Chapter 21
Global Diversity and Importance of Mycorrhizal and Nonmycorrhizal Plants

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21.1 Introduction

Morphological features, host plants and fungal associates for different types of mycorrhizas are summarised in Table 21.1. Mycorrhizal associations are classified according to the way in which the fungi interact with the host plant root, in particular, the structure of fungal hyphae that form a symbiotic interface with host cells (Brundrett 2004). There are five distinct types of mycorrhizal associations, but only the two most abundant associations, arbuscular mycorrhizas (AM) and ectomycorrhizas (EcM), occur in multiple plant families. Orchid and ericoid mycorrhizas are confined to genera within the Orchidaceae and Ericaceae families, respectively. The sub-epidermal associations of *Thysanotus* species are restricted to a single genus in the family Asparagaceae (Chap. 17).

Mycorrhizal association types are usually consistent within plant species, genera and families, but there are exceptions to this rule as discussed below. Families of plants with multiple root types can be designated as families with both AM and NM species, such as many Australian plants in the families Fabaceae and Myrtaceae, which have both AM and EcM (Chaps. 17 and 19). The designation of plants with nonmycorrhizal (NM) or inconstantly mycorrhizal (NM-AM) roots can also be difficult.

Objectives of this chapter are to discuss issues with the identification of mycorrhizal plants and provide updated information on the global importance of mycorrhizas, as well as regional case studies where mycorrhizal plant diversity or dominance has been determined. The lists of plants provided here are updated from Brundrett (2009) to reflect changes in plant phylogeny and newer databases of plant diversity following the

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Table 21.1 Structural definitions, roles, host plants and associated fungi for different types of mycorrhizas (after Brundrett 2004)

Category	Definition	Main role	Hosts plants	Fungal symbionts
Arbuscular mycorrhizas (AM)	Associations formed within roots that usually have arbuscules and often have vesicles	Nutrient acquisition for plant (P, K, N, etc.)	Most families of vascular plants and some bryophytes	Glomerales (formerly Glomeromycota is now part of the Mucoromycota)
Ectomycorrhizas (EcM)	Associations with a hyphal mantle enclosing short lateral roots and a Hartig net of labyrinthine hyphae that penetrate between root cells	Nutrient acquisition for plant (N, P, etc.)	Certain families or genera of flowering plants and some gymnosperms (some host AM also; Chap. 19)	Most are higher fungi (some ascomycetes and many basidiomycetes; Chap. 6)
Orchid mycorrhizas	Associations where coils of hyphae (pelotons) penetrate within cells in a root or stem in the plant family Orchidaceae	Nutrient acquisition for plant (N, P, etc.)	Orchidaceae	Mostly basidiomycetes in *Rhizoctonia* alliance, also EcM fungi in some cases (Chap. 8)
Ericoid mycorrhizas	Coils of hyphae within very thin roots (hair roots) of the Ericaceae	Nutrient acquisition for plant	Ericaceae	Most are Ascomycetes (Chap. 9)
Thysanotus (subepidermal) mycorrhizas	Hyphae in cavities under epidermal cells, only known from a monocot genus	Expected to be nutrient uptake	*Thysanotus* spp. (Laxmaniaceae)—all but one species is Australian	Unknown (Chap. 17)

latest family classifications (Angiosperm Phylogeny Group 2016) and using revised plant species totals for families (Christenhusz and Byng 2016). Values for the diversity of EcM plants presented here include monotopoid and arbutoid mycorrhizas which are now recognised as variants of EcM (Brundrett 2004). Values for the diversity of mycorrrhizal hosts also include mycoheterotrophic variants of their associations.

21.2 Defining Mycorrhizal and Nonmycorrhizal Plants

Current knowledge about the diversity and ecology of plants with NM, NM-AM or facultatively AM roots is summarised in Tables 21.2 and 21.3. Our knowledge of these plants is substantially limited due to problems with consistency of identification of mycorrhizas in roots, especially in cases where only hyphae and vesicles are present (Brundrett 2009). These issues are summarised in Box 21.1.

Table 21.2 List of all plant known families with nonmycorrhizal (NM) or nonmycorrhizal and arbuscular mycorrhizal (NM-AM) roots

Order	Family	Habit	Ecology	NM-AM	NM
Nymphaeales	Nymphaeaceae	Herbs	H	70	
Ceratophyllales	Ceratophyllaceae	Herbs	H		4
Laurales	Lauraceae (Cassytha only)	Climber	P		19
Piperales	Hydnoraceae (now in Aristolochiaceae)	Herbs	P		7
Piperales	Piperaceae	Woody, herbs	E	3700	
Acorales	Acoraceae	Herbs	H	2	
Alismatales	Alismataceae	Herbs	H	115	
Alismatales	Aponogetonaceae	Herbs	H	56	
Alismatales	Araceaea (some only)	Herbs	H, E	1300	
Alismatales	Butomaceae	Herbs	H	1	
Alismatales	Cymodoceaceae	Herbs	M		17
Alismatales	Hydrocharitaceae	Herbs	M, H		135
Alismatales	Juncaginaceae	Herbs	H	34	
Alismatales	Posidoniaceae	Herbs	M		9
Alismatales	Potamogetonaceae	Herbs	H	110	
Alismatales	Ruppiaceae	Herbs	M, H		8
Alismatales	Zosteraceae	Herbs	M		22
Pandanales	Cyclanthaceae	Herbs	E	230	
unplaced	Dasypogonaceae	Herbs	SB		16
Commelinales	Commelinaceae	Herbs	R (E)		731
Commelinales	Haemodoraceae	Herbs	SB		102
Commelinales	Pontederiaceae	Herbs	H	34	
Poales	Bromeliaceae	Herbs	E	3475	
Poales	Cyperaceae	Sedges	RD, SB, A	5500	
Poales	Hydatellaceae	Herbs	H		12
Poales	Juncaceae	Rushes	H, RD, R		464
Poales	Restionaceae (includes Centrolepidaceae)	Herbs	AT, SR		572
Poales	Typhaceae	Herbs	H		51
Poales	Xyridaceae	Herbs	H		399
Proteales	Nelumbonaceae	Herbs	H		3
Proteales	Proteaceae	Woody	RC		1660
Fabales	Fabaceae (*Lupinus, Daviesia* only)	Shrubs, herbs	CR (a few)		700
Ranunculales	Papaveraceae	Herbs	R	775	
Caryophyllales	Aizoaceae (includes Mesembranthaeae)	Herbs, woody	X, S		1900
Cucurbitales	Apodanthaceae	Herbs	P		10

(continued)

Table 21.2 (continued)

