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# Myco-heterotroph/epiparasitic plant interactions with ectomycorrhizal and arbuscular mycorrhizal fungi

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More than 400 achlorophyllous plant species in 87 genera are parasitic upon fungi, and exploit them as their principle source of carbon. With a few exceptions, most of these myco-heterotrophic plants are now thought to be 'cheats', stealing carbon and nutrients from the mycorrhizal associates of adjacent autotrophic plants. Most myco-heterotrophs are therefore considered to be epiparasitic on green plants. Both the ectomycorrhizal and arbuscular mycorrhizal symbioses have been invaded by myco-heterotrophic epiparasites. DNA analysis is revealing the identities of many of the fungal partners of myco-heterotrophs, and their exceptionally high specificity. Myco-heterotrophs have distinctive stable isotope signatures, which can be used to establish the dependence upon fungal carbon of green plants that are partially myco-heterotrophic.

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## Abbreviations

**AM** arbuscular mycorrhiza  
**EM** ectomycorrhiza  
**MH** myco-heterotrophic  
**MHP** MH plant

## Introduction

The myco-heterotrophs remain the least studied and most poorly understood of the holo-parasitic plants [1]. They are the only group of parasitic plants for which, in over 90% of cases, the host species that provide their carbon and nutrients remain unidentified, and their ultimate sources of carbon are therefore generally unknown. Rapid advances made in the past three years through use of DNA-based fungal identification have, however, enabled fungal partners to be identified for almost all species in the Monotropoideae, for many myco-heterotrophic (MH) orchids, and for the first time, for representatives of several of the most important South American and Tropical genera. These identifications

have provided important new insights into the biotic factors that control the distributions of MH plants (MHPs), and into plant–fungus co-evolutionary processes. They have also revealed a consistent pattern of extreme fungal specificity in MHPs, as well as frequent dependence upon adjacent autotrophic plants from which they gain carbon indirectly by cheating the shared mycorrhizal fungal partners. In taking both carbon invested in the mycorrhizal fungi by the autotrophs and some of the nutrients passing through the mycelial network, these MHPs are epiparasitic on the green plants that support the shared fungal partners with sugars [2]. Because mycorrhizal mutualisms are diffuse, with many species sharing the same fungal partners [3] many of which can inter-link between plants [4], and because the costs and benefits of green plants joining these networks are not shared equally, the mutualism may be particularly vulnerable to exploitation by 'cheaters' [5\*\*]. Both major types of mycorrhiza, ectomycorrhiza (EM) and arbuscular mycorrhiza (AM), have been invaded by MH epiparasites.

## Epiparasites specialised on ectomycorrhizal fungi

Epiparasitism was first recognised in the Monotropoideae [2], whose roots are covered with fungal mantles that are characteristic of EM fungi. The unambiguous identification of the fungal partners of ten of the twelve species of Monotropoideae using DNA analysis has, however, become possible only recently. The epiparasitic status of ten of the 12 species in the Monotropoideae has been confirmed, and their specific fungal partners have been identified as ectomycorrhizal associates of adjacent trees and shrubs [5\*\*,6]. It is now known that epiparasitism via ectomycorrhizal fungi occurs in other groups of myco-heterotrophs in the Orchidaceae [7–10,11\*\*,12,13\*,14\*\*] and is also known in one non-vascular plant species [15\*\*].

The development of epiparasitism in some orchids is of particular interest because they are arguably the most successful family of myco-heterotrophs [1,12]. The family is relatively young but has diversified rapidly, and is estimated to contain approximately 30 000 species distributed widely over most terrestrial ecosystems [16]. Although the majority of orchids are autotrophic when fully established, the early stages of their growth and development are normally entirely dependent upon myco-heterotrophy. The orchid's strategy of producing vast numbers of 'dust' seeds means that young seedlings have insufficient reserves to enable growth without fungus-supplied carbon [1,12]. The carbon supplies that are required for the establishment of green orchids are norm-

