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ORIGINAL PAPER

Arbuscular, ecto-related, orchid mycorrhizas—three independent structural lineages towards mycoheterotrophy: implications for classification?

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Abstract The classification of mycorrhizas in seven equally ranked types glosses over differences and similarities and, in particular, does not acknowledge the structural diversity of arbuscular mycorrhizas. This article emphasizes the parallel continua of ecto-related mycorrhizas and arbuscular mycorrhizas, exemplified within Ericaceae and Gentianales, respectively, as well as the proprietary development of orchid mycorrhizas, all three of which have independently developed mycoheterotrophic plants. A hierarchical classification according to structural similarities is suggested.

Keywords Arbuscular mycorrhiza · Ectomycorrhiza · Orchid mycorrhiza · Mycorrhizal structures · Mycorrhizal classification · Mycoheterotrophy

Introduction

Classification of mycorrhizas started with Frank (1887) who distinguished between ectotrophic and endotrophic mycorrhizas (including ericoid and orchid mycorrhizas), which were amended by Melin (1923, p. 95) adding "ectendotrophic." In a rarely cited paper, Dominik (1956) accepted the two main types of Frank (1887) and the subdivision of endotrophic mycorrhizas by Burgeff (1943) but suggested a refined classification of ectotrophic mycorrhizas in 12 subtypes (A through L). After some debate on the suffix instead of -trophic, suggesting -cellular (Wilde and Lafond 1967) and -mycorrhiza (Peyronel et al. 1969), Lewis (1973) proposed a new classification using "sheathing," "vesicular-arbuscular" (formerly treated as an endomycorrhiza), "ericaceous," and "orchidaceous," which is close to the top level types suggested much later by Brundrett (2004). Interestingly, Trappe (1987), not explicitly categorizing mycorrhizas, summarized "zygomycotous" and "asco- and basidiomycotous" (including ericoid mycorrhiza) in his taxonomic accounts of mycorrhizas, coming close to the view expressed in the present article.

Currently, mycorrhizas are classified into seven types of equal rank: arbuscular (AM), ecto- (ECM), ectendo-, arbutoid, ericoid, monotropoid, and orchid mycorrhiza (Smith and Read 2008). However, AM have turned out to be much more diverse in structural features than previously thought (e.g., Widden 1996; Imhof 1997, 1999a, 2003, 2007; Dickson 2004; Dominguez and Sérsic 2004), whereas the distinctions between ecto-, ectendo-, and arbutoid mycorrhizas are slight (e.g., Brundrett 2004; Smith and Read 2008). Thus, ranking all these types at the same level runs the risk of overemphasizing the distinctions between ecto-related types and glosses over the considerable structural diversity of AM.

The present article argues for the recognition of three structural lineages of mycorrhizas, ecto-related, arbuscular, and orchid, as mycorrhizal groups in a hierarchical system keeping the established names for the well-known mycorrhizal syndromes as mycorrhizal types. This approach is from the plant perspective and based on the notion that the phenotype of mycorrhizas, like any other functional feature of plants and fungi, is subject to evolution. Hence, it is not surprising that ecto-related associations can be linked by gradual morphological-anatomical changes (Fig. 1) and thus represent an analogous mycorrhizal continuum as stated for AM by Dickson (2004). These changes become even more convincing if they are paralleled by other

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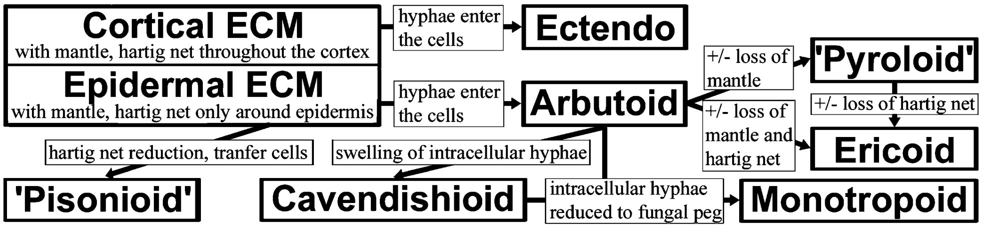

Fig. 1 Hierarchy of structural changes linking the types and morphotypes of ECM group, "Pyroloid" based on Robertson and Robertson (1985) and "Pisonioid" based on Ashford and Allaway (1982)

structural trends pointing in the same direction. In fact, the two monophyla Ericaceae and Gentianales (APG 2003) exemplify the evolutionary trend from trees to mycoheterotrophic herbs paralleled by changes of ecto-related mycorrhizal types and AM, respectively.

