Parasitism and mycoheterotrophy

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In plant parasitism, two groups can be distinguished based on two different mechanisms. The first group of **parasitic plants** includes those directly parasitizing on another plant. These plants are called haustorial parasites. Using a specialized organ, the haustorium, they attach themselves to other plants and uptake resources from the host's vascular bundles. The second group comprises **mycoheterotrophic plants**, which parasitise fungi via mycorrhizal interactions and gain organic carbon from them. Plants in both groups display variable dependence on their host organism.

The functional categorization of **parasitic plants** has been a topic of an active debate that is still ongoing. The traditional categories are based on the ability to perform photosynthesis (photosynthetic hemiparasites and non-green holoparasites) and the location of the haustoria (root and stem parasites) (Heide-Jørgensen 2008). However, such a classification system struggles with phenomena such as rudimentary photosynthesis in some species, variable photosynthetic activity throughout the life cycle, and the existence of parasitic plants that integrate with their host to such an extent that they can be considered endophytic. For the functional classification of European parasitic plants, we have adopted the most recent classification system proposed by Teixeira-Costa & Davis (2021) with small further modifications. This system relies primarily on ontogenetic development and strategies of attachment to the host. The values of other important functional traits, including photosynthetic capacity, type of vascular bundle connection, development of the primary haustorium, and location of haustoria on the host are also well discriminated by the categories of Teixeira-Costa & Davis (2021).

- *Euphytoid hemiparasites* represent a great majority of European parasitic plants. These are root-parasitic, photosynthetic plants that germinate independently of the presence of the host and produce exclusively lateral (secondary) haustoria with a vascular connection to the host xylem only. All European species belong to the *Orobanchaceae* and *Santalaceae*. Teixeira-Costa & Davis (2021) call these plants "euphytoid parasites", but we prefer keeping "hemiparasites" in the name of this category to preserve this well-established term.

- *Obligate root parasites* comprise all species of non-green root holoparasites (such as *Orobanche* spp.), but also hemiparasitic species, which are more dependent on their host than the euphytoid hemiparasites due to the absence of photosynthesis in the initial life stage (e.g. *Striga* spp.). Most of them produce terminal (primary) haustoria immediately after seed germination, triggered by chemical cues of host presence. However, several European obligate root parasites (holoparasitic *Lathraea* spp., hemiparasitic *Tozzia alpina*, and perennial species of *Rhynchocorys*) deviate from this developmental pattern by germinating without host cues and not forming primary haustoria (Těšitel 2016).

- *Mistletoes* are epiphytic parasitic shrubs. They germinate on host stems or branches and penetrate the host with a primary haustorium. The level of photosynthesis varies among the mistletoe species from efficient to rudimentary. The most widespread mistletoes of *Loranthus* and *Viscum* display efficient photosynthesis. By contrast, the Mediterranean

genus *Arceuthobium* connects to the host's phloem and takes up substantial amounts of carbon from the host (Rey et al. 1991). The photosynthetic capacity of *Arceuthobium* is probably limited, as shown by physiological data from their American congeners (Miller & Tocher 1975).

- *Parasitic vines* are herbaceous parasites that attach themselves to the stems of their hosts by haustoria that are formed on the parasite stem. They germinate on the soil surface and, during a period of independent growth, forage for a host to which they attach themselves with lateral haustoria. All European parasitic vines belong to the genus *Cuscuta* and have only rudimentary photosynthesis, which however has an important function in seedling metabolism and seed production (McNeal et al. 2007).

- *Endophytic parasites* (or *Endoparasites*) are the most integrated with the host body among parasitic plants. They are rootless, stemless and leafless, grow most of their life as filaments within their host and are only visible outside the host body when flowering. The holoparasitic *Cytinus hypocistis* and *Pilostyles haussknechtii* are the only species of this category in the European flora.

In **mycoheterotrophic plants**, the initial developmental stages (gametophytes in lycophytes and ferns or belowground seedling stages of other plants) are not green, obtaining all their organic carbon and other resources from the fungus. The adult stages are still dependent on the mycorrhizal fungi as a source of water and mineral nutrients but vary in their dependence on heterotrophic carbon: there is a continuum from autotrophy, where the adult plants no longer use fungal carbon (this strategy is further called 'initial mycoheterotrophy'), through mixotrophy (the adult plants combine autotrophic with heterotrophic nutrition; further called 'partial mycoheterotrophy'), to heterotrophy (further called 'full mycoheterotrophy') (Merckx 2012). Two categories are distinguished here:

- *Initial and partial mycoheterotrophs* have been combined here into a common category because the level of carbon heterotrophy may be low or depend on light conditions (Preiss et al. 2010), which makes it difficult to distinguish between partial mycoheterotrophs and initial mycoheterotrophs. Furthermore, new partially mycoheterotrophic species may be identified due to the advancement of the stable-isotope methodology (e.g., Schiebold et al. 2018). This category includes mycoheterotrophic species from *Ophioglossaceae*, *Lycopodiaceae*, green mycoheterotrophic species from *Ericaceae* (subfamily *Pyroloideae*) and all green *Orchidaceae*. Species that obtain nearly all of their carbon from mycorrhizal fungi but still contain chlorophyll and can be photosynthetically active, such as *Corallorhiza trifida* (Zimmer et al. 2008, Cameron et al. 2009) and *Limodorum* species (Bellino et al. 2014) from *Orchidaceae*, are also included in this category. Interestingly, achlorophyllous individuals, which completely lack chlorophyll and wholly depend on their mycorrhizal fungi, are rarely found among partially mycoheterotrophic species (e.g., in the genera *Cephalanthera* and *Epipactis*).

