Mycorrhizas in Natural Ecosystems

M. BRUNDRETT

I. Summary 171
II. Introduction........ 172
III Mycorrhizal Ecology 173
A. Mycorrhizal Fungi........ 175
B. Edaphic or Climatic Factors and Mycorrhizal Fungi 176
C. The Host Plant 194
D. Plants and Mycorrhizal Fungi 196
E. Edaphic/Environmental Factors, Plants and Mycorrhizas 202
F. The Ecology of Mycorrhizal Plants 235
IV. Conclusions. 257
Appendix 1........ 262
Acknowledgements 271
References 271

I. SUMMARY

There is now ample evidence to support the common assertion that most plants in natural ecosystems have mycorrhizal associations. Information about the worldwide distribution of plants with different types of mycorrhizal associations is used to establish correlations with the major climatic factors (water, temperature) which regulate the distribution of plants, as well as more localized edaphic conditions. Ecological implications of mycorrhizal associations in natural ecosystems and the role of soil or environmental factors, mycorrhizal fungus characteristics or host plant properties alone or in combination are considered. Factors which can influence the occurrence and effectiveness of mycorrhizal associations include (i) root properties (ii) edaphic or climatic factors (iii) soil

ADVANCES IN ECOLOGICAL RESEARCH
Vol 21 pp 171-313
Begon, M, Fitter, A. H. & Macfadyen, A. (Eds.)

ISBN 0-12-013921-9

organisms, (iv) soil disturbance and (v) host-fungus compatibility. More complex ecological topics (involving, the environment. plants and mycorrhizal fungi) that are discussed include (i) mycorrhizal phenology, (ii) factors responsible for varying degrees of mycorrhizal dependency in host plants, (iii) the role of mycorrhizal hyphae in soil, (iv) nutrient competition involving mycorrhizal and non-mycorrhizal plants and (v) mycorrhizal interactions involving pollution and other stresses, the rhizosphere, soil properties and allelopathy. The population ecology of mycorrhizal fungi and the influence of their associations on plant population ecology are also considered.

II. INTRODUCTION

Mycorrhizas are highly evolved, mutualistic associations between soil fungi and plant roots. The partners in this association are members of the fungus kingdom (Zygomycetes, Ascomycetes and Basidiomycetes, but not protoctistan fungi such as Oomycetes) and most vascular plants (Harley and Smith, 1983; Kendrick, 1985). In the mycorrhizal literature the term symbiosis is often used to describe these highly interdependent mutualistic relationships where the host plant receives mineral nutrients while the fungus obtains photosynthetically derived carbon compounds (Harley, 1989; Harley and Smith, 1983). At least seven different types of mycorrhizal associations have been recognized, involving different groups of fungi and host plants and distinct morphology patterns (see Hadley, 1982; Harley, 1989, Table 1; Harley and Smith, 1983; Read, 1983). The most common associations are (i) vesicular-arbuscular mycorrhizas (VAM) in which zygomycetous fungi produce arbuscules, hyphae and vesicles within root cortex cells, (ii) ectomycorrhizas (ECM) where Basidiomycetes and other fungi form a mantle around roots and a Hartig net between root cells, (iii) orchid mycorrhizas where fungi produce coils of hyphae within roots (or stems) of orchidaceous plants and (iv) ericoid mycorrhizas involving hyphal coils in outer cells of the narrow "hair roots" of plants in the Ericales. In this review, hyphae of a mycorrhizal fungus originating from one entry point in roots or one propagule in soil are referred to as colonies, and colonization refers to the degree of root occupation by mycorrhizal fungi.

It has often been stated that most plants in ecosystems have mycorrhizal associations, but there have been no attempts to catalogue the evidence which supports this assertion since Kelly (1950) last summarized information about the worldwide distribution of mycorrhizal plants. However, there have been recent literature surveys which consider correlations between mycorrhizal strategies and plant taxonomy (Newman and Reddell, 1987; Trappe, 1987) and one concise regional compilation of host plants (Harley and Harley, 1987). A survey of information about the mycorrhizal status of plants occurring in each of the world's major ecosystems and edaphic communities is provided in Appendix 1 at the end of this review. This compilation provides a summary of our knowledge about the distribution of mycorrhizal associations in natural ecosystems and allows correlations between these distribution patterns and climactic and edaphic factors to be established. Various aspects of the ecology of mycorrhizal fungi and their associations with plants in natural ecosystems are considered in this review.

III. MYCORRHIZAL ECOLOGY

Mycorrhizal associations are regulated by features of the host plant and rnycorrhizal fungus, as well as by soil conditions and environmental factors (Harley and Smith, 1983; Mosse and Hayman, 1980). Mycorrhizal ecology can be viewed as regions of overlap between one or more of these three factors (Fig. 1) and the discussion here reflects this

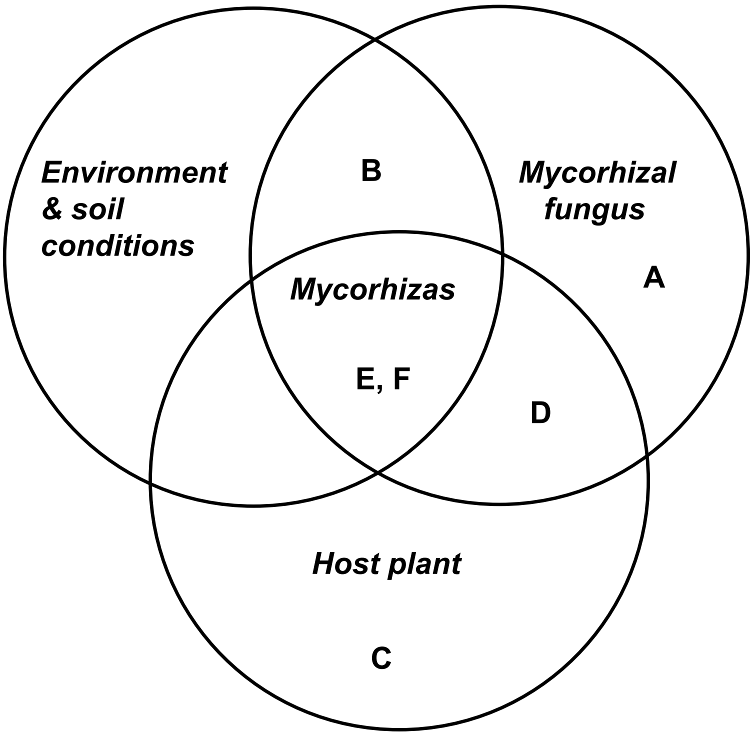

Fig. 1. Mycorrhizal associations result from three-way interactions between mycorrhizal fungi, host plants and environment/soil conditions, as is illustrated by three overlapping regions in this figure. The labeled regions refer to mycorrhizal ecology subject areas that are sections in this review.

The life cycle of a mycorrhizal association

1 . Fungal propagules *[spores hyphae, old roots etc*]

- survival
    - disturbance, predation
    - adverse conditions
- dispersal
- dormancy, quiescence
- activation- fungi may respond to:
    - environmental conditions
    - time intervals
    - presence of roots or other organisms

3. Root growth *[young roots required to form associations]*

- regulated by phenology and environmental factors
- production of soluble or volatile signals*

2. Active soil hyphae

- mineral nutrient acquisition by fungus
- microhabitat preferences?
- limited saprobic potential?
- spread through soil
- attraction to roots*?, tropic responses?
- contact with young host roots

4. Hyphae on root surface

- proliferation on root surface
- recognition of potential host?
- fungus morphology changes
    - appressoria (VAM), mantle (ECM)

5. Hyphal penetration into or between root cells

- avoidance or tolerance of host defenses
- recognition by host? (minimal response)
- further fungus morphology changes

6. Formation of exchange sites

- most pronounced fungus morphology changes
- highly branched hyphal structures
    - arbuscules (VAM), Hartig net (ECM)
- obvious host responses (protoplasm synthesis, etc.)

7. Active exchange processes

- limited in duration influence of host, fungus or environment.

8. Senescence of hyphal structures within roots

- disorganization of exchange site hyphae
- fungal resources withdrawn for
    - storage by hyphae, vesicles within root (VAM)
    - storage in mantle (ECM)
    - export into external mycelium

9. Propagule formation *[the cycle recommences]*

- resting spores in soil or root (VAM)
- sexual spores from mushrooms, truffles (ECM)
- mycelial strands and sclerotia (ECM)
- mycelial networks in soil
- long-lived roots

10. Root senescence

- root cortex lost due to:
    - root death or secondary growth
    - parasitism or consumption
- nutrients in root and fungus structures recycled
    - decomposition food web

Fig. 2. This chart illustrates the sequence of events during mycorrhizal formation, senescence and propagule formation.

structure. Discussion topics also follow the sequence of events presented in Fig. 2, which is a schematic representation of the life-cycle of a mycorrhizal association. as much as possible. The influence of environmental factors on soils or plants alone have been considered in detail elsewhere (Barbour *et al.,* 1987; Etherington, 1982; Fitter and Hay, 1987). Most of the discussion which follows concerns VAM and ECM associations because there have been most studied, but other association types are also considered.

A. Mycorrhizal Fungi

Members of the fungus kingdom obtain nutrition from many sources. including decomposition of organic substrates (saprobes). predation and parasitism and involvement in mutualistic associations (Christensen, 1989; Kendrick, 1985). Many soil fungi are saprobes with the enzymatic ability to digest organic substrates of varying degrees of complexity, but some subsist on very low levels of organic or inorganic substrates (Wainwright, 1988). Mycorrhizal fungi are a major component of the soil microflora in many ecosystems (Harley, 1971) and usually have limited saprobic abilities (Section III.F.l). Endophyte properties which would help determine the effectiveness of mycorrhizal associations include the amount of soil hyphae produced relative to root colonization, the rate of hyphal growth and root colony initiation, and physiological characteristics which regulate nutrient absorption or nutrient translocation by hyphae and exchange with the host (Kottke and Oberwinkler, 1986; Smith and Gianinazzi-Pearson, 1988).

Fungi forming VAM associations include about 150 species belonging to the genera *Gigaspora* and *Scutellispora* (Gigasporaceae), *Glomus* and *Sclerocystis* (Glomaceae) and *Acaulospora* and *Entrophospora* (Acaulosporaceae) in the Zygomycete order Glomales (Morton and Benny, 1990). Mycorrhizal fungi apparently can occupy a particular habitat for thousands of years with little genetic change (Trappe and Molina, 1986) and fossil evidence suggests that VAM associations have been present throughout most of the history of vascular plants (Pirozynski and Dalpé, 1989; Stubblefield and Taylor, 1988). The relatively small number of extant species and the scarcity of sexual reproduction in this group of fungi also suggest that the potential for genetic change within these species is limited (Morton, 1988; Tommerup, 1988). Morton (1990) has proposed that most of the evolution of species in the Glomales occurred early in their evolutionary history and that they have changed relatively little since then. However, the hyphae and spores of VAM fungi are multinucleate and probably also heterokaryotic, so genetic changes may occur through hyphal anastomosis or somatic recombination involving different nuclei (Tommerup, 1988; Trappe and Molina, 1986). Careful taxonomic studies (Morton, 1988). the use of new methods such as isoenzyme analysis (Hepper *et al.,* 1988) and variable responses to soil and environmental conditions (Section III.B.5) have demonstrated considerable variation within currently defined taxa of VAM fungi.

A wide range of fungi, including thousands of species, belonging to 25 families of Basidiomycetes, seven families of Ascomycetes and a single Zygomycete family, can form ECM associations (Miller, 1982a). Some hosts form associations with many fungi while others are more specific (Duddridge, 1987; Trappe, 1962). Host preferences, metabolic diversity and responses to habitat conditions provide evidence that considerable diversity occurs within this group of fungi (Section III. B.6). Debaud *et al.* (1988) found that homokaryotic mycelia of the fungus *Hebeloma cylindrosporum* produced ECM associations that were similar to those produced by hyphae of the dikaryotic parent. Unfortunately, little is known about the genetics (cytology, nuclear behavior, mating systems, etc.) of ECM fungi (Harley and Smith, 1983; Trappe and Molina, 1986). The ericoid mycorrhizal fungi that have been identified include Ascomycetes such as *Hymenoscyphus (Pezizella), Myxotrichum* and *Gymnascella* (Dalpe, 1989; Read, 1983). Fungi forming mycorrhizal associations with orchids include many *Rhizoctonia* anamorphs (some of which have known teliomorphs), as well as other fungi that may form specific or non-specific associations with their hosts (Currah *et al.,* 1987; Ramsay *et al.,* 1987; Warcup, 1981, 1985).

B. Edaphic or Climatic Factors and Mycorrhizal Fungi

1. Propagules of *Mycorrhizal Fungi*

The spread to new roots, long-range dispersal and persistence of mycorrhizal fungi in ecosystems is dependent on the formation of propagules and their interactions with soil and environmental conditions (Fig. 2). It is important that infective propagules are present when root growth activity occurs, since roots have a limited period of susceptibility (Brundrett and Kendrick, 1990a; Hepper, 1985) and rapid colonization of the root system is required for an effective association (Abbott and Robson, 1984a; Bowen, 1987). The activity of VAM fungi in soils is usually quantified by measuring mycorrhizal formation within roots with a microscope using a clearing and staining procedure (see Brundrett *et al.,* 1990; Kormanik and McGraw, 1982). When these methods are used to quantify propagules of mycorrhizal fungi it is important to consider the total length as well as the proportion of host root occupied by VAM colonies (Abbott and Robson, 199la). The number of successful root contacts (ECM short roots, or individual VAM colonies within roots (which are often called infection units) is the best criterion to measure the infectivity of soil fungi (Huisman, 1982), but hyphal spread along roots and colony extension within roots also contributes to total colonization levels (Sanders and Sheikh, 1983; Smith and Walker, 1981). Increased soil hyphae activity often follows association establishment so it is also important to grow bait plants in the soil being tested for only a short period (several weeks) before enumeration.

Propagules of VAM fungi include spores, root fragments containing hyphae and vesicles (storage structures) and soil hyphae (Biermann and Lindermann, 1983; Manjunath and Bagyaraj, 1981; Tommerup and Abbott, 1981). The large soil-borne spores of VAM fungi, are considered by many to be the most important type of inoculum, but their numbers are often poorly correlated with mycorrhizal formation in soils (Abbott and Robson, 1984a, 1991a; Ebbers *et al.,* 1987; McGee, 1989; Mukerji and Kapoor, 1986; Schmidt and Reeves, 1984). Spore production by VAM fungi is influenced by many factors including the host plant (Section III.D.I), and soils in ecosystems often contain low numbers of living spores (Brundrett and Kendrick, 1988; Gay *et al.,* 1982; Janos, 1980b; Read *et al.,* 1976; Schenck and Kinloch, 1980). Living spores of VAM fungi present in the soil may not function as propagules, if they are quiescent (inactive because soil conditions are unsuitable) or have an innate period of dormancy-mechanisms which may help them survive periods of adverse soil conditions (Tommerup, 1987). Melanins (fungal pigments) within their relatively thick walls may help protect the contents of VAM spores, which sometimes receive further protection by forming within structures such as old seed coats (Daniels Hetrick, 1984). Spores are generally considered to be more resistant to adverse conditions than other VAM fungus propagules (Abbott and Robson, 1990).

A poor correlation between spore numbers and mycorrhizal initiation, and the rapid initiation (within a few days) of VAM infection that often occurs in ecosystems suggest that a pre-existing network of soil hyphae is often the main source of VAM inoculum (Birch, 1986; Jasper *et al.,* 1989a; McGee, 1989; Powell, 1977; Read *et al.,* 1976). Fragments of dead roots present in the soil can also initiate VAM, provided they are in close proximity to the new roots (McGee, 1987; Rives *et al.,* 1980), which would happen if they occupy the same soil channels (Went and Stark, 1968). The vesicles produced by many VAM fungi (hyphal swellings containing cytoplasm and lipids) are considered to function as temporary storage organs, but often elaborate multilayered walls like spores. Vesicles can function as propagules When isolated from roots (Biermann and Lindermann, 1983). Some plants in a deciduous forest community were found to have roots which maintained a living cortex for 2-10 years without undergoing secondary growth and still contained inactive hyphae and vesicles of VAM fungi (Brundrett and Kendrick. 1988). These species with long-lived roots may function as keystone mutualists (Gilbert, 1980). benefiting all host plants by allowing VAM fungi to perenniate within them (Brundrett and Kendrick, 1990a). Coarse soil organic matter colonized by VAM fungus hyphae can also contribute to their survival (Warner, 1984) and function as propagules (Koske, 1987b; Nicolson, 1960).

There is evidence that some endophytes do not produce spores (Johnson, 1977; McGee, 1989; Powell, 1977), or fail to survive in dried root fragments (Tommerup and Abbott, 1981). The relative importance of spores, old roots and soil hyphae as propagules apparently varies between species of VAM fungi occurring in the same site (McGee, 1989). Since the most important propagules of VAM fungi in soils are generally unknown, it is best to find some measure of the total infectivity of these fungi. The mycorrhizal infectivity of soils can be estimated by most probable number methods (serial dilutions using increasing proportions of sterilized soil), or "bioassays" (where the degree of colonization of a bait plants are measured). but it can also be difficult to interpret results obtained by these methods (see Abbott and Robson, 1991a). Mycorrhizal fungus activity, measured by the presence of mycorrhizal roots and spores, is generally thought to be concentrated near the soil surface, but propagules can be more numerous at greater depths (up to 2-4 m) in arid ecosystems (Virginia *et al.,* 1986; Zajicek *et al.,* 1986).

Propagules of ECM fungi include hyphae, mycelial strands and rhizomorphs (Ogawa, 1985; Read *et al.,* 1985). basidiospores (Bowen and Theodorou, 1973; Fox, 1983, 1986b), sclerotia (Fox, 1986a; Gibson *et al.,* 1988) and probably also mycorrhizal roots, but these fungi typically do not produce asexual (conidial) spores (Hutchinson, 1989). Boreal forest soil and leaf litter contains basidiospores which can initiate mycorrhizas (Amaranthus and Perry, 1987; Parke *et al.,* 1983, 1984). Localized patterns of ECM fungus proliferation depend on the production of hyphae, mycelial strands, or rhizomorphs by a particular endophyte (Ogawa, 1985). Hyphal strands of some ECM fungi will only initiate new mycorrhizas if attached to living host roots (Fleming, 1984). Roots with ECM usually live for one or more years and are protected by mantle hyphae (Harley and Smith, 1983), suggesting that they may be important perenniating structures.

2. Dispersal of Mycorrhizal Fungi

The spread of mycorrhizal fungi can occur by active processes (hyphal growth through soil) or passive dispersal mechanisms (Daniels Hetrick, 1984). Hyphae of VAM fungi radiate outward from mycorrhizal plants and thus can slowly spread the association to adjacent plants (Warner and Mosse, 1982; Scheltema *et al.,* 1985b). Dispersal mechanisms are responsible for introduction of mycorrhizal fungi to new geographic locations and the transfer of genetic information. The large (for a fungus) spores of VAM fungi can be suspended in moving air currents (Tommerup, 1982) and wind dispersal has been observed in arid ecosystems (Allen, 1988; Warner *et al.,* 1987). Transportation of spores by water erosion and human activities (transport of soil and living plants) probably also occurs (Daniels Hetrick, 1984; Walker, 1988). Koske and Gemma (1990) observed that VAM fungus spores produced in rhizome leaf sheaths or quiescent fungal structures within old roots could function as inoculum, even after exposure to sea water. They suggest that this provides a mechanism for the dispersal of mycorrhizal fungi along with fragments of plants which occupy early successional coastal habitats.

The ingestion and subsequent defecation of spores by animals can result in the introduction of VAM into new locations, as was observed during the revegetation of Mt. St Helens (Allen, 1988). Trappe and Maser (1976) observed that VAM spores remained viable after passage through the digestive tract of a rodent. Animals which probably transport VAM fungus spores include small mammals, grasshoppers, worms, ants, wasps and birds (see Table 1). Macroarthropod detritivores such as woodlice (Isopoda) and millipedes (Diplopoda) ingest and disperse mycorrhizal inoculum and may in turn be eaten by predatory beetles (Rabatin and Stinner, 1988). Earthworms, which frequently ingest VAM fungi and expel their spores in casts, are eaten by many small animals which may thus act as vectors for the mycorrhizal fungi (Rabatin and Stinner, 1988). Mycorrhizal fungus spores have been found within organisms which may act as vectors that belong to many trophic levels, but the distances involved and the importance of these dispersal mechanisms in ecosystems is usually not known.

Many fungi forming ECM associations have large fruiting structures (mushrooms) that produce abundant quantities of wind-borne spores, but survival and dispersal of these spores may be limited (Bowen and Theodorou, 1973; Harley and Smith, 1983). Sclerotia, including those produced by ECM fungi, can be moved in spring run-off water by floating or adhering to organic material (Malloch *et al.,* 1987). Some ECM fungi produce hypogeous fruiting bodies that are excavated and

Table 1

Organisms associated with mycorrhizal fungi

Organism	**Mycorrhizal fungus**	**Type of association**	**References**
Bacteria			
bacteria-like organelles	VAM	1	Macdonald and Chandler (1981)
spiroplasma-like organisms	VAM	1	Tzean *et al.* (1983)
Actinomycetes	VAM	2	Ames *et al.* (1989)
Actinomycetes	ECM	2	Richter *et al.* (1989)
Protoctistan fungi (Chytrids)			
Rhizidiomcopsis sp.	VAM	3	Ross and Ruttencutter (1977)
Spizellomyces sp.	VAM	3	Daniels and Menge (1980)
Protoctistan animals (Amoebae)			
Saccamoeha and *Gephramoeba* sp.	ECM	4	Chakraborty *et al.* (1985)
True fungi			
Anguillospora and *Humicola* sp.	VAM	3	Daniels and Menge (1980)
various fungi	VAM	2	Secilia and Bagyaraj (1988)
various fungi	ECM	2	Summerbell (1989)
Stachybotrys chartarum	VAM	2,5	Siqueira *et al.* (1984)
unidentified fungi	VAM	3	Ross and Ruttencutter (1977)
"Rhizoctonias"	VAM	2,3	Williams (1985)
aphyllophoralean fungi	ECM	2	Fries and Swedjemark (1985)
various "fungicolous" fungi	ECM	2,6	Barnet (1964), Hawksworth (1981)
Nematodes			
Aphelenchoides sp.	Ericoid	4	Shafer *et al.* (1981)
fungus-feeding nematodes	VAM	4	Jngham (1988) (review)
Meloidodera sp.	ECM	4	Zak (1967)
Aphelenchus sp.	ECM	4	Sutherland and Fortin (1968)
Arthropods			
mites	all?	4	see text
collembola (springtails)	VAM	4,7	Moore *et al.* (1985), Finlay (1985), Rabatin and Stinner (1988)
Pemphigus sp. (aphid)	ECM	8	Zak (1965)
Tetraneura sp. (aphid)	VAM	8	Reddy and Sharma (1981)
Coleoptera (25+ sp.)	ECM	6,9	Fogel and Peck (1976) (review)
Onicus sp. (sowbugs)	VAM	7,10	Rabatin and Stinner (1988)
Gryllus sp. (crickets)	VAM	7,10	Rabatin and Stinner (1988)
ants and wasps	VAM	10	McIlveen and Cole (1976)
Earthworms			
Lumbricus sp.	VAM	7,10	Mcllveen and Cole (1976)
Birds			
Hirundo sp. (barn swallow)	VAM	10	Mcllveen and Cole (1976)
Animals			
squirrels, other small mammals and marsupials	ECM & VAM	7,9,10	Blaschke and Baumler (1989), Maser and Maser (1988), McIntire (1984), Malajczuk *et al.* (1987), Cowan (1989)

Table 1 Notes.

* Association types:
1, found in cytoplasm (role unknown);
2, associated with fungi;
3, occupy or attack spores (parasitic or necrotrophic);
4, feed on hyphae;
5, inhibit spore germination;
6, feed on epigeous sporophores;
7, ingest spores;
8, feed on mycorrhizal roots;
9, feed on hypogeous sporophores;
10, move spores with soil.

About this version of the review:

This version has been scanned from the original and converted to searchable text by an OCR program. The OCR process results in numerous minor errors, some of which may remain. A number of minor errors have been corrected from the original, especially in spelling and references. Typesetting differs from the original, but the content of each page is the same (except for some tables). Hyphenated words were removed to facilitate searching

Citation: as for original.

Mark Brundrett 2009

consumed by small mammals or marsupials and thus spread to new locations (Table 1). Spores of ECM fungi contained in animal faeces can be a viable source of inoculum (Kotter and Farentinos, 1984; Lamont *et al.,* 1985). In western North America, hypogeous fungi form a major part of the diet of squirrels, which in turn are beneficial to the community by transporting nitrogen-fixing bacteria and fungal spores which can establish new mycorrhizal fungus colonies or transfer genetic material to existing colonies (Maser and Maser, 1988). Similar tree-mycorrhizal fungus-dispersing animal inter-relationships also occur in Europe, Australia and New Zealand (Blaschke and Baumler, 1989: Malajczuk *et al.,* 1987; Cowan, 1989). The supply of mycorrhizal inoculum could be limited in some recently created or disturbed habitats if these fungi were less readily dispersed than their host plants (Section III. F.4).

3. Soil Organisms Associated with Mycorrhizal Fungi

The wide variety of mycophilous (Barnet, 1964; Hawksworth, 1981) soil organisms that are known to ingest, inhabit, or associate with hyphae or spores/sporophores of mycorrhizal fungi are listed in Table 3. This table contains members of most of the trophic levels of organisms which feed in or on soils. Rhizosphere micro-organisms associated with mycorrhizal roots are considered in Section III. E.3.

Some organisms listed in Table 1 may be associated with moribund hyphae or spores and thus have little effect on mycorrhizal associations. but others apparently kill living hyphae and spores of these fungi. Chytrids may occupy VAM fungus spores that already are moribund (Paulitz and Menge, 1984), but in other cases contamination by these organisms is correlated with reduced spore germination (Sylvia and Schenck, 1983). Fungivorous mites are an important component of soil food webs (Coleman, 1985) and are also likely to be major consumers of mycorrhizal fungi (St John and Coleman, 1983). Dense mats of ECM roots and fungi in forest soils can have substantially higher populations of microbes and microarthropods than other areas (Cromack *et al.,* 1988). Fungi that may be parasitic on ECM roots have been observed to form hyphae in the mantle and haustoria within root cells (Agerer, 1990; Brundrett *et al.,* 1990). Several mycorrhizal root associates, including root inhabiting fungi, nematodes and an aphid-fungus partnership were observed during a study of Canadian forest tree roots (Brundrett *et al.,* 1990) and it is certain that many more interesting mycorrhizal root-soil organism associations will be unearthed. Because of the widespread occurrence and abundance of mycorrhizal fungi in soils, we would expect them to be an important food source for many soil organisms (Daniels Hetrick, 1984; Harley, 1971; Odum and

Biever, 1984). Fungus-feeding nematodes and springtails have been observed to reduce the efficacy of mycorrhizal associations in some cases (Warnock *et al.,* 1982; Finlay, 1985; Ingharn, 1988; Rabatin and Stinner, 1988). Differences in the susceptibility of mycorrhizal fungi to antagonistic microbes has been reported to influence the outcome of competition between endophytes (Godfrey, 1957; Ross and Ruttencutter, 1977).

Spores of VAM fungi isolated from soils in natural ecosystems frequently show signs of predation (Brundrett and Kendrick, 1988; Berliner and Torrey, 1989; Janos, 1980a; Koske, 1988) that may be partially responsible for seasonal fluctuations in their abundance (Section III. E.1). Hyphal grazing by soil organisms has the potential to significantly reduce the efficacy of mycorrhizal associations in ecosystems-by limiting the transport of mineral nutrients to roots (Finlay, 1985; Ingham, 1988; McGonigle and Fitter, 1988b; Rabatin and Stinner, 1988). but also allows nutrients contained in hyphae to be recycled (Coleman, 1985; Perry *et al.,* 1987).

4. Soil Disturbance and Mycorrhizal Fungi

Mycorrhizal propagules can be severely influenced by damage to vegetation and soils resulting from natural processes or human intervention. These destructive processes include intense fires (Dhillion *et al.,* 1988; Klopatek *et al.,* 1988; Wicklow-Howard, 1989), exposure of subsurface soil by erosion (Day *et al.,* 1987; Habte, 1989), or by burrowing animals (Koide and Mooney, 1987) and volcanic activity (Allen, 1988). Human activities which influence mycorrhizas include; topsoil disturbance and stockpiling during mining (Danielson, 1985; Jasper *et al.,* 1987; Rives *et al.,* 1980; Stahl *et al.,* 1988) and clear-cut logging (Janos, 1987; Parke *et al.,* 1984; Perry *et al.,* 1987). Agricultural practices such as tillage (Evans and Miller, 1988), long fallow periods (Thompson, 1987), soil compaction (Wallace, 1987). growth of non-mycorrhizal crops (Section III. F.3.a), biocide application (Haas *et al.,* 1987; Medve, 1984), or flooding for rice culture (Hag *et al.,* 1987; Nopamornbodi *et al.,* 1987) can also adversely influence mycorrhizas. These processes usually result in greatly reduced VAM or ECM fungi formation. Forest decline associated with air and/or precipitation borne pollution has become a serious problem in Europe and North America (Klein and Perkins, 1988; Smith, 1990) and various forms of pollution can inhibit mycorrhiza formation in experimental systems (Section III. E.6). Small scale disruptions due to frost action, shrinkage of drying soil, or the activities of soil animals may also be detrimental to mycorrhizal hyphae in soil (Read and Birch, 1988). Klopatek *et al.* (1988) found that high soil temperatures resulting from a fire were correlated with reductions in subsequent VAM formation.

Soil disturbance may Have a direct impact on propagules of mycorrhizal fungi or an indirect affect through changes to soil properties. Disturbance impacts on VAM fungi that have been hypothesized include; (i) a reduction numbers of viable spores, (ii) loss of a hyphal network in the soil, or (iii) the prevention of hyphal growth from root inoculum to new roots (Evans and Miller, 1988; Jasper *et al.,* 1989abc; Rives *et al.,* 1980). The relative importance of these mechanisms has not been fully established and may vary in different situations.

A reduction in VAM endophyte diversity from 11 to one species occurred after disturbance in an alpine area (Allen, *et al.,* 1987). Spores of these fungi are fairly resistant to physical and chemical stress (Tommerup and Kidby, 1980) but apparently are killed or removed by severe disturbance. During fallow periods or when soil is stockpiled. the infectivity of spores could decline as their population structure becomes older (without host plants to support new spore production) and as a result of premature germination (Section III.E.1). Daft *et al.* (1987) found that spores were still viable after topsoil storage for 12 weeks if temperature and humidity were moderate. They found that spores were more resistant to these conditions than root fragments and much more resistant than hyphae. A network of mycorrhizal fungus hyphae in soil is considered to be an important source of inoculum in natural ecosystems (Section III.B.1). Disruption of this network can result in a substantial loss of mycorrhizal infectivity (Evans and Miller, 1990; Jasper *et al.,* 1989a,b), or reduce the vigour of mycorrhizas that do form perhaps because they were no longer connected to a common resource pool (Read & Birch 1988). Soil structure changes resulting from disturbance could disrupt the spatial association between old and new roots, or otherwise reduce the effectiveness of root inoculum (Evans and Miller, 1988; Rives *et al.,* 1980). Changes to soil properties and populations of soil organisms which occur during soil stockpiling can reduce the efficacy of surviving VAM endophytes (Abdul-Kareem and McRae, 1984; Stahl *et al.,* 1988; Waaland and Allen, 1987).

Loss of ECM inoculum can occur rapidly in the absence of host plants after clear-cutting. especially with burning and scarification and soil property changes can prevent the reestablishment of surviving fungi (Amaranthus and Perry, 1987; McAfee and Fortin, 1986, 1989; Parke *et al.,* 1984; Perry *et al.,* 1987). During revegetation "early stage" mycorrhizal fungi (Section III. B.6) such as *Pisolithus tinctorius,* which are well adapted to growth in mineral soils, become dominant until forest soil conditions develop (Danielson, 1985; Gardner and Malajczuk, 1988; Stahl *et al.,* 1988). During the recovery process a succession involving increasing numbers of ECM fungi occurs as soil organic matter builds up (Section III.B.6). After disturbance, surviving ECM fungus inoculum may be concentrated in localized soil pockets high in organic materials (Christy *et al.,* 1982; McAfee and Fortin, 1989).

Following ecosystem disturbance, a reduction in mycorrhizal inoculum apparently is often responsible for reduced mycorrhiza formation. The level of inoculum in disturbed soil will depend on initial propagule concentrations, the resilience of propagules, their reintroduction by dispersal mechanisms and on the impact of changes to soil conditions on the activity of surviving fungi. The mycorrhizal dependency of recolonizing vegetation also varies (Section III.F.4), In some cases it may be advantageous or necessary to introduce mycorrhizal fungi to replace lost inoculum or, that provide a greater benefit than indigenous fungi (Danielson, 1985; Cook and Lefor, 1990; Jasper *et al.,* 1988; Perry *et al.,* 1987; Stahl *et al.,* 1988).

5. Climatic or Edaphic Specificity of Mycorrhizal Fungi

Environmental factors and soil conditions influence the occurrence of mycorrhizal associations in ecosystems (Section III.F.5), but it is hard to examine the direct impacts of these factors on mycorrhizal fungi because they rarely occur in nature without a host and members of the Glomales can not be grown axenically (Harley and Smith, 1983). However, some evidence of the physiological diversity of mycorrhizal fungi has been provided by comparing experimental responses to soil pH, soil nutrient levels, soil moisture, salinity, temperature and other factors (Abbott and Robson, 1991a; Daniels Hetrick, 1984; Morton, 1988; Slankis, 1974; Trappe and Molina, 1986). Most of this data has been collected using simplified experimental systems which allow the influence of one factor on one mycorrhizal fungus to be examined, but some field data are also available for comparison.

Changes to soil properties occurring during succession or between sites with similar climates can be correlated with the predominance of different species or isolates of VAM fungi (Bethenfalvay *et al.,* 1982; Gerschefske Kitt *et al.,* 1987; Puppi and Reiss, 1987; Rose, 1988). There is limited evidence that climatic factors can influence the distribution of mycorrhizal fungus taxa (Section III.B.6). Ebbers *et al.,* (1987) and Anderson *et al.* (1984) discovered changes in predominate species of VAM fungi across a soil moisture (soil fertility) gradient in a prairie site, which had a much greater influence on plant populations. Henkel *et al.,* (1989) observed that isolates of four VAM fungi from adjacent ridgetop, mid-slope and basal sites in an arid plant community were most infective in the soil from which they were collected and less infective in soil from the other two sites. They suggested that these isolates had adapted to phosphorus levels or other factors in the soil where they occur. Adelman and Morton (1986), Graham *et al.* (1982b), Molina *et al.* (1978). Porter *et al.* (1987b) and Stahl *et al.* (1988) also observed that clonal isolates of VAM fungi were more effective when used in their native soil type.

Further evidence of the physiological diversity of VAM fungi is Provided by comparing responses of different species or isolates to physical conditions (Table 2). These comparisons have demonstrated variations between taxa and intraspecific variability within species of VAM fungi in their ability to promote plant growth when exposed to the factors listed in Table 2. These fungi apparently have a limited tolerance range to environmental conditions (Stahl *et al.,* 1988) and possess specific adaptations to the soil in which they occur (Lambert *et al.,* 1980). These adaptations apparently can influence the outcome of competition between VAM fungi (Gerschefske Kitt *et al.,* 1987). The effect of low soil pH on VAM associations is discussed by Howeler *et al.* (1987) and Robson and Abbott (1989). Some endophytes can still provide substantial benefits to the host plant in soils with low pH and high aluminium levels, while others are less effective (Table 2). It has sometimes been observed that the fine endophyte called *Glomus tenue* is more abundant in acidic soils (Gianinazzi-Pearson *et al.,* 1980; Wang *et al.,* 1985). Porter *et al.,* (1987a) found the distribution of VAM fungus taxa in Western Australia to be highly correlated with soil pH. Bethlenfalvay *et al.,* (1989) proposed that the term "edaphotype" be used to describe intraspecific variants of mycorrhizal fungi isolated from different soils that differ in their physiological response to various conditions. There are many statements in the mycorrhizal literature about the physiological, ecological, or mutualistic characteristics of species of VAM fungi that actually only describe one particular clonal isolate (Morton, 1990).

Unfortunately, VAM research has been concerned with plant responses to mycorrhizas with little consideration of specific endophytes, thus creating the impression that these fungi are functionally equivalent (Abbott and Robson, 1991a; Morton, 1988; Walker, 1988). This impression has been strengthened by the classification problems of fungi such as *Glomus fasciculatum* which originally had a worldwide distribution and was accredited with remarkable genetic and physiological plasticity (Morton, 1988); this fungus has now been more precisely defined (Walker and Koske, 1987). It is probable that many of the earlier reports of the occurrence of *Glomus fasciculatum* and experiments conducted with this fungus refer to other, as yet unnamed fungi. If the taxonomy problems associated with many of the VAM fungi originally considered to have wide geographical ranges and the physiological variations that often occur within species of these fungi are considered, it becomes apparent that these fungi do exhibit considerable.

Table 2

Evidence of the adaptation of mycorrhizal fungi to localized soil conditions as Provided by comparisons between species or geographic isolates of species in responses to various conditions

Soil or environmental condition	References
VAM fungi	
high or low soil P levels	Boerner (1990), Davis *et al.* (1984), Henkel *et al.* (1989), Haas and Krikun (1985), Johnson (1976), Krikun (1983), Thomson *et al.* (1986)
soil micronutrient levels	Killham (1985)
aridity	Bethlenfalvay *et al.* (1989). Sieverding and Toro (1988), Simpson and Daft (1990a), Stahl and Smith (1984)
salinity	Pond *et al.* (1984)
low soil pH	Adelman and Morton (1986), Hayman and Tavares (1985), Howeler *et al.* (1987), Koomen *et al.* (1987), Porter *et al.* (1987b)
toxic levels of metals	Dueck *et al.* (1986), Gildon and Tinker (1983) Koslousky and Boerner (1989)
low or high temperatures	Dodd and Jeffries (1986), Raju *et al.* (1990) Schenck and Smith (1982), Sieverding (1988)
ECM fungi	
water stress	Coleman *et al* (1989), Parke *et al.* (1983), Slankis (1974)
calcium availability	Lapeyrie and Bruchet (1986)
different pH levels	Hung and Trappe (1983), McAfee and Fortin (1987)
toxic levels of metals	Denny and Wilkins (1987), Jones and Hutchinson (1988), Thompson and Medve (1984)
high or low temperatures	Cline *et al.* (1987), Gibson *et al.* (1988), Ingleby *et al.* (1985), Slankis (1974)

physiological diversity and probably have evolved specific adaptations to the edaphic and environmental conditions of the sites where they occur.

The distribution and mycorrhizal efficacy of fungi forming ECM associations is also influenced by climatic and edaphic factors (Bowen and Theodorou, 1973; Slankis, 1974; Harley and Smith, 1983). These fungi are generally considered to be acidophilic (preferring a low soil pH) inhabitants of litter layers near the soil surface (A horizon), but some "early stage fungi" prefer calcareous mineral soils (Section III.B.6). Isolates of ECM fungi show considerable inter- and infraspecific variations in responses to the factors listed in Table 2. Most of these results correlated with responses to similar factors in soils (Cline *et al.,* 1987; Coleman *et al.,* 1989; Hung and Trappe, 1983). It has been suggested that variations in tolerances to physical factors may be responsible for soil specificity (Last *et al.,* 1984) and restricted geographic ranges (Ingleby *et al.,* 1985), and may influence the outcome of fungal competition (McAfee and Fortin, 1987) or host responses to factors such as drought (Parke *et al.,* 1983). It is apparent that a wide range of variations in tolerance to edaphic and climatic factors (such as temperature extremes, drought, soil toxicity etc.) often occur both between and within species of mycorrhizal fungi and these variations may represent adaptation to specific site conditions by poorly understood genetic mechanisms (Morton, 1990; Tommerup, 1988; Trappe, 1977; Trappe and Molina, 1986).

6. The Population Ecology of Mycorrhizal Fungi

Detailed surveys of VAM fungus spores have provided information on the numbers of endophyte species occurring in some plant communities (Table 3). From these surveys it can be seen that the soil in one location normally contains more than one VAM fungus and may contain a fairly wide diversity of these fungi (considering that only about 150 species are known – (Morton 1990). It is not possible to use the results in Table 2 to examine the influence of soil conditions or environmental factors on VAM fungus diversity, because of differences in sampling methodologies (sampling intensity and the area surveyed vary considerably) and the limited number of surveys involved.

Several VAM fungi can occur within a single root (Abbott and Robson, 1984b, 199la). It is possible to identify particular endophytes by comparing their colonization patterns within roots (Abbott and Robson, 1982), or using recently devised immunological or biochemical techniques (Hepper *et al.,* 1988; Morton, 1988; Rosendahl *et al.,* 1989). However, in most cases investigators measure overall root colonization levels without considering the relative contribution of particular endophytes, so our knowledge of the ecology of VAM fungi is based on the occurrence of their spores. Spore occurrence data may be misleading because spore abundance can be poorly correlated with mycorrhiza formation (Section III.B.l), fungi which do not produce recognizable spores may be present (Johnson, 1977; McGee, 1989; Morton, 1988) and roots of different plants often intermingle so spores could occur under plants that they were not associated with. The spore characteristics used to identify species of VAM fungi are thought to be relatively conservative features so that considerable genetic variations may well occur within a species of VAM fungus (Morton, 1990) and this intraspecific diversity may also have to be considered.

Table 3
Populations of VAM fungi occurring at various sites

VAM species	Habitats sampled (*n*)	Location	References
9-18	Coastal, sand dunes (1)	Eastern USA	Tews and Koske (1983)
11-18	Coastal, sand dunes (6)	Eastern USA	Koske (1987a)
2-12	Coastal, sand dunes (4)	Hawaii, USA	Koske (1988)
9	Coastal, sand dunes (4)	Florida, USA	Sylvia and Will 1988
18	Arid mountains (region)	Arizona, USA	Bloss & Walker (1987)
4	Arid grassland (3)	Wyoming, USA	Henkel *et al.* (1989)
2-5	Grasslands (27)	Western USA	Molina *et al.* (1978)
21	Prairie (1)	Kansas, USA	Daniels Hetrick and Bloom (1983)
3-6	Wheat fields (4)	Kansas, USA	Daniels Hetrick and Bloom (1983)
6	Mediterranean shrubland (1)	Southern Australia	McGee (1989)
3-5	Pasture, crop or native (20)	Western Australia	Abbott and Robson (1982)
18	Native cerrado vegetation (1)	Brazil	Schenck *et al.* (1989)
7-15	Field crops (4)		
10	Forest (1)	Florida, USA	Schenck and
7-12	Field crops (6)		Kinloch (1980)
10	Forest (1)	New Zealand	Johnson (1977)
1-5	Pasture or forest (37)	New Zealand	Powell (1977)
3-8	Seminatural or agricultural (4)	southern USA	Adelman and Morton (1986)
10-12	Agro-forestry (2)	Iowa, USA	Walker *et al.* (1982)
7	Apple orchard (1)	Quebec, Canada	Dalpé *et al.* (1986)

The occurrence of several VAM fungi in soils or within roots suggests that interspecific competition between them is possible. Koske (1981) could find no evidence that any of the VAM endophytes occurring in a coastal ecosystem were better competitors than others and considered environmental factors and host plants to be more important factors influencing their distribution. However, Gemma *et al.* (1989) observed seasonal variations in spore production between co-existing endophytes and the fact that abundant spore production by one VAM fungus was usually correlated with lower levels of spore production by others, which may have been due to antagonism between species.

When several isolates of VAM fungi are inoculated together in pot culture experiments, some have proven to be better competitors than others (Lopez-Aguillon and Mosse, 1987; Van Nuffelen and Schenck, 1984; Wilson, 1984). In these kinds of studies the most successful fungi generally were those that colonized roots most rapidly (Abbott and Robson, 1984b; Wilson, 1984). The outcome of competition between endophytes would be expected to depend on the placement and amount of their inoculum, their hyphal growth rates in soil and interactions within roots (Abbott and Robson, 1991ab; Hepper *et al.,* 1988). Root elongation rates of the plants in natural ecosystems, for which this has been measured, are substantially slower than those of crop plants (Brundrett and Kendrick, 1990a; Huisman, 1982; Lyr and Hoffmann, 1967; Russell, 1977), so rapid responses to the presence of roots and hyphal elongation rates should be less important in nature. It is possible that mycorrhizal fungi with slow hyphal growth rates would preferentially occupy slowly elongating roots, while faster fungi in the same soil colonize roots with greater rates of elongation.

Competition between endophytes occurring in the same soil could be reduced if their activities were chronologically separated by phenological differences, or spatially separated by substrate preferences, or host specificity. but the microhabitat preferences of VAM fungi have rarely been considered. Fungi with narrow hyphae (called fine endophytes or Glomus tenue) can be readily distinguished from other VAM fungi when cleared and stained roots are examined. Dodd and Jeffries (1986) observed that a fine endophyte was most active during the winter, while other endophytes predominated at other times. It might be expected that mycorrhizal fungi which have periods of activity and quiescence would preferentially associate with roots that were active at the same times of the year. McGee (1989) observed that propagules of a fine endophyte were more abundant near the soil surface while other fungi were more abundant at greater depths. Anderson *et al.* (1984) found that different VAM fungi were most common at opposite ends of a soil moisture-fertility gradient at a prairie site. Factorial experiments involving many combinations of host plants and VAM fungi have rarely demonstrated specificity (Section III.D.1), but almost nothing is known about the specificity of interactions between host plants and mycorrhizal fungi in nature. McGonigle and Fitter (1990) have observed that fine endophyte hyphae preferentially colonized roots of the grass *Holcus lanatus,* while endophytes with coarse hyphae were more common in other plants at the site throughout the year. This report of "ecological specificity" and the other examples discussed above suggest that specialization in the phenology, and microhabitat preferences, and perhaps some degree of host specificity may limit interactions between the isolates of VAM fungi present in a soil.

The fungi forming ECM associations include a large group of Basidiomycetes as well as other fungi and it is normal for a wide diversity of these fungi to be present on the roots of one host tree (Mason *et al.,* 1987). While it is possible to identify the ECM fungi associated with roots by anatomical studies (Agerer, 1986) or other means, most of our information about the occurrence of these fungi comes from observations of their above-ground reproductive structures-which are usually closely associated with mycorrhizal roots (Hilton *et al.,* 1989; Trappe, 1962). Villeneuve *et al.* (1989) observed that the diversity of ECM fungi occurring in several temperate deciduous and coniferous forest sites was positively correlated with the dominance of potential host trees. Bills *et al.* (1986) observed that ECM fungus diversity was greater in mixed hardwood forests than in coniferous forests where one tree predominated. Tyler (1985) examined the influence of edaphic factors on the distribution of macrofungi in European forest sites (dominated by the ECM tree *Fagus*). In this study the relative importance of ECM fungi increased (and saprobes decreased) in more acidic soils and the distribution of many fungi was correlated with edaphic factors, such as soil organic matter and metal ion content.

Many ECM fungi have a wide host range and will form associations with hosts which originate on the other side of the globe, but others specifically associate with particular host taxa (Duddridge, 1987; Le Tacon *et al.,* 1987; Malajczuk *et al.,* 1982; Molina, 1981; Molina and Trappe, 1982b). Kropp and Trappe (1982) have suggested that plants such as *Alnus rubra* and *Pseudotsuga menziesii.* which often form pure stands during early succession, tend to form specific associations with ECM fungi, while species such as *Tsuga heterophylla* which become established in the shaded understorey of other trees usually have non-specific ECM associates. Fungi that have specific ECM associations will be restricted in their distribution by the occurrence of their hosts, but other fungi may have specialized habitat preferences etc. which influence their occurrence. When ECM fungi are introduced to a site, as when inoculated host seedlings are transplanted, their success depends on their ability to spread through the soil to new roots and on the outcome of competition with indigenous fungi (McAfee and Fortin, 1986).

When ecosystems recover from severe disturbance a succession of different ECM fungi will associate with host plants growing at a site, beginning with "early stage" and ending with "late stage" fungi (Fleming, 1985; Gardener and Malajczuk, 1988; Mason *et al.,* 1987). "Early stage" but not "late stage" fungi can be easily introduced in disturbed sites (Danielson, 1985; Fox, 1986b). Physiological differences between these two groups of fungi are apparent in aseptic culture experiments (Gibson and Deacon, 1990). Early stage fungi are associated with young forests where ECM roots occur in mineral soil, while late stage fungi form ECM in the litter layer of mature forest soils (Dighton and Mason. 1985; Mason *et al.,* 1987). Fungi in the former group may be inhibited by changes to soil chemical and physical properties associated with tree leaf litter. etc. which occur during succession (Perry and Choquette, 1987). Gardener and Malajczuk (1988) observed five ECM fungi associated with *Eucalyptus* seedlings in a 1-year-old revegetation site which contrasted with 40 species in a mature Eucalyptus forest. Fungal diversity generally increases until late in succession. when the number of species present may decline because those with more specialized host or substrate preferences predominate (Bills *et al.,* 1986; Mason *et al.,* 1987).

Different clones of a mycorrhizal fungus may be present in the same soil and form colonies which expand by directional or radial hyphal growth. When colonies of the same mycorrhizal fungus overlap they may join by hyphal anastomosis (non-reproductive cell fusion). Hyphal anastomosis is a distinguishing characteristic of higher (Basidiomycete and Ascomyete) fungi and is considered not to occur in the Zygomycetes (Kendrick, 1985), but does occur in members of the Glomales (Tommerup, 1988). Anastomosis is an important mechanism by which mycorrhizal fungi can maintain continuity, exchange nuclear and extra-nuclear genetic information and reproduce sexually (Tommerup, 1988; Trappe and Molina, 1986). We would expect hyphal anastomosis to be common in ECM fungi (most of which are Basidiomycetes or Ascomycetes), but the frequency with which this event occurs between clones of VAM fungi in soil is unknown. Frequent anastomosis would appear to be essential, especially after a period of quiescence when fungal activity may have to be re-initiated form various scattered propagules. Otherwise clones would remain separate and compete for soil resources and host roots with which to form associations (this may occur to some extent). Tommerup (1988) has observed that spores of mycorrhizal fungi isolated 5 m apart formed compatible anastomoses (evidence for original continuity). while the compatibility of spores which originated 150 m apart was lower (71%). Fries (1987b) found that many genetically distinct isolates of one species of ECM fungus could occur in a small forest area.

