1993). Recent investigations suggest that mycorrhizal status could be treated as a genetic trait (Krishna et al., 1985; Mercy et al., 1990). Allen et al. (1989) reported the adverse effects of VAM fungus on the non-host Salsola kali (Chenopodiaceae) which were seen in the form of localised lesions on the roots around aborted points. Sanders and Koide (1994) reported that mycorrhizal fungi reduced the growth of non-mycorrhizal Amaranthus retroflexus. In addition ineffective VAM associations have been discovered in a few host VAM fungal combinations under experimental and field conditions (Johnson, 1977; Giovannetti and Hepper, 1985; Hendrix, 1993).

*Root Characters:* Mycorrhizal development occurs in primary root
tissues prior to suberization (Wilcox, 1990). Considerable variation exists between plant species in the degree of root system architecture, changes that occur in response to the nutrients and water contents of the soil. But such variations occurring within species are small compared to variations in root systems between species (Grime et al., 1986; Fitter, 1987; Crick and Grime, 1987). VAM infection in woody plants appear to occur over longer axial increments of root growth. However, little definite information is available on VA mycorrhizal development in relation to architecture and seasonal activity of woody plants.

In herbaceous species, VAM infection occurs and functions over a considerable portion of the total root length. Infected lengths of individual root axes are built up of discrete "infection units", which may not overlap longitudinally (Cox and Sanders, 1974). The expansion and senescence of infection units is co-ordinated with senescence of root axes, and in annual plants the mutualistic association terminates with the life cycle of the plants. In herbaceous perennials, infection may remain systemic in older root systems (Wilcox, 1990). Koide et al. (1988) noted that wild oats had root systems that is more responsive to soil nutrient levels than cultivated oats which received more benefit from mycorrhizas. Extensive or highly active root systems alone may not ensure adequate mineral uptake by plants. Fohse et al. (1988) observed that onion, tomato and bean plants (mycorrhizal dependent) had substantially lower P uptake efficiency per unit root length than rape or spinach (non-mycorrhizal species). Van Ray and Van Diest (1979) found that the non-mycorrhizal buckwheat (Fagopyrum esculentum) (Harley and Harley, 1987), was able to obtain P from sources that were unavailable to other species. Mycorrhizal fungal hyphae primarily function by increasing the soil volume from which immobile nutrients are absorbed and provided to roots (Harley and Smith, 1983). Furthermore fungal hyphal maintenance would be
approximately 100 times less expensive compared to root formation and their maintenance (Harley, 1989).

Carbohydrates: Bjorkman (1942) first proposed that carbohydrates in roots was the controlling factor in ectomycorrhizal formation. This hypothesis has been tested and developed by others (Hacskaylo, 1985; Nylund, 1988) for endomycorrhizal system. Two separate considerations embracing Bjorkman’s hypothesis were pointed out by Lewis (1975). First, there might have been initial causal relationship between carbohydrates concentration and infection and secondly, the infection might influence the carbohydrates concentration in the infected tissues once its has been established.

Two relevant theories exists on the role of carbohydrates on mycorrhizal formation. According to the first theory, the relation between VAM infection and concentration of carbohydrates in roots are casual (Jasper et al., 1979; Same et al., 1983; Thomson et al., 1986). Phosphorus applied to the soil has been shown to influence the soluble carbohydrates concentrations within roots (Same et al., 1983; Thomson et al., 1986). The application of small quantities of P to soils deficient in P has been shown to increase the soluble carbohydrates concentrations within roots (Same et al., 1983; Amijee et al., 1990), while further addition of P have shown to reduce soluble carbohydrate concentrations of subterranean clover roots (Same et al., 1983; Thomson et al., 1991). The second theory indicates that the exudation of carbohydrates from roots is an important variable, as relationships were found between the rate of exudation and percentage of mycorrhizal colonisation (Ratnayake et al., 1978; Graham et al., 1981, 1982; Ferguson and Menge, 1982; Johnson et al., 1982). A negative relationship between root colonisation and concentrations of soluble carbohydrates has been reported in *Trifolium subterraneum* (Pearson and Schweiger, 1993; Pearson
et al., 1994). Pearson et al. (1994) indicated that root carbohydrates directly influence the competition between VAM fungal species within roots. Douds and Schenck (1990) found that soluble carbohydrates concentration of *Paspalum notatum* roots were related to mycorrhizal root infection levels and sporulation for isolates of *A. longula* and *Gi. margarita* but not for *Gl. intraradices*.

