Plants living on fungi: a short review of mycoheterotrophy[*]

by

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KEYWORDS. — Plant evolution, Biogeography, Mycorrhizal Fungi, Tropical rainforests, Parasitism.

SUMMARY. — Most land plants live in close association with a large variety of soil organisms. The interaction with mycorrhizal fungi is of particular importance. Most mycorrhizal fungi can only obtain carbon from the plants of which they colonize the roots. In exchange for these carbohydrates they extract water and minerals from the soil for their host plants. In general, this interaction does not show high specificity: mycorrhizal fungi often colonize the roots of multiple plant species simultaneously. And the root system of a plant is mostly colonized by multiple species of mycorrhizal fungi. This creates underground networks, linking plants of different species by shared mycorrhizal fungi. Some leafless plants, termed ‘mycoheterotrophic’ plants, use this underground fungal network to obtain carbon. They grow in the deep shade in forests and obtain carbon from surrounding green plants through shared mycorrhizal fungi. Mycoheterotrophic plants are often rare and inconspicuous. Yet, the mycoheterotrophic mode of life is relatively widespread in land plants and had evolved multiple times independently. There are more than 500 species of mycoheterotrophic plants and they belong to ten families and 89 genera of flowering plants. Most species are restricted to the tropics. In this overview I discuss the ecology and evolution of mycoheterotrophic plants and how they influenced our view on the mycorrhizal symbiosis.

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TREFWOORDEN. — Plantenevolutie, Biogeografie, Mycorrhizaschimmels, Tropische regenwouden, Parasitisme.

SAMENVATTING. — De meeste landplanten leven nauw samen met allerlei bodemorganismen. Vooral de interactie met mycorrhizaschimmels is erg belangrijk. Deze schimmels kunnen niet aan fotosynthese doen en zijn voor hun koolstofbehoefte meestal volledig afhankelijk van de planten waarvan ze de wortels koloniseren. In ruil voor de koolhydraten die ze daarbij ontvangen voorzien ze hun gastheerplant van water en minerale verbindingen die ze met hun fijne hyfen uit de bodem extraheren. De interactie tussen planten en mycorrhizaschimmels is meestal weinig specifiek: de schimmels koloniseren vaak de wortelsystemen van verschillende naburige planten. Daarenboven is het wortelsysteem van een plant is doorgaans gekoloniseerd door verschillende mycorrhizaschimmels tegelijkertijd. Hierdoor ontstaan ondergrondse netwerken, waarbij planten van verschillende soorten door gemeenschappelijke mycorrhizaschimmels verbonden worden. Sommige bladloze planten, de zogenaamde mycoheterotrofe planten, gebruiken dit ondergrondse schimmelnetwerk om aan koolstof te komen. Ze groeien in bossen en onttrekken koolstof van mycorrhizaschimmels die op hun beurt de wortels van omliggende bomen koloniseren. Mycoheterotrofe planten leiden een erg onopvallend bestaan. De mycoheterotrofe levenswijze tientallen keren onafhankelijk van elkaar ontstaan tijdens de evolutie van de landplanten. Er zijn meer dan 500 soorten mycoheterotrofe planten die behoren tot tien families en 89 verschillende geslachten van de bloemplanten. De meeste soorten komen enkel in de tropen voor. In deze uiteenzetting bespreek ik de ecologie en evolutie van mycoheterotrofe planten en hoe hun bijzondere levenswijze van invloed geweest is op onze kijk op de mycorrhizasymbiose.

MOTS-CLES. — Evolution des plantes, Biogéographie, Champignons Mycorhiziens, Forêts tropicales, Parasitisme.