Order	Family	Habit	Ecology	NM-AM	NM
Caryophyllales	Amaranthaceae (includes Chenopodiaceae)	Herbs, shrubs	S, R		2040
Caryophyllales	Caryophyllaceae	Herbs	R, AA		2625
Malvales	Cytinaceae	Internal	P		10
Caryophyllales	Droseraceae	Herbs	C		180
Caryophyllales	Drosophyllaceae	Herb	C		1
Caryophyllales	Frankeniaceae	Shrubs	S		90
Caryophyllales	Molluginaceae	Herbs	X, R		80
Caryophyllales	Nepenthaceae	Climbers	C		150
Caryophyllales	Nyctaginaceae	Woody	Other		400
Caryophyllales	Phytolaccaceae	Woody, herbs	R		33
Caryophyllales	Plumbaginaceae	Herbs, woody	X, R, S	725	
Caryophyllales	Polygonaceae	Most herbs	R		1200
Caryophyllales	Portulacaceae (s.s)	Woody, herbs	X	115	
Caryophyllales	Tamaricaceae	Woody	D, S	78	
Santalales	Olacaceae (parasites only)	Woody	P		59
Santalales	Balanophoraceae	Herbs	P		39
Santalales	Opiliaceae	Woody	P		36
Santalales	Loranthaceae	Mistletoes	P		1039
Santalales	Misodendraceae	Mistletoes	P		8
Santalales	Santalaceae s.l.	Woody	P		1097
Saxifragales	Cynomoriaceae	Herbs	P		2
Saxifragales	Crassulaceae	Herbs, shrubs	D	?	1400
Saxifragales	Haloragaceae (aquatics only)	Herbs	H	50	
Saxifragales	Saxifragaceae	Herbs	AA, X	640	
Zygophyllales	Zygophyllaceae	Herbs, woody	X, S	285	
Fagales	Myricaceae	Woody	RC		57
Malpighiales	Erythroxylaceae	Woody	Other	242	
Malpighiales	Podostemaceae	Herbs	H	300	
Malpighiales	Quiinaceae (Ochnaceae s.l.)	Woody	Other		50
Malphigiales	Rafflesiaceae	Internal	P		25
Malpighiales	Rhizophoraceae	Woody	M	147	
Oxalidales	Cephalotaceae	Herb	C		1
Rosales	Urticaceae	Herbs, woody	R	2625	
Brassicales	Brassicaceae	Herbs	AA, D, R		3628

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Table 21.2 (continued)

Order	Family	Habit	Ecology	NM-AM	NM
Brassicales	Capparaceae	Shrubs, herbs	R, S		450
Brassicales	Cleomaceae	Herbs, shrubs	X, S		346
Brassicales	Limnanthaceae	Herbs	H		8
Brassicales	Resedaceae	Herbs, shrubs	DR		107
Cornales	Loasaceae	Herbs, shrubs	R		308
Ericales	Roridulaceae	Shrubs	C		
Ericales	Mitrastemonaceae	Internal	P		2
Ericales	Sarraceniaceae	Herbs	C		34
Boraginales	Lennoaceae	Herbs	P		4
Boraginales	Hydrophyllaceae (Boraginaceae s.l.)	Herbs, woody	D	300	
Lamiales	Avicenniaceae (Acanthaceae s.l.)	Trees	M		8
Lamiales	Byblidaceae	Herbs	C		8
Lamiales	Callitrichaceae (Plantaginaceae s. l.)	Herbs	M	75	
Lamiales	Hippuridaceae (Plantaginaceae s. l.)	Herbs	H		3
Lamiales	Lentibulariaceae	Herbs	C		316
Lamiales	Orobanchaceae (Scrophulariaceaea s.l.)	Herbs	P		1957
Solanales	Convolvulaceae (Cuscuta only)	Climbers	P		172
Asterales	Menyanthaceae	Herbs	H	60	
Total				21,044	24,814

Based on Brundrett (2009) with updated species allocation and numbers following Christenhusz and Byng (2016), Nickrent (1997-onwards) and The plant list 1.1 (www.theplantlist.org)

SB Sand-binding roots, *H* Hydrophytes (aquatic), *M* Marine hydrophytes, *AA* Arctic or alpine, *CR* Cluster (proteoid) Roots, *RD* Dauciform Roots, *P* Parasitic, *R* Disturbed habitats, *S* Saline soils, *E* Epiphytic, *X* Arid habitats, *C* Carnivorous

Table 21.3 Global diversity of different ecological categories of plants with nonmycorrhizal (NM) roots or predominantly NM roots (updated from Brundrett 2009)

Root trait category	Families	Species	Notes
Cluster and dauciform roots	6	7853	Dauciform roots occur in some sedges and rushes
Carnivores	7	689	Sundews, bladderworts and pitcher plants (occasional AM in some)
Parasites and hemiparasites	15	4244	Some hemiparasites have AM
Epiphytes	4	11,155	Most epiphyte families also include AM plants
Arctic and Alpine	1	640	Most belong to families with many AM plants
Aquatic	29	2236	Plants with species growing partly of fully submerged (also many AM plants in the same families)
Marine	3	48	Seagrasses, mangroves, etc.
Halophytes	4	701	Samphires and other salt-tolerant species, some may have AM depending on soil conditions
Arid	10	2265	Many succulent plants are AM
Disturbance opportunists	13	14,909	Short-lived weedy plants in disturbed habitats
Total	95	46,737	Includes many NM-AM plants which sometimes have AM

Families are listed in Table 21.2 and all species are allocated to the most important category

Box 21.1 Mycorrhizal Diagnosis Issues

1. Arbuscular mycorrhizal (AM) roots can be misdiagnosed as nonmycorrhizal (NM) if arbuscules are not seen due to poor sample preparation or root quality (arbuscules are digested in older roots).
2. AM or NM roots with superficial hyphal growth are sometimes diagnosed as ectomycorrhizal (EcM) despite the lack of a Hartig net (Chap. 19). Growth of hyphae on non-host roots is common and can lead to growth responses in sterilised soils (Chap. 17). Some plants have both AM and EcM roots, but this is uncommon or rarely reported in most ecosystems.
3. NM plants are defined as plants that fail to form mycorrhizas when inoculum of these fungi are present, so they have roots that are highly resistant to fungal colonisation (Tester et al. 1987; Giovannetti and Sbrana 1988; Schreiner and Koide 1993; Brundrett 2009). These families are listed in Table 21.2.
4. NM roots become less resistant to fungal colonisation with age, and many NM plants will contain vesicles and hyphae of AM fungi along with

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saprophytic and endophytic organisms (Brundrett 2006). This endophytic activity by mycorrhizal fungi has been referred to as Glomalean Fungus Colonisation (GFC) and is normally asymptomatic (Brundrett 2006). GFC also occurs in other subterranean plant organs such as rhizome scales and seeds.