The ECM group

In order to sketch a putative morphological progression within ecto-related mycorrhizas (Fig. 1), we may start with ECM as listed by Smith and Read (2008), who did not distinguish between cortical and epidermal types. Cortical ECM in gymnosperms (Brundrett 2004) already shows the tendency towards intracellular colonization in the ectendomycorrhiza (e.g., Yang and Wilcox 1984; Scales and Peterson 1991; Yu et al. 2001). The epidermal ECM (Brundrett 2004) not only of the Fagales but also in Ericaceae (Largent et al. 1980; Smith et al. 1995; Richard et al. 2005) only differ in being restricted to the root epidermis. The switch to arbutoid mycorrhiza of some Ericaceae (Scannerini and Bonfante-Fasolo 1983; Massicotte et al. 1993) is an identical structural change as from cortical ECM to ectendomycorrhiza. It still keeps hyphal mantle and hartig net of the epidermal ECM but shows intracellular colonization of the epidermis.

Recently, a morphotype of arbutoid mycorrhiza, coined cavendishioid, was reported from the hemiepiphytic *Cavendishia nobilis* (Ericaceae), where the hartig net is less prominent and the intracellular hyphal phase comprises swollen hyphae (Setaro et al. 2006). In the herbaceous *Pyrola* (Furman and Trappe 1971), either considered to be arbutoid mycorrhizal (e.g., Peterson and Farquhar 1994) or ectendomycorrhizal (Wang and Qiu 2006), it is not the hartig net but the hyphal mantle that can be reduced, whereas the hyphae still build dense intracellular coils in the epidermis (Robertson and Robertson 1985). These "pyroloid" (as such referred to by Cullings 1996) and cavendishioid morphotypes underline the plasticity of ecto-related mycorrhizas and corroborate the notion of gradual evolutionary changes within the lineage. There might be even more findings in the future, showing other combinations of lack or differentiation of the three components mantle, hartig net, and intracellular colonization. In fact, one conceivable combination, namely the reduction of both the hyphal mantle and the hartig net keeping the hyphal coils in the rhizodermis, have already been found: the ericoid mycorrhiza. The similarities of ectomycorrhizas, ectendomycorrhiza, arbutoid, and monotropoid mycorrhizas have been already acknowledged by Brundrett (2004). However, the ericoid mycorrhizas also (see Read 1996) have much closer morpho-anatomical affinities to ectomycorrhiza than to orchid or arbuscular mycorrhiza (e.g., Cullings 1996, Wang and Qiu 2006). Not only are the fungi involved in ectomycorrhizas and ericoid mycorrhizas closely related so that one fungus species may develop ecto-, ectendo-, as well as ericoid mycorrhizas in different hosts (e.g., Björkman 1960; Monreal et al. 1999; Bergero et al. 2000; Vrålstad et al. 2000; Yu et al. 2001; Perotto et al. 2002; Villarreal-Ruiz et al. 2004). There are also reports of intermediate structural features in ericoid mycorrhizas such as hyphal mantles (Xiao and Berch 1996; Rains et al. 2003) and residues of a hartig net (Bergero et al. 2000; Rains et al. 2003) and likewise reports of arbutoid mycorrhizas with hardly a hyphal mantle (Fusconi and Bonfante-Fasolo 1984). Moreover, arbutoid and ericoid mycorrhiza have obvious structural similarities with the only difference of some intercellular hyphae in the former (compare e.g., Figures 188/189 and 171 in Peterson et al. 2004) and already Harley (1969) assumed the arbutoid mycorrhiza to link ectomycorrhiza and ericoid mycorrhiza.

Eventually, in the monotropoid mycorrhizas of the achlorophyllous *Sarcodes sanguinea* and *Pterospora andromedea* (Robertson and Robertson 1982) and *Monotropa hypopitys* (Duddridge and Read 1982), the intracellular phase of the mycorrhiza is reduced to a fungal peg (Duddridge and Read 1982). Taking the advanced character of these achlorophyllous species and their necessity for an efficient mycorrhiza into account, the fungal pegs are best interpreted as coil rudiments, as such omitting the presumably retarding coil development, and directly "burst" (Duddrigde and Read 1982) their content into the cells. Within the monotropoid mycorrhizas, we may even distinguish two morphotypes: in *Monotropa* the pegs go through the outer periclinal wall of the epidermis (Lutz and Sjolund 1973; Duddridge and Read 1982), whereas in *Sarcodes* and *Pterospora* they penetrate the radial walls (Robertson and Robertson 1982).

