

Mycoheterotrophy and mixotrophy in orchids: an update

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A particularity of orchids is their mycoheterotrophic germination, where reserveless seeds develop into a heterotrophic seedling, thanks to the colonization and carbon provided by a symbiotic fungus (Dearnaley *et al.*, 2016). The seedling later forms green leaves in most case: the fungus, generally belonging to the polyphyletic 'rhizoctonia' aggregate (Dearnaley *et al.*, 2013), then turns into a purely mycorrhizal fungus, and colonizes roots only. At this adult stage, green orchids are believed to become autotrophic and to reward the fungus with their own photosynthetic carbon, as in most other mycorrhizal associations.

However, some species rely on mycoheterotrophy at adulthood and lost photosynthesis. This evolution of non-green species occurred ca. 50 times independently in the orchid family. It was more recently realized that some green orchids, phylogenetically related to mycoheterotrophic species, although photosynthetic, are partially mycoheterotrophic, a strategy called mixotrophy (Selosse and Roy, 2009). In the later species, difference in isotopic abundance (¹³C) between fungal and photosynthetic carbon and the examination of albinos (rare achlorophyllous variants that survive *in natura* thanks to full mycoheterotrophy) were instrumental in the elucidation of mixotrophy. Mycoheterotrophic and mixotrophic species rely on the symbiotic shifts from the usual rhizoctonia partners to totally different fungal taxa, which are either saprotrophic (in the tropics mainly) or mycorrhizal on surrounding trees (Hynson *et al.*, 2013). Moreover, mixotrophy is viewed as an evolutionary step toward mycoheterotrophy.

More recently, isotopic particularities found in most green orchids that are putatively considered autotrophic raised the possibility that they are mixotrophic as well (Selosse and Martos, 2014; Gebauer *et al.*, 2016). We discuss this issue in an evolutionary perspective, and also address the limits of isotopic approaches, in order to suggest next steps in research on mixotrophy in the orchid family

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