5. NM plants with GFC are often misdiagnosed as AM (Brundrett 2009). These roots often contain hyphae and vesicles but not arbuscules. Arbuscules are the defining feature of AM, but are not always used for diagnosis, since they are missing in old AM roots.
6. Plants with roots that can be mycorrhizal or not depending on soil or habitat conditions are known as NM-AM (Table 17.1). These include members of the Cyperaceae, Chenopodiaceae and other NM-AM families listed in Table 21.3. They often grow in the same habitats as NM plants.
7. The mycorrhizal status of many species in NM-AM families such as the Cyperaceae, Papaveraceae and Chenopodiaceae cannot be resolved with existing data (Brundrett 2009). Most species in these families have NM roots (often with GFC), but there are also plants in these families that are considered to have AM (see Sect. 21.3).
8. Some plant families include both fully AM and fully NM species. These are also referred to as AM-NM families in Table 21.2. A few plant species have both AM and NM in healthy primary roots at the same time, because AM fungi only grow in the finest lateral roots, which are attached to coarser NM roots (e.g. *Sanguinaria canadense*—Brundrett and Kendrick 1988). This seems to be rare and has been linked to the patterns of accumulation of fungistatic chemicals in roots.
9. A comparison of published lists of mycorrhizal plants suggests that about 5% of taxa have been misdiagnosed (Brundrett 2009). This error rate has little impact on estimated numbers of host and non-host plants, but there is a tendency for errors to accumulate in lists of mycorrhizal plants. Many NM plant families are misclassified in Wang and Qiu (2006), who do not attempt to resolve conflicting information within families. Their list includes about 100 families that are incorrectly diagnosed relative to lists of NM plants produced by Tester et al. (1987) and Brundrett (2009). There are also many errors in the list of EcM taxa in Wang and Qiu (2006) and Smith and Read (2008), for the same reason.
10. Resolving apparent misidentifications requires more consistent diagnosis of roots with sparse fungal colonisation by the rigorous application of definitions of AM and EcM associations (Brundrett 2009). In many cases, errors can be detected by comparing results to other studies that include plants in the same families, since mycorrhizal status of plants is usually consistent within families (but see Chap. 19).

As explained in Box 21.1, several categories of inconsistently or weakly mycorrhizal plants can be recognised based on patterns of root colonisation by mycorrhizal fungi (see also Table 17.1). However, distinguishing these NM-AM plants from NM plants is difficult since it is very rare of any NM plant to have roots that are consistently free of mycorrhizal fungi (Brundrett 2006; Toju et al. 2014). Most NM-AM plants have inconsistent associations where the degree of AM formation is limited by habitat conditions that cause mycorrhizal fungus activity to be inhibited. The main categories of NM-AM plants are hydrophytes, halophytes, xerophytes and epiphytes, as well as alpine and arctic plants (Table 21.3). Some aquatic plants and halophytes have roots that are mycorrhizal at times but not at other times due to soil conditions that vary seasonally or spatially. Both NM-AM and fully NM plants also tend to be more common in colder arctic and alpine habitats (Brundrett 2009; Newsham et al. 2009). Roots of aquatic plants are often NM or NM-AM, but some fully submerged plants have AM roots (Brundrett 1991, 2009). Marine seagrasses are fully NM but have endophytes in their roots (Vohník et al. 2015). Weedy plants also tend to be NM (Miller 2005; Brundrett 2009; Betekhtina and Veselkin 2011). Daehler (1998) summarised the taxonomic distribution of the worst weeds in agricultural habitats, and his list includes 15 NM or NM-AM families and only 2 AM families in the top 17. However, weeds that invade natural areas include a more even mixture of mycorrhizal and NM plants (Daehler 1998).

Most NM plants have a replacement strategy for nutrient acquisition (Table 21.3). With only rare exceptions, plants lose the capacity to form mycorrhizas if these are no longer required for nutrient uptake, as in the case of parasitic and carnivorous plants (Brundrett 2009; but see Chap. 19). Table 21.3 provides estimates of the overall number of species of plants in these categories. NM plants with specialised means of nutrition also include cluster-rooted species and sedges with dauciform roots that excrete organic acids to “mine” soil for immobile forms of soil phosphorus (Shane and Lambers 2005; Lambers et al. 2006). These root systems tend to have high production costs, but plants with NM roots seem to be more competitive in extremely infertile soils (Lambers et al. 2006). Delaux et al. (2014) found that some of the symbiosis specific genes in mycorrhizal plants were missing in NM plants such as *Lupinus* sp. Their data suggest that once plants evolve another nutrient uptake adaptation strategy such as cluster roots, the ability to form AM is lost and will not be readily reacquired. Some of these genes are now known to be ancestral in land plants (Wang et al. 2010b) and their presence in NM plants is worthy of further study.

The category of facultative AM was first originally applied to plants, which consistently had low levels of colonisation (Janos 1980; Brundrett 1991, 2009), but other authors use this term to refer to NM-AM plants. Figure 21.1 shows that samples need to be taken throughout the year to resolve differences in mycorrhizal colonisation between species. This graph of seasonal AM levels in Canadian deciduous forest shows that there is a continuum of mycorrhizal colonisation intensity and that these levels are fairly consistent within species with perennial roots throughout the year. There seems to be a threshold of 40% of root length colonised by AM that separates plants with high or low root colonisation levels, but

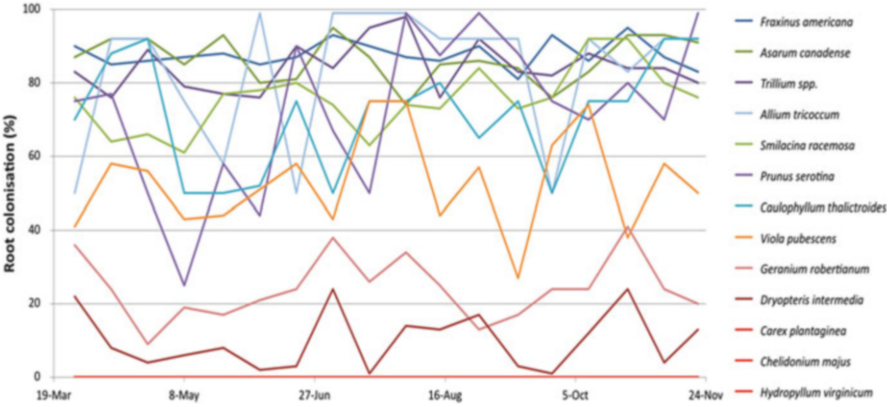

Fig. 21.1 Seasonal variations in arbuscular mycorrhizal colonisation for Canadian deciduous forest plants. Data are root length colonised (RLC) from 735 root samples taken every 2 weeks times throughout the year, except when soil was frozen (from Brundrett and Kendrick 1988). Three geophyte species with short-lived roots are omitted for clarity

this requires further investigation. In reality, most mycorrhizal studies do not include sufficient sampling within a species over time or space to allow facultative mycorrhizas to be recognised or to allow meaningful comparison of colonisation intensity between species or habitats. Consequently, plants with facultative AM will be designated only as AM plants in most mycorrhizal studies. There do not seem to be any facultative EcM plants, as few if any EcM host plants have sparse or intermittent root colonisation as adults, unless they are growing in extremely inhospitable or highly disturbed substrates. Some possible exceptions to this rule (listed in Chap. 19) include EcM-AM plants that form AM, when conditions are not favourable for EcM (facultative with respect to EcM but not to AM). A few EcM hosts also form NM roots when they are submerged in water (Khan 1993).

