REVIEW OF LITERATURE
Arbuscular mycorrhizae are fungus-root symbiosis that occurs in the vast majority of plants have existed since the Devonian period and might have been essential for the evolution of land plants (Pirozynski and Malloch, 1975).

Research on arbuscular mycorrhizal association from the initial comprehensive description (Gallaud, 1905) entered a lag phase, until workers in the 1950’s demonstrated convincingly that arbuscular mycorrhizae 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 arbuscular mycorrhizae from orchid and ericoid mycorrhizae and described that arbuscules and vesicles 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 arbuscular mycorrhizae. Hence, this review is focused on ecology, taxonomy and arbuscular mycorrhizal fungal benefits to the host plants.
ECOLOGY

A. OCCURRENCE AND DISTRIBUTION OF ARBUSCULAR MYCORRHIZAL FUNGI

Several workers have published excellent general reviews about mycorrhizae (Gerdemann, 1975; Hayman, 1978; Smith, 1980; Mosse et al., 1981) and also reviewed on specific aspects of the symbiosis such as nitrogen uptake (Bowen and Smith, 1981), and nutrient translocation (Rhodes and Gerdemann, 1980).

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 arbuscular mycorrhizal plants in natural ecosystems. Since then several studies have appeared widening the knowledge of arbuscular mycorrhizal fungi and their distribution in natural ecosystems. Koske et al., (1992) and Gemma et al., (1992), have reported the mycorrhizal status of Hawaiian angiosperms and pteriophytes. Ueda et al., (1992) found arbuscular mycorrhizal association in twenty six of the thirty three species of medicinal plants they examined.

In India, occurrence of arbuscular mycorrhizal association has been studied by different workers in various ecosystems viz., subtropical evergreen forests (Sharma et al., 1984), Seasonally dry tropical and subtropical forests (Parameswaran and Augustine, 1988; Jha et al., 1988; Raman et al., 1992; Bhat Narayana, 1993; Appaswamy and Ganapathy, (1995); Mohankumar and Mahadevan, 1987; Muthukumar et al., 1996; Santhaguru et al., 1995), Semiarid and arid (Mukerji and Kapoor, 1986; Rachel et al., 1989 & 1991; Tarafdar and Rao, 1990; Neeraj et al., 1991; Gupta and Mukerji, 1996),

However, as further ecosystem types are explored for arbuscular mycorrhizal associations, surprises still appear (Allen, 1996). Arbuscular mycorrhizal association can also be found in unexpected plant groups and habitats. *viz.*, in aquatic plants (Khan, 1993); floating *Typha* mats (Stenlund and Charvat, 1994), parasitic plants (Palacios-Mayorga and Perez-Silva, 1993) and in Proteaceae (Bellgard *et al.*, 1994).

**B. ROLE OF ARBUSCULAR MYCORRHIZAL ASSOCIATION**

The role of arbuscular mycorrhizal fungi in stimulating plant growth through enhanced nutrient and water uptake is now widely recognised. Mineral nutrients especially phosphorus appear to be the major constrain for plant growth in natural ecosystem (Brundrett, 1991). But plants have developed 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 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. Byalis (1975) has pointed out that plant species with poor development of root hairs tend to be mycotrophic i.e. dependent upon mycorrhizal fungi for nutrient uptake. These plants in natural ecosystem further conserve resources within long-lived shoot and root structures, efficiently reclaim minerals from senescing tissues (Boerner, 1986; Chapin, 1988) and establish carefully regulated mycorrhizal associations (Brundrett and Kendrick 1990).

