MARSCHNER REVIEW

Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis

Mark C. Brundrett

Abstract A comprehensive appraisal of the mycorrhizal literature provides data for 336 plant families representing 99% of flowering plants, with regard to mycorrhizas and other nutritional adaptations. In total, arbuscular (AM), orchid, ectomycorrhizas (EM) and ericoid mycorrhizas and nonmycorrhizal (NM) roots occur in 74%, 9%, 2%, 1% and 6% of Angiosperm species respectively. Many families of NM plants have alternative nutritional strategies such as parasitism, carnivory, or cluster roots. The remaining angiosperms (8%) belong to families reported to have both AM and NM species. These are designated as NM-AM families here and tend to occur in habitats considered non-conducive to mycorrhizal fungi, such as epiphytic, aquatic, extremely cold, dry, disturbed, or saline habitats. Estimated numbers of species in each category of mycorrhizas is presented with lists of NM and EM families. Evolutionary trends are also summarised by providing data on all clades and orders of flowering and non-flowering vascular plants on a global scale. A case study of Western Australian plants revealed that plants with specialised nutritional modes such as carnivory, cluster roots, or EM were much more diverse in this ancient landscape with infertile soils than elsewhere. Detailed information on the mycorrhizal diversity of plants presented here is linked to a website (mycorrhizas.info) to allow data to remain current. Over a century of research effort has resulted in data on mycorrhizal associations of >10,000 plant species that are of great value, but also somewhat of a liability due to conflicting information about some families and genera. It is likely that these conflicts result in part from misdiagnosis of mycorrhizal associations resulting from a lack of standardisation in criteria used to define them. Families that contain both NM and AM species provide a second major source of inconsistency, but even when these are excluded there is a ~10% apparent error rate in published lists of mycorrhizal plants. Arbuscules are linked to AM misdiagnosis since they are used less often than vesicles to recognise AM associations in roots and apparently occur sporadically in NM plants. Key issues with the diagnosis of mycorrhizal plants are discussed using the Cyperaceae as a case study. Detailed protocols designed to consistently distinguish AM from endophytic Glomeromycotan Fungus Colonisation (GFC) are provided. This review aims to stimulate debate and provide advice to researchers delving into root biology.

M. C. Brundrett (✉)
School of Plant Biology (M090),
Faculty of Natural and Agricultural Sciences,
The University of Western Australia,
35 Stirling Highway,
Crawley 6009 WA, Australia
e-mail: mark.brundrett@uwa.edu.au

Abbreviations

AM	arbuscular mycorrhizas (vesicular-arbuscular mycorrhizas VAM)
NM	nonmycorrhizal plants
EM	ectomycorrhizas (ECM)
NM-AM	plants with variable AM or NM roots
GFC	endophytic or unspecified colonisation by Glomeromycotan Fungi
RLC	root length colonised

Introduction

For over a century, a substantial proportion of the research effort on mycorrhizal symbioses has focussed on identifying plant and fungal partners in samples of roots obtained from natural ecosystems. Newman and Reddell (1987), Trappe (1987) and Wang and Qiu (2006) have provided comprehensive summaries of the mycorrhizal literature [e.g. 723 papers consulted by Harley and Harley (1987) and a dataset of 3000 papers summarised by Trappe (1978)]. A second major source of information is provided by mycorrhizal surveys or data compilations on regional scales for Japan by Maeda (1954), the UK by Harley and Harley (1987) and Peat and Fitter (1993), Hawaii by Koske et al. (1992), South Africa by Allsopp and Stock (1993) and Australia by Brundrett (2008-mycorrhizas.info). Additional information is provided by mycorrhizal data compilations for hydrophytes by Khan and Belik (1995), xerophytes by Trappe (1981), ectomycorrhizal Fabaceae by Alexander (1989), the Cyperaceae by Muthukumar et al. (2004) and the Brassicaceae by DeMars and Boerner (1996).

In total, mycorrhizologists have presented data on over 10,000 plant species, which equates to about 3% of vascular plants. This comprehensive dataset is of great scientific value, but also a source of confusion, due to inconsistent reports of associations within some families and genera. Mycorrhizas are defined by microscopic features that are used to identify associations (Brundrett 2004). However, it is often not clear which structures were used to identify associations in published studies of field-collected roots. Perhaps as a consequence, it is relatively common to find examples of conflicting data on mycorrhizas for plant families, genera and even species in the scientific literature. Dickie et al. (2007) identify one

example of misdiagnosis for *Buddleja davidii*, but there are many others. The most confusion concerns the status of plant families, such as Chenopodiaceae and Cyperaceae, that are considered to contain NM plants by most authors, but have also been reported to have AM (Hirrel et al. 1978; Muthukumar et al. 2004). Apparent misdiagnosis of EM in plants that normally have AM is also common, especially in the older mycorrhizal literature (mycorrhizas.info/ecm). Our knowledge of the mycorrhizal status of some plant families is becoming less clear over time, as errors accumulate in host plant lists. It is important that such contradictory information be resolved since data on the importance of mycorrhizas at local, regional and global scales is of great value to land mangers, for restoration ecology and conservation and also required for applied use of plants in forestry, horticulture and agriculture. Inconsistencies in the diagnosis of mycorrhizas result in a number of key questions:

1. Is existing information of sufficient scope and consistency to determine which plant families contain species that typically have mycorrhizal or NM roots?
2. Can plant families of NM species be allocated into categories based on nutritional or ecological strategies?
3. How can inconsistencies caused by misdiagnosis be distinguished from those due to real variation in mycorrhizal associations within some plant families and genera?
4. Can we resolve uncertainty about the relative importance of habitats where plants tend to be NM, relative to plant families that have variable mycorrhizas, especially when both occur together?
5. Are reported inconsistencies within plant families linked to inconsistent use of criteria for identification of mycorrhizal associations such as arbuscules for AM and a Hartig net for EM?
6. Are more reliable protocols for diagnosis of mycorrhizas required?

The purpose of this review is to address these questions by: (1) a critical appraisal of the literature to designate plant families with mycorrhizal or NM roots and identify families with well established mycorrhizal relationships, NM roots, or conflicting information, (2) use these data to determine the total diversity of plants with different types of mycorrhizas or alternative means of nutrition, and (3) discuss the

importance of mycorrhizal survey data and suggest objectives for future surveys. The second part of this review aims to identify the most common errors that have been perpetuated in the mycorrhizal literature and recommend protocols to reduce error rates in the diagnosis of mycorrhizal associations in the future.

Methods

Two contrasting approaches were used to provide estimates of the relative diversity of mycorrhizal and other nutrition strategies in plants to provide the most accurate estimates possible and to allow comparison of results.

Mycorrhizal status of plant families, orders and clades

The first approach estimated mycorrhizal plant diversity based on current plant phylogeny data to minimise the effect of sampling biases on outcomes. A comprehensive and critical screening of the mycorrhizal literature using criteria listed below provided mycorrhizal status data for 336 families that included 99% of flowering plant species. Data on mycorrhizal and NM species was obtained from the regional survey publications listed below and many additional references only listed at mycorrhizas.info. It is conservatively estimated that over 10,000 plant species were included in the analysis. Family classification followed this approach:

1. Families were not allocated to categories unless there was sufficient sampling of taxa (several species or corroborative studies).
2. In families well established to be AM, occasional contradictory reports of NM roots were considered to be due to habitat conditions, sampling, or diagnosis errors.
3. Families where most species consistently lack mycorrhizas are designated as NM.
4. Families where both NM and AM roots were repeatedly diagnosed were assigned to the variable NM-AM category.
5. Parasitic plants without roots were designated as NM.
6. Studies that explain how mycorrhizal structures were used in diagnosis or illustrate such structures were given preference over other reports.

7. Data for plants growing in habitats that are non-conducive for mycorrhizas (e.g. arctic, epiphytic and marine plants) were not used to determine the mycorrhizal status of families that also occur in other habitats.
8. Families with substantial numbers of species with more than one root type were split across categories using estimated number of species at the genus level.

Data on the mycorrhizal status of plant families were incorporated into a table listing the 506 currently recognised flowering plant families (Soltis et al. 2000; Heywood et al. 2007), with current estimates for numbers of species in each family compiled from the data sources listed below. These data were combined with mycorrhizal records in a table to estimate of the total taxonomic diversity of all flowering plants with each type of mycorrhizas or NM roots. Data on mycorrhizas of major groups of primitive plants was compiled separately for online publication (mycorrhizas.info/evol). The estimates of mycorrhizal diversity for primitive plants and flowering plants were then combined to provide an overall estimate for all vascular plants.

A more detailed estimate of the number of species of EM plants was compiled at the genus level, using comprehensive taxonomic data from the sources listed below. Separate diversity estimates were also compiled for specialised categories on NM plants such as parasites, carnivores and species with root clusters, as was the diversity of plant families with variable NM-AM roots from different habitats. Some of these data tables were first published online at mycorrhizas.info, where they will be kept updated.

Data on estimated numbers of species in plant families were compiled primarily from Heywood et al. (2007). Additional information as provided by Florabase (florabase.calm.wa.gov.au), the Catalogue of Life (www.catalogueoflife.org), the International Plant Names Index (www.ipni.org), Angiosperm Phylogeny Website by Stevens (2001-, www.mobot.org/MOBOT/research/APweb). The diversity of lower plants was obtained from Gymnosperms Homepage (www.conifers.org) and the Tree of Life (www.tolweb.org), and Chapman (2005). Lists of parasitic plants follow Nickrent (2006, www.parasiticplants.siu.edu/ListParasites.html). Myco-heterotrophs follow Leake (1994) and Nickrent (1997-). The orchid diversity estimate is from Chase et al. (2003).

Mycorrhizal survey data summary

Data on mycorrhizas of plants in natural habitats were summarised from 128 publications, covering most major habitats and geographic regions of the world, estimated to include over 8,000 plant species. Data on habitats likely to be non-conducive to mycorrhizas, such as arctic, alpine, aquatic and epiphytic plant communities, were summarised separately for ~2,000 plant species. This approach was used to minimise the impact of habitat conditions on overall measures of mycorrhizal occurrence. Thus, data from published lists of mycorrhizal species incorporated over 10,000 plant species. References were chosen that:

1. Use modern definitions of mycorrhizal types.
2. Included at least 10 species of plants from an ecosystem.
3. Used roots collected in natural habitats.
4. Minimised duplication of species in lists by maximising distance or habitat separation between surveys in similar habitats,
5. Primarily focussed on flowering plants (gymnosperms and ferns were included in totals, but bryophytes were excluded).

Papers listing mycorrhizal plants in ecosystems were: Alarcón and Cuenca (2005), Allen et al. (1987), Allen et al. (1998), Allen et al. (2006), Allsop and Stock (1993), Andrade et al. (2000), Bagyaraj et al. (1979), Bakarr and Janos 1996), Barnola and Montilla (1997), Bauer et al. (2003), Beck-Nielsen and Madsen (2001), Bellgard (1991), Berch and Kendrick (1982), Berch et al. (1988), Béreau et al. (1997), Berliner and Torrey (1989), Bethlenfalvay et al. (1984), Blaschke (1991), Blaszkowski (1994), Bledsoe et al. (1990), Brockhoff and Allaway (1989), Brundrett and Abbott (1991), Brundrett and Kendrick (1988), Brundrett et al. (1995), Camargo-Ricalde et al. (2003), Carrillo-Garcia et al. (1999), Cázares et al. (2005), Chaudhry et al. (2005), Clayton and Bagyaraj (1984), Collier et al. (2003), Cooke and Lefor (1988), Cooper (1976), Cornwell et al. (2001), Cripps and Eddington (2005), Currah and Van Dyk (1986), da Silva et al. (2001), de Alwis and Abeynayake (1980), DeMars (1996), Dhillion et al. (1995), Dodd et al. (2002), Ducousso et al. (2008), Eriksen et al. (2002), Ernst et al. (1984), Farmer (1985), Fisher and Jayachandran (2005), Fontenla et al. (1998), Fontenla et al. (2001), Frenot et al. (2005), Frioni et al. (1999), Fuchs and Haselwandter (2004),

Gai et al. (2006), Gehring and Connell (2006), Gemma and Koske (1995), Giovannetti and Nicolson (1983), Gorsi (2002), Grippa et al. (2007), Hartnett et al. (2004), Hetrick et al. (1992), Hildebrandt et al. (2001), Högberg and Piearce (1986), Högberg (1982), Hopkins (1987), Hurst and Turnbull (2002), Janos (1993), Johnson-Greene et al. (1995), Kagawa et al. (2006), Kai and Zhiwei (2006), Katenin (1964), Khan (1974), Kohn and Stasovski (1990), Koske and Gemma (1990), Koske et al. (1992), Kottke et al. (2004), Kühn et al. (1991), Kumar and Ghose (2008), Laursen et al. (1997), Lesica and Antibus (1986), Lesica and Antibus (1990), Logan et al. (1989), Louis (1990), Lovera and Cuenca (1996), Maeda (1954), Mafia et al. (1993), Malloch and Malloch (1981, 1982), Maremmani et al. (2003), McGee (1986), McGuire et al. (2008), Medve (1984), Menoyo et al. (2007), Michelsen (1993), Miller (1979, 1982), Mishra et al. (1980), Moyersoen et al. (2001), Muthukumar and Udaiyan (2000), Muthukumar et al. (2003), Muthukumar et al. (2006), Nadarajah and Nawawi (1993), Newbery et al. (1988), O'Connor et al. (2001), Olsson et al. (2004), Onguene and Kuyper (2001), Onipchenko and Zobel (2000), Pendleton and Smith (1983), Perrier et al. (2006), Peterson et al. (1985), Powlowski et al. (1996), Radhika and Rodrigues (2007), Ragupathy and Mahadevan (1993), Ragupathy et al. (1990), Rains et al. (2003), Read and Haselwandter (1981), Reddell and Milnes (1992), Reddell et al. (1996), Reeves et al. (1979), Rosales et al. (1997), Rose (1981), Ruotsalainen et al. (2002), Rowe and Pringle (2005), Saif (1975), Santos et al. (2000), Schmidt and Scow (1986), Sengupta and Chaudhuri (2002), Sharma et al. (1986), Shi et al. (2006), Siqueira et al. (1998), Šraj-Kržič et al. (2006), St John (1980), Straker et al. (2007), Tao and Zhiwei (2005), Tao et al. (2004), Thomazini (1973), Titus et al. (2002), Tori and Coley (1999), Tawaraya et al. (2003), Treu et al. (1996), Tsuyuzaki et al. (2005), Turnau et al. (1992), Väre et al. (1992), Väre et al. (1997), Weishampel and Bedford (2006), Wetzel and van der Valk (1996), Wilson and Hartnett (1998), Wubet et al. (2003), Yamato and Iwasaki (2002), Zhang et al. (2004), Zangaro et al. (2002).

Mycorrhizal studies providing survey data for 100 or more plant taxa from natural habitats were used in comparison with data summaries described above. These 14 surveys were of plants from Cameroon (Onguene and Kuyper 2001), New Zealand (Cooper

1976), China (Muthukumar et al. 2003), India (Muthukumar and Udaiyan 2000, Muthukumar et al. 2006, Ragupathy and Mahadevan 1993), Australia (Brundrett and Abbott 1991, Brundrett et al. 1995), Guyana (McGuire et al. 2008), Hawaii (Koske et al. 1992), Argentina (Fontenla et al. 2001), Canada (Currah and Van Dyk 1986), South Africa (Allsop and Stock 1993) and Japan (Maeda 1954).

Data from arctic habitats were used to investigate the relationship between latitude and mycorrhizas. These studies of arctic habitats were by Bledsoe et al. (1990), Olsson et al. (2004), Kohn and Stasovski (1990), Väre et al. (1992, 1997), Miller (1982), Treu et al. (1996), Allen et al. 2006, Ruotsalainen et al. (2002) and Katenin (1964).

A case study contrasting global averages to one of the world's oldest landscapes in Western Australia (WA) is also presented. The ratio of expected to actual diversity in families from WA with different types of mycorrhizas, specialised roots or mycorrhiza-suppressive habitats was determined. Data on plant diversity were obtained from the Western Australian Herbarium (florabase.calm.wa.gov.au, calculated in June 2007).