ally provided by their associations with basidiomycetes in the polyphyletic form genus *Rhizoctonia*, which are generally assumed to be saprophytes or plant parasites [13<sup>\*</sup>,17]. However, there are more than 100 species of non-photosynthetic species in the Orchidaceae, comprising almost a quarter of known MHPs [1]. Among those orchid species examined to date that are fully MH and do not photosynthesise, many have switched from the ancestral associations with orchid *Rhizoctonias* to exclusive dependence upon basidiomycetes from ectomycorrhizal groups, such as the Thelephoraceae and Russulaceae, or in a few cases, to dependence upon aggressive wood-decay fungi [7,8,12,14<sup>\*\*</sup>]. The greater requirements of fully MH orchids for sustained supplies of fungal carbon is likely to have driven their switch to associating with such fungi [7,12]. Ectomycorrhizal fungi have access to an exceptionally large supply of carbon, receiving as much as 30% of the net photosynthate of their hosts [18], and this supply is potentially sustained over the lifespan of the trees.

### Epiparasites specialised on ectomycorrhiza-forming *Rhizoctonias*

Recent molecular phylogenetic studies of the orchid *Rhizoctonias* confirm that they fall into three polyphyletic lineages: the Ceratobasidiales, the Sebacinaceae and the Tulasnellales [13<sup>\*</sup>]. The specific associates of several epiparasitic MH orchids are in the genus *Sebacina* [10,11<sup>\*\*</sup>,13<sup>\*</sup>], and a *Tulasnella* is the partner of the achlorophyllous MH liverwort *Cryptothallus mirabilis* [15<sup>\*\*</sup>]. An earlier report of the MH orchid *Rhizanthella gardneri* associating with a fungus thought to be in the third group of *Rhizoctonia* fungi, the Ceratobasidiales [19], requires confirmation.

A striking feature of all of these myco-heterotrophs is that their specific *Rhizoctonia* fungal associates are all ectomycorrhizal on trees and shrubs [11<sup>\*\*</sup>,15<sup>\*\*</sup>,19]. *Sebacina* spp. are known to be common ectomycorrhizal associates of *Eucalyptus* in Australia [20]. In Europe, *Sebacina* spp. are the exclusive fungal associates of the most common MH orchid, *Neottia nidus-avis*, in the UK, Germany [10] and throughout its range in France and Corsica [11<sup>\*\*</sup>]. The same group of *Sebacina* species are found on adjacent EM tree roots, confirming the epiparasitic status of *N. nidus-avis* [11<sup>\*\*</sup>]. In North America and Mexico, the MH orchid *Hexalectris spicata*, which is only very remotely related to *Neottia*, is also almost exclusively associated with Sebacinoid fungi that are phylogenetically intermixed with the ectomycorrhizal and *N. nidus-avis* fungal associates [13<sup>\*</sup>].

The *Tulasnella* fungus' association with *C. mirabilis* provides the first record of ectomycorrhiza formation [15<sup>\*\*</sup>] by this major clade of *Rhizoctonia* fungi, which is also frequently associated with green orchids [21]. The carbon flux from birch trees to *Cryptothallus* liverwort thalli via the linked mycorrhizal mycelium has been quantified by <sup>14</sup>C-pulse labelling [15<sup>\*\*</sup>]. The failure to detect

Tulasnelloid ectomycorrhizas previously can be explained by the fact that these fungi are so divergent from other basidiomycetes that they do not share priming sites with standard universal fungal oligonucleotides. Hence, they remained undetected by standard PCR-based identification methods [15<sup>\*\*</sup>]. As a consequence, the abundance, distribution and host range of Tulasnelloid ectomycorrhizas is currently unknown and needs investigating.

The third group of orchid *Rhizoctonias*, the Ceratobasidiales, includes strains or species of *Ceratobasidium* that form mutualistic or pathogenic endophytic infections on trees and also partner green orchids, such as *Goodyera repens* [22] and many epiphytic tropical orchids [23]. The ectomycorrhiza-forming ability of fungi in this group has not been established unequivocally. One MH orchid has been reported to associate with ectomycorrhiza-forming fungi from this group, but the characteristics of these fungi were atypical [19] and their taxonomic placement requires confirmation by molecular phylogenetic analysis.

