Myco-heterotrophy: A new vision about fungi-plants interactions

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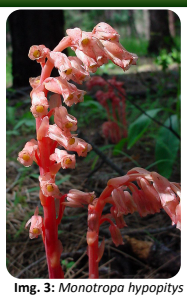
1 INTRODUCTION

Myco-heterotrophy is the process in which a plant obtains carbon and nutrients from fungi. They are generally **achlorophyllous** and known as "cheater" plants: an individual that obtains a benefit offered to mutualists without reciprocating, with little fitness costs for the mutualists with which it associates . Myco-heterotrophic plants (MHPs) are also known as "epiparasitic" on green plants. This resulting **tripartite symbiosis** is composed by photosynthetic plants, fungi and MHPs, and in this relationship there is a carbon flow from the photosynthetic plant through the mycorrhizal fungus to the myco- heterotroph. The main difference between parasitic plants and MHPs is the lack of haustoria in MHPs, since the connection to the photosynthetic plant is the mycorrhizal fungi, which has filaments closely associated with the root systems of both plants.

Img. 1: *Neottia nidus-avis*, a fully myco-heterotrophic plant.



Img. 3: *Monotropa hypopitys*

Initial myco-heterotroph
- a plant which is myco-heterotrophic only during germination

Partial myco-heterotroph
- a plant with limited photosynthetic capacity as a mature plant

Fully myco-heterotroph
- a plant lacking photosynthetic capacity during its entire life span.

2 FUNGI-PLANTS SYMBIOSIS

Fungi

Arbuscular mycorrhizal fungi (Glomeromycota)
Ectomycorrhizal fungi (Ascomycota & Basidiomycota)
Saprotrophic fungi (Orchidaceae early development)

Specificity

The specificity of MHPs towards fungi is normally extremely high. This has led to diversification of some lineages, each of them phylogenetically tracks one specific distantly related fungal lineages, and this can lead to some co-evolution cases.
MHPs can also track fungi in regional terms → *Pterospora andromedea* **(Img. 2),** sympatric genotypes discriminate between two *Rhizopogon* sp. different groups.

Img. 2: *Pterospora andromedea*

HABITATS AND DISTRIBUTION

Worldwide, most of them have **pantropical distribution**
Some in temperate forests
From **0m to 4000m** high
Moist rotting wood, wet rocks, moist soil, muddy ground
Deeply shaded forest **undestorey**

Img. 4: *Parasitaxus usta*

MYCO-HETEROTROPHY IN NUMBERS

-Has evolved **40 times** within different plant lineages
- **400 spp.** fully MHPs
- **20.000 spp.** initial and partial MHPs
- **1 sp.** gymnosperm fully myco - heterotroph → *Parasitaxus usta* **(Img. 4)**
- **1 sp.** liverwort fully myco-heterotroph → *Aneura mirabilis*
- First MHPs appeared **170ma** ago (Mid Jurassic)

Physiological ecology

NUTRIENT TRANSFER
Some methodologies have helped to the understanding of MHPs physiology → **analysis of the natural abundance of C ($_{13}C/_{12}C$) and N ($_{15}N/_{14}N$) stable isotopes.** With these tools is possible to infer strategies of resource acquisition and metabolic pathways in plants.
It has been shown that **fully MHPs that associate with ectomycorrhizal fungi are enriched in $_{13}C$ and $_{15}N$**, compared with the "cheated" autotrophic plants

GERMINATION
Germination is often initiated only when the appropriate fungi are in the immediate surroundings of the seeds of MHPs. In the Orchidaceae, almost all species produce "dust seeds" with few reserves. This model (**Fig. 1**) from **Bidartondo (2005)** shows the process of "dust seeds germination".