RESUME. — La grande majorité des végétaux terrestres vivent en étroite collaboration avec de nombreux organismes du sol parmi lesquels les champignons mycorhiziens jouent un rôle primordial. Ces champignons sont incapables de faire de la photosynthèse et sont dépendants de la plante qu'ils colonisent pour obtenir des substances carbonées. Ils fournissent en retour de l'eau et des substances minérales qu'ils sont capables de mobiliser grâce à leurs connexions hyphales avec le sol. La symbiose mycorhizienne n'est pas une relation entre deux partenaires seulement: peu spécifiques, les champignons mycorhiziens colonisent souvent les systèmes racinaires de plusieurs plantes voisines, parfois d'espèces différentes. Cette symbiose constitue donc un réseau, qui peut entraîner des synergies ou des parasitismes indirects entre végétaux. Certaines plantes non-chlorophylliennes, dites mycohétérotrophes, utilisent le réseau mycorhizien souterrain comme source de carbone. Ces plantes forestières reçoivent leur carbone de leurs champignons mycorhiziens qui, eux-mêmes, s'associent aux arbres voisins. Des mycohétérotrophes sont relativement discrètes dans les écosystèmes et ils sont apparues à diverses reprises dans l'évolution des plantes terrestres. Il existe plus de 500 espèces mycohétérotrophes réparties essentiellement dans dix familles indépendantes et 89 genres d'angiospermes. Ces espèces sont principalement tropicales. Dans cet exposé, je discute des aspects généraux écologiques et évolutifs des mycohétérotrophes tropicales et comment leur interaction avec des champignons a influencé notre point de vue sur la symbiose mycorhizienne.

Introduction

Almost all land plants are green: they obtain most of their energy from sunlight via photosynthesis using chlorophyll contained in chloroplasts, which gives them their green colour. Some plants, however, have lost the ability for photosynthesis and are heterotrophic. Heterotrophs include the holoparasitic plants, which obtain their nutrition directly from other plants through a special organ, the haustorium. There are approximately 350 species of holoparasitic plants. Arguably the most famous of all parasitic plants is *Rafflesia arnoldii* from rain forest in Sumatra and Borneo. The flower of *R. arnoldii* may be over 100 centimetres in diameter, and weigh up to 10 kilograms. It is considered the largest "single" flower of any flowering plant (Heide-Jørgensen 2008). However, in addition to holoparasitic plants, there is another, larger but less-known, category of plants that are leafless and heterotrophic: mycoheterotrophic plants.

Unlike holoparasitic plants, mycoheterotrophic plants are able to obtain carbohydrates from root- or rhizoid-associated fungi. The association between plant roots or rhizoids and soil fungi is very common: the majority of land plants and a wide variety of fungi are involved in this interaction, commonly described as the “mycorrhizal symbiosis”. In general, this symbiosis is mutualistic because both partners benefit: mycorrhizal fungi improve the nutrient uptake of their host plants, and in return they receive photosynthetically fixed carbon that is essential for growth and reproduction of the fungi. In contrast, in a mycoheterotrophic plant-fungal interaction plants are able to obtain carbon from their mycorrhizal fungi and thus exploit their fungi rather than support them. Most mycoheterotrophic plants obtain carbon from fungi that are simultaneously mycorrhizal with surrounding green plants. In this case these green plants are the ultimate source of the carbon in the system and the mycoheterotrophic plant can be considered as indirectly parasitic on green plants through shared mycorrhizal fungi. In some cases mycoheterotrophic plants are associated with fungi that obtain carbon by decomposing organic material (“saprotrophy”).