The principal benefit of arbuscular mycorrhizal symbiosis for higher plants is an increased supply of phosphorus which is taken up by hyphae outside the root, translocated to internal fungal structures, and ultimately released cortical cells of the roots. As the phosphorus level of the soil or growth medium is increased, mycorrhizal colonization is reduced. This apparently results from physiological changes accompanying high concentrations of phosphorus in plant tissue, rather than a direct effect of phosphorus on growth of mycorrhizal fungus (Sanders, 1975; Ratnayake et al., 1978). 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. It is known that some species in nature fail to grow in the absence of arbuscular mycorrhizal association. (Janos, 1980). In some cases this is because of an ineffective coarse root system (Byalis, 1975). The presence of arbuscular mycorrhizal propagules in the most undisturbed natural ecosystem, ensure mycorrhization of these plants, thus facilitating the capture of nutrients and survivability to such species contributing to the maintenance of the diversity (Read, 1993).
C. FACTORS INFLUENCING ARBUSCULAR MYCORRHIZAL FUNGI

I. Season

Seasonal changes in mycorrhizal colonization 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); salt marshes (Lee and Koske, 1994); tropical forests (Louis and Lim, 1987; Jha et al., 1992) arid and dry land (Allen, 1983; Meney et al., 1993) communities. In India, seasonal changes in mycorrhizal colonization and spore numbers have been recorded in semievergreen forest, mixed deciduous forest, Teak forest and scrub jungle (Mohankumar and Mahadevan, 1986).

Large variations in arbuscular mycorrhizal colonization 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 colonized by arbuscular mycorrhizal fungi increase rapidly when roots grow and decrease when roots senesces (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 arbuscular mycorrhizal fungi to penetrate within them (Brundrett and Kendrick 1990a).
Seasonal fluctuations in arbuscular mycorrhizal spore numbers have been attributed to germination activities (Gemma and Koske, 1988), soil micro- and macrofaunal activities (Rabatin and Stinner, 1988; McGee and Baczocha, 1994) and destruction of arbuscular mycorrhizal spores by soil fungi and other parasites (Ross and Rottencutter 1977; Lee and Koske, 1994a). The variation in arbuscular mycorrhizal fungal spores to initiate mycorrhization may also contribute to seasonal changes, as newly formed spores require a period of dormancy (Tommerup, 1983; Gemma and Koske, 1988). The spore numbers generally decline during periods of mycorrhizal formation and increases during periods of root senescence (Brundrett, 1991).

II. Climatic factors

a. Rainfall and Relative Humidity

Literature on ecological studies related to the effect of climatic factors on arbuscular mycorrhizae is scarce. Michelini et al., (1993) found significant relationship between arbuscular mycorrhizal fungal colonization and rainfall in Citrus. According to Hayman (1974) seasonal changes, which includes changes in both climatic and edaphic factors play a key role in controlling sporulation of arbuscular mycorrhizal fungi. The number of mycorrhizal spores and extent of colonization decreased especially during rainy season. Braunberger et al., (1994) found that "false break" (rain during summer) decreased mycorrhizal colonization and proportion of root length colonized by arbuscular mycorrhizal structures. Udaiyan et al., (1996) reported a positive relation between arbuscular mycorrhizal fungal spore numbers and Relative Humidity in Acacia farnesiana, but a negative relationship in Acacia planiforms.
b. Temperature

It has been shown that temperature significantly influences arbuscular mycorrhizal fungal colonization and sporulation both under field and glasshouse conditions. Higher root colonization is generally known to occur during higher temperature (Furlan and Fortin, 1973). Increased temperature is known to decrease the lag phase of colonization. Jarstfer and Sylvia, 1993) noted decreased sporulation under high temperatures. Schenck and Schroder (1974) observed maximum arbuscule development in soyabean near 30°C, but mycelial colonization was greater between 28-34°C. Daniels and Trappe (1980) observed that the optimum temperature for germination of *Glomus* and *Acaulospora* species were found 20-25°C, whereas, *Gigaspora* had much higher optima. These studies indicate that increased soil temperature fastens the development of arbuscular mycorrhizal fungi.