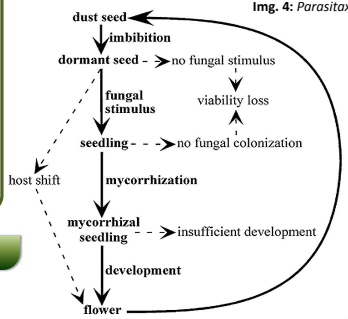


Fig. 1: *Adapted from Bidartondo, 2005*. A model for the symbiotic development of MHPs with "dust seeds".

Systematics & evolution: where they come from?

Making a phylogeny of MHPs is complicated:
- Reduction or loss of key morphological characters
- Lack or divergence of chloroplast genes
- Nuclear & mitochondrial substitution rates
- Getting samples of MHPs is difficult → spaced life cycles

Mycorrhizal green plants → **Myco – heterotrophic plants**

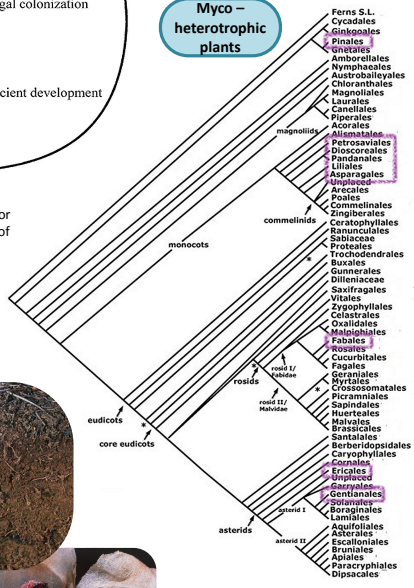


Fig. 2: *Adapted from Angiosperm Phylogeny Website, 2014, and The Taxonomicon Project.* Taxonomic vascular plant tree in order terms. Here are, highlighted, all orders of vascular plants in which there are MHPs.

Myco-heterotrophy has appeared **different times in plant evolution (Fig. 2)** → **evolutionary convergence process**

3 STATE OF THE ART & CONSERVATION

Threatening factors for MHPs

- Change of land uses
- Forest undestorey clearing operations
- Increasing pressure from mountain activities
- Increasing quantity of dry soils ← land use change and climate change

Most of species are assumed to be endangered!

DARK SPOTS IN MHPs RESEARCH

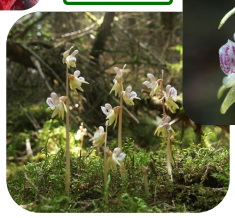
Isotope signatures of MHPs depending on arbuscular mycorrhizal fungi
Nutrient transfer mechanism
All MHPs are physiologically convergent?
The signals involved in triggering MHP seed germination and mycorrhization
Timing of the myco-heterotroph process
Are there measurable costs for mycorrhizas invaded by a MHPs?

Interesting cases

Aneura mirabilis

Rhizanthella gardneri

Epipogium aphyllum



4 CONCLUSIONS

Investigation about myco-heterotrophy has made great advances the recent years but there are some dark spots and unanswered questions, and few gaps in our knowledge of evolution and ecology of MHPs. For some genera is lacking a lot of information: since distribution, life history, pollination biology, dispersal agents, ecology and taxonomic position. This lack of information is primarily due to the fact that a lot of MHPs genera are rare and ephemeral, and the first step to get this understanding about them is fieldwork. This field sampling is very important to know about both aerial and subterranean parts of MHPs and their fungal partners, and therefore is important to have collections of MHPs, mycorrhizal fungi and green plants that are involved in the relationship. Further investigation about their biology and conservation status is needed to get a global perspective about.

REFERENCES: Bidartondo, Martin I. 2005. The evolutionary ecology of myco-heterotrophy. Tansley Reviews, New Phytologist 167: 335 – 352 | Angiosperm Phylogeny Website: www.mobot.org/MOBOT/research/APweb/ | Arkive: www.arkive.org/underground-orchid/rhizanthella-gardneri/photos.html | The Taxonomicon Project: taxonomicon.taxonomy.nl