The data compilation from 125 published papers described above was also used to estimate rates of errors for diagnosis of AM, EM and NM roots as well as the frequency of use of different definitions of AM (arbuscules, or hyphae, vesicles and arbuscules, or not stated). The types of data on root colonisation by mycorrhizal fungi presented is also reported. Misdiagnosis was considered likely when reports are contrary to expectations based on the mycorrhizal literature, as explained in the Section on Resolving conflicting information in published data.

Part I. the relative importance of mycorrhizas and other means of plant nutrition

Determining the total diversity of mycorrhizal and nonmycorrhizal plants

An estimation of the relative diversity of plants with different types of mycorrhizas provided by assigning mycorrhizal associations to Angiosperm families is shown in Fig. 1. In this analysis, the majority of flowering plants (>99%) belonged to families that could be reliably assigned to mycorrhizal categories
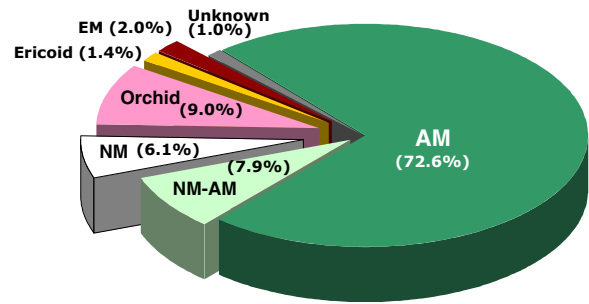

Fig. 1 The relative diversity of angiosperms with different types of mycorrhizal or nonmycorrhizal roots. The mycorrhizal status of the majority of species in plant families was determined from literature citations for >10,000 plants and combined with estimated numbers of species in each family (see "Methods" for data sources). Less than 1% of angiosperms could not be allocated (unknown). *AM* arbuscular mycorrhizas, *NM* nonmycorrhizal, *NM-AM* variable NM or AM, *EM* ectomycorrhizal

with existing data. This approach is much more reliable than summaries produced from averaging published data alone, as it corrects for sampling biases (e.g. more data from the Northern Hemisphere). There are < 200 families yet to be sampled and the majority of these are very small (the average size of un-sampled families is 15 species and 1/4 are monotypic). Most of these unallocated families are likely to contain AM plants as they are sister to, or nested within clades known to predominantly contain AM plants.

Of the 336 Angiosperm families which could be assigned to categories, 217 contained AM plants, 40 had variable NM-AM, 53 only NM, 23 included EM hosts and 3 other types of mycorrhizas were confined to one family (Orchidaceae, Ericaceae, *Thysanotus* in the Laxmaniaceae). A key finding is that, on a global scale, the importance of fully NM plants is less than suggested in the past (i.e. ~6% of flowering plants). Even if families reported to contain both NM and AM species (NM-AM) is added to the NM total, 86% of flowering plants are mycorrhizal.

The mycorrhizal associations of the majority of large families of flowering plants are now well resolved and it is unlikely that the overall trends presented in Fig. 1 would change much with more data. However, there are several potential error sources in estimates of numbers of mycorrhizal species:

i. Estimates of plant diversity in Figs. 1, 2, 3, 4 will change as taxonomy is resolved and new species
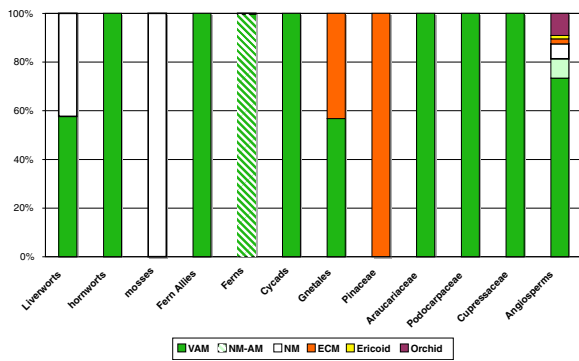
Fig. 2 The mycorrhizal status of different clades of lower plants, using data sources summarised at mycorrhizas.info and including Angiosperm data from Fig. 1 for comparison (see Fig. 1 for abbreviations)

are described. However, this is not expected to substantially alter the relative sizes of categories.

ii. The relative diversity of the orchids varies considerably in estimates (from 18,000 to 25,000 species (Heywood et al. 2007), but the larger estimated by Chase et al. (2003) was considered to be most realistic so is used here.

The proportions of AM, EM and NM plants in different primitive plant clades is summarised in Fig. 2 using data provided at mycorrhizas.info. This website should be consulted for references and further information on mycorrhizas of these plant groups. Bryophytes such as mosses and liverworts included in Fig. 2, have been reported to contain AM-like associations, hyphae of other fungi, or be NM, but the nature of associations are unclear in some cases (Ligrone et al. 2007). Combined data from Figs. 1 and 2
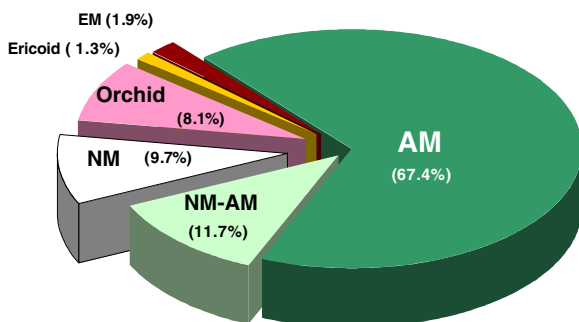

Fig. 3 The relative diversity of mycorrhizal or nonmycorrhizal plants summarised for all vascular plants. Data sources are explained for Figs. 1 and 2 (see Fig. 1 for abbreviations)
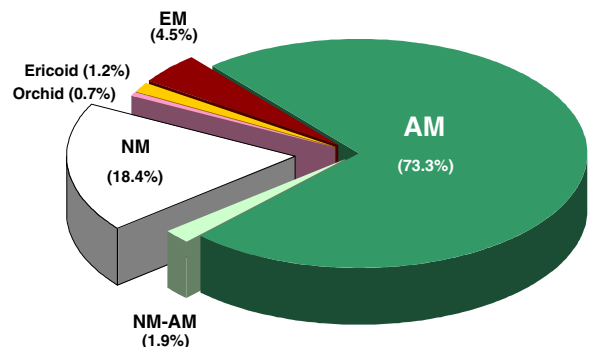
Fig. 4 The relative diversity of mycorrhizal or nonmycorrhizal plants summarised by calculating totals from published lists of mycorrhizal or nonmycorrhizal vascular plants. Data are from 128 publications from most regions of the world, estimated to include 8,000 plant species. See "Methods" for a list of these papers and Fig. 1 for abbreviations

provides an overview of the relative importance of mycorrhizas for all vascular plants in Fig. 3.

In total, over 200,000 flowering plants have AM, out of about 280,000 species in total. These 217 families are too numerous to list here. Most of the remaining families have EM or predominantly NM roots so are listed in Tables 1 and 2. Host plants with orchid (~25,000 spp.), ericoid (~3,900 spp.), and *Thysanotus* (~50 spp. in the Laxmanniacae) mycorrhizas occur in a single family or genus, so will not be discussed further. Plants with *Thysanotus* mycorrhizas were excluded from Figs. 1, 2, 3, 4 as they would not be clearly visible.

Summary of mycorrhizal survey data

Estimates of the relative diversity of mycorrhizal and NM plants compiled using data from 128 published host plant lists which included about 8,000 plant taxa are shown in Fig. 4. When these results are compared with plant classification-based estimates for mycorrhizal plant diversity (Figs. 1, 2, 3), it can be seen that both approaches provide similar estimates of the relative diversity of AM plants, but surveys have tended to over-sample NM and EM plants and under-sample orchids. It is not surprising that orchids are under-sampled as their highest diversity occurs in specialised tropical epiphytic habitats (Chase et al. 2003) and mycorrhizas of epiphytes as a group are poorly studied (Janos 1993). In contrast, habitats where NM plants predominate tend to be over-

Table 1 Families and genera of ectomycorrhizal plants with estimated number of species (see "Methods" for data sources)

Clade	Order	Family	Genera	No. Gen	No. Spp.	Habit	Habitat
Gymnosperms							
Gymnosperms	Gnetales	Gnetaceae	*Gnetum*	1	35	Shrubs	Tropical
Gymnosperms	Conifers	Pinaceae	*Abies, Cathaya, Cedrus, Keteleeria, Larix, Picea, Pinus, Pseudolarix, Pseudotsuga, Tsuga*	11	250	Trees	Boreal
Angiosperms—monocotyledons							
Commelinids	Poales	Cyperaceae	*Kobresia*	1	132?	Sedge	Alpine, arctic
Angiosperms—dicotyledons							
Core Eudicots	Caryophyllales	Asteropeiceae	*Asteropeia* (Madagascar)	1	8	Trees	Tropical
		Nyctaginaceae	*Guapira, Neea, Pisonia*	3	5	Trees	Tropical
		Polygonaceae	*Polygonum*	1	15?	Herb	Alpine, arctic
		Polygonaceae	*Coccoloba*	1	14	Trees	Tropical
Rosids	Myrtales	Myrtaceae	*Allosyncarpia, Agonis, Angophora, Baeckea, Eucalyptus, Leptospermum, Melaleuca, Tristania, Tristaniopsis, etc.*	10	1,800?	Trees, shrubs	Most semi-arid Australia
Eurosids I	Fabales	Fabaceae I Caesalpinioideae (Caesalpiniaceae)	*Afzelia, Anthonotha, Aphanocalyx, Berlinia, Brachystegia, Cryptosepalum, Dicymbe, Didelotia, Eperua, Gilbertiodendron, Gleditsia, Intsia, Isoberlinia, Julbernardia, Microberlinia, Monopetalanthus, Paraberlinia, Paramacrolobium, Pellegriniodendron, Tetraberlinia, Toubaouate*	21	250	Trees	Tropical
		Fabaceae II Papiloinoideae (Papilionaceae)	*Aldinia, Gastrolobium, Gompholobium, Jacksonia, Lonchocarpus, Mirbelia, Oxylobium, Pericopsis*	12	610?	Shrubs	Semi-arid, most in Australia
		Fabaceae III Mimosoideae (Mimosaceae)	*Acacia, Calliandra*	2	240?	Shrubs, trees	Semi-arid or wet
	Fagales	Betulaceae	*Alnus, Betula, Carpinus, Corylus, Ostrya, Ostryopsis*	6	130	Trees, shrubs	Boreal
		Casuarinaceae	*Allocasuarina, Casuarina*	2	80	Trees, shrubs	Australasia
		Fagaceae	*Castanea, Castanopsis, Fagus, Lithocarpus, Quercus*	8	750	Trees	Most boreal
		Junglandaceae	*Carya, Engelhardtia*	2	32	Trees	Temperate
		Nothofagaceae (Fagaceae)	*Nothofagus*	1	35	Trees	Southern
	Malpighiales	Phyllanthaceae (Euphorbiaceae)	*Uapaca, (Ampera), Poranthera*		105	Trees	Tropical
		Salicaceae	*Populus, Salix*	2	385	Trees, shrubs	Boreal
	Rosales	Rhamnaceae	*Cryptandra, Pomederris, Spyridium, Trymalium*	4	130	Shrubs, trees	Australia
		Rosaceae I	*Dryas* (arctic and alpine herbs),	1	16	Shrubs	Arctic, alpine
		Rosaceae II	*Cercocarpus*, Purshia* *VAM also*	2	13	Shrubs	Temperate

Table 1 (continued)

Clade	Order	Family	Genera	No. Gen	No. Spp.	Habit	Habitat
Eurosids II	Malvales	Cistaceae	*Cistus, Fumana, Helianthemum, Hudsonia, Lechea, Tuberaria*	8	180	Shrubs	Temperate
		Dipterocarpaceae	*Anisoptera, Dipterocarpus, Hopea, Marquesia, Monotes, Shorea, Vateria, Vateriopsis, Vatica*	17	500	Trees	Tropical
		Sarcolaenaceae	*Leptolaena, Sarcolaena, Schizolaena*	8	60	Trees	Tropical
		Tiliaceae	*Tilia*	1	22	Trees	Boreal
	Sapindales	Meliaceae	*Owenia*	1	5	Trees	Tropical
Asterids	Ericales	Ericaceae I	*Arbutoid category of ECM and/or ECM: Arbutus, Arctostaphylos, Cassiope, Chimaphila, Comarostaphylis, Gaultheria, Kalmia, Leucothoe, Pyrola*	8	119	Shrubs, trees	Boreal
		Ericaceae II	*Monotropoid category of ECM: Monotropa, Pterospora, Sarcodes*	9	11	Herbs	Boreal
		Sapotaceae	*Manilkara*	1	80	Tree	Tropical

? number of species with EM uncertain

represented in published lists, perhaps because they are relatively accessible or easier to sample (e.g. annual plants in disturbed habits). The relative diversity of EM hosts is also higher in Fig. 4, but this probably reflects the dominance of EM trees in many of the habitats that have been sampled most often.

Despite the fact that Fig. 4 is based on a much larger dataset than was used in earlier compilations of mycorrhizal species data [i.e. 2075 spp. in Newman and Reddell (1987), 6507 spp. in Trappe (1987), 843 spp. in Peat and Fitter (1993), 3617 spp. in Wang and Qui (2006)], some results are in close agreement as shown in Fig. 5. Only the overall importance of mycorrhizal and NM roots can be compared in Fig. 5, since the other reviews used fewer categories of mycorrhizas to summarise data. Families and taxa with variable mycorrhizas are more common in the literature summaries of Trappe 1987 and Harley and Harley 1987, which rely more heavily on older literature than the data presented here. Newman and Reddell (1987) were unable to allocate any families as totally NM, because of contradictory information in the literature, even though some families were reported to comprise ~90% NM species. This example illustrates why it is necessary to designate such families as predominantly NM, recognise a category of families with NM-AM plants and/or exclude data that are likely to be incorrect when the majority of reports are in agreement.

Figure 6 includes data for all types of mycorrhizas from 14 large surveys for comparison with the data from Figs. 1 and 4 included for comparison. The proportion of plants with mycorrhizas varies considerable between surveys, from 100% of ferns sampled in New Zealand (Cooper 1976) to 50% of plants sampled in India (Muthukumar and Udaiyan 2000). The proportion of mycorrhizal species is substantially lower than expected in some surveys, which may be related to the habitats sampled (aquatic, epiphytic and disturbed plants were included in some surveys), but also may reflect issues with diagnosis as explained in Part II.

