Diversity and classification of mycorrhizal associations

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ABSTRACT

Most mycorrhizas are 'balanced' mutualistic associations in which the fungus and plant exchange commodities required for their growth and survival. Myco-heterotrophic plants have 'exploitative' mycorrhizas where transfer processes apparently benefit only plants. Exploitative associations are symbiotic (in the broad sense), but are not mutualistic. A new definition of mycorrhizas that encompasses all types of these associations while excluding other plant-fungus interactions is provided. This definition recognises the importance of nutrient transfer at an interface resulting from synchronised plant-fungus development. The diversity of interactions between mycorrhizal fungi and plants is considered. Mycorrhizal fungi also function as endophytes, necrotrophs and antagonists of host or non-host plants, with roles that vary during the lifespan of their associations. It is recommended that mycorrhizal associations are defined and classified primarily by anatomical criteria regulated by the host plant. A revised classification scheme for types and categories of mycorrhizal associations defined by these criteria is proposed. The main categories of vesicular-arbuscular mycorrhizal associations (VAM) are 'linear' or 'coiling', and of ectomycorrhizal associations (ECM) are 'epidermal' or 'cortical'. Subcategories of coiling VAM and epidermal ECM occur in certain host plants. Fungus-controlled features result in 'morphotypes' within categories of VAM and ECM. Arbutoid and monotropoid associations should be considered subcategories of epidermal ECM and ectendomycorrhizas should be relegated to an ECM morphotype. Both arbuscules and vesicles define mycorrhizas formed by glomeromycotan fungi. A new classification scheme for categories, subcategories and morphotypes of mycorrhizal associations is provided.

Key words: mycorrhiza, ectomycorrhiza, vesicular-arbuscular mycorrhiza, exploitative, balanced, mutualism, symbiosis, terminology.

CONTENTS

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I. INTRODUCTION

Mycorrhizas are multifaceted associations comprising diverse morphological, functional and evolutionary categories (Smith & Read, 1997; Brundrett, 2002). Some types of mycorrhizas are similar and share plant lineages while others have highly distinct anatomical features and separate evolutionary histories (Brundrett, 2002). Vesicular-arbuscular mycorrhizal associations (VAM), which are also called arbuscular mycorrhizas or glomeromycotan mycorrhizas, are the most widespread and common root-fungus associations (the usage of arbuscular or vesicular-arbuscular mycorrhizas is discussed in the Appendix). Ectomycorrhizal associations (ECM) are also important in many habitats, but restricted to certain plant families. Other types of mycorrhizas are restricted to the Orchidaceae or the Ericales, while some angiosperm families typically have nonmycorrhizal (NM) roots (Brundrett, 1991; 2002). This review considers symbiosis and mutualism from a mycorrhizologist's perspective, the nature of interactions in other types of symbiotic associations have been summarised elsewhere (e.g. Starr, 1975; Cook, 1977; Boucher, James & Keeler, 1982; Paracer & Ahmadjian, 2000).

The purpose of this review is to consider the diversity of mycorrhizal associations and contrast them with other root-fungus associations. Unique characteristics of mycorrhizas are identified and used to formulate a comprehensive definition of these associations that excludes other plant-fungus interactions. The diversity of interactions between mycorrhizal fungi and plants and factors regulating their associations are examined. A modified hierarchical classification scheme for mycorrhizal associations consistent with the regulation of association morphology by plants and fungi is proposed. This review was written as a sequel to earlier reviews on mycorrhizal ecology (Brundrett, 1991) and the evolution of mycorrhizal associations (Brundrett, 2002), which should be consulted for further information.

# II. DEFINING MYCORRHIZAL ASSOCIATIONS

The terms symbiotic and mutualistic have been used interchangeably to describe mycorrhizal associations. Symbiosis was originally used to define both lichens and parasites (DeBary, 1887 – cited by Paracer & Ahmadjian, 2000), but many scientists now use this term to describe beneficial associations only (Lewis, 1985; Paracer & Ahmadjian,

2000). Fungal symbioses have been defined as 'all associations where fungi come into contact with living host from which they obtain, in a variety of ways, either metabolites or nutrients' (Cook, 1977). However, this definition excludes associations of myco-heterotrophic plants that are entirely supported by a fungus (Section III.3). Only the broadest definition of symbiosis (e.g. 'living together of two or more organisms') applies universally to mycorrhizal associations (Lewis, 1985; Smith & Read, 1997).

The term mutualism implies mutual benefits in associations involving two or more different living organisms (Boucher, 1985; Lewis, 1985). Mutualistic associations occupy the mutual benefit $(+ +)$ quadrant in diagrams contrasting the relative benefits $(+)$ or harm $(-)$ to two interacting organisms (Fig. 1). Fig. 1 is similar to other phase plane diagrams describing biological interactions arising from the Lotka-Volterra equation (see Lewis, 1985), or cost-benefit models for associations (Tuomi, Kytoviita & Hardling, 2001). Mutualism is an isocline in these diagrams indicating that both species are more successful together than they are alone (Boucher, 1985).

Mycorrhizas cannot be universally categorised as mutualistic associations because benefits to fungi are implausible in associations of myco-heterotrophic plants, as explained in Section III.3. Mutualistic associations include a wide range of direct and indirect, or symbiotic and non-symbiotic associations, many of which function by means other than nutrient transfer (Boucher *et al.*, 1982; Paracer & Ahmadjian, 2000). As explained above, all mycorrhizal associations are symbiotic, but some are not mutualistic. In this review, the terms 'balanced' and 'exploitative' are proposed for mutualistic and non-mutualistic mycorrhizal associations respectively (Section III). The use of specific terms for mycorrhizal associations avoids problems resulting from inconsistent use of the terms symbiosis and mutualism.

The term mycorrhiza (meaning fungus-root) was originated by Frank (1885), who was fairly certain that these symbiotic plant-fungus associations were required for the nutrition of both partners. More recently, mycorrhizas have been defined as associations between fungal hyphae and organs of higher plants concerned with absorption of substances from the soil (Harley & Smith, 1983). Broader definitions have also been published (e.g. Hawksworth *et al.*, 1995), but are of little value as they do not exclude pathogenic associations. Mycorrhizas are now considered to differ primarily from other plant-fungus associations because they are intimate associations with a specialised interface where
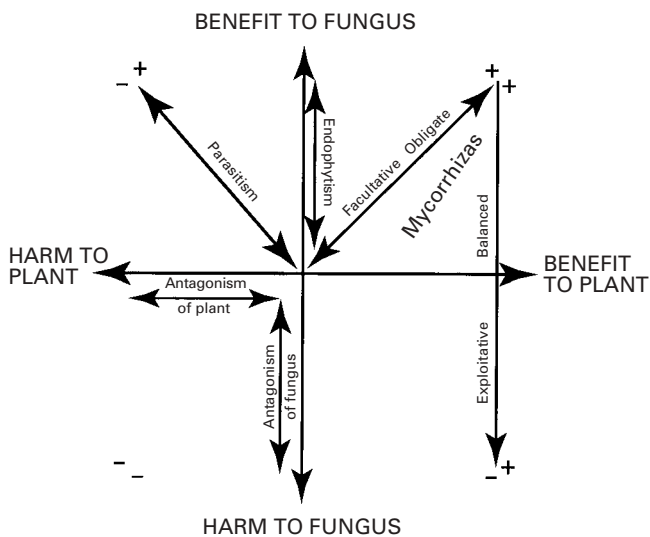
Fig. 1. Phase plane diagram comparing types of mycorrhizas and other categories of plant-fungus interactions. These categories are explained in Section III.

exchange of materials occurs between living cells (Nehls *et al.*, 2001; Pfeffer, Bago & Shachar-Hill, 2001). Most mycorrhizas occur in roots, which evolved to house fungi (Brundrett, 2002), but they also occur in the subterranean stems of certain plants and the thallus of bryophytes (Smith & Read, 1997; Read *et al.*, 2000). Pathogenic associations also involve intimate plant-fungus contact, but differ from mycorrhizas because they lack fungus to plant nutrient transfer, and are highly detrimental to their host plants – resulting in disease symptoms (Cook, 1977). Pathogenic fungi are typically not specialised for efficient mineral nutrient acquisition from soil (see Table 2 in Brundrett, 2002). A new, broader definition of mycorrhizas that embraces the full diversity of mycorrhizas while excluding all other plant-fungus associations is presented here. A mycorrhizas is: *a symbiotic association essential for one or both partners, between a fungus (specialised for life in soils and plants) and a root (or other substrate-contacting organ) of a living plant, that is primarily responsible for nutrient transfer. Mycorrhizas occur in a specialised plant organ where intimate contact results from synchronised plant-fungus development.*

Any plant containing a fungus can be designated as a 'host', regardless of whether the association is beneficial or not. As in the case of a person hosting a party, the plant cannot be assumed to be in control of the situation. Many terms (symbiont, associate, mycobiont, inhabitant, etc.) can be used to designate mycorrhizal fungi within plants, but it is usually sufficient to call them fungi. Mycorrhizal fungi should not be called endophytes to avoid confusion with other plant inhabiting fungi (Section III.1). The neutral term 'colonisation' is preferential to infection (implying disease) when describing mycorrhizal fungus activity (Brundrett *et al.*, 1996; Smith & Read, 1997). Similarly, 'inoculum potential' or 'inoculum levels' should be used to designate fungal activity in soil, rather than infectivity, as is the case with other soil fungi (Baker, 1978). Fungal entities in roots

should be identified as 'colonies' rather than infection units (Brundrett *et al.*, 1996).