The temperature effect may explain the slow development of colonization in temperate soils (Black and Tinker, 1979) where soil temperature is low compared to tropical soils. Since many species of arbuscular mycorrhizal fungi are worldwide in distribution, it is possible that strains and species may be temperature adapted. Schenck *et al.*, (1975) found that two isolates of *Glomus mosseae* from Florida germinated best at 34°C, whereas one from Washington had an optimum of 20°C. McGee *et al.*, (1987) have shown that propagules of some isolates of arbuscular mycorrhizal fungi can survive in dry soil temperatures upto 70°C and subsequently colonize roots of ephemeral plants following rain.
Many reports have shown that isolates may differ in their optimum temperature for germination, root colonization and spore production. (Graham et al., 1982; Tommerup, 1983a). Though, there have been a number of studies on the effect of temperature on the mycorrhizal formation (Farlan 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 colonization occurred at 36°C indicating complex interactions between survival and germination of propagules and plant process such as root growth.

c. Edaphic factors

i) Water

The arbuscular mycorrhizal colonization has been found in plants around the world over a wide range of soil water content like in xerophytes of arid regions (Khan, 1974; Mukerji and Kapoor, 1986), wet soil of marshes (Chaubal et al., 1982; Ragupathy et al., 1990; Rickerl et al., 1994), free floating (Bagyaraj et al., 1979) and submerged aquatic plants (Clayton and Bagyaraj, 1984).

Water logging may substantially reduce the number of spores in mangrove soils and may abolish mycorrhizal colonization (Mohankumar and Mahadevan, 1986). Water logging may inhibit mycorrhizal formation through lack of aeration as oxygen is necessary for fungal growth (Crawford, 1992). Excessively high soil water potential reduced arbuscular mycorrhizal colonization (Khan, 1974). The distribution of spores in
the rhizosphere and arbuscular mycorrhizal colonization of roots is affected by soil moisture and seasons (Khan, 1974). Khalil and Loyanachan, (1994) reported a higher arbuscular mycorrhizal fungal spore populations in poorly drained soils compared to well drained and moderately drained soils. Water has been shown to affect arbuscular mycorrhizal fungal sporulation. Non-saturated and non stressed water conditions are best for spore production both in high and low phosphorus conditions (Nelson and Safir, 1982). Water activity has been found to be the important determinant of arbuscular mycorrhizal fungal spore germination in vitro (Douds and Schenck, 1991).

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). Tommerup (1987) indicated that spores of arbuscular mycorrhizal fungi can probably survive for atleast 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, 1983). Mc Gee et al., (1987) observed the survival of arbuscular mycorrhizal propagules in an Australian soil reaching 70°C during summer. Jha et al., (1992) reported a positive relation between soil moisture and root colonization levels but a negative relationship between soil moisture and spore numbers.
ii) pH

The soil pH is one of the important factors considered by several authors (Abbott and Robson, 1991) in the mycorrhizal study. The study on soil pH can be subdivided into effects on spore germination (Daniels and Trappe, 1980), spore production (Kruckelmann, 1975; Read *et al.*, 1976) and effects on plant growth and nutrients uptake (Lambert and Cole, 1980).

Natural soils of the world cover a pH range of 2.8 to >10 (Bass Becking *et al.*, 1960). Daft *et al.*, (1975) reported considerable arbuscular mycorrhizal colonization in plants growing in a mine spoils of pH 2. Sparling and Tinker (1978) found no obvious effect of pH on mycorrhizal colonization in three grassland sites at pH 4.9, 5.9 and 6.2. Previous studies indicate some evidence for differences in adaptations of strains and species of arbuscular mycorrhizal fungi to soil pH. Lambert and Cole (1980) reported that an isolate of *Gigaspora gigantea* failed to colonize at low pH and six isolates of *Glomus tenue* differed in their ability to form mycorrhizas at low pH. Janarthanan *et al.*, (1994) reported that the typical arbuscular mycorrhizal fungi occur at extreme alkaline pH (10.5) which occurs in natural soils of saline regions. Peat and Fitter (1993) indicated that mycorrhizal dependent plant species occur at higher pHs than infrequently mycorrhizal species.