Ectomycorrhizal plants

There are about 6000 ectomycorrhizal (EM) plant species in 145 genera and 26 families (approximately 5600 angiosperms and 285 Gymnosperms), most of which are trees or shrubs (Table 1). Most of the families listed in Table 1 are well known EM hosts, but designation of EM hosts becomes more complex when variation occurs within large families such as the Fabaceae and Myrtaceae where numbers of EM species are most uncertain. The Sarcolaenaceae (the sister group to the Dipterocarpaceae and Cistaceae) and the Asteropeiaceae are new EM families that have been recently discovered (Ducousso et al. 2004, 2008). Table 1 is based on the data summary discussed above and

Table 2 Families of nonmycorrhizal (NM) and NM-AM (variable mycorrhizal) plants listed with data on habits, nutritional strategies, habitats and estimated number of species (see "Methods" for data sources)

Clade	Order	Family	Habit	Ecology	NM-AM	NM
Basal	Basal	Nymphaeaceae	Herbs	Aquatic	60	
	Ceratophyllales	Ceratophyllaceae	Herbs	Aquatic		3
Magnoliids	Laurales	Lauraceae[a]	Climber	Parasites		16
	Piperales	Hydnoraceae	Herbs	Parasites		7
		Piperaceae	Woody, herbs	Epiphytes	3,000	
Monocots	Acorales	Acoraceae	Herbs	Aquatic	4	
	Alismatales	Alismataceae	Herbs	Aquatic	80	
		Aponogetonaceae	Herbs	Aquatic	45	
		Araceae[a]	Herbs	Aquatic and epiphytes	1,600	
		Butomaceae	Herbs	Aquatic	1	
		Cymodoceaceae	Herbs	Aquatic-marine		15
		Hydrocharitaceae	Herbs	Aquatic-marine	75	
		Juncaginaceae	Herbs	Aquatic	15	
		Limnocharitaceae	Herbs	Aquatic	8	
		Najadaceae	Herbs	Aquatic-marine	40	
		Posidoniaceae	Herbs	Aquatic-marine		9
		Potamogetonaceae	Herbs	Aquatic	100	
		Ruppiaceae	Herbs	Aquatic-marine	8	
		Zosteraceae	Herbs	Aquatic-marine		18
	Pandanales	Cyclanthaceae	Herbs	Epiphytes	255	NM?
Commelinids	unplaced	Dasypogonaceae	Herbs	Sand binding		16
	Commelinales	Commelinaceae	Herbs	Other NM		650
		Haemodoraceae	Herbs	Sand binding		100
		Pontederiaceae	Herbs	Aquatic	33	
	Poales	Bromeliaceae	Herbs	Epiphytes	2,600	
		Centrolepidaceae	Herbs	Many aquatic		35
		Cyperaceae	Sedges	Dauciform roots, sand binding, aquatic, etc.	4,500	
		Hydatellaceae	Herbs	Aquatic		10
		Juncaceae	Rushes	Many aquatic, some root clusters		440
		Restoniaceae	Herbs	Cluster, sand binding		500
		Typhaceae	Herbs	Aquatic		25
		Xyridaceae	Herbs	Many aquatic		300
Eudicots	Proteales	Nelumbonaceae	Herbs	Aquatic	2	
	Proteales	Proteaceae	Woody	Cluster roots		1,700
	Ranunculales	Papaveraceae	Herbs	Many weeds	760	
Core eudicots	Caryophyllales	Aizoaceae	Herbs or woody	Succulent, halophytes		170
		Amaranthaceae	Herbs, shrubs	Many saline or weeds		1,000
		Droseraceae	Herbs	Carnivores		180
		Drosophyllaceae	Herb	Carnivore		1
		Frankeniaceae	Shrubs, saline	Arid saline		80
		Molluginaceae	Herbs	Succulent, weedy		90
		Mesembranthaceae	Succulents	Succulent		1,680
		Nepenthaceae	Climbers	Carnivores		85
		Nyctaginaceae#	Woody	Other NM		395
		Phytolaccaceae	Woody, herbs	Many weeds		31
		Plumbaginaceae	Herbs, woody	Arid saline	840	
		Polygonaceae#	Most herbs	Many weeds		1,100
		Portulacaceae	Woody, herbs	Succulent	500	
		Tamaricaceae	Woody	Arid saline	80	

Table 2 (continued)

Clade	Order	Family	Habit	Ecology	NM-AM	NM
	Santalales	Eremolepidaceae	Shrubs	Parasites		12
		Olacaceae[a]	Woody	Parasites		154
		Opiliaceae	Woody	Parasites		33
		Loranthaceae	Mistletoes	Parasites		906
		Misodendraceae	Mistletoes	Parasites		10
		Santalaceae	Woody	Parasites	490	
		Viscaceae	Mistletoes	Parasites		350
	Saxifragales	Crassulaceae	Herbs, shrubs	Succulent		1,500
		Haloragaceae[a]	Herbs	Aquatic	50	
		Saxifragaceae	Herbs	Alpine, arctic, etc.	630	
Eurosids I	unplaced	Zygophyllaceae	Herbs, woody	Arid saline	275	
	Fagales	Myricaceae	Woody	Cluster		62
	Malpighiales	Erythroxylaceae	Woody	Other NM	140	
		Podostemaceae	Herbs	Aquatic	300	
		Quiinaceae	Woody	Other NM	51?	
		Rhizophoraceae[a]	Woody	Marine	145	
	Oxalidales	Cephalotaceae	Herb	Carnivore		1?
	Rosales	Urticaceae	Herbs, woody	Many weeds	1,700	
Eurosids II	Brassicales	Brassicaceae	Herbs	Many weeds		3,350
		Capparaceae	Shrubs, herbs	Close to Brassicaceae		470
		Cleomaceae	Herbs, shrubs	Many in arid and or saline	310?	
		Resedaceae	Herbs, shrubs	Arid	70	
Asterids	Cornales	Loasaceae	Herbs, shrubs	Many in arid habitats		230?
	Ericales	Roridulaceae	Shrubs	Carnivores		2
		Sarraceniaceae	Herbs	Carnivores		20?
Euasterids I	unplaced	Hydrophyllaceae	Herbs, woody	Many in arid habitats	300	
		Lennoaceae	Herbs	Parasitic		4
	Lamiales	Avicenniaceae	Trees	Marine	8	
		Byblidaceae	Herbs	Carnivores		6?
		Callitrichaceae	Herbs	Aquatic	75	
		Hippuridaceae	Herbs	Aquatic		4
		Lentibulariaceae	Herbs	Carnivores		320
		Orobanchaceae (Scrophulariaceae[a])	Herbs	Parasites		2,046
	Solanales	Convolvulaceae[a]	Climbers	Parasites		180
Euasterids II	Asterales	Menyanthaceae	Aquatic	Aquatic	62	
	Dipsacales	Adoxaceae	Herbs	Boreal	3	
Taxa of uncertain position	unplaced	Apodanthaceae	Herbs	Parasites		23
		Balanophoraceae	Herbs	Parasites		45
		Cynomoriaceae	Herbs	Parasites		2
		Cytinaceae	Internal	Parasites		10
		Mitrastemonaceae	Internal	Parasites		2
		Rafflesiaceae	Internal	Parasites		20

EM plants in family, *?* insufficient data or inconsistent data to determine if NM or NM-AM

[a] Family includes AM species not included in total

additional information published online at mycorrhizas. info/ecm, which should be consulted for references and further information. Families and genera described as EM in the past, but now well established not to have EM are excluded from Table 1. Atypical EM-like associations are also excluded, as discussed in Part II.

Ectomycorrhizal roots of *Gnetum* are substantially different from those of conifers (Pinaceae) as illus-
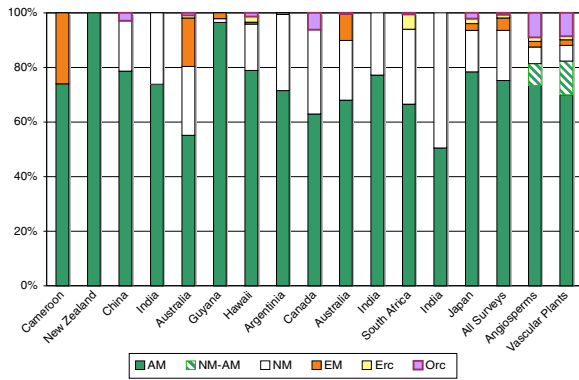
Fig. 5 Comparing results of 14 mycorrhizal studies that include at least 100 plant species in different regions of the world. The last three columns include data from Figs. 1, 3 and 4 for comparison. These papers are listed in the "Methods"

trated in Fig. 7a. The fungal interface in *Gnetum* EM occurs on numerous densely arranged finger-like projections, most likely derived from root hairs, embedded in matrix of hyphae. Epidermal cells are exceptionally narrow and densely packed. It is very unlikely this complex type of epidermal Hartig net evolved from the cortical Hartig net of other gymnosperms in the Pinaceae, or vice versa.
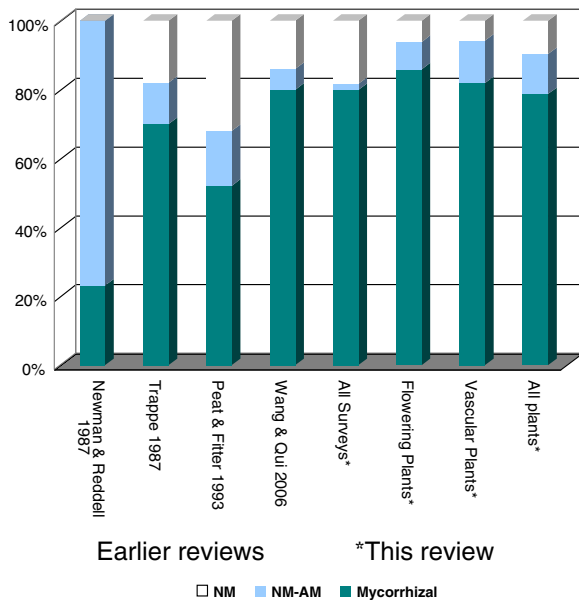
Fig. 6 Comparison of results from different reviews where the relative diversity of mycorrhizal plants was calculated from published data. The last four columns include data from Figs. 1, 2, 3, 4 for comparison
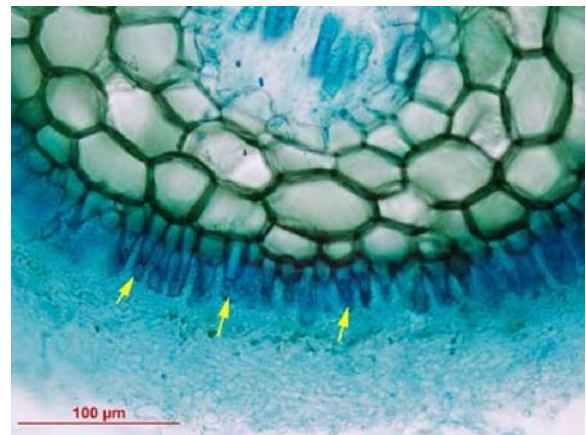
A. *Gnetum* Hartig net
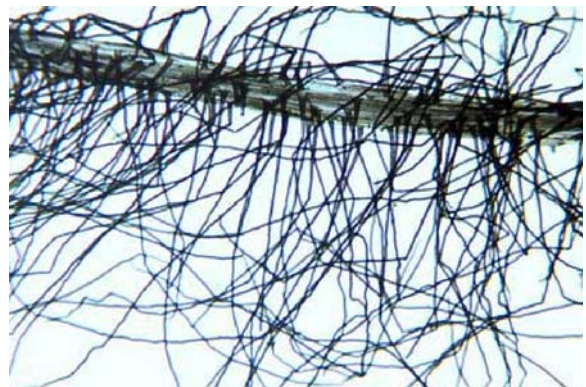
B. *Drosera erythrorhiza* root hairs

Fig. 7 Photos of roots **a** *Gnetum gneum* ectomycorrhizal roots have a unique type of Hartig net. **b** Nonmycorrhizal roots of a carnivorous sundew (*Drosera erythrorhiza*) with very long root hairs

Predominantly nonmycorrhizal plant families with specialised nutrition

NM plants include about 17,000 species, or approximately 6% of flowering plants and NM-AM plants include a further 22,000 or more species, or 8% of the flowering plants. As listed in Table 2, NM or NM-AM plants occur in 90 Angiosperm families. Families were included in this list if the majority of reports are consistent and it will be updated online at mycorrhizas. info/nmplants. Despite some inconsistencies in published data, it is clear that some plant families are predominantly NM, and many of these families have been recognised for some time (e.g. Maeda 1954; Gerdemann 1968; Selivanov and Eleusenova 1974; Trappe 1981; Harley and Harley 1987; Tester et al.

1987; Brundrett 1991; Molina et al. 1992; Allsopp and Stock 1993; Schreiner and Koide 1993; Cripps and Eddington 2005). However, many of the 90 families listed in Table 2 are recognised here for the fist time. Most of the newly recognised families are parasites or carnivores that are unable or unlikely to have mycorrhizas, as explained below.

Nonmycorrhizal (NM) plants have roots that are highly resistant to mycorrhizal fungus hyphae, so usually remain free of fungi in habitats where other plants are mycorrhizal (Tester et al. 1987; Brundrett 1991; Giovannetti and Sbrana 1998). However, in many NM families, there are occasional reports of AM (usually lacking arbuscules). Families with a substantial number of reports of both NM and AM families are designated as having variable NM-AM roots. In the mycorrhizal literature, endophytic hyphae and vesicles of Glomeromycotan fungi (GFC) are interpreted as AM by some authors, but not by others, as discussed in Part II. NM plants tend to have very fine lateral roots with long root hairs, as illustrated for the NM carnivore *Drosera erythrorhiza* in Fig. 7b.

Figure 8 shows the relative importance of flowering plants with consistently NM roots belonging to different ecological and habitat categories. Most lineages of NM plants have evolved in directions that result in reduced benefits from mycorrhizas (loss of mycorrhizal dependency). Overall, these evolutionary trends can be summarised as "root function reduction or transformation", where nutrient uptake by mycorrhizal roots becomes less common than other means of nutrition (Table 2). Categories of NM or NM-AM

plants where mycorrhizal roots are likely to become redundant for nutrient uptake include:

1. Parasites with haustoria attached to host plants,
2. Carnivores that trap and digest invertebrates,
3. Highly specialised hydrophytes, and
4. Plants with root clusters.

These highly specialised NM plants differ from more generalist families of NM species, which acquire nutrients from soils via more conventional means. Many species in NM or NM-AM families tend to occur in specialised habitats, as discussed below. Several predominantly NM families also contain a few EM hosts. These include *Kobresia* spp. in the Cyperaceae, *Pisonia grandis*, *Neea* and *Guapira* spp. in the Nyctaginaceae and *Polygonum* sp. in the Polygonaceae (Table 1).

Parasites (18 families, ~4500 spp.)

There are over 4500 parasitic plants in total and this is equivalent to about 1% of the global diversity of flowering plants (Nickrent 1997-). It is safe to assume that all holoparasites are NM due to loss of roots, or their conversion into haustoria. The most highly evolved parasitic plants grow directly attached to or within other plants, but many hemiparasites maintain a connection to the soil (Kuijt 1969). The majority of hemiparasites where roots have been assessed are NM in families such as the Orobanchaceae (Scrophulariaceae), where Lesica and Antibus (1986) found 27 species all had

Fig. 8 Exploded pie graph segments for the nonmycorrhizal (NM) and variable mycorrhizal (NM-AM) plant families from Fig. 1. Plant families are allocated to ecological or habitat categories as explained in the text (see Fig. 1 for abbreviations)
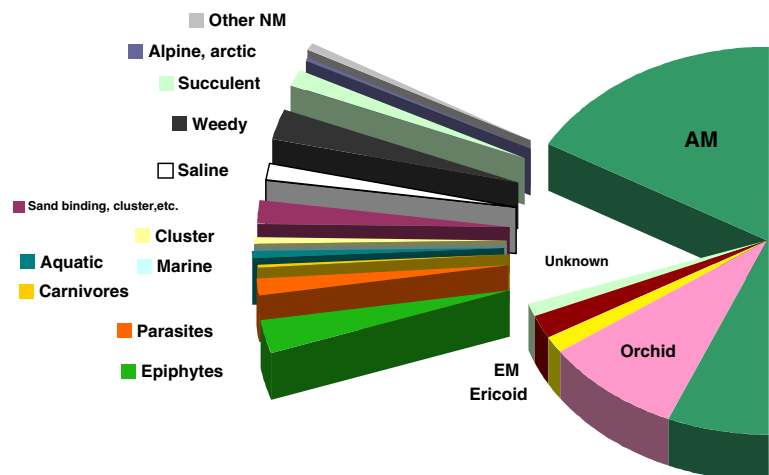
< 5% colonisation without arbuscules. However, there are reports of AM in hemiparasites in the Santalaceae and Krameriaceae (Lesica and Antibus 1986). It is not known if these AM associations contribute to nutrition, or are relictual but tolerated as a minor drain on resources.

Carnivores (8 families, ~615 spp.)

Carnivores with highly specialised nutrient-capture strategies usually have NM roots, as is the case of carnivorous plants in the genera *Drosera*, *Utricularia* and *Aldrovanda* (the latter has no roots). *Drosera* species have roots that are very fine with very long root hairs (see Fig. 7b). Experiments have demonstrated that carnivorous plants acquire a substantial proportion of their nutrients by digestion of prey (Juniper et al. 1989; Schulze et al. 1997). Consequently, mycorrhizas are likely to have become partially or fully redundant. Carnivorous plants with roots that have not been examined for mycorrhizas include *Brocchinia*, *Catopsis* (Bromeliaceae) and *Triphyophyllum* (Dioncophyllaceae). *Roridula gorgonias* (Roridulaceae), a semi-carnivorous plant endemic to South Africa, has AM but also acquires nutrition from insects (Midgley and Stock 1998).

Cluster roots and related root types (8 families, ~7000 spp.)

Some NM plants, including ~1800 members of the Proteaceae and Myricaceae and some genera of the Fabaceae (i.e. *Lupinus* and *Daviesia*) have cluster roots—dense aggregations of lateral roots with long root hairs (Skene 1998; Lambers et al. 2006). Mycorrhizas become redundant in many plants with cluster roots, but others retain AM or EM, such as *Viminaria* and *Aspalanthus* of the Fabaceae and members of the Betulaceae, Casuarinaceae and Eleagnaceae (Allsopp and Stock 1993; Skene 1998; Lambers et al. 2006). Cluster roots can form a dense mat near the soil surface and promote nutrient uptake by their large surface area and production of exudates that increase nutrient availability (Lambers et al. 2006; Shane et al. 2006).