III. DIVERSITY OF MYCORRHIZAS

Any attempt to define mycorrhizal associations must be based on an understanding of the full spectrum of variation in these associations. Mycorrhizal associations occur across several continua representing varying degrees of interdependence and morphological specialisation (Fig. 1). The isocline in the upper right quadrant of Fig. 1 (+ +) is a continuum of increasing plant dependence, starting with facultatively mycorrhizal and nonmycorrhizal plants and culminating in plants with obligate mycorrhizal associations (defined in Section III.2.a). Obligately mycorrhizal plants serve as a fulcrum between the isocline and a second continuum of decreasing fungal benefits culminating in mycorrhizas of myco-heterotrophic plants (without photosynthesis). The second continuum is parallel to the vertical axis (representing harm or benefit to fungi), because fungal benefits decrease while plant benefits remain high. Both of these continua correspond to major differences in the biology of fungi and the functioning of their associations with plants, as discussed in Sections III.2 and III.3. Parasitic and antagonistic associations occupy the other two quadrants in the plant-fungus benefits continuum (Fig. 1). The relationship between plant harm and fungal benefits would vary considerably between different categories of pathogenic or endophytic fungi (only generalised relationships are shown in Fig. 1). Antagonisms of plants by fungi or fungi by plants are discussed in Section III.4.

(1) Endophytic activity

The most appropriate definition of endophytism is *symptomless associations of other living organisms that grow within living plant tissues* (Wilson, 1995; Stone, Bacon & White, 2000). Many fungi can rapidly colonise the cortex of living roots without causing disease, including pathogenic or necrotrophic fungi with latent phases as well as beneficial fungi that offer protection against pathogens, but it is not easy to categorise precisely roles of these fungi (Sivasithamparam, 1998). Endophytic associations differ from mycorrhizas primarily by the absence of a localised interface of specialised hyphae (present in most mycorrhizas), the absence of synchronised plant-fungus development, and the lack of plant benefits from nutrient transfer (Section II). However, plants may benefit indirectly from endophytes by increased resistance to herbivores, pathogens or stress, or by other unknown mechanisms (Saikkonen *et al.*, 1998).

Fungi are the most commonly studied endophytes, but these can also include bacteria, algae and other plants (Stone *et al.*, 2000). Endophytic associations have various strategies for transmission and impacts on plants that range from harmful to beneficial (Saikkonen *et al.*, 1998; Stone *et al.*, 2000). Predominantly phytopathogenic fungus genera such as *Fusarium* and *Colletotrichum* also include endophytes (Kuldau & Yates, 2000; Redman, Dunigan & Rodriguez,

Table 1. Summary of evidence supporting the hypothesis that the majority of mycorrhizas are balanced associations. Evidence for both ectomycorrhizal associations (ECM) and vesicular-arbuscular mycorrhizal associations (VAM) is provided, unless otherwise stated

Evidence	Selected references
Host plant and mycorrhizal fungus productivity is correlated	
Correlation between plant benefit (yield or reproduction) and the degree of mycorrhizal fungus colonisation*	Clapperton & Read (1992); Shumway & Koide, 1995; Gange (1999)
Correlation between ECM fungus productivity and host tree dominance	Fogel & Hunt (1979); Vogt *et al.* (1982); Högberg & Högberg (2002)
Fungus sporulation requires mycorrhizal formation	Pearson & Schweiger (1993); Douds (1994); Lamhamedi *et al.* (1994)
Plant productivity is low when soil factors inhibit mycorrhizal fungi (fungicides, disturbance, pH, salinity, waterlogging, temperature, etc.)	Evans & Miller (1988); Sidhu & Chakravarty (1990); Juniper & Abbott (1993); McInnes & Chilvers, 1994; Setälä (1995); Thomson *et al.* (1996); Soulas *et al.* (1997)
Fungus productivity is decreased by factors that harm plants (herbicides, pollution, disturbance, etc.)	Termorshuizen & Schaffers (1987); Brundrett & Abbott (2002)
Both partners occur together	
VAM fungi are incapable of saprotrophic survival and can only be grown with a host plant	Douds *et al.* (2000); Smith *et al.* (2001)
ECM fungi normally only occur with compatible host plants in nature	Brundrett (1991); Molina *et al.* (1992); Brundrett *et al.* (1996)
Mycorrhizal fungus biomass and diversity increases in parallel with that of plants after severe disturbance (volcanism, glaciation, or mining)	Allen *et al.* (1987); Gemma & Koske (1990); Gange *et al.* (1993); Brundrett & Abbott (2002); Helm *et al.* (1996); Corkidi & Rincón (1997)
ECM fungus introduction often is required to grow host trees in exotic locations	Brundrett *et al.* (1996); Dunstan *et al.* (1998)
Co-dispersal of plants and VAM fungi in early succession	Koske & Gemma (1990)
Simultaneous reciprocal exchange of commodities between plant and fungus	
Synchronised bi-directional fluxes of nutrients have been measured	Pearson & Jakobsen (1993); Nehls *et al.* (2001); Pfeffer *et al.* (2001)
Substantial energy (metabolite) fluxes from plant to fungus during active associations	Rygiewicz & Andersen (1994); Smith *et al.* (1994); Markkola *et al.* (1995); Högberg *et al.* (1999); Douds *et al.* (2000); Miller & Kling (2000)
Substantial fungus-mediated mineral nutrient fluxes from soil to plant during active associations	Smith *et al.* (1994); Marschner (1995); Kahiluoto & Vestberg (1998); Näsholm *et al.* (1998); Miller & Kling (2000)
Nutrient fluxes or plant growth responses are proportional to the area of the symbiotic interface	Burgess *et al.* (1994); Dickson *et al.* (1999)
Soil hyphal development in response to plant growth or nutrient requirements	Miller & Kling (2000); Wallander *et al.* (2001)
Nutrient accumulation in plants can be explained by mycorrhizal phenology	Newton (1991); Mullen & Schmidt (1993); Lapointe & Molard (1997)
Physiological interdependence of plant and fungus	
Mycorrhizal dependency has been established for many plants at realistic soil nutrient levels	See Table 6 in Brundrett & Abbott (2002)
Roots of most plants are more efficient at mycorrhizal formation than direct nutrient uptake	Baylis (1975); Janos (1980); Brundrett & Kendrick (1988); Manjunath & Habte (1991); Wilson & Hartnett (1998); Siqueira & Saggin-Júnior (2001)
Most mycorrhizal fungi are obligate symbionts	Brundrett *et al.* (1996); Smith & Read (1997)
Synchronised development	
Root growth is required for mycorrhizal formation	Hepper (1985); Chilvers & Gust (1982)
Nutrient uptake is synchronised with mycorrhizal formation and soil hyphal activity	Bethlenfalvay *et al.* (1982); Cairney & Alexander (1992); Mullen & Schmidt (1993); Merryweather & Fitter (1995); Lussenhop & Fogel (1999); Wallander *et al.* (2001)

* See text for further explanation.

Table 2. *Contrasting the nature of plants and fungi with balanced or exploitative mycorrhizas*

Factor	Balanced	Exploitative
Plant form	All types	Typically small herbs without lignification
Plant habitat	Dominate most terrestrial habitats, limited capacity to grow in very deep shade	Restricted to particular habitats, often in deep shade
Plant shoots	Efficient photosynthesis	Non-photosynthetic or weakly photosynthetic
Plant roots	Substantial root system	Roots often highly reduced or absent
Plant dependency on fungus	Obligate or facultative	Obligate
Fungus life-mode	Specialised for efficient growth both in soil and plants	Saprophytes or parasites without dual specialisation, or balanced mycorrhizal associate of another host plant
Fungus dependency on plant	Most are obligate symbionts, incapable of independent growth in nature	Do not benefit from mycorrhizal associations (unless with another host)
Exchange processes	Reciprocal transfer of essential resources for both the plant and fungal partner	Unidirectional transfer of essential resources for the plant at the expense of the fungus
Exchange location	Root (or stem)	Stem or root
Interface	Specialised hyphae in specialised plant organs	Unspecialised or specialised hyphae in highly specialised plant organ
Development	Fungus colonisation synchronised with plant organ growth. Requires young plant organ	Fungus may recolonise the same cells. May continue to function in older plant organs

See Table 1, Brundrett (2002) and Leake (1994) for references.

2001). Root endophytes with dark septate hyphae (called dark septate endophytes or DSE) are common in many habitats, and may provide benefits to their hosts (Jumpponen & Trappe, 1998). These widespread root inhabitants are closely related to some ECM and ericoid fungi (Vrålstad, Schumacker & Taylor, 2002), but do not form mycorrhizal associations as defined by morphological criteria (Section IV).

Endophytic growth of mycorrhizal fungi in plants is fairly common, but differs primarily from mycorrhizal associations formed by the same fungi elsewhere by the lack of coordinated development and specialised interface hyphae (see Section IV.1). Fungal benefits from these associations are uncertain as mycorrhizal fungi apparently are incapable of long-term endophytic survival. Glomeromycete fungi are not capable of saprobic existence, probably because their soil hyphae cannot absorb sugars, and ECM fungi generally only occur in the presence of compatible host plants (Table 1).

Glomeromycete fungi are ubiquitous soil organisms that often proliferate within patches of soil organic material (St John, Coleman & Reid, 1983; Joner & Jakobsen, 1995; Azcón-Aguilar, Bago & Barea, 1999). These fungi commonly grow in living plant tissues other than roots (e.g. rhizome scales – Brundrett & Kendrick, 1988; Imhof, 2001). They also occupy dead soil animals and spores of other VAM fungi, presumably to acquire nutrients or avoid predation, or perhaps as mycoparasites (Rabatin & Rhodes, 1982; St John *et al.*, 1983; Koske, 1984; Warner, 1984). Glomeromycete fungi commonly grow in roots of ECM plants (e.g. Harley & Harley, 1987; Cázares & Trappe, 1993; Smith, Johnson & Cázares, 1998). This endophytic activity is distinguished from functional dual ECM/VAM associations by the absence of arbuscules (Section V). Endophytic colonisation of NM plants by VAM fungi is common, but considered to be

of limited functional significance because it typically occurs in old moribund roots and does not result in plant growth responses (Ocampo, 1986; Muthukumar *et al.*, 1997; Giovannetti & Sbrana, 1998). However, some species in predominantly NM families like the Cyperaceae have VAM associations (see Table 4 in Brundrett, 2002; Muthukumar, Udaiyan & Shanmughavel, 2004).