**(ii) Other soil microorganisms:** Among the various microorganisms inhabiting the rhizosphere, VAM fungi occupy a unique ecological position, as they are partly inside and partly outside the host. The extra-radical mycelia in the "bulk soil" enters into association with the biotic components of the soil. The site where the interactions between VAM fungi and soil biota takes place has been called the "mycorrhizosphere" (Linderman, 1988). The general soil microflora may have a significant influence on mycorrhization. Sutton and Sheppard (1976) showed that non-sterile soil filtrate added to the pasteurized soil increased the extramatrical hyphae of VAM fungi in some undetermined manner. St. John et al. (1983) showed that VAM formation was stimulated by volatile compounds produced by soil microflora. Meyer and Linderman (1986) reported a qualitative change in the mycorrhizosphere. Bagyaraj and Menge (1978) showed an increase in rhizosphere populations of bacteria and actinomycetes when plants were inoculated with mycorrhiza.

VAM fungal spores are highly vulnerable to parasitism from other soil organisms principally chytridiaceous fungi (Sylvia and Schenck, 1983; Paultz and Menge, 1986) and Vampyrellid amoebae (Boyetchko and Tewari, 1991). Ross and Ruttencutter (1977) suggested that parasites of VAM fungi play an important role in regulating mycorrhizal spore populations. Germination of VAM fungal spores could be inhibited in natural soils by antagonistic microflora (Linderman, 1988). However some rhizosphere and spore-associated bacteria and their culture filtrates are known to enhance
mycorrhizal formation (Azcon-Aguilar et al., 1986; Mayo et al., 1986; Linderman and Paulitz, 1990). Tylka et al. (1991) suggested that specific interactions between Streptomyces spp., and VAM fungi can occur as the former had varied effect on the germination of VAM fungal spores. Azcon (1989) has shown the selective influence of rhizosphere bacteria on mycorrhizal formation by different Glomus species. Bacteria such as fluorescent Pseudomonas proliferate in the hyphosphere of the mycorrhizal fungi (Klyuchnikov and Kozhevin, 1990).

Though the results of Tarafdar and Marschner (1995) indicate that the presence of Aspergillus fumigatus increased VAM fungal colonisation, other studies (Clavet et al., 1992; 1993) indicate the detrimental effect of A. fumigatus on VAM mycelium. McAllister et al. (1995) demonstrated that A. niger inhibited spore germination and hyphal growth of Gl. mosseae. Campurbi et al. (1995) reported that Tricoderma aureoviride did not affect the mycorrhizal development in Citrus reshni. Calvet et al. (1992) reported the stimulatory effect of T. aureoviride on Gl. mosseae. The results of research on the interactions between saprophytic fungi and VAM fungi differ widely when some genus is involved. For example Trichoderma spp., have been found to have both antagonistic (Chu and Wu, 1981; Cook and Baker, 1983; Camporota, 1985; Wyss et al., 1992) and stimulatory (Calvet et al., 1992; 1993), effects on VAM fungi. Mc Allister et al., (1994) reported a reduction in the populations of T. koningii and Fusarium solani in the rhizosphere of mycorrhizal maize and lettuce and attributed the effect to modification of root exudates.