21.3 Resolving Conflicting Mycorrhizal Information

It has long been recognised that a definition of mycorrhizas based on morphology is required to identify associations consistently (Harley and Harley 1987; Brundrett 2004, 2009). Errors in published data most often result from diagnosis problems, especially when trying to distinguish endophytic activity of mycorrhizal fungi from mycorrhizal associations. A protocol to address common diagnosis problems was published (Brundrett 2009), but it has not been widely adopted, so it is still common for mycorrhizal studies to lack a clear definition of mycorrhiza types (note to journal editors and reviewers). The most common errors are listed in Box 21.1, and some specific examples are provided in Table 21.4.

Further research is required to resolve the status of some families of plants reported to have both AM and NM roots, which are called NM-AM families

Table 21.4 Case studies showing examples of endophytic activity by glomalean fungi (GFC) in NM or NM-AM plants

Plant (family)	Habitat	Status	Evidence	References
NM-AM families				
Chenopodiaceae (3 sp.), Cyperaceae (1 sp.)	Desert spring ephemerals	GFC	No arbuscules, limited colonisation	Shi et al. (2006)
Ceratocarpus arenarius (Chenopodiaceae)	Desert annual	GFC	No arbuscules or P increase but growth responses and 15% colonisation	Zhang et al. (2012)
Chenopodium quinoa (Amaranthaceae)	Alpine	GFC	Endophytes common	Urcelay et al. (2011)
Stelleria media (Amaranthaceae)	Glasshouse study	GFC	AM fungi cause growth reduction	Veiga et al. (2013)
Cyperaceae (3 genera, 5 sp.)	Tropical ultramaphic soils	GFC	Some hyphae but few or no arbucules	Lagrange et al. (2013)
Amaranthaceae, Brassicaceae (12 sp.)	Temperate	GFC in 7 sp.	Colonisation (<5%) requires a companion plant, no arbuscules	Hirrel et al. (1978)
Carnivorous plants				
Drosera (2 sp.)	Tropical	GFC or NM-AM?	Low colonisation with few arbuscules	Harikumar (2013)
Drosera rotundifolia	Temperate	GFC?	Many endophytes present including AM and EcM fungi	Quilliam and Jones (2010)
Halophytes				
Mangrove vegetation (10 sp.)	Tropical	NM-AM or GFC	AMF hyphae and spores, arbuscules rare	Wang et al. (2010a, b)
Mangrove vegetation (17 sp.)	Tropical	NM-AM, NM	AMF in most species (1 sp. NM)	D'Souza and Rodrigues (2013)
Seasonally dry saline habitats (12 spp.)	Mediterranean	AM (4), GFC (9)	Asteraceae AM, Amaranthaceae, Caryophyllaceae and Pumbaginaceae NM	Sonjak et al. (2009)
Hydrophytes				
Aquatic and wetland plants (20 spp.)	Tropical	NM (5), GFC (12), AM (3)	Hyphae and vesicles in most, arbuscles in 3 spp. only	Radhika and Rodrigues (2007)
Aquatic (8 sp.) and wetland plants (50 sp.)	Tropical	NM (37), AM (21)	Most species had limited or no AM	Seerangan and Thangavelu (2014)
Hydrophytes (32 sp.)	Temperate	NM (25), AM (7)	Most hydrophytes NM	Kai and Zhiwei (2006)

(continued)

Table 21.4 (continued)

Plant (family)	Habitat	Status	Evidence	References
Parasites				
Cuscuta (2 sp.)	Temperate	GFC	Ephemeral root-like organ colonised by hyphae	Behdarvandi et al. (2015)
Cytinus (2 sp.)	Mediterranean	GFC?	Ephemeral colonisation by hyphae	De Vega et al. (2010)

here. The most important plant families in this category are the Cyperaceae, Papaveraceae and Chenopodiaceae, which seem to include a majority of NM species with a few exceptions. Many investigators have looked at roots of the Cyperaceae, which is one of the largest NM-AM plant families, but interpreting their data is difficult. For example, most of the roots examined did not contain arbuscules, but these sedge species were designated as AM due to the presence of hyphae and vesicles formed by glomalean fungi (Powell 1975; Miller et al. 1999; Muthukumar et al. 2004; Brundrett 2009). Thus, the designation of these species was based on a definition of AM that does not require arbuscules to be formed, which is contrary to the normal practice by mycorrhizal researchers. It seems that most of the sedge roots, which have been examined, have GFC but are not AM, but there may also be a few species with functional AM (see Table 21.4).

The endophytic growth of AM fungi (GFC) is common in non-host plants, but is not consistently interpreted by mycorrhizal scientists. Toju et al. (2014) found that EcM and AM fungi were present in most of the 36 tropical plants they studied, but in many cases these were obviously growing as endophytes in non-hosts. Endophytes including AM, EcM, ericoid and orchid mycorrhizal fungi seem to be common in NM plants (Brundrett 2006; Quilliam and Jones 2010; Lekberg et al. 2015). Issues also arise with the diagnosis of the roles of fungi in EcM and EcM-AM plants. (Chap. 19). These issues can be tested by using consistent definitions of mycorrhizal and NM roots when gathering new data. Other ecological categories of plants, where roots are typically NM but often contain endophytic AM fungi, include carnivores and parasites (Table 21.4).