When initiated by spores or other limited sources of inoculum in experiments, ECM fungi weakly colonise root surfaces before they have sufficient energy to form typical mycorrhizas (Clowes, 1951; Chilvers & Gust, 1982; Brundrett *et al.*, 1996). This establishment phase may equate to a transition from saprotrophic to mutualistic activity. Some ECM fungi form associations with a mantle but no Hartig net on non-host roots (e.g. Harrington & Mitchell, 2002). The opportunistic growth of fungal hyphae on the surface of roots is common in nature and could be considered to be a form of endophytic association in which fungi feed on root exudates without penetrating cells. Morphological criteria defining ECM associations are discussed in Section IV.2 *a*.

Formation of a second type of mycorrhizal association by fungi seems to be rare, in contrast to the widespread occurrence of their endophytic activity. Exceptions include members of the *Hymenoscyphus ericae* aggregate that form both ericoid and ECM associations with different hosts (Vrålstad, Fossheim & Schumacher, 2000; Vrålstad *et al.*, 2002). However, other studies found that ericoid fungi colonised roots of several ECM hosts, but do not form ECM (Bergero *et al.*, 2000; Piercey, Thormann & Currah, 2002). Sen, Hietala & Zelmer (1999) found that some *Rhizoctonia* isolates that associate with orchids also colonise conifer roots, presumably as endophytes or parasites. Some fungal associates of myco-heterotrophic orchids (e.g. species of *Corallorhiza* and *Rhizanthella*) primarily are ECM associates of dominant

plants in their habitats (Warcup, 1985; Taylor & Bruns, 1999; McKendrick *et al.*, 2002). The significance of endophytic activities of mycorrhizal fungi is not clear; it may provide benefits to these fungi, or simply be a consequence of their high inoculum levels in soils.

(2) Balanced mycorrhizas

The majority of mycorrhizal associations provide substantial benefits to both plants and fungi (Table 1). I propose that these be called 'balanced' mycorrhizas (as opposed to other possibilities such as reciprocal or mutualistic) to imply that exchange processes are in dynamic equilibrium. *Balanced mycorrhizal associations are those in which both organisms receive essential commodities through reciprocal exchange*. Thus, the balance of costs *versus* benefits may shift to favour one partner over the other at times, but must later shift back to a more equitable arrangement or both partners will be disadvantaged in the long term.

The term balanced defines a particular category of mutualism to distinguish mycorrhizas from the many other types of these associations. Balanced associations have remained the dominant type of mycorrhizas throughout the evolutionary history of land plants (Brundrett, 2002). Perhaps mycorrhizal plants and fungi have some capacity to associate selectively with the partners that provide the most benefits. However, the coupling of costs and benefits by simultaneous exchange across a common interface (Pfeffer *et al.*, 2001; Smith, Dickson & Smith, 2001) is the key attribute likely to result in the stability of associations on evolutionary timescales (Brundrett, 2002). Reciprocal exchange was believed to be the key to mycorrhizal functioning long before the physiological processes involved were known (e.g. Rayner, 1928; Hacskaylo, 1973). After a comprehensive review of early mycorrhizal literature, Rayner (1928) summarised the available evidence by stating that most types of mycorrhizas functioned by 'regular and demonstrable periodic exchange of nutritive material' and these associations were 'relatively stable in equilibrium'. These quotes demonstrate that the key ideas behind the definition of balanced associations provided above are supported by early mycorrhizal research as well as by the modern research summarised in Table 1.

Pathogenic associations are not balanced, because plant-fungus development may not be highly coordinated and nutrient transfer only benefits the fungus (Section II). Mycorrhizal fungi also typically have more consistent growth patterns in plants than do parasitic or endophytic fungi, due to regulation by root features resulting from plant-fungus coevolution (Anderson, 1992; Brundrett, 2002). Most other types of mutualism have less metabolic and morphological coordination than balanced mycorrhizas (Boucher *et al.*, 1982; Paracer & Ahmadjian, 2000).

Ideally, evidence is required that substantial benefits accrue to both the mycorrhizal plant and fungus due to reciprocal transfer in order to designate associations as balanced. However, in practice, it is often difficult to measure the benefits mycorrhizal fungi provide to plants, especially in the field, and most available information comes from experimental synthesis of mycorrhizas using artificial

conditions (McGonigle, 1988; Brundrett *et al.*, 1996; Johnson, Graham & Smith, 1997). Nevertheless, there now is ample evidence, as outlined in Table 1, that mycorrhizal plants typically have correlated productivity and co-occurrence of partners, reciprocal exchange, and synchronised development. Evidence for plant-fungus interdependence includes increased fitness or fecundity of both partners when they occur together, or their failure to exist alone. Physiological interdependence has been established by links between carbohydrate utilisation and mycorrhizal development, fungus biomass and host plant productivity to the degree of mycorrhizal formation (Table 1). Synchronised development has been confirmed by detailed morphological studies, which also demonstrated the short lifespan of the active interface (Hartig nets, arbuscules, or coils). The link between mycorrhizal development and plant benefit is supported by experimental studies where valid comparisons were made (Table 1), but this relationship is often obscured by other factors in field trials (McGonigle, 1988).

The majority of mycorrhizal fungi are known to be obligate symbionts, so the benefits they receive from balanced associations with plants are not in doubt (Table 1). However, there are exceptions to this generalisation, such as plants that require a companion plant linked by a common hyphal network, which probably do not support their associated fungi (Section III.3). Plants also provide important non-nutritional benefits to mycorrhizal fungi, especially by providing shelter within roots (Brundrett, 2002). The fact that most host plants benefit substantially from mycorrhizal associations is a well-established scientific paradigm (Smith & Read, 1997). Substantial non-nutritional benefits to the disease resistance, water relations, or photosynthetic capacity of mycorrhizal plants can also occur (e.g. Ruiz-Lozano & Azcón, 1995; Cordier *et al.*, 1998; Nehls *et al.*, 2001). However, there are also plants which are not mycorrhizal, or which have facultative associations where benefits are conditional on soil conditions (see below).

(a) Facultatively mycorrhizal and nonmycorrhizal plants

Symbiotic associations include organism which may be: 'obligate' symbionts that are necessary for the partner being considered which does not normally occur alone, and 'facultative' symbionts that are not always required by the partner being considered which can occur alone (Starr, 1975; Cook, 1977). All VAM, and most ECM fungi are considered obligate symbionts incapable of independent life without plants, but ericoid fungi may not be obligate plant associates, and orchid fungi probably are fully independent of their hosts (Brundrett, 2002). Plants can be described as 'obligately mycorrhizal', 'facultatively mycorrhizal', or 'nonmycorrhizal' (Janos, 1980; Brundrett, 1991, 2002; Habte & Manjunath, 1991; Marschner, 1995). Detailed explanations of these categories are provided by the cited references, so only a brief summary is provided here.

Nonmycorrhizal plants have roots that are highly resistant to colonisation by mycorrhizal fungi and do not form functional associations (Brundrett, 2002). Facultative mycorrhizas are balanced associations, where plant benefits are conditional on soil fertility. Experiments have shown

that facultatively mycorrhizal plants benefit from VAM only when soil phosphorus levels are relatively low and these plants typically have relatively long, narrow and highly branched roots with long root hairs in comparison with obligately mycorrhizal species (Table 1). Facultatively mycorrhizal plants apparently have the capacity to limit the extent of their associations to reduce costs in cases where fungi provide little benefit (Koide & Schreiner, 1992). Soil moisture and aeration levels can also regulate mycorrhizal colonisation for wetland plants (Cantelmo & Ehrenfeld, 1999; Beck-Nielsen & Madsen, 2001).

There is a continuum from obligately mycorrhizal plant species that benefit from associations across a wide range of soil fertility levels to those which only benefit in infertile soils. In some studies, the benefit provided by mycorrhizas decreased as the degree of mycorrhizal colonisation of roots increased (Clapperton & Read, 1992; Gange, 1999). This seems to be a rare phenomenon that would probably be confined to facultatively mycorrhizal plants growing in relatively fertile soils, because the majority of species used in experiments respond positively to increased inoculum levels of mycorrhizal fungi (Table 1). A study of Brazilian native plants found that most were highly dependent on VAM, and many were incapable of absorbing phosphorus without mycorrhizas even in highly fertile soils (Siqueira & Saggin-Júnior, 2001). A theoretical model has shown that associations with reciprocal transfer of carbon and nutrients are likely to evolve regardless of the costs to the plant if mineral nutrients strongly limit plant growth (Tuomi *et al.*, 2001), as is often the case in natural ecosystems (Brundrett, 1991).

Mycorrhizas only increase plant fecundity if the benefits provided by improved mineral nutrition or other factors outweigh the production costs of mycorrhizal associations (see Johnson *et al.*, 1997). Mycorrhizal associations have been considered to be parasitic in cases where the costs outweigh the benefits, as occurs in several cropping systems (Hendrix, Jones & Nesmith, 1992; Johnson *et al.*, 1997). However, crops that benefit from mycorrhizas may eventually replace those that do not, because of crop rotation or the implementation of sustainable agricultural systems. These subsequent crops would benefit from mycorrhizal inoculum maintained by earlier crops that did not benefit from these fungi. In some cases, mycorrhizas result in increased fecundity or disease resistance rather than increased yield (Newsham, Fitter & Watkinson, 1995; Shumway & Koide, 1995; Cordier *et al.*, 1998). We must remember that mycorrhizal benefits are calculated in highly artificial situations by measuring the growth of non-mycorrhizal control plants that normally do not occur in this state in nature (Brundrett, 1991). I suggest that facultative mycorrhizas should be considered to be balanced associations, as reciprocal plant-fungus exchange processes benefit both species except when external conditions negate fungal benefits. It is not appropriate to designate ineffective mycorrhizal fungi as parasitic if they are capable of providing substantial benefits to plants in more natural situations.