The soil VAM fungal mycelia and spores are vulnerable to grazing by soil fauna (Fitter and Sanders, 1992). Soil animals are known to graze mycorrhizal mycelium and hyphal fragments and spores have been identified in gut contents (Warnock et al., 1982; Rothwell and Victor, 1984). Grazing
may either limit the development of external mycelium or severe the internal mycelium by grazing in the rhizosphere on entry points (Fitter and Sanders, 1992). Nematodes within roots physically disrupt tissues and so impede the spread of VAM mycelium (OBannon and Nemec, 1979). VAM fungi are also known to impart resistance in the host to nematodes infestation (Schonbeck, 1979; Muchovej et al., 1991). *Rhizobium* (and *Bradyrhizobium*) and *Frankia* associated plants are normally mycorrhizal (Fitter and Garbaye, 1994). VAM fungi markedly improve nodulation and N-fixation mainly by satisfying the high P requirement for N fixation process. Similarly free living N-fixer *Azospirillum* is also known to enhance mycorrhizal formation (Pacovsky et al., 1985).

II. TAXONOMY

Taxonomy of Glomalean fungi is less than 30 years old, starting with the formal Linnaean classification by Gerdemann and Trappe (1974). Approximately 150 species (Schenck and Perez, 1990) have been described based on morphological features of spores. More than 65 of these had been described by 1983; but taxonomy concepts of them have advanced (Walker, 1983; Morton, 1987) and only a few have been redescribed using modern concepts and terminologies (Koske and Walker, 1985; Walker and Koske, 1987). Subsequently the matching of new collections with old descriptions has led to innumerable difficulties in their identification. Additionally many species (42%) of the described Glomalean fungi have never been proved mycorrhizal (Morton, 1990).

A. Morphology of VAM fungi

The most important taxonomical parameters of Glomales can be summerized as follows:
a. **Sporocarp occurrence, shape, colour and size**: Sporocarp phenotype is highly variable and great variations exist within the same genus. For example in *Glomus* it varies from single spores evolved in a hyphal mantle (*Gl. coronatum* Giovannetti) to clusters of disorderly aggregated spores (*Gl. aggregatum* Schenck & Smith emend. Koske) or true sporocarps with [*Gl. mosseae* (Nicol. & Gerd.) Gerd. & Trappe] or without (*Gl. epigaeum* Daniels & Trappe) a peridium.

b. **Peridium occurrence and characteristics**: Peridial characters are of great significance in the genus *Sclerocystis* where species known till now in this genus are strictly sporocarpic.

c. **Spore colour, size and shape**: Spore colour varies from hyaline through white to yellow, red, brown and black with all intermediate shades. Spore size is also variable even within same species and can range from <20 μm (*G. tenue* (Greenhall) Hall) to >800 μm (*Gi. gigantea*) (Nicol. & Gerd.) Gerd. & Trappe) between different genera. In contrast spore shape vary very little from globose to subglobose, elliptical or pear-like, but sometimes peculiar shapes can be observed as the result of physical constrains during spore development.

d. **Spore wall number, colour, thickness and ornamentation**: Number, size, structure and ornamentation of spore walls vary considerably between species of the same genus. These wall features have assumed a major role in recent descriptions and their importance has been emphasized by many workers (Walker, 1983; Morton, 1988).

e. **Hyphal attachment, shape and type of occlusion**: The shape of subtending hyphae is also a character which is quite stable within each species (eg. *Gl. constrictum* Trappe, *Gl. mosseae*), but the mode of occlusion may vary probably depending on the age of the spores.
The order Endogonales formalised by Benjamin (1979) had a single family Endogonaceae, containing the zygosporic *Endogone* as well as the VAM fungi and the other genera *scleragone*. The placement of VAM fungi along with *Endogone* in the zygomycetes appears to result from historical precedent, superficial similarity of morphology and occasional involvement of both *Endogone* and *Glomus* in ectomycorrhizal symbiosis (Warcup, 1985). Pirozynski and Dalpe (1989) separated *Glomus* and *Sclerocystis* into a separate family Glomaceae on the geological appearance of these two genera. Morton and Benny (1990) delimited the order Glomales which encompass only fungi either known or assumed to form mycorrhizal association with plants. The order Glomales consist of two new suborders Glomineae (Families: Acaulosporaceae and Glomaceae) and Gigasporineae (Family : Gigasporaceae). The fungi in the suborder Gigasporineae forms only arbuscules within roots (Walker, 1992). At present there are 6 genera included in Glomales which are clearly defined and easy to separate (Walker, 1987). These are *Glomus*, *Sclerocystis* (Glomaceae), *Acaulospora Entrophospora* (Acaulosporaceae), *Gigaspora* and *Scutellospora* (Gigasporaceae).