The natural distribution of plant species is limited by their tolerance to environmental conditions. especially periods of extremely cold temperatures, or when soils are dry, but biotic and soil factors are also important (Barbour *et al.,* 1987; Woodward, 1987). One might also expect that the distribution of mycorrhizal fungi would also be influenced by similar factors, since it would be impossible for one isolate of these fungi to be well adapted to both high and low extremes in temperature, moisture, pH, etc. Some evidence for the climatic adaptation of endophytes is provided by the optimum, maximum and minimum germination temperatures of mycorrhizal fungi (Tommerup, 1983b) which can be higher in isolates from warmer regions than for fungi originally from cooler locations (Schenck *et al.,* 1975). Koske (1987a) found that some VAM fungi were more abundant at the northern or southern end of a 355-km latitudinal (temperature) gradient of sites with similar coastal vegetation.

Environmental factors might be expected to override the more localized mycorrhizal fungus distribution influences (soil conditions, preferred host plants, dispersal effects) considered in previous sections, Unfortunately, there has been a tendency to promote the use of one particular fungus isolate (that would have a limited distribution in nature) as if it had universal applicability in mycorrhizal applications. Considerable thought has been given the criteria used to select "superior" isolates of mycorrhizal fungi for field inoculation programmes (Abbott and Robson, 1991b; Howeler *et al.*. 1987; Trappe, 1977), but we must also consider the limits to their ecological adaptability if one isolate is to be successfully used in a wide range of habitats/soils.

The diversity of ECM fungi present in communities of associated plants is typically much higher than that of VAM fungi (although additional intraspecific genetic diversity may also be important). A diverse assemblage of ECM fungi is present in communities which generally contain relatively low diversity of host plants (Section III.F.5). It is necessary to envisage a high degree of ecological specialization of ECM fungi (with regards to host, microhabitat, phenology, or substrate preferences), or complex biotic interactions between these fungi to understand why so many of them can coexist in relatively small volumes of soil. Little is known about the ecology of fungi forming less common types of mycorrhizal associations.

Massive destruction of native vegetation is occurring because of deforestation in tropical regions (Jordan, 1985) and forest decline in temperate regions (Klein and Perkins, 1988). While mycorrhizal fungi often exhibit little host specificity, evidence is accumulating that they have become adapted to specific edaphic conditions. Substantial losses in fungal diversity occur when ecosystems are disturbed or converted to agriculture (Allen *et al.,* 1987; Daniels Hetrick and Bloom, 1983; Schenck and Kinloch, 1980; Schenck *et al.,* 1989). These processes are likely to result in a permanent loss of some of the isolates of mycorrhizal fungi which have become highly adapted to local conditions. During subsequent attempts at ecosystem reconstruction, the impact of this reduction in genetic resources of mycorrhizal fungi will depend on how rapidly surviving fungi adapt to changing soil conditions during succession and how effectively well-adapted isolates are dispersed from remnants of native vegetation.

C . The Host Plant

l. The Structural Diversity *and Function of Roots*

With few exceptions. roots are essential to the growth and survival of plants. As much as 30% of the plant genome is involved in defining root characteristics (Zobel, 1986) and roots are normally responsible for acquiring the resources (water and mineral nutrients) most often limiting plant growth in ecosystems (Chapin *et al.,* 1986; Fitter, 1986a). The primary functions of roots include (i) absorption of water and mineral nutrients, (ii) anchorage and physical support, (iii) storage and (iv) mycorrhizal formation (Esau, 1965; Russell, 1977). Roots may also support symbiotic nitrogen fixing associations (Gibson and Jordan, 1983; Torrey, 1978), influence shoot growth by growth-regulator production (Carmi and Heuer, 1981; Richards and Rowe, 1977) and in specialized cases may be involved in vegetative propagation or parasitic attachment (Esau, 1965).

The structural and functional diversity in roots is generally considered to be much lower than that of plant shoots (Fitter, 1987). It is certainly true that roots essentially are elongated cylinders which often appear superficially similar. However. anatomical or chemical variations between the roots of different species can be sufficient to allow their identification in soils collected from natural ecosystems (Brundrett and Kendrick, 1988; Brundrett *et al.,* 1990; Chilvers, 1972). Thus with practice it may often be possible to identify roots in mixed samples by examination of their superficial characteristics, or during the course of mycorrhizal assessment. Individual roots can pass through three distinct developmental phases: (i) growth, (ii) maturation and (iii) (in some cases) secondary growth. The importance and duration of these stages varies between plants and root system components. Plants produce a number of types (orders) of roots, including tap, lateral, basal and adventitious roots, that are physiologically, structurally and genetically distinct (Zobel, 1986). For example, lateral roots typically are narrower in diameter, grow less rapidly and have shorter lifespans than roots with higher branching orders (Russell, 1977). The fine laterals (feeder roots) of trees, especially those forming ECM, are often heterorhizic differentiated into long and short elements, while those with VAM usually have more extensive lateral root systems, without heterorhizy (Brundrett *et al.,* 1990; Kubíková, 1967). Tree roots belong to four categories resulting from structural differences between Angiosperms and Gymnosperms and those with VAM or ECM associations (Brundrett *et al.,* 1990). In the later group, distantly related trees have evolved similar, heterorhizic roots with epidermal Hartig nets.

Correlations between root structure and function in natural ecosystems are hard to establish because of the scarcity of careful morphological investigations and the frequent use of vague expressions such as "brown" or "suberized" roots (which do not distinguish between tannin accumulation, exodermis, periderm suberization, or root death Richards and Considine, 1981). There is also a paucity of information about root phenology (which could be used to predict when mycorrhizal associations are likely to be active Section III.E.1). Root structural complexity (protective features such as suberized epidermal, hypodermal, or periderm cell walls) is often correlated with long root lifespans (Brundrett and Kendrick, 1988; Pienaar, 1968), or difficult substrates such as alpine soils (Luhan, 1955). Plants which grow in waterlogged soils generally have large air spaces in their cortex which helps them survive in anaerobic soils (Armstrong, 1979; Justin and Armstrong, 1987). Roots occurring in arid regions often have a cortex which collapses to leave an epidermal/exodermal sheath surrounding roots when the soil is dry (Drew, 1987; Hayden, 1919; Ginzburg, 1966). It is probable that many other correlations between root structure and function occur in natural ecosystems and would be discovered if the roots of plants in a variety of habitats were examined. Roots absorb and translocate nutrients by mechanisms that have been well examined in experimental systems (Marschner, 1986), but it may be difficult to apply some of this knowledge to plants in ecosystems because of many complicating factors (Tinker, 1990). These factors include pH changes, root hairs, exudates and bacteria in the rhizosphere (Tinker, 1990).

Root morphological criteria of relevance to any consideration of root nutrient acquisition and mycorrhizal formation include the presence of an exodermis (a barrier to solutes and microbes (Peterson, 1988)), heterorhizy (long and short roots). the proportion of roots at different developmental stages (primary roots with a cortex, secondary roots with a periderm, or senescent roots) and their duration and differences in root activity (lifespan and growth rate). Interactions between root structure and mycorrhiza formation will be considered in Section III.E.4.b.

D. Plants and Mycorrhizal Fungi

The physiology of mycorrhizal associations has been well discussed by Hayman (1983), Harley and Smith (1983) and Smith and Gianinazzi-Pearson (1988). Mycorrhizal associations are generally considered to benefit host plants by enhancing mineral nutrient acquisition, especially with regards to phosphorus (Section III.E.5). Nitrogen supply by ECM and ericoid associations is also considered to be important (Section III.F.1) and VAM associations may also improve nitrogen uptake (Barea *et al.,* 1989). Increase in the absorption of minor nutrients, such as Mg, Cu and Zn have also been observed, but Mn uptake can be reduced (Arines and Vilarino, 1989; Harley and Smith, 1983; Hayman, 1983; Killham, 1985; Pacovsky, 1986). Other less specific changes to host physiology, which include alterations in nutrient requirements. membrane composition and metabolite levels, apparently occur even when nutrient input is negligible (Dehne, 1986; Pacovsky, 1986). Mycorrhizal fungi (ECM and ericoid) apparently can influence host morphology and physiology by producing plant hormones, such as ethylene and auxins, which may be responsible for the reduced apical growth of mycorrhizal short roots (Berta *et al.,* 1988; Gay and Debaud, 1987; Rupp *et al.,* 1989). Root growth is usually only slightly affected by VAM (Section III.E.5.b), but a detrimental reduction in root elongation occurs in some cases (Jones and Hendrix, 1987). Mycorrhizal associations have been implicated in increased host resistance to disease and other stresses (Section III.E.6).

1. Compatibility and Specificity

Figure 2 illustrates the series of events which result in mycorrhizal formation. At the beginning of the process, root and mycorrhizal fungus activity is independently initiated and regulated (both partners may be responding to the same soil or environmental conditions), but there is strong evidence of genetic interactions between the mutualistic partners in the later stages of this process. Evidence of genome expression changes in the fungal partners is provided by hyphal structure and behavior at the root surface, but the response by roots apparently is largely restricted to individual cells forming exchange sites (Gianinazzi-Pearson, 1984). The widespread susceptibility of plant roots to colonization by mycorrhizal fungi may be explained by specific comparability systems. or because mycorrhizal fungi somehow avoid or fail to elicit host defence mechanisms (Gianinazzi-Pearson and Gianinazzi, 1989). There is little evidence of host-fungus specificity in most types of mycorrhizal associations (Duddridge, 1987; Gianinazzi-Pearson, 1984; Harley and Smith, 1983). Ineffective VAM associations have been discovered in only a few of the many host plant and mycorrhizal fungus combinations tried in synthesis experiments (Johnson, 1977; Giovannetti and Hepper, 1985). Thus relatively few endophytes (±150 members of the Glomales) can form associations with most members of the plant kingdom (Morton, 1988, 1990). Genotypic variations within a host species can influence the degree of VAM formation (Azcón and Ocampo, 1981: Krishna *et al.,* 1985; Lackie *et al.,* 1988; Sieverding and Galvez, 1988; Thomas and Ghai, 1987). Some hosts provide more benefit to VAM fungi than others, as is suggested by differences in the magnitude of spore production. but in most cases spore formation is closely related to the total length of mycorrhizal roots produced by a given host (Giovannetti *et al.,* 1988; Daniels Hetrick and Bloom, 1986; Howeller *et al.,* 1987; Pellet and Sieverding, 1986; Simpson and Daft, 1990b; Struble and Skipper, 1988).

The adaptation of mycorrhizal fungi to particular soil conditions (Section III.B.5). apparently is more common than specific interactions with host plants. Thus in experimental systems incompatible host-fungus combinations are rare, but in ecosystems many of these combinations may be less successful because the fungi are poorly adapted to the normal habitat of plants. However, even if environmental and soil conditions could somehow be excluded from consideration, particular endophytes are also likely to exhibit differences in metabolic competence (the ability to obtain and transport nutrients) (Smith and Gianinazzi-Pearson, 1988). McGonigle and Fitter (1990) observed the preferential association between a VAM fungus with fine hyphae and a grass species, but there have been few other attempts to identify the VAM fungus associates of plants in natural ecosystems (Section III.B.6). The assertion that VAM associations lack host-fungus specificity may well be a reflection of how little we known about these fungi. Observations of the occurrence of above-ground fructifications of ECM fungi has provided much information about associated host plants and the geographic ranges of these fungi (Mason *et al.,* 1987). There is usually a high correlation between the occurrence of fruiting structures and mycorrhizal formation by ECM fungi (Gardner and Malajczuk, 1988; Trappe, 1962), but association lists produced in this way are certain to contain some errors. One such erroneous report involved ash trees *(Fraxinus* sp.), which are known to have VAM associations, and the fungus *Boletinellus merulioides,* which is now known to associate with root-feeding aphids (Brundrett and Kendrick, 1987).

Details of mantle structure have also been used to identify associated ECM fungi in some cases (Agerer, 1986; Mason *et al.,* 1987). Most ECM fungi associate with a broad range of host plants, but incompatible host-fungus combinations have been found and some fungi specifically associate with one genus (or possibly a single species) of host trees (Duddridge, 1987). Clonal variations within Sitka spruce can influence populations of ECM fungi associated with their roots (Walker *et al.,* 1986). The compatibility of host plant-ECM fungus combinations has been tested using artificial conditions (host seedlings grown in aseptic media) and fungi that colonize roots best under these conditions are often those that form sporocarps in close association with the same host in the field (Molina and Trappe, 1982b). Attempts to form associations between ECM fungi and host plants that are incompatible (at least with the experimental conditions used) can result in a "wounding response" (lignification or phenolic accumulation and cell disruption) in the root cortex (Malajczuk *et al.,* 1984; Molina and Trappe, 1982b). There is strong evidence of cellular and genetic interactions between host plants and mycorrhizal fungi (Gianinazzi-Pearson and Gianinazzi, 1989), but these relatively subtle interactions may be hard to separate from environmental/edaphic influences (Section III.B.6) on the occurrence of mycorrhizal fungi in natural ecosystems.

2. Mycorrhizal Definitions

Researchers have used different criteria to designate the mycorrhizal status of plants. The Hartig net-hyphae forming a labyrinthic exchange site between root cells (Kottke and Oberwinkler, 1986; Massicotte *et al.,* 1987) should be used to identify roots with functional ECM associations. In most cases ECM associations are quantified by counting ECM short root tips (using superficial dissecting microscope examinations) and making occasional sections to confirm the presence of a Hartig net (Grand and Harvey, 1982). Unfortunately, some reports of ECM are only substantiated by the presence of fruiting structures produced by putatively mycorrhizal fungi in the vicinity of a plant (Harley and Smith, 1983). There are many early reports of VAM or ECM associations of trees which have since been well established to form mycorrhizas of the other type (see Harley and Harley, 1987 for examples). These designations should perhaps be re-evaluated if they were not originally based on careful morphological observations. However, there are well documented cases of trees belonging to taxa which normally have ECM also forming VAM. especially as seedlings (Chilvers *et al.,* 1987; Lodge, 1989; Vozzo and Hacskaylo, 1974) and such dual associations apparently are common in Australian arid communities (Kope and Warcup, 1986; Warcup, 1980, 1988). Samples collected in natural ecosystems will almost inevitably contain roots of more than one species, which must be carefully separated on the basis of their anatomical characteristics to avoid misinterpretations.

The presence of arbuscules (the main site of host-fungus nutrient exchange: Harley and Smith, 1983; Smith and Gianinazzi-Pearson, 1988), is normally used to designate VAM associations, but the presence of hyphae and vesicles alone have also been used as evidence. With practice, these latter structures can usually be distinguished from those produced by saprobic or parasitic fungi, but they make unreliable indicators since they also occur in senescent roots of non-host species, rhizome scales, etc. (Brundrett and Kendrick, 1988; Hirrel *et al.,* 1978; Stasz and Sakai, 1984). Arbuscules are ephemeral structures, which may be absent if samples are collected when roots are inactive (Section III.E.1). Thus it may be difficult to designate plants as mycorrhizal if they only have old or senescent roots when harvested. In ecosystem surveys it may be best to define VAM colonization levels as the proportion of a plant's root system that, when susceptible to colonization, supported an active association with arbuscules (Brundrett and Kendrick, 1988). This requires a prior understanding of host root phenology, or the collection of root samples throughout the year.

Mycorrhizal surveys independently conducted in diverse localities have shown that members of certain plant families rarely form mycorrhizal associations. These typically non-mycorrhizas families are listed in Table 4. but their have been some reports of mycorrhizas in most of these families (Section III.E.4). Studies of plants in ecosystems which have found plants within the same genus or family to have consistent mycorrhizal associations greatly outnumber reports of variable mycorrhizal relations within taxa (Brundrett and Kendrick, 1988; Brundrett *et al.,* 1990; Maeda, 1954; Pendleton and Smith, 1983; Selivanov and Eleusenova, 1974; Trappe, 1981, etc.).

Host plants forming Ericoid and Orchid mycorrhizas are taxonomically restricted, so these associations usually do not present identification problems (Hadley, 1982; Read, 1983). Members of the Ericales (Ericaceae

Table 4

Plant families which are predominantly nonmycorrhizal

CLASS Subclass Order	Family*	Habit and habitat§	Accumulated chemicals				
			Primative†			Advanced‡	
MAGNOLIOPSIDA							
Magnoliidae							
Nymphaelales	5 families	Aq	T±	P+	E±	Ak+	
Papaverales	Papaveraceae(?)	Hb	T-	P-	E-	Ak+	
	Fumariaceae	Hb	T-	P-	E-	Ak+	
Hamamelidae							
Urticales	Urticaceae(?)	Hb	T+	P+			
Caryophyllidae							
Caryophyllales	Phytolaccaceae(?)	Hb	T-	P-	E-	B+	Sp+
	Nyctaginaceae	Hb (Sb)	T-	P-	E-	B+	Sp±
	Aizoaceae	Hb	T-	P-	E-	B+	Ak+
	Chenopodiaceae	Hb Sa	T-	P-	E-	B+	Sp+ Ak+
	Amaranthaceae	Hb	T-	P-	E-	Sp+	B+
	Portulacaceae	Hb	T-	P-	E-	B+	
	Caryophyllaceae	Hb	T-	P±	E-	Sp+	
Polygonales	Polygonaceae	Hb (Sb)	T+	P+	E+	Aq+	
Dilleniidae							
Lecythidales	Lecythidaceae(VAM)	Tr (Sb)	T+	P+	E+	Sp+	
Nepenthales	3 Families	Carn	T+	P+	E±		
Capparales	Brassicaceae	Hb	T-	P-	E-	Gs+	Cy+
Ebenales	Sapotaceae(?)	Tr Sb	T+	P+	E+	St+	Tp+
Rosidae							
Proteales	Proteaceae	Sb (Tr)	T+	P+	E-	Ak+	Cy±
Podostemales	Podostemaceae	Aq	?				
Haloragales	2 families	Aq	T+	P+	E+	Cy+	
Rhizophorales	Rhizophoraceae(VAM)	Tr ±Aq Sa	T+	P+	E+	Ak+	
Santalales	10 Families(VAM)[1]	Para	T+	P+	E-	Cy±	Sp±
Rafflesiales	3 Families[1]	Para	?				
Sapindales	Zygophyllaceae	Sb	T-	P-	E-	Sp+	Ak± Gs±
Asteridae							
Solanales	Hydrophyllaceae(?)	Hb	T-	P-	E-	Tp±	Fl±
Scrophulariales	Scrophulariaceae(VAM)	Para±	T-	P-	E-	Ir+	Sp+ Or+
	Orobanchaceae[1]	Para	T+	P-	E-	Ir+	Or+
	Lentibulariaceae[1]	Carn	T-	P-	E-	Ir+	
LILIOPSIDA							
Alismatidae							
Alismatales	3 Families	Aq	T+	P+	E-		
Hydrocharitales	Hydrocharitaceae	Aq	T+	P+	E-		
Najadales	10 Families	Aq	T+	P±		Cy±	
Commelinidae							
Commelinales	Commelinaceae	Hb	T±			Fl+	
Eriocaulales	Eriocaulaceae(?)	Aq	?				
Restionales	Restionaceae(?)	Hb	T+	P+			
Juncales	Juncaceae	Hb	T+	P+		Cy±	Fl+
Cyperales	Cyperaceae	Hb	T+	P+		Al±	Fl+
Zingiberidae							
Bromeliales	Bromeliaceae[1]	Epi	T+	P±		Enz	Sp±

and Epacridaceae) almost always form ericoid (or arbutoid) associations (Read, 1983; Reed, 1987). but also form VAM associations in Hawaii (Koske *et al.,* 1990). Mycorrhizas of achlorophyllous plants. including monotropoid plants and some orchids, may superficially resemble ECM but are functionally different (Furman and Trappe, 1971; Harley and Smith, 1983). Root-colonizing fungi that do not form recognized types of mycorrhizal associations can often be observed in natural ecosystems and are especially common in arctic and alpine habitats (Currah and Van Dyk, 1986; Haselwandter and Read, 1982; Kohn and Stasovsky, 1990). Root colonization by one of these fungi (which has dark septate hyphae) can be beneficial to alpine plants (Haselwandter and Read, 1982). Root-colonizing fungi that do not form mycorrhizal associations may benefit plants by conferring disease resistance (Dewan and Sivasithamparam, 1988). These other beneficial root-fungus associations differ from mycorrhizal associations because they show little evidence of morphological or physiological specialization by either organism.

The concept that plants have varying degrees of dependence on mycorrhizal associations is gaining acceptance (see Janos, 1980b; Marschner, 1986; Miller, 1987). Detailed examinations of plants in natural ecosystems often show consistently differences between host plants occurring in a particular habitat in the degree (proportion of roots) supporting rnycorrhizal associations. These observations have shown that species generally either have consistently high levels of mycorrhizas, intermediate or variable levels of mycorrhizas, or are non-mycorrhizal (Brundrett and Kendrick, 1988; Dominik *et al.,* 1954b; Janos, 1980b; Koske and Gemma, 1990). Plants belonging to these categories have been designated as obligatorily mycorrhizal, facultatively mycorrhizal, or non-mycorrhizal.

Notes to Table 4 (opposite)

* ? = mycorrhizal status requires further study; VAM = family also contains species with VAM; 1 = highly reduced roots.

§ Hb = herbaceous; Sb = shrub; Tr = tree; Aq = aquatic herb; Para = parasitic on other plants; Carn = carnivorous; Sa = saline habitats, Epi = epiphytes.

† T = tannins; P = proanthocyanins; E = ellagic acid; + = present; - = absent; ± = present in some.

‡ Ak = alkaloids; B = betalains; Sp = saponiferous; Aq = anthraquinone glycosides; Gs = glucosinolates; St = sterols;
Tp = terpinoids; Al = aluminum; Cy = cyanogenic; Ir = iridoid compounds;
Or = orobanchin; Enz = proteolytic enzymes.

Obligatorily mycorrhizal plants have been defined as those which will not survive to reproductive maturity without being associated with mycorrhizal fungi in the soils (or at the fertility levels) of their natural habitats (Janos, 1980b; Kormanik, 1981). These species consistently support mycorrhizal colonization throughout most of their young roots. *Facultatively mycorrhizal plants* are those that benefit from mycorrhizal associations only in some (of the least fertile) soils in which they naturally occur (Janos, 1980b) (see Section III.E.4). In ecosystem surveys inconsistent mycorrhization (Trappe, 1987) or low levels of mycorrhizal colonization (less than 25%) (Brundrett and Kendrick (1988) have been used to designate facultatively mycorrhizal species when soil fertility levels could not be manipulated. The various factors, including soil nutrient levels, root system characteristics and host plant physiology, that determine the net benefit of mycorrhizal associations to plants are considered in Section III.E.5.

Non-mycorrhizal plants have roots that consistently resist colonization by mycorrhizal fungi, at least when they are young and healthy. These observations provide evidence that intrinsic properties of roots may regulate mycorrhiza formation, at least in some cases and possible mechanisms for this regulation are discussed in Section III.E.4.c. Nutrient levels and other soil properties (Section III. E.5) and mycorrhizal propagule dynamics (Section III. B.1) can also influence mycorrhizal associations, but in a less consistent manner.

E. Edaphic / Environmental Factors, Plants and Mycorrhizas

The events which occur during the life-cycle of a mycorrhizal association are shown in Fig. 2. The formation, survival and dispersal of mycorrhizal propagules have already been considered (Section III.B.1). Environmental factors, soil conditions, root properties, rhizosphere effects, etc. that influence the activity of these propagules, mycorrhizal fungus hyphae and roots, as well as the remaining stages in mycorrhizal formation and activity illustrated in Fig. 2 will now be considered.

1. Mycorrhizal Phenology

Seasonal variations in the periodicity of root growth and mycorrhizal activity occur in ecosystems and may be substantial enough to change the apparent mycorrhizal status of plants (Allen, 1983; Brundrett and Kendrick, 1988; Gay et *al.,* 1982; Giovannetti, 1985; Louis and Lim, 1987; Rabatin, 1979). There were no significant seasonal variations in the degree of mycorrhizal colonization of the roots of many herbaceous plants in a deciduous forest community, because only a fraction of their roots were replaced each year (Brundrett and Kendrick, 1988, 1990a).

These species consequently had high levels of VAM at all times year, but active associations with arbuscules only in their youngest roots, which only comprised a fraction of their root systems. Other species of deciduous forest plants had annual roots with well defined periods of growth and senescence, resulting in abrupt transitions in mycorrhizal colonization levels. These seasonal changes in VAM activity were regulated by root phenology, since VAM associations only formed in young roots and had a limited period of activity (Brundrett and Kendrick, 1990a; Harley and Smith, 1983). Moderate seasonal variations in the extent of mycorrhizas in the roots of European deciduous forest species (Mayr and Godoy, 1989) and salt marsh plants (Van Duin *et al.,* 1989) were also associated with new root production during the growing season. Allen and Allen (1986) found that mycorrhizas delayed the phenology of a grass that received little benefit from the association. Mycorrhizal strategies of plants may be correlated with the environmental conditions prevailing when plants produce new roots, as was observed in a temperate deciduous forest community (see Fig. 3). In this community, most species with root growth in summer (in warm soil) were mycorrhizal, while those with active roots in the spring or fall (in cold soils). had little or no mycorrhizas (Fig. 3). Species in a European

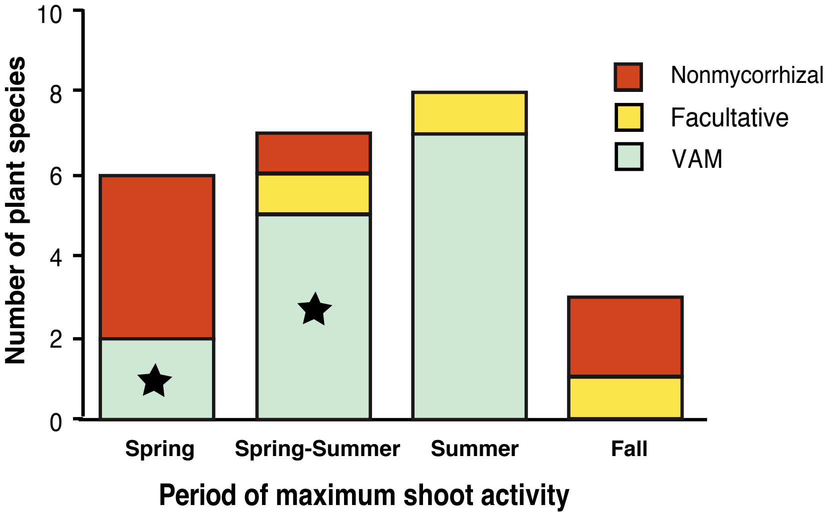

Fig. 3. This chart shows correlations between phenological categories (major period of shoot activity) and mycorrhizal relationships for common species of herbaceous woodland plants in a temperate deciduous forest community (data from Brundrett and Kendrick, 1988). Species with high levels of VAM which grow in the spring or spring and summer periods (indicated by stars) generally had roots which grow in the summer, even though their shoot activity occurred earlier in the year. (Abbreviations; VAM = vesicular-arbuscular mycorrhizal, facultative = low levels of VAM**,** non-mycorrhizal = without any mycorrhizas.)

grassland community could be divided into similar summer and spring root phenology groups (Fitter, 1986c). Co-existing North American prairie grasses also belong to warm and cool season phenology groups and only those most active at warm times of the year are highly mycorrhizal (Daniels Hetrick and Bloom, 1988; Daniels Hetrick *et al.,* 1989). Correlations between low ambient temperatures and reduced mycorrhizal colonization have also been reported in a desert shrub (Allen, 1983), cultivated winter wheat (Daniels Hetrick and Bloom, 1983) and with increasing altitude or latitude in arctic and alpine ecosystems (Appendix 1). The predominance of non-mycorrhizal plants in situations where cold temperatures prevail probably results because these conditions restrict the activity of mycorrhizal fungi (Brundrett and Kendrick, 1988; Daniels Hetrick *et al.,* 1989), but this correlation could also have resulted because cool conditions favoured plants from non-mycorrhizal families (Table 4) for other reasons.

Roots forming ECM associations can live for several years (Harley and Smith, 1983). However, ultrastructural studies have shown that only subapical regions of ECM roots have an active host-fungus interface that must be renewed by further root extension (Kottke and Oberwinkler, 1986; Massicotte *et al.,* 1987). Root growth and mycorrhizas formation often parallel shoot development in crop plants, but in many trees root growth is suppressed during periods of rapid leaf formation (Lyr and Hoffmann, 1967) and some herbaceous plants form roots and VAM when shoots are dormant (Brundrett and Kendrick, 1988; Daft *et al.,* 1980). Root growth in natural ecosystems generally occurs at times when both temperature and soil moisture conditions are favourable (Allen, 1983; Gregory, 1987; Hayes and Seastead, 1986; Lyr and Hoffmann, 1967; Richards, 1986). Consequently, overall communitywide trends in mycorrhizal activity would be regulated by these environmental constraints on root (and fungus) activity, but variations between hosts would be the result of genetically regulated differences in their root phenology.

Experimental investigations have found that the benefits provided by mycorrhizal associations are often reduced by low temperatures and may be eliminated at 5-10 °C (Andersen *et al.,* 1987; Chilvers and Daft, 1982; Furlan and Fortin, 1973; Hayman, 1983; Smith and Bowen, 1979). Reduced VAM activity may result because the activity of these fungi stops below a cut-off temperature (±7 °C) (Hayman, 1983) while roots of some plants continue to grow, or because mycorrhizal exchange processes become inefficient at low temperatures. Smith and Bowen (1979) observed that low temperatures reduced VAM initiation, which suggests that fungal activity was affected. There are differences between VAM fungi in the optimum and upper and lower temperature limits for spore germination (Tommerup, 1983b; Schenck *et al.,* 1975). The activity of ECM fungi is also considerably influenced by temperature (Peredo *et al.,* 1983; Slankis, 1974). Winter wheat (Dodd and Jeffries, 1986) and *Endymion non-scriptus* (Daft *et al.,* 1980) form VAM associations during mild winter conditions in the UK and some species are mycorrhizal (VAM, ECM or Ericoid) in all but the most extreme arctic and alpine sites (Appendix 1), suggesting that some host-endophyte combinations are effective at low temperatures. Under experimental conditions the efficacy of mycorrhizal associations can also be reduced by low light levels (Section III.E.4.a). However, woodland plants growing in heavily shaded conditions can be highly mycorrhizal, but with associations that form and senesce at relatively slow rates (Brundrett and Kendrick, 1990a).

Seasonal variations in mycorrhizal spore numbers can occur (Ebbers *et al.,* 1987; Dhillion *et al.,* 1988; Gemma and Koske, 1988b; Gemma *et al.,* 1989; Giovannetti, 1985; Louis and Lim, 1987). In most cases spores are less abundant during periods of mycorrhizal formation and become more numerous during periods of root senescence, These reductions in spore numbers may result from spore germination, limited spore lifespans, or the activities of antagonistic soil organisms-which may coincide with root growth (Mosse and Bowen, 1968; Sutton and Barron, 1972). Peak periods of spore production are generally thought to coincide with periods of fungal resource remobilization from senescing roots (Gemma *et al.,* 1989; Hayman, 1970; Sutton and Barron, 1972). This hypothesis is supported by observations that spore production is greatest when root activity is interrupted by a long dry season or plants are harvested for agricultural purposes (Janos, 1980b; Mosse and Bowen, 1968; Redhead, 1977). However, substantial variations in the timing of spore production occur between VAM fungi associated with a host plant, suggesting that competition between fungi (Section III.B.6) and environmental factors probably also influence spore production (Gemma and Koske, 1989).

Spore numbers are not always well correlated with the degree of mycorrhizal formation (Section III.B.1) and their germination potential varies at different times of the year (Tommerup, 1983a; Gemma and Koske, 1988b). Other inoculum types are often considered to be more important in natural ecosystems (Section III.B.2), but the total inoculum potential of undisturbed soils been measured (by bioassays) in only a few cases. Bioassays of undisturbed soil did not find large seasonal variations in the inoculum potential of soils in Australia pasture or ecosystem soils (Jasper *et al.,* 1989c; McGee, 1989; Scheltema *et al.,* 1985a). Fructifications of ECM fungi occur at a specific time of the year (usually in the fall), when spores of these fungi would be abundant in their natural habitats. While seasonal variations in the capability of mycorrhizal fungi to initiate associations can occur, mycorrhizal formation requires root growth and factors influencing the latter process appear to be of overriding importance.

2. The Activity of Mycorrhizal Fungus Hyphae in Soils

Mycorrhizal fungi form a hyphal network in soil which can obtain and transport nutrients, propagate the association and interconnect plants (Read *et al.,* 1985; Newman, 1988). Production of external hyphae varies between species and isolates of VAM fungi, can be influenced by soil properties and is an important determinant of mutualistic effectiveness (Abbot and Robson, 1985; Graham *et al.,* 1982b; Gueye *et al.,* 1987).

Mycorrhizal fungus hyphae are normally thought to obtain poorly mobile nutrients from beyond the zone of nutrient depletion surrounding roots in soils (Section III.E.S), but may also respond to soil heterogeneity. Harvey *et al.* (1976) found that most of the ECM roots in a forest soil occurred within organic soil fractions, where litter, woody debris and charcoal decomposition was occurring. Hyphae of these fungi may exploit soil heterogeneity by occupying substrates with lower carbon/nutrient ratios (Coleman *et al.,* 1983). Hyphae of VAM fungi may also preferentially occupy soil organic material (Mosse, 1959; St John *et al.,* 1983; Warner, 1984), where they produce fine, highly branched, septate hyphae that may have an absorptive function (Mosse, 1959; Nicolson, 1959). Roots also respond to spatial and temporal variations in soil nutrient supply, but they may be less efficient at this than are mycorrhizal hyphae (Section III.E.5). Mycorrhizal associations can provide the greatest benefit when plants are supplied with forms of phosphorus that dissolve very slowly, so producing highly localized point sources within soils (Bolan *et al.,* 1987). Some mycorrhizal fungi apparently can utilize organic or insoluble nutrient sources that are normally thought to be unavailable to plants (Section III.F.1). Absorption of inorganic nutrients by mycorrhizal hyphae and their transport through soil to roots over distances measured in centimeters has been demonstrated by tracers such as ^{32}P (Harley and Smith, 1983; Hayman, 1983). Similar experiments have shown rapid transport of carbon, nitrogen, phosphorus and water by hyphal networks of VAM and ECM fungi (Finlay and Read, 1986; Finlay *et al.,* 1988; Francis *et al.,* 1986; Haystead *et al.,* 1988; Newman, 1988; Read *et al.,* 1985; Ritz and Newman, 1986). In some of these experiments, nutrients transfer occurred between plants of the same or different species. The rapidity of this transfer and its correlation with the presence of mycorrhizal fungi, suggests that it occurs within mycorrhizal fungus hyphae, but this has not been fully established (Haystead *et al.,* 1988; Newman, 1988). Francis *et al.* (1986) reported that mycorrhizal mediated inter-plant nutrient transfer significantly enhanced the growth of recipient plants. but Ritz and Newman (1986) considered the P-transfer rates they measured to be substantially less than uptake rates in the field. Experiments invoking competition between mycorrhizal plants suggest that hyphal interconnections provide little benefit to other plants (Section III.F.2).

In pot cultures, the proportion of living soil hyphae increases only after root colonization is established and declines rapidly when this process stops (Schubert *et al.,* 1987; Sylvia, 1988). However, these hyphal growth and viability trends might not occur in ecosystems, where host plants with different periods of root activity could co-operate to support a network of mycorrhizal hyphae and where environmental constraints (temperature, soil moisture levels) would likely be the most important determinants of fungus activity. It has been observed that seedlings form mycorrhizas more rapidly, or to a greater extent when growing near companion plants that are already mycorrhizal (Birch, 1986; Eissenstat and Newman, 1990; Miller *et al.,* 1983; Read *et al.,* 1976). The simultaneous introduction of mycorrhizal fungi and plants to pots in experiments may ultimately impose a greater drain on the host than would occur in nature, because of the costs of creating a new hyphal network from quiescent propagules. The reductions in mycorrhizal colonization resulting from soil disturbance provide further evidence of the importance of pre-existing hyphae as propagules (Evans and Miller, 1988, 1990; Jasper *et al.,* 1989ab). These hyphal networks may facilitate the absorption and transport of nutrients in soil, since their disruption can reduce the efficacy of mycorrhizal associations in a way that is independent of colonization levels (Evans and Miller, 1990). Mycorrhizal fungus hyphae can influence soil structure by helping to produce humic acids, weathering soil minerals and stabilizing large soil aggregates (Oades, 1984; Perry *et al.,* 1987; Rothwell, 1984), but organic acids and polysaccharides produced by bacteria, fungi and roots and organic debris resulting from root, hyphae, or soil animal activity are also important components of soil structural stability (see reviews by Lynch and Bragg, 1985; Perry *et al.,* 1987). Major structural contributions to soils by hyphae of VAM or ECM fungi has been observed in arctic communities (Miller, 1982b), sand dunes (Jehne and Thompson, 1981; Rose, 1988), deserts (Went and Stark, 1968), revegetating minesites (Rothwell, 1984) and agricultural fields (Thomas *et al.,* 1986; Tisdall and Oades, 1979). Meyer (1964) considered hyphae of the ECM fungus *Cenococcum* to be an important structural component of a boreal forest soil and Hunt and Fogel (1983) found this fungus alone can comprise as much as 64% of all soil hyphae. Humic acids-organic chemicals which are important components of soil structure and fertility. are produced by partial decomposition of plant residues such as lignin. as well as microbial products-especially fungal melanins (Martin and Haider, 1980; Vaughan and Malcolm, 1985). Similar substances can accumulate in cultures of ECM fungi (Tan *et al.,* 1978). The abundance of mycorrhizal fungus hyphae in many soils suggests that they may be important as source of humic acids as well as influencing soil structural properties.

3. The Rhizosphere and Mycorhizosphere

Whipps and Lynch (1986) describe the rhizosphere as consisting of three zones, the ectorhizosphere (soil in close proximity too roots), the rhizoplane (root surface) and endorhizosphere (apoplastic space within roots). In the rhizosphere soil properties are changed and microbial activity is enhanced by dead cells. mucilages and exudates from roots and these influences are most pronounced near young roots (Curl and Truelove, 1986; Newman, 1985; Uren and Reisenaur, 1988). Root exudates include inorganic ions, sugars, amino acids and organic acids which escape from root cells (Curl and Truelove, 1986).

Roots with ECM associations are encased by a mantle of fungal hyphae which would influence or mediate any exudation and cell loss processes that occur, so that the zone or influence surrounding these roots should be called a mycorrhizosphere (Fogel, 1988). The mycorrhizosphere of ECM roots may be expected to hate unique properties, including more gradual but sustained exudation, micro-organisms which have evolved to utilize substrates such as trehalose or mannitol. and tolerate defensive secondary metabolites which are of fungal rather than root origin (Fogel, 1988). Fogel (1988) also suggests that mycorrhizal fungi may have a greater influence on rhizosphere properties than host roots, so that the common association of one host with many ECM fungi could result in mycorrhizosphere heterogeneity, It would also be expected that VAM associations (which are a major sink for substrates within roots) would have a substantial influence on mycorrhizosphere properties. Mycorrhizosphere effects, which include many interactions between mycorrhizal fungi and other soil organisms. have been considered in reviews by Fogel (1988), Linderman (1988), Perry *et al.* (1987) and Rambellini (1973).

The VAM mycorrhizosphere may support substantially altered population of soil bacteria, actinomycetes and fungi when compared with non-mycorrhizal roots (Ames *et al.,* 1984; Lawley *et al.,* 1982; Meyer and Linderman, 1986b; Secilia and Bagyaraj, 1988). Vancúra *et al.,* (1989) observed that soil hyphae of VAM fungi had bacteria growing on them and these "hyphosphere" bacteria were a subset of the host rhizosphere population. Soil micro-organisms may enhance (Azcón-Aguilar and Barea, 1985; Meyer and Linderman, 1986a), reduce (Baas *et al.* 1989a; Daniels Hetrick *et al.,* 1987; Koide and Li, 1989), or have no effect (Paulitz and Linderman, 1989) on the effectiveness of VAM associations (to increase host growth), relative to pasteurized soil controls. Different soil micro-organisms can enhance or reduce ECM formation, but enhancement is more common (Garbaye and Bowen, 1986, 1989; Richter *et al.,* 1989; Strzelczyk and Kampert, 1987). Garbaye and Bowen (1989) isolated micro-organisms from ECM roots and found that some were capable of enhancing the growth of ECM fungi. They suggest that a community of microbes has evolved in association with ECM roots. However, Summerbell (1989) found that most fungi associated with the mantle of ECM black spruce roots also occurred on non-mycorrhizal roots and roots of a non-host species. Wilkinson *et al.* (1989) found that some strains of soil bacteria, when co-inoculated with mycorrhizal fungi. enhanced the symbiotic germination of aseptic orchid seeds.

Spore dormancy and subsequent activation in response to relatively specific signals, allows fungi to survive in soil when conditions are unfavorable (Sussman, 1976). Germination of VAM spores and subsequent hyphal growth may be enhanced (Azcón, 1987; Azcón-Aguilar *et al.,* 1986; Azcón-Aguilar and Barea, 1985), or may be inhibited (Paulitz and Linderman, 1989) by the presence of free-living bacteria and fungi isolated from soils. Germination of the spores of some VAM fungi only occurs after the completion of a specific period of dormancy (Bowen, 1987; McGee, 1989; Tommerup, 1983a). Roots exudates can promote germination and hyphal growth from VAM spores (Graham, 1982; Elias and Safir, 1987). within a narrow zone of influence in soils (Smith *et al.,* 1986). Gianinazzi-Pearson *et al.* (1989) observed that host root exudates and flavonoids they contained elicited rapid germination and hyphal growth responses in a VAM fungus. Volatile factors from roots can also attract soil hyphae or germ tubes from VAM spores (Gemma and Koske, 1988a; Koske, 1982; St John *et al.,* 1983). Germination and survival of propagules of VAM fungi (spores) is also influenced by soil moisture, temperature, pH and salinity levels (Daniels Hetrick, 1984; Bowen, 1987). Enhancement of ECM fungus basidiospore germination occurs in the presence of some yeasts and filamentous fungi, but host root exudates often produce a greater response (Ali and Jackson, 1988; Fries, 1987a; Theodorou and Bowen, 1987). Hyphae of ECM fungi can be attracted by exudates of both host and non-host species (Duddridge, 1987).

The rhizosphere influence is most pronounced near young roots (Curl and Truelove, 1986; Newman, 1985; Uren and Reisenaur, 1988), which may explain their greater attraction to mycorrhizal hyphae (Chilvers and Gust, 1982; Mosse and Hepper, 1975; Smith and Walker, 1981). Mycorrhizal hyphae require several days to respond to the presence of a growing root tip, so would first interact with root cells that are at least 2 days old and take several more days to establish an effective association with a Hartig net or arbuscules (Alexander *et al.,* 1989; Piché and Peterson, 1985). Gemma and Koske (1988a) found that host root growth and lateral root production could be stimulated by the presence of VAM fungi before an association was formed.

Plants belonging to certain families have mutualistic associations with N2-fixing bacteria contained within root nodules (Gibson and Jordan, 1983; Torrey, 1978) and associative N2-fixing bacteria may occur in the rhizosphere of other plants (Giller and Day, 1985; Ho, 1988; Pacovsky, 1989), or within ECM roots or basidiocarps (Li and Hung, 1987). There can be interactions between mutualistic nitrogen-fixing bacterial associations and mycorrhizas, which may result because plants with dual associations tend to have higher phosphate requirements (Barea and Azcón-Aguilar, 1983). Soil bacteria which solubilize rock phosphate may increase nutrient uptake by mycorrhizal associations (Piccini and Azcón, 1987). Additional mycorrhizosphere interactions that may occur include inhibition of pathogenic organisms (Section III.E.6) and competition with other soil organisms for nutrients (Section III.F.1).

The rhizosphere consists of two zones inside and outside the root (the endorhizosphere and ectorhizosphere) which are considered to be more or less contiguous (Whipps and Lynch, 1986). However, roots often have an exodermis with suberin lamellae and Casparian bands which function as a peripheral apoplastic permeability barrier (Peterson, 1988). It seems that many roots which contain VAM associations also have an exodermis-the role of which should be considered in mycorrhizal studies (Brundrett and Kendrick, 1988, 1990b; Smith *et al.,* 1989). The exodermis is a peripheral root layer, which is similar in structure and apparently also in function to the endodermis, that can reduce root permeability to water and mineral nutrients (see reviews by Drew, 1987; Passioura, 1988; Peterson, 1988) and thus may restrict the diffusion of exudates from roots. However, these substances would still be available in the apoplatic spaces within the root and this internal-root exudation could help maintain quiescent VAM fungi perenniating within roots (Section III.B.1). Cell walls in the exodermis and fungal mantle hyphae can function as permeability barriers which would isolate the site of nutrient exchange to Hartig net hyphae and adjacent epidermal cells in angiosperm roots with ECM associations (Ashford *et al.,* 1989). Endodermal and exodermal Casparian bands may also help to prevent losses during nutrient-exchange processes in roots with VAM associations. It has been suggested that mycorrhizas are more important to plants with a suberized exodermis than those without this layer (Brundrett and Kendrick, 1988; Von Endrigkeit, 1933). Unfortunately, little is known about root exudation in natural ecosystems. or the influence of mycorrhizal associations or root anatomy features such as the exodermis on this process.

4. Regulation of Mycorrhizal Associations

Thousands of unsuccessful root-fungus contacts may be required for every successful establishment of a pathogenic fungus within roots (Huisman, 1982), but unsuccessful contacts between mycorrhizal fungi and host roots apparently are rare. However, there are some plants in natural ecosystems which unyieldingly resist the advances of mycorrhizal fungi by as yet unexplained mechanisms (Section III.D.2). The roots of these non-mycorrhizal species may co-exist with mycorrhizal roots of other species, so the problem is not always a lack of inoculum (Brundrett and Kendrick, 1988). The failure of mycorrhizal fungi to colonize roots could occur at a number of the stages illustrated in Fig. 2. but most likely involve a lack of hyphal attraction to the root, or prevention of hyphal penetration of the root, since hyphal activity is aborted before colonies form inside the root. It has been proposed that mycorrhizal fungus ingress can be prevented by physical or chemical barriers or the absence of a factor which promotes hyphal growth (Bowen, 1987; Brundrett and Kendrick, 1988; Testier *et al.,* 1987). Chemical, morphological and physiological properties of roots that may influence mycorrhizal formation are considered below.

(a) Root morphology and mycorrhiza formation. Associations between soil fungi and roots are thought to involve contact between fungus propagules with limited mobility and more rapidly growing roots; the number of these contacts which are successful will ultimately determine the intensity of the association (Huisman, 1982). If we assume that most root-fungus contacts will result in root colonization, the intensity of a mycorrhizal association will be regulated by an interaction between (i) the distribution of active propagules (hyphae or germ tubes) in the soil and the rapidity of their response to the presence of roots and (ii) the number of growing tips, growth rate, spatial distribution and duration of susceptibility of host roots (mycorrhizal initiation occurs in young roots and effective associations have limited lifespan) (Brundrett and Kendrick, 1990a; Hepper, 1985). We would normally only expect mycorrhizal inoculum to be in short supply in disturbed sites (Sections III.B.4,

III.F.4). or areas where extreme climatic or edaphic conditions favour plants with low levels of mycorrhizas (Section III.F.5). The balance between fungus and root activity would result in relatively low levels of mycorrhizal formation if plants have active root systems in which highly branched, rapidly growing, narrow and relatively short-lived roots predominate. As will be considered further in the next section, species with low mycorrhizal dependency often have root systems of this type. The narrow cortex of fine roots may also limit mycorrhization because relatively few exchange sites (arbuscules) would result from each contact with a mycorrhizal fungus, whose hyphae may reach less of these rapidly growing roots while they are still young enough to form an association. However, species with extensive root systems may require lower levels of mycorrhizal colonization (measured as a proportion of root length) to achieve similar nutrient inflow rates than species with coarse roots. This hypothesis should be examined by comparing phosphorus inflow rates. the total volume of mycorrhizal colonies, or numbers of arbuscules between roots of facultatively and obligately mycorrhizal species.

Host roots are capable of much faster growth than ECM fungus hyphae, which also must contact young root cells to form an association. so formation of ECM associations apparently only occurs in roots with reduced rates of elongation (Bowen and Theodorou, 1973; Chilvers and Gust, 1982; Duddridge, 1987). This may explain why only plants belonging to a limited number of families form ECM associations and members of these diverse families have independently evolved similar heterorhizic root systems in which some lateral roots have very limited elongation (Brundrett *et al.,* 1990; Kubíková, 1967). The interdependence of root growth and fungus activity should be considered to be one of the main attributes of mycorrhizal associations,

Some idea of the relative contribution of host and endophyte features to regulation of VAM formation can be obtained by contrasting different combinations of host plants and mycorrhizal fungi. Consistent features of mycorrhizal morphology that are associated with particular mycorrhizal fungi have sometimes been used to identify endophytes (Abbott, 1982; Agerer, 1986; Haug and Oberwinkler, 1987), but root features can also regulate mycorrhizal morphology. Their is evidence that arbuscule formation is primarily under fungal control but there were some differences in the size of arbuscules that may be attributed to the host (Alexander *et al.,* 1989; Lackie *et al.,* 1987). Gallaud (1905) observed that two distinct VAM morphology types occurred in the roots of different species, (i) the *Arum* series where hyphae proliferated by growing between cortex cells and (ii) the *Paris* series where hyphae formed coils within cells. These morphological distinctions arise because hyphae grow along longitudinally continuous intercellular air spaces in

Arum series hosts, but these longitudinal channels are absent in *Paris* series roots (Brundrett and Kendrick, 1988, 1990ab). This provides morphological evidence that the efficiency of VAM associations (arbuscule location and abundance within roots) can be regulated by root anatomy features and it seem likely that some aspects of root form evolved as means to control these associations.

The subepidermal layer of roots of many angiosperms differentiates into a suberized exodermis with Casparian bands and suberin lamellae (Brundrett and Kendrick, 1988; Peterson, 1988; Shishkoff, 1987). Cells in this layer can play an important role in the resistance of roots to plant pathogens (Brammall and Higgins, 1988) and may also restrict the passage of mycorrhizal fungi. In roots with this potential barrier, it may consist of uniformly suberized cells or alternating suberized long cells and unsuberized short cells (Shishkoff, 1987). In plants with short cells rnycorrhizal fungus penetration typically occurs through these "passage cells" (Bonfante-Fasolo and Vian, 1989; Brundrett and Kendrick, 1988; Gallaud, 1905), while in other cases fungal entry has been observed to proceed uniform exodermis suberization (Brundrett and Kendrick, 1990a). It is not known if cells with suberized walls restrict the passage of mycorrhizal fungi (which may lack the enzymes necessary to degrade them) or if these fungi avoid them by following paths of lesser resistance into roots.