### Epiparasites specialised on arbuscular mycorrhizal fungi

The AM symbiosis is found in roughly 70% of all plant species and is the major type of mycorrhizal symbiosis found in most tropical forests, in which there is also the greatest diversity of myco-heterotrophs. Most of the MHPs in the families Gentianaceae (more than 20 species), Triuridaceae (more than 50 species), Burmanniaceae (more than 80 species) and Corsiaceae (more than 20 species) are found in tropical forests and other environments in which the majority of plants have arbuscular mycorrhizas (Figure 1). The fungal structures in representatives of the MHPs in all of these families appear to conform to a highly modified form of AM [1,24–26], which involves fungi in the Glomeromycota. This has been confirmed by DNA analysis of MHPs including one species in the Triuridiaceae [27], a species in the Corsiaceae and several species in the Gentianaceae [28<sup>\*\*</sup>]. The obligate requirements of AM fungi for carbon from their autotrophic partners, and the confirmed presence of these AM fungi in the roots of autotrophs adjacent to some of the MHP species, suggest that AM fungal associations are also exploited by epiparasites [28<sup>\*\*</sup>].

Epiparasites that are specialised on the AM symbiosis have evolved independently several times, in families that span from the dicotyledons to the monocotyledons. On the basis of molecular and morphological evidence, albeit it still rather limited, it seems likely that this is the type of association found in the majority of myco-heterotrophs.

The invasion of the AM mutualism by epiparasitic plants has several important implications. First, it establishes that biologically significant quantities of carbon can be transferred between plants that are inter-linked by a

Figure 1



Epiparasitic myco-heterotrophs in the Gentianaceae. *Voyria corymbosa* (left) and *Voyria rosea* (right), pictured growing in a tropical rainforest in French Guiana, are epiparasitic via different AM fungi [28\*\*].

common AM mycelial network, thereby refuting the suggestion that there is no evidence for such transfers having any significance for plant community composition or functioning [29]. Second, it strengthens the suggestion that significant transfers of carbon may occur even between green-leaved plants that are linked by a common mycelial network. In families such as the Gentianaceae and Burmanniaceae, in which the majority of species produce green leaves, some dependence upon fungal-derived carbon is likely to have been an ancestral trait that led to the development of fully MH genera, a pattern that is clearly seen in the Orchidaceae [12].

### Extreme fungal specificity characterises epiparasites

Both arbuscular and ectomycorrhizal fungi are typically characterised by low host specificity, most fungi normally associating with a wide range of plant species [3,30]. Many ectomycorrhizal plants associate with as many as thousands of distantly related fungi across their geographic ranges, with tens of fungal species often associating with individual trees at a single location [31]. In tropical rainforests, as many as 30 or more AM fungi can be found at a single location [32].

In contrast to the low specificity of EM and AM fungi for autotrophic hosts, recent studies on MHPs have consistently revealed that these plants form highly specific associations with very narrow ranges of fungi, with the fungal distributions strictly controlling those of the plants [8,10,12,14\*\*,33]. In the Monotropoideae, the MHP

family in which the most complete analysis of fungal associates has been carried out, extreme fungal specialisation is ubiquitous. In each of the ten *Monotrope* genera examined, the plants are specialised to a different genus or species group within five families of ectomycorrhizal basidiomycetes [5\*\*]. This level of specificity is remarkable; for example, *Sarcodes sanguinea* in the Sierra Nevada of California is associated exclusively with a single species of *Rhizopogon*, whereas its sister species *Pterospora andromedea*, which can grow within metres of *S. sanguinea*, is specialised on another closely related *Rhizopogon* species [32].

Extreme fungal specificity and epiparasitism has now been confirmed in other major groups of MHPs, irrespective of which of the major groups of mycorrhizal fungi they associate with. It is seen in orchids that are associated with Sebacinoid ectomycorrhiza-forming *Rhizoctonias* [10,11\*\*,13\*], in orchids associated with other major groups of ectomycorrhizal fungi [12,14\*\*], in the association of the liverwort *C. mirabilis* with *Tulasnella* [15\*\*], and in achlorophyllous members of the families Gentianaceae and Corsiaceae species that are specialised on a single narrow lineage of AM fungi [28\*\*].