Some members of the Cyperaceae have root clusters that consist of swollen "dauciform" roots that are functionally similar to cluster roots (Davies et al. 1973; Shane et al. 2006). It is not clear if the Cyperaceae is a NM or NM-AM family as is discussed as the case

study in Part II. Root clusters also occur in some rushes in the Restionaceae and Juncaceae (Lamont 1982; Shane et al. 2006). Other monocotyledons with NM roots that are not as well studied include the Commelinaceae, as well as the Dasypogonaceae and Haemodoraceae which have "sand-binding roots" with a thick soil sheath covering root hairs.

Predominantly nonmycorrhizal plants in mycorrhiza suppressing habitats

Plants in some families are mycorrhizal in some locations and NM in others, especially when soil conditions are not conducive to mycorrhiza formation. In other cases, families are known to include both mycorrhizal and NM species, or the family status is in doubt due to conflicting evidence. These are referred to here as NM-AM plants and plant families and Glomeromycotan fungal hyphae in roots as GFC if AM diagnosis is not certain. Possible explanations for the variable mycorrhizal status of these families are discussed in Part II. NM-AM families are included with NM plants in Fig. 8, as they often occur in the same habitats. The category of variable NM-AM mycorrhizas includes 40 families, or 8% of flowering plants (Table 2, Fig. 8). Many ferns also have variable NM-AM roots (Fig. 2). There are many NM-AM monocotyledons, especially hydrophytes (Table 2).

Situations where NM or NM-AM species are most likely to occur can be characterised as stressful and include aquatic, epiphytic, arctic, saline, disturbed, very cold (arctic and alpine) and very arid habitats (Trappe 1987; Brundrett 1991). As shown in Fig. 9, the relative importance of mycorrhizal roots is greatly reduced in arctic and alpine habitats, as well as aquatic and epiphytic habitats. These are habitats where mycorrhizal fungi may not be present, or if present, inoculum levels are likely to be low and fungal distribution very patchy. This results in a feedback loop because most mycorrhizal fungi need host plants to survive, but reduced fungal inoculum will favour non-host plants.

Hydrophytes in aquatic, wetland or marine habitats (28 families, ~1600 spp.)

Mycorrhizas are more likely to be absent, or sparsely/intermittently/inconsistently present in roots of hydrophytes than in other plants (Table 2, Fig. 9).
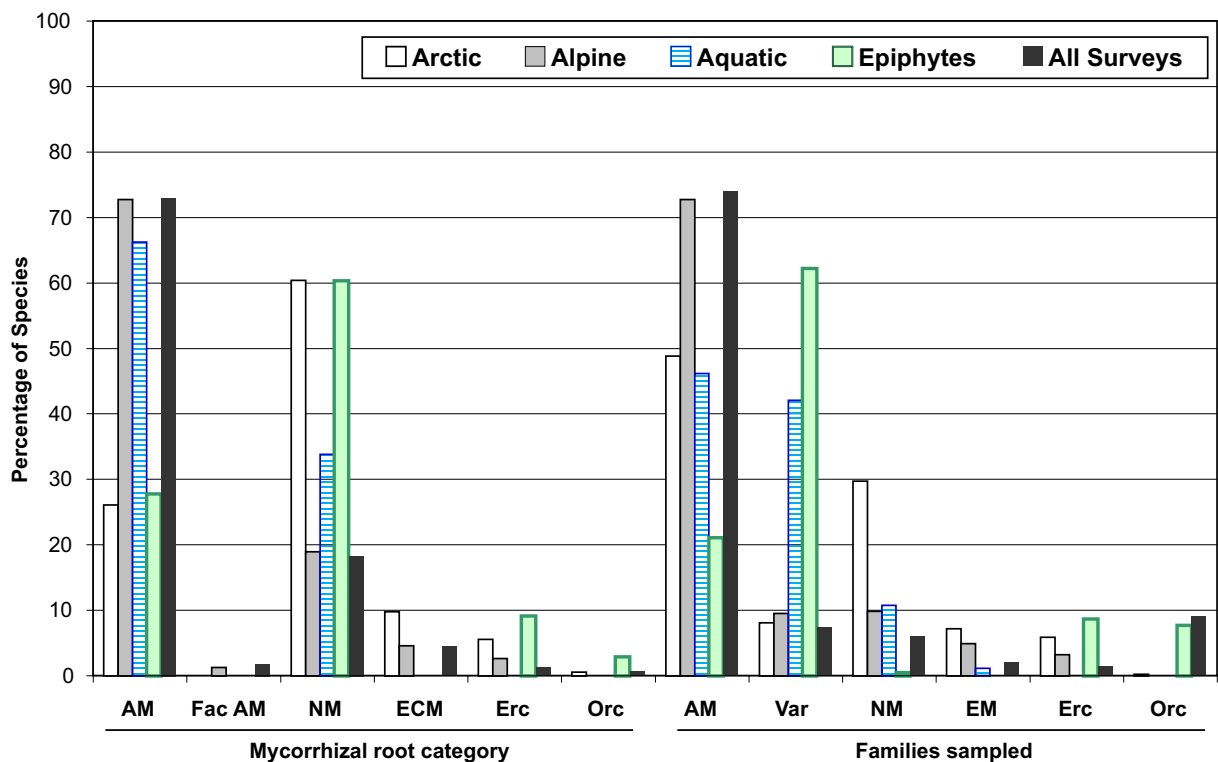
Fig. 9 The relative diversity and frequency of sampling of mycorrhizal or nonmycorrhizal plants in comparatively stressful habitats. The first 5 groups of bars show the relative diversity of plants reported to have AM, NM-AM, NM, EM, ericoid (Erc) or orchid (Orc) roots in 4 habitat types. The next 5 groups of bars show the relative frequency of plant families with roots in each of these categories were sampled in the same studies. Overall results for non-stressful habitat (Fig. 4) are included for comparison as the last bar in each group. See Methods for a list of papers

However, some submerged aquatic plants rooted in sediment are typically mycorrhizal and experiments have demonstrated benefits from mycorrhizas for some of them (Clayton and Bagyaraj 1984; Beck-Nielsen and Madsen 2001; Cornwell et al. 2001; Jayachandran and Shetty 2003). The most highly specialised hydrophytes, floating plants with few or no roots, such as *Ceratophyllum* sp., are unlikely to ever be mycorrhizal and floating aquatic plants such as *Azolla, Eichhornia, Lemna* and *Marsilea* spp. are usually considered to be NM (Maeda 1954; Ragupathy and Mahadevan 1993; Beck-Nielsen and Madsen 2001; Kai and Zhiwei 2006; Radhika and Rodrigues 2007). In some hydrophytes, the majority of root samples with GFC lack arbuscules (Radhika and Rodrigues 2007).

Comparisons of habitats show submerged individuals are less likely to be mycorrhizal than emergent hydrophytes, or other wetland plants (Clayton and Bagyaraj 1984; Peat and Fitter 1993; Beck-Nielson

and Madsen 2001; Šraj-Kržič et al. 2006). Khan and Belik (1995) list aquatic plants with NM or AM roots in different habitats, including aquatic members of the Alismataceae, Araceae, Butomacaea, Cyperaceae, Haloragaceae, Nymphaeaceae, Podostemonaceae, Pontederiaceae, Potamogetonaceae and Typhaceae. Plants in these families tend to have well developed aerenchyma and fine roots with long root hairs (Khan and Belik 1995; Beck-Nielsen and Madsen 2001). The monocotyledon families Juncaceae, Centrolepidaceae and Xyridaceae also tend to occur in wet habitats and have NM roots.

Plants with NM-AM or NM roots are even more prevalent in saline aquatic habitats. Mangroves (Avicenniaceae, Rhizophoraceae) are reported to have AM in one study, but not in 3 others (Maeda 1954; Rose 1981; Mohankumar and Mahadevan 1986; Sengupta and Chaudhuri 2002). Seagrasses (Cymodoceaceae, Hydrocharitaceae, Posidoniaceae, Zosteraceae) are
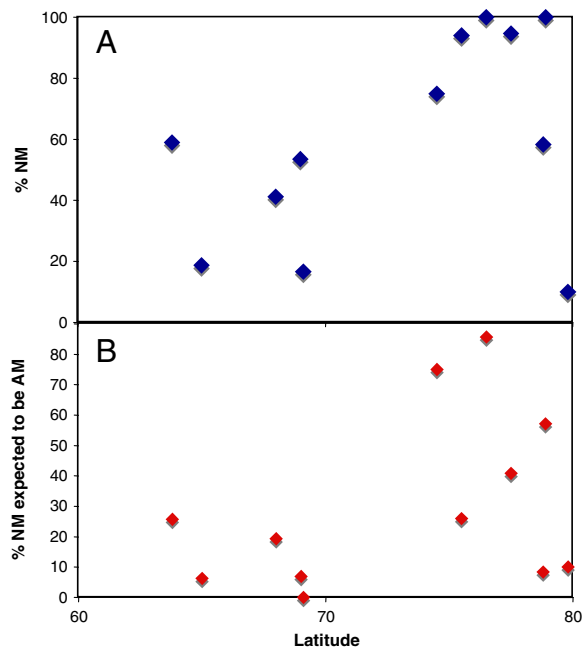
Fig. 10 Correlations between arctic latitude (degrees N) and the relative frequency of inclusion of plants with nonmycorrhizal roots in publications. **a** Plants lacking mycorrhizas. **b** Nonmycorrhizal plants in families that are typically mycorrhizal in other habitats. See "Methods" for the list of papers

NM (Nielsen et al. 1999; Brundrett and Cambridge unpublished).

Epiphytes (3 families, ~7200 spp. of Angiosperms + many ferns)

The epiphytes that have been sampled in mycorrhizal studies predominantly belong to NM-AM families (Fig. 9). For ferns and angiosperms in families such as the Bromeliaceae, Piperaceae and Araceae, habitat is a principal determinant of mycorrhizal status, as epiphytes are often NM, while most terrestrial plants in the same families usually have AM (Lesica and Antibus 1990; Janos 1993; Maffia et al. 1993; Michelsen 1993; Gemma and Koske 1995; Grippa et al. 2007). Epiphytic ferns in a plantation had NM roots (Nadarajah and Nawawi 1993), but those growing in natural habitats are more likely to have AM (Gemma and Koske 1995; Rains et al. 2003).

The Araceae (aroids) have complex mycorrhizal relationships as they include terrestrial plants with AM, as well as NM hydrophytes such as *Lemna* and *Pistia* spp. and NM-AM epiphytes such as *Philodendron* spp.

(Maeda 1954; Santos et al. 2000). Species in the Araceae were split between AM and AM-NM categories in Table 2. Epiphytic orchids are also often mycorrhizal, but require further study (Hadley and Williamson 1972; Otero et al. 2002). Ericoid mycorrhizas also occur in epiphytic Ericaceae in South America (Rains et al. 2003). The overall importance of epiphytic mycorrhizas is not as well resolved, as that of other plants, due to limited sampling (Janos 1993). In some cases the significance of GFC in epiphytes is unclear since only hyphae and vesicles were observed (Nadjarajah and Nawawi 1993; Maffia et al. 1993).

Arctic and alpine plants (1 family, ~650 spp.)

Many alpine and arctic plants belong to variable NM-AM or NM families such as the Cyperaceae, Brassicaceae and Caryophyllaceae, but only the Saxifragaceae occurs most often in these habitats. Nonmycorrhizal plants tend to become more dominant at high latitudes (Väre et al. 1997), as is also the case in sub-antarctic islands (Laursen et al. 1997). Figure 10a uses data from studies of arctic plants to illustrate this point. Extremely cold habitats also seem to induce some plants to switch to EM, as is the case with arctic species of *Kobresia, Dryas* and *Polygonum*. Plants belonging to families which are typically AM elsewhere are also likely to have NM roots in the coldest arctic sites (Fig. 10b). The impact of altitude on mycorrhizas in alpine habitats seems to be less pronounced than the impact of latitude in arctic sites (Fig. 9), but this could result from the choice of sampling locations.

Arid and arid saline habitats (12 families, ~7800 spp.)

Non-succulent predominantly NM plant families with species that often occur in salt-affected areas, such as desert saltpans and salt lake margins, include the Amaranthaceae, Chenopodiaceae, Cleomaceae, Frankeniaceae, Plumbaginaceae, Tamaricaceae and Zygophyllaceae (Table 2). Selivanov and Eleusenova (1974) summarised data for 234 desert plants, of which a comparatively high proportion (35%) were NM. They observed that families such as the Brassicaceae, Caryophyllaceae, Frankeniaceae, Juncaceae and Polygonaceae were fully NM while the Chenopodiaceae, Cyperaceae, Plumbaginaceae and Papaveraceae had a majority of NM plants.

The families Aizoaceae, Crassulaceae, Mesembranthaceae, Portulacaceae and Molluginaceae have succulent leaves and NM-AM or NM roots. They also frequent arid habitats where mycorrhizas may be less beneficial than elsewhere because plant productivity is very low and periods of root activity are brief. However, many other succulents, such as members of the Agavaceae, Cactaceae and Euphorbiaceae have AM roots (Bethlenfalvay et al. 1984; Carrillo-Garcia et al. 1999; Camargo-Ricalde et al. 2003).

Disturbed habitats and weedy plants (5 families, ~7000 spp.)

It is well known that many NM plants are herbs that occur in disturbed habitats (Trappe 1987; Harley and Harley 1987; Peat and Fitter 1993). Families that include many annual weeds and often have NM roots include the Amaranthaceae, Brassicaceae, Capparaceae, Caryophyllaceae, Chenopodiaceae, Cyperaceae, Molluginaceae, Papaveraceae, Polygonaceae, Portulacaceae, Urticaceae and Zygophyllaceae (Hirrel et al. 1978; Pendleton and Smith 1983; DeMars and Boerner 1996). These families are fully NM, or include some AM hosts such as *Atriplex* which is a shrub in the NM-AM family Chenopodiaceae (Miller 1979; Schmidt and Reeves 1984; Asghari et al. 2005). Nonmycorrhizal families also tend to be early colonisers of habitats created by disturbances such as volcanism, glaciation or erosion, but mycorrhizal plants soon become established in these new habitats (Allen 1988; Gemma and Koske 1990; Cázares et al. 2005). It has been well established that severe soil disturbance reduces the inoculum potential of mycorrhizal fungi, but they tend to be present in all but the most recently/severely impacted sites (Brundrett et al. 1996a; Jasper 2007). Consequently, lack of mycorrhizal fungus inoculum may contribute to the NM/AM status of plants in some habitats, where more intensive sampling is required to resolve the mycorrhizal status of plants (see Section on Resolving issues with diagnosis of mycorrhizas).

In a comprehensive study of 649 taxa in the Brassicaceae, DeMars and Boerner (1996) observed that 20 taxa contained hyphae and vesicles and the rest were fully resistant to an aggressive root colonising AM fungus. No samples had arbuscules. In contrast, Orlowska et al. (2002) considered *Biscutella laevigata* in the Brassicaceae to be AM, but arbuscules were only present in mature specimens of these annual plants. A detailed study of *Thlaspi* spp. in the Brassicaceae by Regvar et al. (2003) found GFC in some samples, but arbuscules were very rare. They concluded these associations were probably of no functional significance.

The Papaveraceae include many weeds and species well established to be NM such as *Chelidonium majus* (e.g. 43 samples all NM—Brundrett and Kendrick 1988), as well as those with AM such as *Sanguinaria canadensis* (18 samples all AM—Brundrett and Kendrick 1988). However, mycorrhizal relations of the later species are complex, because AM occurs in fine laterals, but not in coarser roots where orange-coloured metabolites that include fungistatic alkaloids are most visible (Brundrett and Kendrick 1988; Brundrett 1991). This example where AM and NM roots apparently occur simultaneously in a single host is worthy of further study. The Hydrophyllaceae are another family reported to include both NM and AM plants in separate genera.

Other NM or NM-AM families (8 families, ~1,700 spp.)