The Hartig net of ECM associations is normally confined to the epidermis of the roots of angiospenn hosts (Alexander and Högberg, 1986; Massicotte *et al.,* 1987, 1989), but occupies much of the cortex of gymnosperm roots (Harley and Smith, 1983; Kottke and Oberwinkler, 1986). It seems likely that structural or chemical properties of outermost cortex cells prevent further ingress by ECM fungi in angiosperm roots. Inner-cortex cells with thick, highly refringent walls also function as fungal barriers in the roots of some gymnosperms (Brundrett *et al.,* 1990). The distribution of ECM fungus hyphae can be correlated with the distribution of "pectins" (acid polysaccharides that are relatively flexible) in root cell walls (Nylund, 1987).

Plants with mycorrhizal associations become less important than non-mycorrhizal species in some habitats with adverse soil conditions (Appendix 1) and this may be correlated with root structural specializations of plants in these communities (Section III.C.1). Mycorrhizal associations generally are sparse or absent in the roots of hydrophytes which generally have adapted to growth in anoxic substrates by having large cortex air spaces in their roots. We would expect these roots to be structurally less compatible with VAM associations, because mycorrhizal fungus hyphae would impede oxygen flow if they grew along air channels and in the case of roots with large spaces, there would be few remaining cells with which to form an association. Plants which do not have roots as adults (including some parasitic, epiphytic, or submerged aquatic members of families in Table 4) would not be able to form mycorrhizal associations. Plants adapted to growth in regions were soils are dry most of the time. often have deep root systems or shallow roots that proliferate rapidly when the soil becomes wet (Eissenstat and Caldwell, 1988; Franco and Nobel, 1990; Richards and Caldwell, 1987). The rapid growth of these roots and the brief period of their activity could make them inefficient mycorrhiza formation.

(b) Host plant physiology. Cost benefit analysis can be used to weight the benefits provided by mycorrhizal associations (enhanced mineral nutrient uptake) against the costs (carbon supplied by the host) of the association (Section III.E.7). In situations where the cost of mycorrhizas outweigh their benefits. one would expect the host plant to restrict mycorrhizal formation in some way. Situations where mycorrhizal formation is not regulated by a balance between root growth and mycorrhizal fungus propagule activity (as was considered above) are most likely to occur when the host already has ample supply of nutrients or is unable to supply sufficient amounts of carbohydrates to the fungus, The inability to supply carbohydrates may explain why plants growing at suboptimal light levels and/or at low temperatures (both of which reduce photosynthesis) can have reduced or inefficient mycorrhizal associations (Graham *et al.,* 1982a; Hayman, 1983; Son and Smith, 1988). It has also been proposed that the formation of ECM associations is regulated by root carbohydrate levels (which are influenced by plant mineral nutrition and light). although plant growth hormones (auxins or ethylene) produced by mycorrhizal fungi may also be involved (Harley and Smith, 1983; Nylund, 1988; Rupp *et al.,* 1989).

It has often been observed that VAM formation can be considerably reduced by growing plants at high phosphorus levels, even in the presence of abundant mycorrhizal fungus propagules (Amijee *et al.,* 1989; Menge *et al.,* 1978; Mosse, 1973; Thomson *et al.,* 1986), although at much lower levels phosphorus addition can enhance VAM formation (Bolan *et al.,* 1984; Koide and Li, 1990). The greatest reduction in mycorrhizal fungus activity apparently occurs because of phosphorus levels and processes inside the root (Jasper *et al.,* 1979; Koide and Li, 1990; Menge *et al.,* 1978; Thomson *et al.,* 1986). Son and Smith (1988) reported that reductions in VAM caused by high phosphorus were more severe at low light levels and Thomson *et al.* (1986) associated high phosphorus level VAM inhibition with reductions in soluble carbohydrates within roots and their exudates. High phosphorus levels, which are correlated with reductions in root carbohydrate levels, can also inhibit ECM formation (Marx *et al.,* 1977).

Phosphate deficiency can increase root exudation by a potential host plant, which may be correlated with the degree of VAM formation (Elias and Safir, 1987; Graham *et al.,* 1982a; Thomson *et* al., 1986), However, in other cases their appears to be no clear relationship between root exudation and VAM formation (Ocampo and Azcón, 1985; Schwab *et al.,* 1983). Mosse (1973) and Amijee *et al.* (1989) observed that many VAM fungus entry points aborted when *Allium* species where grown at very high phosphorus levels. These reports of reduced mycorrhizal formation caused by low light levels or high phosphorus supply in experiments may be applicable to some agricultural situations, but are less relevant to plants in nature where such high phosphorus levels are unlikely to occur and plants generally are exposed to the fertility and light levels to which they are adapted.

(c) Chemical root features. It has frequently been observed that plants belonging to families such as the Brassicaceae (Hirrel *et al.,* 1978; Medve, 1983), Cyperaceae and Juncaceae (Powell, 1975), Proteaceae (Lamont, 1982), or Zygophyllaceae (Khan, 1974, Trappe, 1981) rarely form mycorrhizas. Additional families and orders of plants which are predominantly non-mycorrhizal are listed in Table 4, which is compiled from many sources. Some of these families contain species. which are aquatics, epiphytes, or parasites with much reduced roots, but in other cases their lack of mycorrhizas cannot be explained by habitat preferences. Major chemical constituents of these families (after Cronquist, 1981) are also listed in Table 4. Many of the secondary metabolites listed in Table 4 can also be found in plants from predominantly mycorrhizal families. However, it would seem that plants in "non-mycorrhizal families" are more likely to accumulate chemicals which are considered to be evolutionarily advanced (see Cronquist, 1977, 1981) in comparison with more primitive chemical components, such as phenolics, which are often scarce or absent in these same families.

Plants have evolved a very wide diversity of secondary metabolites, but the function of these chemical is often unknown. Potential roles include interactions with other plants, herbivores and pathogens (Bell, 1981). It seems likely that many of these chemicals are accumulated in plants for defensive purposes and that relatively advanced chemicals evolved because herbivores and pathogens developed resistance to older chemicals (Cronquist, 1977, 1981). There is reason to believe that many of the secondary metabolites accumulated by plants belonging to the families listed in Table 4 (cyanogenic glucosides, betalains, alkaloids, etc.), can be antagonistic to fungi. It has been suggested that these chemicals are responsible for the absence of mycorrhizas in plants in which they accumulate (Bowen, 1987; Hayman *et al.,* 1975; Iqbal and Qureshi, 1976; Kumar and Mahadevan, 1984; Lesica and Antibus, 1986) and there is some evidence to support this hypothesis.

Flavonoids include a diverse group of common root constituents. some of which have been implicated in plant protection from fungal pathogens. insects and nematodes, as well as allelopathic interactions (Rao, 1990). Morandi *et al.* (1984) reported that VAM colonization enhanced flavonoid production in soybean roots and in a later study (Morandi, 1989) could find no immediate correlations between their concentration (as influenced by pesticide treatments) and VAM colonization. Gianinazzi-Pearson *et al.* (1989) observed that flavonoids in root exudates produced by soybean roots induced rapid spore germination and hyphal growth responses in a VAM fungus, but exudates from *Lupinus* roots did not. Members of the genus *Lupinus* (in the predominantly VAM family Fabaceae) are resistant to colonization by VAM fungi (Trinick, 1977) and can inhibit mycorrhizal formation in adjacent roots of other plants (Moriey and Mosse, 1976). *Lupinus* roots are known to contain isoflavonoids and alkaloids with antifungal properties (Lane *et al.,* 1987; Wink, 1987), which may have an adverse influence on VAM fungi if contained in their exudates. Betalains replace flavonoids in most members of the predominantly non-mycorrhizal order Caryophyllales (Cronquist, 1981) and their influence on fungi warrants investigation. Glucosinolates (isothiocyanate derivatives), which are characteristic components of the Brassicaceae and other Capparales (Cronquist, 1981; Testier *et al.,* 1987; Table 3), also have antifungal properties (Drobnica *et al.,* 1967). However, Testier *et al.* (1987) found that these compounds are also contained within many mycorrhizal plants.

In a study of Canadian deciduous forest plants most were found to have VAM associations, but several species had roots that remained free of mycorrhizal fungi (Brundrett and Kendrick, 1988). These include *Chelidonium majus* and several other members of the families Papaveraceae and Fumariaceae, which are known to accumulate fungistatic isoquinoline alkaloids (Gheorghiu *et al.,* 1971: Hakim *et al.,* 1961; Hejtmankova *et al.,* 1984). Of these related plants, C. *majus* and *Dicentra* spp. were non-mycorrhizal, while *Sanguinaria canadensis* had VAM in its fine. but not its coarse lateral roots. This restriction of VAM to fine *S. canadensis* roots was negatively correlated with the occurrence of orange substances (that were likely to be isoquinoline alkaloids) in coarse roots. Kumar and Mahadevan (1984) found that all of the Indian medicinal plants they examined (which contain large amounts of secondary metabolites) were non-mycorrhizal. The above evidence suggests that mycorrhizal strategies can be correlated with plant chemistry, but there is insufficient information is to test this hypothesis for many of the families listed in Table 4.

Tommerup (1984) compared the time-course of VAM colonization in *Brassica* and *Trifolium* roots. She found that *Brassica* roots induced considerably lower rates of spore germination, germ tube growth and successful appressoria formation than occurred in the presence of *Trifolium* roots (a potential host). In addition. few arbuscules and no vesicles were produced in the *Brassica* roots. Tommerup (1984) suggested that volatile or soluble compounds in *Brassica* roots were probably responsible for the observed inhibition, but a shortage of specific substances required by the fungus could also have been a factor. El-Atrach *et al.* (1989) found that roots of the non-host *Brassica oleracea* reduced mycorrhiza formation in *Medicago sativa* when spores, but not when bulk soil was used as inoculum. They also observed that *Glomus mosseae* spore germination was not influenced by *Brassica* root exudates, but was inhibited by a volatile factor produced by these roots. These experiments provide some evidence that secondary metabolites produced by non-host plants can adversely influence mycorrhizal fungi. However, Glenn *et al.* (1988) found that VAM formation was not correlated with the glucosinolate content of *Brassica* cultivars. In their study, host roots stimulated VAM fungus growth, but roots of *Brassica* did not, which may suggest that they were lacking a diffusible hyphal growth promoter. Ocampo *et al.* (1980) and Testier *et al.* (1987) have also proposed that the absence of mycorrhiza formation in non-mycorrhizal plants was the result of internal root or cell wall properties rather than secondary metabolites, but there is little evidence to support this theory. Further evidence that secondary metabolites can influence mycorrhizal fungi is provided by reports that non-mycorrhizal plants and their residues sometimes have an allelopathic influence on mycorrhizal formation (Section III.F.3.a).

The potential role of secondary metabolites in regulating mycorrhizal relationships is complex and would involve many factors that are not well understood. These factors include (i) the accumulation and compartmentalization of secondary metabolites in active or inactive forms, (ii) the susceptibility of mycorrhizal fungi to these chemicals, (iii) the quantity and activity of these chemicals released as soluble or volatile forms from roots and (iv) if they are released or activated by plants in response to mycorrhizal fungi.

Many secondary metabolites are toxic to the cells that make them, so are stored in inactive forms, are compartmentalized in vacuoles, or are detoxified in the cytoplasm (Matile, 1987; McKey, 1979). Thus, it may be possible for mycorrhizas to form an association with roots without being exposed to appreciable quantities of chemicals they contain.

Suberized or lignified structures (which may function as constitutive mechanical defences) were usually well developed in the roots of obligately mycorrhizal deciduous forest plants. but were conspicuously absent from those of non-mycorrhizal species (Brundrett and Kendrick, 1988). This may provide evidence that other more potent chemical defences are present. Primitive chemical constituents of plants, frequently include phenolics and flavonoids which are also potentially fungitoxic (Friend, 1981; Rao, 1990). However, most roots contain phenolics, so mycorrhizal fungi may well have developed tolerance to these chemicals or detoxification mechanisms (Duchesne *et al.,* 1987). in a similar fashion to non-biotrophic plant pathogens (De Wit, 1987) and may even use them as signals to indicate susceptible roots (Brundrett and Kendrick, 1990b: Gianinazzi-Pearson *et a1.,* 1989). Wacker *et al.* (1990) observed that ferulic acid (a simple phenolic compound) produced by asparagus roots was inhibitory to VAM fungus growth at higher soil concentrations.

Unlike physical defences, chemical defences apparently decline in effectiveness as roots age. Low levels of colonization have been reported in the roots of non-mycorrhizal plants, especially when they are old or growing in close proximity to mycorrhizal roots (Glenn *et al.,* 1985; Hirrel *et al.,* 1978; Miller *et al.,* 1983; Ocampo *et al.,* 1980; Ocampo and Hayman, 1981). These atypical VAM infections did not supply nutrients to non-mycorrhizal plants (Ocampo, 1986) and often occur in moribund roots (Ocampo and Hayman, 1981; Brundrett and Kendrick, 1988). It is possible that many of the reports of VAM in non-mycorrhizal families (see Harley and Harley, 1987; Testier *et al.,* 1987; Table 2) represent non-functional infections (without arbuscules) that were induced by the presence of host roots or occurred in senescent roots.

Non-mycorrhizal plants may passively release secondary metabolites into their rhizosphere. Morphological comparisons between the roots of non-mycorrhizal and highly mycorrhizal plants provide evidence (such as highly active and extensive roots systems and the absence of an exodermis) that the roots of non-mycorrhizal plants would be likely to produce more exudates (Table 5). Darnall and Burns (1987) were able to detect glucosinolates (but not free HCN) released into the rhizosphere by plants, but the influence the concentrations they measured would have on fungi is unknown. The volatile factor released by *Brassica* roots that El-Atrach *et al.* (1989) found could inhibit *Glomus* spore germination may have resulted from glucosinolate breakdown. Rhizosphere factors have been implicated in the inhibition (in the case on non-mycorrhizal plants) or promotion (in the case of potential hosts) of mycorrhizal fungus activity. It is not known if mycorrhizal fungi can

Table 5
Root system features correlated with mycorrhizal dependency

Typical trends in root features	Mycorrhizal dependency continuum	
	High	Low
Surface area of absorbing roots [a]	Low	High
Root length/biomass ratio [b]	Low	High
Lateral root branching orders	Few	More
Branching frequency	Sparse	Frequent
Root hairs	Few/short	Many/long
Root system activity	Low	High
Root growth	Slow	Fast
Responsiveness [c]	Slow	High
Root lifespan (in primary growth)	Months/years	Weeks/months
Protective features		
Structural [d]	Strong	Weak
Chemical [e]	Relatively primitive	Relatively advanced
Rhizosphere influences [f]	Slight	May occur
Root activity at low temperatures	Usually stops	May be considerable
Formation of mycorrhizas	Efficient Well regulated	Inefficient May be inhibited

a Relative to plant biomass; *b* specific root length; *c* roots respond to temporary or localized soil conditions; *d* suberization or lignification of primary root structures; *e* accumulated secondary metabolites may be relatively primitive (tannins etc.) or advanced (alkaloids, cyanogens, etc.); *f* that influence the availability of soil nutrients.

detect differences in the rhizosphere properties of susceptible vs non-susceptible roots (which would result in fungus gene expression changes) or if they are influenced by these properties in other ways (perhaps through physiological processes).

A distinction also needs to be made between chemicals which are part of a plant's constitutive defences and those induced as a result of injury. Codignola *et al.* (1989) did not detect increased cell-wall phenolic production in *Allium* epidermal and exodermal cells after colonization by a VAM fungus, but phenolic wall depositions in these cell layers can be an important part of a resistant host plant's response to invasion by a pathogenic fungus (Brammall and Higgins, 1988). Amijee *et al.* (1989) and Mosse (1973) observed that very high phosphorus levels resulted in aborted VAM fungus penetration of roots by a reaction at the root periphery and their illustrations suggest that this process occurred within exodermal short cells. Allen *et al.* (1989a) found that a similar wounding response resulted in aborted VAM fungus colonization of roots of the non-host plant *Salsola kali.* Duc *et al.,* (1989) produced mutants of two normally mycorrhizal species which would not allow VAM fungi to occupy their roots. Their results suggest that host plants have potential mechanisms for excluding fungi from their roots which can be used to exclude pathogens, but which are normally not activated during mycorrhizal formation. Interactions between biotrophic plant pathogens and compatible hosts apparently also involve a failure of the host to respond adequately to the presence of the fungus (De Wit, 1987). Roots of host plants forming VAM or ECM associations often intermingle in natural ecosystems and would be exposed to propagules of both types of fungi, but normally only form one type of association (Section III.D.2). This may suggest that roots of ECM hosts repel or fail to attract VAM fungi and vice versa.

It would appear that the major difference between facultatively mycorrhizal and non-mycorrhizal plant species is that facultative species lack the ability possessed by non-mycorrhizal species to exclude mycorrhizal fungi from their roots completely. Plants in both these categories are more likely to grow in habitats where mycorrhizal fungi would be of limited benefit (Section III.F.5). As a consequence, it may have been advantageous for these plants to evolve mechanisms which prevent mycorrhizal colonization and the resultant loss of energy to the fungus. Alternatively, they might have been excluded indirectly by a process evolved as a defence against pathogenic organisms, if mycorrhizas no longer were of much value. It appears likely that non-mycorrhizal plants have evolved potent mechanisms for excluding mycorrhizal fungi from their roots, which may include the stockpiling of fungistatic chemicals such as the alkaloids in *Chelidonium* roots, active defensive reactions, the absence of signals mycorrhizal fungi use to "recognize" susceptible roots, or other forms of chemical or structural incompatibility. There is insufficient evidence to determine which of these hypothetical mechanism(s) are used by non-mycorrhizal plants in natural ecosystems. These complex interactions provide evidence of the co-evolution of host plant chemical root properties and mycorrhizal fungi.

5. Mycorrhizal Dependency

(a) Soil properties. Plants in natural ecosystems have varying degrees of dependence on mycorrhizal associations which are the result of inherent properties of the plants themselves and the availability of nutrients in the soils in which they naturally occur (Janos, 1980b). Mycorrhizal dependency is simply a measure of the benefit provided by mycorrhizas and will depend on the relative contribution of root and

mycorrhizal mediated nutrient uptake to plants. The outcome of this competition between the roots themselves and their mycorrhizal associations would depend on the root system properties considered in the next section and soil characteristics influencing nutrient availability.

The supply of a particular mineral nutrient to a plant depends on its availability and mobility in soils, as well as the plants internal requirement for that nutrient (Marschner, 1986; Russell, 1977). Phosphorus is generally considered to be the most important plant-growth limiting factor which can be supplied by mycorrhizal associations, because of the many abiotic and biotic factors which can restrict its mobility in soils (Harley and Smith, 1983; Hayman, 1983; Marschner, 1986; Wood *et al.,* 1984). Reductions in the benefit provided by mycorrhizal associations (mycorrhizal dependency) to plants caused by increasing soil phosphorus levels have often been observed (Baylis, 1975; Crush, 1973b; Daniels Hetrick *et al.,* 1989, 1990; Gerschefske Kitt *et al.,* 1988; Johnson, 1976).

In general, both mycorrhizal and non-mycorrhizal roots access the same "available" sources of soil phosphorus (Harley and Smith, 1983; Hayman, 1983), but there is some evidence that mycorrhizas may have a greater effect when phosphorus is present in less soluble forms. Bolan *et al.* (1987) observed that VAM provided the greatest benefit when plants were supplied with iron phosphates, which are poorly soluble, so would provide highly localized phosphorus sources. Jayachandran *et al.* (1989) observed enhanced growth of plants with VAM (but not non-mycorrhizal plants) after the addition of an iron chelator to an infertile soil. These studies suggest that a high phosphorus fixing capacity within a soil may contribute to mycorrhizal dependency by impeding the uptake of “available phosphorus" to plants. Sainz and Arines (1988) reported that soil sterilization and the activities of mycorrhizal fungi can result in changes in the relative proportion of phosphorus contained in different organic or inorganic soil fractions (as measured by different extraction procedures). The abundance of organic *vs* inorganic nutrient sources (see Section F.1) and variations in soil phosphorus-fixing capabilities, may influence the relative availability of phosphorus to roots and mycorrhizal fungi in natural soils, but this requires further investigation.

(b) Root properties. Considerable variations in root system extensiveness, geometry, depth distribution and plasticity occur between plant species (Crick and Grime, 1987; Fitter, 1987; Richards and Caldwell, 1987). Plants with extensive (highly branched, fine, long roots with numerous root hairs) have often been observed to have sparse mycorrhizas in natural ecosystem soils or derive little benefit from mycorrhizas in experiments. Observations of this type have involved plants in Amazonian rainforests (St John, 1980b). New Zealand forests (Baylis,

1975; Johnson, 1976), prairies (Daniels Hetrick *et al.,* 1988; Miller, 1987), temperate deciduous forests (Fig. 4), arctic communities (Miller, 1982a) and peatlands (Hoveler, 1892).

Mineral nutrients such as phosphorus have very limited mobility in soils so that depletion zones, where much of the available nutrient has been utilized, quickly form around roots (Kraus *et al.,* 1987; Marschner, 1986; Russell, 1977). Thus to obtain more phosphorus, plants must bypass the depletion zones surrounding existing roots by further root activity elsewhere in the soil. The outcome of this quest for phosphorus (and other relatively immobile soil resources) should largely be determined by the surface area of a plant's root system, which in turn is a product of the length and diameter of roots, the abundance and length of root hairs and branching properties (architecture). These properties have been found to be positively correlated with a plant's ability to absorb phosphorus in a variety of situations (Bolan *et al.,* 1987; Cardus, 1980; Crush, 1974; Fohse *et al.,* 1988; Itoh and Barber, 1983, etc.). Mengel and Steffens (1985) found that absorption of potassium (a nutrient of intermediate soil mobility) was also correlated with root length differences between species.

Some plants, like rye grass, have narrow, highly branched roots with

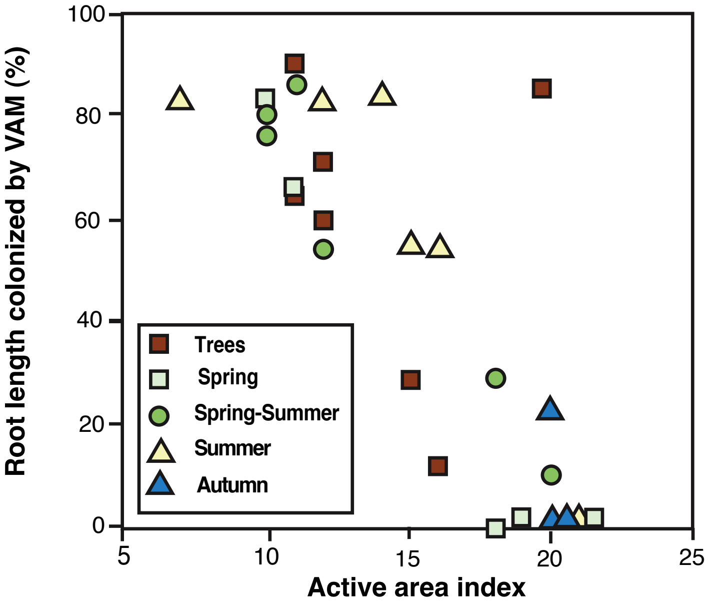

Fig. 4. The relationship between active area index (which is an arbitrary sum of root diameter, branching order, hair developments, lifespans and suberization indices) and VAM colonization (% of primary root length). Data was obtained from a study of deciduous forest plants (Brundrett and Kendrick, 1988) and includes common trees, shrubs and herbaceous plants-which have been separated into the phenological categories used in Fig. 3.

numerous root hairs forming a vast surface area in contact with the soil: one rye plant can produce 600 km roots with a 600 m2 surface area (Dittmer, 1937). Other plants. such as onion (Bhat and Nye, 1974) and most of the temperate forest plants examined by Brundrett and Kendrick (1988), have coarse, infrequently branched roots with few root hairs. resulting in substantially less soil contact. Root hairs can make a large contribution to root surface area, but usually are short-lived structures and considerable variations in their length and abundance occur between species (Dittmer, 1949) or as a result of soil conditions (MacKay and Barber, 1985).

In ecosystem studies, total biomass is the parameter most often used to quantify roots, but provides much less information than root length or specific root length (length/unit root weight) data (Fitter and Hay, 1987; Kummerow, 1983). Parameters that could be used to predict nutrient absorption are; total root biomass < fine root biomass < root length < root surface area < root surface area and activity < rhizosphere volume, arranged in increasing order of predictive ability. These measurements would all be relative to whole plant (or shoot) biomass. It is sometimes possible to provide good estimates of root surface area from root biomass after careful study of roots in a particular ecosystem (Kummerow, 1983). Investigations of crop plants have shown that the biomass, length. volume, growth rate. activity, depth and water conductance and strength of roots can influence cultivar responses to nutrient levels, temperature, drought, hard soil layers, wind, disease and poor drainage (O'Toole and Bland, 1987).

There are considerable variations between plant species in the degree of root system architecture (distribution and branching pattern) changes that occur in response to localized sources of nutrients and water in soil, but it appears that variations occurring within species are considerably less than variations in root system plasticity between species (Crick and Grime, 1987; Drew and Saker, 1975, 1978; Fitter, 1987; Grime *et al.,* 1986; St John *et al.,* 1983). The responsiveness of plant root systems to small scale or short duration changes in water or nutrient availability is thought to be an important determinant of their success during competition for soil resources (Campbell and Grime, 1989; Franco and Nobel, 1990; Jackson and Caldwell, 1989). Powell (1974) found that non-mycorrhizal *Carex coriacea* plants grown at low soil phosphorus levels had a greater specific root length (finer roots) but a similar root:shoot ratio than plants grown at a higher fertility levels. Moderate reductions or increases in the relative area of root systems have been observed when mycorrhizal plants were compared to non-mycorrhizal controls (Anderson and Liberta, 1989; Daniels Hetrick *et al.,* 1988; Graham, 1987; Price *et al.,* 1989). However, these responses (which probably result from competition for carbohydrates or differences in phosphorus nutrition) are apparently much less plastic than those of plants with little mycorrhizal dependency. Koide *et al.* (1988) observed that wild oats had a root system that is more responsive to soil nutrient levels than cultivated oats and the latter received more benefit from mycorrhizas. Root system plasticity (or responsiveness to changes in soil heterogeneity) apparently allows plants to forage for soil nutrients without relying on mycorrhizal associations, but probably results in high root system maintenance costs (due to growth and respiration rates).

Extensive, highly active root systems alone may not be enough to ensure adequate mineral nutrient capture for non-mycorrhizal plants. Fohse *et al.* (1988) observed that onion, tomato and bean plants (which often benefit from VAM) had substantially lower phosphorus uptake efficiency per unit root length than rape and spinach (non-mycorrhizal species). Van Ray and Van Diest (1979) found that buckwheat *(Fagopyrum esculentum),* a plant that has been reported to be non-mycorrhizal (Harley and Harley, 1987), was able to obtain phosphorus from sources that were unavailable to other species. Some plants have the ability to change rhizosphere conditions, such as pH, which influence nutrient availability (see Marschner, 1986; Uren and Reisenaur, 1988). However, this influence of roots on soil will also depend on the extensiveness and activity of their root system, since young roots are the primary source of exudates (Curl and Truelove, 1986; Uren and Reisenaur, 1988).

Mycorrhizal fungus hyphae primarily function by effectively increasing the soil volume from which immobile nutrients are absorbed and provided to roots (Hayman, 1983; Harley and Smith, 1983). By comparing their relative diameters, Harley (1989) has estimated that, per unit length, fungus hyphae would be approximately 100 times less expensive to form and maintain than roots. Mycorrhizal associations and extensive, highly active root systems are two alternatives in the quest for non-mobile soil nutrients and mycorrhizal fungus hyphae should be a more cost-effective means of exploring large soil volumes. It is becoming increasingly apparent that variations between species in roots system properties such as extensiveness, responsiveness, growth rates, rhizosphere modification and mycorrhizal colonization (which are often correlated) correspond to substantial differences in their below-ground strategies for nutrient uptake. Root system features that are often correlated with the mycorrhizal dependency of plants are summarized in Table 5.

The root system properties described above can be used to formulate an *active area index,* which is the sum of separate arbitrary scales referring to root hair length and abundance, root diameter, branching orders. root suberization and root lifespan data. An index of this kind has been formulated for 26 temperate deciduous forest plants and contrasted with their degree of mycorrhizal colonization in Fig. 4. The inverse correlation between this index (which provides a crude estimate of a plant's ability to absorb nutrients from the soil) and mycorrhizal formation suggests that a continuous range of mycorrhizal strategies apparently exists-ranging from species with coarse, long-lived roots of which almost all form mycorrhizas at one end of the continuum, to those with little or no mycorrhizas that have highly active and extensive roots at the other.

6. Mycorrhizas and Plant Responses to Pollution and Other Stresses

Plants that are dependent on mycorrhizas require them to supply nutrients at adequate levels to sustain "normal" growth and reproduction where they occur in natural ecosystems (Section III.E.7), but mycorrhizas may have other less-direct influences on plant fitness and survival. The indirect mycorrhizal benefits that have been most often reported include increased tolerance to various biotic or abiotic stresses.

Associations with ECM or VAM fungi have been reported to increase host resistance to pathogens (Chakravarty and Unestam, 1987; Dehne, 1986; Duchesne *et al.,* 1987). This increased resistance may involve improvements to host plant mineral nutrition, physical protection of roots by mantle hyphae in the case of ECM, phytoalexin production antimicrobial chemicals such as flavonoids or phenolics – or other mechanisms that are not well understood (Bagyaraj, 1984; Duchesne *et al.,* 1987; Harley and Smith, 1983; Morandi *et al.,* 1984). Davis and Menge (1980) were able to demonstrate disease-suppression benefits from a VAM association when mycorrhizal roots were isolated from diseased roots (in a split root experiment), which suggested that the beneficial effects of VAM were due to enhanced host plant mineral nutrition. Fungi forming ECM can be antagonistic to other microbes, perhaps by producing antibiotics (Garrido *et al.,* 1982; Kope and Fortin, 1989; Rambelli, 1973). Kope and Fortin (1989) found that cell-free extracts from cultures of 7 out of 16 isolates of ECM fungi they screened inhibited the growth of many of the root-pathogenic fungi they tested and in some cases cell lysis was observed. Duchesne *et al.* (1989) reported that oxalic acid, which was produced by an ECM fungus *(Paxillus involutus),* inhibited a *Fusarium* pathogen of pine roots. There are some instances when mycorrhizal associations do not reduce disease severity. For example. Afek *et al.* (1990) observed a negative interaction with VAM (reduced root colonization) caused by several common soil pathogens when crop plants were grown in non-fumigated soil.

Interactions between nematodes and VAM are complex (see review by Ingham, 1988). Plant-feeding nematodes generally reduce the growth of mycorrhizal plants, but they still usually grow better than non-mycorrhizal control plants. Plant-feeding nematodes generally avoid roots already containing VAM and vice versa (although in some cases the activity of VAM fungi and nematodes are mutually enhanced). Fungal-feeding nematodes can reduce root colonization or mineral nutrient uptake by the soil hyphae VAM fungi, but these effects may not be large enough to influence host plants. Nematodes and other mycophilous soil organisms can also have detrimental influences on ECM associations (Section III.B.3).

There is a report that the fitness of insect larvae feeding on mycorrhizal plants can be reduced relative to those feeding on non-mycorrhizal plants (Rabin and Pacovsky, 1985). There apparently is little interaction between herbivore grazing of leaves and mycorrhizal colonization of roots (Allen *et al.,* 1989b; Wallace, 1987). although severe grazing can substantially reduce mycorrhizal colonization, presumably due to a reduction in photosynthate available to maintain root processes (Bethlenfalvay *et al.,* 1985; Borowicz and Fitter, 1990).

Lapeyrie and Chilvers (1985) reported that a *Eucalyptus* species could grow in calcareous soil when associated with ECM but not with VAM. Mycorrhizal associations with certain isolates of VAM and ECM fungi can reduce hosts plant susceptibility to toxic metal ions (Denny and Wilkins, 1987; Dixon, 1988; Dueck *et al.,* 1986; Jones and Huchinson, 1988; Koslowsky and Boerner, 1989; Schuepp *et al.,* 1987). However, mycorrhizal fungi themselves exhibit varying degrees of susceptibility to these factors and may enhance metal ion uptake in some cases (Smith, 1990). Ericoid mycorrhizal associations effectively "detoxify" metal ions and phenolic compounds which can occur in phytotoxic levels the acidic soils in which their host plants grow (Leake *et al.,* 1989; Read 1983). Pesticides generally have little effect on mycorrhizal associations if used at recommended rates, but there are exceptions (Trappe *et al.,* 1984). There is evidence that VAM associations can increase the uptake of soil pesticide residues by plants (Nelson and Khan, 1990).

Acidic precipitation and atmospheric ozone and sulphur dioxide pollution have been implicated in the serious forest decline problems occurring in Europe and Eastern North America (Klein and Perkins, 1988; Smith, 1990). Forest decline is a complex process involving many biotic and abiotic factors, of which the disruption of nutrient cycling appears to be one of the most important (Klein and Perkins, 1988). In experiments, pollution in the form of O_3, SO_2, S dust, or acid rain can reduce VAM or ECM formation, but mycorrhizal plants were more tolerant to these stresses in some cases (Danielson and Visser, 1989;

Garret *et al.,* 1982; Ho and Trappe, 1984; Reich *et al.,* 1985; Shafer *et al.,* 1985). Reductions in the biomass of feeder roots and mycorrhizas have been observed in forests where trees are declining (Mejstrik, 1989; Vincent. 1989), but it has not been determined if this is a cause or a symptom of tree decline.

VAM colonization of roots may be associated with increased salinity tolerance in some saltmarsh plants (Rozema *et al.,* 1986), but many plants in these habitats are non-mycorrhizal (Appendix 1). Graham and Syvertsen (1989) found that associations with a VAM fungus did not influence the tolerance of citrus seedlings to salinity, but enhanced chloride uptake. Pfeiffer and Bloss (1988) found that a VAM association increased plant growth in a saline soil, but so did the application of additional phosphorus.

There is experimental evidence that mycorrhizal fungus hyphae can transport water, perhaps in sufficient quantities to help sustain plants during periods of water stress (Read and Boyd, 1986). However, the increased growth of mycorrhizal plants in dry soils is normally considered to occur by less direct mechanisms and often involves enhanced transpiration (Allen and Allen, 1986; Nelsen, 1987; Parke *et al.,* 1983; Sieverding and Toro, 1988). Mycorrhizal increases to drought tolerance can be explained by improved phosphorus nutrition in many cases (Fitter, 1988; Nelsen, 1987). but there may still be transpirational differences between mycorrhizal and non-mycorrhizal plants of similar size and phosphorus content (Augé, 1989).

In many of the experiments described above, mycorrhizal benefits to plants were assessed by contrasting the response of mycorrhizal and non-mycorrhizal plants to stresses at the same fertility levels, so it is often difficult to separate mycorrhizal benefits due to mineral uptake from other less-direct mechanisms (see Fig. 5). While there may be more subtle indirect effects of mycorrhizas on plants, it seems that most of the increased stress tolerance of mycorrhizal plants can be directly related to enhanced uptake of mineral nutrients, especially phosphorus (Graham, 1987; Marschner, 1986; Nelsen, 1987).

7. The Value of Mycorrhizas to Plants in Natural Ecosystems

The numerous factors which interact to determine if mycorrhizal associations are beneficial to plants in natural ecosystems or experiments are summarized in Fig. 5. As was considered in Section III.E.5, the cost-effectiveness of mycorrhizal *vs* non-mycorrhizal root systems will largely depend on the availability of nutrients in soils and the relative expense of producing and maintaining root systems which are well suited for direct *vs* mycorrhizally mediated uptake (Table 5). Baylis (1975) was

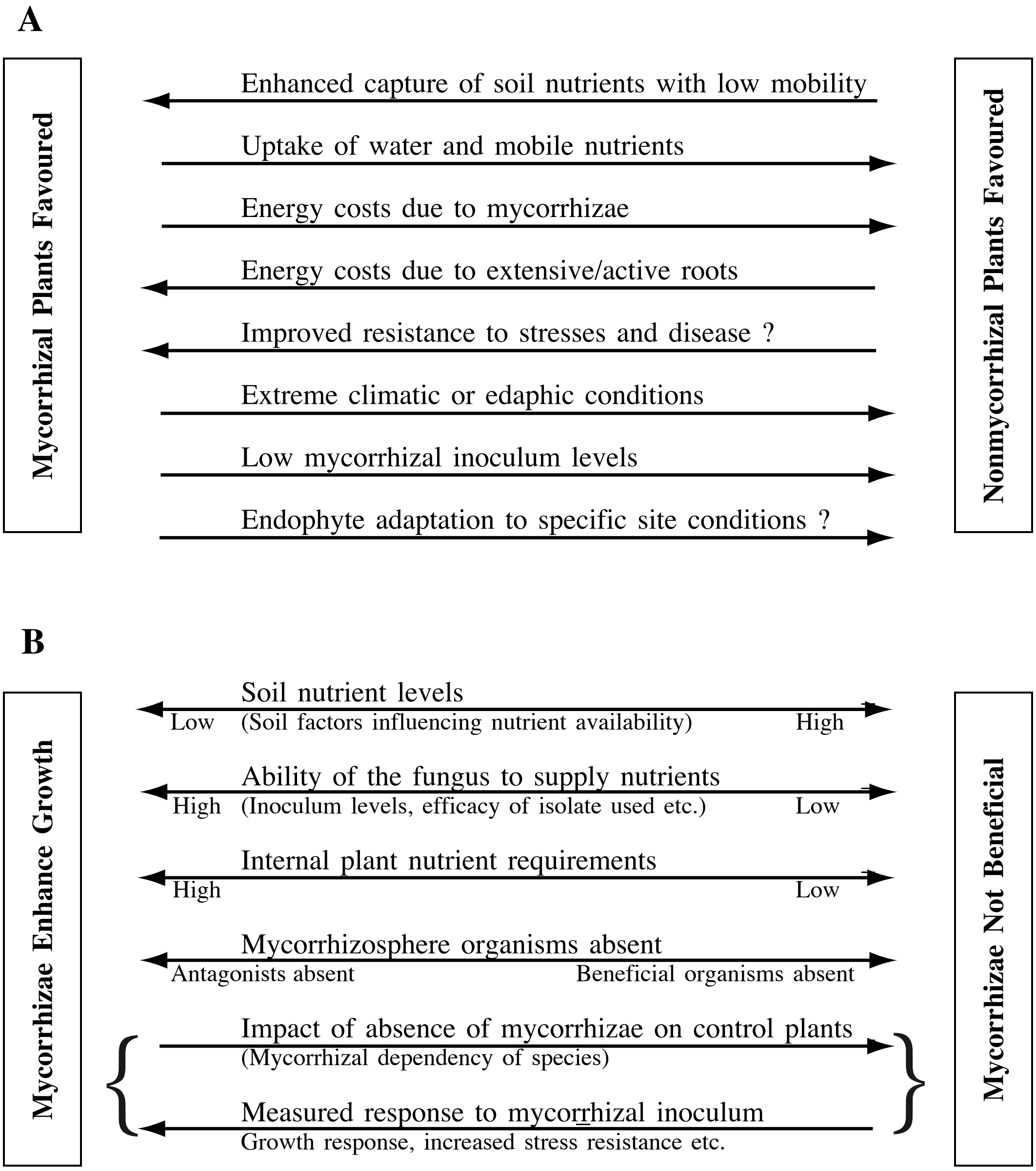

Fig. 5. Diagrammatic summary of factors with the potential to influence the effectiveness of mycorrhizal associations in natural ecosystems (part A: upper) and experimental systems (part B: lower). These factors are discussed in various sections of the review, but their relative importance is unknown. The last two factors in part B (lower) indicate that measured plant responses to mycorrhizas are relative to control plants grown without mycorrhizas (see text).

one of the first systematically to consider that these factors regulated variations between plants in their responsiveness to mycorrhizal colonization and the critical levels of nutrients, especially phosphorus, above which they no longer benefited from mycorrhizas. Evidence that there are variations in the mycorrhizal dependency of plants has been provided by experiments where plant mycorrhizal responses are determined at soil nutrient levels comparable to those found in their natural habitats (Table 6). Many of the plants in Table 6 were found to be highly dependent on mycorrhizas, but these associations provided little or no benefit in other cases.

Despite having relatively extensive fibrous root systems, most sand dune and prairie grasses benefit from VAM associations, but grasses from other habitats may not (Table 6, Miller, 1987). Reports of non-mycorrhizal trees are rare and there is a substantial body of physiological evidence that trees normally are highly dependent on VAM or ECM associations (Fitter and Hay, 1987; Harley and Smith, 1983; Kormanik, 1981; Le Tacon *et al.,* 1987: Lyr and Hoffman, 1967; Meyer, 1973). This may result because trees generally have relatively low root:shoot ratios and they often have short, heterorhizic lateral roots (Kubíková, 1967; Lyr and Hoffman, 1967). *Salix nigra,* a tree which grows in wet soils, is an exception to this rule, since it has elongated lateral roots, of which only a fraction develop ECM (Brundrett *et al.,* 1990).

Variations in mycorrhizal colonization resulting from changes in the nutrient status of plants/soils have been demonstrated in many experiments (Section III.E.4), but correlations between mycorrhizal colonization and plant or soil phosphorus contents are usually weak or non-existent in field trials (Abbott and Robson, 1991a; McGonigle, 1988) or natural ecosystems (Franklin and Harrison, 1985; Lee and Lim, 1989; McAfee and Fortin, 1989; Noordwijk and Hairiah, 1986). Boerner (1986) observed that more VAM colonization occurred in *Geranium* and *Polygonatum* spp. roots from less-fertile North American deciduous forest soils. Species in these genera have relatively finer root systems and lower levels of VAM when compared with many other plants in deciduous forests (Brundrett and Kendrick, 1988), so may have more facultative (and thus more variable) VAM associations. Correlations between soil nutrient levels and mycorrhizal formation in natural ecosystems would be expected to be uncommon, because natural soil nutrient levels are normally much lower than those reported to reduce mycorrhization in experiments, many plants are highly dependent over a range of soil fertility levels and plants and mycorrhizal fungi are adapted to the fertility of the soils in which they occur.

It is an interesting paradox that plants in natural ecosystems are often less efficient at absorbing nutrients from soil than more opportunistic ruderal species or crop plants, but they generally also have lower requirements for nutrients such as phosphorus (Begg, 1963; Cardus, 1980; Chapin, 1988: Chapin *et al.,* 1986). Herbaceous plants which grow

Table 6

Mycorrhizal growth responses of plants from natural ecosystems

Ecosystem type plant	Mycorrhizal dependency*	References
Tropical forest		
trees, herbs (28 spp.)	23+ ,5 –	Janos (1980a)
Mediterranean		
shrub (*Cistus* sp.)	+ (ECM)	Berliner *et al.* (1986)
shrubs (*Acacia* spp.)	+	Jasper *et al.* (1988, 1989c)
Broadleaved evergreen forest		
trees, herbs	+	Baylis (1967), Hall (1977), Johnson (1977)
Deciduous forest		
trees	+	Kormanik (1981), Kormanik *et al.* (1982), Pope *et al.* (1982), Tobiessen and Werner (1980)
shrubs (3 spp.)	+	Sylvia (1987)
herbs (4 spp.)	+	Mosse (1978)
herb (Geranium sp.)	±	Boerner (1990)
Prairie		
grass (*Schizachyrium* sp.)	–	Anderson and Liberia (1989),
grass (*Andropogon* sp.)	+	Gerschefske Kitt *et al.* (1988, 1989),
warm-season grasses and forbs	+	Daniels Hetrick *et al.* (1989), Daniels Hetrick and Bloom (1988)
cool-season grasses	–	Daniels Hetrick *et al.* (1989)
forbs (3 spp.)	+	Anderson and Liberta (1987), Zajicek *et al.* (1986a)
Temperate arid ecosystems		
grasses (*Agropyron* spp.)	–	Allen and Allen (1986), Loree and Williams (1987), Henkel *et al.* (1989)
shrub (*Atriplex* sp.)	+	Miller *et al.* (1983)
Alpine		
grasses	–	Allen *et al.* (1987)
Coastal sand dunes		
Grass (*Uniola* sp.)	+	Sylvia (1989)
Disturbed habitats		
weed (*Ambrosia* sp.)	+	Crowell and Boerner (1988)
wild oats (*Avena* sp.)	–	Koide *et al.* (1988)
Rushes and sedges (4 spp.)	–	Powell (1975)
Aquatic plants		
submerged (*Ranunculus* sp.)	–	Tanner and Clayton (1985)

Notes: Responses are to VAM unless otherwise stated: + substantial growth response to mycorrhizal inoculation when grown at realistic nutrient levels: – little or no growth response to inoculation; ± response varied with soil used.

in fertile soils often have greater relative growth rates than plants from infertile sites (Grime, 1979; Tilman, 1988). Plants in natural ecosystems may be more tolerant of low nutrient levels because their slow growth results in less demand for nutrients. These plants also 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, 1990b). Long-lived roots (with structural defensive features, such as an exodermis – (Section III.C.I) would initially be more expensive to produce, but thereafter confer increased resistance to adverse physical or biological soil factors.

Despite their extremely fine lateral roots, plants with ericoid mycorrhizas are considered to be highly dependent on these associations, which are required to detoxify the soils in which they often occur (Leake *et al.,* 1989). The achlorophyllous. subterranean protocorms of orchid seedlings are completely dependent on mycorrhizas but photosynthetic adult plants may be less so (Harley and Smith, 1983). Some adult plants with monotropoid, arbutoid, or orchid mycorrhizal associations lack chlorophyll and are completely dependent on these associations for their sustenance (see Section III.F.1).

Most of our knowledge about mycorrhizal benefits comes from studies of crop and forage plants. Pasture plants often occur naturally in similar habitats, but many crop plants have been changed considerably by selection and breeding programs. Wild oat *(Avena fatua)* is less dependent on mycorrhizas than cultivated oat *(Avena sativa)* because the former has a higher root/shoot ratio and adaptations to low nutrient levels such as inherently slower growth (Koide *et al.,* 1988). Other comparisons between domesticated plants and their wild relatives would be instructive, since selection of plants that perform well in agricultural conditions may well also have resulted in the opposite situation reduced mycorrhizal dependency. Many crop plants might be expected to be facultatively mycorrhizal because they have ruderal ancestors and were selected for rapid growth in high fertility soils. Mycorrhizal associations have been found to provide little benefit or even reduce the yield of some temperate field crops or pasture species (Jones and Hendrix, 1987; McGonigle and Fitter, 1988a). but many other cultivated plants receive a substantial benefit from these fungi (Hayman, 1987; Mosse and Hayman, 1980). Tropical crops and forage species often grown in acidic, highly infertile soils and many are highly dependent on mycorrhizas (Crush, 1974; Saif, 1987; Howeler *et al.,* 1987).

Morphological criteria (the proportion of a plants absorbing root system containing mycorrhizas) have been used to designate plants with different degrees of mycorrhizal dependency (Section III.D.2), but physiological evidence (the relative benefit provided by mycorrhizas at realistic nutrient levels) would provide a more consistent basis for these designations. Unfortunately, it is difficult to use physiological definitions during mycorrhizal surveys in natural ecosystems, because it usually is not possible to manipulate (and may be difficult to measure) soil nutrient availability. Plants in natural ecosystems belong to a continuum ranging from plants which consistently have mycorrhizas in almost all of their roots to those that never do (Fig. 4). Morphological and physiological definitions of mycorrhizal dependency would probably be in close agreement when applied to plants from either end of this spectrum. However, there is likely to be less agreement about the value of mycorrhizas to plants with intermediate levels of mycorrhizas. since there is little information about the proportion of a plant's root system which is required to form an effective association (and this proportion may be influenced by soil and other environmental conditions).

The use of fungicides which fairly selectively inhibit mycorrhizal fungi, provides another approach to analysing the benefit of mycorrhizal associations in natural communities. Benomyl application to soils can substantially reduce VAM formation. phosphorus inflow and shoot biomass in experiments (Borowicz and Fitter, 1990; Fitter and Nichols, 1988; Daniels Hetrick *et al.,* 1989; Trappe *et al.,* 1984). When applied to an alpine grassland community, benomyl reduced mycorrhizal infection, but had no consistent influence on plant phosphorus content (Fitter, 1986b). Gange *et al.* (1990) reduced mycorrhizal colonization and plant productitity by applying the fungicide Rovral (iprodione) to an early successional community. Koide *et al.* (1988) found that fungicide application had little effect on VAM. but increased plant abundance in an annual plant community. Ideally, it would be possible to find a mycorrhizal inhibitor that could be applied to shoots and would be phloem-translocated to active roots, which would then remain free of mycorrhizas (Fitter, 1989). A fungicide of this type would have minimal influence on soil nutrient cycling processes or the mycorrhizal associations of untreated plants. Poor correlations between experimentally induced changes in mycorrhizal colonization levels and plant growth responses or phosphorus contents in field experiments may occur because; (i) mycorrhizal associations provided little benefit to the species involved or are only required during certain stage in their life history (Fitter, 1989), (ii) plants normally form more mycorrhizas than they actually need so that changes have little effect below a certain threshold (McGonigle, 1988), (iii) roots were not very active at the time of application, or (iv) the effects require long periods to develop because plants grow very slowly.

A detailed cost-benefit analysis of a rnycorrhizal association must balance productivity gains (resulting from enhanced mineral nutrient uptake) against the costs of maintaining these associations (Koide and Elliott, 1989). Root production and turnover rates are difficult to measure accurately but are thought to account for 40-85% of the net primary productivity of plants in ecosystems (Fogel, 1985; Hayes and Seastedt, 1986; Vogt *et al.,* 1987). This energy is used to support root growth, respiration, exudation, as well as mycorrhizas and other associations (Lambers, 1987). By comparing mycorrhizal and phosphorus fertilized plants with similar relative growth rates. Baas *et al.* (1989b) found that mycorrhizal *Plantago major* sp. plants had 30% higher root respiration rates. Koch and Johnson (1984) found that 3-5% of ^{14}C labeled photosynthate was supplied to mycorrhizal fungi in half of the root system in a split root experiment. Jakobsen and Rosendahl (1990) found that approximately 20% of the photoassimilate of cucumber plants with VAM was required for mycorrhizal events (using a "CO2 labeling experiment). It is considered that trees in boreal forests expend about 50% of their primary productivity below ground (Fogel, 1980, 1985; Vogt *et al.,* 1982) and it has been estimated that 20-30% of this energy is supplied to ECM fungi to form mycorrhizas. hyphae, sclerotia and reproductive structures (Harley, 1971; Odum and Biever, 1984). However, these estimates of mycorrhizal costs are rather preliminary (because of inaccuracies in root turnover rate measurements and yearly variations in ECM fungus reproduction). In general it seems that VAM associations utilize 7-17% of the energy translocated to roots (Harris and Paul, 1987; Lambers, 1987), but ECM associations may require 20-30% of this energy (Harley, 1971; Odum and Biever, 1984).