### Geographic, phylogenetic and genotypic controls on fungal specificity

Fungal specificity in MHPs extends to regional specialisation on different fungal partners in different geographic areas and to races of the plants that selectively exploit different fungal partners, both providing fine-scale specificity. Results obtained in the past three years have provided the first proof of plant-genotype-level control on fungal specificity in MHPs. In the *Monotrope Pterospora andromedea*, sympatric genotypes discriminate between two *Rhizopogon* species groups [5\*\*,31].

By combining the internal transcribed spacer (ITS) phylogeny of the three *Monotrope* species that target fungi in the Tricholomataceae with ITS-based phylogenetic analysis of their *Tricholoma* associates, relationships between the plant and fungal phylogenies were investigated [5\*\*]. The most widely distributed *Monotrope* species, *Monotropa hypopitys*, comprises several lineages with distinct geographical ranges, each of which was found to normally associate with closely related *Tricholoma* species from particular parts of the fungal lineage [5\*\*]. Genotype-controlled fungal specificity has also been confirmed for the MH orchid *Corallorhiza maculata*, in which races have narrower specificity than the species as a whole with co-occurring genotypes at the same sites remaining faithful to their different ectomycorrhizal fungal partners in the Russulaceae [14\*\*]. Similarly, genotype-linked fungal specificity is indicated in varieties of the orchid *Hexalectris spicata* and in the closely related *H. revoluta* [13\*]. Regional variations in the sebacinoid associates of *N. nidus-avis* in France have suggested that geographic controls on

fungal distributions or genotype controls on fungal specificity also occur in this species [11\*\*].

### The significance of fungal specificity in myco-heterotrophs

Two hypotheses have been advanced to explain the extreme fungal specificity seen in myco-heterotrophs [31]. First, specialisation might allow the plants to adapt to particular fungi to enable the most effective capture of fungal carbon. Second, most fungi may develop resistance to exploitation by the MH plants, forcing them to specialise on fungi without this resistance. Because MHPs are rare, and are typically of insignificant biomass in comparison to mycorrhizal fungi, the first hypothesis seems to be the more plausible. Symbiotic germination has been investigated in a few MHPs; in the species examined, seed dormancy appears to be broken only by chemical signals from specific fungal associates [8,10,31,34]. This enables the tiny seeds to lie dormant in the soil for long periods, thereby increasing their chances of being encountered by their fungal partners. Germination is often only initiated when the appropriate fungi are in the immediate vicinity of the seeds (Figure 2).

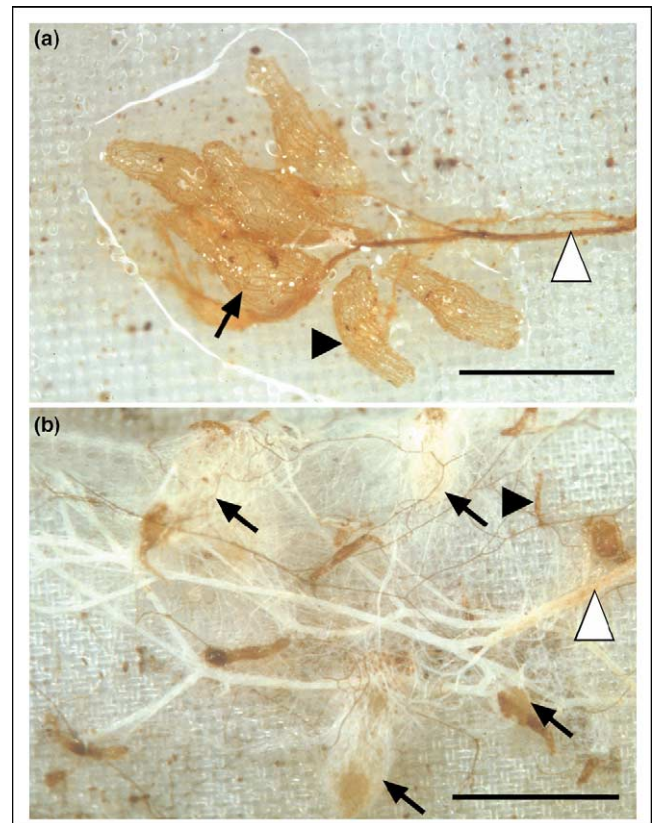
The extreme fungal specificity seen in myco-heterotrophs provides one of the few compelling examples of the importance of mycorrhizal biodiversity for the maintenance of plant diversity and ecosystem functions. It demonstrates that individual mycorrhizal fungal species, irrespective of their relative abundance at the ecosystem-scale, can have a crucial controlling influence on the success of other species [5\*\*,6–10,11\*\*,12,13\*,14\*\*,15\*\*].