Other families reported to have NM species where the majority of species are not associated with harsh habitats are the Adoxaceae, Erythroxylaceae, Quiinaceae, Resedaceae, Capparaceae (sister to Brassicaceae), Hydrophyllaceae, Nyctaginaceae and Loasaceae (Table 2). Of these families, the Adoxaceae and Loasaceae, are poorly sampled. Members of the Erythroxylaceae and Quiinaceae accumulate very toxic alkaloids (Heywood et al. 2007). Fungistatic chemical accumulation is characteristic of many NM plant families (see Brundrett 1991).

Case Study 1: The relative importance of mycorrhizal and nonmycorrhizal roots in an ancient landscape with nutrient-poor soils

This case study is presented to demonstrate how knowledge of the nutrition of plant families can be scaled to a regional scale.

The Southwest Floristic Region of Western Australia is an internationally recognised biodiversity hotspot (Myers et al. 2000). High plant diversity in this region is linked to highly infertile soils and a long geological history without major tectonic or glacial disturbance

Fig. 11 The relative importance of specialised nutritional strategies for flowering plants in Western Australia (WA) in comparison with the whole World. Data are the ratio of actual over expected numbers of species, as explained in the text. Categories of plants with bars extending above the expected line (*1*) are more diverse in WA than they are on a global scale
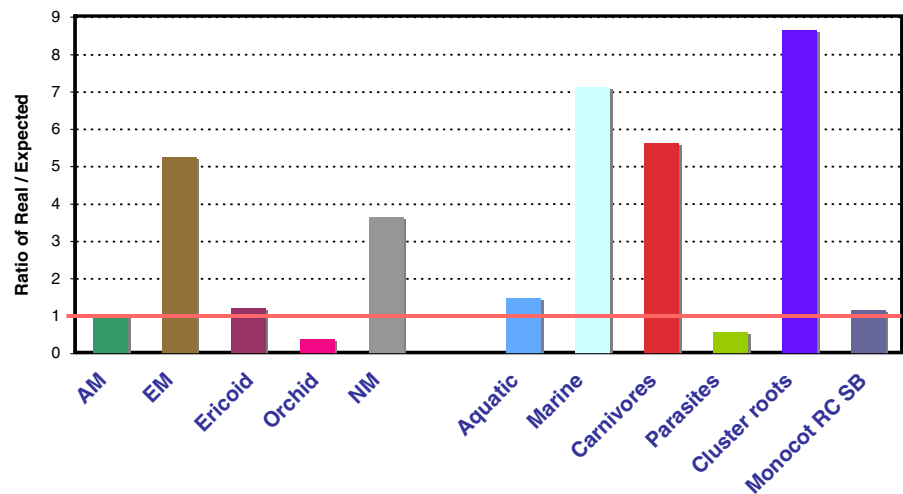
(Hopper and Gioia 2004). Figure 11 clearly shows that certain functional categories of roots or plant nutrition have become much more important in the ancient landscapes of Western Australia (WA) than elsewhere. These include NM plants in the cluster root, carnivore and marine plant categories, as well as EM hosts. Parasitic plants and orchids are less diverse than other highly specialised plants in WA (their centres of diversity are in the humid tropics). Western Australia has about 150 species of carnivores, most of which are endemic, which represents almost 1/4 of all carnivorous plants. These include over 100 *Drosera* spp. and 39 *Utricularia* spp (Florabase 2007). Western Australia is also a hotspot of diversity for marine angiosperms (seagrasses) with about 30% of known species (M. Cambridge pers. comm.).

It is well known that highly leached soils in the ancient landscapes of WA include many habitats where plants with cluster roots tend to be more abundant than elsewhere in the world (Lamont 1982; Lambers et al. 2006). However, plants with AM roots are also common in these habitats and there is a much higher diversity of plants with EM roots than would be expected (e.g. the Myrtaceae and Fabaceae are often dominant). In conclusion, it seems that the ancient landscapes and infertile soils of WA are linked to an exceptionally high relative diversity of plants with specialised means of mineral nutrition. It is likely that the former provided time for a high degree of speciation of plants in these categories, while the latter could explain their increased relative diversity relative to other ecosystems.

Mycorrhizal evolution revisited

The evolution of mycorrhizal associations has been discussed in considerable detail elsewhere (Pirozynski and Malloch 1975; Trappe 1978; Read et al. 2000; Brundrett 2002; Bidartondo 2005; Wang and Qui 2006), so only updated information is provided here. Detailed summaries of the relative importance to clades and orders of flowering and non-flowering plants are discussed in the previous sections and summarised in Figs. 12 and 13. Figure 13b includes the same data as Fig. 13a with AM hosts omitted to allow other categories to be seen more clearly. Only a very small basal group of flowering plants is poorly sampled and there is a high degree of consistency within many clades of angiosperms (Figs. 12, 13). As has already been well established, AM is the basal condition in all major groups of vascular plants and is still dominant in most orders and clades. At the clade level, most contain 2 or more nutrient strategies, but, the Euasterids I and II are predominantly AM plants (Fig. 13). Of the 54 orders of flowering plants, 22 are predominantly AM hosts.

Ectomycorrhizas occur in at least 10 separate lineages of the angiosperms and 2 in the Gymnosperms, but there almost certainly are multiple origins of EM within orders such as the Caryophyllales, and within families such as the Ericaceae, Fabaceae and Myrtaceae.

There are 90 families of NM or NM-AM plants (Table 2, Figs. 12, 13). These are dispersed throughout the angiosperms in at least 30 clades (the NM strategy likely originated more than once in some
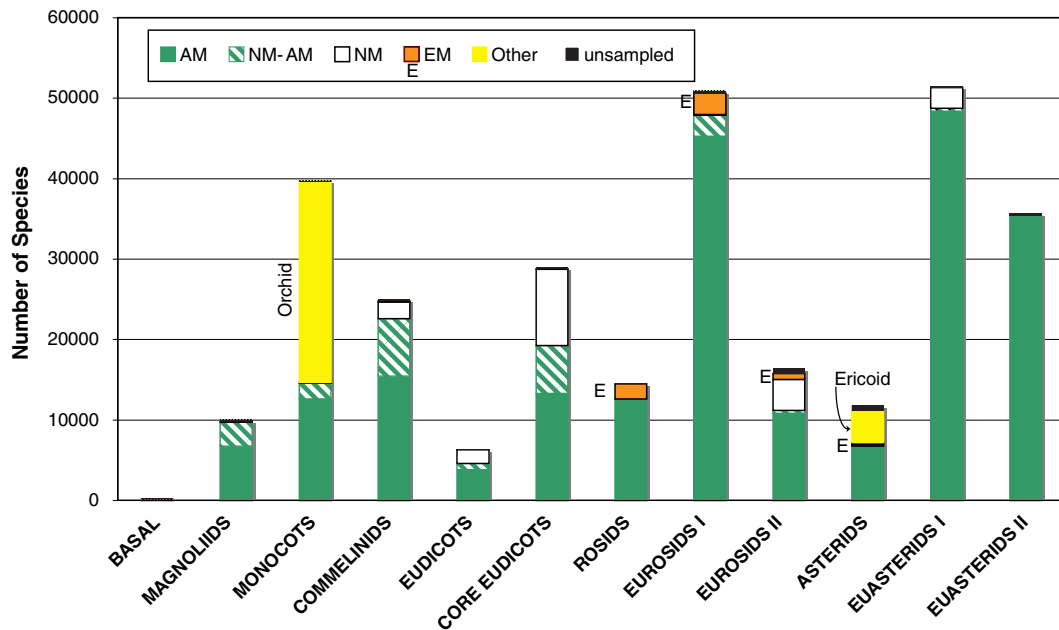
Fig. 12 The occurrence of mycorrhizas in clades of flowering plants (see Fig. 1 for Abbreviations)

clades). The largest aggregations of NM or NM-AM families within a clade are in:

- The Alismatales with 13 families including many hydrophytes.
- The Poales with 8 families including the Restionaceae, Cyperaceae and Juncaceae, with the Poaceae being an AM in-group. This clade also includes many variable NM-AM aquatic or epiphytic plants in the Typhaceae, Bromeliaceae, Sparganiaceae.
- The Caryophyllales with 14 families including halophytes and carnivores.
- The Santalales with 7 families of parasites (Der and Nickrent 2008).
- The Brassicales with 4 families.
- The Lamiales with 6 families of carnivores, parasites, or aquatic plants.

There are also many NM families that are isolated within clades of predominantly mycorrhizal plants, such as the Proteaceae and a number of other isolated groups of parasites, epiphytes and aquatic plants (some are unplaced within clades due to unresolved phylogeny). In other cases NM plants exist as a group or groups within families that also include AM hosts such as the Papaveraceae and Hydrophyllaceae. This situation also

occurs in families such as the Araceae, Piperaceae, Bromeliaceae that include substantial numbers of both terrestrial and epiphytic species, as well as in families with both aquatic and terrestrial members.

Orders with highly specialised NM plants, or myco-heterotrophs are displayed in Fig. 13c. Each of these strategies has arisen more than once in distantly related species including; 6 or more lineages of parasites, 4 of epiphytes, 5 of myco-heterotrophs outside the Orchidaceae, 3 of NM cluster roots, 6 or more of aquatics and 4 or more of carnivores. Assessment of the phylogeny of carnivorous plants has shown that *Drosera, Dionaea, Aldrovanda, Drosophyllum, Nepenthes* and *Triphyophyllum* are 2 closely related clades in the Caryophyllales (Cameron et al. 2002). Thus, the majority of carnivorous plants belong to a single lineage of predominantly NM plants in an order including many other NM plants (Aizoaceae, Caryophyllaceae, Chenopodiaceae, Polygonaceae, etc.). There are also many parasitic plants in a single lineage within the Santalales (Der

Fig. 13 The occurrence of mycorrhizas in orders of flowering plants. **a** All types of mycorrhizas. **b** Data as in **a**, but omitting AM to allow other categories to be seen more clearly. **c** Orders of plants with highly specialised nonmycorrhizal or myco-heterotrophic (MH) plants (see Fig. 1 for other abbreviations)
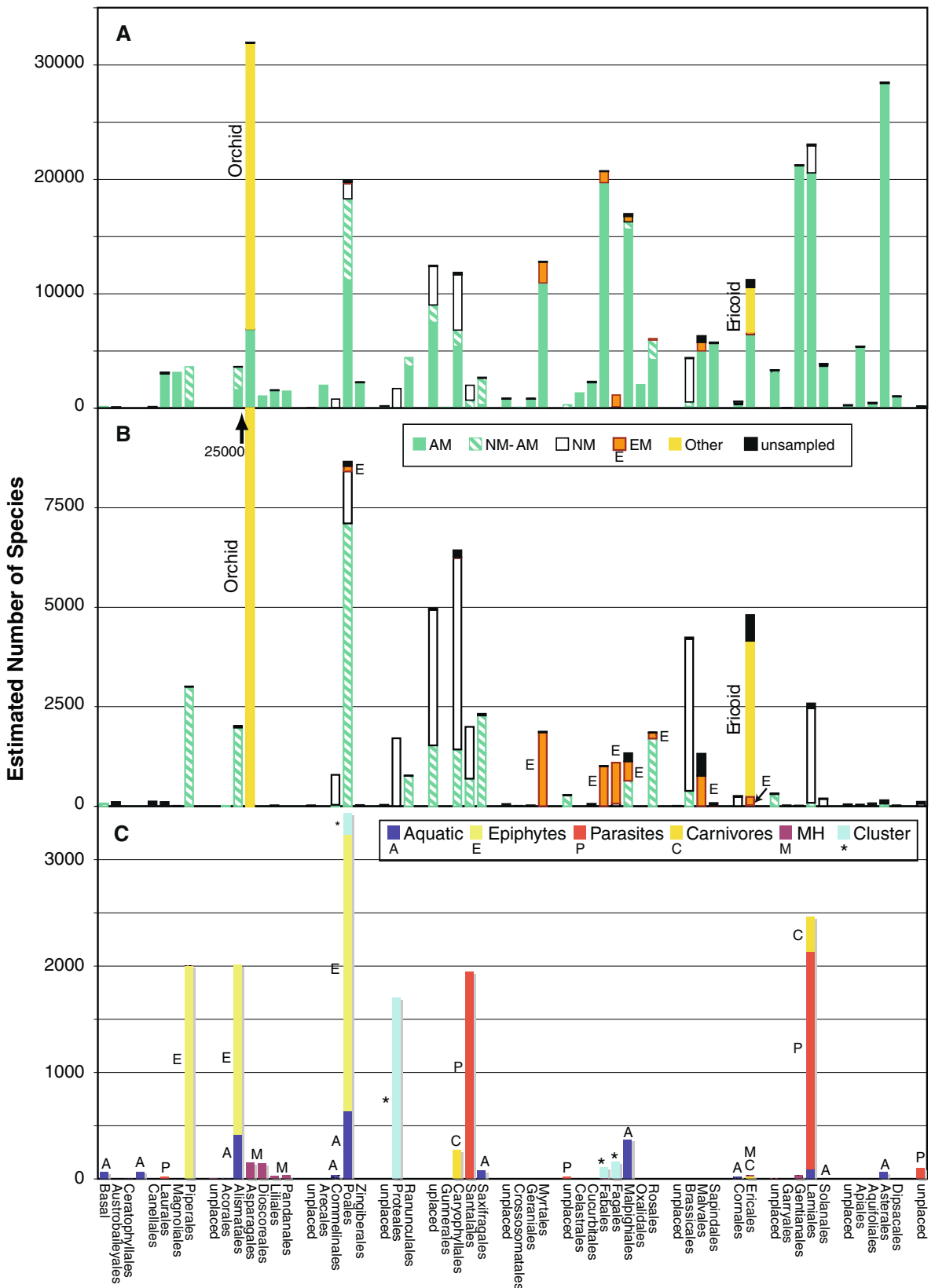
and Nickrent 2008). In some orders, plants that have lost the capacity to host AM seem to be more likely to evolve new nutrient acquisition mechanisms such as carnivory. In other cases, specialisations such as cluster roots or parasitism probably preceded the loss of mycorrhizas, which became redundant or impossible in the case of those parasites or aquatic plants that lack soil contacting roots at maturity.

Earlier reviews by Trappe (1987) and Wang and Qui (2006) also summarised data for substantial numbers of flowering plants. Reorganisation of the "tree of life" for plants makes it difficult to compare clades in Trappe (1987) with those presented here. However, results are in agreement for aquatic mono-cots with NM or NM-AM roots (Alismatales, etc.) and for some orders of NM or EM plants (Fagales, Santalales, etc.). Wang and Qui (2006) list families as NM that are known to have mycorrhizal roots (Isoetaceae, Adoxaceae, Bromeliaceae, Butomaceae, Cannaceae, Erythroxylaceae, Loasaceae, Menyantha-ceae and Nymphaeaceae), or were only represented by a single report (Cyclanthaceae, Limnocharitaceae, Bataceae, Butomaceae). As stated by Harley and Harley (1987), single reports are not sufficiently reliable to make a diagnosis about the presence or absence of mycorrhizas for a family. Wang and Qui (2006) also list several families as AM that are considered by most mycorrhizologists to consists predominantly of NM species (Brassicaceae, Junca-ceae, Proteaceae, Restionaceae) and classify some NM-AM families as AM (Cyperaceae, Papaveraceae). The approach in the current review differs from that of Wang and Qui (2006) by developing a consensus view of the literature for each family, by discounting occasional contradictions that are likely to be errors and by allocating inconsistently mycorrhizal families in the NM-AM category. In summary, the majority of NM families designated by Wang and Qui (2006) are not in accordance with those recognised here (i.e. they only recognised 21 NM families, of which 9 are probably incorrect, while over 90 are recognised here).

The evolution of nutrient-uptake mechanisms, such as new types of mycorrhizas or NM cluster roots, seems to have coincided with the origin of many plant families which apparently became more competitive in certain habitats (Brundrett 2002). We would assume that these mechanisms provided a selective advantage due to increased nutritional efficiency relative to associated costs. However, analysis of the costs and benefits of root nutrient-uptake mechanisms is complex, because mycorrhizal plants remain dominant in most habitats, while most NM plants are marginalised in wet, saline, dry, disturbed, or cold habitats or extremely infertile soils, where plant productivity is low and inoculum of mycorrhizal fungi could be scarce (Brundrett 1991).