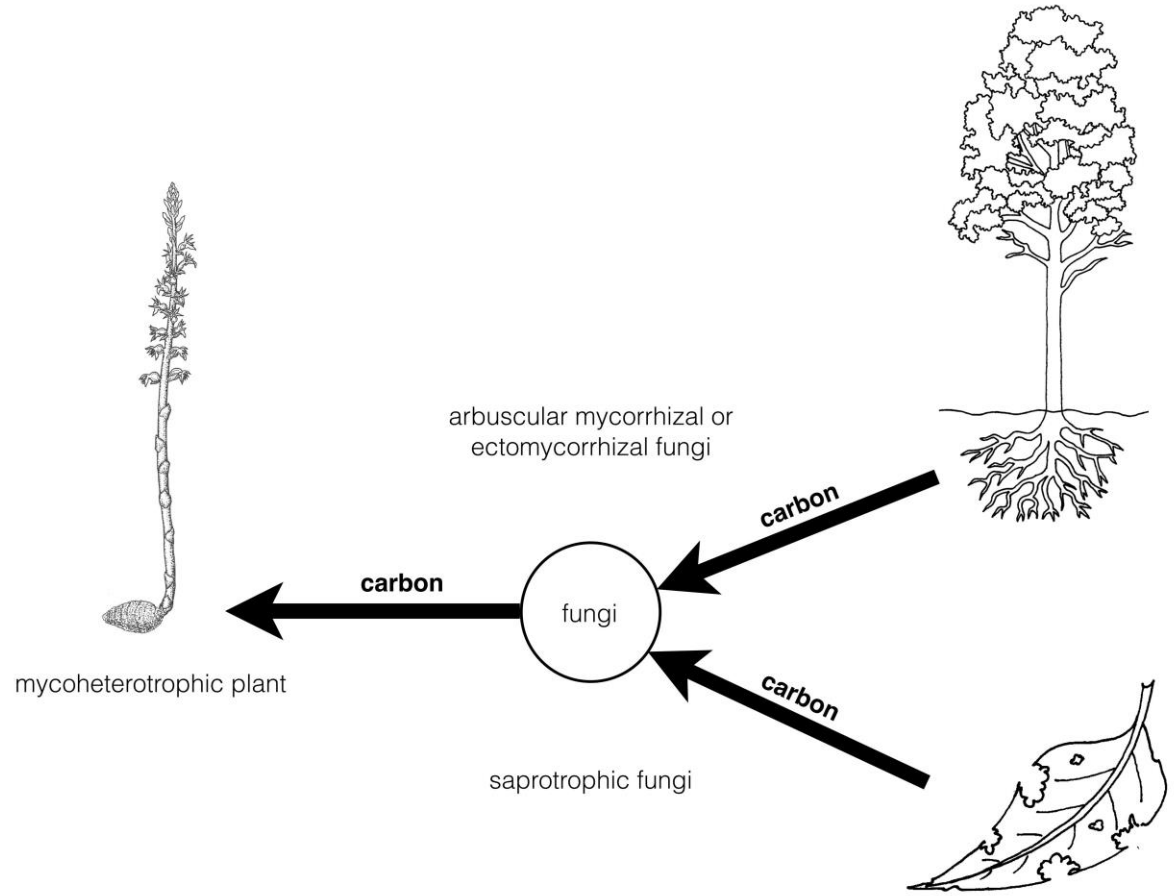

Figure 1. Mycoheterotrophic plants obtain carbohydrates either from fungi that are simultaneously mycorrhizal with surrounding green plants (above), or from fungi that are saprotrophic, *i.e.*, decompose organic material (below).

It must be noted that in neither case a mycoheterotrophic plant is living directly from carbohydrates obtained from degradation of organic material. Thus mycoheterotrophic plants are not “saprophytes” as is often incorrectly assumed (Leake 2005).

There are different types of mycoheterotrophic plants. Fully mycoheterotrophic plants are completely dependent on fungal carbon during their entire life cycle. As a result they have lost the ability for photosynthesis: they are non-green (“achlorophyllous”) and leafless. Not all mycoheterotrophic plants are achlorophyllous, however, or at least not during their entire life cycle. Initial mycoheterotrophs are dependent on fungal carbon for germination and their early development, but become green, autotrophic adult plants. Partially mycoheterotrophic plants can combine autotrophy and mycoheterotrophy as adults, and thus while still green they can also obtain carbon from fungi, for example when they are growing in shady habitats where there is not enough light to survive on photosynthesis alone.