**B. Problems in Glomalean Taxonomy**

Spores are the most retrievable part of the fungal organism, because each can be manipulated as discrete objects. Most taxa described in the first classification were sporocarpic (Gerdemann and Trappe, 1974), because they were more easily detected in soil sievings. As additional procedures were introduced (Daniels and Skipper, 1982), more non-sporocarpic species were discovered. The presence of spore propagules in field soil sample is unpredictable even when most plants are mycorrhizal (McGee, 1989). Modifications of collection procedures are often necessary when spores are present for each set of circumstances. For example many species tend to sporulate preferably inside roots (*Gl. intraradices*). In addition soil samples
collected from field usually contain spores of different VAM fungal species. Molina et al. (1978) recovered an average of two to five species from *Festuca* plants in western United States and species mixtures are common even in extreme soil conditions.

Spores of VAM fungi are recovered under a dissecting microscope, but characters observable at this level often overlap among different species and even among different genera (eg. *Scutellospora, Gigaspora*). In nature most spores are either deteriorated or modified in some way to cause misinterpretation of characters, properties or their occurrence (Morton, 1993). For example Morton (1993) states that spores of an *Acaulospora* and *Scutellospora* species isolated from west Virginia soil samples were indistinguishable because they lacked diagnostic hyphal attachments and overlapped in colour, size and shape. As all structural components of VAM fungal spores for taxonomic decisions are susceptible to alteration or deterioration by a wide range of biotic or abiotic agents in the soil environment, the assumption that field collected spores possess intact informative character is erraneous. Many species-level characters are outer components of spores (ie., walls) exposed to soil environment (Morton and Benny, 1990). They may be ephemeral and therefore absent in field collected specimens. So collection of spores from pot cultures are essential for identification or characterization of Glomalean fungi.

The taxonomy of Glomalean fungi is further plagued by inaccurate descriptions and the type method in the present form has failed to provide a fixed reference point at study (Morton, 1993). New taxa are in danger of redundant and inconsequential unless a high priority is placed on re-evaluation of known taxa. A number of taxa has been inadequately described. New structures or new properties of existing structures are often missed if more obvious diagnostic features are present. For example, the sub cellular
wall structure of *Acaulospora bireticulata* was not noted because of the striking ornamentation pattern of the laminated spore wall (Rothwell and Trappe, 1979). Certain taxa are described from preserved (e.g., *Scu. aurigloba* (Hall) Walker & Sanders; *A. sporocarpia* Berch.) or parasitized spores (*Gi. candida* Bhattacharjee, Mukerjii, Tewari & Skoropad) and characters are interpreted as those in live or healthy spores. In addition type descriptions of certain species are based on a few spores collected from a heterogenous field sites and are generalised as archetypal of the whole species [e.g., *Gl. botryoides*, (Rothwell and Victor, 1984); *A. bireticulata* (Rothwell and Victor, 1974)]. Hence, as Walker (1992) stated “the identification of fungi in Glomales is a difficult and specialised task”.