The laboratory studies indicate a good germination of arbuscular mycorrhizal spores 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 arbuscular mycorrhizal fungal species and to environments to which each is indigenous (Gerdman and Trappe, 1974; Green et al., 1976). It has been established that spore germination is pH sensitive, but different species have different pH optima (Robson and Abbott, 1989). Hepper and Smith (1976) showed that arbuscular mycorrhizal fungal spore germination on agar is sensitive to metals such as Manganese, Copper and zinc, whose activities in soil solutions is dependent of pH.

iii) Nutrients

a) Nitrogen:

In general, nitrogen is very important nutrient which limits plant growth. Plants require nitrogen in large amounts for their growth. There have been a few studies on the effects of nitrogen on arbuscular mycorrhizal fungi compared to phosphorus. Studies indicate that nitrogen supresses root colonization (Mosse and Phillips 1971; Menge, 1984). Hepper (1983) demonstrated that increased application of NO₃ increased the levels of root colonization in lettuce. In contrast, Chambers et al., (1980) reported that both NH₄⁺ and NO₃⁻ depressed arbuscular mycorrhizal formation and suggested the effect to a drop in rhizosphere pH. Sylvia and Neal (1990) suggested that plants nitrogen stress like phosphorus stress promotes mycorrhization. Thomson (1986) reported that pH modification by nitrogen sources influenced mycorrhization. Jha et al., (1992) found that soil N was positively related to arbuscular mycorrhizal colonization and negatively to spore numbers. Like phosphorus, the effect of soil nitrogen on arbuscular mycorrhizal colonization and spore number can vary with plant species (Muthukumar et al., 1994a; Udaiyan et al., 1996).
b) Phosphorus

A relationship exists between the extent of mycorrhizal colonization and the concentrations of soil phosphorus. The sites with large amount of soil P may have high levels of colonization and large spore numbers. In contrast, sites with small amount of phosphorus may have low levels of colonization or spore numbers (Hayman, 1978; Gianinazzi-Pearson et al., 1980; Jeffries et al., 1988). Positive (Jha et al., 1992; Udayian 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 phosphorus and arbuscular mycorrhizal colonization.

The root colonization of arbuscular mycorrhizal fungi are adversely affected by application of phosphorus through inhibition of spore germination (Miranda and Harris, 1994), depressing the development of arbuscles, vesicles, internal and external hyphae and penetration points (Menge et al., 1978; Schwab et al., 1983; Miranda and Harris, 1994; Suriyapperuma and Koske, 1995). However arbuscular mycorrhizal fungi vary in their sensitivity to soil phosphorus (Trouvelot et al., 1987; Lamar and Davey 1988).

The important factor for controlling arbuscular mycorrhizal colonization has been as plant tissue phosphorus (Sylvia and Neal, 1990; Menge et al., 1978). This conclusion has been extended to changes in root membrane permeability and to the availability and quantity of root exudates (Ratnayake et al., 1978; Graham et al., 1981; Bolan et al., 1984). They however, reported that increasing soil phosphorus gradually from a severely
deficient condition could increase mycorrhizal colonization before the expected decrease occurred as soil phosphorus become sufficient. This increase in arbuscular mycorrhizal colonization due to small amounts of phosphorus application suggest that mycorrhization may to certain extent depend on soil phosphorus and not totally on plant phosphorus (Graham et al., 1981). Sanders and Fitter (1992a), however, have found no relationship between plant phosphorus and arbuscular mycorrhizal colonization in grassland species. Sylvia and Neal (1990) reported that root colonization by arbuscular mycorrhizal fungi was not affected when plants were deficient in nitrogen, but when nitrogen was sufficient, phosphorus addition suppressed root colonization. But the response of arbuscular mycorrhizal colonization and spore number to soil phosphorus can vary with host species (Muthukumar et al., 1994a).

c) Potassium

There are very less reports on role of potassium. Daniels and Trappe, (1980) has reported that the potassium has no effect on arbuscular mycorrhizal fungi. But Ebbers et al., (1987) reported significantly positive correlation between spore abundance and available soil potassium in prairie drop seed (Sporobolus heterolepsis). Zahka et al. (1995) indicated that concentration of soil potassium was a key predictor for variations observed in colonization levels and for the occurrence of arbuscules in the root cortical cells.
d) Other nutrients