Nutrient uptake without mycorrhizal mediation also requires respiratory energy and in the case of *two Carex* species (most sedges are non-mycorrhizal: Powell, 1975) this can amount to 25 to 35% of their total respiration (Van der Werf *et al.,* 1988). Mycorrhizal roots would still expend some energy on direct ion uptake, but these expenditures would almost certainly be much less than those of non-mycorrhizal species. which generally have more extensive and active root systems and higher root/shoot ratios than mycorrhizal plants (Table 5). There is also some evidence that plants growing in full sunlight can have excess photosythetic energy that overflows into an alternative (cyanide-resistant) respiratory pathway where it is lost (Lambers, 1985). Cost-benefit analysis calculations based on photosynthetic energy would be less relevant if plants in natural ecosystems are able to capture photosynthetic energy that is in excess of their needs for well regulated growth, respiration and storage. When plants that would obtain little or no benefit from mycorrhizas in natural ecosystems are compared with plants that are dependent on mycorrhizas, the former would normally have root systems that are more expensive to maintain. However, when the costs *vs* benefits of one plant's mycorrhizal associations are being considered the results may well depend on soil fertility levels and other factors.

The benefit provided by mycorrhizal associations to plants has been established by numerous glass-house and growth-chamber experiments. but less often under field conditions and rarely in ecosystems (Abbott and Robson, 1991a; Fitter, 1985; Nelson, 1987). There has also been a tendency to use experimental conditions which would maximize mycorrhizal growth responses, without considering complicating factors (as shown in Fig. 5) which would reduce mycorrhizal efficacy (Fitter, 1985). Despite these criticisms, there is little doubt that mycorrhizal associations have an important role in nutrient uptake in natural ecosystems. This assertion is supported by the following indirect evidence:

(i) The majority of plants growing in natural ecosystems have mycorrhizal associations (Appendix 1).

(ii) Experiments with plants from natural ecosystems have demonstrated benefits from mycorrhizas at appropriate nutrient levels (Table 6). In places where mycorrhizas are absent. their reintroduction may result in increased plant productivity (Sections III.B.4. III.F.4). Application of fungicides to natural communities has resulted in measurable reductions in plant production or diversity, at least in some cases. As was considered in the previous section, mycorrhizal associations may reduce the impact of various plant stresses, largely through enhanced plant nutrition.

(iii) Mineral nutrients (especially phosphorus and nitrogen) provide most of the beneficial effects of mycorrhizal associations observed in experimental studies (Hayman, 1983; Harley and Smith, 1983) and are amongst the most important factors limiting plant production in ecosystems (Coleman *et al.,* 1983; Chapin *et al.,* 1986; Kramer, 1981; Fitter, 1986a). Mineral nutrient constraints on plant growth are considered to be important in tropical forests (Janos, 1987; Jordan, 1985), deserts (Noy-Meir, 1985), mediterranean regions of South Africa and Australia (Jeffrey, 1987; Lamont, 1982). temperate deciduous forests (Wood *et al.,* 1984). prairies (Risser, 1985). boreal coniferous forest (Larsen, 1980) and arctic vegetation communities (Chapin and Shaver, 1985; Tieszen, 1978). In these regions many plants have strategies to ensure nutrient uptake and conservation, including long-lived evergreen or xeromorphic (desiccation resistant) leaves which thought to conserve nutrients as well as water (Chabot and Hicks, 1982; Fitter, 1986a; Jeffrey, 1987). (iv) In experiments radioactive tracers have demonstrated the rapid transfer of nutrients to roots, that most probably occurs through a network of mycorrhizal fungus hyphae (Section III.E.2).

(v) The extensiveness, responsiveness and activity of a plant's root system will determine its ability to obtain relatively immobile soil resources and these root characteristics are often negatively correlated with mycorrhizal colonization or mycorrhizal dependency (Table 5). Some mycorrhizal species in natural ecosystems have coarse, relatively inactive roots that would be hopelessly inefficient at direct nutrient absorption. Comparing the biomass of similar lengths of roots and mycorrhizal fungus hyphae, suggests that hyphae are a considerably less expensive way of exploring the soil (Harley, 1989).

(vi) As was considered above, host plants spend a significant proportion of their energy budget to support mycorrhizal fungi. Ecological factors (such as low light levels) that should limit the plant's ability to supply photosynthate, if anything favour mycorrhizal species over those that are non-mycorrhizal (Brundrett and Kendrick, 1988).

F. The Ecology of Mycorrhizal Plants

Interactions between plants which are mediated by above-ground processes include competition for light and space and variations in direct responses to the physical environment (Grime, 1979; Tilman, 1988), but it is difficult (and perhaps irrelevant) to completely eliminate soil factors and mycorrhizal fungal influences from consideration. Many mycorrhizal ecology topics are poorly understood, because plant ecologists rarely consider mycorrhizas and mycorrhizal investigations usually are not conducted in ecosystems (Fitter, 1985; 1989; Harley and Harley, 1987; St John and Coleman, 1983). However, much relevant information about both mycorrhizal partners alone, or in association has been obtained from experimental or agricultural situations and is of value in predicting the response of mycorrhizas in ecosystems. Papers on mycorrhizas in ecosystems (especially regarding regeneration after disturbance or forestry) are now appearing in the literature with increasing frequency.

1. Mycorrhizas and Nutrient Cycling in Natural Ecosystems

Mycorrhizal fungi are generally considered to be incapable of utilizing complex substrates such as cellulose and lignin as energy sources and to depend on their host plant for nutritional support (Harley and Smith, 1983). The intimate association of mycorrhizal roots with leaf litter has resulted in the hypothesis that mycorrhizal fungi could be directly involved in leaf litter decomposition, but there is no good evidence that this occurs in ecosystems (Harley and Smith, 1983). Some ECM fungi have the enzymatic ability to degrade cellulose and pectin, but this activity is generally much less than that of saprobes (Dahm *et al.,* 1987; Harley and Smith, 1983; Haselwandter *et al.,* 1987). It has recently been discovered that some ECM fungi can utilize organic (protein) sources of nitrogen (Abuzinadah *et al.,* 1986; Abuzinadah and Read, 1986) and phosphorus (Haussling and Marschner, 1989; Ho, 1989). In soils where ECM trees occur. 50% of the phosphorus can be in organic forms that could be broken down by rhizosphere phosphatases produced by ECM fungi (Haussling and Marschner, 1989).

Soil minerals are weathered by microbial activity as well as physical processes (Coleman *et al.,* 1983; Robert and Berthelin, 1986). Hyphae of the ECM fungi *Hystangium* sp. and *Paxillus involutus* apparently weather clay minerals by producing calcium oxalate (Cromack *et al.,* 1979; Lapeyrie, 1988). Oxalates produced by ECM fungi may chelate iron to release phosphorus from iron phosphates (Cromack *et al.,* 1979; Lapeyrie, 1988) and siderophore production has also been proposed as a mechanism for enhanced phosphorus absorption by VAM fungi (Bolan *et al.,* 1987; Jayachandran *et al.,* 1989). Reducing activity can be detected in the rhizosphere of ECM roots and may be an important mechanism to enhance the absorption of oxides of nutrients such as manganese (Cairney and Ashford, 1989). Ericoid mycorrhizal fungi apparently normally utilize organic sources of nitrogen (amino acids) and phosphate (Bajwa and Read, 1986; Read, 1983; Straker and Mitchell, 1986) and can degrade lignin, at least in some cases (Haselwandter *et al.,* 1987). These specialized nutritional abilities of ericoid mycorrhizal fungi are likely to be particularly valuable in heathland soils where organic forms of nutrients, such as free amino acids, may predominate (Abuarghub and Read, 1988; Leake *et al.,* 1989). The influence of mycorrhizal fungi on forms of soil minerals that are generally considered not to be available to plants requires further investigation.

Monotropoid and some arbutoid and orchid mycorrhizal hosts have a highly reduced root system and are without chlorophyll, so must rely on mycorrhizal fungi to supply all of their needs (Furman and Trappe, 1971) - a reverse of most relationships between higher plants and fungi. Isotope tracer studies have demonstrated nutrient transfer to plants with monotropoid mycorrhizas from nearby trees, presumably through a common mycorrhizal fungus (Bjorkman, 1960; Newman, 1988; Vreeland *et al.,* 1981). Plants with arbutoid mycorrhizas usually have chlorophyll, but also associate with the same fungi as adjacent trees (Molina and Trappe, 1982a). Members of the Gentianaceae that have VAM associations may not support further spread of the fungus (Jacquelinet - Jeanmougin and Gianinazzi - Pearson, 1983; McGee, 1985). Warcup (1988) found that Australian members of the genus *Lobelia* (and its allies) were often highly dependent on VAM or ECM associations during seedling establishment and apparently required the presence of a companion plant for subsequent growth. These experiments with gentians and lobelias suggest that some plants in natural ecosystems greatly benefit from mycorrhizal associations, but provide little to the fungus in return, so these fungi (and to some extent the lobelia or gentian) would be supported by other members of their community.

Orchid mycorrhizal fungi can transfer ^{14}C to their host plant especially when they are young (Alexander and Hadley, 1985). but the source of this carbon has not been determined. Endophytes isolated from orchid roots are often designated as *Rhizoctonias – a* diverse group of non-sporulating fungi which include plant pathogens as well as saprophytes (Hadley, 1982; Warcup, 1981; 1985) and similar fungi have been found to occupy hyphae and spores of VAM fungi (Williams, 1985). However, detailed studies of orchid endophytes suggest that many of these fungi may have fairly specialized associations with orchids (Currah *et al.,* 1987; Ramsay *et al.,* 1987; Warcup, 1981). The nature of interactions between orchid mycorrhizal fungi and other plants in their native habitats warrants investigation. Orchid endophytes may be saprophytes, but it is possible that many of these fungi have a detrimental influence on other plants or their mycorrhizal fungi and this is almost certain to be the case with achlorophyllous orchids that require photosynthetically acquired energy from some other source. *Armillariella mellea,* a fungus which can be parasitic on plants, forms mycorrhizal associations with some chlorophyll-free orchids (Campbell, 1962; Terashita, 1985). It is interesting to note that chlorophyll-free and green individuals of the normally photosynthetic orchid *Epipactis helleborine* apparently had a common mycorrhizal fungus, which was able to support the growth of fully heterotrophic individuals (Salmia, 1988; 1989). It has been suggested that epiphytic orchids sometimes have a detrimental effect of their host trees (Johansson, 1977). Plants such as orchids. gentians and lobelias are renowned for their showy flowers, which are often disproportionately large. It may be that growth of these plants occurs partially at the expense of other members of the community (by way of their mycorrhizal fungi). However, these fascinating plants are usually not abundant in ecosystems so would have little impact on their fully autotrophic neighbours.

Energy and nutrients from plants are recycled through six major pathways in ecosystems; (i) grazing, (ii) seed consumption, (iii) feeding on nectar, (iv) loss of soluble exudates, (v) active extraction by parasitic and mutualistic organisms and (vi) decomposition of plant structures

(Odum and Biever, 1984). The last process (litter decomposition) is the most important, but energy and nutrient flow through the other cycles is usually also significant (Odum and Biever, 1984). Decomposition processes in the soil involve many organisms in a complex food web, which culminates in nutrient absorption by roots (Coleman, 1985). This food web consists of hierarchies of microbes, microbe-feeding and predatory soil fauna, which form a pyramid with the more primitive organisms that feed on organic substrates at its base (Price, 1988). Measurements of root litter production in natural ecosystems indicate that below-ground litter (dead roots and mycorrhizas) can amount to 2-5 times aboveground litter production (Fogel, 1988; Raich and Nadelhoffer, 1989).

It has been suggested that the presence of mycorrhizal roots can reduce the rate of leaf litter decomposition, perhaps by absorbing nutrients required by saprobic organisms (Cuenca *et al.,* 1983; Gadgil and Gadgil, 1975). However, mycorrhizal roots had a greater influence on moisture levels in litter and their exclusion did not influence decomposition rates in other cases (Harmer and Alexander, 1985; Staaf, 1988). It seems likely that factors other than mycorrhizal fungus activity are responsible for the slow nutrient cycling which occurs in ECM tree dominated forests (Section III.F.5). In a microcosm experiment, Dighton *et al.* (1987) reported increased rates of decomposition of some organic substrates when mycorrhizal roots were present and this effect on decomposition was reduced by the presence of a saprobic fungus

Hyphae from one mycorrhizal fungus are often associated with several different host plants in ecosystems to form a common pool of nutrients, but it is not known if all associated plants have equal access to this pool (Newman, 1988). It has been hypothesized that mycorrhizal fungus hyphae that are already present in senescing host roots may scavenge mineral nutrients before they escape into the soil solution or are absorbed by saprobes. and then transfer them to other associated roots, thus partially bypassing the soil food web (Newman, 1988; Newman and Eason, 1989). Dying plants roots can loose 60% of their nitrogen and 70% of their phosphorus within 3 weeks and much of this ends up in neighboring plants (Eason and Newman, 1990). The magnitude of this rapid dying-living root nutrient transfer was substantially greater if cohabitating plants were mycorrhizal, providing evidence that the transfer occurs through VAM fungus hyphae links (Newman and Eason, 1989).

As was considered above, mycorrhizal fungi are generally considered to enhance plant uptake of inorganic nutrients, but organic nutrient sources may also be important in some ecosystems and much of the soil nutrient pool is likely to be contained within the living biomass of organisms belonging to a complex decomposition food web. This likely results in competition between mycorrhizal fungi and other soil organisms for nutrients, but the nature and importance of this competition is unknown (St John and Coleman, 1983). It is possible that mycorrhizal fungi co-operate with other soil organisms to obtain nutrients that are spatially or chronologically separated from roots. There are seasonal variations in the availability of nutrients in natural ecosystem soils (Gupta and Rorison, 1975; Versoglou and Fitter, 1984), which may not always coincide with periods of maximum mycorrhizal root activity. Other soil microbes and non-mycorrhizal plants may help to prevent nutrient loss from the system at these times.

Mycorrhizal roots or hyphae are often spatially associated with soil organic material in natural ecosystem soils (Section III.E.2). Efficient conservation of minerals, especially phosphorus, has been observed in deciduous forests, eucalyptus forests and tropical rain forests and is thought to result from the combined activities of microbes and roots (Attiwill and Leeper, 1987; Jordan, 1985; Wood *et al.,* 1984). This efficient conservation suggests that the release of nutrients by the activities of saprobic organisms is tightly coupled with uptake by roots. bacteria and fungus hyphae concentrated near the soil surface (Wood *et al.,* 1984). It is probable that mycorrhizal fungi have an important role in the later stages of this process, but this role has not been directly investigated.

2. *Mycorrhizas and Plant Nutrient Competition*

The supply of resources such as light, water and nutrients often limits the growth of plants in natural habitats, but to obtain a greater proportion of one resource, plants must allocate more of their growth to the structures responsible for obtaining it, which may reduce their ability to compete for other resources (Tilman, 1988). For example, plants must balance their expenditures on stem and leaf growth required to obtain light against root costs associated with water and nutrient uptake. Root competition for soil resources is often more important than shoot interactions (Wilson, 1988) and root biomass in a particular site has been found to be inversely correlated with soil nutrient levels in natural ecosystems (Lyr and Hoffmann, 1967; Gower, 1987; Vogt *et al.* 1987). Plant root systems usually intermingle with those of other plants, so would normally be competing for the same soil resources (Brundrett and Kendrick, 1988; Caldwell, 1987; Caldwell and Richards, 1986; Chilvers, 1972; Kummerow, 1983; Richards and Caldwell, 1987).

The relative availability of different soil resources can influence the outcome of competition between species with different capacities to obtain these resources (Tilman, 1982). Genetically determined characteristics of root systems that would influence the ability of plants to obtain immobile soil nutrients such as phosphorus include total root length. rooting depth, geometry and plasticity (Section III.E.5). Root length and rooting depth relative to leaf transpirational area are particularly important for water acquisition, but other factors such as root xylem characteristics and the proportion of roots which can absorb water are also important (Crombie *et al.,* 1988; Eissenstat and Caldwell, 1988; Fitter and Hay, 1987; Hamblin and Tennant, 1987; Richards, 1986; Richards and Caldwell, 1987). Differences in root system responsiveness to temporarily available water or nutrients also influence the outcome of interspecific competition (Campbell and Grime, 1989; Franco and Nobel, 1990; Jackson and Caldwell, 1989). Co-existing plants in natural communities may avoid competition for nutrients by having roots which are active at different times of the year (Brundrett and Kendrick, 1988; Fitter, 1986c; Daniels Hetrick *et al.,* 1989; Veresoglou and Fitter, 1984).

The outcome of competition between plants with different mycorrhizal strategies will depend on the nature of soil resource(s) that are limiting plant productivity. Resources such as water and some mineral nutrients can move rapidly through soil by diffusion and would be obtained directly by roots even if they were non-mycorrhizal. while poorly mobile nutrients such as phosphorus are more efficiently obtained by fungus hyphae if plants are mycorrhizal (Section III.E.5). Thus, the outcome of competition between mycorrhizal and non-mycorrhizal plants should favour the former species if phosphate is limiting, but the extensive roots of non-mycorrhizal of facultative species should be more effective if water is in short supply. These differences in the efficiency of resource acquisition may be less important than other factors in communities where plant growth is restricted by severe edaphic or climatic conditions and non-mycorrhizal species are often common (Section III.F.5). When growing together, plants with the same type of mycorrhizal association may be more equal competitors than plants without mycorrhizas or with different types of mycorrhizas (Newman, 1988). Mycorrhizas should partially alleviate differences in the competitive ability of species to obtain immobile nutrients such as phosphorus by increasing the functional similarity of roots that differ in form. This may explain why species with highly mycorrhizal, coarse roots as well as those with extensive, fine root systems and lower levels of mycorrhizas successfully coexist in habitats such as deciduous forests and prairies (Brundrett and Kendrick, 1988; Daniels Hetrick and Bloom, 1988). However, in these communities plants belonging to these two contrasting groups also avoid competition by having periods of maximum root activity at different times of the year.

Different forms of competition may occur between plants which differ in their mycorrhizal dependency, but there is little available experimental evidence to support these suggestions. Fitter (1977) reported that the addition of VAM to two grasses increased dominance of *Holcus lanutus* over Lolium perenne when compared to root competition alone. Crush (1974) and Hall (1978) found that VAM increased the growth of clover grown in competition with ryegrass (which suffered from nitrogen deficiency) at low soil phosphate levels. In experiments with A*gropyron* species. which receive little benefit from mycorrhizas, these associations had little impact on the outcome of competition with other species (Allen and Allen, 1986). Daniels Hetrick *et al.* (1989) studied competition between two prairie grasses – *Andropogon gerardii*, a species which was highly dependent on mycorrhizas (in the soils used) and *Koeleria pyramidata*, which did not respond to VAM. They found that the outcome of competition favoured *A. gerardii* when mycorrhizas were present or phosphorus was added, while *K. pyramidata* was only successful when mycorrhizas were suppressed and phosphorus levels were low.

In natural ecosystems the diversity of host plants is often substantially greater than the diversity of mycorrhizal fungi and there is no reason to believe that individual plants could maintain separate networks of mycorrhizal hyphae. Thus, it would be normal for different individuals, species, ages or growth forms of plants to be interconnected by one or more mycorrhizal fungus (Harley and Smith, 1983). It has been suggested that these mycorrhizal hyphae networks could reduce plant nutrient competition and help support subordinate species (such as seedlings, shaded by a canopy of mature plants) by interplant nutrient transfer (Francis *et al.,* 1986; Grime *et al.,* 1987; Newman, 1988; Ocampo, 1986). In the experiments described above, mycorrhizal influences on the outcome of competition do not seem to involve nutrient transfer (or ryegrass would have obtained nitrogen from clover in Crush's (1974) or Hall's (1978) experiments).

Grime *et al.* (1987) demonstrated increased diversity (survival of subordinate species) in a microcosm experiment when species were growing with VAM fungi. They proposed that interplant nutrient transfer (measured by ^{14}C) was an important mechanism for maintaining higher plant diversity in this system. However, Bergelson and Crawley (1988) and Newman (1988) consider it more likely that this microcosm experiment demonstrated that the subordinate species had a greater requirement for mycorrhizas so their growth was increased relative to that of dominant grass plants when mycorrhizas were present in the system, while the grass plants (which have fine root systems) were at a greater competitive advantage when mycorrhizas were withheld. In separate experiments using *Sorghum* and *Plantago*, Ocampo (1986) and

Eissenstat and Newman (1990) could detect little P-transfer between mature plants and seedlings of these species when they shared the same VAM fungus and competition with mature plants adversely influenced the seedlings. Mycorrhizas may reduce nutrient competition between plants by some interplant nutrient transfer (Section III.E.2), but they also increase the functional similarity of roots and this later role would appear to be more likely to help maintain plant diversity in ecosystems. It seems likely that competition occurs between plants connected to a common network of mycorrhizal fungus hyphae for nutrients obtained by that fungus (Newman, 1988). It might be expected that the outcome of this type of competition would depend on the energy a particular host invests on mycorrhizal formation, since exchange across mycorrhizal interfaces occurs simultaneously in both directions. Thus plants which support more active mycorrhizal exchange sites in their roots (arbuscules, Hartig nets, etc.) should be at a competitive advantage, but subtle differences in the efficiency or compatibility of different host-fungus combinations may also be a factor. The level of support plants provide to mycorrhizal fungi (in the form of root carbohydrates) is thought to be an important regulator of mycorrhizal formation (Section III.E.4.a). However, some heterotrophic or partially heterotrophic plants have unexplained mechanisms that allow them to obtain inorganic and organic nutrients from hyphal networks in sufficient quantities to sustain their growth, without providing any reciprocal benefit to the mycorrhizal fungus (Section III.F.1).

A wide range of different ECM fungi may be present in a community and some of these fungi preferentially associated with a certain host (Section IlI.D.1), suggesting that interactions between mycorrhizal fungi may sometimes be a factor in plant nutrient competition. Perry *et al.* (1989) conducted competition experiments using two different coniferous host trees growing together with different combinations of ECM fungi. In these experiments mycorrhizal fungi greatly reduced competitive effects by increasing phosphorus uptake by both species. In another microcosm experiment, Finlay (1989) grew seedlings of *Pinus sylvestris* and *Larix eurolepis* together with one of three ECM fungi, two of which are considered to be specific associates of *Larix* spp. Growth of *Pinus* was found to be substantially better when the non-specific ECM fungus was present than when *Larix* - associates were used, while these latter fungi resulted in the best growth and phosphorus uptake by *Larix* seedlings. This experiment provides evidence that the presence of host-specific fungi can shift the balance of nutrient competition in favour of their hosts.

The outcome of nutrient competition between mycorrhizal and non-mycorrhizal plants has also rarely been considered. In a study of early successional species, Crowell and Boerner (1988) found that non-mycorrhizal *Brassica* plants could have a greater influence on mycorrhizal *Ambrosia* plants than other *Ambrosia* neighbours, but this effect was not consistent. The presence of VAM fungi can increase the growth of host plants (grasses) in the presence of non-mycorrhizal competitors (Allen and Allen, 1984; Ocampo, 1986). In studies of this type it can be difficult to separate the competition for resources by roots and mycorrhizas from the growth benefits provided by mycorrhizas (when compared to growth when mycorrhizas are withheld – (see Fig. 5). Other factors such as allelopathy (Section III.F.3.a), that way influence the outcome of competition between mycorrhizal and non-mycorrhizal species, also need to be considered. It has been suggested that mycorrhizal fungi may have an adverse effect on non-mycorrhizal plants that is not related to nutrient competition (Allen and Allen, 1984). The sequestering of nutrients in mycorrhizal fungus hyphal pools may provide a competitive advantage to highly mycorrhizal over those with other nutrient uptake strategies (Newman, 1988).

Root systems must evolve in response to the environmental factors most limiting to plant growth (Caldwell, 1987; Fitter, 1986a; Tilman, 1988). However, these factors may be in conflict (for example a root system optimized for water uptake would be very different than one that is most efficient at mycorrhizal formation), so it is not surprising that results of evolutionary processes have often produced plants with substantially different root systems (strategies) even in the same habitat. These differences in root strategies may influence the outcome of competition between species and ultimately the composition of plant communities.

3. Other Mycorrhizally Mediated Interactions Between Plants

In addition to their roles in nutrient cycling and competition for soil resources, mycorrhizal associations may be involved in other interactions between coexisting plants. The presence of plants which are strongly dependent on VAM can substantially increase mycorrhizal colonization of more facultative plants that would otherwise form little VAM (Hirrel *et al.,* 1978; Miller *et al.,* 1983; Stejskalová, 1989). However, it is known if this type of mycorrhizal enhancement is detrimental or beneficial to facultative species, or if this depends on soil fertility. Attempted colonization of non-host roots by mycorrhizal fungi can result in wounding responses which may have an adverse influence on these plants (Allen *et al.,* 1989a).

(a) Allelopathic interactions involving mycorrhizal fungi. Chemical substances liberated in soil by plants can have adverse effects on other

plants (Rice, 1984) and these amensalistic interactions may involve mycorrhizal fungi (Perry and Choquette, 1987). Leachates from the leaves of some plants (Coté and Thibault, 1988; Iyer, 1980; Rose *et al.,* 1983) and lichens (Brown and Mikola, 1974; Fisher, 1979; Goldner *et al.,* 1986) can inhibit ECM fungi. However, *Pteridium aquilinum* (bracken), *Helianthus occidentalis* and *Salsola kali*, which are considered to be allelopathic, have little influence on the mycorrhizas of other species (Acsai and Largent, 1983; Anderson and Liberia, 1987; Schmidt and Reeves, 1989). Roots of *Calluna vulgaris,* a species with ericoid mycorrhizas, produce factors inhibitory to fungi forming other types of mycorrhizas (Robinson, 1972). The growth of plants with ericoid mycorrhizas can result in the accumulation in soils of phenolic compounds (as well as a low pH and metal ions) which can be toxic to plants and mycorrhizal fungi but are detoxified by ericoid mycorrhizal endophytes (Leake *et al.,* 1989). Tobiessen and Werner (1980) and Kovacic *et al.* (1984) have suggested that chemical properties of leaf litter from *Pinus* trees with ECM may inhibit VAM fungi in soils under these trees. Chemical properties of leaf litter produced by trees may specifically inhibit some ECM fungi allowing other more tolerant fungi to become dominant (Perry and Choquette, 1987). There is some evidence that ECM fungi can produce substances that inhibit the growth of other ECM fungi (Kope and Fortin, 1989).

The roots of non-mycorrhizal species apparently contain chemical factors inhibitory to mycorrhizal fungi (Section III.E.4.c), so these substances could adversely influence mycorrhizal formation in other species if released into the soil. The previous growth of non-mycorrhizal plants in a soil has been observed to have a detrimental effect on the subsequent infectivity of VAM fungi, in some cases (Baltruschat and Dehne, 1988; Hayman *et al.,* 1975; Iqbal and Qureshi, 1976; Morley and Mosse, 1976; Powell, 1982), but not in others (Ocampo and Hayman, 1981; Schmidt and Reeves, 1984; Testier *et al.,* 1987). Ferulic acid, an allelopathic agent produced by *Asparagus officinalis,* has an inhibitory effect on VAM fungus activity, even though this plant normally benefits from mycorrhizas (Wacker *et al.,* 1990). Roots contain many secondary metabolites that have the potential to have allelopathic influences on plants and their mycorrhizal associates, but the role of these substances in soils is very difficult to resolve (Section III.E.4.c). Allelopathic interactions between mycorrhizal and non-mycorrhizal species, plants with separate types of mycorrhizas, or trees with different populations of ECM fungi may be one of the factors that influences the composition or stability of plant communities.

4. Mycorrhizas and Plant Succession

Successional changes to plant populations occur during ecosystems recovery from disturbance or establishment on new substrates (Barbour *et al.,* 1987; Grime, 1979). During this process opportunistic (ruderal) species are gradually replaced by more specialized plants as competition for space and soil resources becomes more important (Grime, 1979). Ruderal species, which are usually rare or absent from undisturbed sites (Grime, 1979), apparently often have root systems that would make them less dependent on mycorrhizas (Table 5) than climax vegetation species. The proportion of mycorrhizal roots has been observed to increase along with plant cover during succession in several natural ecosystems (Khan, 1974; Lesica and Antibus, 1985; Miller *et al.,* 1983; Pendelton and Smith, 1983; Red and Haselwandter, 1981; Rose, 1988). In tropical forests (Janos, 1980b) and arid shrub/grass communities (Allen, 1984; Allen and Allen, 1984; Miller, 1979; 1987; Reeves *et al.,* 1979) the first colonizers of disturbed sites are often non-mycorrhizal or facultative species, while obligately mycorrhizal plants became dominant later in succession. Miller (1987) has suggested that obligately mycorrhizal plants are more likely to be found where soil nutrient levels are low and disturbance is minimal, while moderate disturbance and soil nutrient levels favour facultatively mycorrhizal species and a combination of severe disturbance and high nutrient levels will favour non-mycorrhizal plants (severe disturbance and low nutrient levels tends to eliminate plants altogether) (Grime, 1979). There is evidence that succession in many communities follows these generalized trends, but there are also many exceptions.

In arid regions non-mycorrhizal plants may dominate severely Disturbed sites and the proportion of mycorrhizal plants may only reach previous levels after 20-30 years, but in other regions with more mesic, climates mycorrhizal plants are often common during the initial stages of succession (Miller, 1987). In the temperate deciduous forest region plants with VAM such as *Solidago* and *Aster* are important in early succession and non-mycorrhizal species only become dominant after massive fertilizer or biocide applications (Medve, 1984). Gange *et al.* (1990) found that the inhibition of VAM formation by the application of a fungicide significantly reduced the growth and recruitment of some species during the first year of succession after cultivation. In some arid habitats mycorrhizas may provide little benefit if the establishment of early successional species with low mycorrhizal dependency normally precedes successful establishment of mycorrhizal species (Allen and Allen, 1988; Loree and Williams, 1987). In coastal sand dunes most colonizing species form VAM and benefit greatly from this association, even though propagules of VAM fungi must often be in short supply (Koske, 1978b). Apparently propagules of both host plants and VAM fungi are co-dispersed to coastal habitats as plant colonization begins (Koske, 1988; Koske and Gemma, 1990). During succession in prairie ecosystems the proportion of mycorrhizal roots (but not total colonization levels) can decline during succession as fine roots (which are poorly colonized) become more prevalent (Cook *et al.,* 1988).

In deciduous forests, annuals and other ruderal (weed-like) species Which are normally present only in disturbed sites (Rogers, 1982), tend to be non-mycorrhizal or have facultative VAM associations (Brundrett and Kendrick, 1988). These relatively opportunistic species respond to openings in the tree canopy more rapidly than obligately mycorrhizal species, which generally have slow growth rates and lower reproductive potentials, but mycorrhizal species gradually regain dominance. Janos (1980b) observed similar trends in tropical forests and found that early successional species often had lighter seeds (aiding long range dispersal) than obligately mycorrhizal plants from climax communities (where seedling survival would be more important).

In boreal coniferous forests ECM inoculum levels decline rapidly after clear-cutting and changes to soil properties can inhibit surviving fungi, thus preventing tree regeneration (Section III.B.4). In these forests a succession of increasingly specialized fungi parallels re-establishment of host trees and soil conditions (Section III.B.6). It has been proposed that the absence of ECM inoculum may be one of the factors responsible for the absence of host trees in temperate grasslands (Harbour *et al.,* 1987). While it is true that propagules of ECM fungi are generally absent from prairie soils (Meyer, 1973; White, 1941; Wilde, 1954), other factors such as low water availability and frequent fires are considered to be responsible for the absence of trees (Risser, 1985). Abundant VAM fungus inoculum is normally present (Liberia and Anderson, 1986; Miller, 1987), but poor growth of trees with VAM associations has also been reported in prairie soils (White, 1941; Wilde, 1954). In some boreal coniferous forests the soil does not contain VAM inoculum (Kovacic *et al.,* 1984; Tobiessen and Werner, 1980). Seedlings of some trees may initially have VAM associations when growing in disturbed sites, but generally only form ECM when they are mature (Gardener and Malajczuk, 1988; Lapeyrie and Chilvers, 1985). This mycorrhizal flexibility may help them colonize sites where inoculum of ECM fungi is absent, but suggests that mature plants are more specific in their mycorrhizal requirements than seedlings. In boreal forests species with VAM and nitrogen fixing shrubs with ECM are important during early succession before ECM trees regain dominance and may help maintain mycorrhizal fungi (Cromack, 1981; McAfee and Fortin, 1989). The impact of soil disturbance, which may precede succession, on mycorrhizal fungus propagules was considered in Section III.B.4.

After the last ice age, the revegetation of glaciated regions in North America and Europe was a gradual process (Davis, 1981; Delcourt and

Delcourt, 1987). Initially tundra was replaced in North America by *Picea* spp. forests which dominated until *Larix, Abies, Betula* and *Pinus* species migrated northwards and finally trees from present day deciduous forests (such as *Fraxinus, Ulmus* and *Quercus,* which were early migrants, and *Acer, Carya* and *Fagus,* which were slower) extended to their present ranges. From our knowledge of the present day mycorrhizal associations of these trees, it seems that postglacial succession initially resulted in the dominance of trees with ECM, while trees with VAM were slower to become dominant or codominant. These trends may have resulted because the prevailing climatic conditions favoured trees with ECM associations, VAM fungi were slower to disperse than ECM fungi, VAM host trees had more limited dispersal than trees with ECM, or a combination of these factors were involved. The early pleistocene occurrence of fossil VAM fungus spores (Pirozynski and Dalpé, 1989) suggests that inoculum dispersal was not the most important limiting factor.

There is evidence that in some situations mycorrhizal inoculum levels may be one factor influencing the rate of succession, but changes to soil properties, or root system characteristics of plants may also be important and the gradual replacement of non-mycorrhizal species by those with VAM or ECM does not always occur during this process. While, successional processes often result in the increasing dominance of obligately mycorrhizal plants, there are many exceptions to this generalization and facultatively mycorrhizal or non-mycorrhizal plants may remain dominant or co-dominant in communities where severe edaphic or climatic conditions prevail, as will be considered in the next section.

5. The Distribution of Plants with Different Mycorrhizal Strategies

A compilation of reports on the mycorrhizal status of selected plants in major world ecosystems and edaphically limited vegetation communities is presented in Appendix 1. Trappe (1987) has calculated that about 3% of angiosperms have been examined for mycorrhizal associations (coverage of the pteridophytes would be similar, but a much higher proportion of the gymnosperms have been examined). Mycorrhizas have been most studied in temperate ecosystems, especially in the northern hemisphere, where there have been numerous studies especially of dominant trees (there are more than 75 reports concerning *Pinus sylvestris* or *Fagus sylvatica* (Harley and Harley, 1987), but in other areas sampling has been sparse (in tropical forests very high plant diversity makes this almost impossible) (Janos, 1987). From the evidence presented in Appendix 1 and other compilations of the mycorrhizal literature (Harley and Harley, 1987; Kelly, 1950; Meyer, 1973; Newman and Reddell, 1987; Trappe, 1987) correlations between environmental or soil conditions and the distribution of plants with different types of mycorrhizas can be established. Less is known about the occurrence of species with low or highly variable levels of mycorrhizas, since many separate reports are required to determine if a species is inconsistently mycorrhizal (Trappe, 1987). Plants that can form more than one type of functional mycorrhiza are rare in most ecosystems (Section III.D.2). The available evidence is more than sufficient to conclude that plants in most ecosystems are predominantly mycorrhizal and this fact is now as well established as many of the other assumptions on which science is based.

Trappe (1987) has compiled information about the mycorrhizal status of angiosperms from the mycorrhizal literature to allow comparisons with plant growth forms and ecological functions (Fig. 6). In general there are few correlations between mycorrhizal strategies and plant life history (annuals *vs* perennials) or growth form (herbaceous plants, trees, etc.). Exceptions to this rule include the fact that trees and shrubs are much more likely to have ECM associations than annuals and herbaceous plants (Harley and Smith, 1983). Parasitic plants usually are

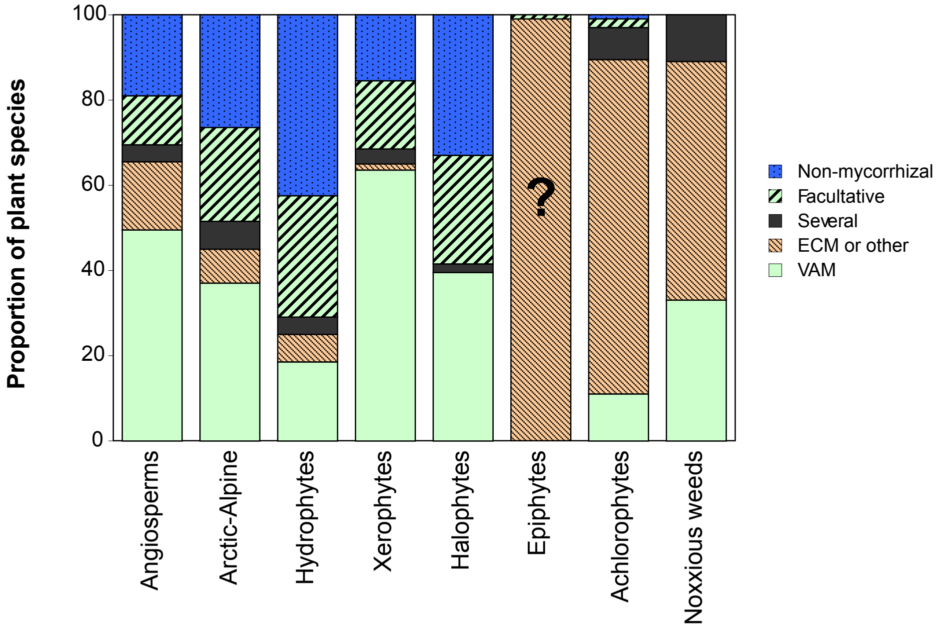

Fig. 6. Data from a mycorrhizal database compiled by Trappe (1987) is charted to illustrate mycorrhizal trends amongst the Angiosperms as a whole and within some specialized groups of plants (numbers of species examined for each category = 6507, 674, 679, 455, 293, 53, 66, 84 respectively). The question mark for epiphytes indicates that sampling of this group has been very limited and biased. "Several" refers to species which have been reported to have more than one type of mycorrhizas, while other terminology is the same as that used in Fig. 2.

non-mycorrhizal (Currah and Van Dyk, 1986; Harley and Harley, 1987; Lesica and Antibus, 1986): some plant families, such as the Scrophulariaceae, contain both mycorrhizal non-parasitic and non-mycorrhizal parasitic members, the latter having probably evolved from the former (Alexander and Weber, 1984). The proportion and importance of plants with different mycorrhizal strategies in a North American hardwood forest community are shown in Fig. 3. In this community, the mycorrhizal relations of plants is more closely related to root phenology than plant growth forms or above-ground phenology.

Epiphytes, plants which grow attached to tree branches or rocks rather than in soil. are most common in humid tropical sites (Benzing 1973). Limited surveys of epiphytic Orchidaceae have found many to have sporadic infection by orchid mycorrhizas (Benzing, 1982; Hadley and Williamson, 1972). The mycorrhizal status of other important groups of epiphytes – Filicales, Araceae, Bromeliaceae, Gesneriaceae, etc. has largely remained unexplored, although there is a report of ECM roots within bromeliad leaf-base tanks (Pittendrigh, 1984).

A shortage of mycorrhizal inoculum can occur during early succession (Section III.F.4), or in habitats where host plants normally do not occur (Berliner *et al.,* 1986; White, 1941; Wilde, 1954), but it seems that factors influencing the distribution of plants with a particular type of rnycorrhizal strategy are usually more important. However, the distribution of individual mycorrhizal fungi could influence the occurrence of plants which have relatively specific associations with these fungi, as is the case with some terrestrial orchids (Ramsay *et al.,* 1987; Warcup, 1981).

Vegetation on the Earth's surface can be classified into a number of distinct ecosystems with characteristic climates, soils and vegetation (Walter, 1979). These natural ecosystems occupy different parts of the Earth's land surface as a result of variations in the climatic factors with the greatest influence on plants-temperature and moisture availability (Billings, 1974; Osmond *et al.,* 1987; Whittaker, 1975). Thus tropical vegetation changes along a moisture gradient extending from rain forests to deserts, while temperate ecosystems follow a similar gradient from deciduous forests to grasslands and cool deserts (see Fig. 7). Other factors which can influence the distribution of vegetation include competition (which is most extreme in moist and warm regions and least severe in extremely cold or dry habitats) excessive radiation in arctic or alpine sites, localized edaphic factors and human activities such as agriculture and forestry (Barbour *et al.,* 1987; Osmond *et al.,* 1987).

One ecosystem type may occur in widely separate regions or continents with similar climates (Walter, 1979). Despite overall similarities in growth form, major taxonomic differences often occur between the

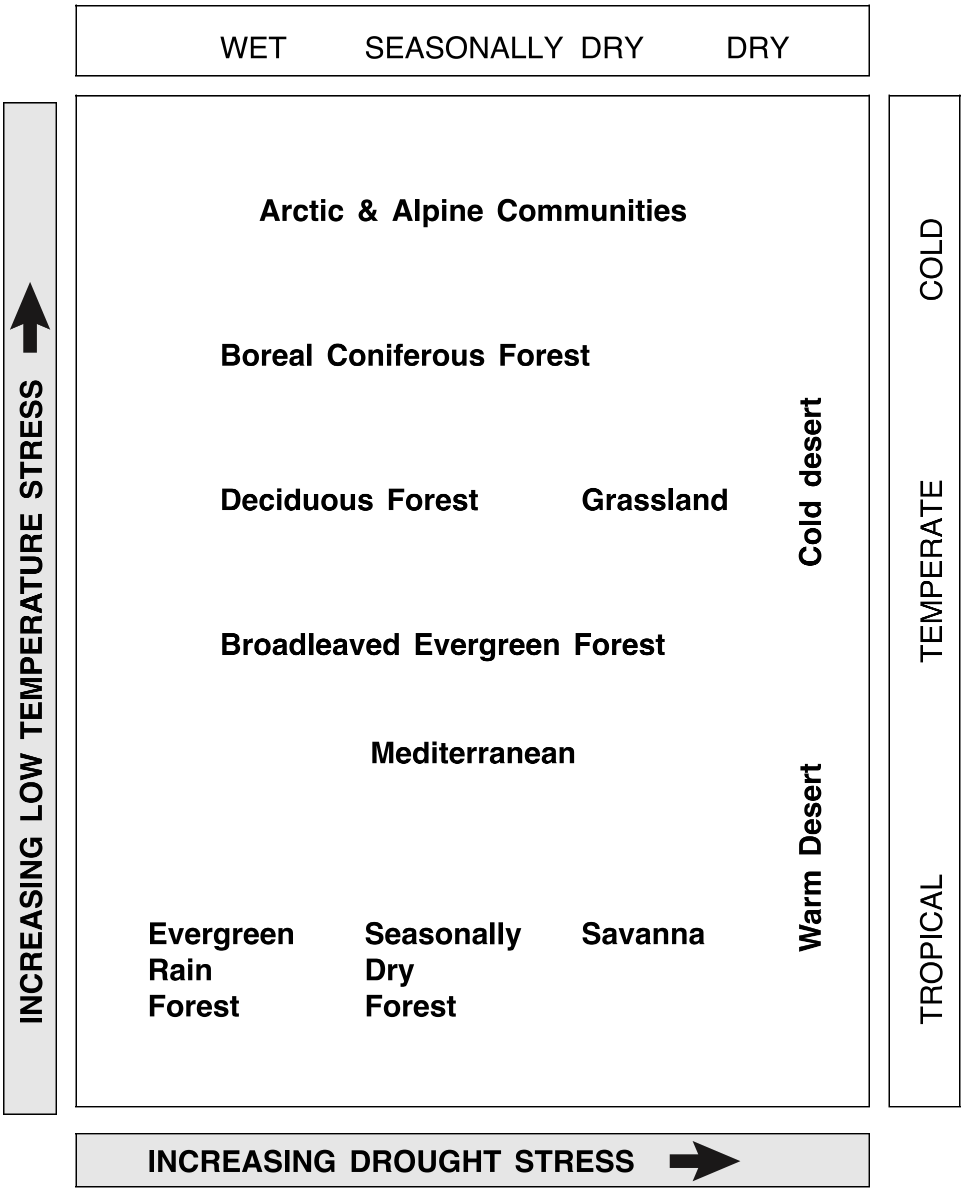

Fig. 7. Low temperature and drought stress are the two most important factors responsible for the distribution of world ecosystem types. Competition and other biological interactions are also important and would have the greatest influence in warm and/or wet ecosystems and less important in cold or dry habitats. This figure is based on similar charts in Billings (1974). Osmond *et al.* (1987) and Whittaker (1975).

vegetation in these separate floristic regions (Takhtajan, 1986). Because of these differences in host genetic background. generalizations about the mycorrhizal status of plants in one floristic region should not be indiscriminately applied to another. However, the relative importance of host genetic background and environmental factors in determining mycorrhizal strategies may be elucidated by their comparison. In general, it appears that similar mycorrhizal strategies occur throughout an ecosystem, even though they often include plants which are widely separated taxonomically or geographically (Appendix 1). Thus, environmental influences would appear to be more important determinants of mycorrhizal strategies than host taxonomic relationships or geographic barriers to host and fungus dispersal.

Within an ecosystem, variations in soil conditions. such as excess water and salinity, can cause localized changes in community structure (Etheringion, 1982; Whittaker, 1975). Mycorrhizal strategies in edaphic communities have been separately considered in Appendix 1, in an attempt to gain some understanding of the influence of gradients in soil factors or climatic conditions on these associations. Care must be taken in drawing conclusions from correlations between these gradients and the mycorrhizal relations of plants in natural ecosystems, because of the limits to our current knowledge of the environmental physiology of mycorrhizas.

Excess water and/or poor drainage in wetlands and aridity or excessive salinity in arid regions can restrict root growth (Gregory, 1987) as well as influencing the composition of plant communities (Etherington, 1982). Vegetation in temperate, arid, tropical or arctic regions has been observed to have less mycorrhizas where soils are wet (Anderson *et al.,* 1984; Khan, 1974; Miller and Laursen, 1978; Read *et al.,* 1976, etc.), but plants with VAM or ECM are usually present and some plants that are totally emersed in water can still form VAM (Appendix 1). The mycorrhizal inoculum potential of soils can be much reduced by flooding, as is the case with VAM after rice culture (Hag *et al.,* 1987; Nopamornbodi *et al.,* 1987). Mejstrik (1965) observed that most VAM activity in the roots of plants in a wetland community occurred at the times when the water table was lowest. The occurrence of plants with ericoid mycorrhizal associations is thought to be restricted in waterlogged soils, where plants with air-channels in their roots (such as non-mycorrhizal members of the Cyperaceae) become dominant (Leake *et al.,* 1989).

Kim and Weber (1985) found that mycorrhizas declined in sites with higher salinity and were absent in the centre of salt playas where salinity levels were extremely high. Members of the plant family Chenopodiaceae frequent saline soils (Etherington, 1982) and are usually non-mycorrhizal (Harley and Harley, 1987; Trappe, 1981), although some woody members of the genus *Atriplex* have VAM (Williams *et al.,* 1974).

Soil parent material composition influences soil chemical properties and vegetation types (Jefirey, 1987; Proctor and Woodell, 1975). Soil pH and calcium levels can also influence plant distribution since some species (calcicoles) prefer alkaline, calcareous soils while others (calcifuges) characteristically occur on acidic soils where metal ions may occur at toxic levels (Kinzel, 1983; Rorison and Robinson, 1984). In alpine vegetation communities plants growing on crystalline substrates had significantly lower levels of mycorrhizas than plants growing on calcareous substrates (Lesica and Antibus, 1985). In alpine or arctic regions many plants growing in rocky soils were non-mycorrhizal, while plants growing in soils with more organic matter were more likely to have VAM (Currah and Van Dyk, 1986; Miller, 1982b). Soils based on serpentine rock parent materials often have distinctive vegetation and may have toxic metal ion levels or lower nutrient levels (Proctor and Woodell, 1975). Plants in a serpentine grassland in California were mostly well colonized by VAM (Hopkins, 1986). Further investigations are likely to unearth other correlations between soil properties and plant mycorrhizal strategies, but these factors apparently have a much greater direct influences on plants.

There are many reports of mycorrhizal plants in arid ecosystems (Appendix I), but within these habitats gradients of decreasing soil moisture availability can be correlated with reductions in the proportion of mycorrhizal plants (Selavinov and Elusenova, 1974; Schmidt and Scow, 1986). Mycorrhizal activity in arid regions may also occur at greater soil depths than is usual in other habitats (Virginia *et al.,* 1986; Zajicek *et al.,* 1986b).

There are substantial reductions in the proportions of plants with any kind of mycorrhizal association in high altitude or high latitude sites where cold climatic conditions prevail (Christie and Nicolson, 1983; Dominik *et al.,* 1965a; Haselwandter, 1979; Read and Haselwandter, 1981; Trappe, 1988). Christie and Nicolson (1983) observed that some plants had VAM on sub-Antarctic islands but no mycorrhizal plants were found on continental Antarctic sites and they suggest that inoculum of VAM fungi may be lacking from the latter sites. Plants with VAM can be uncommon relative to those with ECM or ericoid associations, or non-mycorrhizal roots in high arctic habitats (Appendix 1), perhaps because the short growing season, or very slow nutrient cycling limit the effectiveness of VAM in these habitats (Kohn and Stasovski, 1990). The root length (relative to leaf surface area) of alpine vegetation is greater at higher altitudes and may compensate for lower mycorrhizal levels (Korner and Renhardt, 1987).