Tight species interdependencies of the kinds described in this review support the hypothesis that biodiversity begets biodiversity. Although specificity and host-compatible races may be features dictated by the parasitic lifestyle of MHPs, the selection of the same specific host fungi by very distantly related MHPs raises questions as to why these particular fungi and not others are involved. The sharing of the narrow clade of *Glomus* species by MH plants in the Gentianaceae (Dicotyledonae) and Corsiaceae (monocotyledonae) or the specialisation of both European *N. nidus-avis* and the remotely related North American orchids *Hexalectris spicata* and *H. revoluta* on closely related *Sebacina* species is intriguing. What are the features of these fungi or of the co-evolutionary processes that have led to these specific interactions?

### The stable isotope 'fingerprint' of myco-heterotrophy

Epiparasites that associate with ectomycorrhizal fungi are enriched in  $^{15}\text{N}$  and  $^{13}\text{C}$  to an exceptionally high level that sets them apart from autotrophs (Figure 3; [35\*\*,36\*\*]). This is a consistent feature across representatives of the Monotropoideae and Orchidaceae, and in the latter family, applies both to species that are depen-

Figure 2

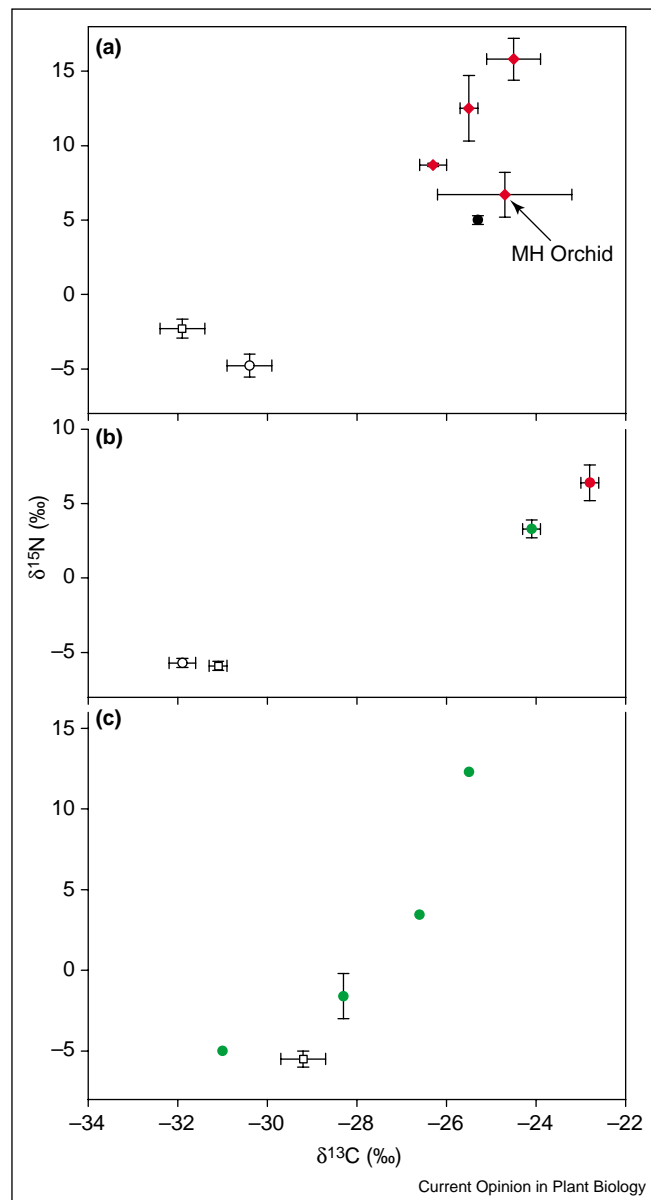


Symbiotic germination of seeds of MHPs buried in their natural habitats in nylon mesh bags. (a) *Neottia nidus-avis* with EM *Sebacina* spp. [10] and (b) *Monotropa hypopitys* with EM *Tricholoma cingulatum*. Black arrow heads point to ungerminated seeds; arrows point to representative seedlings; and white arrow heads point to fungal partners. The scale bars represents 500 μm.

dent upon ectomycorrhiza-forming sabacinoid fungi [36\*\*] and those associated with *Russula* [35\*\*]. Strong correlations have been observed between the  $^{15}\text{N}$  enrichment in the epiparasites and that in their putative ectomycorrhizal fungal partners [35\*\*].

The isotopic 'fingerprint' of myco-heterotrophy in orchids that are epiparasitic via ectomycorrhizal fungi is so strong and consistent that, by using isotope-mixing models, the proportion of carbon and nitrogen that is supplied to partially MH green orchids by their fungal partners can be estimated [36\*\*]. A further feature of interest is the high concentration of nitrogen in orchids in general. This is particularly surprising in MH orchids as they presumably do not need to produce the main plant protein, ribulose biphosphate carboxylase, yet maintain N concentrations in the range 1.9–2.9% dry weight, which are as high as those in nitrogen-fixing plants [36\*\*]. In autotroph associations with ectomycorrhizal fungi, some of the carbon supplied by the host plant is used by the fungi to assimilate ammonium into amino acids and then returned