Identity of the plants

Mycoheterotrophy occurs in almost all major lineages of land plants (table 1). In liverworts, which are considered the sister group of all other land plants, there is one fully mycoheterotrophic species in the family Aneuraceae: *Aneura mirabilis* Malmb. This peculiar species is found in the United Kingdom, Germany, France, Portugal, Russia, Sweden, Norway, and Greenland. It often grows buried under mosses in peat bogs. In Lycopodiaceae, and several families of ferns the gametophytes of many species are achlorophyllous and mycorrhizal. This is a strong indication that they are mycoheterotrophic, but the trophic status of most species remains to be investigated. While mycoheterotrophy in the gametophytes of clubmosses and ferns appears to be common, there is no indication of mycoheterotrophy in the sporophytes of any of these groups.

In gymnosperms there is a single heterotrophic species: *Parasitaxus usta* (Vieill.) de Laub. of the Podocarpaceae. *Parasitaxus usta* only occurs in New Caledonia and is always found sprouting from roots and trunks of another podocarp, *Falcatifolium taxoides* (Brongn. & Gris) de Laub., and is therefore often regarded as a holoparasitic plant. Some evidence shows that a fungal partner is involved in the interaction between *Parasitaxus* and *Falcatifolium*, in which case this would qualify as mycoheterotrophy

In angiosperms mycoheterotrophy is most common in monocots, where it occurs in seven families. Most of these families contain relatively few species and are restricted to the tropics. Thismiaceae, Triuridaceae, and Corsiaceae comprise entirely of fully mycoheterotrophic species. Petrosaviaceae and Burmanniaceae both contain fully mycoheterotrophic and autotrophic species. All species of Orchidaceae are presumably initially mycoheterotrophic, but while most species develop into autotrophs some species remain partially mycoheterotrophic and c. 235 species are full mycoheterotrophs. Besides monocots, mycoheterotrophy in angiosperms occurs in the eudicot families Polygalaceae, Gentianaceae, and Ericaceae. A small portion of the species in these families is fully mycoheterotrophic, and the latter two families also contain a few known partial mycoheterotrophic species.

Identity of the fungi

In the nineteenth century naturalist started to investigate the roots of mycoheterotrophic plants with their microscopes and observed that they were infected with fungi. In particular, the detailed observations of Kaminski (1882) lead to a breakthrough paper in which he postulates that *Hypopitys monotropa* Crantz lives on a fungus that is connected to tree roots. However, due to the lack of diagnostic morphology of mycorrhizas it was not until the development of molecular tools that the identity of the fungi forming mycorrhizas with mycoheterotrophic plants was unambiguously revealed. These investigations show that the two most common types of mycorrhizal symbioses are used by mycoheterotrophic plants: ectomycorrhizal symbioses involve fungi of the phyla Basidiomycota and Ascomycota. Arbuscular mycorrhizal symbioses occur through fungi of the phylum Glomeromycota. With few exceptions, mycoheterotrophic Aneuraceae, Orchidaceae and Ericaceae exploit ectomycorrhizal networks that mostly consist of Basidiomycota or sometimes Ascomycota fungi. Mycoheterotrophy in other families, including clubmosses and ferns, occurs through Glomeromycota networks that form arbuscular mycorrhizas (Leake 2005). As an alternative to associations with mycorrhizal fungi, a few tropical mycoheterotrophic orchids grow on litter- and wood-decay Basiodiomycota fungi (Ogura-Tsujita et al. 2009).

The plant-fungus mycorrhizal interactions are generally characterized by high promiscuity. An autotrophic mycorrhizal plant typically associates with multiple fungi and a mycorrhizal fungus often associates simultaneously with plants of different species (Bidartondo 2005). In contrast to autotrophic plants mycoheterotrophic plants often show high specificity towards fungi even though the fungi remain generalists. In extreme cases mycoheterotrophic plant species are found to be associated with only a single fungal genotype (e.g. Bidartondo et al. 2002), and there are reports that even within a species different plant genotypes preferentially associate with a different host fungus (e.g. Taylor et al. 2004). However, not all mycoheterotrophic plants are characterized by high fungal specificity. The mycoheterotroph *Pyrola aphylla* Sm. (Ericaceae) for example has been shown to be a fungal generalist as it is able to associate with a wide range of root-inhabiting fungi (Hynson & Bruns 2009).