It would seem that the climatic gradients that have resulted in the formation of ecosystems (Fig. 7) have had little influence on the distribution of mycorrhizal associations as a whole (especially VAM which occur in almost all habitats), except that increasing severity of soil or environmental conditions is often correlated with a gradual decline in the importance or mycorrhizal plants relative to those that are non-mycorrhizal. There is evidence that mycorrhizal roots are more efficient at nutrient capture than non-mycorrhizal roots in most communities (Section III.E.5). In communities where plant productivity is severely restricted by environmental factors, photosynthetic energy capture is less likely to be limited by above-ground competition for light, while soil resources are often in short supply. Apparently this excess in photosynthate production relative to nutrient supply allows plants with diverse capture strategies-including extensive non-mycorrhizal or proteoid roots, carnivory, or parasitism, to compete more effectively with mycorrhizal plants. Indeed, plants with these specialized nutrient strategies are more common in communities such as mediterranean shrublands, where nutrient supply is severely limited (Jeffrey, 1987; Lamont, 1982).

More specialized types of mycorrhizas (Ericoid, Orchid, Monotropoid etc.) are present in most ecosystems but are rarely dominant (Appendix 1). Ericaceous shrubs (presumably with ericoid mycorrhizas) are common in the understorey of many dry, nutrient-poor forests in North America (Hicks and Chabot, 1985). Plants with ericoid mycorrhizas are more likely to be abundant or dominant in soils which are acidic and very nutrient deficient (Leake *et al.,* 1989; Read, 1983). Ericoid mycorrhizal fungi can greatly increase the tolerance of host roots to the toxic phenolic compounds and metal ions that occur on these soils (Leake *et al.,* 1989). Non-mycorrhizal plants or those with other types of mycorrhizas would be at a disadvantage in these communities if they cannot tolerate these soil conditions, or utilize organic nutrient sources (Section III.F.l). Litter from plants with ECM or ericoid mycorrhizal associations, apparently influences soil properties in ways that would be deleterious to plants with other other root strategies (Section III.F.3.a), which suggests that these plants may form communities which have a tendency to be self-perpetuating.

Trees are the dominant form of vegetation in habitats where they are not excluded by adverse environmental conditions (aridity or low temperatures) or disturbance. Forests containing mixtures of tress with VAM and ECM associations are generally less common than those where trees with one type of mycorrhizas predominate and non-mycorrhizal trees have rarely been observed (Appendix 1). Trees with VAM occur in many families, while those with ECM belong to a smaller number of diverse families (Harley and Smith, 1983; Malloch *et al.,* 1980).

Lodge (1989) compared VAM and ECM formation in *Populus* and *Salix* (trees which can form both types of associations) over a range of natural and experimental soil moisture levels. He found that VAM associations were more common in field soils that were drier or wetter than those in which ECM predominated, although VAM activity also found to be optimal in soils that were not flooded or dry in experiments. These results provide evidence of antagonistic interactions between mycorrhizal associations since VAM was only dominant where ECM activity was low (Lodge, 1989).

Trees with ECM are dominant in forests with relatively low plant diversity at high longitudes or altitudes where cool temperatures prevail (Appendix 1; Harley and Smith, 1983; Read, 1983; Singer and Morello, 1960). It has been suggested that only trees with ECM can grow in these forests (Tranquillini, 1979). However, this restriction is not due to the mycorrhizal fungus, since herbaceous plants with VAM are present in these forests and well beyond the tree line in arctic and alpine communities (Appendix 1). Similarly, the lack of trees above the tree line does not result from the absence of ECM fungi which still form associations with shrubs in much more severe sites.

Trees with ECM dominate most deciduous forests in Europe (Appendix 1). In North America, trees with ECM are more likely to be dominant in sites in warmer and dryer regions or where soils are poor (ridgetops, sandy glacial till) (Chabot and Hicks, 1982). In Europe, management practices have resulted in the predominance of F*agus sylvatica* (Walter and Breckle, 1985), an ECM tree, while in northeastern North America, human activities have favoured *Acer saccharum* (VAM) over *Fagus grandifolia* (ECM). Girard and Fortin (1985) observed that coniferous forests in Quebec occurred on sites with soils that were less fertile, more acidic and had much slower organic matter decomposition rates, relative to sites with similar climates where VAM trees were also present.

Most tropical plants have VAM associations, but areas where ECM trees are locally dominant occur in tropical forests throughout the world (Appendix 1). These ECM forests are warm throughout the year, but in some cases are subject to periodic drought (in Africa), or flooding (in South America). In these forests, trees with ECM are not randomly distributed but tend to occur in low-diversity stands or "groves" where VAM trees are excluded (Högberg, 1986; Newbery *et al.,* 1988; Singer and Araujo, 1979). Hart *et al.* (1989) considered reasons for the local dominance of *Gilbertiodendron deweveri* (which has been reported to have ECM) in tropical forests in Zaire. These reasons were complex, but included the large seeds with limited dispersal and shade tolerance of seedlings of *G. deweveri*, which apparently were related to a gradual increase in dominance by this species during long periods without disturbance. Trees that form low-diversity stands in other tropical regions, often have similar reproductive characteristics (Hart *et al.*,

1989) and in many cases represent islands of ECM activity surrounded by larger regions where trees with VAM are dominant (Malloch *et al.,* 1980). In temperate regions forests dominated by ECM trees also generally have lower plant diversity than those containing trees with VAM (Berliner and Torrey, 1989; Malloch *et al.,* 1980).

Högberg (1986) reported that soil phosphate levels were lower in ECM forests than in VAM communities in tropical Africa, but Newbery *et al.* (1988) found that seasonal variations in nutrient levels obscured these trends. Semi-arid African forests are often dominated by leguminous trees in the families Papilionaceae and Caesalpiniaceae, which have either ECM or both VAM and nitrogen fixing *Rhizobium* associations) suggesting that conservation of soil nitrogen by tight nutrient cycling may reduce the benefit of nitrogen fixing associations in ECM communities (Högberg, 1986). Ammonium and organic forms of nitrogen, are considered to be more restricted in supply that phosphorus in ECM forests, while phosphorus and nitrate may be more important limiting factors in VAM communities (Alexander, 1983; Girard and Fortin, 1985; Read, 1983). In the Amazon basin of South America, ECM trees occur in Igapó forests-areas where periodic inundation by "black water" rivers occurs, but trees in Várzea forests-where "white water” rivers cause flooding, have VAM (Singer, 1988). "Black water" rivers carry water which is nutrient poor and acidic relative to "white water" rivers (Kubitzki, 1989). In this case there appears to be a good correlation between soil quality (low-nutrient supply, or acidity) and ECM tree dominance.

It has been suggested that forests of trees with ECM can "degrade" soils by causing increased soil acidification (Harley, 1989). However, these trees may also be more likely to occur on soils that are naturally acidic, because they have a greater tolerance to low soil pH and high levels of aluminium or other toxic ions (Högberg, 1986). Litter characteristics of ECM trees may be responsible for changes to soil properties, such as slow nutrient cycling, soil acidification and adverse allelopathic influences on other species (Section III.F.3.a). Leaf litter accumulation, as apposed to rapid mineralization or consumption of leaves by soil biota, is a distinguishing feature of both tropical and temperate ECM forests (Chabot and Hicks, 1982; Singer and Araujo, 1979). In ECM-dominated boreal forests nutrient cycling occurs slowly because decomposition is inhibited by the high lignin and tannin content of leaf litter (Horner *et al.,* 1988). Litter decomposition may be further inhibited by low soil pH, or the withdrawal of water and nutrients by mycorrhizal fungi and roots (Section III.F.l). The activity and diversity of litter decomposing fungi can be substantially lower in ECM forests than in VAM forests (Singer and Araujo, 1979). Earthworms play an important role in decomposition processes in forests with VAM hut are absent in boreal forests (Girard and Fortin, 1985) and termites may also be important in tropical forests with VAM. There is evidence that substantial differences in decomposition processes, which regulate the form and availability of nutrients, occur between ECM and VAM communities, but how this relates to the mycorrhizal strategies of dominant trees is uncertain.

Estimates of carbon cycling in mycorrhizal associations support the contention that ECM associations are more expensive to maintain than VAM associations (Section III.E.7), originally proposed because of the higher fungal biomass associated with ECM roots (Harley, 1989, Harley and Smith, 1983; Read, 1983). Thus ECM associations require more investment in energy from the host than VAM associations, but in regions with short growing seasons ECM may be more advantageous if the function as perennial storage organs (Harley and Smith, 1983; Högberg, 1986). Limited seed dispersal by ECM trees in tropical forests (Hart *et al.,* 1989; Newbery *et al.,* 1988) and support of seedlings by a pre-existing hyphal network (Newman, 1988) may also favour seedling establishment close to trees with the same type of mycorrhizas. It appears that ECM forests are more likely to occur in regions with cool climates or nutrient-poor acidic soils that limit plant productivity. However, there is no evidence that trees with ECM associations in temperate regions are inherently less productive than those with VAM associations. In tropical regions ECM trees may be marginally more efficient than VAM trees, since groves of ECM trees gradually expand into VAM forests during long periods without disturbance. It would appear that host leaf-litter characteristics, substrate utilization by mycorrhizal fungi, soil pH, nutrient levels, etc. and environmental factors are the most important factors correlated with the mycorrhizal strategies of dominant trees, but their relative importance has not been established.

The best way to summarize the information presented in this section is to present the following list of generalizations. (i) Most of the plant species present in natural communities throughout the world normally have mycorrhizal associations. (ii) On a worldwide basis, plants with VAM are predominant, ECM relationships are very common (and tend to dominate where they occur), while other association types (ericoid, orchid, etc.) are present in most ecosystems, but usually form only a small part of the community. (iii) Non-mycorrhizal or facultatively mycorrhizal plants are more likely to occur in habitats where (a) there has been severe, recent disturbance, (b) soils are very dry and/or saline and/or wet, (c) low temperatures prevail, or (d) soil fertility is abnormally high or extremely low. (iv) Dominant trees in a community may have either ECM or VAM associations, less often trees with both occur together, but trees rarely if ever are non-mycorrhizal. (v) Throughout the world, plants in similar habitats usually have similar mycorrhizal strategies. (vi) Plants within a family usually have similar mycorrhizal relationships and plants within a genus nearly always do. We can be fairly confident that these generalizations would be reliable when used to predict mycorrhizal relationships at the community or ecosystem level, but they obviously should not be used to predict the mycorrhizal status of individual plants.

IV. CONCLUSIONS

There has been considerable progress in our understanding of the occurrence and multifaceted role of mycorrhizas in ecosystems during the last 100 years, but despite increasing interest there is still much to be learned. It is now well established that the most plants in ecosystems have mycorrhizas, so studies of nutrient uptake, soil resource competition. nutrient cycling etc. in ecosystems may be of little value if they do not consider the role of these associations. The value of mycorrhizal associations to plants which occur in natural ecosystems, has been demonstrated for a limited number of species by growth experiments at realistic nutrient levels (Table 6). However, mycorrhizas provided little benefit to host plants in some of these experiments and attempts to demonstrate their value in natural communities (using fungicides which inhibit mycorrhizal activity) have largely been unsuccessful (Section III.E.7). While it is possible successfully to manipulate mycorrhizal associations in experiments using controlled conditions in a glasshouse or growth chamber, there may be difficulties when extrapolating these results to natural ecosystems. In particular, it is difficult to (i) find a substitute for undisturbed soil, (ii) remove mycorrhizal fungi from soils without substantially altering other biotic and abiotic soil properties and (iii) grow control plants without mycorrhizas without changing many aspects of their physiology.

Experimental systems that have been used include (i) axenic culture of mycorrhizal fungi, (ii) mycorrhizal synthesis experiments using sterilized soil or axenic conditions, (iii) microcosm experiments, (iv) experiments using soil from ecosystems and (v) experiments in ecosystems arranged in increasing order of complexity and predictive ability. The axenic culture of mycorrhizal fungi allows the influence of a single factor such as temperature to be tested on a range of endophytes, but some fungi cannot be grown in this way and in other cases results can be misleading (Section III.B.5). Mycorrhizal synthesis experiments are more laborious but can allow the influence of one factor on a range of host-fungus combinations to be considered while environmental conditions are carefully controlled. Microcosm experiments can be used to study the influence of additional microbes or host plants in mycorrhizal experiments. These experiments have been used to study mycorrhizal influences on interplant nutrient transfer, competition between plants and decomposition processes (Dighton *et al.,* 1987; Finlay, 1989; Grime *et al.,* 1987; Perry *et al.,* 1989). The interpretation of data from mycorrhizal synthesis experiments is complicated by the absence of complicating factors that occur in nature (Fig. 5.A) and the interactions between root properties. soil nutrient availability and mycorrhizal fungus activity which determine mycorrhizal responses in experiments (Fig. 5.B). Intact cores of unmodified soil from natural ecosystems can be used to study mycorrhizal establishment while maintaining control of environmental factors (Jasper *et al.,* 1989c; Scheltema *et al.,* 1985a) and it is also possible to transplant seedlings into ecosystems and measure mycorrhizal formation (McAfee and Fortin, 1986; 1989; McGee, 1989; McGonigle and Fitter, 1988a).

Most mycorrhizal experiments have been conducted using simplified systems (monocultures, dual-organism cultures, or sterilized soils) because it is expected that more complex systems would produce results that were highly variable or difficult to interpret. However, real soil conditions must still be kept considered when interpreting results of these experiments. For example, soil sterilization can create toxic conditions or increase nutrient levels (Sparling and Tinker, 1978b) and may enhance plant growth by removing pathogens (Afek *et al.,* 1990). The relatively small volume of soil available to plants in pots can reduce mycorrhizal benefits (Bääth and Hayman, 1984). Additional complicating factors that may be important in ecosystems, but are usually excluded from experimental systems include preferences by endophytes for certain hosts or soil conditions which may occur in nature (Section III.D.l), soil organisms that may enhance the growth or germination of (Section III.E.3), or are antagonistic to mycorrhizal fungi (Section III.B.3) and the impact of mixing or storing soil on mycorrhizal fungi (Section III.B.4). It should also be noted that pre-existing hyphal networks which may influence nutrient completion or reduce association costs are absent from most experiments (Section III.E.2) and variations in the mycorrhizal dependency of plants can mask competition effects in experiments (Newman, 1988). It is easy to criticise experiments conducted under controlled conditions because of their artificial nature, but results from experiments in natural ecosystems may not produce clear cut results if treatment effects are overwhelmed by other sources of variability (Allen and Allen, 1986; Allen *et al.,* 1989b).

Measured responses of plants to mycorrhizal fungi will largely depend on soil properties which regulate nutrient availability (Section III.E.4). host plant nutrient requirements (Section III.E.7) and root system characteristics which determine nutrient uptake efficiency (Table 5). These mycorrhizal responses must be measured by comparing improvements in plant growth, stress tolerance, etc. with those in a non-mycorrhizal control plant. However, most plants in natural ecosystems are normally mycorrhizal, so we are really measuring the magnitude of growth depression resulting from mineral deficiency in the non-mycorrhizal control plants and this will depend on the factors listed above (see Fig. 5b). When quantifying mycorrhizal benefits, it is best to construct response curves that compare the nutrient use efficiency of mycorrhizal and non-mycorrhizal plants over a wide range of nutrient levels (Abbott and Robson, 1984a, 1990b), or compare mycorrhizal and non-mycorrhizal plants with similar relative growth rates and phosphorus contents by manipulating soil phosphorus levels (Augé, 1989; Baas *et al.,* 1989b; Graham, 1987; Pacovsky, 1986). Facultatively mycorrhizal plants should make the best experimental subjects, because these species can occur naturally without mycorrhizas. The existence of non-nutritional physiological differences between mycorrhizal and non-mycorrhizal control plants has not been properly established (Section III.E.6), but these would be more likely to occur in obligately mycorrhizal species which are not found without these associations in nature.

Roots in ecosystems have a much greater diversity in morphological features than is usually considered and this diversity involves features with the potential to influence water uptake, nutrient absorption and mycorrhizal formation (Sections III.C.l, III.E.4). For example, the mycorrhizal dependency of plants is influenced by root surface area and activity; long-lived roots often have suberized or lignified peripheral layers, which may enhance their survival when exposed to desiccation, pathogens etc., but should also restrict nutrient absorption; mycorrhizal associations may be regulated by root anatomical or chemical features; and root phenology can also influence the mycorrhizal relations of plants (Table 5). Many mycorrhizal morphology studies would benefit from a greater understanding of root phenology and structure and ultrastructural investigations should include a preliminary survey of root features using histochemical staining procedures (Brundrett *et al.*, 1990).

It is likely that root systems have evolved in response to the plants need to obtain adequate soil resources (water and nutrients) while minimizing carbon costs, but optimal root system features for obtaining different resources may be in conflict (Section III.F.2). Correlations between root structure and mycorrhizal formation (Section III.E.4-5) suggest that the regulation of mycorrhizal associations as well as the need for efficient water and nutrient acquisition have influenced the evolution of root form. Agricultural selection may have also resulted in changes to root parameters that influence nutrient uptake and mycorrhizal formation (Section III.E.5; O'Toole and Bland, 1987).

We are just beginning to understand the attributes of clonal isolates of mycorrhizal fungi that would result in the greatest benefit to associated plants and how they interact with environmental factors or soil conditions (Section III.B.5). In the future, careful identification of mycorrhizal isolates and progress in mycorrhizal taxonomy (especially with VAM fungi) may well reveal a much higher degree of fungus specialization with regard to these conditions. For this reason, it is advisable to assign isolate numbers to endophytes used in experiments, keep herbarium specimens and accurate information about where fungi were isolated so that future knowledge about taxonomic relationships and edaphic or climatic interactions can be taken into account (Morton, 1988, 1990; Trappe and Molina, 1986; Walker, 1988). Careful taxonomic studies and investigations of mycorrhizas in undisturbed ecosystems should be considered to be essential foundations which ultimately benefit all mycorrhizal research. It could also be argued that we have much to learn about the ecology of mycorrhizal fungi in the natural ecosystems and soils where they evolved. Unfortunately, it is much easier to receive funding for research with more practical objectives involving domesticated plants or disturbed ecosystems.

There are many questions involving the ecology of roots and mycorrhizal ecology that cannot be adequately answered at this time. There is evidence that the evolution of root form is regulated by trade-offs between features required for efficient direct nutrient absorption and water uptake on one hand and efficient mycorrhiza formation on the other, while minimizing root system costs (Section III.E.5). Roots exhibit less structural diversity than shoots. Has the need to form associations with a limited group of fungi (especially in the case of VAM) placed restrictions on the chemical and morphological evolution of roots? Have roots of non-mycorrhizal plants diverged more substantially (at least chemically) because this constraint on selection has been removed? Are processes such as rhizosphere modification, in addition to extensive root systems, used to help extract soil nutrients by non-mycorrhizal plants, such as members of Cruciferae, Cyperaceae and Proteaceae? Plants have evolved a very wide range of secondary metabolites and these chemicals appear to be more highly evolved in many non-mycorrhizal plant families (Table 4). Do these chemicals play a role in preventing mycorrhizal fungus establishment within the roots of non-mycorrhizal species? Are non-mycorrhizal more likely to have adverse allelopathic effects on mycorrhizal plants or their associated fungi? Do mycorrhizal associations with local "edaphotypes" of mycorrhizal fungi help roots adjust to local soil conditions? Do associations with well adapted mycorrhizal fungi increase host tolerance to pollution, disease, etc., or are these benefits entirely due to increased mineral nutrient supply? How rapidly (and how) do mycorrhizal fungi adapt to soil or environmental conditions? How important are organisms or processes which act as dispersal agents and consumers of mycorrhizal fungi in natural ecosystems?

The role of mycorrhizal relationships in competition for soil resources requires further investigation. Nutrient cycling in ecosystems involves a large and complex web of saprobic organisms which usually culminates in mycorrhizally mediated uptake by roots. Thus nutrient uptake likely involves co-operation between mycorrhizal fungi and other members of this food web to obtain nutrients which are spatially or chronologically separated from roots. There is increased evidence that mycorrhizal fungi, especially those forming ECM or ericoid associations, can obtain nutrients from some (relatively simple) organic substrates that are usually not considered to be available to plants. Interplant nutrient transfer through a common mycorrhizal mycelium has been demonstrated experimentally (Section III.F.l). Most evidence suggests that this transfer is not large enough to influence plant population dynamics, but some achlorophyllous plants live entirely by this means.

There are a number of examples where interactions involving mycorrhizal associations appear to be important in ecological interactions between plants. Different forms of nutrient competition may occur between plants with different mycorrhizal strategies (Section III.F.2). Mycorrhizas may ameliorate plant competition by increasing the functional similarity of roots (Section III.F.2). Plant succession may involve changes to dominant mycorrhizal strategies or populations of mycorrhizal fungi (Section III.F.4). Plants with a particular type of mycorrhizal associations can be dominant in some areas and subservient or absent in others, apparently as a result of environmental or edaphic factors (Section III.F.5). Some vegetation communities may have a tendency to be self-perpetuating because plants with other mycorrhizal types are inhibited by allelopathic interactions or soil property changes which they cause (Sections III.F.3.a, III.F.5). There is much scope for future ecological research which considers the role of mycorrhizal associations.

The occurrence of mycorrhizas in ecosystems has been the subject of numerous investigations which have demonstrated their worldwide importance (Appendix 1). However, there is need for more research (i) in ecosystems where sampling has been limited and which allows a range of geographic locations within an ecosystem to be compared, (ii) which considers the relative abundance of plants examined – so that the importance of mycorrhizal strategies can be determined at the community level (St. John and Coleman, 1983), (iii) which measures changes in mycorrhizal relationships or taxa along environmental gradients, such as soil moisture levels (Anderson *et al.,* 1984; Ebbers *et al.,* 1987; Lodge, 1989) or temperature (Koske, 1987a), (iv) which involves in situ identification of endophytes by mycorrhizal morphology or other means (McGee, 1989) and (v) which incorporates an understanding of root phenology and uses rigorously applied definitions to distinguish between different types or degrees of mycorrhizal associations. These types of studies may appear to be of little immediate practical value, but will inevitably be of great benefit to research involving forestry, revegetation etc. and will also help us understand the functioning of roots and mycorrhizas in agricultural situations.

V. APPENDIX 1

The following table contains a summary of our knowledge of the mycorrhizal relations of plants in natural ecosystems. Ecosystems are classified following Walter (1979). Only references in which roots were microscopically examined to confirm the presence and type of mycorrhizas are used in the table. If many references on mycorrhiza in an ecosystem were available, preference has been given to the most recent or concise surveys. The numbers of plant species sampled is provided for surveys of the latter type. Mycorrhizal studies which use the relative abundance of species examined to determine mycorrhizal colonization levels in the community as a whole are rare (St John and Coleman, 1983). but in most ecosystems a good appreciation of the overall importance of mycorrhizal can be obtained by combining floristic data (Hicks and Chabot, 1985; Larsen, 1980; Takhtajan, 1986) with mycorrhizal information from a number of surveys. No attempt has been made to distinguish between facultative (poorly developed or inconsistent) and highly developed mycorrhizas. This table should only be used to obtain an overall picture of the worldwide importance of mycorrhizas and general changes in mycorrhizal strategies resulting from climatic or edaphic trends, since the available data is often insufficient to allow accurate predictions of mycorrhizal relations in vegetation communities.

The occurrence of mycorrhizas in natural ecosystems

Ecosystem type Survey data: Location	Vegetation surveyed	*n*	Proportion of species with types of mycorrhizas	References
A. Evergreen rain forests				
Africa, Asia, South America	trees and herbs	684	93% VAM, 7% NM	Janos 1987 (review)
Southeast Asia	trees — Dipterocarpaceae		ECM	Smits (1983), Alexander (1987), Lee and Lim (1989)
Africa	trees — most areas		VAM	Högberg, 1986 (review), Newbery *et al*. (1988), Hogberg and Piearce (1986)
	trees — locally dominant		ECM	
South America	trees in unflooded forests		VAM	Singer and Araujo (1979)
	trees in seasonally flooded forests		ECM	
B. Seasonally dry tropical and subtropical forests				
Australia	dominant trees: Myrtaceae		ECM	Chilvers and Pryor (1965), Warcup (1980)
	shrubs, herbs	30	most VAM	Langkamp and Dalling (1982)
	shrubs: Ericales		ERC	Reed (1987)
	herbs, shrubs	93	70% VAM, 30% ECM, 10% NM (ORC, ERC)	McGee (1986)
Africa	most forest trees		VAM	Högberg (1986) (review)
	locally dominant trees		ECM	Högberg and Piearce (1986)

Continued

The occurrence of mycorrhizas in natural ecosystems *Continued*

Ecosystem type Survey data: Location	Vegetation surveyed	*n*	Proportion of species with types of mycorrhizas	References
C. Savanna				
Kenya	common grasses	5	VAM	Newman *et al*. (1986)
Cuba	trees	6	VAM	Herrera and Ferrer (1980)
Africa	trees: “Miombo” woodlands		70% ECM	Högberg (1986) (review)
	most other savanna trees		VAM	
South America	herbs, shrubs: “Cerrado” vegetation		most VAM, also ORC, ECM	Thomazini (1974)
D. Hot deserts and semideserts				
North America, Galápagos Islands, Zambia, Algeria, India, Pakistan	herbs and shrubs		most have VAM NM plants usually also common	Bethlenfalvay *et al*. (1984), Bloss (1985), Bloss and Walker (1987), Högberg and Piearce (1986), Khan (1974), Mejstrik and Cudlin (1983), Mukerji and Kapoor (1986), Rose (1980), Schmidt and Scow)1986)
E. Mediterranean regions				
Australia	shrubs, herbs		most VAM, NM, ERC and ECM also common	Lamont 1982 (review)
	trees: Myrtaceae		ECM also common	Chilvers and Pryor (1965), Gardner and Malajczuk (1988)
	herbs: Orchidaceae	144	ORC	Ramsay *et al*. (1986)
Western Australia	trees, shrubs, herbs	110	55% VAM, 17% ECM+VAM, 27% NM, ORC, ERC also	M. Brundrett (unpublished data) (=Brundrett and Abbott 1991)

South Africa	shrubs, herbs	41	42% VAM, 58% NM	Berliner *et al*. (1989)
Europe	trees		most ECM	Meyer (1973) (review)
California	shrubs		VAM or ECM	Kummerow (1981)
F. Temperate broadleaved evergreen forests				
Northern hemisphere	trees: mostly *Quercus* spp.		ECM	Harley and Smith (1983), Meyer (1973)
Southern hemisphere	trees: mostly *Nothofagus* and *Eucalyptus*		ECM	Meyer (1973)
New Zealand	herbs: limited surveys		most VAM	Baylis (1967), Johnson (1977)
Japan	herbs: large surveys		most VAM	Asai (1934), Maeda (1954)
G. Temperate deciduous forests				
North America	trees: dominant species well studied		VAM or ECM	Brundrett *et al*. (1990), Kelly (1950), Kormanik (1981)
	herbs (understorey): many surveys		most VAM, also NM and ERC	Girard (1985), Lohman (1927), McDougall and Liebtag (1928)
Ontario, Canada	trees, herbs, shrubs	68	80% VAM, 4% ECM, 13% NM, 3% ORC	Brundrett and Kendrick (1988)
Massachusetts, USA	trees, herbs, shrubs	45	71% VAM, 22% ECM, also NM, ERC and MON	Berliner and Torrey (1989)
Europe	trees: dominant species well studied		most ECM, some VAM	Le Tacon *et al*. (1987), Meyer (1973), Harley and Harley (1987), Dominik (1957), Dominik and Pachlewski (1956), Gallaud (1905), Read *et al*. (1976)
	herbs (understorey): many surveys		most VAM	
Europe FRG	beech forest herbs, trees	28	79% VAM, 18% NM, 4% ECM	Mayr and Godoy 1989

Continued

The occurrence of mycorrhizas in natural ecosystems *Continued*

Ecosystem type Survey data: Location	Vegetation surveyed	*n*	Proportion of species with types of mycorrhizas	References
H. Temperate grasslands				
North America	grasses and forbs		most VAM	Miller (1987) (review), Anderson *et al.* (1984), Davidson and Christensen (1977)
Alberta, Canada	grasses and forbs	85	95% VAM, 5% NM	Currah and Van Dyk (1986)
California, USA	herbs: serpentine grasslands	27	98% VAM	Hopkins (1986)
Russia	herbs, forbs: steppe vegetation	68	88% VAM, 12% NM	Selivanov and Eleusenova (1974)
New Zealand	tussock grasses		VAM	Crush (1973a)
Europe and North America	herbs: semi-natural grasslands		most VAM	Gay *et al*. (1982), Read *et al*. (1976), Sparling and Tinker (1978a), Rabatin (1979)
I. Cold deserts and semideserts				
Colorado, USA	herbs, shrubs: undisturbed site	42	95% VAM, 5% NM	Reeves *et al*. (1979)
	disturbed site	21	71% NM, 29% VAM	
Wyoming, USA	herbs: undisturbed site	22	95% VAM, 5% NM	Miller (1979)
	disturbed site	16	NM	
Utah, USA	herbs: disturbed sites	74	57% VAM, 43% NM	Pendleton and Smith (1983)
Russia, Kazakistan	herbs, shrubs	234	65% VAM, 35% NM	Selivanov and Eleusenova (1974)

Worldwide	herbs, shrubs, trees	263	72% VAM, 26% NM, 2% ECM	Trappe (1981) (review)
J. Boreal coniferous forests				
Northern hemisphere	trees: many studies		ECM	Brundrett *et al*. (1990), Harley and Harley (1987), Le Tacon *et al*. (1987), Meyer (1973)
North America	shrubs, herbs: understorey		many VAM, also ERC, ECM, ARB, ORC, MON also	Girard (1985), Malloch and Malloch (1981, 1982)
British Columbia, Canada	herbs	27	78% VAM, 22% NM	Berch *et al*. (1988)
Europe	shrubs, herbs: understorey		many VAM, also ERC, ECM, ARB, ORC, MON also	Dominik *et al*. (1954b), Harley and Harley (1987)
K. Arctic vegetation				
Northern hemisphere	herbs, shrubs		VAM, NM, ERC, ECM	Katenin (1965), Laursen and Chmielewski (1982), Likins and Antibus (1982), Stutz (1972)
Alaska, USA	dominant tundra plants	16	38% ECM, 31% ERC, 19% NM, 6% VAM, 6% ARB	Miller (1982)
Canada, Ellesmere Is.	high artic plants	24	54% NM, 25% ECM, 4% VAM, 4% ARB	Kohn and Stasovski (1990)
Sub-Antarctic islands	herbs	24	most VAM	Smith and Newton (1986)
Continental Antarctica	herbs	2	NM	Christie and Nicolson (1983)

continued

The occurrence of mycorrhizas in natural ecosystems *Continued*

Ecosystem type Survey data: Location	Vegetation surveyed	*n*	Proportion of species with types of mycorrhizas	References
L. Alpine vegetation				
Europe, Asia, North and South America	trees: subalpine boreal forests		ECM	Dominik *et al*. (1954b), Keke and Yu (1986), Meyer (1973), Trappe (1988), Singer and Morello (1960)
	shrubs: above tree line		ECM, ERC	Haselwandter (1979, 1987), Dominik *et al*. (1954a)
	herbs: many surveyed		many VAM, ERC, NM and DSF also common	Haselwandter and Read (1980), Lesica and Antibus (1985), Miller (1982), Nespiak (1953), Read and Haselwandter (1981)
Canada	herbs, shrubs: alpine and montane	44	16% VAM, 61% DSF, 9% NM, 14% ORC	Currah and Van Dyk (1986)
M. Edaphic vegetation communities				
1. Wet coastal vegetation				
Saltmarshes in Europe	dominant herbs: *Juncus*, *Spartina* etc.		NM	Boullard (1958), Fries (1944)
	herbs	18	56% VAM, 44% NM	Rozema *et al*. (1986)
Saltmarsh, USA	herbs	7	71% VAM, 29% NM	Cooke and Lefor (1990)
Saltmarsh, India	herbs	4	VAM	Sengupta and Chaudhuri (1990)
Mangrove vegetation	trees, herbs	26	NM	Lee and Baker (1973), Mohankumar and Mahadevan (1986), Rose (1981)

Seagrasses	herbs: detailed root structure studies		NM (VAM not seen)	Cambridge and Kuo (1982), Kuo *et al*. (1981), Tomlinson (1969)
2. Terrestrial wetlands				
North America, Europe, Asia and New Zealand	herbs: hydrophytes in marshes, lakes and rivers	82	56% NM, 44% VAM	Anderson *et al*. (1984), Bagyaraj *et al*. (1979), Clayton and Bagyaraj (1984), Farmer (1985), Khan (1974), Read *et al*. (1976), Sondergaard and Laegaard (1977)
India	tropical hydrophytes	70	53% NM, 47% VAM	Ragupathy *et al*. (1990)
Europe	herbs: wet meadows	73	86% VAM, 14% NM	Mejstrik (1965, 1972)
	herbs, shrubs: peatlands.	40	68% NM, 15% VAM, also ECM, ERC and ORC	Höveler (1982)
Temperate regions	trees, shrubs		VAM or ECM	Brundrett *et al*. (1990), Keeley (1980), Lodge (1989), Harley and Harley (1987), Marshall and Pattulo (1981)
3. Dry Saline Soils				
North America and Asia	herbs, shrubs: moderately saline soils		VAM or NM	Ho (1987), Khan (1974), Pond *et al*. (1984)
	highly saline soils		NM	Trappe (1987), Kim and Weber (1985)

Continued

The occurrence of mycorrhizas in natural ecosystems *Continued*

Ecosystem type Survey data: Location	Vegetation surveyed	*n*	Proportion of species with types of mycorrhizas	References
N. Ecosystems created by disturbance				
1. Sand Dune Vegetation				
Europe, Holland	herbs, shrubs	15	VAM	Ernst *et al*. (1984)
Europe, U. K.		6	most VAM	Nicolson (1960)
Europe, Italy		7	86% VAM, 14% NM	Puppi and Riess (1987)
North America			VAM	Koske (1987b) (review), Rose (1988), Sylvia and Will (1988)
Australia, Heron Island		42	57% VAM, 43% NM	Peterson *et al*. (1985)
Australia, New South Wales		41	88% VAM, 19% NM, 2% ERC	Logan *et al*. (1989)
Hawaii		31	74% VAM, 26% NM	Koske and Gemma (1990)

Abbreviations used: herb = herbaceous plant, VAM = vesicular-arbuscular mycorrhizas, ECM = ectomycorrhizas, NM = non-mycorrhizal, ERC = ericoid mycorrhizas, ORC = orchid mycorrhizas, ARB = arbutoid mycorrhizas, MON = monotropoid mycorrhizas, DSF = dark septate fungus.

ACKNOWLEDGEMENTS

Most of this review was written while the author was supported by a postdoctoral fellowship from the Natural Sciences and Engineering Research Council of Canada. I am especially gratefull to Abbott and Allan Robson for their support. Some parts of this review developed during my tenure as graduate student under the guidance of Bryce Kendrick and Larry Peterson. A. H. Fitter, Lyn Abbott, David Jasper provided comments on the manuscript. I would also like to thank Jim Trappe for his generous hospitality and access to his extensive collection of rare mycorrhizal papers.

REFERENCES

Abbott, L. K. (1982). Comparative anatomy of vesicular-arbuscular mycorrhizas formed on subterranean clover. *Aust. J. Bot.* **30,** 485-499.

Abbott, L. K. and Robson, A. D. (1982). Infectivity of vesicular-arbuscular mycorrhizal fungi in agricultural soils. *Aust. J. Agric. Res.* **33,** 1049-1959.

Abbott, L. K. and Robson, A. D. (1984a). The effect of VA mycorrhizae on plant growth. In: *VA Mycorrhiza* (Ed. by C. L. Powell and D. J. Bagjaraj). pp. 113-130. CRC Press, Boca Raton, Florida.

Abbott, L. K. and Robson, A. D. (1984b). Colonization of the root system of subterranean clover by three species of vesicular-arbuscular mycorrhizal fungi. *New Phytol.* **96,** 275-281.

Abbott, L. K. and Robson, A. D. (1985). Formation of external hyphae in soil by four species of vesicular-arbuscular mycorrhizal fungi. *New Phytol.* **99,** 245-255.

Abbott, L. K. and Robson, A. D. (1991a). Factors influencing the occurrence of vesicular-arbuscular mycorrhizas. *J. Agric. Ecos. Envir.* **35,** 121-150.

Abbott, L. K. and Robson, A. D. (1991b). Field management of va mycorrhizal fungi. In: *The Rhizosphere and Plant Growth* (Ed, by D.L. Keister and P.B. Cregan) pp. 355–362. Kluwer, Dordrecht.

Abdul-Kareem, A. W. and McRae, S. G. (1984). The effects on topsoil of long-term storage in stockpiles. *Plant Soil* **76,** 357-363.

Abuarghub, S, M. and Read, D. J. (1988). The biology of mycorrhizae in the Ericaceae XI. The distribution of nitrogen in soil of a typical upland Callunetum with special reference to the "free" amino acids. *New Phytol.* **108,** 425-431.

Abuzinadah, R. A. and Read, D. J. (1986). The role of proteins in the nitrogen nutrition of ectomycorrhizal plants. III. Protein utilization by *Betula, Picea* and *Pinus* in mycorrhizal association with *Hebeloma crustulinaforme. New Phytol.* **103,** 507-514.

Abuzinadah, R. A., Finlay, R. D. and Read, D. J, (1986). The role of proteins in the nitrogen nutrition of ectomycorrhizal plants. II. Utilization of protein by mycorrhizal plants of *Pinus contorta. New Phytol.* **103,** 495-506.

Acsai, J. and Largent, D. L. (1983). Ectomycorrhizae of selected conifers growing in sites which support dense growth of bracken fern. *Mycotaxon* **16,** 509-518.

Adelman, M. J. and Morton, J. B. (1986). Infectivity of vesicular-arbuscular mycorrhizal fungi: influence of host-soil diluent combinations on MPN estimates and percentage colonization. *Soil Biol. Biochem.* **18,** 77-83.

Afek, U., Menge, J. A. and Johnson, E. L. V. (1990). Effect of *Pythium ultimum* and metalaxyl treatments on root length and mycorrhizal colonization of cotton, onion, and pepper. *Plant Dis.* **74,** 117-120.

Agerer, R. (1986). Studies of ectomycorrhizae II. introducing remarks on characterization and identification. *Mycotaxon* **26,** 473-492.

Agerer, R. (1990). Studies of ectomycorrhizae XXIV. Ectomycorrhizae of *Chroogomphys helveticus* and *C. rutilus* (Gomphidiaceae, Basidiomycetes) and their relationship to those of *Suillus* and *Rhizopogon. Nova Hedwegia* **50,** 1-63.

Alexander, C. and Hadley, G. (1985). Carbon movement between host and mycorrhizal endophyte during the development of the orchid *Goodyera repens* Br. *New Phytol.* **101,** 657-665.

Alexander, I. J. (1983). The significance of ectomycorrhizas in the nitrogen cycle. In: *Nitrogen As An Ecosystem Factor* (Ed. by J. A. Lu, S. McNeill and I. H. Rorison). pp. 69-93. Blackwell, Oxford.

Alexander, I. J. (1987). Ectomycorrhizas in indigenous lowland tropical forest and woodland. In: *Mycorrhizae in the Next Decade, Practical Applications and Research Priorities* (Ed. by *D.* M. Sylvia, L. L. Hung and J. H. Graham). pp. 115-117. Institute of Food and Agricultural Sciences. University of Florida, Gainesville.

Alexander, I. J. and Högberg, P. (1986). Ectomycorrhizas of tropical angiosperms. *New Phytol.* **102,** 541-549.

Alexander, T., Toth, R., Meier, R., and Weber, H. C. (1989). Dynamics of arbuscule development and degeneration in onion, bean. and tomato with reference to vesicular-arbuscular mycorrhizae in grasses. *Can. J. Bot.* **67,** 2505-2513.

Alexander. V. T. and Weber, H. C. (1984). Zur parasitischen lebensweise von *Parentucellia latifolia* (L.) Caruel (Scrophulariaceae). *Beitr. Biol. Pflanzen.* **60,** 23-34.

Ali, N. A. and Jackson, R. M. (1988). Effects of plant roots and their exudates on germination of spores of ectomycorrhizal fungi. *Trans. Br. Mycol. Soc.* **91,** 253-260.

Allen, E. B. (1984). VA mycorrhizae and colonizing annuals: implications for growth. competition and succession. In: *VA Mycorrhizae and Reclamation of Arid and Semi-arid Lands* (Ed. by *S.* E. Williams & M. F. Allen), pp. 45-52. Wyoming Agr. Expt. St. Univ. Wyoming. Sci. Rep. No. SA1261.

Allen, E. B. and Allen, M. F. (1984). Competition between plants of different successional stages: mycorrhizae as regulators. *Can. J. Bot.* **62,** 2625-2629.

Allen, E. B. and Allen, M. F. (1986). Water relations of xeric grasses in the field: interactions on mycorrhizas and competition. *New Phytol.* **104,** 559-571.

Allen, E. B. and Allen, M. F. (1988). Facilitation of succession by the nonmycotrophic colonizer *Salsola kali* (Chenopodiaceae) on a harsh site: effects of mycorrhizal fungi. *Am. J. Bot.* **75,** 257-266.

Allen, E. B., Chambers, J. C., Connor, K. F., Allen, M. F. and Brown, R. W. (1987). Natural re-establishment of mycorrhizae in disturbed alpine ecosystems. *Arctic Alpine Res.* **19,** 11-20.

Allen, M. F. (1983). Formation of vesicular-arbuscular mycorrhizae in *Atriplex gardneri* (Chenopodiaceae): seasonal response in a cool desert. *Mycologia* **75,** 773-776.

Allen, M. F. (1988). Re-establishment of VA mycorrhizas following severe disturbance: comparative patch dynamics of a shrub desert and a subalpine volcano. *Proc. R. Soc. Edinb. B* **94,** 63-71.

Allen, M. F. and MacMahon, J. A. (1980). Direct VA mycorrhizal inoculation of colonizing plants by pocket gophers *(Thomomys talpoides)* on Mount St. Helens. *Mycologia* **80,** 754-756.

Allen, M. F., Allen, E. B. and Friese, C. F. (1989a). Responses of the non-myotrophic plant *Salsola kali* to invasion by vesicular-arbuscular mycorrhizal fungi. *New Phytol.* **111,** 45-49.

Allen, M. F., Richards, J. H. and Busso, C. A. (1989b). Influence of clipping and soil water status on vesicular-arbuscular mycorrhizae of two semi-arid tussock grasses. *Biol. Fertil. Soils* **8,** 285-289.

Amaranthus, M. P. and Perry, D. A. (1987). Effect of soil transfer on ectomycorrhiza formation and the survival and growth of conifer seedlings on old, nonreforested clear-cuts. *Can. J. For. Res.* **17,** 944-950.

Ames, R. N., Reid, C. P. P. and Ingham, E. R. (1984). Rhizosphere bacterial population responses to root colonization by a vesicular-arbuscular mycorrhizal fungus. *New Phytol.* **96,** 555-563.

Ames, R. N., Mihara, K. L. and Bayne, H. G. (1989). Chitin-decomposing actinomycetes associated with a vesicular-arbuscular mycorrhizal fungus from a calcareous soil. *New Phytol.* **111,** 67-71.

Amijee, F., Tinker, P. B. and Stribley, D. P. (1989). The development of endomycorrhizal root systems. VII. A detailed study of effects of soil phosphorus on colonization. New *Phytol.* **111,** 435-446.

Andersen, C. P., Sucoff. E. I. and Dixon. R. K. (1987). The influence of low soil temperature on the growth of vesicular-arbuscular mycorrhizal *Fraxinus pennsylvanica. Can. J. For. Res.* **17,** 951-956.

Anderson, R. C. and Liberia, A. E. (1987). Variation in vesicular-arbuscular mycorrhizal relationships of two sand prairie species. *Am. Midl. Nat.* **118,** 56-63.

Anderson, R. C. and Liberia, A. E. (1989). Growth of little bluestem *(Schizachyrium scoparium)* (Poaceae) in fumigated and nonfumigated soils under various inorganic nutrient conditions. *Am. J. Bot.* **76,** 95-104.

Anderson, R. C. Liberia, A. E. and Dickman, L. A. (1984). Interaction of vascular plants and vesicular-arbuscular mycorrhizal fungi across a soil moisture- nutrient gradient. *Oecologia (Berl.)* **64,** 111-117.

Arines, J. and Vilarino, A. (1989)- Use of nutrient-phosphorus ratios to evaluate the effects of vesicular-arbuscular mycorrhizaa on nutrient uptake in unsterilized soils. *Biol. Fertil. Soils* **8,** 293-297.

Armstrong, W. (1979). Aeration in higher plants. In: *Advances in Botanical Research* (Ed. by H. W. Woolhouse). pp. 225-332. Academic Press, Toronto.

Asai, T. (1934). Uber das vorkommen und die bedeutung der wurzelpilze in der landpflanzen. *Jap. J. Bot.* **7,** 107-150.

Ashford, A. E., Peterson, C. A., Carpenter, J. L., Cairney, J. W. G. and Allaway, W. G. (1988). Structure and permeability of the fungal sheath in *Pisonia mycorrhiza. Protoplasma* **147,** 149-161.

Ashford, A. E., Allaway, W. G., Peterson, C. A. and Cairney, J. W. G. (1989). Nutrient transfer and the fungus-root interface. *Aust. J. Plant Physiol.* **16,** 85-97.

Attiwill, P. M. and Leeper, G. W. (1987). *Forest Soils and Nutrient Cycles.* Melbourne University Press, Melbourne.

Augé, R. M. (1989). Do VA mycorrhiza enhance transpiration by affecting host phosphorus content. *J. Plant Nut.* **12,** 743-753.

Azcón-Aguilar, C. and Barea, J. M. (1985). Effect of soil microorganisms on formation of vesicular-arbuscular mycorrhizas. *Trans. Br. Mycol. Soc.* **84,** 536-537.

Azcón-Aguilar, C., Diaz-Rodriguez, R. M. and Barea, J. M. (1986). Effect of free-living fungi on the germination of *G. mosseae* on soil extract. In: *Physiology and Genetical Aspects of Mycorrhizae* (Ed. by V. Gianinazzi-Pearson and S. Gianinazzi). pp. 515-519. INRA, Paris.

Azcón, R. (1987). Germination and hyphal growth of *Glomus mosseae in vitro:* effects of rhizosphere bacteria and cell-free culture media. *Soil. Biol. Biochem.* **19,** 417-419.

Azcón, R. and Ocampo, J. A. (1981). Factors affecting the vesicular-arbuscular infection and mycorrhizal dependency of thirteen wheat cultivars. *New Phytol.* **87,** 677-685.

Baas, R. Van Dijk, C. and Troelstra, S. R. (1989a). Effects of rhizosphere soil, vesicular-arbuscular mycorrhizal fungi and phosphate on *Plantago major* L. ssp. *pleiospenna* Pilger. *Plant soil* **113,** 59-67.

Baas, R., Van der Werf, A. and Lambers, H. (1989b). Root respiration and growth in *Plamago major* as affected by vesicular-arbuscular mycorrhizal infection. *Plant Physiol.* **91,** 227-232.

Bääth, E. and Hajman, D. S. (1984). Effect of soil volume and plant density on mycorrhizal infection and growth response. *Plant Soil* **77,** 373-376.

Bagyaraj, D. J. (1984). Biological interactions with VA mycorrhizal fungi. In: *VA Mycorrhizae* (Ed. by C. L. Powell and D. J. Bagyaraj), pp. 131-154. CRC Press, Boca Raton, Florida.

Bagyaraj, D. J., Manjunath, A. and Patil, R. B. (1979). Occurrence of vesicular-arbuscular mycorrhizas in some tropical aquatic plants. *Trans. Br. Mycol. Soc.* **72,** 164-167.

Bajwa, R. and Read, D. J. (1986). Utilization of mineral and amino N sources by the cricoid mycorrhizal endophyte *Hymenoscyphus ericae* and by mycorrhizal and non-mycorrhizal seedlings of *Vaccinium. Trans. Br. Mycol. Soc.* **87,** 269-277.

Baltruschat, H. and Dehne, H. W. (1988). The occurrence of vesicular-arbuscular mycorrhiza in agro-ecosystems. *Plant Soil* **107,** 279-284.

Barbour, M. G., Burk, J. H. and Pitts, W. D. (1987). *Terrestrial Plant Ecology.* Benjamin Cummings Company. Menlo Park, California.

Barea, J. M. and Azcon-Aquilar, C. (1983). Mycorrhizas and their significance in nodulating nitrogen-fixing plants. *Adv. Agron.* **36,** 1-54.

Barea, J. M., El-Atrach, F. and Azcón, R. (1989). Mycorrhiza and phosphate interactions as affecting plant development, N2-fixation, N-transfer and N-uptake from soil in legume-grass mixtures by using a ^{15}N dilution technique. *Soil Biol. Biochem.* **21,** 581-589.

Barnet, H. L. (1964). Mycrotropism. *Mycologia* **56,** 1-19.

Baylis, G. T. S. (1967). Experiments on the ecological significance of phycomycetous mycorrhizas. *New Phytol.* **6,** 231-243.

Baylis, G. T. S. (1975). The magnolioid mycorrhiza and mycotrophy in root systems derived from it. *Endomycorrhizas* (Ed. by F. E. Sanders, B. Mosse and P. B. Tinker), pp. 373-389. Academic Press, New York.

Begg, J. E. (1963). Comparative responses of indigenous, naturalized, and commercial legumes to phosphorus and sulphur. *Aust. J. Exp. Agric. Anim. Husbandry* **3,** 17-19.

Bell, E. A. (1981). The physiological role(s) of secondary (natural) products. In: *The Biochemistry of Plants a Comprehensive Treatise Vol. 7: Secondary Plant Products* (Ed. by *E.* E. Conn). pp. 1-19. Academic Press. New York.

Benzing, D. H. (1973). The monocotyledons: their evolution and comparative biology I. Mineral nutrition and related phenomena in Bromeliaceae and Orchidaceae. *Q. Rev. Biol.* **48,** 277-290.

Benzing, D. H. (1982). Mycorrhizal infections of epiphytic orchids in southern Florida. *Am. Orchid Soc. Bull.* **51,** 618-622.

Berch, S. M., Garriet, S. and Deom, E. (1988). Mycorrhizal status of some plants of southwestern British Columbia. *Can. J. Bot.* **66,** 1924-1928.

Bergelson, J. M. and Crawly, M. J. (1988). Mycorrhizal infectivity and plant species diversity. *Nature* **334,** 202.