It seems to be far more common for plants to exploit mycorrhizal fungi than for these fungi to exploit plants (Brundrett, 2002). Reports of growth depression caused by VAM fungi are surprisingly rare considering how ubiquitous these associations are, and seem to be even rarer for other types of mycorrhizas. For example, significant growth depression did not occur in any of the VAM inoculation trials using natural soil fertility levels summarised in Table 6 of Brundrett & Abbott (2002): These data were from 23 studies of plants from 11 natural ecosystems in which 63 % of 235 plant species were highly responsive to mycorrhizas and the rest did not respond significantly. Most plants with ECM are considered to be highly dependent on these associations, but some hosts (e.g. *Eucalyptus* spp. in plantations) may not benefit in highly fertile soils (Brundrett *et al.*, 1996). Trees grown in exotic locations may associate with less-compatible fungi than when growing in their indigenous habitats (Lu *et al.*, 1999). Both VAM and ECM fungi vary in carbon sink strength and apparently also in symbiotic effectiveness (e.g. Abbott, Robson & Gazey, 1992; Burgess, Dell & Malajczuk, 1994; Cullings, Azaro & Bruns, 1996). However, fungal isolates that perform poorly in some experiments may provide substantial benefits to plants in other trials where growing conditions are more suitable for that particular fungus (Dickson, Smith & Smith, 1999).

The practical designation of plants as facultatively mycorrhizal is often not based on physiological data. Field surveys have shown that plant species generally have (i) consistently high levels of mycorrhizas, (ii) inconsistent, low levels of mycorrhizas or (iii) are not mycorrhizal; those in the second category have traditionally been designated as facultatively mycorrhizal (Janos, 1980; Brundrett, 1991, 2002). This designation was originally based on experiments where both the mycorrhizal colonisation and mycorrhizal dependency of plant species were measured (Baylis, 1975; Janos, 1980). Facultatively mycorrhizal plants defined in this way are common in many natural ecosystems, but typically are much less important than obligately mycorrhizal species in most undisturbed habitats (Brundrett, 1991). Facultatively mycorrhizal species have also been recognised by inconsistent reports about their mycorrhizal status (e.g. Trappe, 1987) but some conflicting results probably result from problems with the methodology used for sampling or assessment (see Brundrett, 2002).

(3) Exploitative mycorrhizal associations

The evolutionary trend for increasing plant control over mycorrhizal fungi culminates in associations of myco-heterotrophic plants without chlorophyll that are fully dependent on highly specific relationships with fungi (Leake, 1994; Bidartondo & Bruns, 2001; Brundrett, 2002; McKendrick *et al.*, 2002). Nutrient exchange in these associations is unidirectional because the plant functions as a very large sink for fungal nutrients, but cannot, or does not, provide a significant contribution to the growth or nutrition of the associated fungus (Table 2). Mycorrhizal associations where fungi do not seem to receive any benefits from plants have been called epiparasitic, myco-heterotrophic, or cheating associations (Furman & Trappe, 1971; Leake, 1994; Taylor & Bruns, 1999). *Associations where only the plant receives substantial benefits from nutrient exchange are defined here as 'exploitative mycorrhizas'*. This term more accurately

reflects the nature of the associations from both plant and fungus perspectives ('exploitative' plant, 'exploited' fungus). These mycorrhizas are the reverse of relationships between higher plants and parasitic fungi (Fig. 1).

Exploitative associations generally occur in myco-heterotrophic plants with little or no photosynthetic ability (Leake, 1994; Cummings & Welschmeyer, 1998), but some associations of green plants can also be partially or fully exploitative (see below). Plants with exploitative mycorrhizas are typified by shoot and root reduction, as well as the lack of visible photosynthetic pigments (Table 2). Parasitic plants often share these features, but are usually not mycorrhizal and have physical attachment to other plants (haustoria). Separate lineages of plants with exploitative mycorrhizas have evolved from plants with VAM, ECM or orchid mycorrhizas (Brundrett, 2002).

Myco-heterotrophic plants are unable to synthesise metabolites to sustain their fungi, and so are indirectly subsidised by other members of their plant community that provide energy and nutrients to their fungi (Björkman, 1960; Newman, 1988). They probably also acquire most of their water and nutrients through fungal connections (since they have few if any roots). Bidartondo *et al.* (2000) observed higher than normal concentrations of mycorrhizal roots of the primary host (*Abies magnifica*) in soils near the myco-heterotrophic plant *Sarcodes sanguinea*. They interpreted this as evidence that *S. sanguinea* benefited the mycorrhizal fungus by providing additional habitat for it. However, a cost-benefit analysis would suggest that the overall impact of a greater concentration of mycorrhizal activity is likely to be detrimental to the fungus (*Rhizopogon ellenae*) in the long-term, as it could only occur at the expense of distal parts of the mycelial network required for nutrient uptake. Further research is required to establish (i) if the presence of exploitative plants like *S. sanguinea* results in an overall reduction or increase in the fecundity of associated fungi, and (ii) if the fecundity of exploitative plants is determined by the original size and density of patches of the fungus.

Plants with exploitative mycorrhizas have extremely high host-fungus specificity with ECM, orchid or VAM fungi (e.g. Bidartondo & Bruns, 2001; Bidartondo *et al.*, 2002), and thus would be more vulnerable to fluctuations in fungal populations than plants with less specific fungal associates. If myco-heterotrophic plants have an adverse effect on an exploited fungus, this would probably result in their eventual decline in a particular location and explain why some of these plants are very rare and can disappear from particular locations (Leake, 1994; Rasmussen, 1995). It is normal for both ECM and VAM fungi to have very patchy distribution patterns in soils (e.g. de la Bastide, Kropp & Piché, 1994; Brundrett & Abbott, 1995; Dahlberg & Stenlid, 1995). Perkins & McGee (1995) found orchid fungi were concentrated close to a host plant, but other seed baiting studies have also found orchid fungi a considerable distance from their hosts (Masuhara & Katsuya, 1994; Batty *et al.*, 2001). It is very difficult to separate cause from effect in studies contrasting the distribution of mycorrhizal plants and their fungi.

Mycorrhizas are generally considered to function by two-way exchange processes across a symbiotic interface between plant and fungus cells (Section III.2). However, the symbiotic interface is unlikely to work in the same way in exploitative associations as it does in balanced associations. There is no selective advantage for the fungus to evolve the means to transport nutrients into the plant because it gains nothing in return, and some exploited fungi have not co-evolved as mycorrhizal associates with plants (Brundrett, 2002). Ultrastructural studies of exploitative associations have shown that lipids (a major storage product of fungi) can be released into host cells after the collapse of hyphae (Peterson, Howarth & Whittier, 1981; Schmid & Oberwinkler, 1994). This process has been described as lysis or digestion, but the latter is not appropriate since it has not been established whether the plant or fungus controls it. Mycorrhizal scientists no longer consider hyphal lysis an important means of nutrient transfer in balanced mycorrhizal associations (Smith & Smith, 1990), but lysis seems to be more important in exploitative associations. Exploitative associations have unique, highly complex interfaces that function by means that are not fully understood (Burgeff, 1959; Robertson & Robertson, 1982; Leake, 1994; Schmid & Oberwinkler, 1994; Rasmussen, 2002). Further work is required to determine how these mycorrhizas function. The collapse of old hyphae allows reinvasion of the same host cells, making more efficient use of limited space within the reduced organs of exploitative plants (Brundrett, 2002).

Photosynthetic orchids seem to have a greater capacity to regulate the growth of invading fungi than other hosts, as the fungi involved have not evolved as mutualistic plant inhabitants (Brundrett, 2002; Rasmussen, 2002). Orchid mycorrhizal associations are thought to require a delicate balance between the aggression of the fungus and the plant's defences, and only certain host-fungus combinations are successful (Burgeff, 1959; Hadley, 1982). Fungistatic metabolites produced by the plant are believed to be important for controlling compatible fungi (Burgeff, 1959; Xu *et al.*, 1998). The evolution of many lineages of orchids with fully exploitative associations provides further evidence of a highly evolved capacity to control fungi (Molvray, Kores & Chase, 2000; Brundrett, 2002).

Plants which are not fully myco-heterotrophic may also exploit mycorrhizal fungi, if they are part of the continuum from balanced to exploitative associations (Fig. 1). Most plants with the arbutoid type of ECM have chlorophyll, but also associate with the same fungi as adjacent trees and may receive some advantages from this (Molina & Trappe, 1982*a*). Mycelial connections by ECM fungi between different hosts can result in transfer of carbon between plants and a net carbon gain by one host (Simard *et al.*, 1997). Carbon transferred between plants interconnected by VAM generally stays in roots and thus would not directly benefit the second host, but may provide indirect benefits by reducing association costs (Robinson & Fitter, 1999). It has been suggested that seedlings growing under mature trees of the same species are partially supported by shared associations (Newbery, Alexander & Rother, 2000; Onguene & Kuyper, 2002). However, support of seedlings by their parents is unlikely to be substantial, as only a very small proportion of tree seedlings survive (Newman, 1988; Newbery *et al.*, 2000). Dickie, Koide & Steiner (2002)

compared seedling establishment near trees with the same (ECM) or different mycorrhizas (VAM). These seedlings established better near ECM trees, and this was considered primarily to result from increased mycorrhizal colonisation. Sharing a common type of mycorrhiza may also increase the functional similarity of the root systems of different species competing for soil nutrients (Brundrett, 1991). The role of plant connections by shared fungal networks requires further study, as in most cases the transfer of substances appears to be insufficient to influence the growth and survival of plants, yet myco-heterotrophic plants are able to live entirely by this means. The ecological importance of shared hyphal networks is the focus of other reviews (Newman, 1988; Brundrett, 1991; Perry, 1998; Wilkinson, 1998).