- *Full mycoheterotrophs* include achlorophyllous species that cannot photosynthesize and obtain carbon only from mycorrhizal fungi during their life cycle. *Neottia nidus-avis* and *Epipogium aphyllum* from *Orchidaceae* and *Hypopitys monotropa* and *H. hypophegea* from *Ericaceae* are the only species in this category in the European flora.

Categories

- autotroph
- euphytoid hemiparasite
- obligate root parasite
- mistletoe
- parasitic vine
- endophytic parasite
- initial or partial mycoheterotroph
- full mycoheterotroph

Further references

Bellino, A., Alfani, A., Selosse, M.-A., Guerrieri, R., Borghetti, M., & Baldantoni, D. (2014). Nutritional regulation in mixotrophic plants: New insights from *Limodorum abortivum*. *Oecologia*, 175(3), 875–885. https://doi.org/10.1007/s00442-014-2940-8

Cameron, D. D., Preiss, K., Gebauer, G., & Read, D. J. (2009). The chlorophyll-containing orchid *Corallorhiza trifida* derives little carbon through photosynthesis. *New Phytologist*, 183(2), 358–364. https://doi.org/10.1111/j.1469-8137.2009.02853.x

Heide-Jørgensen, H. S. (2008). Parasitic flowering plants. Brill, Leiden.

Kubat, R. & Weber, H. C. (1987). Zur Biologie von *Rhynchcorys elephas* (L.) Griseb. (*Scrophulariaceae*). *Beiträge zur Biologie der Pflanzen*, 62, 239–250.

McNeal, J. R., Arumugunathan, K., Kuehl, J. V., Boore, J. L., & dePamphilis, C. W. (2007). Systematics and plastid genome evolution of the cryptically photosynthetic parasitic plant genus *Cuscuta* (*Convolvulaceae*). *BMC Biology*, 5(1), 55. https://doi.org/10.1186/1741-7007-5-55

Merckx, V. S. F. T. (Ed). (2012). Mycoheterotrophy: the biology of plants living on fungi. Springer, Berlin.

Miller, J. R., & Tocher, R. D. (1975). Photosynthesis and respiration of *Arceuthobium tsugense* (*Loranthaceae*). *American Journal of Botany*, 62(7), 765–769. https://doi.org/10.2307/2442068

Preiss, K., Adam, I. K. U., & Gebauer, G. (2010). Irradiance governs exploitation of fungi: Fine-tuning of carbon gain by two partially myco-heterotrophic orchids. *Proceedings of the Royal Society B: Biological Sciences*, 277(1686), 1333–1336. https://doi.org/10.1098/rspb.2009.1966

Rey, L., Sadik, A., Fer, A., & Renaudin, S. (1991). Trophic relations of the dwarf mistletoe *Arceuthobium oxycedri* with its host *Juniperus oxycedrus*. *Journal of Plant Physiology*, 138(4), 411–416. https://doi.org/10.1016/S0176-1617(11)80515-8

Schiebold, J. M.-I., Bidartondo, M. I., Lenhard, F., Makiola, A., & Gebauer, G. (2018). Exploiting mycorrhizas in broad daylight: Partial mycoheterotrophy is a common nutritional strategy in

meadow orchids. *Journal of Ecology*, 106(1), 168–178. https://doi.org/10.1111/1365-2745.12831

Teixeira-Costa, L., & Davis, C. C. (2021). Life history, diversity, and distribution in parasitic flowering plants. *Plant Physiology*, 187(1), 32–51. https://doi.org/10.1093/plphys/kiab279

Těšitel, J. (2016). Functional biology of parasitic plants: A review. *Plant Ecology and Evolution*, 149(1), Article 1. https://doi.org/10.5091/plecevo.2016.1097

Těšitel, J., Těšitelová, T., Blažek, P., & Lepš, J. (2016). Parasitism and mycoheterotrophy. www.pladias.cz.

Weber, H. C. (1973). Zur Biologie von *Tozzia alpina* L. (Standort, Wirtspflanzen, Entwicklung und Parasitismus). *Beiträge zur Biologie der Pflanzen*, 49, 237–249.

Zimmer, K., Meyer, C., & Gebauer, G. (2008). The ectomycorrhizal specialist orchid *Corallorhiza trifida* is a partial myco-heterotroph. *New Phytologist*, 178(2), 395–400. https://doi.org/10.1111/j.1469-8137.2007.02362.x