Interestingly, this lineage of ecto-related mycorrhizas is roughly parallel to the morphological reduction from trees to mycoheterotrophic plants in Ericaceae. Henderson (1919), based on extensive morphological-anatomical investigations, drew a line of reduction from the woody Ericaceae (trees,

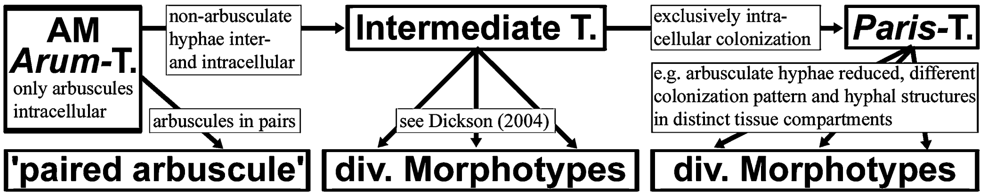

Fig. 2 Hierarchy of structural changes linking the types and morphotypes of AM group (*T.* type, *div.* diverse). "Paired arbuscule" after Dickson et al. (2003)

shrubs, and sub-shrubs) over the herbaceous Pyrolaceae to the achlorophyllous Monotropaceae and already challenged the family delimitations. In fact, the latter two taxa are nowadays considered as Monotropoideae in Ericaceae (Kron et al. 2002). With respect to the Pyrolaceae/Monotropaceae complex, Furman and Trappe (1971) further refined this progression line. They stressed the parallel trends of the reduction of leaves associated with evolution of achlorophylly and the abbreviation of the root systems from fibrous roots over coralloid root systems, reaching the stage of tight root balls in *Monotropa* or *Pterospora* (see Table 2 in Furman and Trappe 1971).

The AM group

The structural diversity of AM apart from the types described by Gallaud (1905) has been discovered rather recently (e.g., Widden 1996; Imhof 1998, 1999b, c, 2001, 2006; Dominguez and Sérsic 2004; Dickson 2004; Beck et al. 2005). Despite the substantial differences between the morphotypes, most authors refrained from naming them, in contrast to the ecto-related mycorrhizas. Nevertheless, the AM morphotypes can likewise be linked according to morphological differences (Fig. 2). The Gentianales are a good example where the predominantly intercellular *Arum* type is linked by intermediate types to the exclusively intracellular *Paris* type (Gallaud 1905; Smith and Smith 1997; Dickson 2004; Appelhans et al. 2008), all types of which are found in Apocynaceae (Tiemann et al. 1994a, 1994b; Untch and Weber 1995; Weber et al. 1995). Furthermore, the *Paris* type shows numerous morphological deviations in achlorophyllous species not only in the Gentianaceae (e.g., Imhof 1998, 1999c, 2001, 2007; Imhof and Weber 2000). The fossil record suggests the *Arum* type to be the oldest mycorrhiza (Kidston and Lang 1921; Remy et al. 1994; Taylor et al. 1995), but it is difficult to detect an evolutionary trend of AM types, since they are scattered all around the plant kingdom (Smith and Smith 1997; Dickson et al. 2007).

At the family level, however, evolutionary changes of AM pattern can be found. Within Gentianaceae, exclusively having *Paris* type AM, there are chlorophyllous (shrubs, sub-shrubs, and herbs), semichlorophyllous (*Obolaria* and *Bartonia*, Holm 1897, 1906), and achlorophyllous genera (*Voyria*, *Voyriella*, and *Sebaea oligantha*) showing pronounced morphological reductions. These are very similar to those described in Ericaceae, also paralleled by changes of mycorrhizal structures. *Voyria truncata* shows runner-like, plagiotropic roots (Imhof et al. 1994); intermediate roots are present in e.g., *Voyria aphylla* (Imhof 1999c) and *Voyria rosea* (Maas and Ruyters 1986); and small

Table 1 Classification of mycorrhizas

AM group (Fig.1)	ECM group (Fig.2)	OM group	Ill-defined group
Arum type[a]	Cortical ECM[d]	Tolypophagous type?[h]	e.g., Mycorrhiza in *Thysanotus* (McGee 1988), Dark Septate Endophyte (Jumpponen 2001; Mandyam and Jumpponen 2005)
Intermediate types[b]	Ectendomycorrhiza	Ptyophagous type?[h]	
Paris type[c]	Epidermal ECM[d,e]		
	Arbutoid mycorrhiza[f]		
	Ericoid mycorrhiza		
	Monotropoid mycorrhiza[g]		

[a] Includes one morphotype with "paired arbuscules" (Dickson et al. 2003)

[b] Morphotypes see Dickson (2004)

[c] Includes many morphotypes especially in mycoheterotrophic plants

[d] Extensive morphotyping done by Dominik (1956) and Agerer (1995)

[e] Includes morphotype in *Pisonia grandis* (Ashford and Allaway 1982)

[f] May include morphotypes in *Cavendishia nobilis* (Setaro et al. 2006) and *Pyrola* (Robertson and Robertson 1985)