(4) Antagonism (allelopathy)

Opportunistic associations of mycorrhizal fungi on non-host plants, or of plants on non-associated fungi, can be interpreted as antagonism if they cause harm to one organism (Fig. 1). Both ECM and VAM fungi have been occasionally reported to cause damage to roots of non-hosts by attempted colonisation (Allen, Allen & Friese, 1989; Plattner & Hall, 1995). For example, colonisation of *Cyperus rotundus* roots by VAM fungi reduced plant growth, especially in the presence of a mycorrhizal companion plant (Muthukumar *et al.*, 1997). Damage to non-host roots by ECM fungi has most often been reported in sterile culture experiments using hosts and fungi that do not normally associate together (Molina & Trappe, 1982*b*). During succession in many habitats, NM plants are outcompeted by mycorrhizal species (Brundrett, 1991; Francis & Read, 1995; Brundrett & Abbott, 2002). This probably occurs because the mycorrhizal species are more efficient at acquiring limiting soil nutrients such as phosphorus (Newman, 1988; Brundrett, 1991), but direct antagonism of non-host plants by mycorrhizal fungi may also occur in some cases as inoculum levels increase during succession (Allen *et al.*, 1989).

Plant communities dominated by plants with one type of mycorrhiza may tend to be self-perpetuating by producing a soil environment hostile to other fungi. This antagonism of plants with another mycorrhiza type could result from restricted mineral nutrient availability, or inhibition of mycorrhizal fungus activity by allelopathy (see Brundrett & Abbott, 2002). It has been reported that trees with ECM often fail to become established in sites dominated by plants with ericoid mycorrhizas such as *Calluna*, *Gaultheria*, *Kalmia* or *Rhododendron* shrublands (Robinson, 1972; Messier, 1993; Yamasaki *et al.*, 1998; Walker *et al.*, 1999). However, Nilsen *et al.* (1999) found that allelopathic effects of ericoid plants could be measured in artificial conditions, but had little impact in the field. Changes to soil properties in ecosystems dominated by ECM trees with decomposition-resistant leaves results in slower nutrient cycling and a predominance of organic nutrient sources which are considered to be less accessible to VAM fungi than to ECM fungi (Allen *et al.*, 1995; Michelsen *et al.*, 1998). Substances in ECM tree leaf litter can have allelopathic influences on AM fungi

(Tobiessen & Werner, 1980; Kovacic, St John & Dyer, 1984). Hyphal mats formed by ECM fungi considerably alter the soil physical and chemical environment (Griffiths, Baham & Caldwell, 1994), perhaps creating inhospitable conditions for establishment of other plants. Interactions between plants with different types of mycorrhizas are discussed in detail elsewhere (Francis & Read, 1995; Brundrett & Abbott, 2002).

Some of the fungi that associate with green orchids may also be parasites of other plants (e.g. Sen *et al.*, 1999). Ruinen (1953) summarised evidence that epiphytes, especially orchids and ferns, were antagonistic to their host trees, a condition he called epiphytosis. This evidence includes (i) correlations between tree health and epiphyte abundance, (ii) histological evidence showing that similar fungi invaded tree branches and leaves as occurred in the roots of orchids, (iii) orchid growth on specific trees, and (iv) sections across orchid roots and tree branches showing continuity between fungal hyphae in both. Johansson (1977) observed that some epiphytic orchids were most abundant in unhealthy trees, but no causal relationship was established. The epiphytosis theory is controversial and most epiphytic orchids are considered to have facultative mycorrhizas (Benzing & Friedman, 1981). However, the mycorrhizal dependency of epiphytic orchids has not been examined. Modern methods are required to confirm or refute Ruinen's (1953) observations of tree-orchid interconnections by a common fungus, and tree-fungus nutrient transfer (e.g. stable isotopes to detect nutrient transfer or systemic fungicide to inhibit orchid fungi in trees). Shared fungi may provide the most plausible explanation for host tree specificity, which occurs for some epiphytic orchids, in much the same way that the distribution of specific fungi in soils can determine where terrestrial orchids grow (Batty *et al.*, 2001).

(5) Variable associations

The same combination of host plant and mycorrhizal fungus can display different types of interactions during the establishment, active phase, and senescence of mycorrhizal associations (Table 3). The range of host-fungus interactions is also affected by variations in the mycorrhizal dependency of the host plant and the impact of soil conditions on mycorrhizal benefits (Section III.2*a*).

Induction of defensive reactions in roots by hyphae during the formation of normal mycorrhizal associations has been reported for both VAM and ECM fungi (Albrecht *et al.*, 1994; Lambis & Mehdy, 1995; Vierheilig *et al.*, 2000). Albrecht *et al.* (1994) found that chitinase and peroxidase enzymes, likely to be key parts of the plant's defences, were induced by some ECM fungal associates of *Eucalyptus* species. They found that the greatest induction of these enzymes occurred with the most compatible strains, so they were not related to poor root colonisation by incompatible strains. VAM fungi also elicit phytoalexins, but this does not constitute a full defence response (Koide & Schreiner, 1992). Partial defence induction may result because mycorrhizal fungi cannot fully evade plant defences, or because initial

Table 3. Different phases in the life histories of mycorrhizal fungi and corresponding aspects of plant-fungus associations

Stage	Vesicular-arbuscular mycorrhizal fungi	Ectomycorrhizal fungi	Other mycorrhizal fungi
Free-living	• Long-term survival requires a host plant • Soil hyphae have a limited capacity for independent survival in soils	• Most have a limited capacity to live and spread without hosts • Some have saprotrophic capabilities	• Extended independent phases as saprotrophs, parasites or mycorrhizas with other plants
Endophytic	• Long-term persistence in older roots of host plants • Hyphae in non-host roots, rhizome scales, etc.	• Partial associations with non-host plants	• Colonisation of bryophytes by ericoid mycorrhizal fungi? • Orchid fungi in other plants
Balanced mycorrhizas	• Normal associations with arbuscules • Root growth and structure of many hosts optimised for mycorrhiza formation	• Compatible associations with a Hartig net • Slow short root growth to allow fungus establishment • Hyphae confined to certain cells	• Mycorrhizas of green orchids? • Ericoid mycorrhizas are considered to be balanced
Exploitative mycorrhizas	• Myco-heterotrophic VAM plants	• Myco-heterotrophic associations of plants such as *Monotropa*	• Myco-heterotrophic orchids
Antagonistic	• Growth reduction can occur in highly fertile soils • Defensive enzymes and chemicals may be induced in host roots • Damage to roots of non-host plants may occur	• Defensive reactions and chemical accumulation (e.g. tannins) in hosts • Partial colonisation of roots of incompatible hosts • Changes to soil properties in hyphal mats detrimental to other plants	• Orchid fungi include pathogens of other plants or fungi
Necrotrophic	• Digestion of arbuscules by plant? • Transfer of nutrients from senescent roots by fungus	• Invasion of senescent root cells by hyphae may occur • Transfer of nutrients to other hosts can occur	• Digestion of hyphal coils by plant? • Incompatible fungi that kill orchids

See text for examples and references.

Table 4. Summary of types and categories of mycorrhizal associations regulated by host plants

1	Vesicular-arbuscular mycorrhiza	Mycorrhizal association formed by glomeromycete fungi in land plants usually with arbuscules and often with vesicles
1.1	Linear	Associations that spread predominantly by longitudinal intercellular hyphae in roots (also known as *Arum* series VAM)
1.2	Coiling	Associations that spread predominantly by intracellular hyphal coils within roots (also known as *Paris* series VAM)
1.2.1	Beaded	Coiling VAM in roots with short segments divided by constrictions
1.2.2	Inner cortex	Coiling VAM with arbuscules in one layer of cells of the root inner cortex
1.2.3	Exploitative	Coiling VAM of myco-heterotrophic plants, with or without arbuscules
2	Ectomycorrhiza	Associations of higher fungi with land plants with short lateral roots where a hyphal mantle encloses the root and a Hartig net comprising labyrinthine hyphae penetrates between root cells
2.1	Cortical	Hartig net fungal hyphae colonise multiple cortex cell layers of short roots (most associations are in gymnosperms)
2.2	Epidermal	Hartig net fungal hyphae are confined to the epidermal cell layer of short roots (occurs in angiosperms)
2.2.1	Transfer cell	Epidermal Hartig net with transfer cells (plant cells with cell wall ingrowths)
2.2.2	Monotropoid	Exploitative epidermal ECM of myco-heterotrophic plants in the Ericales where individual hyphae penetrate epidermal cells
2.2.3	Arbutoid	ECM of autotrophic plants in the Ericaceae where multiple hyphae penetrate epidermal Hartig net cells
3	Orchid	Associations where coils of hyphae (pelotons) penetrate within cells in the plant family Orchidaceae
3.1	root	Associations within a root cortex
3.2	stem	Associations within a stem or rhizome
3.3	Exploitative	Associations of myco-heterotrophic orchids
4	Ericoid	Coils of hyphae within very thin roots of plants in the Ericaceae
5	Subepidermal	Hyphae in cavities under epidermal cells of plants in the monocot genus *Thysanotus*

stages of colonisation are not fully balanced associations. The induction of defences would occur at some cost to the plant, but may increase its resistance to subsequent pathogenic invasion.

Old dead roots are an important source of inoculum for glomeromycete fungi which can survive as endophytes in living roots for up to 10 years after arbuscules have collapsed, presumably functioning as inoculum reservoirs for subsequent generations of roots (Brundrett & Kendrick, 1988). These fungi also have a necrotrophic phase when host roots die, providing the fungus with first access to nutrients that can be transferred to hyphae in other plants (Eason, Newman & Chuba, 1991). ECM fungi can also necrotrophically colonise senescent host roots in some cases (Nylund, Kasimir & Arveby, 1982; Downes, Alexander & Cairney, 1992).

As summarised in Table 3, mycorrhizal fungi have different phases of activity, where the same fungus can be an endophyte, mutualist, saprophyte, or necrotroph at different times or in different situations. As this Table demonstrates, the structural and functional diversity of associations formed by mycorrhizal fungi in natural ecosystems is much greater than is generally acknowledged. An understanding of the changing roles of fungi during the life-cycle of mycorrhizal associations requires careful observation of material of known age, or an understanding of the phenology of plants collected in the wild (Section V).