C. VAM fungal genera

a. *Acaulospora* and *Entrophospora*: *Acaulospora* is defined morphologically by the production of spores laterally on the proximal part (often referred to as the neck) of a swollen sac, singly in the soil or in sporocarps. The sac has been called “mother spore” (Mosse, 1970a, 1970b), a vesicle (Gerdemann and Trappe, 1974), a “hyphal terminus” (Schenck *et al.*, 1984) and a “soporiferous saccule” (Walker *et al.*, 1984). The genus *Entrophospora* is defined by the type species *E. infrequens* (Hall) Ames & Schneider. There are currently only 4 species including the recently reported *E. kentiensis* Wu & Li from Taiwan. Other than formation of spores inside the saccule neck, *Entrophospora* and *Acaulospora* bear little resemblance to each other and differ in sporogenesis (Wu *et al.*, 1995).

b. *Gigaspora*: *Gigaspora* have member species transferred into a recently erected genus *Scutellospora* Walker & Sanders, based primarily on the presence of subcellular structures associated with germination (Walker and Sanders, 1986). Members of this genus have been examined extensively
in spore wall ultrastructure (Sward, 1981a, Maia et al., 1993), germination phenomena (Sward, 1978; 1981b; Gemma and Koske, 1988b), ecological dynamics (Gemma et al., 1989; Lee and Koske, 1994a), in vitro analysis (Becard and Piche, 1989; Becard and Pfeffer, 1993) and commercial use as inocula (Safir, 1994).

Six species remained in the genus Gigaspora after the transfer of most of the species to Scutellospora (Walker and Sanders, 1986). Two additions to the genus were made by Spain et al. (1989) (Gi. ramisporophora) and Neeraj et al. (1993) (Gi. tuberculata). Bentivenga and Morton (1995) redescribed the genus as “spores produced singly in soil, generally greater than 150 µm in diam., usually globose to subglobose but occasionally ovoid, obovoid, or irregular. Spores produced terminally or, rarely laterally on a bulbous sporogenous cell usually greater than 25 µm in diam., often with a slender septate hypha extending from the sporogenous cell towards the spore. Spore wall of three continuous layers a thin outer, hyaline layer which never sloughs; a variable number of laminae which form as spore matures; and a papillate layer formed prior to germination, extending into the lumen of the spore. No inner walls produced. Germ tubes arising from the papillate layer, penetrating directly through the spore wall. Forming endomycorrhizae which stain darkly in trypan blue, with arbuscules and intraradical hyphae but no intraradical vesicles. Intraradical hyphae straight to coiled, 3-11 (-20 µm) in diam. Tightly coiled hyphae, varying in size, produced occasionally within root cortical cells. Extramatrical auxiliary cells produced in clusters of 4-20, individual cells subglobose to ovoid (occasionally clavate) in shape, 15-35 (-55)µm in diam., with echinulate projections 2-10 (-20) µm long; occasionally forking dichotomously. Projections often occluded from the lumen of the cell by a thin septum”. These authors excluded Gi. tuberculata Neeraj et al. as they found it to be a synonym of Scutellospora persica Koske & Walker...
based on the original description. Further, two species were considered to be synonyms of other species (Gi. ramisporophora = Gi. margarita; Gi. candida = Gi. rosea).

c. *Glomus*: The genus *Glomus* presents most difficulty. The possibility is that taxa within *Glomus* may need to be split into different genera because of consistently different morphological characteristics. For example, some species like *Gl. scintillans* Rose and Trappe (= *Gl. dominikii* Blaszokowski) has an ornamented outer wall and a flexible inner wall atypical of the genus *Glomus*. Likewise three distinct groups with regard to occlusion of spore exists in *Glomus*. *Gl. maculosum* Miller & Walker represent one line in which a complete endospore is formed by a more or less flexible wall group. Another is represented by *Gl. fasciculatum* (Thaxter) Gerd. & Trappe emend. Walker & Koske in which the pore is occluded by ingrowth and thickening of the wall of subtending hyphae. In a third group, represented by *Gl. mosseae* the occlusion is by a septum. There are also two known modes of spore germination in the genus *Glomus*. In one, the new hyphae emerge through the lumen of the spore's subtending hyphae and in the other the germ tube directly emerge through the spore wall.