[g] May include morphotypes in *Monotropa* (Duddridge and Read 1982) as well as *Sarcodes* and *Pterospora* (Robertson and Robertson 1982)

[h] More structural investigations required

star-like root systems exist in *Voyria tenella* (Imhof 1997), *Voyria obconica* (Imhof and Weber 2000), or *Voyria flavescens* (Franke 2002). This is strikingly similar to the root systems in Monotropoideae (see Furman and Trappe 1971). Farther like *Pyrola*, *Sarcodes*, *Pterospora*, and *Monotropa* that show specialized mycorrhizal forms of the ECM group, *Voyria* spp. develop little (*V. truncata*, Imhof and Weber, 1997) but also strongly deviant colonization pattern of *Paris* type AM (e.g., *V. tenella*, Imhof 1997), which are linked by a structurally mediating pattern in *V. aphylla* (Imhof 1999c). Ecto-related mycorrhizas and AM thus appear as parallel structural lineages of mycorrhizas, both culminating in the evolution of mycoheterotrophic plants.

The OM group

I propose orchid mycorrhiza (OM) as the third distinct structural lineage of mycorrhizas in addition to ecto-related and arbuscular mycorrhiza. Although the fungi in some, mostly achlorophyllous orchids have been proved to develop ECM in other plants (e.g., Warcup 1985; Taylor and Bruns 1997; McKendrick et al. 2000; Selosse et al. 2002, 2004; Julou et al. 2005; Girlanda et al. 2006; Dearnaley 2007; Ogura-Tsujita and Yukawa 2008; Zimmer et al. 2008), the morpho-anatomical gap between ECM and OM and, most notably, the lack of intermediate forms are good reasons to retain it as a separate mycorrhizal group. Moreover, most root fungi in orchids have no mycorrhizal but saprophytic or parasitic life forms (see list in Rasmussen 2002), signifying a group of fungi newly adopted by orchids for their needs. A morphological progression within OM, as suggested above for the ECM and AM groups, is not yet apparent. Possibly, the two forms of OM already described by Burgeff (1932) as “tolypophagy” (digestion of coils) and “ptyophagy” (releasing fungal content into the cell), which gained a revival after the description of Wang et al. (1997) on *Gastrodia elata* (see also Rasmussen 2002), may be signs of progressive changes.

Interestingly, ptyophagy in OM is restricted to mycoheterotrophic orchids, just as the monotropoid mycorrhiza is restricted to the achlorophyllous Monotropoideae. At all, the ptyophagy in the mycoheterotrophic *G. elata* shows remarkable similarities to the fungal pegs of monotropoid mycorrhiza, both showing vermiform protrusions from the penetrating fungal peg (compare Fig. 2e or 3c in Duddridge and Read 1982 with Figs. 7 and 8 in Wang et al. 1997). Burgeff (1943) even explicitly called the mycorrhiza in *M. hypopitys* ptyophagy, too. So far, the mycorrhizas of six *Gastrodia* species (Kusano 1911; Burgeff 1932; McLennan 1959; Campbell 1962, 1963, 1964; Wang et al. 1997) and *Lecanorchis javanica* (Janse 1896) have been shown to be ptyophagous. Further structural research on more of the over 200 achlorophyllous orchids (Leake 1994) is urgently needed.

Conclusions

The degree of structural diversity within the arbuscular mycorrhizas (rarely named) is as remarkable as the differences among the ecto-related mycorrhizas (ecto-, “pisonioid,” ectendo-, arbutoid, cavendishoid, “pyroloid,” ericoid, and monotropoid mycorrhizas; expressions which have not been explicitly coined in double quotes). Within the monophyla Gentianales (AM) and Ericaceae (ecto-related), both structural lineages of mycorrhiza can even be considered as phylogenetically cohesive, indicated by the gradual changes of mycorrhizal structures in a line from woody autotrophic to herbaceous mycoheterotrophic plants. Hence, ranking all established mycorrhizal types at the same level camouflages known differences and similarities. The three-level hierarchical classification suggested here (Table 1) may still not be able to exactly mirror the structural evolution of mycorrhizas. However, it is useful for both expression of distinction as well as affinities and also is better adaptable to integrate new findings. It distinguishes three mycorrhizal groups representing the most distinctive structural lineages, all of which independently developed mycoheterotrophy: ECM, AM, and OM. Each group comprises mycorrhizal types, where we find the well known and named structural syndromes such as e.g., *Paris* type, ectendomycorrhiza, or, monotropoid mycorrhiza. The mycorrhizal types may be subdivided into morphotypes, which are often less known (e.g. cavendishioid) and even unnamed (e.g., mycorrhiza in *Afrothismia* spp. or *Pisonia grandis*). Little known associations are summarized as “Ill-defined” until more information allows proper integration.

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