Berliner, R. and Torrey, J. G. (1989). Studies on mycorrhizal associations in Harvard Forest. Massachusetts. *Can. J. Bot.* **67,** 2245-2251.

Berliner, R., Jacoby, B. and Zamski, E. (1986). Absence of *Cistus incanus* from basaltic soils in Israel: effect of mycorrhizae. *Ecology* **67,** 1283-1288.

Berliner, R., Mitchell, D. T. and Allsopp, N. (1989). The vesicular-arbuscular mycorrhizal infectivity of sandy soils in the south-western Cape, South Africa. *S. Afr. Tydskr. Plantk.* **55,** 310-313.

Berta, G., Gianinazzi-Pearson, V., Gay, G. and Torri, G. (1988). Morphogenetic effects of endomycorrhizal formation on the root system of *Calluna vulgaris* (L.) Hull. *Symbiosis* **5,** 33-44.

Bethlenfalvay, G. J., Brown, M. S. and Pacovsky, R. S. (1982). Relationships between host and endophyte development in mycorrhizal soybeans, *New Phytol.* **90,** 537-543.

Bethlenfalvay, G. J., Dakessian, S. and Pacovsky, R. S. (1984). Mycorrhizae in a southern California desert: ecological implications. *Can. J. Bot.* **62,** 519-524.

Bethlenfalvay, G. J., Thomas, R. S., Dakessian, S., Brown, M. S. and Ames, R. N. (1985). Mycorrhizae in stressed environments: effects on plant growth, endophyte development, soil stability and soil water. In: *Arid Lands* (Ed. by I. E. E. Whitehead). Westview Press, Boulder, Colorado.

Bethlenfalvay, G. J., Franson, R. L., Brown, M. S. and Mihara, K. L. (1989). The *Glycine-Glomus-Rhizobium* symbiosis. XI. Nutritional, morphological and physiological responses of nodulated soybean to geographic isolates of the mycorrhizal fungus *Glomus mosseae. Physiol. Plant.* **76,** 226-232.

Bhat, K. K. S. and Nye, P. B. (1974). Diffusion of phosphate to plant roots in soil III. depletion around onion roots without root hairs. *Plant Soil* **41,** 383-394.

Biermann, B. and Lindermann, R. G. (1983). Use of vesicular-arbuscular mycorrhizal roots, intraradical vesicles and extraradical vesicles as inoculum. *New Phytol.* **95,** 97-105.

Billings, W. D. (1974). Adaptations and origins of alpine plants. *Arct. Alpine Res.* **6,** 129-146.

Bills, G. F., Holtzmann, G. I. and Miller, O. K. Jr. (1986). Comparison of ectomycorrhizal-basidiomycete communities in red spruce versus northern hardwood forests of West Virginia. *Can. J. Bot,* **64,** 760-768.

Birch, C. P. D. (1986). Development of VA mycorrhizal infection in seedlings in
(Ed. by V. Gianinazzi-Pearson and S. Gianinazzi), pp. 233-237. INRA, Paris.

Bjorkman, E. (1960). *Monotropa hypopitys* L. - an epiparasite on tree roots. *Physiol. Plant.* **13,** 308-327.

Blaschke, H. and Baumler, W. (1989). Mycophagy and spore dispersal by small mammals in Bavarian forests. *For. Ecol.* **26,** 237-245.

Bloss, H. E. (1985). Studies of symbiotic microflora and their role in the ecology of desert plants. *Desert Plants* **7,** 119-127.

Bloss, H. E. and Walker, C. (1987). Some endogonaceous mycorrhizal fungi of the Santa Catalina mountains in Arizona. *Mycologia* **79,** 649-654.

Boerner, R. E. J. (1986). Seasonal nutrient dynamics. nutrient resorption, and mycorrhizal infection intensity of two perennial forest herbs. *Am. J. Bot.* **73,** 1249-1357.

Boerner, R. E. J. (1990). Role of mycorrhizal fungus origin in growth and nutrient uptake by *Geranium robertianum. Am. J. Bot.* **77,** 483-489.

Bolan, N. S., Robson, A. D. and Barrow, N. J. (1984). Increasing phosphorus supply can increase the infection of plant roots by vesicular-arbuscular mycorrhizal fungi. *Soil Biol. Biochem.* **16,** 419-420.

Bolan, N. S., Robson, A. D. and Barrow, N. J. (1987). Effects of vesicular-arbuscular mycorrhiza on the availability of iron phosphates to plants. *Plant Soil* **99,** 401-410.

Bonfante-Fasolo, P. and Vian, B. (1989). Cell wall architecture in mycorrhizal roots of *Allium porrum* L. *Ann. Sci. Nat. Bot. **13,*** 97-109.

Borowicz, V. A. and Fitter. A. H. (1990). Effects of endomycorrhizal infection, artificial herbivory and parental cross on growth of *Lotus cormculatus* L. *Oecologia (Berl.)* **82,** 402-407.

Boullard, B. (1958). Les mycrohizes des especes de contact marin et de contact salin. *Rev. Mycol.* **23,** 282-317.

Bowen, G. D. (1987). The biology and physiology of infection and its development. In: *Ecophysiology of VA Mycorrhii:al Plants* (Ed. by G. R. Safir). pp. 27-57. CRC Press. Boca Raton. Florida.

Bowen, G. D. and Theodorou, C. (1973). Growth of ectomycorrhizal fungi around seeds and roots. In: *Ectomycorrhizae - Their Ecology and Physiology* (Ed. G. C. Marks and T. T. Kozlowski), pp. 107-150. Academic Press, New York.

Brammall, R. A. and Higgins, V. J. (1988). A histological comparison of fungal colonization in tomato seedlings susceptible or resistant to *Fusarium* crown and root rot disease. *Can. J. Bot.* **66,** 915-925.

Brown, R. T. and Mikola, P. (1974). The influence of fruticose soil lichens upon the mycorrhizae and seedling growth of forest trees. *Acta Forest. Fenn.* **141,** 1-23.

Brundrett, M. C. and Kendrick. B. (1987). The relationship between the ash bolete *(Boletinellus merulioides)* and an aphid parasitic on ash tree roots. *Symbiosis* **3,** 315-319.

Brundrett, M. C. and Kendrick, B. (1988). The mycorrhizal status, root anatomy, and phenology of plants in a sugar maple forest. *Can. J. Bot.* **66,** 1153-1173.

Brundrett, M. C. and Kendrick, B. (1990a). The roots and mycorrhizas of herbaceous woodland plants I. Quantitative aspects of morphology. *New Phytol.* **14,** 457-468.

Brundrett, M. C. and Kendrick, B. (1990b). The roots and mycorrhizas of herbaceous woodland plants II. Structural aspects of morphology. *New Phytol.* **114,** 469-479.

Brundrett, M. C., Murase, G. and Kendrick, B. (1990). Comparative anatomy of roots and mycorrhizae of common Ontario trees. *Can.* J. *Bot.* **68,** 551-578.

Cairney, J. W. G. and Ashford, A. E. (1989). Reducing activity at the root surface in *Eucalyptus pilulans-Pisolithus tinctorius* ectomycorrhizas. *Aust. J. Plant Physiol.* **16,** 99-105.

Caldwell, M. M. (1987). Competition between root systems in natural communities. In: *Root Develoment and Function* (Ed. by P. J. Gregory, J. V. Coke and D. A. Rose). pp. 167-185. Cambridge University Press. Cambridge.

Caldwell, M. M. and Richards, J. H. (1986). Competing root systems: morphology and models of absorption. *On the Economy of Plant Form and Function* (Ed. by T. J. Givnish), pp. 251-273. Cambridge University Press, Cambridge.

Cambridge, M. L. and Kuo, J. (1982). Morphology, anatomy and histochemistry of the Australian seagrasses of the genus *Posidonia* König (Posidoniaceae). III. *Posidonia sinuosa* Cambridge & Kuo. *Aquat. Bot.* **14,** 1-14.

Campbell, B. D. and Grime, J. P. (1989). A comparative study of plant responsiveness to the duration of episodes of mineral nutrient enrichment. *New Phytol.* **112,** 261-267.

Campbell, E. O. (1962). The mycorrhiza of *Gastrodia cunninghamii* Hook. f. *Trans. R. Soc. N. Z.* **1 ,** 289-296.

Cardus, J. R. (1980). Distinguishing between grass and legume species for efficiency of phosphorus use. *N. Z. J. Agric. Res.* **23,** 75-81.

Carmi, A. and Heuer, B. (1981). The role of roots in control of bean shoot growth. *Ann. Bot.* **48,** 519-527.

Chabot, B. F. and Hicks, D. J. (1982). The ecology of leaf life span. *Ann. Rev. Ecol. Syst.* **13,** 229-256.

Chakraborty, S., Theodorou, C. and Bowen, G. D. (1985). Mycophagous amoebae reduction of root colonization by *Rhizopogon.* In: *Proceedings of the 6th North American Conference on Mycorrhizae* (Ed. by R. Molina), p. 275. Forest Research Laboratory, Oregon State University, Corvallis, Oregon.

Chakravarty, P. and Unestam, T. (1987). Mycorrhizal fungi prevent disease in stressed pine seedlings. *J. Phytopath.* **118,** 335-340.

Chapin, F. S. III. (1988). Ecological aspects of plant mineral nutrient. In: *Advances in Plant Nutrition Vol. 3* (Ed. by B. Tinker and A. Lachli), pp. 161-191. Praeger, New York.

Chapin, F. S. III, and Shaver, G. R. (1985). Arctic. Pages 16-40 in B. F. Chabot & H. A. Mooney (eds), *Physiological Ecology of North American Plant Communities*. Chapman and Hall, New York.

Chapin, F. S. III, Vitousek, P. M. and Cleve, K. Van. (1986). The nature of nutrient limitations in plant communities. *Am. Natur.* **127,** 48-58.

Chilvers, G. A. (1972). Tree root pattern in a mixed eucalypt forest. *Aust. J. Bot.* **20,** 229-234.

Chilvers, G. A. and Gust, L. W. (1982). Comparison between the growth rates of mycorrhizas, uninfected roots and a mycorrhizal fungus of *Eucalyptus st-johnii* R. T. Bak. *New Phyiol.* **91,** 453-466.

Chilvers, G. A. and Pryor, L. D. (1965). The Structure of eucalypt mycorrhizas. *Aust.* J. *Bot.* **13,** 245-259.

Chilvers, G. A., Lapeyrie, F. F. and Horan, D. P. (1987). Ectomycorrhizal vs endomycorrhizal fungi within the same root system. *New Phytol.* **107,** 441-448.

Chilvers, M. T. and Daft, M. J. F., (1982). Effects of low temperature on development of the vesicular-arbuscular mycorrhizal association between *Glomus caledonium* and *Allium cepa. Trans. Br. Mycol. Soc.* **79,** 153-157.

Christiensen, M. (1989). A view of fungal ecology. *Mycologia* **81,** 1-19.

Christie, P. and Nicolson, T. H. (1983). Are mycorrhizas absent from the Antarctic? *Trans. Br. Mycol. Soc.* **80,** 557-560.

Christy, E. J., Sollins, P. and Trappe, J. M. (1982). First year survival of *Tsuga heterophylla* without mycorrhizae and subsequent ectomycorrhizal development on decaying logs and mineral soil. *Can. J. Bot.* **60,** 1601-1605.

Clayton, J. S. and Bagyaraj, D. J. (1984). Vesicular-arbuscular mycorrhizas in submerged aquatic plants of New Zealand. *Aquat. Bot.* **19,** 251-262.

Cline, M. L., France, R. C. and Reid, C. P. P. (1987). Intraspecific and interspecific growth variation of ectomycorrhizal fungi at different temperatures. *Can. J. Bot.* **65,** 869-875.

Codignola, A., Verotta, L., Spanu, P., Maffei, M., Scannerini, S. and Bonfante-Fasolo, P. (1989). Cell wall bound-phenols in roots of vesicular-arbuscular mycorrhizal plants. *New Phytol.* **112,** 221-228.

Coleman, D. C. (1985). Through a ped darkly; an ecological assessment of root-soil-microbial-faunal interactions. In: *Ecological Interactions in Soil, Plants, Microbes and Animals* (Ed. by A. H. Fitter, D. Atkinson, D. J. Read and M. B. Usher), pp. 1-21. Blackwell, Oxford.

Coleman, D. C., Reid, C. P. P. and Cole, C. V. (1983). Biological strategies of nutrient cycling in soil systems. *Adv. Ecol. Res.* **13,** 1-55.

Coleman, M. D., Bledsoe, C. S. and Lopushinsky, W. (1989). Pure culture response of ectomycorrhizal fungi to imposed water stress. *Can. J. Bot.* **67,** 29-39.

Cook, B. D., Jastrow, J. D. and Miller, R. M. (1988). Root and mycorrhizal endophyte development in a chronosequence of restored tallgrass prairie. *New Phytol.* **11,** 355-362.

Cooke, J. C. and Lefor, M. W. (1990). Comparison of vesicular-arbuscular mycorrhizae in plants from disturbed and adjacent undisturbed regions of a coastal salt marsh in Clinton, Connecticut, USA. *Envir. Mgmt.* **14,** 131-137.

Coté, J. F. and Thibault, J. R. (1988). Allelopathic potential of raspberry foliar leachates on growth of ectomycorrhizal fungi associated with black spruce *Am. J. Bot.* **75,** 966-970.

Cowan, P. E. (1989). A vesicular-arbuscular fungus in the diet of brushtail possums. *N. Z.* J. *Bot.* **27,** 129-131.

Crick, J. C. and Grime, J. P. (1987). Morphological plasticity and mineral nutrient capture of two herbaceous species of contrasted ecology. *New Phytol.* **107,** 403-414.

Cromack, K. Jr. (1981). Below-ground processes in forest Succession. In: *Forest Succession-Concepts and Application* (Ed. by *D.* C. West, H. H. Shugart and D. B. Botkin), pp. 361-373. Springer-Verlag, New York.

Cromack, K. Jr., Sollins, P., Graustein, W. C., Speidel, K., Todd, A. W., Spycher, G., Li, C. Y. and Todd, R. L. (1979). Calcium oxalate accumulation and soil weathering in mats of the hypogeous fungus *Hysterungium crassurn. Soil Biol. Biochem.* **11,** 463-468.

Cromack, K. Jr, Fichter, B. L., Moldenke, A. M., Entry, J. A. and Ingham, E. R. (1988). Interactions between soil animals and ectomycorrhizal fungal mats. *Agr. Ecos. Environ.* **24,** 161-168.

Crombie, D. S., Tippett, J. P. and Hill, T. C. (1988). Dawn water potential and root depth of trees and understory species in south-western Australia. *Aust. J. Bot.* **36,** 621-631.

Cronquist. A. (1977). On the taxonomic significance of secondary metabolites in angiosperms. *Plant Syst. Evol.* (Suppl). **1,** 179-189.

Cronquist, A. (1981). *An Integrated System of Classification of Flowering Plants.* Columbia University Press, New York.

Crowell, H. F. and Boerner, R, E. J. (1988). Influences of mycorrhizae and phosphorus on belowground competition between two old-field annuals. *Env. Expt. Bot.* **28,** 381-392.

Crush, J. R, (1973a). Significance of endomycorrhizas in tussock grassland in Otago, New Zealand. *N. Z. J. Bot.* **11,** 645-60.

Crush, J. R. (1973b), The effect of *Rhizophagus tennis* mycorrhizas on ryegrass, cocksfoot and sweet vernal. *New Phytol.* **72.** 956-973.

Crush, J. R. (1974). Plant growth responses to vesicular-arbuscular mycorrhiza VII. Growth and nodulation of some herbage legumes. *New Phytol.* **73,** 734-749.

Cuenca, G., Aranguren, J. and Herrera, R. (1983). Root growth and litter decomposition in a coffee plantation under shade trees. *Plant Soil* **71,** 477-486.

Curl, E. A. and Truelove, B. (1986). *The Rhizosphere.* Springer-Verlag, Berlin.

Currah, R. S. and Van Dyk, M. (1986). A survey of some perennial vascular plant species native to Alberta for occurrence of mycorrhizal fungi. *Can. Field Nat.* **100,** 330-342.

Currah, R. S., Sigler, L, and Hambleton, S. (1987). New records and new taxa of fungi from the mycorrhizae of terrestrial orchids of Alberta. *Can. J. Bot,* **65,** 2473-2482.

Daft, M. J. (19831. The influence of mixed inocula on endomycorrhizal- development. *plant Soil* **73,** 307-313.

Daft, M. J., Chilvers, M. T. and Nicolson, T. H. (1980). Mycorrhizas of the Liliiflorae I. Morphogenesis of *Endymion non-scriptus* (L.) Garke and its mycorrhizas in nature. *New Phytol.* 85, 181-189.

Daft, M. J., Spencer, D. and Thomas, G. E. (1987). Infectivity of vesicular-arbuscular mycorrhizal inocula after storage under various environmental conditions. *Trans. Br. Mycol. Soc.* **88,** 21-27.

Dahm, H., Strzelczyk, E. and Majewska, L. (1987). Cellulolytic and pectolytic activity of mycorrhizal fungi, bacteria and actinomycetes associated with the roots of *Pinus sylvestris. Pedobiologia* **30,** 73-80.

Dalpé, Y. (1989) Ericoid mycorrhizal fungi in the Myxotrichaceae and Gymnoascaceae. *New Phytol.* **113,** 523-527.

Dalpé, Y., Granger, R. L. and Furlan, V. (1986). Abondance relative et diversité des Endogonaces dans un sol de verger du Québec. *Can. J. Bot.* **64,** 912-917.

Daniels, B. A. and Menge, J. A. (1980). Hyperparasitization of vesicular-arbuscular mycorrhizal fungi. *Phytopathology* **70,** 584-588.

Daniels Hetrick, B. A. (1984). The ecology of VA mycorrhizal fungi. *VA Mycorrhiza* (Ed. by Conway Ll. Powell and D. Joseph Bagyaraj), pp. 35-36. CRC Press, Boca Raton, Florida.

Daniels Hetrick, B. A. and Bloom, J. (1983). Vesicular-arbuscular mycorrhizal fungi associated with native tall grass prairie and cultivated winter wheat. *Can. J. Bot.* **61,** 2140-2146.

Daniels Hetrick, B. A, and Bloom, J. (1986). The influence of host plant on production and colonization ability of vesicular-arbuscular mycorrhizal spores. *Mycologia* **78,** 32-36.

Daniels Hetrick, B. A. and Bloom, J. (1988). Mycorrhizal dependence and growth habit of warm-season and cool-season tallgrass prairie plants. *Can. J. Bot.* **66,** 1376-1380.

Daniels Hetrick, B. A., Thompson Wilson, G., Gerschefske Kitt, D. and Schwab, A. P. (1987). Effects of soil microorganisms on mycorrhizal contribution to growth of big bluestem grass in non-sterile soil, *Soil Biol. Biochem.* **20,** 510-507.

Daniels Hetrick, B. A., Leslic, J. F., Thompson Wilson, G. and Gerschefske Kitt, G. D. (1988). Physical and topological assessment of effects of a vesicular-arbuscular mycorrhizal fungus on root architecture of big bluestem. *New Phytol.* **110,** 85-96.

Daniels Hetrick, B. A., Thompson Wilson, G. W. and Hartnett, D. C. (1989). Relationship between mycorrhizal dependence and competitive ability of two tallgrass prairie grasses. *Can. J. Bot.* **67,** 2608-2615.

Daniels Hetrick, B. A., Wilson, G. W. T. and Owensby, C. E. (1990). Influence of mycorrhizal fungi and fertilization on big bluestem seedling biomass. *J Range Mgmt* **42,** 213-216.

Danielson, R. M. (1985). Mycorrhizae and reclamation of stressed terrestrial environments. *Soil Reclamation Processes - Microorganisms, Analyses and Applications* (Ed. by *R.* L. Tate and D. A. Klein). pp. 173-201. Marcel Dekker, New York.

Danielson, R. M. and Visser, S. (1989). Effect of forest soil acidification on ectomycorrhizal and vesicular-arbuscular mycorrhizal development. *New Phytol.* **112,** 41-47.

Dartnall, A. M. and Burns, R. G. (1987). A sensitive method for measuring cyanide and cyanogenic glucosides in sand culture and soil. *Biol. Fertil. Soil* **5,** 141-147.

Davidson, D. E. and Christensen, M. (1977). Root-microfungal and mycorrhizal associations in a shortgrass prairie. In: *The Belowground Ecosystem: A Synthesis of Plant-associated Processes* (Ed. by *J.* K. Marshall). pp. 279-287 Range Sci. Dep. Sci. Ser. No. 26. Colorado State University, Fort Collins.

Davis, E. A., Young, J. L. and Rose, S. L. (1984). Detection of high-phosphorus tolerant VAM-fungi colonizing hops and peppermint. *Plant Soil* **81,** 29-36.

Davis, M. B. (1981). Quaternary history and the stability of forest communities. In: *Forest Succession Concepts and Application* (Ed. by *D.* C. West. H. H. Shugart and D. B. Botkin), pp. 132-153. Springer-Verlag. New York.

Davis, R. M. and Menge, J. A. (1980). Influence of *Glomus fasciculatum* and soil phosphorus in *Phytophthora* root rot of citrus. *Phytopath.* **70,** 447-452.

Day, L. D., Sylvia, D. M. and Collins, M. E. (19871. Interactions among vesicular-arbuscular mycorrhizae, soil and landscape position. *Soil Sci. Soc. Am. J.* **51,** 635-639.

De Wit, P. J. G. M. (1987). Specificity of active resistance mechanisms in plant-fungus interactions. *Fungal Infection* of *Plants* (Ed. by G. F. Pegg and P. G. Ayes), pp. 1-24. Cambridge University Press. Cambridge.

Debaud, J. C., Gay, C., Prevost, A., Lei, J. and Dexheimer, J. (1988). Ectomycorrhizal ability of genetically different homokaryotic and dikaryotic mycelia of *Hebeloma cylindrosporum. New Phytol.* **108,** 322-328.

Dehne, W. H. (1986). Influence of va mycorrhizae on host plant physiology. In: *Physiology and Genetical Aspects of Mycorrhizae* (Ed. by V. Gianinazzi-Pearson and S. Gianinazzi). pp. 431-435. INRA, Paris.

Delcourt, P. A. and Delcourt, H. R. (1987). *Long-term Forest Dynamics in the Temperate Zone.* Springer Verlag, New York.

Denny, H. J. and Wilkins, D. A. (1987). Zinc tolerance in *Betula* spp. II. Variation on response to zinc among ectomycorrhizal associates. *New Phytol.* **106,** 535-544.

Dewan, M, and Sivasithamparum, K. (1988). A plant-growth promoting sterile fungus from wheat and ryegrass roots with potential for suppressing take-all. *Trans. Br. Mycol. Soc.* **96,** 687-717.

Dhillion, S. S., Anderson, R. C. and Liberia, A. E. (1989). Effect of fire on the mycorrhizal ecology of little bluestem *(Schizachyrium scoparium). Can. J. Bot.* **66,** 706-713.

Dighton, J. and Mason, P. A. (1985). Mycorrhizal dynamics during forest tree development. In: *Development Biology of Higher Fungi* (Ed. by D. Moore, L. A. Caselton. D. A. Wood and J. C. Frankland), pp. 117-139. Cambridge University Press. Cambridge.

Dighton, J., Thomas, E. D. and Latter, P. M. (1987). Interactions between tree roots, mycorrhizas, a saprotrophic fungus and the decomposition of organic substrates in a microcosm. *Biol. Fertil. Soils* **4,** 145-150.

Dittmer, H. J. (1937). A quantitative study of the root hairs of a winter rye plant *Secale cereale. Am. J. Bot.* **24,** 417-420.

Dittmer, H. J. (1949). Root hair variations in plant species. *Am. J. Bot.* **36,** 152-155.

Dixon, R. K. (1988). Response of ectomycorrhizal *Quercus rubra* to soil cadmium, nickel and lead. *Soii Biol. Biochem.* **20,** 555-559.

Dodd, J. C. and Jeffries, J. C. (1986). Early development of vesicular-arbuscular mycorrhizas in autumn-sown cereals. *Soil Biol. Biochem.* **18,** 149-154.

Dominik, T. (1957). [Investigations on the mycotrophy of beech associations on the Baltic coast] (In Polish). *Ekolgia Polska* A **5,** 213-256. (USDA Trans. OTS 61-11329)

Dominik, T, and Pachlewski, R. (1956). [Investigations on mycotrophism of plant associations in the lower timber zone of the Tatra.] (In Polish). *Acta Soc. Bot. Poloniae* **25,** 3-26, (USDA Trans. OTS 60-21384)

Dominik, T., Nespiak, A. and Pachlewski, R. (1954a). [Investigations on the mycotrophy of vegetal associations on calcarious rocks in the Tatra Mts.] (In Polish). *Acta Soc. Bot. Poloniae* **23,** 471-485. (USDA Trans. TT 65-50358)

Dominik, T., Nespiak, A and Pachlewski, R. (1954b). [Investigations on mycotrophy of plant associations of the upper timber zone in the Tatra.] (In Polish). *Acta Soc. Bot. Poloniae* **23,** 487-504. (USDA trans. OTS 61-11330)

Drew, M. C. (1987). Function of root tissues in nutrient and water transport. In: *Root Development and Function (Ed.* by P. J. Gregory, J. V. Lake & D. A. Rose), pp. 71-101. Cambridge University Press, Cambridge.

Drew, M. C. and Saker, L. R. (1975). Nutrient supply and the growth of the seminal root system in barley II. Localized, compensatory increases in lateral root growth and rates of nitrate uptake when nitrate supply is restricted to only part of the root system. *J. Exp. Bot.* **26,** 79-90.

Drew, M. C. and Saker, L. R. (1978). Nutrient supply and the growth of the seminal root system in barley III. Compensatory increases in growth of lateral roots, and in rates of phosphate uptake, in response to a localized supply of phosphate. *J Exp. Bot.* **29,** 435-451.

Drobnica, L., Zemanovi, M., Nemec, P., Kristiin, A., Stullerová, A., Knoppovi, V. and Nemec, P. Jr. (1967). Antifungal activity of isothiocyanates and related compounds. I. Naturally occuring isothiocynates and their analogues. *Appl. Miciobiol.* **15,** 701-709.

Duc, G., Trouvelot. A., Gianinazzi-Pearson, V. and Gianinazzi, S. (1989). First report of non-mycorrhizal plant mutants (Myc-) obtained in pea *(Pisum sativum* L.) and fababean *(Vicia faba* L.). *Plant Sci.* **60,** 215-222.

Duchesne, L. C., Peterson, R. L. and Ellis, B. E. (1987). The accumulation of plant-produced antimicrobial compounds in response to ectomycorrhizal fungi: a review. *Phytoprotection* **68,** 17-27.

Duchesne, L, C., Ellis, B. E. and Peterson, R. L. (1989). Disease suppression by the ectomycorrhizal fungus *Paxilus involutus:* contribution of oxalic acid. *Can. J. Bot.* **67,** 2726-2730.

Duddridge, J. A. (1987). Specificity and recognition in ectomycorrhizal associations. In: *Fungal Infection of Plants* (Ed. by *G.* F. Pegg and P. G. Abres). pp. 25-44. Cambridge University Press, Cambridge.

Dueck, Th. A., Visser, P., Ernst, W. H. 0. and Schat, H. (1986). Vesicular-arbuscular mycorrhizae decrease zinc toxicity to grasses growing in zinc polluted soil. *Soil Biol. Biochem.* **18,** 331-333.

Eason, W. R. and Newman, E. I. (1990). Rapid cycling of nitrogen and phosphorus from dying roots of *Lolium perenne. Oecologia (Berl.)* **82,** 432-436.

Ebbers, B. C., Anderson, R. C. and Liberia, A. E. (1987). Aspects of the mycorrhizal ecology of prairie dropseed. *Sporobolus heterolepis* (Poaceae). *Am. J. Bot.* **74,** 564-573.

Eissenstat, D. M. and Caldwell, M. M. (1988). Competitive ability is linked to rates of water extraction a field study of two aridland tussock grasses. *Oecologia (Berl.)* **75,** 1-7.

Eissenstat, D. M. and Newman, E. I. (1990). Seedling establishment near large plants - effects of vesicular-arbuscular mycorrhizas on the intensity of plant competition. *Func. Ecol.* **4,** 95-99.

El-Atrach, F., Vierheilig and Ocampo, J, A. (1989). Influence of non-host plants on vesicular-arbuscular mycorrhizal infection of host plants and on spore germination. *Soil Biol. Biochem.* **21,** 161 -163.

Elias, K. S. and Safir, G. R. (1987). Hyphal elongation of *Glomus fasciculatus* in response to root exudates. *Appl. Envir. Microbial.* **53,** 1928-1933.

Endrigkeit, A. von. (1933). Beitrage zum ernahrungsphysiologischen problem der mycorrhiza unter besonder berucksichtigung des bauses und der function der wurzel- und pilzmembranen. *Bot. Arch.* **39,** 1-87.

Ernst, W. H. O., Van Duin, W. E. and Oolbekking, G. T. (1984). Vesicular-arbuscular mycorrhiza in dune vegetation. *Acta. Bot. Neerl.* **33,** 151-160.

Esau, K. (1965). *Plant Anatomy.* John Wiley, New York.

Etherington, J. R. (1982). *Environment and Plant Ecology.* John Wiley, Toronto.

Evans, D. G. and Miller, M. H. (1988). Vesicular-arbuscular mycorrhizas and the soil-disturbance-induced reduction of nutrient absorption in maize. I. Causal relations. *New Phytol.* **110,** 67-74.

Evans, D. G. and Miller, M. H. (1990). The role of the external mycelial network in the effect of soil disturbance upon vesicular-arbuscular mycorrhizal colonization of maize. *New Phytol.* **114,** 65-71.

Farmer, A. M. (1985). The occurrence of vesicular-arbuscular mycorrhiza in isoetoid-type submerged aquatic macrophytes under naturally varying conditions. *Aquat. Bot.* **21,** 245-249,

Finlay, R. D. (1985). Interactions between soil micro-arthropods and endomycorrhizal associations of higher plants. In: *Ecological Interactions in Soil: Plants, Microbes and Animals* (Ed. by A. H. Fitter, D. Atkinson, D. J. Read and M. B. Usher), pp. 319-331. Blackwell, Oxford.

Finlay, R. D. (1989). Functional aspects of phosphorus uptake and carbon translocation in incompatible ectomycorrhizal associations between *Pinus sylvestris* and *Suillus grevillei* and *Boletinus cavipes. New Phytol.* **112,** 185-192.

Finlay, R. D. and Read, D. J. (1986). The uptake and distribution of phosphorus by ectomycorrhizal mycelium. In: *Physiology and Genetical Aspects of Mycorrhizae* (Ed. by V. Gianinazzi-Pearson and S. Gianninazzi). pp. 351-355. INRA, Paris.

Finlay, R. D., Ek, H., Odham, G. and Soderstrom, B. (1988). Mycelial uptake translocation and assimilation of nitrogen from ^{15}N-labelled ammonium by *Pinus sylvestris* plants infected with four different ectomycorrhizal fungi. *New Phytol.* **110,** *56*- 66.

Fisher, R. F. (1979). Possible allelopathic effects of Reindeer-moss *(Cladonia)* on Jack Pine and White Spruce. *For. Sci.* **25,** 256-260.

Fitter, A. H. (1977). Influence of mycorrhizal infection on competition for phosphorus and potassium by two grasses. *New Phytol.* **79,** 119-125.

Fitter, A. H. (1985). Functioning of vesicular-arbuscular mycorrhizas under field conditions. *New Phytol.* **99,** 257-265.

Fitter, A. H. (1986a). Acquisition and utilization of resources. In: *Plant Ecology* (Ed. by M. J. Crawley). pp. 375-405, Blackwell, Oxford.

Fitter, A. H. (1986b). Effect of benomyl on leaf phosphorus concentration in alpine grasslands: a test of mycorrhizal benefit. *New Phytol.* **103,** 767-776.

Fitter, A. H. (1986c). Spatial and temporal patterns of root activity in a species-rich alluvial grassland. *Oecologia (Berl.)* **69,** 594-599.

Fitter, A. H. (1987). An architectural approach to the comparative ecology of plant root systems. *New Phytol.* **106** (Suppl.), 61-77.

Filter, A. H. (1988). Water relations of red clover *Trifolium prarense* L. as affected by VA mycorrhizal infections and phosphorus supply before and during drought. *J. Exp. Bot.* **39,** 595-603.

Fitter, A. H. (1989). The role and ecological significance of vesicular-arbuscular mycorrhizas in temperate ecosystems. *Agric. Ecos. Envir.* **29,** 137-151,

Fitter, A. H. and Hay, R. K. M. (1987). *Environmental Physiology of Plants.* Academic Press, London

Fitter, A. H. and Nichols, R. (1988). The use of benomyl to control infection by vesicular-arbuscular mycorrhizal fungi. *New Phytol.* **110,** 201-206.

Fleming, L. V. (1984). Effects of trenching and coring on the formation of ectomycorrhizas on birch seedlings grown around mature trees. *New Phytol.* **98,** 143-153.

Fleming, L. V. (1985). Experimental study of sequences of ectomycorrhizal fungi on birch *(Betula* sp.) seedling root systems. *Soil Biol. Biochem.* **17,** 591-600.

Fogel, R. (1980). Mycorrhizae and nutrient cycling in natural forest ecosystems. *New Phytol.* **86,** 199-212.

Fogel, R. (1985). Roots as primary producers in below-ground ecosystems. In: *Ecological Interactions in Soil: Plants, Microbes and Animals* (Ed. by A. H. Fitter, D. Atkinson, D. J. Read and M. B. Usher), pp. 23-26. Blackwell, Oxford.

Fogel, R. (1988). Interactions among soil biota in coniferous ecosystems. *Agric. Ecos. Envir.* **24,** 69 -85.

Fogel, R. and Peck, S. B. (1975). Ecological studies of hypogeous fungi. I. Coleoptera associated with sporocarps. *Mycologia* **67,** 741 -747.

Fohse, D., Claassen, N. and Jungk, A. (1988). Phosphorus efficiency of plants I. External and internal P requirement and P uptake efficiency of different plant species. *Plant Soil* **110,** 101-109.

Fox, F. M. (19831. Role of basidiospores as inocula of mycorrhizal fungi of birch. *Plant Soil* **71,** 269-273.

Fox, F. M. (1986a). Ultrastructure and infectivity of sclerotium-like bodies of the ectomycorrhizal fungus *Hebelma sacchariolens,* on birch *(Betula* spp.). *Trans. Br. Mycol. Soc.* **87,** 359-369.

Fox, F. M. (1986b). Groupings of ectomycorrhizal fungi of birch and pine, based on establishment of mycorrhizas on seedlings from spores in unsterile soils. *Trans. Br. Mycol. Soc.* **87,** 371-380.

Francis, R., Finlay, R. D. and Read, D. J. (1986). Vesicular-arbuscular mycorrhiza in natural vegetation systems IV. transfer of nutrients in inter- and intra-specific combinations of host plants. *New Phytol.* **102,** 103-111.

Franco, A. C. and Nobel, P. S. (1990). Influences of root distribution and growth on predicted water uptake and interspecific competition. *Oecologia (Berl.)* **82,** 151-157.

Friend, J. (1981). Plant phenolics, lignification and plant disease. In: *Progress* in *Phytochemistry* Vol. 7 (Ed. by L. Reinhold, J. B. Harborne and T. Swain), pp. 197-261. Pergamon Press. Oxford.

Fries, N. (1987a). Ecological and evolutionary aspects of spore germination in the higher basidiomycetes. *Trans. Br. Mycol. Soc.* **88,** 1-7.

Fries, N. (1987b). Somatic incompatibility and field distribution of the ectomycorrhizal fungus *Suillus luteus* (Boletaceae). *New Phytol.* **107,** 735-739.

Fries, N. and Swedjemark, G. (1985). Sporophagy in Hymenomycetes. *Exp. Mycol.* **9,** 74-79.

Furlan, V. and Fortin, J. A. (1973). Formation of endomycorrhizae by *Endogone calospora* on *Allium cepa* under three temperature regimes. *Nat. Can. (Que.)* ***100,*** 467-477.

Furman, T. E. and Trappe, J. M. (1971). Phylogeny and ecology of mycotrophic achlorophyllous Angiosperms. *Q. Rev. Biol. 46,* 219-275.

Gadgil, R. L. and Gadgil, P. D. (1975). Suppression of litter decomposition by mycorrhizal roots ,of *Pinus radiata. N. Z. J. For. Sci.* **5,** 33-41.

Gallaud, I. (1905). Etudes sur les mycorrhizes endophytes. *Rev. Gen. Bot.* **17,** 5-48, 66-83, 123-136, 223-239, 313-325, 425-433, 479-500.

Gange, A. C., Brown, V. K. and Farmer, L. M. (1990). A test of mycorrhizal benefit in an early successional plant community. *New Phytol.* **115,** 85-91.

Garbaye, J. and Bowen, G. D. (1986). Effect of different microflora on the success of ectomycorrhizal inoculation of *Pinus radiata. Can. J. For. Res.* **17,** 941-943.

Garbaye, J. and Bowen, G. (1989). Stimulation of ectomycorrhizal infection of *Pinus radiata* by some microorganisms associated with the mantle of ectomycorrhizas. *New Phytol.* **112,** 383-388.

Gardner, J. H. and Malajczuk, N. (1988). Recolonisation of rehabilitated bauxite mine sites in Western Australia by mycorrhizal fungi. *For. Ecol. Mgmt* **24,** 27-42.

Garrett, H. E., Carney, J. L. and Hedrick, H. G. (1982). The effects of ozone and sulfur dioxide on respiration of ectomycorrhizal fungi. *Can. J. For. Res.* **12,** 141-145.

Garrido, N., Becerra, J., Marticorena, C., Oehrens, E., Silva, M. and Horak, E. (1982). Antibiotic properties of ectomycorrhizae and saprophytic fungi growing on *Pinus radiata* D. Don I. *Mycopathologia* **77,** 93-98.

Gay, G. and Debaud, J. C. (1987). Genetic study on indole-3-acetic acid production by ectomycorrhizal *Hebeloma* species: inter- and interspecific variability in homo- and dikaryotic mycelia. *Appl. Microbial. Biotechnol.* **26,** 141-146.

Gay, P. E., Grubb, P. J. and Hudson, H. J. (1982). Seasonal changes in the concentrations of nitrogen, phosphorus and potassium, and in the density of mycorrhiza in biennial and matrix-forming perennial species of closed chalkland turf. *Ecology* **70,** 571-593.

Gemma, J. X. and Koske, R. E. (1988a). Pre-infection interactions between roots and the mycorrhizal fungus *Gigaspora gigantea:* Chemotropism of germ-tubes an root growth response. *Trans. Br. Mycol. Soc.* **91,** 123-132

Gemma, J. N. and Koske, R. E. (198Sb). Seasonal variation in spore abundance and dormancy of *Gigaspora gigantea* and in mycorrhizal inoculum potential of a dune soil. *Mycologia* **80,** 211-216.

Gemma, J. N., Koske, R. E. and Carriero, M. (1989). Seasonal dynamics of selected species of V-A mycorrhizal fungi in a sand dune. *Mycol. Res.* **92,** 317-32l.

Gerschefske Kitt, D., Daniels Hetrick, B. A. and Thompson Wilson, G. W. (1987). Sporulation of two vesicular-arbuscular mycorrhizal fungi in nonsterile soil. *Mycologia* **79,** 896-899.

Gerschefske Kitt, D., Daniels Hetrick, B. A. and Thompson Wilson, G. W. (1988). Relationship of soil fertility to suppression of the growth response of mycorrhizal big bluestem in non-sterile soil. *New Phytol.* **109,** 473-481.

Gheorghiu, A., E. Ionescu-Matiu, E. and Boteanu, S. (1971). Determinarea cantitativã a chelidoninei, cheleritrinei, sanguinarinei si berberinei din pteparatul "alcaloizii totali". Cercetãri comparative asupra activitãtii lor antibactereine si antifungice. *Communicare de Botanica* **12,** 445-451.

Gianinazzi-Pearson, V. (1984). Host-fungus specificity, recognition and compatibility in mycorrhizae. In: *Genes Involved in Microbe- Plant Interactions* (Ed. by D. P. S. Verma and T. Hohn). pp. 225-249. Springer-Verlag, New York.

Gianinazzi-Pearson, V. and Gianinazzi S. (1989). Cellular and genetic aspects of interactions between hosts and fungal ymbionts in mycorrhizae. *Genoine* **31,** 336-341.

Gianinazzi-Pearson, V., Trouvelot, A., Morandi, D. and Marocke, R. (1980). Ecological variations in endomycorrhizas associated with raspberry populations in the Vosges region. *Acta Oecologia Ecol. Plant* **1,** 111-119.

Gianinazzi-Pearson, V., Branzanti, B and Gianinazzi, S. (1989). *In-vitro* enhancement of spore gemination and early hyphal growth of a vesicular-arbuscular mycorrhizal fungus by host root exudates and plant flavonoids. *Symbiosis* **7,** 243-255.

Gibson, A. H. and Jordan, D, C. (1983). Ecophysiology of nitrogen fixing systems. In: *Physiological Plant Ecology* III: *Responses to the Chemical and Physical Environment* (Ed. by Q. L. Lang, P. S. Nobel, C. B. Osmond and H. Ziegler), pp. 301-390. Springer-Verlag, New York.

Gibson, F. and Deacon, J. W. (1990). Establishment of ectomycorrhizas in aseptic culture: effects of glucose, nitrogen and phosphorus in relation to succession. *Mycol. Res.* **94,** 166-172.

Gibson, F., Fox, F. M. and Deacon, J. W. (1988). Effects of microwave treatment of soil on growth of birch *(Betula pendula)* seedlings and infection of them by ectomycorrhizal fungi. *New Phytol.* **108,** 189-204.

Gilbert, L. E. (1980). Food web organization and the conservation of neotropical diversity. (eds. M. E. Soule, and B. A. Wilcox), *Conservation Biology an Evolutionary-Ecological Perspective.* Sinauer Associates, Sunderland Ma.

Giller, K. E. and Day, J. M. (1985). Nitrogen fixation in the rhizosphere: significance in natural and agricultural systems. In: *Ecological Interactions in Soil: Plants, Microbes and Animals* (Ed. by *A.* H. Fitter, D. Atkinson. D. J. Read and M. B. Usher), pp. 127-147. Blackwell, Oxford.

Ginzburg, C. (1966). Xerophytic structures in the roots of desert shrubs. *Ann. Bot.* **30,** 403-418.

Giovannetti, M. (1985). Seasonal variations of Vesicular-arbuscular mycorrhiza, and endogonaceous spores in a maritime sand dune. *Trans. Br. Mycol. Soc* **84,** 679-684.

Giovannetti, M. and Hepper, C. M. (1985). Vesicular-arbuscular mycorrhizal infection in *Hedysarum coronarium* and *Onobrychis viciaefolia:* host-endophyte specificity. *Soil Biol. Biochem.* **17,** 899-900.

Giovannetti, M., Schubert, A., Cravero, M. C. and Salutini, L. (1988). Spore production by the vesicular-arbuscular mycorrhizal fungus *Glomus monosporum* as related to host species, root colonization and plant growth enhancement. *Biol. Fertil. Soils* **6,** 120-124.

Girard, I. (1985). *Ecologie des mycorhizes: caractere mycorhizien des espèces végétales des fórets climactiques et reflexion sur la relation humus-mycorhize.* MSc Thesis, Univesité Laval, Quebec.

Girard, I. and Fortin, J. A. (1985). Ecological habitat of mycorrhizae of northern temperate climax forests. In: *Proceedings of the 6th North American Conference on Mycorrhizae* (Ed. by Molina. R.) p. 270. Forest Research Laboratory, Oregon State University, Corvallis, Oregon.

Glenn, M. G., Chew, F. S. and Williams, P. H. (1985). Hyphal penetration of *Brassica* (Cruciferae) roots by a vesicular-arbuscular mycorrhizal fungus. *New Phytol.* **99,** 463-472.

Glenn, M. G., Chew, F. S. and Williams, P. H. (1988). Influence of glucosindate content of *Brassica* (Cruciferae) roots on growth of vesicular-arbuscular mycorrhizal fungi. *New Phytol.* **110,** 217-225.

Godfrey, R. M. (1957). Studies of British species of *Endogone* II: fungal parasites. *Trans. Br. Mycol. Soc.* **40,** 136-144.

Goldner, W. R., Hoffman, F. M. and Medve, R. J. (1986). Allelopathic effects of *Cladonia cristatella* on ectomycorrhizal fungi common to bituminous strip-mine spoils. *Can. J. Bot.* **64,** 1586-1590.

Gower, S. T. (19871. Relations between mineral nutrient availability and fine root biomass in two Costa Rican tropical wet forests: a hypothesis. *Biotropica* **19,** 171-175.

Graham, J. H. (1982). Effect of citrus root exudates on germination of chlamydospores of the vesicular-arbuscular mycorrhizal fungus, *Glomus epigaeum. Mycologia* **74,** 831-835.

Graham, J. H. (1987). Non-nutritional benefits of vam fungi-do they exist? In: *Mycorrhizae in the Next Decade, Practical Applications and Research Priorities* (Ed. by D. M. Sylvia, L. L. Hung and J. H. Graham), pp. 237-239. Institute of Food and Agricultural Sciences, University of Florida, Gainesville.

Graham, J. H. and Sylversten, J. P. (1987). Vesicular-arbuscular mycorrhizas increase chloride concentration in citrus seedlings *New Phytol.* **113,** 29-36

Graham, J. H., Leonard, R. T. and Menge, J. A. (1982a). Interaction of light intensity and soil temperature with phosphorus inhibition of vesicular-arbuscular mycorrhiza formation. New *Phyol.* **91,** 683-690.

Graham, J. H., Linderman, R. G. and Menge, J. A. (1982b) Development of external hyphae by different isolates of mycorrhizal *Glomus* spp. in relation to root colonization and growth of troyer citrange. *New Phytol.* **91,** 183-189.

Grand, L. F. and Harvay, A. E. (1982). Quantitative measurement of ectomycorrhizae on plant roots. In: *Methods and Principles of Mycorrhizal Research* (Ed. by N. C. Schenck), pp. 157-164. American Phytopathological Society, St Paul, Minnesota.

Gregory, P. J. (1987). Development and growth of root systems in plant communities. In: *Root Development and Function* (Ed. by *P.* J, Gregory. J. V. Lake and D. A. Rose). pp. 147-166. Cambridge University Press Cambridge.

Grime, J. P. (1979). *Plant Strategies and vegetation Processes.* John Wiley, Toronto.

Grime, J. P., Crick, J. C. and Ricon, J. E. (1986). The ecological significance of plasticity. In: *Plasticity in Plants* (Ed. by D. H. Jennings and A. J. Trewavas). pp. 5-29. The Company of Biologists Limited. Cambridge.

Grime, J. P., Mackey, J. M. L., Hillier, S. M. and Read, D. J. (1987). Floristic diversity in a model system using experimental microcosms. *Nature* **328,** 420-422.

Gueye, M., Diem, H. G. and Dommergues, Y. R. (1987). Variation in N_2 fixation, N and P contents of mycorrhizal *Vigna unquiculata* in relation to the progressive development of extra-radical hyphae of *Glomus mosseae. MIRCEN J.* **3,** 75-86.

Guildon, A. and Tinker, P. B. (1983). Interactions of vesicular-arbuscular mycorrhizal infection and heavy metals in plants. I. The effects of heavy metals on the development of vesicular-arbuscular mycorrhizas. *New Phytol.* **95,** 247-261.

Gupta, P. L. and Rorison, I. H. (1975). Seasonal differences in the availability of nutrients down a podzolic profile. *J. Ecol.* **63,** 521-534.

Haas, J. H. and Krikun, J. (1985). Efficacy of endomycorrhizal-fungus isolates and inoculum quantities required for growth response. *New Phytol.* **100,** 613-621.

Haas, J. H., Bar-Yosef, B., Krikun, J., Barak, R., Markovitz, T. and Kramer, S. (1987). Vesicular-arbuscular mycorrhizal fungus infestation and phosphorus fertilization to overcome pepper stunting after methyl bromide fumigation. *Agron. J.* **79,** 905-910.

Habte, M. (1989). Impact of simulated erosion on the abundance and activity of indigenous vesicular-arbuscular mycorrhizal endophytes in an oxisol. *Biol Fertil. Soils* **7,** 164-167.

Hadley, G. (1982). Orchid mycorrhiza, In: *Orchid Biology Reviews and Perspectives* II (Ed. by J. Arditti), pp. 85-118. Cornell University Press, Ithaca.

Hadley, G. and Williamson, B. (1972). Features of mycorrhizal infections in some Malayan orchids. *New Phytol.* **71,** 1111-1118.

Hakim, S. A. E., Mijovic, V. and Walker. J. (1961). Distribution of certain poppy-fumaria alkaloids and a possible link with the incidence of glaucoma. *Nature* 189, 198-201.

Hall, I. R. (1977). Effect of applied nutrients and endomycorrhizas on *Metrosideros umbellata* and *Leptospermum scoparium. N. Z. J. Bot.* **15,** 481-484.

Hall, I. R. (1978) Effects of endomycorrhizas on the competitive ability of white clover. *N. Z. J. Agric. Res.* **21,** 509-15.

Hamblin, A and Tennent, D. (1987). Root length and water uptake in cereals and grain legumes: how well are they correlated? *Aust. J. Agrzc. Res.* **38,** 513-527.

Harley, J. L. (1971). Fungi in ecosystems. *J. Appl. Ecol.* **8,** 627-642.

Harley, J. L. (1989). The significance of mycorrhiza. *Mycol. Res.* **92,** 129-139.

Harley, J. L. and Harley, E. L. (1987). A check-list of mycorrhiza in the British flora. *New Phytol.* 105, 1-102.

Harley, J. L. and Smith, S. E. (1983). *Mycorrhizal Symbiosis.* Academic Press, Toronto.

Harmer, R. and Alexander, I. J. (1985). Effect of root exclusion on nitrogen transformations and decomposition processes in spruce humus. In: *Ecological Interactions* in *Soils: Plants, Microbes and Animals* (Ed. by A. H. Fitter. D. Atkinson, D. J. Read and M. B. Usher). pp. 279-277. Blackwell, Oxford.

Harris, D. and Paul. E. A. (1987). Carbon requirements of vesicular-arbuscular mycorrhizae. *Ecophysiology of VA Mycorrhizal Plants* (Ed. by G. R. Safir), pp. 93-105. CRC Press, Boca Raton, Florida.