Some published claims about mycorrhizal associations do not make sense, for example the recognition of AM in parasitic plants that lack roots at maturity (de Vega et al. 2010; Kamble and Agre 2014; Behdarvandi et al. 2015). The NM status of most parasitic plants has recently been strengthened by a genomic study by Delaux et al. (2014) which showed that *Cuscuta* and *Orobanche* had lost the symbiosis-specific genes that are normally present in mycorrhizal plants. This implies that attempts by mycorrhizal fungi to form associations with them would fail due to the inability of host cells to recognise beneficial fungi and/or form a functional symbiotic interface. There is also physiological evidence that GFC does not function like AM in roots. For example, Zhang et al. (2012) found hyphae were present in 15% of the roots of *Ceratocarpus arenarius* (Chenopodiaceae), but there were no arbuscules or increase in phosphorus content in colonised plants. They observed growth responses due to the presence of fungi, but the mechanism for this is unclear. It is common for soil fungi to cause growth responses in glasshouse experiments using pasteurised soils, and these responses have been documented for endophytes such as Serendipitaceae as well as putative EcM fungi that failed to colonise roots (Kariman et al. 2014; Ray et al. 2015). Growth promotion by endophytic fungi seems to be fairly common under experimental conditions and perhaps can also occur in agricultural soils, but is much less likely to occur in natural habitats where a high functional diversity or microorganisms is already present. Interpreting growth responses due to fungi that do not form mycorrhizas is challenging as there are no fully effective controls in any mycorrhizal experiment (Brundrett et al. 1996; Chap. 17).

21.4 Mycorrhizal Growth Responses

It makes sense to link mycorrhizal formation to root structures and growth responses, but meta-analysis studies correlating variations in mycorrhizal colonisation may fail to detect meaningful correlations between values for mycorrhizal colonisation and other variables. In particular, it is risky to link colonisation data to soil or environmental conditions because variations between studies in methodology and sampling are likely to be major contributing factor to differences in colonisation levels. For example, some studies measure colonisation relative to total root length while others exclude woody roots, which are not susceptible to mycorrhizal formation, from total root length. In addition, mycorrhizas are very hard to detect in older roots of some species and some species of AM fungi stain very weakly so are easily overlooked. Switching to less toxic (but lower contrast) stains for microscopy may also be a factor in unreliable diagnosis of AM. Despite these limitations, some meta-analyses have detected trends between mycorrhizal colonisation intensity. For example, Treseder (2013) summarised data from many mycorrhizal experiments and found that AM colonisation was linked to plant growth and phosphorus content, but the unexplained variation was substantial. Another meta-analysis by Soudzilovskaia et al. (2015) linked mycorrhizal colonisation intensity to habitat factors, but is also likely to be strongly influenced by inconsistent methodology.

Mycorrhizal associations are balanced mutualisms where both the plant and fungus partner benefit in indirect ways (Brundrett 2004). Examples of studies where plants were grown in realistic soil conditions generally show substantial growth responses to mycorrhizas (Zangaro et al. 2000; Brundrett and Abbott 2002; Johnson et al. 2015; Koziol and Bever 2015). However, measurements of responses to inoculation at a single phosphorus level can be misleading, since nutrient response curve studies are required to quantify mycorrhizal responses (Abbott and Robson 1984). Soil fertility is important for North American prairie plants, which respond to AM in soils where soil P is a limiting factor for plant growth, but not when N supply is limiting (Johnson et al. 2015).

Within the plants which normally have AM, there are variations in mycorrhizal colonisation intensity in a continuum from sparse to intense colonisation of roots. Plants which have sparse colonisation are often referred to as facultatively mycorrhizal and usually have relatively long roots hairs (e.g. Bayliss 1975; Brundrett 1991). However, designating facultatively mycorrhizal plants is often difficult due to limited sampling and lack of standardisation of methods, as explained in Sect. 21.2 above. The Canadian deciduous forest plant species included in Fig. 21.1 all had perennial fine roots, while annual plants and geophytes which replace all their roots each year showed strong seasonal variations in mycorrhizal root length. The majority of plants in natural ecosystems have perennial roots, so annual crop plants are not very good models for studying mycorrhizas in natural ecosystems.

It has long been known that NM plants generally have longer root hairs than mycorrhizal plants, and these major differences in root form are linked to different strategies for nutrient uptake from soils (Bayliss 1975; Lambers and Teste 2013; Fig. 21.2). However, for plants with varying levels of AM colonisation, the link

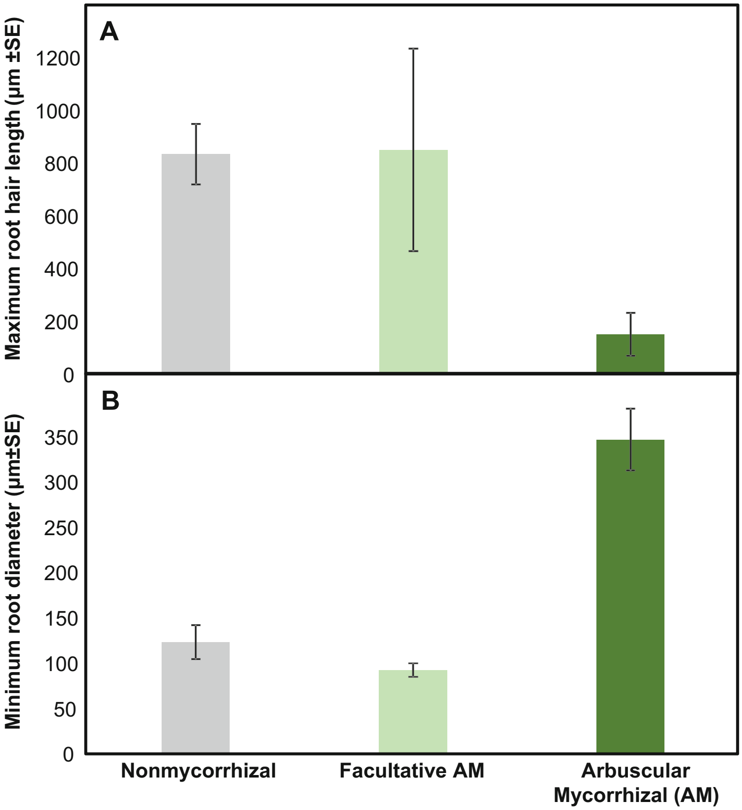

Fig. 21.2 Comparisons of root diameter, maximum root hair length and average AM colonisation levels for Canadian mycorrhizal plants (data from Brundrett and Kendrick 1988)

between mycorrhizal growth responses and root form has been questioned due to a lack of consistent data (Maherali 2014). The lack of correlation between mycorrhizal colonisation and root form in this meta-analysis probably resulted, because these properties are not measured consistently across studies, as explained above. A detailed comparison by Schweiger et al. (1995) found a strong negative correlation between mycorrhizal growth responses and the length of root hairs in pasture species and showed that root hairs were the most important root property for modelling mycorrhizal benefits.