IV. TYPES AND CATEGORIES OF MYCORRHIZAS

Despite the fact that types of mycorrhizas are classified into morphological categories using criteria designed by humans, these categories also seem to have biological relevance as they are highly consistent within plant and fungal lineages and each has characteristic physiological attributes (Smith & Read, 1997; Brundrett, 2002). Seven or more types of mycorrhizas have been recognised, but some are very similar. Early morphological classifications separated mycorrhizas into endomycorrhizal, ectomycorrhizal and ectendomycorrhizal associations based on the relative location of fungi in roots (Peyronel *et al.*, 1969). It is now recognised that VAM, ericoid and orchid mycorrhizas are unrelated types of 'endomycorrhizal' associations with contrasting anatomical features and separate host and fungus lineages (Lewis, 1973; Brundrett, 2002). Thus, the term 'endomycorrhiza' is invalid because it encompasses several phylogenetically and functionally disparate association types.

In theory, mycorrhizas could be defined by structural or physiological characteristics. However, in practice, only anatomical observations can reliably be used to designate categories of these associations, because links between mycorrhizal colonisation and plant physiological parameters

are not known in most cases where identification of associations occurs (Section III.2). The structural features used to define types and categories of mycorrhizas can be regulated by properties of the host, the fungus, or by interactions involving both. However, practical definitions used to classify mycorrhizas must be based primarily on features controlled by the plant, as features controlled by the fungus are too highly variable at the scale of individual plants. For example, it is possible to find most of the fungus-defined categories ('morphotypes') of VAM within a single root and one host plant will have many ECM morphotypes resulting from particular fungi. The two main categories of ECM and VAM associations (defined below) are highly consistent within a given host plant and are believed to be a consequence of genetically defined root structural properties (Smith & Smith, 1997; Brundrett, 2002). Smith & Smith (1997) found that VAM morphology categories were consistent within many, but not all plant families. Plant-defined morphological categories of ECM are also highly correlated with plant lineages (Section IV.2a). Categories of mycorrhizas are summarised in Figs 2 and 3.

(1) Vesicular arbuscular mycorrhizas

Arbuscules are normally used to define VAM associations. They can be quantified by standard microscopic procedures and their abundance is usually correlated with the degree of colonisation of young roots by VAM fungi (McGonigle *et al.*, 1990; Toth *et al.*, 1990). However, arbuscules are ephemeral structures that are often absent or hard to see (due to root age and pigments) in field-collected roots (see Brundrett *et al.*, 1996). Old VAM associations without arbuscules can be consistently identified by characteristic hyphal branching patterns in host plants if the observer has adequate experience. Thus, knowledge of root phenology and experience gained during observations of the same or closely related species is routinely used to determine whether old roots without arbuscules have VAM. Colonisation of non-host plants by glomeromycete fungi has sometimes been designated as vesicular mycorrhizal colonisation (e.g. Smith *et al.*, 1998), but should be called endophytic activity (Section III.1).

Morphological and functional categories of associations formed by glomeromycete fungi in plant organs that may be encountered in field surveys are listed below:

(*a*) Typical balanced VAM in young plant organs with prevalent, even colonisation of roots by hyphae with distinctive growth patterns and arbuscules (common).

(*b*) Older balanced VAM in roots with standard hyphal colonisation patterns (as in *a*), but without intact arbuscules (very common).

(*c*) Endophytic associations in non-host roots and other NM plant organs with diffuse growth of hyphae resulting in sparse, inconsistent colonisation without arbuscules (widespread, sporadic).

(*d*) Exploitative VAM in partially or fully myco-heterotrophic plants with intense colonisation of reduced roots or stems by specialised hyphae forming distinctive patterns that in some cases lack arbuscules (uncommon and restricted to certain plant families).
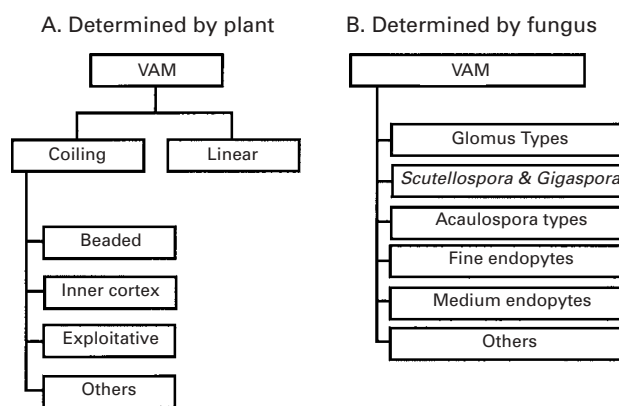
Fig. 2. Morphological classifications of vesicular-arbuscular mycorrhizal (VAM) categories and subcategories resulting from the host properties (A), and morphotypes resulting from fungal properties (B). Fungal morphotypes defined by Abbott (1982) are shown.
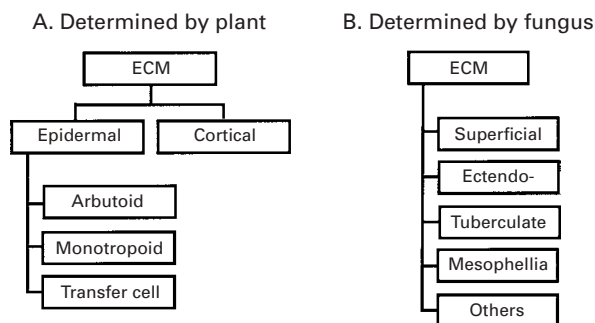
Fig. 3. Morphological classifications of ectomycorrhizal (ECM) categories and subcategories resulting from the host properties (A), and morphotypes resulting from fungal properties (B). Fungal morphotypes shown are major categories defined by Brundrett *et al.* (1996).

Vesicles may be present or absent in all these categories. Note that exploitative associations with glomeromycete fungi should be called VAM, even in hosts where arbuscules are never formed, as their presence is the ancestral condition for these fungi, which presumably simultaneously form associations with arbuscules in other plants.

There is disagreement about whether arbuscular mycorrhizal association (AM) or vesicular-arbuscular mycorrhizal association (VAM) is the most appropriate name for these mycorrhizas (see Smith, 1995; Walker, 1995; Smith & Smith, 1997). The term arbuscular mycorrhizas has gradually become more fashionable because some fungi do not produce vesicles in roots. However, there are problems with the use of arbuscules alone to define VAM because (i) these associations are routinely identified in old roots without intact arbuscules, (ii) their role as the primary site of nutrient transfer has not been fully established (Smith & Smith, 1997), and (iii) glomeromycete fungi have exploitative mycorrhizas without arbuscules in some myco-heterotrophic plants (e.g. Schmid & Oberwinkler, 1994; Imhof, 1999).

The most appropriate terminology for describing VAM associations depends on the particular phylogenetic, structural or functional approach used to classify their components. Classification schemes for glomeromycete fungi assume that storage structures formed in soil and roots are phylogenetically distinct, but fungi without vesicles in roots often produce temporary storage structures in soil (Brundrett *et al.*, 1996; Dalpé & Declerck, 2002; Declerck *et al.*, 2004). Phylogenetic studies have shown that the most primitive taxa of glomeromycete fungi have dimorphic spores (Sawaki, Sugawara & Saito, 1998; Morton & Redecker, 2001). One of these two spore types seems to function primarily as a short-term storage organ (M. Brundrett, unpublished observations). Spores produced by glomeromycete fungi are of unknown phylogenetic origin and may have evolved from a storage structure rather than a sexual spore. Many shared biochemical and genetic events would be involved in the formation of spores and vesicles, as both derive from swellings of relatively unspecialised hyphae and accumulate storage products from the cytoplasmic pool. Fungi without vesicles are likely to be derived from ancestors with them. Thus, it may be as appropriate to use a classification scheme which groups spores and vesicles together as it is to separate them on artificial grounds. The arguments summarised above suggest that the term vesicular-arbuscular mycorrhiza is as accurate as arbuscular mycorrhiza. However, the name arbuscular mycorrhiza is now more widely used (see Appendix).

The VAM fungi have been raised to the rank *Glomeromycota* (= *Glomeromycetes*, glomeromycete, glomeromycotan), so the older name Glomales (which has been corrected to Glomerales) no longer represents the whole phylum (Schüßler, Schwarzott & Walker, 2001). The old name phycomycetous mycorrhizas is invalid as it included fungi now classified in separate kingdoms. Neither can these fungi be referred to as zygomycetous. These fungi should be identified as the *Glomeromycota*, with individual genera listed when appropriate.

(*a*) Categories of vesicular arbuscular mycorrhizas

There are two main types of VAM, named by Gallaud (1905) as *Arum* and *Paris* type associations. In plants with *Paris* VAM associations hyphae grow as coils within cells, while those with *Arum* VAM have colonies that expand primarily by linear hyphal growth along longitudinal air channels between cortex cells (see Fig. 1.11 in Brundrett *et al.*, 1996). It is proposed here that the Arum and Paris categories of VAM should be designated as 'linear' and 'coiling' VAM respectively. Categories of mycorrhizal associations are not always consistent within plant genera (Smith & Smith, 1997), so should not be named after them. There may be physiological differences between linear and coiling VAM, as it has been suggested that substantial host-fungus exchange may also occur within plant cells that contain hyphal coils (Smith & Smith, 1997). The arbuscular interface of these associations is similar in structure to the arbuscular interface of linear VAM associations (Armstrong & Peterson, 2002).

Some plants with coiling VAM fungi have 'inner cortex' associations where hyphae occur throughout the cortex but arbuscules only form in a single inner-cortex cell layer (Brundrett & Kendrick, 1990; Widden, 1996). Plants with 'beaded roots' are a separate subcategory of coiling VAM where roots have many short segments separated by constrictions. These roots have also been called nodular roots, but this causes confusion with nitrogen-fixing associations (Brundrett, 2002). Other subcategories of coiling VAM are recognised in plants with exploitative associations (e.g. Imhof, 1999, 2001), or which have highly irregular coils (Widden, 1996). Inner cortex, beaded, and exploitative associations are only known in plants with coiling VAM. More research is required to determine how many subcategories of VAM exist. Categories and subcategories of VAM are listed in Fig. 2A and defined in Table 4.