Conclusions

Different approaches have been used to summarise data on the relative diversity of plants with mycorrhizas and other plant nutrition adaptations at different scales. These scales include locations, habitats, regions, ecosystems, or the whole world. Data on the relative dominance of mycorrhizal plants at the ecosystem level provides the most accurate indication of the ecological importance of these associations (St John and Coleman 1983), but is available for few locations and cannot be determined on a global scale. In this review, a summary of mycorrhizal association data for families, orders and clades of flowering plants allowed the total diversity of all plants with mycorrhizal roots to be accurately calculated on a global scale for the first time. The same approach was also applied at a regional scale in Western Australia to reveal major trends in plant adaptation in ancient landscapes.

There now is sufficient data to establish the category or categories of mycorrhizal association or other nutritional strategies of most families and orders of flowering plants. Consequently there is little need of further studies that only produce list of mycorrhizal plants unless they target gaps in existing knowledge by including:

1. Poorly sampled habitats.
2. Un-sampled plant families.
3. Families with complex root strategies, such as the Fabaceae in Australia where the relative diversity of plants with AM, EM or NM-cluster roots is unresolved.
4. Plants in variable NM-AM families, especially if detailed information about seasonal variation or habitat effects on colonisation is provided.
5. Mycorrhizal colonisation data linked to data on plant diversity, ecology or physiology at the ecosystem scale.
6. Corrections to the status of families or genera published in earlier studies.

Part II. Mycorrhizal Diagnosis and Misdiagnosis

Quantifying methods and estimating error rates
in published data

Compilation of data from 128 published lists of
mycorrhizal plants, as reported in Part I, also allowed
the relative importance of different criteria for diagno-
sis of AM and data used to make these diagnoses to be
categorised (Figs. 14, 15). This analysis revealed that
despite considerable improvement in our knowledge
of how mycorrhizal associations work over more than
a century of progress, no consensus has emerged
about how they should be identified. Problems with
mycorrhizal definitions can contribute to confusion
about which families have mycorrhizal or NM roots,
as is discussed below.

Since mycorrhizas formed by Glomeromycotan
fungi are now routinely described as arbuscular
mycorrhizas (AM) rather than as vesicular-arbuscular
mycorrhizas (VAM), we would expect that most
reports of the occurrence of these associations to be
based on observations of arbuscules. However, as Fig.
14 shows this is not the case. In fact, arbuscules were
only used to identify about 1/4 of AM species listed
in publications (it is unlikely studies which do not
state which criteria were used relied on arbuscules).
The reasons why arbuscules are important, but should
not be the only criteria used for diagnosis are explained
in Part J below.

Error rates in mycorrhizal diagnosis can only be
estimated by assuming that most plant families
consistently have mycorrhizal or NM roots, when
there is sufficient sampling for this to be determined.
Even when problematic families and habitats are
excluded, the overall error rates in diagnosis of AM,
NM and EM roots are higher than might be expected

(Fig. 15). In Fig. 15, possible misdiagnoses of
mycorrhizas are referred to as;

1. amAM—which is apparently misdiagnosed AM
   in a family of predominantly NM plants,
2. amNM—which is apparently misdiagnosed NM
   in a family of mycorrhizal plants, or
3. amEM—which is apparently misdiagnosed EM.

The overall apparent rate of misdiagnoses for
mycorrhizas of AM, NM and EM is about 10%
(Fig. 15). The largest category for potential errors
(amNM) results when plants in typically mycorrhizal
families are not found to have AM. This could result
from inadequate methods (processing of roots), or
poor samples, and indicates mycorrhizologists are
most likely to err on the side of under-detection.
Overly stringent diagnostic criteria result in an
increased probability of failure to diagnose AM
(Section Resolving issues with diagnosis of mycor-
rhizas). For example, a survey of over 300 species
had a high amNM rate of about 30%, but this can be
reduced to 10% if samples with vesicles but no
arbuscules are considered AM, as is most often the
case in other studies. The errors reported in Fig. 15
result from both a low overall rate across all studies
and a much higher rate of apparent errors in several
large surveys that included many taxa with limited
sampling of each. However, any apparent correlation
between the size of surveys and apparent errors is
contradicted by other large studies with low apparent
error rates, such as Maeda (1954) who sampled >1000
spp. and had very few contradictory results at the
family level.

Types of data presented in publications on mycor-
rhizal plants are also summarised in Fig. 15. As was
the case with diagnosis, data on the occurrence of
arbuscules in root samples is only presented in 1/4 of

Fig. 14 The relative
frequency of use of criteria
used for AM diagnosis
(*A* arbuscules; *HVA* hyphae,
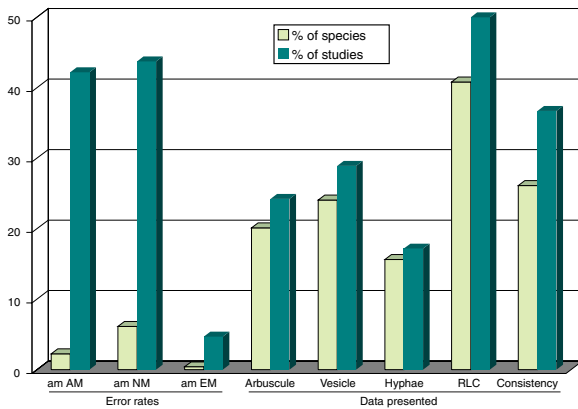vesicles or arbuscules; *?* not
stated)
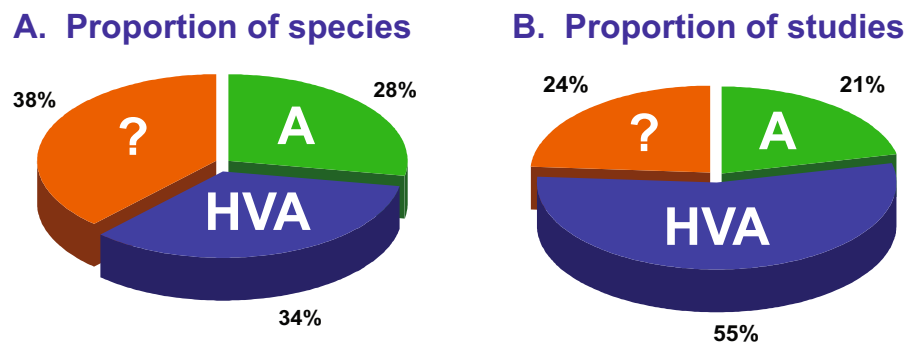
Fig. 15 Apparent error rates for diagnosis of arbuscular mycorrhizas (amAM), nonmycorrhizal roots (amNM), or ectomycorrhizas (amEM) in mycorrhizal studies are shown in the first three double columns. The remaining 5 double bars show the frequency of publication for different categories of data used in mycorrhizal diagnosis. In all cases, the first bar represents the proportion of taxa across all studies (128 publications) and the second column represents the proportion of studies in each category. Data are from the same sources used in Fig. 4

studies, so it is often not possible to check how diagnosis was performed when results are unexpected. Mycorrhizal data presentation in the literature is inconsistent and usually does not allow diagnostic criteria to be applied retrospectively (Fig. 15). In particular:

- Colonisation data may be presented as % RLC, or as a scale, or only presence or absence is noted.
- Sampling replication is often low, or not stated.
- Data on variability or consistency within species is rarely presented. Standard errors are sometimes presented, but may to be pseudo-replication in some cases.
- Arbuscular and vesicular data are often not presented separately from RLC data.
- Morphological criteria for diagnosis of mycorrhizas are often not applied or are not stated in methods.
- In the majority of cases, vesicles and hyphae are of equal or greater importance to arbuscules in the diagnosis of AM.
- Diagnosis of EM is also not always reliable, as some reported associations lack a Hartig net (see Section on Diagnosis of ectomycorrhizas (EM) below).

Case study 2: Resolving conflicting data for the Cyperaceae, Juncaceae and allied families

The purpose of this case study is to summarise data on the Cyperaceae in an attempt to understand why this plant family has been repeatedly diagnosed as NM by many authors, while others consider sedges to be AM hosts. Detailed information on sedge roots from published reports that included many species or samples of sedges is summarised below.

- Powell (1975) found sedges and rushes (Cyperaceae, Juncaceae) were predominantly NM, 36 of 88 spp. had sparse GFC and arbuscules were not reported. They also did not form AM in pots after inoculation.
- Brundrett and Kendrick (1988) found 2 upland *Carex* species were consistently NM throughout the year (28 samples).
- Meney et al. (1993) sampled 12 species of sedges and rushes (Restionaceae) in Western Australia and found 4 species had GFC, but only later in the growing season.
- Cooke and Lefor (1998) found the Cyperaceae (18 spp.), Juncaceae (6 spp.) had highly variable GFC across taxa and sites (AM not defined by arbuscules).
- Miller et al. (1999) reported GFC in 16 of 23 *Carex* spp., but only 9 contained arbuscules.
- Muthukumar and Udaiyan (2002) studied the phenology of 2 tropical sedges and found GFC varied seasonally, but no arbuscules were formed.
- Fuchs and Haselwandter (2004) reported *Carex* sp. in bogs had GFC colonisation that varied seasonally and between sites (4% RLC without arbuscules).
- Ruotsalainen and Aikio (2004) found that the presence of AM fungi reduced the growth of a *Carex* sp. when it was growing in competition with a host plant.
- Gai et al. (2006) found 9 sedges in Tibet had GFC, but only 10 of 22 samples had arbuscules (*Kobresia* spp. apparently lacked EM in this study).
- Perrier et al. (2006) found 3 tropical sedges in New Caledonia had variable GFC, but low mycorrhizal intensity. Arbuscules were not quantified separately.
- Weishanpel and Bedford (2006) studied 10 sedge species that were primarily NM, but 5 of 17

samples had low GFC (2–18% RLC), including 3 of 17 with traces of arbuscular colonisation (<3% RLC).

• A detailed literature review by Muthukumar et al. (2004) summarised data from 221 sedges of which 40% were considered to have AM. However, they noted that the majority of root samples lacked arbuscules and concluded that sedges have a low capacity for mycotrophy.

Several alternative hypotheses that could explain the variable reports of AM and NM in sedges and rushes and may apply to other families with NM-AM roots are:

1. These are NM plants with occasional endophytic GFC (sometimes with arbuscules) due to specificity errors or resistance breakdown in older roots that is misdiagnosed as AM.
2. There is a continuum extending from fully NM to AM species in the Cyperaceae, and some other families resulting from continuing adaptation to variable habitat conditions.
3. Sedges are potentially AM plants, but often occur in mycorrhiza-suppressive habitats.
4. Error rates in published data are too great to allow reliable conclusions.

Some of the evidence cited above supports the first hypothesis, in that GFC is more likely to occur in older sedge roots and most reports of putative AM in sedges state these are inconsistent or sparse and they usually lack arbuscules. This would imply that sedges are functionally NM plants that cannot fully exclude relictual GFC (perhaps the carbon drain from sparse colonisation is negligible). Comprehensive studies of mycorrhizal root phenology using a rigorously applied definition of AM and a high degree of sampling replication, both within species and throughout the growing season, are required to investigate this hypothesis.

The second hypothesis is supported by the fact that the Cyperaceae is a very large family that occupies diverse habitats. Variable mycorrhizal relationships could be linked to habitat factors that result in adaptation to stressful conditions such as waterlogged and cold soils. However, this could also be indicative of flaws in the processes used to designate AM and NM plants, as explained below. Examples that support a high capacity for evolution of new root

types in sedges include arctic sedges in the genus *Kobresia* which are the only monocots to have acquired EM associations, and are presumably descended from a NM ancestor.

There is good evidence to refute the third hypothesis, as some sedges have consistently NM roots in warm dry habitats. The fourth hypothesis seems likely to be a major contributor to conflicting reports of AM in sedges, but is unlikely to be its sole cause.

When assessing the literature on putative AM of sedges it seems most likely that conflicting data results, at least in part, from a failure to use consistent criteria to identify mycorrhizal associations. In this review a precautionary approach has been taken that classifies the Cyperaceae as a variable NM-AM family. However, the balance of information seems to suggest they are a predominantly NM family, with only sporadic GFC in roots. It is possible that all arbuscules in sedges occur in older roots and that young sedge roots are highly resistant to mycorrhizal fungi. If the Cyperaceae are designated as a true NM plants (as opposed to variable NM-AM) the error rate for mycorrhizal diagnoses in published data will increase substantially. This also requires us to acknowledge that arbuscules occur sporadically in NM plants, further weakening the role of arbuscules in defining AM. The confusion about the mycorrhizal status of families such as the Cyperaceae needs to be resolved by more rigorous approaches to diagnosis, as is explained below.

Glomeromycotan fungus colonisation (GFC) in predominantly NM plant families

Since the majority of reports of AM in AM-NM families such as the Cyperaceae did not use arbuscules to diagnose associations, inconsistent colonisation data of these families, may be indicative of misdiagnosis of endophytic growth of hyphae and vesicles without arbuscules in roots as AM. Endophytic activity by Glomeromycotan fungi (which is often referred to as saprophytic growth) is relatively common in various plant organs (e.g. Stasz and Sakai 1984; Warner 1984; Smith et al. 1998; Brundrett 2006; Zhang and Guo 2007). Humans like to have clearly defined boundaries between alternatives we consider important (i.e. we have a tendency to see the world in black and white). However, fungi are not constrained by our world-view and are opportunists

that constantly seek to exploit new situations as endophytes or mycorrhizal partners.

Endophytic GFC is likely to be of only minor ecological significance to plants or fungi and needs to be distinguished from more important plant-fungal associations. It is recommended that Glomeromycotan fungi in roots be labelled GFC in cases where a mycorrhizal association cannot be confirmed (Appendix 2). Fungi known to be mycorrhizal in roots should not be called endophytes, as this contradicts the diagnosis of mycorrhizas. Consistent use of terminology, especially in titles and keywords, is required to avoid confusion and allow knowledge to be retrieved by computerised literature searches.

While it is safe to diagnose roots that never contain arbuscules, but may contain some hyphae and vesicles as NM roots with GFC, the diagnosis of roots with occasional arbuscules is more difficult to resolve, as revealed by the Cyperaceae case study. For example, Hildebrandt et al. (2001) found occasional GFC in roots of members of the Juncaceae, Juncaginaceae and Caryophyllaceae (mostly under 10% RLC) with a few arbuscules (3% RLC in 1 sample). Other examples of occasional arbuscules in plants normally considered NM include the Brassicaceae (Orlowska et al. 2002; Regvar et al. 2003) and Proteaceae (Bellgard 1991; Boulet and Lambers 2005) and epiphytic bromeliads (Rowe and Pringle 2005). In some cases we need to be cautious about calling the observed structures arbuscules, as published images are inconclusive, or no images are provided. Brundrett and Kendrick (1988) distinguished AM and endophytic growth by Glomeromycotan fungi by sampling roots throughout the year to develop an understanding of root and mycorrhizal phenology. They observed that hyphae and vesicles were only present in senescent roots in NM plants, so were not the remnants of mycorrhizal associations.

A key question that arises from the frequent apparent misdiagnosis of AM in sedges reported in case study 2 is: How many arbuscules are required for a functional AM association? If arbuscules are rare, or only occur in old roots they are unlikely to be of major functional significance, but further anatomical and physiological research is required to determine if this is the case. There may also be varying degrees of endophytic activity by Glomeromycotan fungi, perhaps due to differing exclusion mechanisms by non-hosts. GFC could also be strongly influenced

by environmental factors. The declining resistance of NM plants (e.g. annuals growing in seasonal environment) to AM fungi with age often seems to coincide with changes in environmental conditions, such as drying out of aquatic habitats, making them more favourable to GFC. Thus is may be essential to sample roots at different phases of the growing season to resolve association types. The diagnosis of NM and AM roots is inextricably linked, as any roots not diagnosed with mycorrhizas are considered to be NM.

There are several possible explanations for reports of AM in predominantly NM plant families:

i.   There are no fully NM plants since they all have the capacity to occasionally form AM,
ii. There are no fully NM families since they all contain a few species with AM,
iii. The occasional reports of AM in NM families are errors in sampling, assessment, or diagnoses that fall within the expected error rate (~10%), and/or
iv. True NM plants have occasional AM that can include a few arbuscules, but these are not functional mycorrhizas.