Hart, T. B., Hart, J. A. and Murphy, P. G. (1989). Monodominant and species-rich forests of the humid tropics: causes for their co-occurrence. *Am. Natur.* **133,** 613-633.

Harvey, A. E., Larsen, M. J. and Jurgensen, M. F. (1976). Distribution of ectomycorrhizae in a mature douglas-fir/larch soil in western Montana. *For Sci.* **22,** 393-398.

Haselwandter, K. (1979). Mycorrhizal status of Ericaceous plants in alpine and subalpine areas. *New Phytol.* **83,** 427-431.

Haselwandter, K. (1987). Mycorrhizal infection and its possible ecological significance in climatically and nutritionally stressed alpine plant communities. *Angew. Botanik.* **61,** 107-114.

Haselwandter, K. and Read, D. J. (1982). The significance of a root-fungus association in two *Carex* species of high-alpine communities. *Oecologia (Berl.)* **53,** 352-354.

Haselwandter, K., Bonn, G. and Read, D. J. (1987). Degradation and utilization of lignin by mycorrhizal fungi. In: *Mycorrhizae in the Next Decade, Practical Applications and Research Priorities* (Ed. by D. M. Sylvia, L. L. Hung and J. H. Graham). p. 31. Institute of Food and Agricultural Sciences, University of Florida, Gainesville.

Haug, I. and Oberwinkler, F. (1987). Some distinctive types of spruce mycorrhizae. *Tree* **1,** 172-188.

Hausling, M. and Marschner, H. (1989). Organic and inorganic soil phosphates and soil phosphatase activity in the rhizosphere of 80-year-old norway spruce *[Picea abies* (L) Karst.] trees. *Biol. Fertil. Soils* **8,** 128-133.

Hawksworth, D. L. (1981). A survey of the fungicolous conidial fungi. In: *Biology of Conidial Fungi* (Ed. by *G.* T. Cole and B. Kendrick), pp. 171-244. Academic Press, New York.

Hayden, A. (1919). The ecological subterranean anatomy of some plants of a prairie province in central Iowa. *Am. J. Bot.* **6,** 87-105.

Hayes, D. C. and Seastedt, T. R. (1986). Root dynamics of tallgrass prairie in wet and dry years. *Can. J. Bot.* **65,** 787-791.

Hayman, D. S. (1970). Endogone spore numbers in soil and vesicular-arbuscular mycorrhiza in wheat as influenced by season and soil treatment. *Trans. Br. Mycol. Soc.* **54,** *53-63.*

Hayman, D. S. (1983). The physiology of vesicular-arbuscular endomycorrhizal symbiosis. *Can. J. Bot.* **61,** 944-963.

Hayman, D. S. (1987). VA Mycorrhizas in field crop systems. In: *Ecophysiology of* VA *Mycorrhizal Plants* (Ed. by *G.* R. Safir), pp. 171-192. CRC Press. Boca Raton, Florida.

Hayman, D. S. and Tavares, M. (1985). Plant growth responses to vesicular-arbuscular mycorrhiza XV. Influence of soil pH on the symbiotic efficiency of different endophytes. *New Phytol.* **100,** 367-379.

Hayman, D. S., Johnson, A. M. and Ruddlesdin, I. (1975). The influence of phosphate and crop species on *Endogone* spores and vesicular-arbuscular mycorrhiza under field conditions. *Plant Soil* **43,** 489-495.

Haystead, A., Malajczuk, N. and Grove, T. S (1988). Underground transfer of nitrogen between pasture plants infected with vesicular- arbuscular mycorrhizal fungi. *New Phytol.* **108,** 417-423.

Hejtmankova, N., Walterova, D., Preininger, V. and Simanek, V. (1984). Antifungal activity of quaternary benzo [c] phenanthridine alkaloids from *Chelidonium majus. Fitoterapia* **55,** 291-294.

Henkel, T. W., Smith, W. K. and Christensen, M. (1989). Infectivity and effectivity of indigenous vesicular-arbuscular mycorrhizal fungi from contiguous soils in southwestern Wyoming. USA. New *Phytol.* **112,** 205-214.

Hepper, C. M. (1985). Influence of age of roots on the pattern of vesicular-arbuscular mycorrhizal infection in leek and clover. *New Phytol.* **101,** 685-693.

Hepper, C. M., Sen, R., Azcon-Aguilar, C. and Grace, C. (1987). Variation in certain isozymes amongst different geographical isolated of the vesicular-arbuscular mycorrhizal fungi *Glomus clarum, Glomus monosporum* and *Glomus mosseae. Soil Biol. Biochem.* **20,** 51-59,

Hepper, C. M., Azon-Ahuilar, C. Rosenclahl, S. and Sen, R. (1988). Competition between three species of *Glomus* used as spatially introduced and indigenous mycorrhizal inocula for leek *(Allium porrum* L.). *New Phytol.* **110,** 207-215.

Herrera, R. A. and Ferrer, L. (1980). Vesicular-arbuscular mycorrhiza in Cuba. In: *Tropical Mycorrhizal Research* (Ed. by P. Mikola), pp. 156-162. Clarendon Press. Oxford.

Hicks, D. J. and Chabot, B. R. (1985). Deciduous forest. In: *Physiological Ecology* of *North American Plant Communities* (Ed. by B. F. Chabot and H. A. Mooney), pp. 257-277. Chapman and Hall, New York.

Hilton, R. N., Malajczuk, N. and Pearce, M. H. (1989). Larger fungi of the jarrah forest: an ecological and taxonomic survey. In: *The Jarrah Forest* (Ed. by B. Dell, J. J. Havell, and N. Malajczuk), pp. 89-109. Kluwer, Dordrecht.

Hirrel, M. C., Mehravaran, H. and Gerdemann, J. W. (1978). Vesicular-arbuscular mycorrhizae in the Chenopodiaceae and Cruciferae: do they occur? *Can. J. Bot.* **56,** 2813-2817.

Ho, I. (1987). Vesicular-arbuscular mycorrhizae of halophytic grasses in the Alvord desert of Oregon. *Northwest Sci.* **61,** 148-151.

Ho, I. (1988). Interaction between VA-mycorrhizal fungus and *Azotobacter* and their combined effects on growth of tall fescue. *Plant Soil* **105,** 291-293.

Ho, I. (1989). Acid phosphatase, alkaline phosphatase and nitrate reductase activity of selected ectomycorrhizal fungi. *Can. J. Bot.* **67,** 750-753.

Ho, I. and Trappe, J. M. (1984). Effects of ozone exposure on mycorrhiza formation and growth of *Festuca arundinacea. Environ. Exp. Bot.* **24,** 71-74.

Högberg, P. (1986). Soil nutrient availability, root symbioses and tree species composition in tropical Africa: a review. *Trop. Ecol.* **2,** 359-372.

Högberg, P. and Piearce, G. D. (1986). Mycorrhizas in Zambian trees in relation to host taxonomy, vegetation type successional patterns. *J. Ecol.* **74,** 775-785.

Hopkins, N. A. (1986). Mycorrhizae in a California serpentine grassland community. *Can. J. Bot.* **65,** 484-487.

Horner, J. D., Gosz, J. R. and Gates, R. G. (1988). The role of carbon-based secondary metabolites in decomposition in terrestrial ecosystems. *Am. Nat.* **132,** 869-883.

Höveler, W. (1892). Weber die verwerthung des humus bei der ernährune der chlorophyllführenden pflanzen. *Jb. Wiss. Bot.* **24,** 283-316.

Howeler, R. H., Sieverding, E. and Saif, S. (1987). Practical aspects of mycorrhizal technology in some tropical crops and pastures. *Plant Soil* **100,** 249-283.

Hulsman, O. C. (1982). Interrelations of root growth dynamics to epidemiology of root-inhabiting fungi. *Ann. Rev. Phytopathol.* **20,** 203-227.

Hung, L. L. and Trappe, J. M. (1983). Growth variation between and within species of ectomycorrhizal fungi in response to pH *in vitro. Mycologia* **75,** 234-241.

Hunt, G. A. and Fogel, R. (1983). Fungal hyphal dynamics in a western Oregon douglas-fir stand. *Soil Biol. Biochem.* **15,** 614-649.

Hutchinson, L. J. (1989). Absence of conidia as a morphological character in ectomycorrhizal fungi. *Mycologia* **81,** 587-594.

Hag, L. L., Rosales, A. M., Elazegui, F. A. and Mew, T. W. (1987). Changes in the population of infective endomycorrhizal fungi in a rice-based cropping system. *Plant Soil* **103,** 67-73.

Ingham, R. E. (1988). Interactions between nematodes and vesicular-arbuscular mycorrhizae. *Agric. Ecos. Environ.* **24,** 169-182.

Ingleby, K., Last, F. T. and Mason, P. T. (1985). Vertical distribution and temperature relations of sheathing mycorrhizas of *Betula* spp. growing on coal spoil. *For. Ecol.* **12,** 279-285.

Iqbal, S. H. and Qureshi, K. S. (1976). The influence of mixed sowing (Cereals and Crucifers) and crop rotation on the development of mycorrhiza and subsequent growth of crops under field conditions. *Biologia* **22,** 287-298.

Itoh, S. and Barber, S. A. (1983). Phosphorus uptake by six plant species as related to root hairs. *Agron. J.* **75,** 457-461.

Iyer, J. G. (1980). Sorghum-sudan green manure: its effect on nursery stock. *Plant Soil* **54,** 159-162.

Jackson, R. B. and Caldwell, M. M. (1989). The timing and degree of root proliferation in fertile-soil microsites for three cold-desert perennials. *Oecologia* **81,** 149-153.

Jacquelenet-Jeanmougin, S. and Gianinazzi-Pearson, V. (1983). Endomycorrhizas in the Gentianaceae I. the fungi associated with *Gentiana lutea L. New Phytol.* **95,** 663-666.

Jakobsen, I. and Rosendahl, L. (1990). Carbon flow into soil and external hyphae from roots of mycorrhizal cucumber plants. *New Phytol.* **115,** 77-83.

Janos, D. P. (1980a). Vesicular-arbuscular mycorrhizae affect lowland tropical rain forest plant growth. *Ecology* **61,** 151-162.

Janos, D. P. (1980b). Mycorrhizae influence tropical succession. *Biotropica* **12,** (Suppl.), 56-95.

Janos, D. P. (1987). VA mycorrhizas in humid tropical ecosystems. In: *Ecophysiology of VA Mycorrhizal Plants* (Ed. by G. R. Safir), pp. 107-134. CRC Press, Boca Raton, Florida.

Jasper, D. A., Robson, A. D. and Abbott, L. K. (1979). Phosphorus and the formation of vesicular-arbuscular mycorrhizas. *Soil Biol. Biochem.* **11,** 501-505.

Jasper, D. A., Robson, A. D. and Abbott, L. K. (1987). The effect of surface mining on the infectivity of vesicular-arbuscular mycorrhizal fungi. *Aust. J. Bot.* **35,** 641-652.

Jasper, D. A., Robson, A. D. and Abbott, L. K. (1988). Revegetation in an iron-ore mine - nutrient requirements for plant growth and the potential role of vesicular-arbuscular (VA) mycorrhizal fungi. *Aust. J. Soil Res.* **26,** 497-507.

Jasper, D. A., Abbott, L. K. and Robson, A. D. (1989a). Soil disturbance reduces the infectivity of external hyphae of VA mycorrhizal fungi. *New Phytol.* **112,** 93-99.

Jasper, D. A., Abbott, L. K. and Robson, A. D. (1989b). Hyphae of a VA mycorrhizal fungus maintain infectivity in dry soil. except when the soil is disturbed. *New Phytol.* **112,** 101-107.

Jasper, D. A., Abbott, L. K. and Robson, A. D. (1989). The loss of VA mycorrhizal infectivity during bauxite mining may limit the growth of *Acacia pulchella* R. Br. *Aust. J. Bot.* **37,** 33-42.

Jayachandran, K., Schwab, A. P. and Daniels Hetrick, B. A. (1989). Mycorrhizal mediation of phosphorus availability: synthetic Iron chelate effects on phosphorus solubilization. *Soil Sci. Soc. Am. J.* **53,** 1701-1706.

Jeffrey, D. W. (1987). *Soil Plant Relationships: An Ecological Approach.* Croom Helm, Sidney.

Jehne, W. and Thompson, C. H. (1981). Endomycorrhizae in plant colonization on coastal sand-dunes at Cooloola, Queensland. *Aust. J. Ecol.* **6,** 221-230.

Johansson, D. R. (1977). Epiphytic orchids as parasites of their host trees. *Am. Orchid. Soc. Bull.* **46,** 703-707.

Johnson, P. N. (1976). Effects of soil phosphate level and shade on plant growth and mycorrhizas. *N. Z. J. Bot.* **14,** 333-340.

Johnson, P. N. (1977). Mycorrhizal Endogonaceae in a New Zealand forest. *New Phytol.* **78,** 161-170.

Jones, K. and Hendrix, J. W. (1987). Inhibition of root extension in tobacco by the mycorrhizal fungus *Glomus macrocarpum* and its prevention by benomyl. *Soil. Biol. Biochem.* **19,** 297-299.

Jones, M. D. and Hutchinson, T. C. (1988). Nickel toxicity in mycorrhizal birch seedlings infected with *Lactarius rufus* or *Scleroderma flavidum.* I. Effects on growth, photosynthesis, respiration and transpiration. *New Phytol.* 108, 451-459.

Jordan, C. F. (1985). *Nutrient Cycling in Tropical Forest Ecosystems.* Wiley. Toronto.

Justin, S. H. F. W. and Armstrong, W. (1987). The anatomical characteristics of roots and plant response to soil flooding. *New Phytol.* **106,** 465-495.

Katenin, A. E. (1965). Mycorrhiza of artic plants. *(Problemy Severa* **8,** 148-154. 1964) *Problems of the North* **8,** 157-163.

Keeley, J. E. (1980). Endomycorrhizae influence growth of blackgum seedlings in flooded soils. *Am. J. Bot. 67,* 6-9.

Keke, C. and Yu, X, (1986). An investigation of ectomycorrhizal fungi from the subalpine coniferous forest region, N. W. Yunnan (in Chinese). *Acta Botanica Yunnanica* **8,** 399-404.

Kelley, A. P. (1950). *Mycotrophy* in *Plants.* Chronica Bot. Waltham, Mass.

Kendrick, B. (1985). *The Fifth Kingdom.* Mycologue Publications. Waterloo, Ontario.

Khan, A. G. (1974). The occurrence of mycorrhizas in halophytes. Hydrophytes and xerophytes, and of *Endogone* spores in adjacent soils. *J. Gen. Microbial.* **81,** 7-14.

Killham, K. (1985). Vesicular-arbuscular mycorrhizal mediation of trace and minor element uptake in perennial grasses: relation to livestock herbage. In: *Ecological Interactions in Soils: Plants, Microbes and Animals* (Ed. by A. H. Fitter, D. Atkinson, D. J. Read and M. B. Usher), pp. 225-232. Blackwell, Oxford.

Kim, C. and Weber, D. J. (1985). Distribution of VA mycorrhiza on halophytes on inland salt playas. *Plant Soil* **83,** 207-214.

Kidzel, H. (1983). Influence of limestone, silicates and soil pH on vegetation. In: *Physiological Plant Ecology III: Responses to the Chemical and Biological Environment* (Ed. by O. L. Lange, P. S. Nobel, C. B. Osmond and H. Ziegler). pp. 201-224. Springer-Verlag, Berlin.

Klein, R. A. and Perkins, T. D. (1988). Primary and secondary causes and consequences of forest decline. *Bot. Rev.* **54,** 1-43.

Klopatek, C. C., Debano, L. F. and Klopatek, J. M. (1988). Effects of simulated fire on vesicular-arbuscular mycorrhizae in pinyon-juniper woodland soil. *Plant Soil* **109,** 245-249.

Koch, K. E. and Johnson, C. R. (1984). Photosynthate partitioning in split root citrus seedlings with mycorrhizal and non-mycorrhizal root systems. *Plant Physiol.* **75,** 26-21.

Kohn, L. M. and Stasovski, E. (1990). The mycorrhizal status of plants at Alexandra Fiord, Ellesmere Island, Canada, a high Artic site. *Mycologia* **82,** 23-35.

Koide, R. and Elliot, G. (1989). Cost, benefit and efficiency of the vesicular-arbuscular mycorrhizal symbiosis. *Funct. Ecol.* **3,** 252-255.

Koide, R., Li, M., Lewis, J. and Irby, C. (1988). Role of mycorrhizal infection in the growth and reproduction of wild vs. cultivated plants. I. Wild vs. cultivated oats. *Oecologia (Berl.*) **77,** 537-543.

Koide, R. T. and Li, M. (1989). Appropriate controls for vesicular-arbuscular mycorrhiza research. *New Phytol.* **111,** 35-44.

Koide, R. T. and Li, M. (1990). On host regulation of the vesicular-arbuscular mycorrhizal symbiosis. *New Phytol.* **114,** 59-64.

Koide, R. T. and Mooney, H. A. (1987). Spatial variation in inoculum potential of vesicular-arbuscular mycorrhizal fungi caused by formation of gopher mounds. *New Phyol.* **107,** 173-182.

Koomen, I., Grace, C. and Hayman, D. S. (1987). Effectiveness of single and multiple mycorrhizal inocula on growth of clover and strawberry plants at two soil pHs. *Soil Biol. Biochem.* **19,** 539-544.

Kope, H. H. and Fortin, J. A. (1989). Inhibition of phytopathogenic fungi in vitro by cell free culture media of ectomycorrhizal fungi. *New Phytol.* **113,** 57-63.

Kope, H. H. and Warcup, J. H. (1986). Synthesized ectomycorrhizal associations of some Australian herbs and shrubs. *New Phytol.* 104, 591-599.

Kormanik, P. P. (1981). A *Forester's View of Vesicular-Arbuscular Mycorrhizae and their Role in Plant Development and Productivity* pp. 33-37. N. J. Agric. Exp. Stn. Res. Rep. No. R04400-01-81.

Kormanik, P. P. and McGraw, A. C. (1982). Quantification of vesicular-arbuscular mycorrhizae in plant roots. In: *Methods and Principles* of *Mycorrhizal Research* (Ed. by N. C. Schenck), pp. 37-45. American Phytopathological Society, St Paul, Minnesota.

Kormanik, P. P., Schultz, R. C. and Bryan, W. C. (1982). The influence of vesicular-arbuscular mycorrhizae on the growth and development of eight hardwood tree species. *For. Sci.* **28,** 531-539.

Korner, C. and Renhardt, U. (1987). Dry matter partitioning and root length/ leaf area ratios in herbaceous perennial plants with diverse altitudinal distribution. *Oecologia (Berl.)* **74,** 411-418.

Koske, R. E. (1981). A preliminary study of interactions between species of vesicular-arbuscular fungi in a sand dune. *Trans. Br. Mycol. Soc.* **76,** 411-416.

Koske, R. E. (1982). Evidence for a volatile attractant from plant roots affecting germ tubes of a VA mycorrhizal fungus. *Trans. Br. Mycol. Soc.* **79,** 305-310.

Koske, R. E. (1987a). Distribution of VA mycorrhizal fungi along a latitudinal temperature gradient. *Mycologia* **79,** 55-68.

Koske, R. E. (1987b). Ecology of VAM and VAMF in sand dunes. In: *Mycorrhizae in the Next Decade, Practical Applications and Research Priorities* (Ed. by D. M. Sylvia, L. L. Hung and J. H. Graham), pp. 64-65. Institute of Food and Agricultural Sciences, University of Florida, Gainesville.

Koske, R. E. (1988). Vesicular-arbuscular mycorrhizae of some Hawaiian dune plants. *Pacific Sci.* **42,** 217-229.

Koske, R. E. and Gemma, J. N. (1990). VA mycorrhizae in strand vegetation of Hawaii - evidence for long distance codispersal of plants and fungi. *Am. J. Bot.* **77,** 466-474.

Koske, R. E., Gemma, J. M. and Englander, L. (1990). Vesicular-arbuscular mycorrhizae in Hawaiian Ericales. *Am. J. Bot.* **77,** 64-68.

Koslowsky, S. D. and Boerner, R. E. J. (1989). Interactive effects of aluminum, phosphorus and mycorrhizae on growth and nutrient uptake of *Panicum virgatum* L. (Poaceae). *Envir. Pollut.* **61,** 107-125.

Kotter, M. M. and Farentinos, R. C. (1984). Formation of ponderosa pine ectomycorrhizae after inoculation with feces of tassel-eared squirrels. *Mycologia* **76,** 758-760.

Kottke, I. and Oberwinkler, F. (1986). Mycorrhiza of some forest trees - structure and function. *Tree* **1,** 1-24.

Kovacic, D. A., St. John, T. V. and Dyer, M. I. (1984). Lack of vesicular-arbuscular mycorrhizal inoculum in a ponderosa pine forest. *Ecology* **65,** 1755-1759.

Kramer, P. J, (1981). Carbon dioxide concentration, photosynthesis and dry matter production. *Biol. Sci.* **31,** 29-33.

Kraus, M., Fusseder, A. and Beck, E. (1987). Development and replenishment of the P-depletion zone around the primary root of maize during the vegetative period. *Plant Soil* **101,** 247-255.

Krikun, J. (1983). Edaphic and climatic factors in the evolution of vesicular-arbuscular mycorrhizal fungi. In: *Developments in Ecological and Environmental Quality* pp. 31-36. Ecological Society, Hebrew University of Jerusalem, Jerusalem.

Krishna, K. R., Shetty, K. G., Dart, P. J. and Andrews, D. J. (1985). Genotype dependent variation in mycorrhizal colonization and response to inoculation of pearl millet. *Plant Soil* **86,** 113-125.

Kropp, B. R. and Trappe, J. M. (1982). Ectomycorrhizal fungi of *Tsuga heterophylla. Mycologia* **74,** 479-488.

Kubíková, J. (1967). Contribution to the classification of root systems of woody plants. *Preslia* **39,** 236-243.

Kubitzki, K. (1989). The ecogeographical differentiation of Amazonian inundation forests. *Plant. Syst. Evol.* **162,** 285-304.

Kumar, V. M. and Mahadevan, A. (1984). Do secondary substances inhibit mycorrhizal associations. *Curr. Sci.* **53,** 377-378.

Kummerow, J. (1981). Structure of roots and root systems. In: *Ecosystems of the World 11: Mediterranean-type Shrublands* (Ed. by F. di Castri, D. W. Goodall and R. L. Specht), pp. 269-288. Elsevier, New York.

Kummerow, J. (1983). Root surface/leaf area ratios in arctic dwarf shrubs. *Plant Soil* **71,** 359-399.

Kuo, J., McComb, A. J. and Cambridge, M. L (1981). Ultrastructure of the seagrass rhizosphere. *New Phytol* **89,** 139-143.

Lackie, S. M., Garriock, M. L., Peterson, R. L. and Bowley, S. R. (1987). Influence of host plant on the morphology of the vesicular-arbuscular mycorrhizal fungus. *Glomus versiforme* (Daniels and Trappe) Berch. *Symbiosis* **3,** 147-158.

Lackie, S. M., Bowley, S. R. and Peterson, R. L. (1988). Comparison of colonization among half-sib families of *Medicago sativa* L. by *Glomus versiforme* (Daniels and Trappe) Berch. *New Phytol.* **108,** 477-482.

Laheurte, F. and Berthelin, J. (1986). Influence of endomycorrhizal infection by *Glomus mosseae* on root exudation by maize. *Physiology and Genetical Aspects of Mycorrhizae* (Ed. by *V.* Gianinazzi-Pearson and S. Gianinazzi). pp. 425-429. INRA. Paris.

Lambers, H. (1985). Respiration in intact plant and tissue: Its regulation and dependence on environmental factors, metabolism and invaded organism. In: *Higher Plant Cell Respiration, Encyclopedia of Plant Physiology* (Ed. by R. Douce and D. A. Day), pp. 418-473. Springer-Verlag, Berlin.

Lambers, H. (1987). Growth, respiration, exudation and symbiotic associations: the fate of carbon translocated to the roots. In: *Root Development and Function* (Ed. by P. J. Gregory, J. V. Lake and D. A. Rose). pp. 125-145. Cambridge University Press, Cambridge.

Lambert, D, H., Cole, H. Jr. and Baker, D. E. (1980). Adaptation of vesicular-arbuscular mycorrhizae to edaphic factors. *New Phytol.* **85,** 513-520.

Lamont, B. (1982). Mechanisms for enhancing nutrient uptake in plants, with particular reference to mediterranean South Africa and Western Australia. *Bot. Rev.* **48,** 597-689.

Lament, B., Ralph, C. and Chrisiensen, P. E. S. (1985). Mycophagous marsupials as dispersal agents for ectomycorrhizal fungi on *Eucalyptus calophylla* and *Gastrolobium bilobum. New Phytol.* **101,** 651-656.

Lane, G. A., Sutherland, O. R. W. and Skipp, R. A. (1987). Isoflavonoids as insect feeding deterrents and antifungal components from root of *Lupinus angustifolius. J. Chem. Ecol.* **13,** 771-783.

Langkamp, P. J. and Dalling, M. J. (1982). Nutrient cycling in a stand of *Acacia holosericea* A. Cunn, ex. G. Don. II. Phosphorus and endomycorrhizal associations. *Aust. J. Bot.* **30,** 107-19.

Lapeyrie, F. (1988). Oxalate synthesis from soil bicarbonate by the mycorrhizal fungus *Paxillus involutus. Plant Soil* **110,** 3-8.

Lapeyrie, F. F. and Bruchet, G. (1986). Calcium accumulation by two strains, calcicole and calcifuge, of the mycorrhizal fungus *Paxulus involutus. New Phytol.* **103,** 133-141.

Lapeyrie, F. F. and Chilvers, G. A. (1985). An endomycorrhiza-ectomycorrhiza succession associated with enhanced growth of *Eucalyptus dumosa* seedlings planted in a calcareous soil. *New Phytol.* **100,** 93-104.

Larsen, J. A. (1980). *The Boreal Ecosystem.* Academic Press, Toronto.

Last, F. T., Mason, P. A., Pelham, J. and Ingleby, K. (1984). Fruitbody production by sheathing mycorrhizal fungi: effects of "host" genotypes and propagating soils. *For. Ecol. Mgmt* **9,** 221-227.

Laursen, G. A. and Chmielewski, M. A. (1980). The ecological significance of soil fungi in arctic tundra. *Arctic and Alpine Mycology* (Ed. by G. A. Laursen and J. F. Ammirati), pp. 432-492. University of Washington Press, Seattle.

Lawley, R. A., Newman, E. I. and Campbell, R. (1982). Abundance of endomycorrhizas and root-surface microorganisms on three grasses grown separately and in mixtures. *Soil Biol. Biochem.* **14,** 237-240.

Le Tacon, F., Garbaye, J. and Carr, G. (1987). The use of mycorrhizas in temperate and tropical forests. *Symbiosis* **3,** 179-206.

Leake, J. R., Shaw, G. and Read, D. J. (1989). The role of ericoid mycorrhizas in the ecology of ericaceous plants. *Agric. Ecos. Environ.* **29,** 237-250.

Lee, B. K. H. and Baker, G. E. (1973). Fungi associated with the roots of red mangrove, *Rhizophora mangle. Mycologia* **65,** 894-906.

Lee, S. S. and Lim, K. L. (1989). Mycorrhizal infection and foliar phosphorus content of seedlings of three dipterocarp species growing in a selectively logged forest and a forest plantation. *Plant Soil* **117,** 237-241.

Lesica, P. and Antibus, R. K. (1985). Mycorrhizae of alpine fell-field communities on soils derived from crystalline and calcareous parent materials. *Can. J. Bot.* **64,** 1691-1697.

Lesica, P. and Antibus, R. K. (1986). Mycorrhizal status of hemiparasitic vascular plants in Montana U.S.A. *Trans. Br. Mycol. Soc.* **86,** 341-343.

Li, C. Y. and Hung, L. L. (1987). Nitrogen-fixing (acetylene-reducing) bacteria associated with ectomycorrhizae of Douglas-fir. *Plant Soil* **98,** 425-428.

Liberia, A. E. and Anderson, R. C. (1986). Comparison of vesicular-arbuscular mycorrhiza species composition, spore abundance and inoculum potential in an Illinois prairie and adjacent agricultural sites. *Bull. Torrey Bot. Club* **113,** 178-182.

Likens, A. E. and Antibus, R. K. (1982). Mycorrhizae of *Salix rotundifolius* in coastal arctic tundra. In: *Arctic and Alpine Mycology* (Ed. by G. A. Laursen, and J. F. Ammirati), pp. 509-531. University of Washington Press, Seattle.

Linderman, R. G. (1988). Mycorrhizal interactions with the rhizosphere microflora: the mycorrhizosphere effect. *Phytopath.* **78,** 366-371.

Lodge, D. J. (1989). The influence of soil moisture and flooding on formation of VA: endo- and ectomycorrhizae in *Populus* and *Salix. Plant Soil* **117,** 243-253.

Logan, V. S., Clarke, P. J. and Allaway, W. G. (1989). Mycorrhizas and roots attributes of plants of coastal sand dunes of New South Wales. *Aust. J. Plant Physiol.* **16,** 141-146.

Lohman, M. L. (1927). Occurrence of mycorrhiza in Iowa forest plants. *Univ. Iowa Stud. Nat. Hist.* **11,** 5 -30.

Lopez-Aguillon, R. and Mosse, B. (1987). Experiments on competitiveness of three endomycorrhizal fungi. *Plant Soil* **97,** 155-170.

Loree, M. A. J. and Williams, S. E. (1987). Colonization of western wheatgrass *(Agropyron smithii* Rydb.) by vesicular-arbuscular mycorrhizal fungi during the revegation of a surface mine. *New Phytol.* **106,** 735-744.

Louis, I. and Lim, G. (1987). Spore density and root colonization of vesicular-arbuscular mycorrhizas in tropical soil. *Trans. Br. Mycol. Soc.* **88,** 207-212.

Luhan, M. (1955). Das abshluBgewebe der wurzeln unserer alpenpflenzen. *Ber. Deut. Bot. Ges.* **68,** 87-92.

Lynch, J. M. and Bragg, E. (1985). Microorganisms and soil aggregate stability. In: *Advances in Soil Science* Vol. 2. pp. 133-171. Springer-Verlag, New York.

Lyr, H. and Hoffmann, G. (1967). Growth rates and growth periodicity of tree roots. In: *International Review of Forestry Research* (Ed. by J . A. Rornberger and P. Mikola), pp. 181-236. Academic Press, New York.

Macdonald, R. M. and Chandler, M. R. (1981). Bacterium-like organelles in the vesicular-arbuscular mycorrhizal fungus *Glomus caledonius.* New *Phytol.* **89,** 241-246.

MacKay, A. D. and Barber, S, A. (1985). Effect of moisture and phosphate level on root hair growth roots. *Plant Soil* **86,** 321-331.

Maeda, M. (1954). The meaning of mycorrhiza in regard to systematic botany. *Kumamoto J. Sci. B* **3,** 57-84.

Malajczuk, N., Molina, R. and Trappe, J. M. (1982). Ectomycorrhiza formation in *Eucalyptus* I. Pure culture synthesis, host specificity and mycorrhizal compatibility with *Pinus radiata. New Phytol.* **91,** 467-482.

Malajczuk, N., Molina, R. and Trappe, J. M. (1984). Ectomycorrhiza formation in *Eucalyptus* 11. The ultrastructure of compatible and incompatible mycorrhizal fungi and associated roots. *New Phytol.* **96,** 43-53.

Malajczuk, N., Trappe, J. M. and Molina, R. (1987). Interrelationships among some ectomycorrhizal trees, hypogeous fungi and small mammals: Western Australian and northwestern American parallels. *Aust. J. Ecol.* **12,** 53-55.

Malloch, D. and Malloch, B. (1981). The mycorrhizal status of boreal plants: species from northeastern Ontario. *Can.* J. *Bot.* **59,** 2167-2172.

Malloch, D. and Malloch, B. (1982). The mycorrhizal status of boreal plants: additional species from northeastern Ontario. *Can. J. Bot.* **60,** 1035-1040.

Malloch, D., Grenville, D. and Hubart, J.-M. (1987). An unusual subterranean occurrence of fossil fungal sclerotia. *Can. J. Bot.* 65, 1281-1283.

Malloch, D. W., Pirozynski, K. A. and Raven, P. H. (1980). Ecological and evolutionary significance of mycorrhizal symbioses in vascular plants (a review). *Proc. Nat. Acad. Sci.* **77,** 2113-2118.

Manjunath, A. and Bagyaraj, D. J. (1981). Components of VA mycorrhizal inoculum and their effects of growth of onion. *New Phytol.* **87,** 355-361.

Marschner, H. (1986). *Mineral Nutrition of Higher Plants.* Academic Press. London.

Marshall, P. E. and Paitullo, N. (1981). Mycorrhizal occurrence in willows in a northern freshwater wetland. *Plant Soil* **59,** 465-471.

Martin, J. P. and Haider, K. (1980). Microbial degradation and stabilization of ^{14}C labelled lignins, phenols and phenolic polymers in relation to soil humus formation. In: *Lignin Biodegradation: Microbiology, Chemistry and Potential Applications* Vol. 1 (Ed. by T. K. Kirk, T. Higuchi and H. Chang), pp. 77-100. CRC Press, Boca Raton, Florida.

Marx, D. H., Hatch, A. B. and Mendicino, J. F. (1977). High soil fertility decreases sucrose content and susceptibility of loblolly pine roots to ectomycorrhizal infection by *Pisolithus tinctorius. Can. J. Bot.* **55,** 1569- 1574.

Maser, C. and Maser, Z. (1988). Interactions among squirrels, mycorrhizal fungi, and coniferous forests in Oregon. *Great Basin Nat.* **48,** 358-369.

Mason, P. A., Last, F. T., Wilson, J., Deacon, J. W. Fleming, L. V. and Fox, F. M. (1987). Fruiting and successions of ectomycorrhizal fungi. In: *Fungal Infection of Plants* (Ed. by G. F. Pegg and P. G. Ayes). pp. 253-268. Cambridge University Press, Cambridge.

Massicotte, H. B., Ackerley, C. A. and Peterson, R. L. (1987). The root-fungus interface as an indicator of symbiont interaction in ectomycorrhizae. *Can. J. For. Res.* **17,** 846-854.

Massicotte, H. B., Peterson, R. L. and Melville, L. H. (1989). Hartig net structure of ectomycorrhizae synthesised between *Laccaria bicolor* (Tricholomataceae) and two host: *Betula alleghaniensis* (Betulaceae) and *Pinus Resinosa* (Pinaceae). *Am. J. Bot.* **76,** 1654-1667.

Matile, P. (1987). The sap of plant cells. *New Phytol.* **105,** 1-26.

Mayr, R. and Godoy, R. (1989). Seasonal paiterns in vesicular-arbuscular mycorrhiza in melic beech forest. *Agric. Ecos. Envir.* **29,** 281-288.

McAfee, B. J. and Fortin, J. A. (1986). Competitive interactions of ectomjcorrhizal mycobionts under field conditions. *Can. J. Bot.* **64,** 848-852.

McAfee, B. J. and Fortin, J. A. (1987). The influence of pH on the competitive interactions of ectomycorrhizal mycobionts under field conditions. *Can. J. For. Res.* **17,** 859-864.

McAfee, B. J. and Fortin, J. A. (1989). Ectomycorrhizal colonization on black spruce and jack pine seedlings outplanted in reforestation sites. *Plant Soil* **116,** 9-17.

McDougall, W. B. and Liebtag, C. (1928). Symbiosis in a deciduous forest, III. *Bot. Gaz.* **86,** 226-234.

McGee, P. A. (1985). Lack of spread of endomycorrhizas of *Centaurium* (Gentianaceae). *New Phytol.* **101,** 451-458.

McGee, P. A. (1986). Mycorrhizal associations of plant species in a semiarid community. *Aust. J. Bot.* **34,** 585-593.

McGee, P. A. (1987). Alteration of growth of *Solanum opacum* and *Plantago drummondii* and inhibition of regrowth of hypae of vesicular-arbuscular mycorrhizal fungi from dried root pieces by manganese. *Plant Soil* **101,** 227-233.

McGee, P. A. (1989). Variation in propagule numbers of vesicular-arbuscular mycorrhizal in a semi-arid soil. *Mycol. Res.* **92,** 28-33.

McGonigle, T. P. (1988). A numerical analysis of published field trials with vesicular-arbuscular mycorrhizal fungi. *Funct. Ecol.* **2,** 437-478.

McGonigle, T. P. and Fitter, A. H. (1988a). Growth and phosphorus inflows of *Trifolium repens* L. with a range of indigenous vesicular-arbuscular mycorrhizal infection levels under field conditions. *New Phytol.* 108, 59-65.

McGonigle, T. P. and Fitter, A. H. (1988b). Ecological consequences of arthropod grazing on VA mycorrhizal fungi. *Proc. R. Soc. Edinb.* B **94,** 25-32.

McGonigle, T. P. and Fitter, A. H. (1990). Ecological specificity of vesicular-arbuscular mycorrhizal associations. *Mycol. Res.* **94,** 120-122.

McIlveen, W. D. and Cole, H. Jr. (1976). Spore dispersal of Endogonaceae by worms, ants, wasps and birds. *Can. J. Bot.* **54,** 1486-1489.

Mclntire, P. W. (1984). Fungus consumption by the siskiyou chipmunk within a variously treated forest. *Ecology* **65,** 137-146.

McKey, D. (1979). The distribution of secondary compounds within plants. In: *Herbivores, their Interaction with Secondary Metabolises* (Ed. by G. A. Rosenthal and D. H. Janzen). pp. 55-133. Academic Press, New York.

Medve, R. J. (1983). The mycorrhizal status of the Cruciferae. *Am. Midl. Nat.* **109,** 406-408.

Medve, R. J. (1984). The mycorrhizae of pioneer species in disturbed ecosystems in Western Pennsylvania. *Am. J. Bot.* **71,** 787-794.

Mejstrik, V. K. (1965). Study of the development of endotrophic mycorrhiza in the association of *Cladietum marisci.* In: *Plant Microbe Relationships* (Ed. By J. Macura and V. Vancura), pp. 283-290. Publishing House of the Czechoslavak Academy of Sciences, Prague.

Mejstrik, V. K. (1972) Vesicular-arbuscular mycorrhizas of the species of a *Molinietum coeruleae* L.I. association: the ecology. *New Phytol.* **71,** 883-890.

Meistrik, V. (1989). Ectomycorrhizas and forest decline. *Agric. Ecos. Environ.* **28,** 325-337.

Mejstrik, V. K. and Cudlin, P. (1983). Mycorrhiza in some plant desert species in Algeria. *Plant Soil* **71,** 363-366.

Menge, J. A., Steirle, D., Bagyaraj, D. J., Johnson, E. L. V. and Leonard, R. T. (1978). Phosphorus concentrations in plants responsible for inhibition of mycorrhizal infection. *New Phytol.* **80,** 575-578.

Mengel, K. and Steffens, D. (1985). Potassium uptake of rye-grass *(Lolium perenne)* and red clover *(Trifolium pratense)* as related to root parameters. *Biol. Fertil. Soils* **1,** 53-58.

Meyer, F. H. (1964). The role of the fungus *Cenococcum graniforme* (Sow.) Ferd. et Winge in the formation of mor. In: *Soil Micromorphology* (Ed. by A. Jongerius). pp. 23-31. Elsevier, Amsterdam.

Meyer, F. H. (1973). Distribution of ectomycorrhizae in native and man-made forests. In: *Ectomycorrhizae their Ecology and Physiology* (Ed. by G. C. Marks and T. T. Kozlowski). pp. 79-105. Academic Press, New York.

Meyer, J. R. and Linderman, R. G. (1986a). Response of subterranean clover to dual inoculation with vesicular-arbuscular mycorrhizal fungi and a plant growth-promoting bacterium *Pseudomonas putida. Soil Biol. Biochem.* **18,** 185-190.

Meyer, J. R. and Linderman, R. G. (1986b). Selective influence on populations of rhizosphere or rhizoplane bacteria and actinomycetes by mycorrhizas formed by *Glomus fasciculatum. Soil Biol. Biochem.* **18,** 191-196.

Miller, O. K. Jr. (1982a). Taxonomy of ecto- and ectendomycorrhizal fungi. In: *Methods and Principles of Mycorrhizal Research* (Ed. by N. C. Schenck). pp. 91-101. American Phytopathological Society. St Paul. Minnesota.

Miller, O. K. Jr. (1982b). Mycorrhizae. mycorrhizal fungi and fungal biomass in subalpine tundra at Eagle Summit, Alaska. *Holarctic Ecol. 5,* 125-134.

Miller, O. K. Jr. and Laursen, G. **A.** (1978). Ecto- and endomycorrhizae of arctic plants at Barrow, Alaska. In: *Vegetation and Production Ecology of an Alaskan Arctic Tundra* (Ed. by L, L. Tieszen), pp. 230-237. Springer-Verlag New York.

Miller, R. M. (1979). Some occurrences of vesicular-arbuscular mycorrhiza in natural and disturbed ecosystems of the Red Desert. *Can. J. Bot. 57.* 619-623.

Miller, R. M. (1987). The ecology of vesicular-arbuscular mycorrhizae in grassland shrublands. In: *Ecophysiology of VA Mycorrhizal Plants* (Ed. by *G.* R. Safir), pp. 135-170. CRC Press, Boca Raton, Florida.

Miller, R. M., Moorman, T. B. and Schmidt, S. K. (1983). Interspecific plant association effects of vesicular-arbuscular mycorrhiza occurrence in *Atriplex confertifolia. New Phytol.* **95,** 241-246.

Mohankumar, V. and Mahadevan, A. (1986). Survey of vesicular-arbuscular mycorrhizae in mangrove vegetation. *Curr. Sci.* **55,** 936.

Molina, R. (1981). Ectomycorrhizal specificity in the genus *Alnus. Can. J. Bot.* **59,** 325-334.

Molina, R. and Trappe, J. M. (1982a). Lack of mycorrhizal specificity by the ericaceous hosts *Arbutus menziesii* and *Arctostaphylos uva-ursi. New Phytol.* **90,** 495-509.

Molina, R. and Trappe, J. M. (1982b). Patterns of ectomycorrhizal host specificity and potential among pacific northwest conifers and fungi. *Forest Sci.* **28,** 423-458.

Molina, R. J., Trappe, J. M. and Strickler, G. S. (1978). Mycorrhizal fungi associated with *Festuca* in the western United States and Canada. *Can. J. Bot.* **56,** 1691-1695.

Moore, J. C., St. John, T. V. and Coleman, D. C. (1985). Ingestion of vesicular-arbuscular mycorrhizal hyphae and spores by soil microarthropods. *Ecology* **66,** 1979-1981.

Morandi, D. (1989). Effect of xenobiotics on endomycorrhizal infection and isoflavonoid accumulation in Soybean roots. *Plant Physiol. Biochem.* **27,** 697-701.

Morandi, D., Bailey, J. A. and Gianinazzi-Pearson, V. (1984). Isoflavonoid accumulation in soybean roots infected with vesicular-arbuscular mycorrhizal fungi. *Physiol. Plant Pathol.* **24,** 357-364.

Morley, C. D. and Mosse, B. (1976). Abnormal vesicular-arbuscular mycorrhizal infections in white clover induced by lupin. *Trans. Br. Mycol. Soc.* **67,** 510-513.

Morton, J. B. (1988). Taxonomy of VA mycorrhizal fungi: classification, nomenclature. and identification. *Mycotaxon,* **32,** 267-324.

Morton, J. B. (1990). Species and clones of arbuscular mycorrhizal fungi (Glomales, Zygomycetes): Their role in macro and microevolutionary processes. *Mycotaxon* **37,** 493-515.

Morton, J. B. and Benny, G. L. (1990). Revised classification of arbuscular mycorrhizal fungi (Zygomycetes): a new order, Glomales, two new suborders Glomineae and Gigasporineae and two new families Acaulosporaceae and Gigasporaceae with an emendation of Glomaceae. *Mycotaxon,* **37,** 471-491

Mosse, B. (1959). Observations on the extra-matrical mycelium of a vesicular-arbuscular endophyte. *Truns. Br. Mycol. Soc.* **42,** 439-448.

Mosse, B. (1973). Plant growth responses to vesicular-arbuscular mycorrhiza. IV. In soil given additional phosphorus. *New Phytol.* **72,** 127-136.

Mosse, B. (1978). Mycorrhiza and plant growth. In: *Structure and Functioning of Plant Populations* (Ed. by A. H. J. Freysen and J. W. Woldendorp), pp. 269-289. North Holland Publishing Co., Amsterdam.

Mosse, B. and Bowen, G. D. (1986). The distribution of *Endogone* spores in some Australian and New Zealand soils and in an experimental field soil at Rothamsted. *Trans. Br. Mycol. Soc.* **51,** 485-492.

Mosse, B. and Hayman, D. S. (1980). Mycorrhiza in agricultural plants. In: *Tropical Mycorrhizal Research* (Ed. by P. Mikola). pp. 213-230. Claredon Press, Oxford.

Mosse, B. and Hepper, C. (1975). Vesicular-arbuscular mycorrhizal infections in root organ cultures. *Phys. Plant. Path.* **5,** 215-223.

Mukerji, K. G. and Kapoor, A. (1986). Occurrence and importance of vesicular-arbuscular mycorrhizal fungi in semiarid regions of India. *For. Ecol. Mgmt* **16,** 117-126.

Nelsen, C. E. (1987). The water relations of vesicular-arbuscular mycorrhizal systems. In: *Ecophysiology of VA Mycorrhizal Plants* (Ed. by G. R. Safir), pp. 71-79. Academic Press, New York.

Nelson, S. D. and Khan, S. U. (1990). Effect of endomycorrhizae on the bioavailability of bound ^{14}C residues to onion plants from an organic soil treated with ^{14}C Fonofos. *J. Agric. Food Chem.* **38,** 894-898.

Nespiak, A. (1953). Research on the mycotrophism of the alpine vegetation in the granite parts of the Tatra mountains over the limit of *Pinus mughus.* (In Polish). *Am Soc. Bot. Poloniae* 22, 97-125. (USDA Trans. OTS 60-21390)

Newbery, D. M., Alexander, I. J., Thomas, D. W. and Gartlan, J. S. (1988). Ectomycorrhizal rain-forest legumes and soil phosphorus in Korup National Park, Cameroon. *New Phytol.* **109,** 433-450.

Newman, E. I. (1985). The rhizosphere: carbon sources and microbial populations. In: *Ecological Interactions in Soil: Plants, Microbes and Animals* (Ed. by A. H. Fitter, D. Atkinson, D. J. Read and M. B. Usher), pp. ?? Blackwell, Oxford.

Newman, E. I. (1988). Mycorrhizal links between plants: their functioning and ecological significance. *Adv. Ecol. Res.* **18,** *243-270.*

Newman, E. I. and Eason, W. R. (1989). Cycling of nutrients from dying roots to living plants including the role of mycorrhizas. In: *Ecology of Arable Land* (Ed. by M. Clarholm and L. Bergstrom), pp. *133-137.* Kluwer, Dordrecht.

Newman, E. I. and Reddell, P. (1987). The distribution of mycorrhizas among families of vascular plants. *New Phyol.* **106,** *745-751.*

Newman, E. I., Child, R. D. and Patrick, C. M. *(1986).* Mycorrhizal infection in grasses of Kenyan savanna. *Ecology* **74,** *1179-1183.*

Nicolson, T. H. (1959). Mycorrhiza in the Gramineae I. vesicular-arbuscular endophytes, with special reference to the external phase. *Trans. Br. Mycol. Soc.* **42,** *421-438.*

Nicolson, T. H. (1960). Mycorrhiza in the Gramineae II. development in different habitats, particularly sand dunes. *Trans. Br. Mycol. Soc.* **43,** *132-145.*

Noordwijk, M. Van and Hairiah, K. *(1986).* Mycorrhizal infection in relation to soil pH and soil phosphorus content in a rain forest of northern Sumatra. *Plant Soil* **96,** 299-302.

Nopamornbodi, O., Thumsurakul, S. and Vasuvat, Y. (1987). Survival of VA mycorrhizal fungi after paddy rice. In: *Mycorrhizae in* the *Next Decade, Practical Applications and Research Priorities* (Ed. by *D.* M. Sylvia, L. L. Hung and J. H. Graham). p. 53. Institute of Food and Agriculture Sciences, University of Florida, Gainesville.

Noy-Meir, I. (1985). Desert ecosystem structure and function. In: *Ecosystems of the World 12A: Hot Deserts and Arid Shrublands* (Ed. by *M.* Evenari, I. Noy-Meir and D. W. Goodall), pp. 93-103. Elsevier, New York.

Nylund, J.-A. (1988). The regulation of mycorrhiza formation-carbohydrate and hormone theories reviewed. *Scand. J. For. Res.* **3,** 465-479.

Nylund, J. *E. (1987).* The ectomycorrhizal infection zone and it relation the acid polysaccharides of conical cell walls. *New Phytol.* **106,** 505-516.

O'Toole, J. C. and Bland, W. L. (1987). Genotypic variation in crop root systems. *Adv. Agron.* **41,** 91-145.

Oades, J. M. (1984). Soil organic matter and structural stability: mechanisms and implications for management. *Plant Soil* **76,** 319-337.

Ocampo, J. A. (1986). Vesicular-arbuscular mycorrhizal infection of "host" and "non-host" plants: effect on the growth responses of the plants and competition between them. *Soil. Biol. Biochem.* **18,** 607-610.

Ocampo, J. A. and Azcón, R. (1985). Relationship between the concentration of sugars in the roots and VA mycorrhizal infection. *Plant Soil* **86,** 95-100.

Ocampo, J. *A.* and Hayman, D. S. (1981). Influence of plant interactions on vesicular-arbuscular mycorrhizal infections. II. Crop rotations and residual effects of non-host plants. *New Phytol.* **87,** *333-343.*

Ocampo, J. A., Martin, J. and Hayman, D. S. (1980). Influence of plant interactions on vesicular-arbuscular mycorrhizal infections. I. Host and non-host plants grown together. *New Phytol.* **84,** *27-35.*

Odum, E. P. and Biever, L. J. (1984). Resource quality, mutualism and energy partitioning in food chains. *Am. Nat.* **124,** *360-376.*

Ogawa, M. (1985). Ecological characters of ectomycorrhizal fungi and their mycorrhizae - an introduction to the ecology of higher fungi. *JARQ* **18,** *305-314.*

Osmond, C. B., Austin, M. P., Berry, J. A., Billings, W. D., Boyer, J. S., Dacey, J. W. H., Nobel, P. S., Smith, S. D. and Winner, W. E. (1987). Stress physiology and the distribution of plants. *Bioscience* **37,** 38-48.