Figure 3



High enrichment of heavy isotopes of carbon and nitrogen characterises epiparasites that are specialised on EM fungi and reveal the potential MH dependence of green orchids on fungal carbon and nitrogen. The mean values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  are shown for AM/non-mycorrhizal plants ( $\square$ ), EM plants ( $\circ$ ), green orchids ( $\bullet$ ), achlorophyllous epiparasitic orchids specialised on EM fungi ( $\bullet$ ), Monotropes ( $\blacklozenge$ ) and ectomycorrhizal fungal fruit bodies ( $\bullet$ ). The data are re-plotted (a) from Trudell *et al.* [35\*\*], who measured isotopes in samples from the Olympic National Park, Washington, USA; (b) from Gabauer and Meyer [36\*\*], who used samples taken from a *Fagus sylvatica* forest in Bavaria, Germany; and (c) from a *Pinus sylvestris* forest also in Bavaria [36\*\*].

to the host. This may provide an easily exploited pathway for carbon and nitrogen acquisition by epiparasites.

Further work is required to establish whether a switch from association with saprotrophic *Rhizoctonias* to associations with EM-forming basidiomycetes consistently provides distinct isotopic signatures in orchids and other plants. Future work must also determine whether isotopic

signatures can also be used to establish the degree of myco-heterotrophy in green-leaved species in families such as the Burmanniaceae and Gentianaceae, which contain many fully myco-heterotrophic species.

## Conclusions

In the past three years, three major advances have been made in our understanding of myco-heterotrophs. First, it

has been shown that the major groups of MHPs have invaded arbuscular or ectomycorrhizal mutualisms and therefore are epiparasitic on the autotrophic plants that support the mycorrhizal networks. Second, extreme fungal specialisation, including regional and plant-genotype-controlled specificity is emerging as a common feature of myco-heterotrophs and of epiparasites in particular. Third, epiparasites that are specialised on ectomycorrhizas have stable-isotope signatures that are so distinctive that they can be used to identify green plants that obtain much of their carbon through fungal pathways.

New species of MHP are still being discovered [37] and much of the basic biology of these plants remains to be determined, but the progress in the identification of their fungal partners has enabled enormous strides forward.

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