The first of these alternatives has been shown to be incorrect by detailed studies demonstrating that roots of NM plants were resistant to high inoculum levels of Glomeromycotan fungi (e.g. Brundrett and Abbott 1991; Hirrell et al. 1978; DeMars and Boerner 1996). The second alternative has been confirmed for a few NM-AM families such as the Papaveraceae, but seems unlikely for most others. There is strong evidence to support both the third and fourth alternatives for the majority of NM families, as summarised above. Consequently, we should be prepared to expect occasional GFC in the roots of NM plants and may also have to acknowledge that these roots may contain a few arbuscules without having functional AM associations.

Diagnosis of ectomycorrhizas (EM)

Misdiagnoses of EM associations are much less common than misdiagnoses of AM, presumably due to the less frequent occurrence of EM and the major alterations in root structure that normally occur. However, atypical EM-like associations that are difficult to categorise do occur, as shown by examples in Table 3. Misdiagnosis of EM could have major

Table 3 Examples of unusual reports of ectomycorrhizal associations

Families	Genera	Mantle	Hartig net	Apoplast interface	Habitat	Location	References
Apocynaceae, Lamiaceae, Capparidaceae, Oleaceae	*Nerium, Cleome, Mentha, Sida, Olea, Bramia,*	V	?	?	Arid	Pakistan	Saif 1975
Myrtaceae, Fabaceae, Bignoniaceae	*Campomanesia, Bauhinia, Jacaranda?*	V	?	?	Cerrado	Brazil	Thomazini 1973
Ericaceae	*Cavendishia Disterigma, Gaultheria*	V	V	X	Epiphytes	Costa Rica	Rains et al. 2003; Setaro et al. 2006
Cyperaceae	*Carex*	Y	X	?	Temperate	Ireland	Harrington and Mitchell 2002
Melastomataceae	*Graffenrieda*	V	V	X	Tropical	Ecuador	Haug et al. 2004
Asteraceae, Goodeniaceae, Polygalaceae, Sterculiaceae	*Angianthus, Podolepis, Waitzia, Helipterum, Dampiera, Goodenia, Comesperma, Lasiopetalum, etc.*	V	X	X	Temperate	Australia	Kope and Warcup 1986; Warcup and McGee 1983; McGee 1986
Rosaceae	*Adenostoma*	V	X	X	Arid	USA	Allen et al. 1999
Poaceae, Rosaceae, Caryophyllaceae, Asteraceae	*Homogyne, Daphne, Crepis, Helianthemum, Potentilla, Festuca, Silene*	V	?	?	Alpine	Austria	Read and Haselwandter 1981
Asteraceae, Hydrangeaceae, Onagraceae, Sapindaceae	*Anaphalis, Acer, Hydrangea, Weigela, Epilobium*	V	?	?	Alpine	Japan	Tsuyazaki et al. 2005
Asteraceae, Onagraceae, Rosaceae	*Senecio, Epilobium, Potentilla, Sorbus*	V	?	?	Alpine	USA	Cázares et al. 2005
Orobanchaceae (Scrophulariaceae)	*Pedicularis*	V	?	?	Alpine	China	Kohn and Stasovski 1990; Li and Guan 2007

V variable, *Y* present, *X* absent, *?* not described or illustrated

consequences to our understanding of ecosystem processes if dominant trees in ecosystems are involved. However, most EM hosts belong in families well documented to have these associations and nothing else (or have both EM and AM in roots), but some are restricted to particular genera within a family of AM or NM hosts and others have both EM and AM (listed in Table 1).

Most examples listed in Table 3 seem to result from application of an imprecise definition of EM (where the Hartig net is not required), or associations that appear to be intermediate between EM and ericoid or saprobic growth of hyphae on roots (Brundrett 2006). Many of the unusual associations in Table 3 occur in alpine habitats. One example is *Pedicularis* spp. which are hemiparasites in the Orobanchaceae (Scrophulariaceae) reported to be EM in some alpine studies (Kohn and Stasovski 1990; Li and Guan 2007), but not others (Cázares et al. 2005; Gardes and Dahlberg 1996).

It is reasonable to expect that the EM interface (Hartig net) must be connected to the apoplastic space of roots and also must be sealed or enclosed to prevent loss of metabolites into the soil to allow effective nutrient exchange. For example, a strong relationship between the degree of Hartig net formation and growth responses was observed when screening isolates in a glasshouse trial (Burgess et al. 1994). In EM roots the zone of exchange is usually delimited by a suberised exodermis or the endodermis within the root and a well developed mantle on the outside and there are substantial morphological responses by host cells to produce an effective interface (cell enlargement, transfer cells, etc.) (see Brundrett et al. 1990; Vesk et al. 2000; Peterson et al. 2004). In Table 3 it is assumed roots are not EM if they lack a substantial plant-fungus interface.

There are many cases of probable EM misdiagnoses in literature published before morphological definitions of associations to became standardised.

These are not errors as such since they represent the state of knowledge at that time they were originally published, but cause confusion when perpetuated in more recent publications. For example, *Acer, Fraxinus, Ulmus,* the Cupressaceae, etc. were included in EM hosts lists by Trappe (1962) and subsequent authors (e.g. Smith and Read 1997). The Cupressaceae were once assumed to be hosts for EM fungi that fruited in habitats where they co-occur with conifers in the Pinaceae (roots were not sampled). Plants with beaded roots are also more susceptible to confusion than other plants, as they appear heterorhizic if not examined carefully (e.g. *Acer, Ulmus*, and members of the Podocarpaceae), but the AM status of these trees is now well resolved. There are also cases where it seems likely that field-collected root samples were contaminated by roots of other species, such as reports of EM in ferns. Warcup and McGee (1983) observed unusual associations in families such as the Asteraceae and Stylidiaceae, which were not found to be EM by other investigators (Table 4).

As discussed above, the Hartig net-like structures on the root surface will not function as exchange site if substances produced by the fungus escape from the root, but the fungus may benefit by capturing exudates. In the case of *Graffenreda* sp. (Haug et al. 2004) the root primarily hosts AM, which would have much greater access to internally released metabolites. Epiphytic Ericaceae with "cavendishoid mycorrhizas" (Setaro et al. 2006) are unlikely to function as EM since contact between the putative Hartig net, which is inconstantly present and weakly developed, primarily occurs on the outer surfaces of epidermal cells containing ericoid mycorrhizas. Rains et al. (2003) considered these associations to be ericoid mycorrhizas. A patchy mantle has also been observed on other ericoid roots (Massicotte et al. 2005). Other EM-like associations that appear to be non-functional include those of *Morchella* sp. on Pinaceae (Dahlstrom et al. 2000), *Cortinarius* sp. on *Carex* (Harrington and Mitchell 2002) and *Tricholoma* sp. on *Pinus* (Gill et al. 1999). Some fungi considered to be EM associates may actually be parasitic on EM roots (Yun and Hall 2004).

The opportunistic colonisation of root surfaces by fungal hyphae is common in nature and perhaps should be considered a form of endophytism where

Table 4 Criteria to identify mycorrhizas using evidence based on definitions (after Brundrett 2004)

Component	Arbuscular mycorrhizas	Ectomycorrhizas	Other
1. Interface of specialised hyphae with intimate host-fungus contact	Intracellular-arbuscules (coils in exploitative hosts)	Extracellular (but enclosed)– Hartig net + intracellular hyphae in some cases	Intracellular coils
2. Interface occurs in/on specialised plant cells	Temporary cellular response to arbuscules	Radial enlargement of root cells (cell wall ingrowths in some cases)	Cellular responses and digestion of coils (orchid)
3. Plant controls intensity and duration of association	Root growth and arbuscule digestion	Altered root system growth and branching	Hyphae re-colonise cells i(orchid)
4. Coordinated development in young roots	Old roots lack arbuscules	Inactive in old roots	Not coordinated in orchids?
5. Fungus to plant nutrient transfer	Plant consistently has fungal associations in a substantial proportion of young roots (which usually lack substantial modifications for direct nutrient uptake)		
6. Plant to fungus nutrient transfer	Abundant vesicles and/or sporulation	Substantial mantle and/ or fruiting of fungi	May not occur (orchid), expected to occur (ericoid)
7. Fungus is a specialised plant-inhabitant	Fungus growth and sporulation requires a host and fungus always occurs with hosts		Fungus independent (orchid)
8. Fungus is a specialised soil inhabitant	Substantial soil hyphal network, sporulation is usually in/on soil		

fungi feed on root exudates without penetrating cells (see Brundrett 2006). In conclusion, there needs to be a reasonable prospect that mycorrhizal associations can function by providing balanced two-way exchange before we should call them EM. It is not possible to resolve if some of the associations listed in Table 3 are diagnosis errors or unusual new associations without additional anatomical and physiological studies. A list of EM host plants that is as accurate as possible is provided in Table 1 and will be maintained online (mycorrhizas.info/ecm).

Practical definitions of mycorrhizal associations

Anatomical features of mycorrhizas must be observed to distinguish them from other fungi in roots (Brundrett 2004). Any attempt to define mycorrhizas by physiological parameters such growth responses would be impractical, since such information is usually not available. For example, mycorrhizal growth responses have been measured for about 200 host plants from natural ecosystems grown at realistic soil fertility levels (Brundrett and Abbott 2002). In contrast, the anatomy of the root-fungus interface has been used to identify mycorrhizas in over 10,000 plants (see Section on Summary of mycorrhizal survey data). Thus, mycorrhizas are defined by anatomy alone > 99.9% of the time. See Brundrett (2004) for a more comprehensive discussion of this topic.

A revised definition of mycorrhizas was provided by Brundrett (2004) to exclude non-mycorrhizal symbioses in roots and to encompass all types of these symbioses. This definition is based on developmental and functional features that distinguish and unify mycorrhizas, so these features can also be used for diagnosis of associations. These criteria are summarised in Table 4 and explained in the list below:

1. The structure and development of mycorrhizal fungus hyphae is substantially altered in the presence of roots of host plants. These root-inhabiting hyphae are structurally and functionally distinct from hyphae formed in soil by the same fungus.
2. Mycorrhizas require intimate contact between hyphae and plant cells in an enclosed interface where nutrient exchange occurs.
3. The primary role of mycorrhizas is the symbiotic transfer of mineral nutrients from fungus to plant.

In most cases there also is substantial reciprocal transfer of metabolites from plant to fungus (i.e. mutualism).
4. Mycorrhizas require synchronised plant-fungus development for ongoing nutrient exchange, since hyphae normally only colonise young roots in mutualistic associations.
5. Plants control mycorrhizal associations by growth of new roots, digestion of old interface hyphae in plant cells (AM, orchid), or altered root system form (EM).

Existing published reports often provide several lines of evidence for mycorrhizal diagnosis (e.g. percentage root length colonised, and arbuscular colonisation), but rarely link the diagnosis of mycorrhizas to such evidence in a reproducible way. As Figs. 14 and 15 show there are more published reports that do not state which criteria were used and lack detailed root colonisation data than those that do. Consequently, we should not be surprised that there are many examples of contradictory data in the literature that probably arise from differences in interpretation of such data. The misdiagnosis of AM and NM roots is particularly common, as discussed in Part L above. The following subsections discuss criteria for diagnosis of mycorrhizal roots and more detailed protocols are provided in Appendix 2. Methods for processing root samples are available elsewhere (e.g. Brundrett et al. 1996b, mycorrhizas.info/method).

Arbuscular mycorrhizas (AM)

It is ironical that as we increasingly tend to drop the V (vesicles) from the name of arbuscular mycorrhizas (from VAM to AM), evidence is accumulating that some of these associations lack arbuscules, that vesicles are used more often than arbuscules in diagnosis of associations, and that arbuscules may occur in non-host plants where Glomeromycotan fungi grow as endophytes. Examples of AM associations without arbuscules include non-photosynthetic, myco-heterotrophs with exploitative AM and primitive ferns such as *Psilotum* and *Botrychium* (Peterson et al. 1981; Imhof 1999b; Winther and Friedman 2007). A new approach to the diagnosis of AM is required to reconcile discrepancies in lists of host and non-host plants. Thus, while it is fairly safe to use

arbuscules as the main diagnostic criterion in most cases, other evidence is also required to show that the morphology of associations are consistent with AM, as discussed in Appendix 2.

Protocols in Appendix 2 are designed to help prevent errors in the diagnosis of AM. These errors result primarily because arbuscules are not used to define AM in most field-collected roots, since they are difficult to observe in older roots. A more inclusive approach using arbuscules in combination with other diagnostic criteria listed in Table 4 should help distinguish endophytic GFC activity in NM roots from old AM associations. However, in some cases it may not be possible to distinguish AM or endophytic activity by Glomeromycotan fungi and these should be referred to as GFC. However, diagnosis of fungi in roots as GFC does not resolve its mycorrhizal status as it can imply that either a plant is NM with endophytic fungi or that knowledge of its mycorrhizal status is unresolved due to inadequate data.

Ectomycorrhizas (EM)

The presence of a Hartig net defines EM associations (Brundrett 2004). It is easy to recognise typical associations with a prominent mantle and thickened roots with an altered branching pattern. However, there are cases where root branching is not greatly altered, the mantle is thin or absent, or a well-developed Hartig net is not present (Table 3). As explained above, EM-like associations without a normal Hartig net may lack functional significance so should not be recognised as EM, especially when they are not the main type of mycorrhizal association present.

Nonmycorrhizal plants

Nonmycorrhizal plants have roots that remain free of mycorrhizal fungi in habitats where other plants are mycorrhizal (Selivanov and Eleusenova 1974; Tester et al. 1987; Brundrett 1991; Koide and Schreiner 1992). However, in some cases these roots of NM plants contain traces of endophytic hyphae and vesicles of Glomeromycotan fungi and sometimes may also have a few arbuscules. Absence of mycorrhizas in these species is not regulated by habitat conditions, even though they often occur in harsh habitats (Table 2).

Facultative or variable mycorrhizas

The recognition of NM-AM plants in this review as a category of variable mycorrhizas as defined by habitats as well as plant phylogeny differs from earlier approaches where facultatively mycorrhizal plants where defined by inconsistent or sparse mycorrhizal colonisation, or by soil fertility, as is summarised below.

1. Facultative mycorrhizal species were originally defined as plants with roots that remain poorly colonised in soils where other species are highly mycorrhizal (usually < 25% of suitable roots) (Janos 1980; Brundrett 1991). These plants typically have fine roots with long root hairs as observed by Baylis (1975), St John (1980) and many others.

2. More recently, physiological definitions of facultative mycorrhizas have been defined using nutrient response curves regulated by P availability (Abbott and Robson 1984; Schweiger et al. 1995; Janos 2007). In these experiments species with fine roots and long root hairs were less dependant on mycorrhizas than plants with coarse roots and few root hairs. This is a valuable approach for cultivated plants, but is less applicable to plants growing in natural habitats where soil P levels cannot be manipulated.

3. A third concept presented in this review concerns variable mycorrhizas of a species, genus or family where colonisation is regulated by habitat conditions, as explained in Part I. These are designated as variable NM-AM plants. This variability may be linked to sampling time, or habitat conditions and is especially common in epiphytes, hydrophytes and arctic plants. A similar definition of facultative AM was used by Trappe (1987) to deal with contradictions in the mycological literature.

4. A few families are known to include plants in different genera that are consistently either AM or NM plants. Examples include *Atriplex* species in the predominantly NM family Chenopodiaceae and the NM-AM family Papaveraceae (see Section on Predominantly nonmycorrhizal plant families with specialised nutrition).

The first 2 definitions of facultative mycorrhizas listed above are usually only applied at the species

level, while the third concept (NM-AM) can apply to species or families. The fourth concept can only be applied to variability within families. In the current review, only NM-AM families are recognised, since facultative AM as defined by 1 or 2 above can not be designated in most publications due to insufficient data on root colonisation consistency. Facultative mycorrhizas should be suspected if plants have relatively fine roots with long root hairs and are weakly colonised by mycorrhizal fungi.

Resolving issues with diagnosis of mycorrhizas

How do we minimise both Type 1 and Type 2 errors in mycorrhizal diagnosis

In statistics we need to minimise both Type 1 (rejecting a true hypothesis) and Type II (accepting a false hypothesis) errors in analysis of data. In the case of mycorrhizal associations we will commit a Type I error if we overlook, or misinterpret diagnostic criteria, or a Type II error if we reach conclusions not supported by these criteria. Type I errors could include failure to diagnosis AM in old roots due to the absence of arbuscules, but Type 2 errors seem to be more common (i.e. identification of AM from endophytic hyphae and vesicles in non-host plants). In EM associations, examples of Type II errors would also result if EM hosts were designated without a Hartig net. In statistics it is also recognised that these errors cannot be avoided entirely, but analysis protocols are designed to ensure they will be minimised at an acceptably low rate. Mycorrhizal research protocols can be designed to minimise Type I and Type II errors (Appendix 2) and we need to acknowledge that these errors occur in published data.