Habitats

The majority of mycoheterotrophic plants primarily occur in forest biomes, and show a pronounced preference for damp habitats with primary forest and a closed canopy cover. Often they grow in the deep shade where autotrophic plants fail to survive due to the low influx of light. In northern temperate forests only mycoheterotrophic flowering plants of the families Ericaceae and Orchidaceae can be found. These often occur near pine, beech, or oak trees from which they obtain carbohydrates through shared ectomycorrhizal fungi. The flora of Belgium comprises three of these species: *Hypopitys monotropa* (Ericaceae), and the orchids *Neottia nidus-avis* (L.) Rich. and *Limodorum abortivum* (L.) Sw. The diversity of mycoheterotrophic flowering plants peaks in tropical forests and is particularly high in Southeast Asia, where c. 170 species are known. The tropical forests of South America harbour c. 90 species of fully mycoheterotrophic flowering plants, Africa (including

Madagascar) c. 50 species, and about 20 species are known from the restricted tropical forests in India (Merckx et al. 2013b).

Rarity and conservation

Many mycoheterotrophic plants are known from a very limited number of collections – for example most species of *Thismia* (Thismiaceae) in the neotropics have been collected only once or twice – and as a consequence they are considered to be extremely rare. In some cases, however, this apparent rarity may be an artefact of collection bias. Mycoheterotrophic plants often grow on remote locations and they only produce above-ground organs when they are flowering or fruiting, which may last only a few weeks per year. In addition, many species are extremely small and therefore very difficult to find. Some species, such as the enigmatic *Thismia rodwayi* F.Muell. from New Zealand and Australia, mostly remain covered by fallen leaves, which keep them hidden from collectors' eyes.

Figure 2. The flower of *Thismia rodwayi* F. Muell. (Thismiaceae), pictured at Mount Wellington, Tasmania, Australia. This tiny mycoheterotrophic plant lives on arbuscular mycorrhizal fungi that are simultaneously associated with the roots of surrounding trees. The tip of a pencil is shown for scale. Photo by V. Merckx.

In Tasmania *T. rodwayi* had been collected only about five times in the century following its discovery. However, recent intensive searches have revealed that the species is much more common than expected, and it is now known from dozens of sites throughout the eastern part of the state. Another classic example of mycoheterotrophic plants that are nearly impossible to find are the orchid species of the genus *Rhizanthella*, also known as the underground orchids. Underground orchids are endemic to Australia and, as their name suggests, remain completely underground for their whole life. As a result, they are generally only encountered by chance, for example during road constructions and their rarity is very difficult to assess. Despite these apparent observation and collection biases, many mycoheterotrophic plants are truly rare. For example in Britain the mycoheterotrophic orchid *Epipogium aphyllum* has been frequently described as the rarest orchid and even as Britain's rarest plant (Taylor and Roberts 2011). The rarity of mycoheterotrophic plants is probably related to habitat preferences. High specificity toward particular lineages of fungi may significantly limit the dispersal potential of mycoheterotrophs, although specificity toward other biotic (pollinators, dispersal agents, plant communities) and abiotic factors (humidity, soil composition) may be influential as well. The continuous destruction of their habitats and the increase of global temperatures threaten many species with extinction, and a few species have been declared as extinct already. Since the cultivation of fully mycoheterotrophic plants is very difficult, and in most cases currently impossible, the protection of their habitats is the best and only way for the effective conservation of mycoheterotrophic plants.