21.5 Global and Regional Summaries of Mycorrhizal Plant Dominance

Figure 21.3 provides a global summary of the total diversity of flowering plants which are mycorrhizal. The mycorrhizal diversity of vascular plants is very similar (Fig. 21.4). About 92% of flowering plants can form mycorrhizas including 7% of species in plant families with inconsistent associations that vary with habitat or soil conditions (NM-AM). The oldest mycorrhizal association is still the most important, with over 210,000 species of AM hosts. The second largest category is orchid mycorrhizas (Orchidaceae) with about 28,000 plant species, while there are >6000 plants with EcM and about 4000 species in the Ericaceae with ericoid mycorrhizas (some Ericaceae members have a type of EcM and few have AM roots). There are also >40,000 NM or NM-AM plants. The NM-AM category of plants also includes

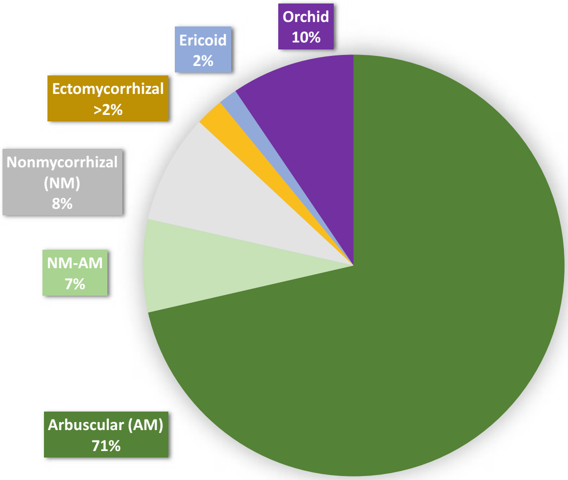

Fig. 21.3 The relative diversity of different categories of mycorrhizal plants on a global scale. All taxa of flowering plants were assigned to categories using data in the scientific literature (updated from Brundrett 2009). See text for data sources and methodology

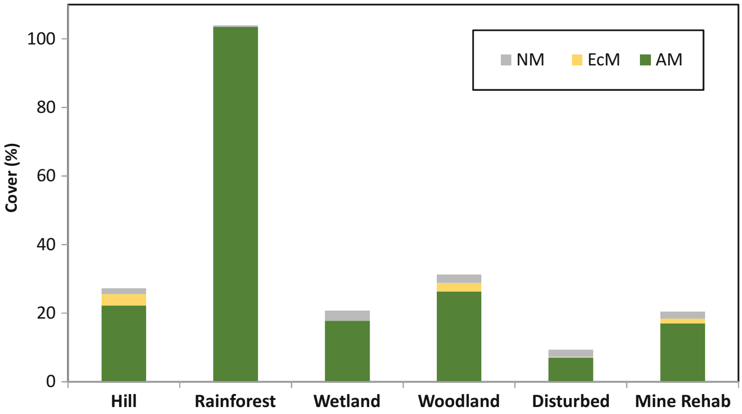

Fig. 21.4 Relative dominance of mycorrhizal and nonmycorrhizal understory plants in different major habits across a region in tropical Australia (data from Brundrett et al. 1995). Data are the relative cover of all species present in quadrats at each site (1 m^2 quadrants located at 10 m intervals along a 100 m transect) averaged by habitat type (25 transects in total)

families such as the Cyperaceae where the mycorrhizal status of many species cannot yet be resolved due to contradictory published information. Thus, it is likely that some of the families listed as NM-AM here will eventually be recognised as NM only. As shown in Table 21.3, the majority of NM-AM families are specialists that grow in habitats where mycorrhizal fungi are inhibited, so are unlikely to be consistently AM.

Other than the Orchidaceae and Ericaceae, members of most of the remaining plant families are known or expected to have AM, EcM or NM roots. Less than 1% of plants belong to families which have not been sampled for mycorrhizas and the majority of plant families have consistent mycorrhizas, so the mycorrhizal status of additional species in these families can be accurately inferred from phylogeny (Brundrett 2009). There are some orders of plants that consistently have AM roots. However, there are also a few plant families in NM-AM clades, where roots need to be sampled to resolve conflicting information (Table 21.2). Several other complex plant families, such as the Fabaceae and Myrtaceae in Australia, include AM and EcM-AM species. There are also cases where relictual associations persist in roots, such as EcM (AM) in *Eucalyptus* spp. that have AM as seedlings, but only rarely do so as adults (Chap. 17). There are also a few plants with both EcM and AM roots as adults, but these plants are normally classified as EcM. These include members of the Salicaceae in the northern hemisphere and some genera in the Fabaceae, Myrtaceae and Casuarinaceae in Australia (Chap. 19).

Lists of mycorrhizal and NM families or genera for all vascular plants can be compiled from the information in this book, which includes comprehensive lists of EcM and NM or NM-AM plants. This approach was used to provide regional summaries of numbers of mycorrhizal plants in Fig. 21.5. It is now possible to repeat these calculations for any region or habitat type with a comprehensive list of

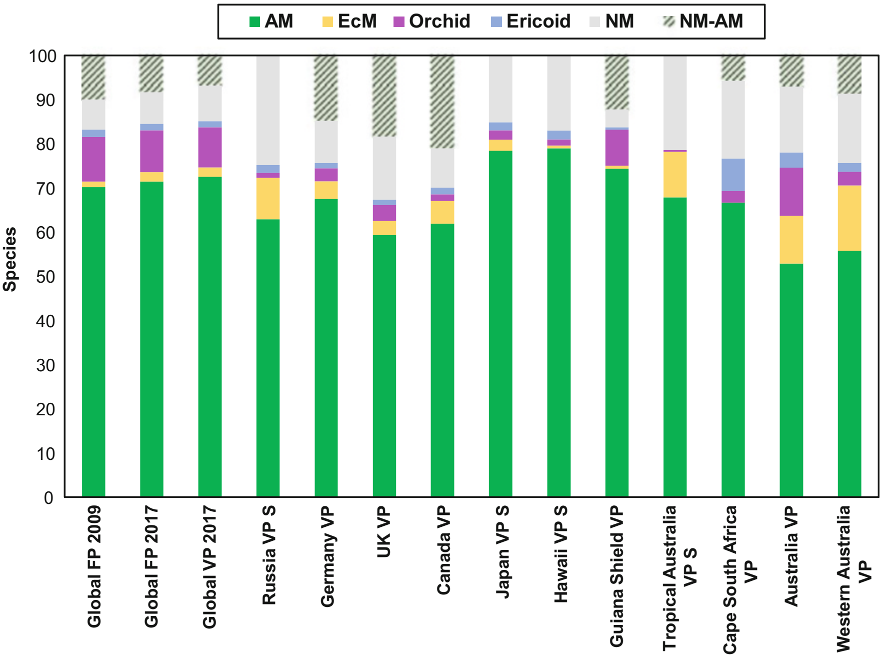

Fig. 21.5 Comparison of the relative diversity of mycorrhizal plants at regional scales for flowering plants (FP) or all vascular plants (VP). These stacked bar graphs were produced by assigning mycorrhizal status to all the species in a region based on phylogeny (see Fig. 21.3), expect for Russia, Japan, Hawaii and tropical Australia which are from large studies where roots were sampled, but do not include all species (S). These samples were from ~3000 species from Russia (Akhmetzhanova et al. 2012), 1037 spp. Japan (Maeda 1954), 147 spp. from Hawaii (Koske et al. 1992) and 247 species form tropical Australia (Brundrett et al. 1995). NM and NM-AM plants were not distinguished in some surveys

plant species. This approach can also be used in combination with more time-consuming approaches (looking at roots) to check for consistency within clades of plants or confirm the status of plants in NM-AM or EcM-AM clades (Table 21.3).