Substantial variations in the growth patterns of hyphae associated with particular VAM fungi should be referred to as 'morphotypes' (Abbott, 1982; Brundrett *et al.*, 1996; Merryweather & Fitter, 1998). Major VAM morphotypes are listed in Fig. 2B. In roots with linear VAM some fungal morphotypes spread by both coils and linear hyphae, especially if these fungi only form small colonies. Some authors have suggested that plants with roots that contain both coils and linear hyphae should be considered an intermediate category (e.g. Smith & Smith, 1997; Cavagnaro *et al.*, 2001). However, these inconsistencies seem to be due to particular fungi, and, thus, do not constitute true categories of VAM as defined here. Morphological studies have demonstrated that the overriding influence of root anatomy on mycorrhizal morphology results in consistent morphological association categories for most plant species.

(2) Ectomycorrhizas

The presence of a Hartig net, consisting of labyrinthine hyphae between root cells, is used to designate ECM associations (Frank, 1885; Harley & Smith, 1983). Correlations between Hartig net thickness and host growth responses to specific strains of inoculated fungi support the hypothesis that the Hartig net is the primary zone of nutrient transfer in these associations (Burgess *et al.*, 1994; Dell *et al.*, 1994). However, correlations between Hartig net structure and mycorrhizal benefits have been established for only a few species. ECM associations can be distinguished from saprotrophic fungi growing on the surface of roots, or casual interactions between ECM fungi and non-host species, by careful microscopic observation (Agerer, 1995; Brundrett *et al.*, 1996).

Observations of the fruiting of putative fungal associates near a potential host plant cannot alone be used to designate ECM associations (Harley & Smith, 1983; Molina, Massicotte & Trappe, 1992). These designations may be incorrect if fungi fruit a considerable distance from their host tree or are wrongly assumed to be ECM associates. These problems are illustrated by literature citations that incorrectly designate VAM trees such as *Acer*, *Fraxinus* and *Ulmus* as ECM hosts (see Table 22 in Harley & Smith, 1983 and Table 11.2 in Molina *et al.*, 1992 for examples taken from the older literature). Many of the trees misclassified as ECM hosts have beaded VAM roots (Brundrett, 2002), as these can be mistaken for ECM short roots in the absence of

careful microscopic examination. The author maintains a list of known genera of ECM plants on the Internet that can be expanded when proof of the mycorrhizal status of other genera is provided (Brundrett, 1999). We must be careful of generalisations about members of fungus families because of exceptions such as *Boletinellus* (*Gyrodon*) *merulioides*, a basidiomycete in a predominantly ECM clade (Kretzer & Bruns, 1999), which only fruits under ash trees. This bolete was erroneously designated as an ECM fungus, but actually associates with subterranean aphids (Brundrett & Kendrick, 1987).

(a) Categories of ectomycorrhizas

There are two basic morphological categories of ECM: (i) associations typical of angiosperms such as *Eucalyptus*, *Betula*, *Populus*, *Fagus* and *Shorea* with a Hartig net confined to epidermal cells, and (ii) those of gymnosperms such as members of the Pinaceae where the Hartig net occupies multiple layers of cells in the cortex (Alexander & Högberg, 1986; Kottke & Oberwinkler, 1986; Massicotte, Ackerley & Peterson, 1987). There are a few exceptions to this rule such as the angiosperm *Dryas integrifolia*, which has a cortical Hartig net (Melville, Massicotte & Peterson, 1987). These categories result from anatomical features of the host root and the same fungus can form both types with different hosts (see Brundrett, 2002). It is proposed that these be designated as 'epidermal' and 'cortical' categories of ECM to reflect these fundamental differences (Fig. 3A). Some reports of cortical Hartig nets in angiosperms result from errors caused by examining root cross sections where slanting epidermal cells can appear multi-layered (Massicotte *et al.*, 1993). Observations of longitudinal sections of roots or cleared whole roots provide a clearer picture of Hartig net organisation than do cross sections (Massicotte *et al.*, 1993; Brundrett *et al.*, 1996). Convergent evolution of plants with ECM results in dimorphic (heterorhizic) root systems, where short roots have limited apical growth and high branching densities (Brundrett, 2002). Plant growth regulators supplied by the ECM fungus influence root swelling, extension and branching, and, when applied experimentally, can induce similar root morphologies in the absence of fungi (Kaska, Myllylä & Cooper, 1999; Barker & Tagu, 2000). Roots with transfer cells in the Hartig net, such as occur in *Pisonia grandis* (Ashford & Allaway, 1982) and *Alnus* spp. (Massicotte *et al.*, 1987), should probably be considered a separate subcategory of epidermal ECM (Fig. 3A). Categories and subcategories of ECM are listed in Fig. 3A and are defined in Table 4.

There are considerable variations in the structure and function of ECM formed by one host associating with different fungi (Agerer, 1995). The degree of short root branching and the structure of the mantle and Hartig net vary because of the presence of different mycorrhizal fungi (Godbout & Fortin, 1985; Newton, 1991; Agerer, 1995). Plant-fungus specificity varies considerably in ECM associations, from narrow host range fungi that associate with a single host species to broad host range fungi that associate with different families of host plants (Molina *et al.*, 1992). Host-fungus combinations that form functional associations

are designated as compatible (Molina *et al.*, 1992). Several morphotypes of ECM with progressively thicker mantles and Hartig nets considered to represent varying degrees of host-fungus compatibility are recognised (Burgess *et al.*, 1994; see Table 4.9 in Brundrett *et al.*, 1996). Tuberculate ECM associations, comprised of dense aggregations of ECM roots, have been reported from *Eucalyptus*, *Pseudotsuga*, *Castanopsis* and *Engelhardtia*, but seem to be uncommon (Trappe, 1965; Haug *et al.*, 1991). The truffle-like fungi in the Australian genera *Mesophellia* and *Castorium* form a unique type of mycorrhizal association, where mycorrhizal roots are incorporated in fungal fruit bodies (Dell *et al.*, 1990). Superficial ECM associations defined by the presence of a thin Hartig net and sparse mantle have been observed in synthesis experiments using host-fungus combinations which are not fully compatible (Burgess *et al.*, 1994; Massicotte *et al.*, 1999), but superficial ECM also occur in natural ecosystems (e.g. Clowes, 1951; Malajczuk, Dell & Bougher, 1987). The morphotypes listed in Fig. 3B result from properties of specific compatible fungi, and most are known to occur in both epidermal and cortical Hartig net hosts.

Associations reported in the literature as atypical ECM include the 'mycorrhiza-like' associations of *Morchella* sp. on members of the Pinaceae (Dahlstrom *et al.*, 2000), *Cortinarius cinnamomeus* on *Carex* spp. (Harrington & Mitchell, 2002), *Tricholoma matsutake* on *Pinus* (Gill *et al.*, 1999), and the variable associations of *Adenostoma fasciculatum* (Allen *et al.*, 1999). ECM associations also can occur in annual plants (McGee, 1988b). Some plants have both ECM and VAM and their relative importance can vary with the age of the plants and their habitats (Moyersoen & Fitter, 1998; Chen, Dell & Brundrett, 2000; van der Heijden, 2001). There also are cases where associations called ectomycorrhizal or ectendomycorrhizal meet none of the required morphological criteria (e.g. Bratek *et al.*, 1996 – a VAM association?). Erroneous designation of mycorrhizas appears to have resulted from mixed root samples in some cases, such as reports of ECM ferns (Brundrett, 2002). See p. 33 in Brundrett *et al.* (1996) for a more comprehensive consideration of ECM designation problems.

(b) Monotropoid, arbutoid and ectendomycorrhizal associations

Arbutoid and monotropoid mycorrhizas have traditionally been considered to be separate from ECM associations, despite their many similarities (Smith & Read, 1997). The fungi which form these associations typically are also ECM associates of other hosts (Molina & Trappe, 1982a; Massicotte *et al.*, 1993), so the unique features of these associations must be controlled by the host plant. A survey of plants in the Ericaceae found that arbutoid mycorrhizas were not consistent, as many of the same plants simultaneously had ECM (Largent, Sugihara & Wishner, 1980). Arbutoid mycorrhizas have been considered to be either a category of ECM (Molina & Trappe, 1982a), or a type of ericoid mycorrhizas (Fusconi & Bonfante-Fasolo, 1984). However, phylogenetic studies have shown that plants in the Ericaceae with ericoid mycorrhizas descended from those with arbutoid associations (Cullings, 1996), so arbutoid

Table 5. Examples provided to demonstrate a proposed classification scheme for types, categories, subtypes and morphotypes of mycorrhizas. Categorical information is listed with the most significant terms last (e.g. *Glomus* linear VAM, or ectendocortical ECM)

Fungal morphotype (if known)	Defined by host plant			Other name
	Subcategory	Category	Type*	
Glomus		Linear	VAM	*Arum* series VAM
	Inner cortex	Coiling	VAM	A type of *Paris* series VAM
Superficial		Epidermal	ECM	
	Arbutoid	Epidermal	ECM	Arbutoid mycorrhizas
Ectendo-		Cortical	ECM	Ectendomycorrhizas

* VAM = vesicular-arbuscular mycorrhiza, ECM = ectomycorrhiza.

associations were derived from ECM rather than ericoid association. It is recommended here that within the hierarchical classification of types of mycorrhizas, arbutoid and monotropoid mycorrhizas should be classified as sub-categories of epidermal ectomycorrhizas (Fig. 3A, Tables 4 and 5).