Biogeography

Despite their local rarity, many groups of mycoheterotrophic plants have very widespread, and often bizarre, global distributions. Although species of Burmanniaceae, Triuridaceae, and Thismiaceae are locally rare, species of these families can be found in virtually all rainforest areas in the world. These wide distributions were often seen as an indication for the old age of these taxa. This would imply that these genera originated before the breakup of Gondwana, allowing a vicariant explanation of the observed patterns. However, the application of molecular dating of lineage divergences has suggested that most transoceanic distributions are unlikely to be the result of tectonic vicariance simply because the lineages are too young to have been dispersed through ancient land connections. These analyses suggest that many mycoheterotrophic plant families obtained their current pantropical distribution by dispersal, probably aided by various land bridges. In particular, dispersal of Burmanniaceae, Thismiaceae, and Triuridaceae between the old and the new world may have been possible by "boreotropical" migration routes: during the Eocene, global temperatures peaked, and tropical vegetation occurred at high latitudes. This allowed for migration of tropical flora between the neotropics and the paleotropics over the "North Atlantic Land Bridge" (Merckx et al. 2013b).

The distributions of a many groups of mycoheterotrophic plants are characterized by remarkable disjunctions (distributions that are geographically separated). Corsiaceae, for example, comprises three genera: *Arachnitis*, which occurs in southern South America, *Corsia,* with species in tropical Australia and New Guinea, and *Corsiopsis,* which has been found once in southern China. Another remarkable distribution pattern is observed in the genus *Oxygyne* (Thismiaceae). One species has been collected once on Mount Cameroon in western Africa. The three other species in the genus are endemic to Japan. However, the most remarkable disjunct distribution is known in *Thismia,* where the closest relative of *T. americana* N.Pfeiff., a species described from a locality near Chicago, is supposedly *T. rodwayi* from Australia and New Zealand. This has been described as the most anomalous disjunction known in flowering plants (Thorne 1972).

Evolution

The taxonomic diversity of mycoheterotrophic plants indicates that the phenomenon has evolved multiple times independently in the evolution of land plants. However, precise phylogenetic hypotheses are lacking for many groups of mycoheterotrophic plants. This is because many mycoheterotrophic plants are rare, or at least difficult to find, which hinders the acquisition of DNA material needed for molecular phylogenetic studies. Also, the chloroplast genome of fully mycoheterotrophic plants suffers from high substitution rates and gene loss, and therefore it is difficult or even impossible to include fully mycoheterotrophic plants in plastid gene data sets often used in plant phylogenetics. However, recently the application of nuclear and mitochondrial DNA data has made it possible to successfully infer the phylogenetic position of many mycoheterotrophic plant clades, often challenging existing taxonomic views. These phylogenetic hypotheses show that fully mycoheterotrophic plants have evolved from green (autotrophic) mycorrhizal ancestors. Although many groups of mycoheterotrophic plants still have to be investigated in detail, current evidence indicates that there have been more than 45 independent shifts towards a fully mycoheterotrophic mode of life in land plants (Merckx et al. 2013a).

Many clades of fully mycoheterotrophic plants are evolutionary isolated lineages with no closely related autotrophic lineages. Consequently, the large evolutionary gap between autotrophic and fully mycoheterotrophic species prevents us to study the putative transitional steps that occurred in the evolution toward full mycoheterotrophy. However, for some fully mycoheterotrophic lineages, particularly in orchids, closely related green relatives are identified. Those lineages provide an interesting evolutionary perspective on the shift to full mycoheterotrophy. In particular, Motomura et al. (2010) demosntrated that full myco-heterotrophic species of *Cymbidium* probably evolved from partially mycoheterotrophic ancestors, which suggests that in this case, full mycoheterotrophy evolved gradually rather than through a direct shift from autotrophy to full mycoheterotrophy. In addition, initial mycoheterotrophy is presumably ubiquitous among orchid species (Rasmussen 1995). Thus partially mycoheterotrophic orchids most likely originated from initially mycoheterotrophic ancestors. A scenario for the evolution toward full mycoheterotrophy in Orchidaceae therefore seems to include shifts from initial mycoheterotrophy to partial mycoheterotrophy and from partial mycoheterotrophy to full mycoheterotrophy. A similar evolutionary scenario is suggested to have occurred in Ericaceae (Merckx et al. 2013a).