The total number of species of mycorrhizal and NM plants in Fig. 21.3 are very similar to the estimates of Brundrett (2009), but were updated using newer databases listing species of flowering plants (the two lists differ by about 5000 species). Table 21.2 also incorporates recent taxonomic changes to plant families (Angiosperm Phylogeny Group 2016), which have resulted in the consolidation of families that are closely related but in some cases ecologically different. The main changes to numbers of mycorrhizal plants since Brundrett (2009) are for recognised species in the Orchidaceae (1% larger) and NM plus NM-AM plants (also 1% larger). These values are provided for comparison in the first two columns in Fig. 21.5. The taxonomic diversity of vascular plants now seems to be relatively stable, but is still not fully resolved (Christenhusz and Byng 2016), so the estimates in Fig. 21.3 may still be subject to minor adjustments in numbers of plant species in some families in the future. The same caveats apply to estimates of numbers of mycorrhizal plants at a regional scale based on phylogeny, as provided in Fig. 21.5. However, lists of mycorrhizal plants derived from phylogeny and lists resulting from studies of roots tend to converge when large data sets of plants growing in similar habitats are compared. For example, the examination of root samples of 2970 Russian plants (Akhmetzhanova et al. 2012) produced very similar results to estimated mycorrhizal totals for German plants based on phylogeny (Fig. 21.5). Both of these regions have similar habitats and plant diversity.

Mycorrhizal plant diversity alone does not represent the importance of associations since the status of under- and overstory plants often differs and mycorrhizal plant lists are commonly dominated by herbs and shrubs. Regional summaries of mycorrhizal species diversity become even more valuable when used in combination with relative dominance data or vegetation maps showing the importance in ecosystems where roots were sampled (Swaty et al. 2016; Fig. 17.4). However, these studies are uncommon (Brundrett 1991). As explained above, the mycorrhizal status of plant species in a region or county can be assigned using phylogeny, and this approach can be extended to datasets of plant dominance. Examples of studies which have determined the total diversity or relative dominance of mycorrhizal plants in a regional flora are provided below.

Hempel et al. (2013) and Menzel et al. (2016) assigned mycorrhizal status to 1752 plant species that occur in Germany. However, their use of the Wang and Qiu (2006) dataset resulted in about 600 misallocated species relative to family allocations in Brundrett (2009). Revised totals for mycorrhizal plants in their list are provided in Fig. 21.5. They also designated species with inconsistent mycorrhizas as facultatively mycorrhizal, but some of this variability is likely to have resulted from variations in methodology in mycorrhizal studies. Despite these potential issues, Hempel et al. (2013) found there were strong relationships between the consistency of mycorrhizal colonisation and soil and climatic factors.

Figure 21.5 includes fewer examples of mycorrhizal plant diversity in tropical habitats, but the overall dominance of AM host plants in most of these habitats has already been well documented (Brundrett 1991). One such study by Bechem et al. (2014) examined roots of 252 species of Cameroun forest trees and found most of the dominant plants in this ecosystem had AM (94%), with only 6 species with EcM (probably an overestimate - see Chap. 19) and 4 species with NM roots. At the opposite end of the global temperature gradient, the proportion of NM plants in Arctic soils increases with proximity to the pole, including both plants from NM families and species that form AM in warmer soils (Brundrett 2009; Newsham et al. 2009). Comparisons in Fig. 21.5 reinforces the idea that AM plants are generally most numerous in tropical habitats while NM plants become more important in colder climates.

Brundrett (1991) provides an overall summary of the mycorrhizal status of all the major ecosystems globally. Despite numerous mycorrhizal studies since then the overall picture has not changed much. In summary, the majority of ecosystems globally are dominated by AM host plants, which are also common in most of the remaining habitats. Ecosystems dominated by EcM tree species are also very important, especially in northern boreal forests and Australia (Read 1991; Chap. 20). Trees or shrubs with EcM are also dominant or co-dominant in many other temperate forests, as well as some tropical and subtropical areas. Orchids are present in most ecosystems but are not dominant. Plants with ericoid mycorrhizas are also widespread, but are only dominant in a few habitat types and have centres of diversity in mountains (Schwery et al. 2015; Chap. 9). Plants with NM roots tend to be specialist that occur in harsh sites or have other nutrient uptake mechanisms (Table 21.3), but are also prevalent in arctic and alpine habitats (Brundrett 2009). Early mycorrhizal research was primarily based in the Northern Hemisphere where soils and plants are atypical on a global scale (more likely to be dominated by EcM trees, highly fertile or disturbed with many weedy plants). But this trend is gradually shifting to include a much better representation of tropical plants in mycorrhizal studies. The impacts of the Anthropocene have resulted in increasing losses of EcM or AM tree coverage with an increasing importance of NM weeds (Betekhtina and Veselkin 2011; Swaty et al. 2016).

My 2009 review predicts that new studies looking at mycorrhizal roots will often be of limited value since the status of most families is well resolved. In many cases, designating mycorrhizal status based on phylogeny will provide more accurate results than sampling roots due to issues with sample quality and the inconsistent interpretation of fungal structures. There is no evidence that the error rate for diagnosis of mycorrhizal roots has reduced since I identified this as an issue in 2009. In fact, advances in molecular techniques make it easier than ever to detect mycorrhizal fungi in NM roots. We need to acknowledge that endophytic activity by mycorrhizal fungi is common, and careful visual observations and adequate root samples are required to diagnose mycorrhizas. Many root samples are inadequate for accurately determining mycorrhizal status (due to their age, mixtures of different species, limited sampling, poor clearing and staining, etc.). These issues with methodology and diagnosis of associations in roots need to be addressed by the mycorrhizal community.