Use of multiple sources of evidence

It is very difficult to distinguish between endophytic and mutualistic colonization of roots by Glomeromycotan fungi (AM vs GFC), as is also the case for some EM-like associations. The presence of arbuscules is normally used to identify AM and the presence of a Hartig net to define EM associations. However, these definitions are not always applied and careful judgement may be required when examining roots collected from the field, particularly if they are old, or have atypical associations. In

Appendix 2, the use of arbuscules is recommended as the main criterion for AM wherever possible, but other evidence such as consistency of root occupation and indirect evidence of metabolite transfer to the fungus (vesicles or sporulation) should also be used to support diagnosis.

Adequate sampling and processing of roots

In most cases the diagnosis of AM or NM roots is straightforward, but it is more difficult if roots are inconsistently or sparsely colonised by fungi. In these cases, roots often contain mixtures of fungi, especially dark septate endophytes, as is most common in arctic and alpine habitats (Ruotsalainen et al. 2002; Cázares et al. 2005). The alternative hypotheses that fungi are (1) endophytic GFC in non-hosts, or (2) AM without arbuscules in older host roots need to be tested when we examine such roots. These problems can be minimised by understanding the phenology of roots to sample active roots, or by sampling at different times to observe colonisation trends. As explained in Appendix 2, It is essential that mycorrhizal diagnosis is based on adequate samples that include young roots and histological procedures used to examine roots reveal diagnostic features (many published images are not sufficiently clear). In some cases better results were obtained by growing plants from seed in soil from natural habitat or applying inoculum of known fungi, than were obtained by excavation of roots of unknown age from the field (Maeda 1954; Brundrett and Abbott 1991). This also avoids the possibility of cross-contamination of root samples with other species.

An understanding of the functional significance of GFC in natural ecosystems may require more comprehensive mycorrhizal colonisation intensity data than is normally obtained by mycorrhizologists. Currently a singe arbuscule in a km or roots, which is unlikely to provide much benefit, can be scored equally to 1000 arbuscules! McGonigle et al. (1990) developed a procedure for detailed assessment of arbuscule, vesicles and hyphae in root segments. However, it is recommended that this approach be modified to distinguish single occurrences from multiple occurrences of fungal structures in each root segment (see Table 6 in Appendix 2). Sufficient sampling replication, examination of seasonal colonisation tends and colonisation intensity data (especially

for arbuscules) are all required to resolve the mycorrhizal status of families such as the Cyperaceae and to distinguish facultative mycorrhizal associations. Physiological data confirming that mycorrhizas are beneficial to plants would also provide valuable supporting evidence of AM associations, but cannot be used alone for diagnosis.

Results

As reported above, few published reports included sufficient data to allow results to be verified. In the future it is recommended that publications about mycorrhizal associations in ecosystems rigorously apply and state definitions used and include the data used to make these diagnoses (listed in Appendix 2). This requires additional columns to be included in results tables, and clear statements in the methods section of papers. This information could also be included in a supplemental table linked to publications available on the web. It is also recommended that result tables organize plants within families and genera to allow comparisons with other published data.

Resolving conflicting information in published data

Misdiagnosis usually results in low error rate, which is acceptable in the context of individual surveys, as it usually does not affect our understanding of the overall importance of mycorrhizas in particular locations. However, the significance of errors in diagnoses are magnified when data from many sources are compiled causing errors to accumulate in lists. These errors have the potential to limit our understanding of the importance of mycorrhizas at the plant family, ecosystem and global scales. Some of this can be resolved by giving detailed studies greater weight than observational studies without sampling replication across habitats or times when interpreting published data. As Harley and Harley (1987) stated, the mycorrhizal status of a family should not be decided by a single record, especially if the habitat is not conducive to mycorrhizal formation. One example is *Batis* sp. (Bataceae) designated as a NM plant by Wang and Qui (2006) after Gemma and Koske (1990) who collected it in a disturbed habitat (sand dunes), but this family may not be NM elsewhere.

Several approaches can be used to resolve conflicting published data on mycorrhizas:

1. A majority rules (consensus) approach, where a family is considered to be AM or NM when most reports are in agreement even if there is some conflicting evidence (within a 10%) error rate in the published data. This works for most plant families if relatively recent data sources are consulted.
2. An "expert system" approach where data are carefully reinterpreted or discarded by using evidence to support diagnosis, if it is provided in publications.

Both approaches require a greater burden of proof when published results contradict expected outcomes based on the phylogeny and habitats of plants. It is probably common for mycorrhizologists to expend additional effort checking unexpected results, but there are no defined protocols for dealing with "outliers" in mycorrhizal data.

This review used a consensus approach to develop lists of mycorrhizal plants that are consistent with plant phylogeny in most cases (see Part I). It is also important to avoid circular reasoning where preconceived ideas help determine conclusions leading to entrenchment of ideas that may not be entirely correct (but it can also be argued that this is how scientific progress normally occurs).

Diagnosis of mycorrhizal fungi

This review primarily concerns the diagnosis of mycorrhizal hosts and not fungi. However, since the propensity for mycorrhizal fungi to grow as endophytes in (or on) non-hosts can result in misdiagnosis of associations, it is necessary to briefly consider the potential impacts of this on the designation of mycorrhizal fungi. It is now common for fungi in roots to be identified by molecular means using extracted DNA, but much harder to establish what the roles of these fungi are by these means. The fact that some of the fungi that are detected may be endophytes needs to be considered, especially if results are contrary to expectations. A relevant study by Allen et al. 2003 found two groups of fungi in ericoid roots, (1) ascomycetes which could be isolated, but were rarely detected by DNA, and (2) *Sebacina* isolates which dominated DNA samples but

could not be isolated. In this study only the ascomycetes were confirmed to be mycorrhizal. *Sebacina* isolates have been detected in the roots of plants with most types of mycorrhizas, but their roles in these roots are rarely tested. While some of these associations are likely to be mycorrhizal, the alternative hypothesis that they may be endophytes also needs to be considered. Despite these issues, most clades of mycorrhizal fungi are now well known (see links in Appendix 1 for lists of taxa).

Conclusions

While there is little doubt about the mycorrhizal status of the majority of large plant families (as established decades ago) there are some whose mycorrhizal status have become more uncertain over time. In part, this results from sampling over a wider range of plant diversity, environmental conditions and habitat types, but it also results because definitions of association types are not rigorously applied and errors accumulate in lists of host plants. It should be possible to eliminate the second source of contradictory data by more consistent protocols for mycorrhizal diagnosis in the future, as recommended here. We also need to address problems with data consistency (adequate replication, providing data used for diagnosis, etc.) and sampling effort, especially in environments where edaphic conditions restrict fungal activity (e.g. epiphytic, aquatic, alpine, arctic, saline and arid habitats).

We should also consider the statistical concept of Type 1 and Type 2 errors that result in either under- or over-allocation of significant results in lists of mycorrhizal plants. For example, we will tend to under-allocate taxa if we only use reports that cite arbuscules, but are likely to over-allocate mycorrhizal plants if reports that do not state if arbuscules were seen are all considered to be correct. In most cases, closely related plants (families and genera) share mycorrhizal associations or other nutrition strategies. However, there are exceptions to any generalisation, so assumptions about mycorrhizal relationships based on plant phylogeny need to be checked.

This review identifies the most common errors that have been perpetuated in the mycorrhizal literature and recommends protocols to reduce error rates in the future. The most frequent cause of misdiagnosis of plants in NM families as AM seems to be caused by misidentification of endophytic

growth of Glomeromycotan fungi in non-hosts as AM. There also is increasing evidence that arbuscules occasionally occur in roots of predominantly NM plants, but their functional significance in these roots is unclear. It is anticipated that in future, more consistent approaches should reduce the misdiagnosis rate for mycorrhizas and resolve the inconsistencies in published list of host plants. After all, it is better to identify mycorrhizal association types accurately for a few species than inaccurately for many.

Appendix 1

List of relevant tables and other data with direct links

Information	Link
Ectomycorrhizal families and genera	http://mycorrhizas.info/ecm.html#hosts/
Nonmycorrhizal families	http://mycorrhizas.info/nmplants.html/
Mycorrhizas of primitive plants	http://mycorrhizas.info/evol.html/
Methods for identifying mycorrhizas	http://mycorrhizas.info/method.html/
Ectomycorrhizal fungi	http://mycorrhizas.info/ecmf.html#list/
Arbuscular mycorrhizal fungi (Arthur Schüßler's site)	http://www.lrz-muenchen.de/×schuessler/amphylo/

Appendix 2

Practical advice for the diagnosis of mycorrhizal associations

Processes required to obtain, process and evaluate samples for accurate mycorrhizal diagnosis are listed in Table 5. It is advisable to use several criteria to identify mycorrhizal associations, especially when roots are of unknown age (field collected). The first criteria (presence of a mycorrhizal interface) should always be used, as it provides the most reliable

Table 5 Stages in the process of accurately identifying mycorrhizal associations

A. Planning

  1. Acquire knowledge about species and habitats to be sampled, especially climate and soils

  2. Determine when roots should be sampled (their growing season), based on plant phenology and climate data

  3. Determine how often roots will be sampled and how many habitats or soil types will be sampled

  4. Recognise that habitats where mycorrhizas are more likely to be inconsistent require more intensive sampling

  5. Summarise existing data for plant species in the same taxonomic groups from earlier studies

B. Sampling roots

  6. Understand categories of roots required in samples (high order lateral roots) and how many roots are required

  7. Confirm there are no mixtures of species in root samples by using monocultures, using whole small plants, or carefully tracing roots. Check uniformity of appearance and anatomy after clearing samples. Expect some contamination of samples from the field by other species

  8. If field collected samples are not adequate, or feasible, grow seedlings in soils from natural habitats (for 1 month or longer)

C. Processing samples

  9. Store samples properly to avoid deterioration

  10. Process roots adequately to allow visualisation of key structures

  11. Check clarity of stained roots and reprocess roots if necessary

D. Designating mycorrhizas

  12. Quantify and identify mycorrhizal associations in roots using standard microscopy procedures

  13. Apply definitions and record which criteria were used to make diagnoses

  14. Admit that accurate diagnosis is not possible without additional sampling in some cases

  15. Check validity by comparing results for closely related species where possible

  16. Use evidence to explain discrepancies and inconsistencies, if any

E. Publishing results

  17. List all criteria used for diagnoses separately in results (Table 6) and also provide a separate column for the overall diagnosis

  18. Discuss any discrepancies with other published work, by indicating which criteria were used or omitted in past diagnoses

  19. Do not assume that mycorrhizal relationships are always directly correlated with plant phylogeny, as habitat conditions have a greater influence on the occurrence of mycorrhizal roots in some situations

evidence, but should not be the only evidence required for diagnosis. Consistency of colonisation is another key criteria. If interface hyphae (arbuscules, Hartig net, or coils) were not observed in roots, reliable identification mycorrhizas may not be possible and it should be stated that further sampling is required for that species. It is important to clearly state which criteria were used in diagnosis in published reports. Lists of mycorrhizal species should be organised into plant families to allow comparison with other studies.

A protocol for diagnosis of AM or NM roots is presented in Fig. 16. Many mycorrhizal studies are already at least partially compliant with these requirements if they include data that allows multiple evidence of diagnosis (e.g. arbuscules, vesicles and colonisation levels). It is most difficult to distinguish functional AM from endophytic root colonisation, especially in extreme habitats where mycorrhizal activity may be suppressed. These habitats usually require more samples or sampling times to determine if plants are mycorrhizal. In some cases it will not be

possible to conclusively state if samples are mycorrhizal or not—in which case sparse associations are likely to be of minor importance.

Diagnosis becomes easier with experience. It is unrealistic to expect accurate diagnosis without experience or guidance from an experience mycorrhizologists. Accuracy in mycorrhizal diagnosis is linked to the following factors:

- Experience and training.
- Sampling intensity.
- Use of standard diagnosis criteria.
- Adequate samples with sufficient replication that include young roots.
- Higher sampling intensity in habitats where NM-AM plants are common.
- Minimising cross contamination of roots by different plant species, but acknowledging it may still occur, especially with fine-rooted species.
- Acknowledging when diagnosis cannot be resolved by GFC designation. It is better to err on the side of caution rather than publish an incorrect diagnosis.

Fig. 16 Flowchart presenting recommended protocol for diagnosis of AM or NM roots

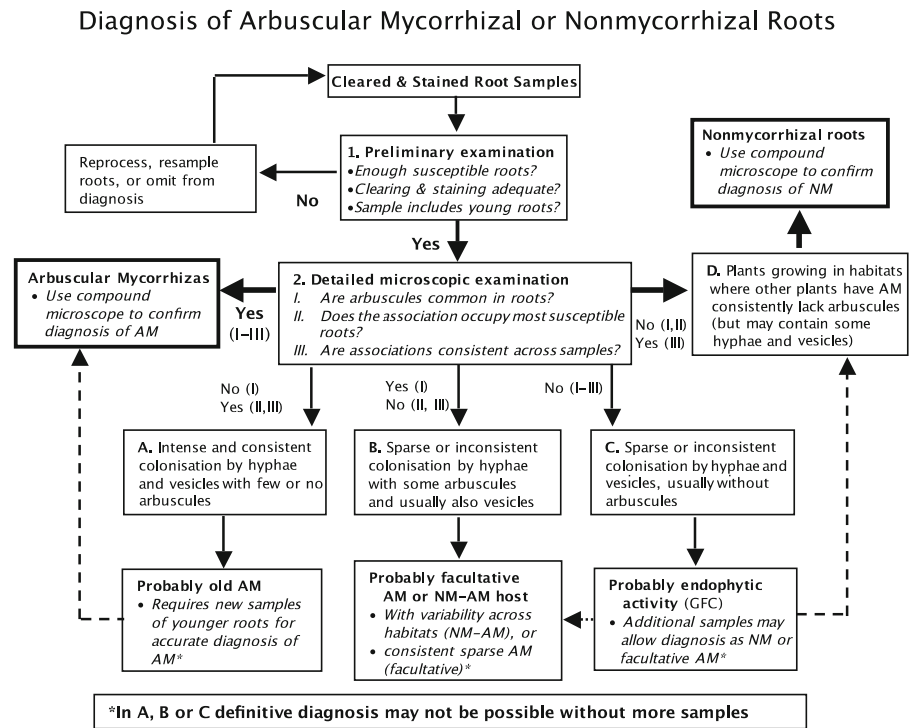Diagnosis of Arbuscular Mycorrhizal or Nonmycorrhizal Roots

Table 6 lists categories of data that should be used to diagnose AM associations. It is best to list all data and protocols used for diagnosis in publications. Protocols used to diagnose AM should be fully explained in the methods section. Detailed information can be presented as supplemental data if not included in the main document. Arbuscule density information is especially important if plants belong to families suspected to have NM-AM roots, have NM roots with some GFC, or are from habitats where NM plants tend to occur. However, in many cases a statement that plants designated as AM contained typical associations with many arbuscules in their roots will be sufficient to confirm diagnosis.

A similar process to that described above can be used to present data used to support diagnosis of EM associations (see Table 4), but usually is not required unless associations are atypical, or occur in an unexpected host plant. Table 3 also provides criteria that could be used for the diagnosis of ericoid or orchid mycorrhizas.

Table 6 Mycorrhizal data categories used for AM diagnosis

No.	Data	Notes
1	Plant family/genus/species	Required for comparison with other data
2	Samples	Number of plants and locations sampled
3	Times	Number of times or seasons sampled
4	Arbuscule presence	Average % root length colonised (RLC)
5	Arbuscule density	Average number per field of view or use Log scale (e.g. 0, 1–3, 4–10, 11–30, 31–100,…)
6	Vesicles (AM or GFC)	Average RLC
7	Hyphae (AM or GFC)	Average RLC
8	Total RLC designated as AM	Average RLC (often the same as 7)
9	AM Consistency	SE or proportion of samples from replicate plants
10	Diagnosis	State if AM, NM or GFC

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