From an ecological point of view the evolution of full mycoheterotrophy represents the breakdown of the mutualistic interaction between plants and their mycorrhizal fungi into a parasitism, in which the plants exploit their mycorrhizal fungi. In theory, breakdown of mutualistic interactions is expected because they are unstable (Sachs et al. 2004). Evolutionary theory stipulated the selfish interest of individuals, thus why would they expend resources to benefit another species when resources could be redirected for one’s own fitness? Yet, despite this theoretical instability, mutualisms are ubiquitous in nature, and many mutualisms have an ancient origin, which suggest that they are evolutionary stable. A prime example is the mycorrhizal symbiosis, which encompasses more than 90% of all land plants and is believed to have played a major role in the invasion of the land by plants (Smith and Read 2008). In one-to-one plant–fungal symbiont interactions, fungal symbionts will increase their own fitness by helping plants grow, and vice versa. However, mycorrhizas are multipartite symbioses because a mycorrhizal plant typically associates simultaneously with multiple fungi and a mycorrhizal fungus often associates simultaneously with multiple plants. This can select for parasitism by exploitation of the benefits provided by others while avoiding the costs of supplying resources. The multipartite nature of the mycorrhizal symbiosis is of vital importance for the evolution of mycoheterotrophs. Since a mycorrhizal fungus needs an association with an autotrophic plant to obtain carbohydrates, an exclusive one-to-one interaction between a mycorrhizal fungus and a fully mycoheterotrophic plant cannot exist.

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Table 1

The occurrence of mycoheterotrophy in land plants. Note that for Orchidaceae, Ericaceae, and Gentianaceae only the fully mycoheterotrophic species are taken into account in the genera and species numbers. Many putative partially and initially mycoheterotrophic species in these families remain to be investigated. Question marks indicate uncertainty

Family	Group	Number of genera with mycoheterotrophic species / total number of genera in the family	Number of mycoheterotrophic species / total number of species in the family	Type of mycoheterotrophy
Aneuraceae	Liverworts	1/4	1/150	Full mycoheterotrophy
Lycopodiaceae	Clubmosses	?3/3	?/300	Mycoheterotrophy in the gametophyte phase
Ophioglossaceae	Ferns	?4/4	?/60	Mycoheterotrophy in the gametophyte phase
Psilotaceae	Ferns	?2/2	?/17	Mycoheterotrophy in the gametophyte phase
Gleicheniaceae	Ferns	1/6	1/130	Mycoheterotrophy in the gametophyte phase

Schizaeaceae	Ferns	1/2	?/30	Mycoheterotrophy in the gametophyte phase
Podocarpaceae	Gymnosperms	1/9	1/180	Full mycoheterotrophy
Petrosaviaceae	Angiosperms	1/2	3/4	Full mycoheterotrophy
Burmanniaceae	Angiosperms	8/8	63/100	Full mycoheterotrophy
Thismiaceae	Angiosperms	5/5	65/65	Full mycoheterotrophy
Triuridaceae	Angiosperms	11/11	50/50	Full mycoheterotrophy
Corsiaceae	Angiosperms	3/3	27/27	Full mycoheterotrophy
Orchidaceae	Angiosperms	43/880	235/22.000	Full, initial, and partial mycoheterotrophy
Iridaceae	Angiosperms	1/66	2/c. 2.000	Full mycoheterotrophy
Polygalaceae	Angiosperms	1/21	6/c. 1,000	Full mycoheterotrophy
Ericaceae	Angiosperms	11/126	16/c. 4.000	Full and partial mycoheterotrophy
Gentianaceae	Angiosperms	4/92	25/c. 1.650	Full and partial mycoheterotrophy