Ectendomycorrhizas are currently recognised by a definition based on fungi rather than plants (Yu, Egger & Peterson, 2001) that does not morphologically distinguish them from arbutoid mycorrhizas. Observations of ectendo-mycorrhizas, defined in this narrow sense, are largely restricted to highly fertile artificial situations where trees grown for forestry are unlikely to benefit from mycorrhizas, and competition from other fungi is limited (Yu *et al.*, 2001). However, ECM with some degree of intracellular hyphal penetration may occur in a wider range of situations than is generally acknowledged (e.g. Brundrett, Murase & Kendrick, 1990). The differences between ECM and ectendomycorrhizal associations are very unclear, because they do not involve separate plant lineages, and some of the fungi involved are poorly known. There may also be cases where hyphae penetrating host cells belong to a different fungus than the one forming the Hartig net, or in which cell penetration occurs only in senescent associations (Yu *et al.*, 2001). Egger & Fortin (1988) originally suggested that ectendomycorrhizas should perhaps be considered a developmental phase or evolutionary stage of ECM. Ectendo-mycorrhizas do not occur in a separate plant lineage and occupy the same level in the classification hierarchy as superficial and tuberculate mycorrhizas. Thus, it is recommended that ectendomycorrhizas be relegated to a fungal morphotype, rather than a true category of ecto-mycorrhizas (Fig. 3, Tables 4 and 5).

(3) Other mycorrhizas

Despite phylogenetic evidence that ericoid mycorrhizas evolved from plants with ECM (Cullings, 1996; Brundrett, 2002), there is ample evidence that they are sufficiently distinct to warrant separate classification from other types of mycorrhizas. Morphological categories have not been recognised within ericoid mycorrhizas, but may exist. Further research is required to confirm if substantial differences in the structure and function of mycorrhizas occur between

the roots and stems of terrestrial orchids, or between chlorophyllous and achlorophyllous orchids (Table 4). The sub-epidermal association of plants in the Australian monocot genus *Thysanotus* discovered by McGee (1988 *a*) is a morphologically distinct type of mycorrhiza (Table 4). The fungi that associate with *Thysanotus* have not been identified.

V. CLASSIFYING MYCORRHIZAS

Mycorrhizal associations are classified primarily by morphological features controlled by the host, but information from fungus-based classification schemes should also be provided. Examples of a proposed classification scheme for mycorrhizal associations are shown in Table 5. *It is vital that consistent definitions are used to distinguish mycorrhizal association types and that these definitions are included in all published work to allow interpretation of data and comparisons between different studies.* The classification in Table 5 uses the categories, sub-categories and morphotypes of mycorrhizal fungi shown in Figs 2 and 3 and defined in Table 4.

It is important to clearly distinguish which functional category of association was observed and to describe the evidence used to make this judgement. A conclusive diagnosis should not be provided when there is uncertainty about the type of association observed. Observational and interpretational problems need to be considered when using data from the literature (see Harley & Smith, 1983; Brundrett *et al.*, 1996), especially if criteria used to identify mycorrhizal associations are not stated (e.g. Hartig nets or arbuscules). Researchers will need to confirm the mycorrhizal status of plants themselves if there are any questions about the reliability of existing information.

In some cases inappropriate methods of observation that reveal minute details of associations are used in mycorrhizal studies without also providing a low-magnification overview that allows associations to be identified. Problems with the identification of association types may also arise from the use of material of unknown age that lacks ephemeral structures such as arbuscules, or inadequate sampling (e.g. observation of a limited number of sectioned roots). It is preferable to identify mycorrhizal associations in whole-root preparations using a clearing and staining technique that allows sufficient sampling volume and replication (Brundrett *et al.*, 1996). In

ecosystem surveys, the degree of mycorrhizal colonisation should be expressed as the proportion of susceptible roots that were mycorrhizal, by excluding woody roots. This requires an understanding of root structure and phenology (Brundrett *et al.*, 1996).

The taxonomic classification of most mycorrhizal fungi has not been fully resolved. Consequently, it is vitally important to submit voucher specimens of any fungi used in experiments to a registered herbarium to allow their names to be confirmed and updated in the future (see Agerer *et al.*, 2000). It is also advisable to include material in a form that will preserve DNA for future studies. Unfortunately, the identity of fungi used in many mycorrhizal studies cannot be precisely determined. This prevents us from establishing relationships between the taxonomy and biology of mycorrhizal fungi used in these experiments.

Mycorrhizas are three-way interactions of plants, fungi, and soils (Brundrett, 1991), so we must expect environmental and edaphic factors to affect their structure and function. Consequently, descriptions of mycorrhiza types should include information about the soils and habitats where they occur which can be as valuable as information about the taxonomic identity of fungi (Brundrett, 1991). Studies of mycorrhizal synthesis under artificial conditions should include comparisons with the same host and fungus in natural habitats to identify artifacts due to cultural conditions. Combinations of host plants, fungi and soils that do not occur in nature may provide inaccurate knowledge of structure and physiology.

Our current knowledge of the physiology of mycorrhizal associations is largely based on generalisations formed by assembling fragmentary evidence from separate measurement of the roles of plants and fungi, in many cases using highly artificial conditions (Miller & Kling, 2000). Consequently, there is much scope for future studies which investigate the reciprocal nature of mycorrhizas by simultaneously measuring the fitness and functioning of both partners. A whole-ecosystem approach to investigating the role of mycorrhizas in nutrient and energy cycling in natural situations will allow us to formulate a better understanding of the typical magnitude of costs and benefits for each partner in mycorrhizal associations (see Miller & Kling, 2000). Assessment of the functional diversity of mycorrhizal associations, and the impact of perturbations such as pollution or climate change on ecosystems dominated by mycorrhizal species requires a more comprehensive understanding of how a balance between the interests of mycorrhizal plants and fungi is maintained.

VI. CONCLUSIONS

1. A new definition of mycorrhizas is provided to encompass the full diversity of these associations. These plant-fungal associations are primarily responsible for nutrient transfer, are essential to one or both organisms and involve synchronised development.

2. Mycorrhizal fungi have a wide diversity of roles and can also function as endophytes, necrotrophs and antagonists of non-host plants, with roles that vary during the life of associations.

3. Most mycorrhizas can be described as balanced mutualistic associations in which the fungus and plant exchange commodities required for the growth and survival of both partners. These occupy a separate isocline from pathogenic, endophytic, or antagonistic associations in the continuum of plant-fungus interactions.

4. Myco-heterotrophic plants have exploitative mycorrhizas where transfer processes benefit only plants. These non-mutualistic associations involve fungi with primary roles as saprophytes, parasites or balanced mycorrhizal associates of other plants.

5. After considering the relative merits of vesicular-arbuscular mycorrhizas and arbuscular mycorrhizas, it is concluded there is no compelling reason to switch to arbuscular mycorrhizas.

6. The main categories of vesicular-arbuscular mycorrhizas are linear and coiling associations, and of ectomycorrhizas are epidermal and cortical associations. Subcategories of coiling and epidermal associations occur in certain host plants. Arbutoid and monotropoid associations are redefined as subcategories of epidermal ectomycorrhizas and ectendomycorrhizas as a morphotype.

7. It is recommended that mycorrhizal associations are defined and classified primarily by anatomical criteria regulated by the host plant as fungal controlled features (morphotypes) vary within plants. A hierarchical classification scheme for types, categories, sub-categories and morphotypes of mycorrhizal associations is proposed.

VII. ACKNOWLEDGMENTS

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IX. APPENDIX

(1) Usage of arbuscular and vesicular-arbuscular mycorrhizas

As shown in Fig. 4 the name arbuscular mycorrhizas (AM) has become more common than vesicular-arbuscular mycorrhizas (VAM), but the latter is still frequently used. Thus, there is no consensus about which name for these associations is most correct. Usage of these terms varied considerably between databases, with a much smaller proportion of papers in *Biological Abstracts* found using VAM than in CAB Abstracts (Fig. 4). Literature searches using 'arbuscular mycorrhizas' as a search term will also find papers with 'vesicular-arbuscular mycorrhizas' in their title or abstract. However, a surprisingly large number of relevant papers (over 10 % of those in *Biological Abstracts* in 2002) were not found by searches using either term, because they used endomycorrhiza, mycorrhiza, abbreviations such as AM, names of fungi, or no useful search terms in their titles.

It is recommended that all papers should include vesicu-lar-arbuscular mycorrhiza or arbuscular mycorrhiza in their title if they primarily concern these associations. Endomycorrhiza, the obsolete name for these associations,
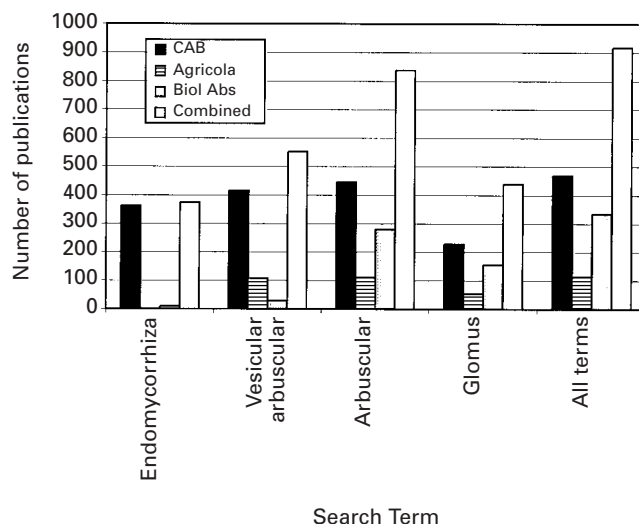
Fig. 4. Publications containing arbuscular mycorrhizas, vesicular-arbuscular mycorrhizas, or other terms in titles or abstracts. This graph summarises 2002 data from three data-bases (*Biological Abstracts*, BIOSIS; *CAB Abstracts*, CAB International; *Agricola*, US Department of Agriculture) using a web-based literature search of the titles and abstracts of scientific publications (www.ovid.com). Combined results include some duplication.

should not be used at all. The International Mycorrhizal Society (www.mycorrhizas.org) should address the issue of association names and provide effective means of communicating recommended nomenclature to all mycorrhizal scientists.