Pacovsky, R, S. (1986). Micronutrient uptake and distribution in mycorrhizal or phosphorus-fertilized soybeans. *Plant Soil* **95,** 379-388.

Pacovsky, R. S. (1989). Influence of inoculation with *Azospillum brasilense* and *Glomus fasciculatum* on sorghum nutrition. In: *Nitrogen Fixation with non-Legumes* (Ed. by F. A. Skinner *et al.),* pp. 235-239. Kluwer, Dordrecht.

Parke, J. L., Linderman, R. G. and Black, C. H. (1983). The role of ectomycorrhizas in drought tolerance of douglas-fir seedlings. *New Phytol.* **95,** 83-95.

Parke, J. L., Linderman, R. G. and Trappe, J. M. (1983). Effects of forest litter of mycorrhiza development and growth of douglas-fir and western red cedar seedlings. *Can. J. For. Res.* **13,** 666-671.

Parke, J. L., Linderman, R. G. and Trappe, J. M. (1984). Inoculum potential of ectomycorrhizal fungi in forest soils of southwest Oregon and northern California. *For. Sci.* **30,** 300-304.

Passioura. J. B. (1988). Water transport in and to roots. *Ann. Rev. Plant Physiol. Plant Mol. Biol.* **39,** 245-265.

Paulitz, T. C. and Linderman, R. G. (1989). Interactions between florescent pseudomonads and va mycorrhizal fungi. *New Phytol.* **113,** 37-45.

Paulitz, T. C. and Menge, J. A. (1984). Is *Spizellomyces punctatum* a parasite or saprophyte of vesicular-arbuscular mycorrhizal fungi? *Mycologia* **76,** 99-107.

Pellet, D. and Sieverding, E. (1986). Host preferential multiplication of fungal species of the Endogonanceae in the field. demonstrated with weeds. In: *Physiology and Genetical Aspects of Mycorrhizae* (Ed. by V. Gianinazzi-Pearson and S. Gianinazzi). pp. 555-557. INRA, Paris.

Pendleton, R. L. and Smith, B. N. (1983). Vesicular-arbuscular mycorrhizae of weedy and colonizer plant species at disturbed sites in Utah. *Oecologia* **59,** 296-301.

Peredo, H., Oliva, M. and Huber, A. (1983). Environmental factors determining the distribution of *Suillus luteus* fructifications in *Pinus radiata* grazing-forest plantations. *Plant Soil* **71,** 367-370.

Perry, D. A. and Choquette, C. (1987). Allelopathic effects on mycorrhizae influence on structure and dynamics of forest ecosystems. In: *Allelochemicals: Role in Agriculture and Forestry* (Ed. by G. R. Waller), pp. 185-194. American Chemical Society, Washington, DC.

Perry, D. A., Molina, R. and Amaranthus, M. P. (1987). Mycorrhizae, mycorrhizospheres and reforestation: current knowlege and research needs. *Can. J. For. Res.* **17,** 929-940.

Perry, D. A., Margolis, H., Choquette, C., Molina, R. and Trappe, J. M. (1989). Ectomycorrhizal mediation of competition between coniferous tree species. *New Phytol.* **112,** 501-511.

Peterson, C. A. (1988). Exodermal Casparian bands: their significance for ion uptake by roots. *Physiol Plant.* **72,** 204-208.

Peterson, R. L., Ashford, A. E. and Allaway, W. G. (1985). Vesicular-arbuscular mycorrhizal associations of vascular plants on Heron Island, a Great Barrier Reef coral cay. *Aust. J. Bot.* **33,** 669-676.

Pfeiffer, C. M. and Bloss, H. E. *(1988).* Growth and nutrition of guayle *(Parthenium argentatum)* in a saline soil as influenced by vesicular-arbuscular mycorrhiza and phosphorus fertilization. *New Phytol.* **108,** *315-321.*

Piccini, D. and Azcón, R. (1987). Effect of phosphate-solubilizing bacteria and vesicular-arbuscular mycorrhizal fungi on the utilization of Bavovar rock phosphate by alfalfa plants using a sand-vermiculite medium. *Plant Soil* **101,** 45-50.

Piché, Y. and Peterson, R. L. (1985). Early events in roots colonization by mycorrhizal fungi. In: *Proceedings of the 6th North American Conference Mycorrhize* (Ed. by R. Molina), pp. 179-180. Forest Research Laboratory, Oregon State University. Covallis, Oregon.

Pienaar, K. J. (1968). 'n anatomiese en ontogenetiese studie van de wortels van suid-afrikaanse Liliaceae: II. Die anatomie van die volwasse bywortels. *J. S. Afr. Bot.* **34,** 91-110.

Pirozynski, K. A. and Dalpé, Y. (1989). Geological history of the Glomaceae with particular reference to mycorrhizal symbiosis. *Symbiosis* **7,** 1-36.

Pittendrigh, C. S. (1948). The bromeliad-*Anopheles*-malaria complex in Trinidad. I - The bromeliad flora. *Evolution* **2,** 58-89.

Pond, E. C., Menge, J. A. and Jarrell, W. M. (1984). Improved growth of tomato in salinized soil by vesicular-arbuscular mycorrhizal fungi collected from saline soils. *Myologia* **76,** 74-84.

Pope, P. E., Chaney, W. R., Rhodes, J. D. and Woodhead, S. H. (1982). The mycorrhizal dependency of four hardwood tree species. *Can. J. Bot.* **61,** 412-417.

Porter, W. M., Robson, A. D. and Abbott, L. K. (1987a). Factors controlling the distribution of vesicular-arbuscular mycorrhizal fungi in relation to soil pH. *J. Appi. Ecol.* **24,** 663-672.

Porter, W. M,, Robson, A. D. and Abbott, L. K. (1987b). Field survey of the distribution of vesicular-arbuscular mycorrhizal fungi in relation to soil pH. *J. App. Eco1.* **24,** 659-662.

Powell, C. L. (1974). Effect of P fertilizer on root morphology and P uptake of *Carex coriacea. Plant Soil* **41,** 661 -667.

Powell, C. L. (1975). Rushes and sedges are non-mycotrophic. *Plant Soil* **42,** 481-484.

Powell, C. L. (1977). Mycorrhizas in hill-country soils I. spore bearing mycorrhizal fungi in thirty-seven soils. *N. Z. J. Agric. Res.* **20,** 53-57.

Powell, C. L. (1982). Effects of kale and mustard crops on response of white clover to VA mycorrhizal inoculation in pot trials. *N. Z. J. Agr. Res.* **25,** 461-464.

Price, N. S., Roncadori, R. W. and Hussey, R. S. (1989). Cotton root growth as influenced by phosphorus nutrition and vesicular-arbuscular mycorrhizas. *New Phytol.* **111,** 61-66.

Price, P. W. (1988). An overview of organismal interactions in ecosystems in evolutionary and ecological time. *Agr. Ecos. Envir.* **24,** 369-377.

Proctor, J. and Woodell, S. R. (1975). The ecology of serpentine soils. *Adv. Ecol. Res.* **9,** 255-366.

Puppi, G. and Reiss, S. (1987). Role and ecology of VA mycorrhizae in sand dunes. *Angew Botanik,* **61,** 115-126.

Rabatin, S. C. (1979). Seasonal and edaphic variation in vesicular-arbuscular mycorrhizal infection of grasses by *Glomus tenuis. New Phytol.* **83,** 95-102.

Rabatin. S. C. and Stinner, B. R. (1988). Indirect effects of interactions between VAM fungi and soil inhabiting invertebrates on plant processes. *Agric. Ecos. Environ.* **24,** 135-146.

Rabin, L. B. and Pacovsky, R. S. (1989). Reduced larva growth of two Lepidoptera (Noctuidae) on excised leaves of soybean infected with a mycorrhizal fungus. *J. Econ. Entomol. 78,* 1358-1363.

Ragupathy, S., Mohankumar, V. and Mahadevan, A. (1990). Occurrence of vesicular-arbuscular mycorrhizae in tropical hydrophytes. *Aquatic Bot.* **36,** 287-291.

Raich, J. W. and Nadelhoffer, K. J. (1990). Below ground carbon allocation in forest ecosystems: global trends. *Ecology* **70,** 1346-1354.

Raju, P. S., Clark, R. B., Ellis, J. R. and Maramille, J. W. (1990). Effects of species of VA-mycorrhizal fungi on growth and mineral uptake of sorghum at different temperatures. *Plant Soil* **121,** 165-170.

Rambelli, A. (1973). The rhizosphere of Mycorrhizae. In: *Ectomycorrhizae: their Ecology and Physiology* (Ed. by G. C. Marks and T. T. Kozlowski). pp. 299-349. Academic Press, New York.

Ramsay, R. R., Dixon, K. W. and Sivasithamparam, K. (1986). Patterns of infection endophytes associated with Western Australia orchids. *Lindleyana* **1,** 203-214.

Ramsay, R. R., Sivasithamparam, K. and Dixon, K. W. (1987). Anastomosis groups among rhizoctonia-like endophytic fungi in southwestern Australian *Pterostylis* species (Orchidaceae). *Lindlyana* **2,** 161- 166.

Rao, A. S. (1990). Root flavonoids. *Bot. Rev.* **56,** 1-84.

Read, D. J, (1983). The biology of mycorrhiza in the Ericales. *Can. J. Bot.* **61,** 985-1004.

Reach, D. J. and Birch, C. P. D. (1988). The effects and implications of disturbance of mycorrhizal mycelial systems. *Proc. R. Soc. Edin. B* **94,** 13-24.

Read, D. J. and Boyd, R. (1986). Water relations of mycorrhizal fungi and their host plants. In: *Water, Fungi and Plants* (Ed. by P. G. Ayes and L. Boddy), pp. 287-303, Cambridge University Press. Cambridge.

Read, D. J. and Haselwandter, K. (1981). Observations on the mycorrhizal status of some alpine plant communities. *New Phytol.* **88,** 341-352.

Read, D. J., Koucheki, H. K. and Hodgson J. (1976). Vesicular-arbuscular mycorrhiza in natural vegetation systems I. the occurrence of infection. *New Phytol.* **77,** 641-653.

Read, D. J., Francis, R. and Finlay, R. (1985). Mycorrhizal mycelia and nutrient cycling in plant communities. In: *Ecological Interactions in Soil: Plants, Microbes and Animals* (Ed. by A. H. Fitter, D. Atkinson, D. J. Read and M. B. Usher) pp. 193-217. Blackwell, Oxford

Reddy, M. V. and Sharma, G. D. (1981). Some observations on an aphid-mycorrhizal association. *Sci. Cult.* **47,** 339-340.

Redhead, J. F. (1977). Endotrophic mycorrhizas in Nigeria: Species of the Endogonaceae and their distribution. *Trans. Br. Mycol. Soc.* **69,** 275-280.

Reed, M. L. (1987). Ericoid mycorrhiza of Epacridaceae in Australia. In: *Mycorrhizae in the Next Decade, Practical, Applications and Research Priorities* (Ed. by *D.* M. Sylvia, L. L. Hung and J. H. Graham), p. 335. Institute of Food and Agricultural Sciences, University of Florida, Gainesville.

Reeves, F. B., Wagner, D., Moorman, T. and Kiel, J. (1979). The role of endomycorrhizae in revegetation practices in the semi-arid west. I. A comparison of incidence of mycorrhizae in severely disturbed vs. natural environments. *Am. J. Bot.* **66,** 6-13.

Reich, P. B., Schoettle, A. W., Stroo, H. F., Troiano, J. and Amundson, R. G. (1985). Effects of O_3, SO_2 and acidic rain on mycorrhizal infection in northern red oak seedlings. *Can J. Bot.* **63,** 2049-2055.

Rice, E. L. (1984). *Allelopathy.* Academic Press. New York.

Richards, D., and Considine, J. A. (1981). Suberization and browning of grapevine roots. In: *Structure and Function of Plant Roots* (Ed. by R. Brower, O. Gasparikova J. Kouk and B. C. Loughman). pp. 111-115. Martinus Nijhoff, Boston.

Richards, D. and Rowe, R. N. (1977). Effects of root restriction, root pruning and 6-benzylaminopurine on the growth of peach seedlings. *Ann. Bot.* **41,** 729-740.

Richards, J. H. (1986). Root form and depth distribution in several biomes. In: *Mineral Exploration: Biological Systems and Organic Matter* (Ed. by D Carlisle. W. L. Berry. I. R. Kaplan and J. R. Wanerson). pp. 82-97 Prentice Hall. New Jersey.

Richards, J. H. and Caldwell, M. M. (1987). Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia (Berl.)* **73,** 486-489.

Richter, D. L., Zuellig, T. R., Bagley, S. T. and Bruhn, J. S. (1989). Effects of red pine *(Pinus resinosa* Ait.) mycorrhizoplane-associated actinomycetes on *in vitro* growth of ectomycorrhizal fungi. *Plant Soil* **115,** 109-116.

Riffle, J. W. (1972). Effect of nematodes on root-inhabiting fungi. In: *Mycorrhizae: Proceedings of the First North American Conference on Mycorrhizae* (Ed. by E. Hacskaylo). pp. 97-113. Misc. Publication 1189. USDA Forest Science, Washington, DC.

Riser, P. G. (1985). Grasslands. In: *Physiological Ecology of North American Plant Communities* (Ed. by B. F. Chabot and H. A. Mooney), pp. 232-256. Chapman and Hall, New York.

Ritz, K. and Newman, E. I. (1986). Nutrient transport between ryegrass plants differing in nutrient status. *Oecologia (Berl.),* **70,** 128-131.

Rives, C. S., Bajwa, M. I., Liberia, A. E. and Miller, R. M. (1980). Effects of topsoil storage during surface mining on the viability of VA mycorrhiza. *Soil Sci.* **129,** 253-257.

Robert, M. and Berthelin, J. (1986). Role of biological and biochemical factors in soil mineral weathering. In: *Interactions of Soil Minerals with Natural Organics and Microbes* (Ed. by P. M. Huang and M. Schnitzer). pp 453-495. Soil Science Society of America, Madison, Wisconsin.

Robinson, R. K. (1972). The production by roots of *Calluna vulgaris* of a factor inhibitory to growth of some mycorrhizal fungi. *J. Ecol.* **60,** 219-224.

Robson, A. D. and Abbott, L. K. (1989). The effect of soil acidity on microbial activity in soils. In: *Soil Acidity and Plant Growth* (Ed. by A. D. Robson). pp. 139-165. Academic Press, Sydney.

Rogers, R. S. (1982). Early spring herb communities in mesophytic forests of the Great Lakes region. *Ecology* **63,** 1050-1063.

Rorison, I. H. and Robinson, D. (1984). Calcium as an environmental variable. *Plant Cell Environ.* **7,** 381-390.

Rose, S. L. (1980). Vesicular-arbuscular endomycorrhizal associations of some desert plants of Baja California. *Can. J. Bot.* **59,** 1056-1060.

Rose, S. L. (1988). Above and below ground community development in a marine sand dune ecosystem. *Plant Soil* **109,** 215-226.

Rose, S. L., Perry, D. A., Pilz, D. and Schoeneberger, M. M. (1983). Allelopathic effects of litter on the growth and colonization of mycorrhizal fungi. *J. Chem. Ecol.* **9,** 1153-1162.

Rosendahl, S., Rosendahl, C. N. and Sochting, U. (l989). Distribution of VA mycorrhizal endophytes amongst plants from a Danish grassland community. *Agric. Ecos. Environ.* **29,** 329-335.

Ross, J. P. and Ruttencutter, R. (1977). Population dynamics of two vesicular-arbuscular endomycorrhizal fungi and the role of hyperparasitic fungi. *Phytopath.* **67,** 490-496.

Rothwell, F. M. (1984). Aggregation of surface mine soil by interaction between VAM fungi and lianin degradation products of *Lespedex. Plant Soil* **80,** 99-104.

Rozema, J., Arp, W., van Diggelen, J., van Esbroek, M., Broekman, R. and Punte, H. (1986). Occurence and ecological significance of vesicular-abuscular mycorrhiza in the salt marsh environment. *Acta Bot. Neerl.* **35,** 457-467.

Rupp, L. A., Mudge, K. W. and Negm, F, B. (1989). Involvement of ethylene in ectomycorrhiza formation and dichotomous branching of roots of mugo pine seedlings. *Can. J. Bot.* **67,** 477-482.

Russell, R. S. (1977). *Plant Root Systems: Their Function and Interaction with the Soil.* McGraw-Hill, London.

Saif, S. R. (1987). Growth responses of tropical forage plant species to vesicular-arbuscular mycorrhizae I. Growth, mineral nutrient uptake and mycorrhizal dependency. *Plant Soil* **97,** 25-35.

Sainz, M. J. and Arines, J. (1988). Effect of indigenous and introduced vesicular-arbuscular mycorrhizal fungi on growth and phosphorus uptake of *Trifolium pratense* and on inorganic phosphorus fractions in a cambisol. *Biol. Fertil. Soil* **6,** 55-60.

Salawu, E. O. and Estey, R. H. (1979). Observations on the relationship between a vesicular-arbuscular fungus, a fungivorous nematode and the growth of soybeans. *Phytoprotection* **60,** 99-102.

Salmia, A. (1988). Endomycorrhizal fungus in chlorophyll-free and green forms of the terrestrial orchid *Epipactis helleborine. Karslenia* **28,** 3-18.

Salmia, A. (1989). Features of endomycorrhizal infection of chlorophyll free and green forms of *Epipactis helleborine* (Orchidaceae). *Ann. Bot. Fennici* **26,** 15-26.

Sanders, F. E. and Sheikh, N. A. (1983). The development of vesicular-arbuscular mycorrhizal infection in plant root systems. *Plant Soil* **71,** 223-246.

Scheltema, M. A., Abbott, L. K. and Robson, A. D. (1985a). Seasonal variation in the infectivity of VA mycorrhizal fungi in annual pastures in a mediterranean environment, *Aust. J. Agric. Res.* **38,** 70-715.

Scheltema, M. A., Abbott, L. K., Robson, A. D. and De'ath, G. (1985b). The spread of *Glomus fasciculatum* through roots of *Trifolium subterraneum* and *Lolium rigidium. New Phytol.* **100,** 105-114.

Schenck, N. C. and Kinloch, R. A. (1980). Incidence of mycorrhizal fungi on six field crops in monoculture on a newly cleared woodland site. *Mycologia* **72,** 445-456.

Schenck, N. C, and Smith, G. S. (1982). Responses of six species of vesicular-arbuscular mycorrhizal fungi and their effects on soybean at four soil temperatures. *New Phyto1.* **92,** 193-201.

Schenck, N. C., Graham, S. O. and Green, N. E. (1975). Temperature and light effect on contamination and spore germination of vesicular-arbuscular mycorrhizal fungi. *Mycologia* **67,** 1189-1192

Schenck, N. C., Siqueira, J, O. and Olixiera, E. (1989). Changes in the incidence of VA mycorrhizal fungi with changes in ecosystems. In: *Interrelationships between Microorganisms and Plants in Soil* (Ed. by V. Vancura and F. Kunc), pp. 125-129. Elsevier, Amsterdam.

Schmidt, S. K. and Reeves, F. B. (1984). Effect of the non-mycorrhizal pioneer plant *Salsiola kali* L. (Chenopodiaceae) on vesicular-arbuscular mycorrhizal (VAM) fungi. *Am. J. Bot.* **71,** 1035-1039.

Schmidt, S. K. and Reeves, F. B. (1989). Interference between *Salsiola kali* L. seedlings: implications for plant succession. *Plant Soil* **116,** 107-110.

Schmidt, S. K. and Scow, K. M. (1986). Mycorrhizal fungi on the Galapagos islands *Biotropica* **18,** 236-240.

Schubert, A., Marzachi, C., Mazzitelli, M., Cravero, M. C. and Bonfante-Fasolo, P. (1987). Development of total and viable extraradical mycelium in the vesicular-arbuscular mycorrhizal fungus *Glomus clarum* Nicol. & Schenck. *New Phytol.* **107,** 193-190.

Schüepp, H., Dehn, B. and Sticher, H. (1987) Interaktionene zwischen VA-Mykorrhizen und Schwermetallbelastungen. *Angew. Botanik* **61,** 85-96.

Schwab, S. M., Menge, J. A. and Leonard, R. T. (1983). Quantitative and qualitative effects of phosphorus on extracts and exudates of sudangrass roots in relation to vesicular-arbuscular mycorrhiza formation. *Plant Physiol.* **73,** 761-765.

Secilia, J. and Bagyaraj, D. J. (1988). Fungi associated with pot cultures of vesicular-arbuscular mycorrhizas. *Trans. Br. Mycol. Soc.* **91,** 117-1 19.

Selivanov, I. A. and Eleusenova, N. G. (1974). [Characteristics of mycosymbiotic relations in the plant communities of north Kazakhstan deserts.] (In Russian). *Boianicheskii Z.* **59,** 18-35. (USD.4 Trans. TT 79-59073,Q)

Sengupta, A. and Chaudhuri, S. (1990). Vesicular-arbuscular mycorrhiza (VAM) in pioneer salt marsh plants of the Ganges river delta in west Bengal (India). *Plant Soil* **122,** 111-113.

Shafer, S. R., Rhodes, L. H. and Riedel, R. M. (1981). *In-vitro* parasitism of endomycorrhizal fungi of ericaceous plants by the mycophagous nematode *Aphelenchoides bicaudatus. Mycologia* **73,** 1414-149.

Shafer, S. R., Grand, L. F., Bruck, R. I. and Heagle, A. S. (1985). Formation of ectomycorrhizae on *Pinus taeda* seedlings exposed to simulated acidic rain *Can. J. For. Res.* **15,** 66-71,

Shishkoff, N. (1987). Distribution of the dimorphic hypodermis of roots in Angiosperm families. *Am. J. Bot.* **60,** 1-15.

Sievarding, E. (1988). Effect of soil temperature on performance of different VA mycorrhizal isolates with cassava. *Angew. Botanik* **62,** 295-300.

Sievarding, E. and Glavez, A. (1988). Performance of different cassava clones with various VA mycorrhizal Fungi. *Angew. Botanik* **62,** 273-282.

Sieverding, E. and Toro, T. T. (1988). Influence of soil water regimes on VA mycorrhiza. V. performance of different VAM fungal species with cassava. *J. Agron. Crop Sci.* **161,** 322-332.

Simpson, D. and Daft, M. J. (1990a). Interactions between water-stress and different mycorrhizal inocula on plant growth and mycorrhizal development in maize and sorghum. *Plant Soil* **121,** 179-186.

Simpson, D. and Daft, M. J. (1990b). Spore production and mycorrhizal development in various tropical crop hosts infected with *Glomus clarum. Plant Soil* **121,** 171-178.

Singer, R. (1988). The role of fungi in periodically inundated Amazonian forests. *Vegetatio* **78,** 27-30.

Singer, R. and Araujo, I. (1979). Litter decomposition and ectomycorrhiza in amazonian forests I. a comparison of litter decomposition and ectomycorrhizal basidiomycetes in latosol-terra-firme rain forest and white podzol campinarana. *Acta Amazonica* **9,** 25-41.

Singer, R. and Morello, J. H. (1960). Ectotrophic forest tree mycorrhizae and forest communities. *Ecology* **41,** 549-551.

Siqueira, J. O, Hubbell, D. H., Kimbrough, J. W. and Schenck, N. C. (1984). *Stachyobotrys chatarum* antagonistic to azygospores of *Gigaspora margarita in vitro. Soil Biol. Biochem.* **16,** 679-481.

Slankis, V. (1974). Soil factors influencing formation of mycorrhizae. *Ann. Rev. Phytopath.* **12,** 437-457.

Smith, S. E. and Bonen, G. D. (1979). Soil temperature, mycorrhizal infection and nodulation of *Medicago truncatula* and *Trifolium subterraneum. Soil Biol. Biochem.* **11,** 469-473.

Smith, S. E. and Gianinazzi-Pearson, V. (1988). Physiological interactions between symbionts in vesicular-arbuscular mycorrhizal plants. *Ann. Rev. Plant Physiol. Plant Mol. Biol.* **39,** 221-244.

Smith, S. E. and Walker, N. A. (1981). A quantitative study of mycorrhizal infection in *Trifolium:* separate determination of the rates of infection and of mycelial growth. *New Phytol.* **89,** 225-240.

Smith, S. E., Walker, N. A. and Tester, M. (1986). The apparent width of the rhizosphere of *Trifolium subterraneum* L. for vesicular-arbuscular mycorrhizal infections: effects of time and other factors. *New Phytol.* **104,** 547-558.

Smith, S. E., Long, C. M. and Smith, F. A. (1989). Infection of roots with a dimorphic hypodermis: possible effects on solute uptake. *Agric. Ecos. Environ.* **29,** 403-407.

Smith, V. R. and Newton, I. P. (1986). Vesicular-arbuscular mycorrhizas at a sub-Antarctic island. *Soil Biol. Biochem.* **18,** 547-549.

Smith, W. H. (1990). Air *Pollution and Forests Interactions between Air Contaminants and Forest Ecosystems.* Springer-Verlag, New York.

Smits, W. Th. M. (1983). Dipterocarps and mycorrhiza. An ecological adaptation and a factor in forest regeneration. *Flora Malesiana Bull.* **36,** 3926-3937.

Son, C. L. and Smith, S. E. (1988). Mycorrhizal growth responses: interactions between photon irradiance and phosphorus nutrition. New *Phytol.* **108,** 305-314.

Sondergaard, M. and Laegaard, S. (1977). Vesicular-arbuscular mycorrhiza in some aquatic vascular plants. *Nature* **268,** 232-233.

Sparling, G. P. and Tinker, P. B. (1978a). Mycorrhizal infection in pennine grassland, I. levels of infection in the field. *J. Appl. Ecol. 15,* 943-950.

Spading, G. P. and Tinker, P. B. (1978b). Mycorrhizal infection in pennine grassland II. Effects of mycorrhizal infection on the growth of some upland grasses on ϒ-irradiated soils. *J. M. Ecol.* **15,** 951-958.

St John, T. V. (1980a). A survey of mycorrhizal infection in an Amazonian rain forest. *Acta Amazonica* **10,** 527-533.

St John, T. V. (1980b). Root size, root hairs and mycorrhizal infection: a re-examination of Baylis's hypothesis with tropical trees. *New Phytol.* **84,** 483-487.

St John, T, V. and Coleman, D.C. (1983). The role of mycorrhizae in plant ecology. *Can. J. Bot.* **61,** 1005-1014.

St John, T. V., Coleman, D. C. and Reid, C. P. P. (1983). Growth and spatial distribution of nutrient-absorbing organs: selective exploitation of soil heterogeneity. *Plant Soil* **71,** 487-493.

Staaf, H. (1988). Litter decomposition in beech forest - effects of excluding tree roots. *Biol. Fertil. Soils* **6,** 302-305.

Stahl, P. D. and Smith, W. K. (1984). Effects of different geographic isolates of *Glomus* on the water relations of *Agropyron smithii. Mycologia* **76,** 261-267.

Stahl, P. D., Williams, S. E. and Christensen, M. (1988). Efficacy of native vesicular-arbuscular mycorrhizal fungi after severe soil disturbance. *New Phytol.* **110,** 347-354.

Stasz, T. E. and Sakai, W. S. (1984). Vesicular-arbuscular mycorrhizal fungi in the scale-leaves of Zingiberaceae. *Mycologia* **76,** 754-757.

Stejskalová, H. (1989). The role of mycorrhizal infection in weed-crop interactions. *Agric. Ecos. Env.* **29,** 415-419.

Straker, C. J. and Mitchell, D. T. (1986). The activity and characterization of acid phosphateases in endomycorrhizal fungi of the Ericaceae. *New Phytol.* **104,** 243-256.

Struble, J. E. and Skipper, H. D. (1988). Vesicular-arbuscular mycorrhizal fungal spore production as influenced by plant species. *Plant Soil* **109,** 277-280.

Strzelczyk, E. and Kampert, M. (1987). Growth of mycorrhizal fungi cultured with bacteria. *Angew. Botanik.* **61,** 157-162.

Stubblefield, S. P. and Taylor, T. N. (1988). Recent advances in paleomycology. *New Phytol.* **108,** 3-25.

Stutz, R. C. (1972). Survey of mycorrhizal plants. In; *Devon Island I.B.P. Project, High Arctic Ecosystem, Project Report 1970 and 1971* (Ed. by L. C. Bliss). pp. 214-216. Dept. of Botany, University of Alberta.

Summerbell, R. C. (1989). Microfungi associated with the mycorrhizal mantle and adjacent microhabitats within the rhizosphere of black spruce. *Can. J. Bot.* **67,** 1085-1095.

Sussman, A. S. (1976). Activators of fungal spore germination. In: *The Fungal Spore Form and Function* (Ed. by D. J. Weber and W. M. Hess), pp. 101-137. John Wiley, New York.

Sutherland, J. R. and Fortin, J. A. (1968). Effect of the nematode *Aphelenchus avenae* on some ectotrophic, mycorrhizal fungi and on a Red Pine Mycorrhizal relationship. *Phytopath.* **58,** 519-523.

Sutton, J. C. and Barren, G. L. (1972). Population dynamics of *Endogone* spores in soil. *Can. J. Bot.* **50,** 1909-1914.

Sylvia, D. M. (1987). Growth response of native woody plants to inoculation with *Glomus* species in phosphate mine soil. *Proc. Soil Crop Sci. Soc. Florida* **47,** 60-64.

Sylvia, D. M. (1988). Activity of external hyphae of vesicular-arbuscular mycorrhizal fungi. *Soil Biol. Biochem.* **20,** 39-43.

Sylvia, D. M. (1989). Nursery inoculation of sea oats with vesicular-arbuscular mycorrhizal fungi and outplanting performance on Florida beaches. *J. Coastal Res.* ***5,*** 747-754.

Sylvia, D. M. and Schenck, N. C. (1983). Germination of chlamydospores of three *Glomus* species as affected by soil matric potential and fungal contamination. *Mycologia* **75,** 30-35.

Sylvia, D. M. and Will, M. E. (1988). Establishment of vesicular-arbuscular mycorrhizal fungi and other microorganisms on a beach replenishment site in Florida. *Appl. Environ. Microbiol.* **54,** 343-352.

Takhtajan, A. (1986). *Floristic Regions of the World.* University of California Press, Berkley.

Tan, K. H., Silhanonth, P. and Todd, R. L. (1978). Formation of humic like compounds by the ectomycorrhizal fungus, *Pisolithus tinctorius. Soil Sci. Soc. Am. J.* **42,** 906-908.

Tanner, C. C. and Clayton, J. S. (1985). Effects of vesicular-arbuscular mycorrhizas on growth and nutrition of a submerged aquatic plant. *Aquatic Bot.* **22,** 377-386.

Terashita, T. (1985). Fungi inhabiting wild orchids in Japan (II). A symbiotic experiment with *Armillariella mellea* and *Galeola septentrionalis. Trans. Mycol. Soc. Japan* **26,** 47-63.

Testier, M., Smith, S. E. and Smith, F. A. (1987). The phenomenon of "nonmycorrhizal" plants. *Can. J. Bot.* **65,** 419-431.

Tews, L. and Koske, R. E. (1986). Toward a sampling strategy for vesicular-arbuscular mycorrhizas. *Trans. Br. Mycol. Soc.* **87**, 353-358.

Theodorou, C. and Bowen, G. D. (1987). Germination of basidiospores of mycorrhizal fungi in the rhizosphere of *Pinus radiata* D. Don. *New Phytol.* **106,** 217-223.

Thomas, G. V. and Ghai, S. K. (1987). Genotype dependent variation in vesicular-arbuscular mycorrhizal colonisation of coconut seedlings. *Proc. Indian Acad. Sci. (Plant Sci.)* **97,** 289-294.

Thomas, R. S., Dakessian, S., Ames, R. N., Brown, M. S. and Bethlenfalvay, G. J. (1986). Aggregation of a silty clay loam soil by mycorrhizal onion roots. *Soil Sci. Soc. Am. J.* **50,** 1494-1499.

Thomazini, L. I. (1973). Mycorrhiza in plants of the 'Cerrado'. *Plant Soil* **41,** 707-711.

Thompson, G. W. and Medve, R. J. (1984). Effects of aluminium and manganese on the growth of ectomycorrhizal fungi. *Appl. Env. Microbiol.* **48,** 556-560.

Thompson, J. P. (1987). Decline of vesicular-arbuscular mycorrhizae in long fallow disorder of field crops and its expression in phosphorus deficiency of sunflower. *Aust. J. Agric. Res.* **38,** 847-67.

Thompson Wilson, G. W., Daniels Hetrick, B. A. and Gerschefske Kitt, D. (1987). Suppression of vesicular-arbuscular fungus spore germination by nonsterile soil. *Can. J. Bot.* **67,** 18-23.

Thomson, B. D., Robson, A. D. and Abbott, L. K. (1986). Effects of phosphorus on the formation of mycorrhizas by *Gigaspora calospora* and *Glomus fasciculatum* in relation to root carbohydrates. *New Phytol.* **103,** 751-765.

Tieszen, L. L. (1978). Summary. In: *Vegetation and Production Ecology of an Alaskan Arctic Tundra* (Ed. by *L.* L. Tieszen), pp. 601-645. Springer-Verlag, New York.

Tilman, D. (1982). *Resource Competition* and *Community Structure.* Princeton University Press, Princeton, New Jersey.

Tilman, D. (1988). *Plant Strategies and the Dynamics and Structure of Plant Communities.* Princeton University Press, Princeton, New Jersey.

Tinker, P. B. (1990). Nutrient uptake by plant roots in natural systems. In: *Nutrient Cycling in Terrestrial Ecosystems: Field Methods, Application and Interpretation* (Ed. by A. F. Harrison, P. Ineson and O. W. Heal). pp. 322-334. Elsevier, London.

Tisdall, J. M. and Oades, J. M. (1979). Stabilization of soil aggregates by the root systems of ryegrass. *Aust. J. Soil Res.* **17,** 429-441.

Tobiessen, P. and Werner, M. B. (1980). Hardwood seedling survival under plantations of scotch pine and red pine in central New York. *Ecology* **61,** 25-29.

Tomlinson, P. B. (1969). On the morphology and anatomy of turtle grass, *Thalassia testudinum* (Hydrocharitaceae). II Anatomy and development of the root in relation to function. *Bull. Marine Sci.* **19,** 57-71.

Tommerup, I. C. (1982). Airstream fractionation of vesicular-arbuscular mycorrhizal fungi: Concentration and enumeration of propagules. *Appl. Envir. Microbiol.* **44,** 533-539.

Tommerup, I. C. (1983a). Spore dormancy in vesicular-arbuscular mycorrhizal fungi. *Trans Br. Mycol. Soc.* **81,** 37-45.

Tommerup, I. C. (1983b). Temperature relations of spore germination and hyphal growth of vesicular-arbuscular mycorrhizal fungi in soil. *Trans. Br. Mycol. Soc.* **81,** 381-387.

Tommerup, I. C. (1984). Development of infection by a vesicular-arbuscular mycorrhizal fungus in *Brassica napus* L. and *Trifolium subterraneum* L. *New Phytol.* **98,** 487-495.

Tommerup, I. C. (1987). Physiology and ecology of VAM spore germination and dormancy in soil. In: *Mycorrhizae in the Next Decade, Practical Applications and Research Priorities* (Ed. by *D.* M. Sylvia, L. L. Hung and J. H. Graham), pp. 175-177. Institute of Food and Agricultural Sciences. Unhersity of Florida, Gainesville.

Tommerup, I. E. (1988). The vesicular-arbuscular mycorrhizas. *Adv. Plant Path.* **6,** 81-91.

Tommerup, I. C. and Abbott, L. K. (1981). Prolonged survival and viability of VA mycorrhizal hyphae after root death. *Soil Biol. Biochem.* **13,** 431-433.

Tommerup, I. C. and Kidby, D. K. (1980). Production of aseptic spores of vesicular-arbuscular endophytes and their viability after chemical and physical stress. *Appl. Env. Microbiol.* **39,** 1111-1119.

Torrey, J. G. (1978). Nitrogen fixation by actinomycete-nodulated angiosperms. *Bioscience* **28,** 586-592.

Tranquillini, W. (1979). Physiological ecology of the alpine timberline. Springer- Verlag, New York.

Trappe, J. M. (1962). The fungus associates of ectotrophic mycorrhizae. *Bot. Rev.* **28,** 538-606.

Trappe, J. M. (1977). Selection of fungi for ectomycorrhizal inoculation in nurseries. *Ann. Rev. Phytopath.* **15,** 203-222.

Trappe, J. M. (1981). Mycorrhizae and productivity of arid and semiarid rangelands. In: *Advances* in *Food Producing Systems for Arid and Semi And Lands.* pp. 581-599.

Trappe, J. M. (1987). Phylogenetic and ecologic aspects of mycotrophy in the Angiosperms from an evolutionary standpoint. In: *Ecophysiology of VA Mycorrhizal Plants* (Ed. by G. R. Safir). pp. 5-25. CRC Press, Boca Raton, Florida.

Trappe, J. M. (1988). Lessons from alpine fungi. *Mycologia* **80,** 1-10.

Trappe, J. M. and Maser, C. (1976). Germination of spores of *Glomus macrocarpus* (Endogonaceae) after passage through a rodent digestive tract. *Mycologia* **68,** 433-436.

Trappe, J. M. and Molina, R. (1986). Taxonomy and genetics of mycorrhizal fungi: their interactions and relevance. In: *Physiology and Genetical Aspects of Mycorrhizae* (Ed. by V. Gianinazzi-Pearson and S. Gianinazzi). pp. 133-146. INRA. Paris.

Trappe, J. M., Molina, R. and Castellano, M. (1984). Reactions of mycorrhizal fungi and mycorrhizal formation to pesticides. *Ann. Rev. Phytopath.* **22,** 331-359.

Trinick, M. J. (1977). Vesicular-arbuscular infection and soil phosphorus utilization in *Lupinus* spp. *New Phytol.* **78,** 297-304.

Tyler, G. (1985). Macrofungal flora of Swedish beech forest related to soil organic matter and acidity characteristics. *For. Ecol. Mgmt* **10,** 13-29.

Tzean, S. S., Chu, C. L. and Su, H. J. (1983). Spiroplasma-like organisms in a vesicular-arbuscular mycorrhizal fungus and its mycoparasite. *Phytopath.* **73,** 989-991.

Uren, N. C. and Reisenaur, H. M. (1988). The role of root exudates in nutrient acquisition. In: *Advances* in *Plant Nutrition Vol. 3* (Ed. by B. Tinker & A. Lachli), pp. 79-114. Praeger. New York.

Van der Werf, M., Kooijman, A, Welschen, R. and Lambers, H. (1988). Respiratory energy costs for the maintenance of biomass, for growth and for ion uptake in roots of *Carex diandra* and *Carex acutiformis. Physiol. Plantarum* **72,** 483-491.

Van Duin, W. E. Rozema, J. and Ernst, W. H. O.(1989). Seasonal and spatial variation in the occurrence of vesicular-arbuscular (VA) mycorrhiza in salt marsh plants. *Agric. Ecos. Environ.* **29,** 107-1 10.

Van Nuffelen, M. and Schenck, N. C. (1984). Spore germination penetration and root colonization of six species of vesicular-arbuscular mycorrhizal fungi on soybean. *Can. J. Bot.* **62,** 624-628.

Van Ray, B. and Van Diest, A. (1979). Utilization of phosphate from different sources by six plant species. *Plant Soil* 51, 577-589.

Vančura, V., Orozco, M. O., Grauová, O. and Přikryl Z. (1989). Properties of bacteria in the hyphosphere of a vesicular-arbuscular mycorrhizal fungus. *Agric. Ecos. Envir.* **29,** 421-427.

Vaughan, D. and Malcolm, R. E. (1985). *Soil Organic Matter and Biological Activity.* Martinus Nijhoff / W. Junk, Dordrecht.

Veresoglou, D. S. and Fitter. A. H. (1984). Spatial and temporal patterns of growth and nutrient uptake of five Co-existing grasses. *J. Ecol.* **72,** 359-272.

Villeneuve, N., Grandtner, M. M. and Fortin, J. A. (1989). Frequency and diversity of ectomycorrhizal and saprophytic macrofungi in the Laurentide Mountains of Quebec. *Can J. Bot.* **67,** 2626-2629.

Vincent, von J. -M. (1989). Feinwurzelmasse und mykorrhiza von altbuchen *(Fagus sylvatica* L.). in waldschadensgebieten bayer&. *Eur. J. For. Path.* **19,** 167-177.

Virginia, R. A., Jenkins, M. B. and Jarrell, W. M. (1986). depth of root symbiont occurrence in soil. *Biol. Fertil. Soils* **2,** 127-130.

Vogt, K. A., Grier, C. C., Meier, C. E. and Edmonds, R. L. (1982). Mycorrhizal role in net primary production and nutrient cycling in *Abies amabilis* ecosystems in western Washingon. *Ecology* **63,** 370-380.

Vogt, K. A., Vogt, D. J., Moore, E. E., Fatuga, B. A., Redlin, M. R. and Edmonds, R. L. (1987). Conifer and Angiosperm fine-root biomass in relation to stand age and site productivity in douglas-fir forests. *J. Ecol.* **75,** 857-870.

Vozzo, J. A. and Hacskaylo, E. (1974). Endo- and ectomycorrhizal associations in five *Populus* species. *Bull. Torrey Bot. Club* **101,** 182-186.

Vreeland, P., Kleiner, E. F. and Vreeland, H. (1981). Mycorrhizal symbiosis of *Sarcodes sunguinea. Environ. Exp. Bot.* **21,** 15-25.

Waaland, M. E. and Alien, E. B. (1987). Relationships between VA mycorrhizal fungi and plant cover following surface mining in Wyoming. *J. Range Mgmt* **40,** 271-276.

Wacker, T. L., Safir, G. R. and Stephens, C. T. (1990). Effects of ferulic acid on *Glomus fasciculatum* and associated effect on phosphorus uptake and growth of asparagus *(Asparagus officinalis* L). *J. Chem. Ecol.* **16,** 901-909.

Wainwright, M. (1988). Metabolic diversity of fungi in relation to growth and mineral cycling in soil - a review. *Trans. Br. Mycol. Soc.* **90,** 159-170.

Walker, C. (1988). Formation and dispersal of propagules of endogonaceous fungi. In: *Fungal Infection in Plants* (Ed. by G. F. Pegg & P. C. Ayes), pp. 269-284. Cambridge University Press, Cambridge.

Walker, C. and Koske, R. E. (1987). Taxonomic concepts in the Endogonaceae: IV. *Glomus fasciculatum* redescribed. *Mycotaxon* **30,** 253-262.

Walker, C., Biggin, P. and Jardine, D. C. (1986), Difference in mycorrhizal status among clones of sitka spruce. *For. Ecol. Mgmt.* **14,** 275-283.

Walker, C., Mize, C. W. and McNabb, H. S. Jr. (1982). Populations of Endogonaceous fungi at two locations in central Iowa. *Can. J. Bot.* **60,** 2518-2529.

Wallace, L. L. (1987). Effects of clipping and soil compaction on growth, morphology and mycorrhizal colonization of *Schizachyzum scoparium,* a C4 bunchgrass. *Oecologia (Berl.)* **72,** 423-428.

Walter, H. (1979). *Vegetation of the Earth and Ecological Systems of the Geo-biosphere.* Springer-Verlag. New York.

Walter, H. and Breckle, S. W. (1985). *Ecological Systems of the Geobiosphere 1: Ecological Principles in Global Perspective.* Springer-Verlag. New York.

Wang, G. M. A., Stribley, D. P., Tinker, P. B. and Walker, C. (1985). Soil pH and vesicular-arbuscular mycorrhizas. In: *Ecological Interactions in Soil* (Ed. by A. H. Fitter), pp. 219-224. Blackwell, Oxford.

Warcup, J. H. (1980). Ectomycorrhizal associations of Australian indigenous plants. *New Phytol.* **85,** 531-535.

Warcup, J. H. (1981). Mycorrhizal relationships of Australian orchids. *New Phytol.* **87,** 371-381.

Warcup, J. H. (1985). Pathogenic *Rhizoctonia* and orchids. In: *Ecology and Management of Soilborne Plant Pathogens* (Ed. by *C.* A. Parker. A. D. Rovira, K. J. Moore, P. T. W. Wong, J. F. Kollmorgen), pp. 69-70. The American Phytopathological Society, St Paul. Minnesota.

Warcup, J. H. (1988). Mycorrhizal associations and seedlings development in Australian Lobeliadeae (Campanulaceae). *Aust. J. Bot.* **36,** 461-472.

Warner, A. (1984). Colonization of organic matter by vesicular-arbuscular mycorrhizal fungi. *Trans. Br. Mycol. Soc.* **82,** 352-354.

Warner, A. and Mosse, B. (1982). Factors affecting the spread of vesicular-arbuscular mycorrhizal fungi in soil I. root density. *New Phytol.* **90,** 529-536.

Warner, N. J., Alien. M. F. and MacMahon. J. A. 09871. Dispersal agents of vesicular-arbuscular mycorrhizal fungi in a disturbed arid ecosystem. *Mycologia* **79,** 721-730.

Warnock, A. J., Fitter, A. H., and Usher, M. B. (1982). The influence of a springtail *Folsomia candida* (Insecta Collembola) on the mycorrhizal association of leek *Allium porrum* and the vesicular-arbuscular mycorrhizal endophyte *Glomus fasciculatum. New Phytol.* **90,** 285-292.

Went, F. W. and Stark, N. (1968). The biological and mechanical role of soil fungi. *Proc. Natl. Acad. Sci.* **60,** 497-504.

Whipps, J. M. and Lynch, J. M. (1986). The influence of the rhizosphere on crop productivity. *Adv. Microb. Ecol.* **9,** 187-244.

Whtie, D. P. (1941). Prairie soil as a medium for tree growth. *Ecology* **22,** 398-407

Whittaker, R. H. (1975). *Communities and Ecosystems.* Macmillan, New York.

Wicklow-Howard, M. (1989). The occurrence of vesicular-arbuscular mycorrhizae in burned areas of the Snake River Birds of Prey area, Idaho. *Mycotaxon* **34,** 253-257.

Wilde, S. A. (1954). Mycorrhizal fungi: their distribution and effect on tree growth. *Soil Sci.* **78,** 23-31.

Wilkinson, K. G., Dixon, K. W. and Sivasithamparam, K. (1989). Interaction of soil bacteria, mycorrhizal fungi and orchid seed in relation to germination of Australian orchids. *New Phytol.* **112,** 429-435.

Williams, P. G. (1985). Orchidaceous rhizoctonias in pot cultures of vesicular-arbuscular mycorrhizal fungi. *Can. J. Bot.* **63,** 1329-1333.

Williams, S. E., Wollum, A. H. II and Aldon, E. F. (1974). Growth of *Atriplex canescens* (Pursh) Nutt. improved by formation of vesicular-arbuscular mycorrhizae. *Proc. Soil Soc. Am.* **38,** 962-965.

Wilson, J. B. (1988). Shoot competition and root competition. *J. Appl. Ecol.* **25,** 279-269.

Wilson, J. M. (1984). Comparative development of infection by three vesicular-arbuscular mycorrhizal fungi. *New Phytol.* **97,** 413-426.

Wink, M. (1987). Chemical ecology of quinolizine alkoids. In: *Allelochemicals: Role in Agriculture and Forestry* (Ed. by *G.* R. Waller), pp. 524-533. American Chemical Society. Washington, DC.

Wood, T., Bormann, F. H. and Voigt, G. K. (1984). Phosphorus cycling in a northern hardwood forest: biological and chemical control. *Science* **223,** 391-393.

Woodward, F. I. (1987). *Climate and Plant Distribution.* Cambridge University Press, Cambridge.

Zajicek, J. M., Daniels Hetrick, B. A. and Albrecht, M. L. (1986a). Influence of drought stress and mycorrhizae on growth of two native forbs. *J. Am. Soc. Hort. Sci.* **112,** 454-459.

Zajicek, J. M., Daniels Hetrick, B. A. and Owensby, C. E. (1986b). The influence of soil depth on mycorrhizal colonization of forbs in the tallgrass prairie. *Mycologia* **78,** 316-320.

Zak, B. (1965). Aphids feeding on mycorrhizae of douglas-fir. *For. Sci.* **11,** 410-411.

Zak, B. (1967). A nematode *(Meloidodera* sp.) on douglas-fir mycorrhizae. *Plant Dis. Reptr.* **51,** *264.*

Zobel, R. W. (1986). Rhizogenetics (root genetics) of vegetable crops. *Hortscience* **21,** 956-959.

Begon, M, Fitter, A. H. & Macfadyen, A. (Eds.)
Advances in Ecological Research 1991
Volume 21 pp 171-313
Academic Press Limited, London

I. SUMMARY *171*
II. INTRODUCTION *172*
III. MYCORRHIZAL ECOLOGY *173*
A. Mycorrhizal Fungi *175*
B. Edaphic or Climatic Factors and Mycorrhizal Fungi *176*
1. Propagules of Mycorrhizal Fungi *176*
2. Dispersal of Mycorrhizal Fungi *179*
3. Soil Organisms Associated with Mycorrhizal Fungi *182*
4. Soil Disturbance and Mycorrhizal Fungi *183*
5. Climatic or Edaphic Specificity of Mycorrhizal Fungi *185*
6. The Population Ecology of Mycorrhizal Fungi *188*
C. The Host Plant *194*
1. The Structural Diversity and Function of Roots *194*
D. Plants and Mycorrhizal Fungi *196*
1. Compatibility and Specificity *196*
2. Mycorrhizal Definitions *198*
E. Edaphic/Environmental Factors, Plants and Mycorrhizas *202*
1. Mycorrhizal Phenology *202*
2. The Activity of Mycorrhizal Fungus Hyphae in Soils *206*
3. The Rhizosphere and Mycorrhizosphere *208*
4. Regulation of Mycorrhizal Associations *211*
5. Mycorrhizal Dependency *220*
6. Mycorrhizas and Plant Responses to Pollution and Other Stresses *225*
7. The Value of Mycorrhizas to Plants in Natural Ecosystems *227*
F. The Ecology of Mycorrhizal Plants *235*
1. Mycorrhizas and Nutrient Cycling in Natural Ecosystems *235*
2. Mycorrhizas and Plant Nutrient Competition *239*
3. Other Mycorrhizally Mediated Interactions Between Plants *243*
4. Mycorrhizas and Plant Succession *244*
5. The Distribution of Plants with Different Mycorrhizal Strategies *247*
IV. CONCLUSIONS *257*
APPENDIX 1 *262*
Acknowledgements *271*
REFERENCES *271*