The role of other nutrients on root colonization and spores abundance of arbuscular mycorrhizal fungi is little known compared nitrogen, phosphorus and potassium. Micronutrients like copper, zinc and manganese are reported to inhibit arbuscular mycorrhizal fungi at low concentration and arbuscular mycorrhizal fungal colonization levels and suggested a combined effect of Zn-pH leading to this inhibition. In contrast, McIlw een and Cole (1978) reported the stimulatory effect of zinc on spore germination at low concentrations. Sreenivasa and Bagyaraj (1988) reported that the sub-optimal levels of zinc, copper and manganese would enhance root colonization and sporulation of *Glomus fasciculatum* associated with Rhodes grass (*Chloris gayana)*.

**TAXONOMY**

Taxonomy of Glomalean fungi is less than 30 years old, starting with the formal Linnaean classification by Gerdman 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 the year 1983. But since then the taxonomical concepts about arbuscular mycorrhizae 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.
Problems in Glomalean Taxonomy

Spores are the most retrievable part of the fungal organisms, because each can be manipulated as discrete object. 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 were mycorrhizal (McGee, 1989). Modification of collection procedures is often necessary when spores are present for each set of circumstances. In addition, soil samples collected from field usually contains spores of different arbuscular mycorrhizal 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 arbuscular mycorrhizal fungi are recovered under a dissecting microscope, but characters observable at this level often overlap among different species and even among different genera. In nature most spores are either deteriorated or modified in same way to cause misinterpretation of characters, properties of their occurrence (Morton, 1993). It is true that all structural components of arbuscular mycorrhizal fungal spores for taxonomic decisions are susceptible to alterations or deterioration by a wide range of biotic or abiotic agents in the soil environment. The assumption that field collected spores possesses intact informative character is erroneous. Many species-level characters like spore wall are exposed to soil environment (Morton and Benny, 1990). They may be ephemeral and therefore absent in field collected
specimens. So collections of spores from pot cultures are essential for identifications 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 have been inadequately described. New structures or new properties of existing structures are often missed if more obvious diagnostic features are present. Hence, as Walker (1992) stated “The identification of the fungi in Glomales is a difficult and specialized task”.

ROLE OF MYCORRHIZAE

Mycorrhiza constitutes the most striking example of symbiosis in plant kingdom. Mycotrophy represents a specialized mode of tree nutrition, the significance of which has been realized during the last few decades. They help in the faster uptake and translocation of water and nutrients, particularly phosphorus, nitrogen and potassium, besides other elements like zinc, calcium etc. Plants equipped with mycorrhizae are better adapted to withstand drought and invasion by pathogenic organisms.
Nutritional benefits

a) Nitrogen

In arbuscular mycorrhizal research on nitrogen nutrition, the most attention has been paid to legumes. When arbuscular mycorrhiza improves the phosphorus nutrition of the host plant there may be corresponding increase in nodulation, nitrogen fixation and growth (Robson et al., 1981). In view of the high phosphorus requirements for nodulation, many legume species growing on low phosphorus soils are highly dependent on arbuscular mycorrhizal colonization. However, the symbioses impose a strong competition for photosynthates, usually at expense of root growth. Accordingly, the beneficial effects on nitrogen fixation are either confined to, or at least most distinct, in low phosphorus soils. The ability of mycorrhizal plants to utilize nitrogen sources has been attributed to an indirect effect associated with improved phosphorus nutrition. Some studies have demonstrated that the arbuscular mycorrhizal fungi were able to metabolise inorganic nitrogen (Ames et al., 1983; Smith et al., 1985) The presence (Coxwell and Johnson, 1985) and absence (Rose and Youngberg, 1981) of the involvement of arbuscular mycorrhizal on the nitrogen nutrition of the host plants have been reported. Studies have suggested that mycorrhizal plants can derive nitrogen 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 N^{15} from labeled ammonium salts by the external arbuscular mycorrhizal fungal hyphae. The existence of inter-plant hyphal bridges between individual plants permits transfer of nutrients such as nitrogen in a non-legume and legume combination (Newman et al., 1992).
b) Phosphorus