d. *Sclerocystis*: The genus *Sclerocystis* encompass species with *Glomus*-like spores that are formed in sporocarps in an orderly manner around a 'sterile central plexus' (Gerdemann and Trappe, 1974). The genus was revised by Almeida and Schenck (1990) and defined as having unbranched sporophores formed around a central sterile hyphal plexus, with each sporophore bearing a single spore occluded by a basal septum. Based on this all species then known except *Scl. coremeoides* Berkely & Broome were transferred to the genus *Glomus* based on the resemblance of spore ontogeny and sporocarp formation of *Glomus*. Seven species were considered as synonyms and excluded (*Scl. alba, Scl. coccogena, Scl. dusii* = *Scl. coremeoides,*
Scl. indicus, Scl. pachycaulis = Scl. rubiformis, Scl. pakistanica = Scl. sinuosa, Scl. microcarpus = Scl. clavispora).

However, Walker (1992) suggested that the retention of the monospecific genus in Glomales should be reconsidered when more is known of its biology. Wu (1993a) retained the generic concept of *Sclerocystis* as proposed by Gerdemann and Trappe (1974) based on spore ontogeny and sporocarp formation. The emended description defines *Sclerocystis* as “sporocarps globose or subglobose or hemispherical, enclosed by a peridium or naked, with a multihyphal stipe or monohyphal stalks; chlamydospores arranged side by side in a single layer radiating out from a central plexus of hyphae; central plexus composed of a broad, stellate thick walled cells or interwoven hyphae; development of chlamydospores within sporocarps synchronous or asynchronous; side branches frequently produced from the base of the chlamydospores, becoming spores or intersporal hyphae.

**e. Scutellospora**: Taxa in *Scutellospora* form spores terminally on a swollen hyphal tip called a bulbous hyphal attachment (Nicolson and Gerdemann, 1968) or bulbous suspensor-like cell (Gerdemann and Trappe, 1974) or a sporogenous cell (Blaszkowski, 1992). The bulbous attachment usually bears one or more peg like structures which subtend an extremely fine hyphae that extends towards and often touches the surface of the spore. Spore wall structure, ornamentation of auxiliary cells and manner of spore germination are fundamental differences which separate *Scutellospora* from *Gigaspora* (Walker and Sanders, 1986). Spores of *Scutellospora* possess at least one flexible wall, auxiliary cells lumpy to knobby and the germ tube emerge from the “germination shield”. *Scutellospora* is distributed over a wide biogeographical range than *Gigaspora* (Walker, 1992). Vesicles within roots are absent as in *Gigaspora*. However, the one report of vesicle formation
brought up by Stuessy (1992) was found to be auxiliary cells which are occasionally formed within roots.

**D. Spore in spore syndrome**

Spores of VAM fungi are intimately associated with a wide range of soil microorganisms (Lee and Koske, 1994b). Frequent occurrence of fungal hyphae has been observed inside spores of VAM fungi (Gerdemann and Trappe, 1974; Hall, 1977). Spores of VAM fungi can develop certain features that are likely caused by the action of soil microorganisms. Perforations and ingrowths often develop within walls in many species of *Glomus, Gigaspora* and *Sclerocystis* (Gerdemann and Trappe, 1974; Lee and Koske, 1994b). Further, many investigations have found VAM fungal spores in unusual sites like insect integument (Dowding, 1959), infolds of leaf fragments (Graham and Stone, 1975; Rabitin and Rhodes, 1982), dead seeds and seed coats (Ferrer and Herrera, 1980), inside basidiocarps of hypogeous *Melanogaster* (Bakerspigel, 1958) and nematode cysts (Graham and Stone, 1975; Tribe, 1977).

There are a few reports on the occurrence of VAM fungal spores within spores of VAM fungi. These may be either due to internal proliferation of spores as in *Gl. aggregatum* (Koske, 1985; Blaszkowski, 1991) or occupation by other VAM fungal species. Hall (1977) reported the occurrence of *Gl. pallidus* spores within spores of *G. macrocarpus* var. *macrocarpus*. Khan's (1971) illustration suggests the presence of endospores within an unidentified *Endogone (=Glomus)* spore. Spores of *A. scrobiculata* (as “yellow punctate”) inside an unidentified *Gigaspora* spore has been illustrated by Koske (1975) from Australian sand dunes. But a later study by Koske (1984) revealed the wide occurrence of this phenomenon in Atlanta Coast, U.S. and Great lakes. Wu and Chen (1993) reported the presence of 'Glomus-like' spores within chlamydospores of *Scl. sinuosa* from Taiwan. More recently, Mehrotra (1995)
reported the occupation of *A. scrobiculata* spores by hyaline punctate spores of the same species from a coal mine site in Maharastra (India).

