Mycoheterotrophs: Plants that feed on fungi

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By Sue Lancelle

We usually think of plants as being green because most of them contain chlorophyll. This chlorophyll allows green plants to “fix” carbon from carbon dioxide into useable organic carbon compounds, utilizing the energy of sunlight. But if you’ve been out hunting for mushrooms, you have undoubtedly come across organisms such as those pictured above, which are white or pale pink, and don't contain a hint of green. You may have even wondered if it was a plant or a fungus or something else! In fact the organism in the photo is *Monotropa uniflora*, the “ghost pipe” or “Indian pipe,” a flowering plant that does not produce chlorophyll. So how does it get carbon?

In the past, scientists thought that plants without chlorophyll were “saprophytic,” meaning that they obtained carbon directly from decaying organic matter. But it turns out that there are no saprophytic land plants[1]. Instead, plants that don’t have chlorophyll fall into one of two categories: those that are parasitic on other plants via direct root-root interactions, and those that get their carbon from fungi. The latter plants are called “mycoheterotrophs,” meaning “fungus feeders.” In contrast, green plants are termed “autotrophs” or “self-feeders” because they can fix carbon themselves.

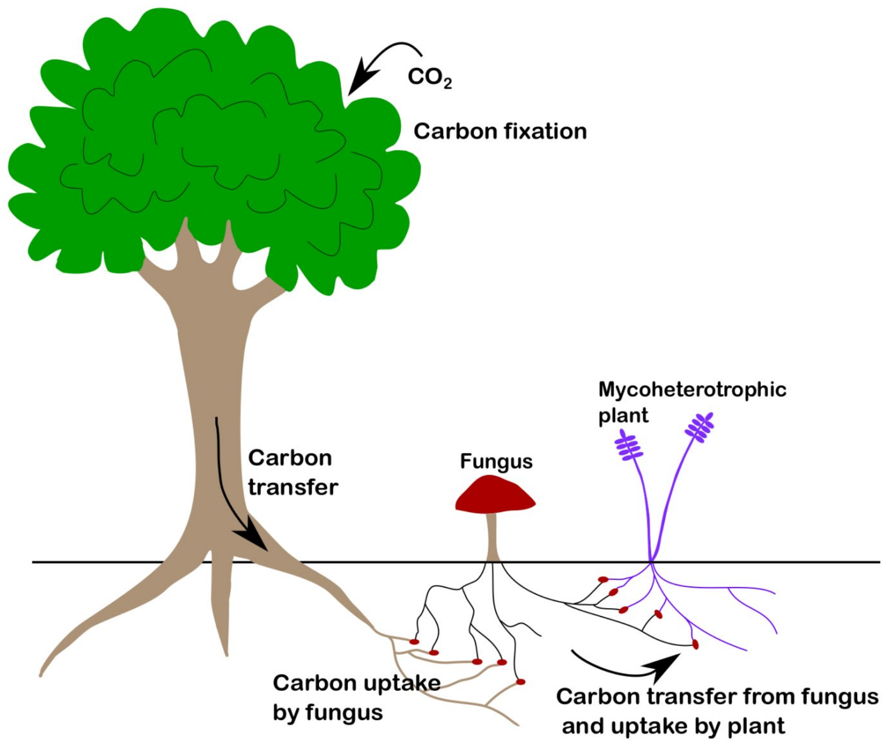

Figure 1. Carbon transfer from a tree to a plant via a fungus, the most common form of mycoheterotrophy. Drawn after Hynson, 2018[2].

Mycoheterotrophy (MHT) probably evolved from initially mycorrhizal interactions[3]. Recall that mycorrhizae are associations between a plant's roots and a fungal partner. Approximately 90% of vascular land plants have a mycorrhizal association[4]. The fungus provides increased water and nutrients to the plant while the plant provides organic carbon to the fungus. This is an example of a mutualistic symbiosis, where both partners benefit. In contrast, MHT appears to be one-way in that the plant nabs carbon and possibly other nutrients from the fungus but apparently doesn't provide anything to the fungus in return (Figure 1). The carbon is initially fixed by the autotrophic plant, and flows through the mycorrhizal fungus to the MHT plant. Thus, these plants are sometimes referred to as "cheats" on the process of mycorrhizal symbiosis[1].