In general large growth enhancement effects of root colonization with mycorrhizal fungi are occurred by increase in phosphorus absorption, particularly from sparingly soluble phosphorus sources (Bolan et al., 1987). The low diffusion rate of phosphorus in soils limits its uptake by plants root system (Silberbush and Barber, 1983). When root uptake is restricted, upto 80% of the plant phosphorus can be delivered by the extramatrical arbuscular mycorrhizal hyphae to the host over a distance of more than 10 centimeters from the root surface (Li et al., 1991). Convincing experimental evidences is still lacking for the speculation that arbuscular mycorrhizal plants obtain phosphorus from sources that are not available to non-mycorrhizal plants (Bolan, 1991). With increasing levels of soil phosphorus, 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 phosphorus concentrations per unit dry weight are higher and thus the phosphorus use efficiency is lower than non-mycorrhizal plants. (Koide, 1991; Marschner and Dell, 1994).

c) Potassium and other nutrients

Very little is known on the role of mycorrhiza in uptake of K, Ca, Mg and S. Although for arbuscular mycorrhizae, there are many results on effects of colonization on concentrations and amounts of K in shoots, these results are inconsistent and difficult to interprete (Sieverding and Toro, 1988). The ability of the extramatrical arbuscular mycorrhizal fungal hyphae to uptake and transport potassium has also been demonstrated
in compartmented pots (George et al., 1992). Significant differences in growth response of soyabean to different geographical isolates of *Glomus mosseae* seemed to be more related to improved potassium rather than phosphorus nutrition of the host (Bethlenfalvay et al., 1989). The hyphal uptake of calcium (Rhodes and Gerdmann, 1978) and SO₄-S (Cooper and Tinker, 1978) has been shown through supplying radio isotopes (⁴⁵Ca, ³⁵SO₄). The uptake and transport rate of calcium is very low compared to phosphorus.

There are numerous reports on the enhancement of zinc and copper uptake by arbuscular mycorrhizal colonized plants. At least in part, this enhancement can be attributed to uptake and transport in external hyphae to the host plant (Kothari et al., 1990 & 1990a). The hyphal contribution of *Glomus mosseae* to the uptake of zinc ranged from 16-25% compared to 13-20% for phosphorus in maize grown in calcareous soil (Kothari et al., 1991). In the same soil, Li et al., (1991a) demonstrated that the delivery of copper from the hyphal compartment ranged from 52 to 6% of the total copper uptake under restricted rooting space. In contrast, manganese uptake and concentration in plants are either unaffected but more often are lower in arbuscular mycorrhizal plants (Lambert and Weidensaul, 1991). The decrease in concentration of manganese in plants is most likely an indirect effect caused by arbuscular mycorrhizal induced changes in the rhizosphere micro-organisms in general and particularly the decline in population of manganese reducers (Kothari et al., 1991 & 1991a). The role of arbuscular mycorrhizal fungi on boron nutrition of the host plant is either lacking or inconclusive. Arbuscular mycorrhizal fungi may decrease boron concentration in host plants (Kothari et al., 1991 & 1991a). Plants have varying mechanisms for mobilizing, chelating and reducing ferric (Fe) in
order to facilitate uptake (Marshner, 1986). Treeby (1992) indicated that arbuscular mycorrhizal fungi may facilitate the iron uptake in acidic but not in alkaline soils.

d) Non-nutrient benefits

Many experiments have shown that the rate of photosynthesis is higher in mycorrhizal plants 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 phosphorus availability (Lewis, 1986; Sivak and Walker, 1986). The direct role of phosphorus 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 phosphorus deficiency (Dietz and Foyer, 1986), may be a possible basis for differences in response to mycorrhizal colonization.

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 phosphorus 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 allowed 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).

Colonization by arbuscular mycorrhizal fungi 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).