21.6 Mycorrhizal Evolutionary Trends

The evolution of mycorrhizal associations is briefly updated here, to complement information available elsewhere (Brundrett 2002, 2009). The two most common evolutionary trends for species are to switch from AM to NM roots or from AM to EcM roots with about 45,000 species of flowering plants in the former category and over 6000 in the latter. In most cases, these trends are consistent across families, but in a few cases, there are diverse root types within one family, such as the separate clades of EcM, AM or NM plants in the Australian Fabaceae (see Chap. 17). As shown in Table 21.5, there are intermediate stages in both of these evolutionary trends where plants have multifunctional roots with both EcM and AM symbioses, or can acquire nutrients directly and/or by the AM symbioses, as

Table 21.5 The two most common evolutionary trends in mycorrhizal roots (see text)

	Stage 1	Stage 2	Stage 3
A. AM to NM Evolutionary Continuum			
Stage	Obligate AM	Facultative AM or NM-AM	NM
Hyphae in root	AM fungi efficiently colonise the root cortex using longitudinal or coiling hyphae to extend colonies in roots. Hyphal growth primarily occurs in young roots	Colonisation of the root cortex is relatively inefficient in thin highly branched roots Root colonisation may be regulated by soil conditions that suppress fungal activity	Absent or diffuse and most common in older roots. If present, AM fungi typically occur in combination with other endophytic fungi
Arbuscules (Interface area)	Numerous in young roots, forming in one or more layers of cortex cells	Less numerous, inconsistently present or absent from roots	Absent or rarely present in some older roots
Vesicles (storage)	Many, few or none (fungus dependent)	Sparse or absent and highly variable	Rare or absent (roots may be short-term fungal refuges, but carbon stored is imported from elsewhere)
Root Form	Usually fairly thick (due to cortex) with short root hairs	Usually thinner and highly branched with fewer rows of cortex cells and longer root hairs than AM hosts. Roots are primarily optimised for direct nutrient uptake from soil	
Root evolution	Plants have root systems adapted for efficient mycorrhiza formation and symbiosis regulation genes responsible for recognition and formation of a host–fungus interface	The plant–fungal interface becomes less efficient due to root adaptations for direct nutrient uptake. Some symbiosis genes may be lost?	Symbioses regulation genes lost (interface nonfunctional if present) Roots further optimised for direct nutrient uptake and cluster roots may develop
B. AM to EcM Evolutionary Continuum			
Stage	AM	EcM-AM	EcM or EcM (AM)
Hyphae on root	Patchy colonisation by EcM fungi occurs on long laterals	Some lateral roots have a thin or thick mantle of hyphae	Many short lateral roots have a thick mantle of hyphae
Hartig net (interface)	Absent (hyphae may grow between epidermal cells but they do not form an interface)	Present but relatively inefficient due to root length and thickness. Arbuscules are also present, especially in longer roots	Substantially increased Hartig net area due to elongation of root cells in the epidermis
Root Form	No specialised lateral roots (roots optimised for AM or NM roles) Root form does not	Ultimate lateral roots have reduced growth rates and increased branching to allow a larger fungal interface to	Ultimate lateral roots have highly reduced growth rates and more lateral roots to increase interface area

(continued)

Table 21.5 (continued)

	Stage 1	Stage 2	Stage 3
	change in the presence of EcM fungi	form Root form is altered in the presence of EcM fungi	Root form is highly responsive to EcM fungi
Root evolution	Plants have root systems adapted for efficient AM formation and symbiosis regulation genes responsible for recognition and formation of host–fungus interface (in some cases NM or ericoid roots develop EcM)	Root system form and symbioses genes change to allow EcM formation, but roots retain adaptations for AM (or NM) root functionality	Root systems are optimised for EcM only, so AM specific genes may be lost or have altered roles. In some cases AM fungi are not fully excluded, but are usually rare or primarily found in young plants as EcM (AM) associations

determined by soil conditions. Other, less common, trends, which have occurred in one or more plant lineages, include (1) switching from NM to EcM roots, (2) from Ericoid to EcM or even AM, or (3) switching from balanced to mycoheterotrophic associations in plants with AM, EcM or orchid mycorrhizas (Brundrett 2002).

One of the strongest root evolution trends for plants that are exposed to hostile soil or environmental conditions is to develop NM-AM or NM roots. NM and NM-AM plants are more likely to be epiphytes, grow in wet, salty or cold soils or become parasitic on other plants. The alternative hypothesis (plants in these habitats lose mycorrhizas more often) has less support because families of NM plants with different ecological preferences tend to cluster together in phylogenetic trees. Evolutionary trends linked to soil conditions also include the increased importance of both EcM and NM plants in extremely infertile soils in Australia (Chap. 17).

Table 21.5 shows mycorrhizal evolution as a three-stage process starting from AM roots and progressing forward to NM or EcM roots, but there may be some cases where reversions back to AM occur. The presence of both AM and NM families in the Poales provide one example of complex evolution, as it seems likely that ancestral plants in this group had NM roots, but the Poaceae has AM roots in most species. Reports of some mycorrhizal species in the otherwise NM Cyperaceae may also represent recent switching from NM to AM or EM roots, provided that these are functional associations. It has yet to be confirmed that there are lineages of plants that have re-acquired mycorrhizal associations that descended from ancestors with fully NM roots. It is possible that plant lineages with newly acquired mycorrhizal associations do not function in the same way as ancient mycorrhizal lineages and that their associations are regulated by a different suite of symbiotic genes. The complex lineages of EM-AM plants in the Australian Fabaceae and Myrtaceae provide an excellent opportunity to investigate the functional and genetic processes in symbiotic associations of different ages (Chap. 17).

Not all plants follow the trends in Table 21.5 to their conclusion (fully EcM or fully NM roots), as there are also many plants that remain in an intermediate state such as EcM-AM or NM-AM. These plants have retained several root functions with overlapping roles that may provide them with greater ecological flexibility, but this may come at a greater cost. In other cases, different root functions are utilised by plants at different times or in different habitats, which can be the case for hydrophytes or halophytes that have seasonal mycorrhizal associations, or for plants with NM roots as epiphytes and AM roots when growing in soil. Examples of plant families with very complex roots include the Australian Fabaceae and Casuarinaceae where some species have several types of mycorrhizas as well as a nitrogen fixing symbiosis (Chaps. 17 and 19). The ability of some plants to support multifunctional roots and remain competitive provides strong evidence that soil fertility is the most important factor limiting plant productivity in their habitats.

As explained in Chap. 17, there have been three waves of mycorrhizal evolution that started with AM in early land plants, followed by a second major phase of root functional diversification in the Cretaceous when EcM, orchid, ericoid and NM plants would have originated. The third phase of root diversification is currently underway in some habitats in response to changing soil conditions. Lineages of plants that have acquired new root traits are most common in hostile habitats. Some examples include the EcM roots of sedges in the genus *Kobresia* that grow in arctic habitats or cluster roots in some members of the Fabaceae that grow in extremely infertile soils. However, these examples are not typical of the majority of vascular plants, which have remained associated with AM fungi throughout their evolutionary history.

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