An exception to the mycorrhizal origin of MHT is that of a few tropical orchids that are known to obtain their carbon from saprobic fungi[5], often aggressive pathogens such as *Armillaria*[1] rather than through a mycorrhizal association.

In practice, there is a whole range of degrees of MHT. Interestingly, the orchid family displays all of these! *Fully mycoheterotrophic* plants have no chlorophyll and obtain all of their carbon from fungi. Plants that are only *initially mycoheterotrophic* utilize MHT during seed or spore germination and then may switch to autotrophy later in development. *Partially mycoheterotrophic* plants develop chlorophyll and are able to produce at least some of their own organic carbon while obtaining the rest from fungi. There exists among partial MHT species a continuum of dependence on MHT for carbon needs; some are almost fully MHT while others extract only a small amount of their necessary carbon this way[6]. Interestingly, the degree of MHT in some plants can change seasonally as light levels change[7,8]. The various degrees of partial MHT that plants exhibit probably reflect the evolutionary steps that led to full MHT[1,9].

Locally, there are at least three fully MHT plants that you might come across while out searching for fungi. The ghost pipe or Indian pipe (*Monotropa uniflora*) pictured on the previous page is a member of the Monotropoideae, a subfamily of the Ericaceae, or heath family, one that includes such common green plants as blueberries and rhododendrons. All members of the Monotropoideae are mycoheterotrophic. Another member of this subfamily, *Hypopitys monotropa* or pinesap (Figure 2), is a beautiful plant that appears in various shades of yellow, pink, or orange. It blooms from midsummer into fall. The orchid family contains by far the highest number of MHT species, and a local one that you might see blooming in midsummer is spotted coral root (*Corallorhiza maculata*, Figure 3). Notice that MHT plants tend to have very reduced, scaly leaves if they have any at all (because they don't really need them); the most prominent thing you notice is the flowers.

Unlike mutualistic mycorrhizal associations, the MHT-fungal association is generally highly specific[1]. Ghost pipes and spotted coral root only associate with a few species from the Russulaceae family, pinesap with certain species of *Tricholoma.*

Why would it be advantageous for a plant to adapt this lifestyle? After all, obtaining carbon this way limits the size that these species can attain, and being very specific as to the fungal host means MHT plant distribution is reliant on distribution of the fungus[1]. As a result, although MHT is widespread, numbers of individuals are relatively low. However, because the trees from which MHT plants indirectly obtain carbon are much taller and have easier access to the sun, utilizing MHT allows the smaller plants to grow and reproduce on dimly lit forest floors, where other plants might have trouble thriving[3]. Think about ghost plants and pinesap, for instance. They start to appear in midsummer after the tree canopy has closed, and they

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Figure 2. Hypopitys monotropa, or pinesap, a member of the Monotropoideae.

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Figure 3. Corallorhiza maculata, or spotted coral root, an orchid.

continue blooming into the fall. Spotted coral root also blooms in midsummer on the forest floor. This is a very different strategy from, for instance, spring ephemeral plants, which bloom and set fruit before the trees have fully leafed out. In tropical forests, the forest floor can be very dark, and plants must utilize various strategies to survive there, mycoheterotrophy among them. In fact, the majority of mycoheterotrophic plants live in tropical regions[10].

Mycoheterotrophy is not rare and it has evolved independently at least 46 times throughout the plant kingdom[2]. There are at least 500 known species of plants worldwide that utilize MHT[5], and there are undoubtedly many more awaiting discovery. Green plants that are able to thrive in very low light conditions on the forest floor are good candidates[5].

Mycoheterotrophy is another example of the fascinating, intertwined, and important roles that fungi play in our ecosystems. It seems that the more we learn about fungi, the more we realize there is so much more to discover!

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From *Fungi Kingdom News*, Fall 2019