### III. MYCORRHIZAL BENEFITS

#### A. Nutritional

**a. Phosphorus**: The beneficial influence of VAM fungi on plant growth has mostly been attributed to an increase in the uptake of nutrients especially P. The low diffusion rate of P in soils limit its uptake by plants root system (Silberbush and Barber, 1983). When root uptake is restricted, upto 80% of the plant P can be delivered by the extramatrical VAM hyphae to the host over a distance of more than 10 cm from the root surface (Li *et al.*, 1991a). Besides this increase in surface area, effective P acquisition by the fungal hyphae is related to:

a) Polyphosphate formation in the hyphae and thus maintaining low phosphate concentrations.

b) The small hyphal diameter leading to a relatively large soil volume delivering P per unit surface area compared to root surface area (Jungk and Claassen, 1989).

c) A correspondingly 2-6 times higher P influx rate per unit length of hyphae (Jakobsen *et al.*, 1992).

d) Production of extracellular acid phosphatases which catalyse the release of P from organic complexes in the soil (Tarafdar and Marschner, 1994).

Convincing experimental evidence is still lacking for the speculation that VAM plants obtain P from sources that are not available to non-mycorrhizal plants (Bolan, 1991). With increasing levels of soil P, the
mycorrhizal response on plant growth declines and may either be abolished or lead to growth depressions (Peng et al., 1993). The shift in root length: shoot dry weight ratio is a typical response to improved P nutrition in both mycorrhizal and non-mycorrhizal plants. In mycorrhizal plants, the P concentration per unit dry weight are higher and thus, the P use efficiency is lower than non-mycorrhizal plants (Koide, 1991; Marschner and Dell, 1994). This suggests that the other growth factors (mineral nutrients, carbohydrates) become limiting, or that in mycorrhizal root systems, the feed-back regulation between nutrient uptake rates and shoot demand are less well regulated than in non-mycorrhizal root systems (Douds et al., 1988).

b. Nitrogen: The status on VAM-N nutrition has focussed on the effect on legumes. When the P nutrition of the host plant is substantially improved by VAM fungi, there may be a corresponding increase in nodulation, N-fixation and growth (Azcon, 1994). Many legumes growing in P deficient soils are highly mycorrhizal dependent due to the high P requirement for nodulation and N-fixation. The ability of mycorrhizal plants to utilize nitrogen sources has been attributed to an indirect effect associated with an improved P nutrition. Some studies have demonstrated that VAM fungi were able to metabolize inorganic N (Ames et al., 1983; Smith et al., 1985). The presence (Coxwell and Johnson, 1985) and absence (Rose and Youngberg, 1981) of the involvement of VAM fungi on the N-nutrition of the host plants have been reported. Studies have suggested that mycorrhizal plants can derive N from both organic as well as inorganic sources that are not available to non-mycorrhizal plants (Ames et al., 1984; Barea et al., 1987, 1989). Johansen et al. (1992, 1994) recently reported the uptake of $^{15}$N from labelled ammonium salts by the external VAM fungal hyphae. The existence of inter-plant hyphal connections between individual plants permit the transfer of nutrients such as N in a non-legume and legume combinations (Newman et al., 1992).
c. Potassium and other nutrients: The role of VAM fungi in the uptake of K, Ca, Mg and S is little known. Eventhough there are many reports on the effect of VAM on concentrations and the amounts of K in the plants these results are inconsistent and difficult to interpret (Sieverding and Toro, 1988). The ability of the extramatrical VAM fungal hyphae to uptake and transport K has also been demonstrated in compartmented pots (George et al., 1992). Significant differences in growth response of soybean to different geographical isolates of Gl. mosseae seemed to be more related to improved K rather than P nutrition of the host (Bethlenfalvay et al., 1989). The hyphal uptake of Ca (Rhodes and Gerdemann, 1978) and SO₄-S (Cooper and Tinker, 1978) has been shown through supplying radio isotopes (⁴⁵C, ³⁵SO₄). The uptake and transport rates of Ca is very low compared to P. A substantial contribution of hyphal delivery to the host plant is not likely under most cases because of high mobility of Ca²⁺ and SO₄²⁻ in the soil.

The numerous reports on the enhancement of Zn and Cu uptake by VAM plants can be attributed to the uptake and transport in external hyphae to the host plant (Kothari et al., 1990a,b). The hyphal contribution (of Gl. mosseae) to the uptake of Zn ranged from 16-25% compared to 13 to 20% for P in maize grown in calcareous soil (Kothari et al., 1991a). In the same soil Li et al. (1991b) demonstrated that the delivery of Cu from the hyphal compartment ranged from 52 to 6% of the total Cu uptake under restricted rooting space. In contrast, Mn uptake and concentration in plants are either unaffected but more often are lower in VAM plants (Lambert and Weidensaul, 1991). The decrease in concentrations of Mn in plants is most likely an indirect effect caused by VAM induced changes in the rhizosphere microorganisms in general and particularly the decline in population of Mn reducers (Kothari et al., 1991a,b). The role of VAM on boron (B) nutrition of host plant is either lacking or inconclusive. VAM may decrease B concentrations in host plants.
Plants have varying mechanisms for mobilizing, chelating and reducing ferric Fe in order to facilitate uptake (Marschner, 1986). Treeby (1992) indicated that VAM fungi may facilitate the Fe uptake in acidic but not in alkaline soils.

B. Non-nutrient benefits: Several experiments have shown that the rate of photosynthesis is higher in mycorrhizal compared to non-mycorrhizal plants (Allen et al., 1981; Kucey and Paul, 1982; Snellgrove et al., 1986). The rate of photosynthesis in vitro can be limited by P availability (Lewis, 1986; Sivak and Walker, 1986). The direct role of P in photosynthesis and in subsequent mobilization or storage of photosynthates has now been clearly demonstrated. But, the differences in the sensitivity of photosynthetic mechanism of plant species to P deficiency (Dietz and Foyer, 1986), may be a possible basis for differences in response to mycorrhizal infection.

Mycorrhizal plants may be drought tolerant (Allen and Allen, 1986; Osonubi, 1989) but it has been difficult to distinguish direct mycorrhizal effect on water relations from those mediated via improved mineral nutrition. The increased growth of mycorrhizal plants under drought conditions than non-mycorrhizal plants has been attributed to increased stomatal conductance (Osonubi, 1989; Subramanian et al., 1995) and increased root conductivity provided by increased surface area of mycorrhizal hyphae (Read and Boyd, 1986). These reported changes in mycorrhizal plants under drought conditions could be either due to the secondary response to better P nutrition (Michelsen and Rosendahl, 1990; Osonubi et al., 1990) or mediated via direct mycorrhizal effect (Henderson and Davies, 1990). The relief of nutrient stress might also be followed by increased rates of root growth and more efficient extraction of water from soil profile (Fitter, 1985). The improved water availability reduces severe drought stress symptoms such as proline accumulation (Levy and Krikun 1980; Nemec and Meredith, 1981; Cooper, 1984).
Mycorrhizal infection enhances hormone accumulation in host tissues with changes in the levels of cytokinin, abscissic acid and gibberellin-like substances (Baas and Kuiper, 1989; Danneberg et al., 1992). Isoflavonoids and phytoalexins which are inhibitory to pathogenic fungi have been isolated from mycorrhizal plants (Morandi et al., 1984; Morandi and Gianinazzi-Pearson, 1986).