

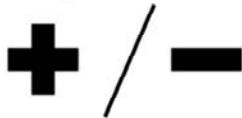
Invisible Connections: Introduction to Parasitic Plants

Dr. Vanessa Beauchamp
Towson University

What is a parasite?

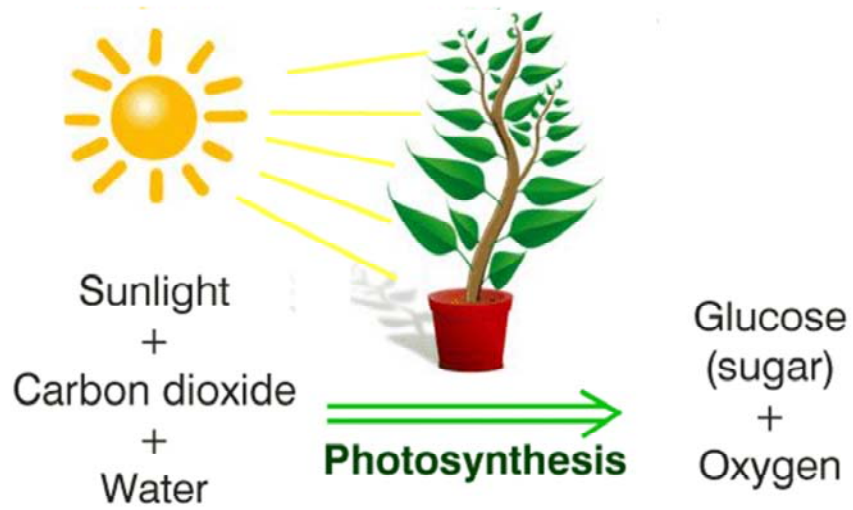
- An organism that lives in or on an organism of another species (its host) and benefits by deriving nutrients at the other's expense.

Symbiosis



<https://www.superpharmacy.com.au/blog/parasites-protozoa-worms-ectoparasites>

Food acquisition in plants: Autotrophy



Heterotrophs (“different feeding”)

- True parasites: obtain carbon compounds from host plants through haustoria.
- Myco-heterotrophs: obtain carbon compounds from host plants via mycorrhizal fungal connection.
- Carnivorous plants (not parasitic): obtain nutrients (phosphorus, nitrogen) from trapped insects.



Image Credit: Flickr User wackybadger, via CC



https://commons.wikimedia.org/wiki/File:Pink_indian_pipes.jpg



<http://www.welivealot.com/venus-flytrap-facts-for-kids/>

Parasite is from the Greek para (beside) and sitos (grain or food) which literally means “beside the food”. If a plant also induces disease symptoms in a host, then it is a pathogen as well as parasite. A general term that refers to both parasites and mycotrophs that derive carbon from sources other than their own photosynthesis is heterotrophic, which simply means “different feeding.”

Parasite vs. Epiphyte



<https://chatham.ces.ncsu.edu/2014/12/does-mistletoe-harm-trees-2/>



By © Hans Hillewaert, CC BY-SA 3.0, <https://commons.wikimedia.org/w/index.php?curid=6289695>

True Parasitic Plants

- Gains all or part of its nutrition from another plant (the host).
- Does not contribute to the benefit of the host and, in some cases, causing extreme damage to the host.
- Specialized peg-like root (haustorium) to penetrate host plants.



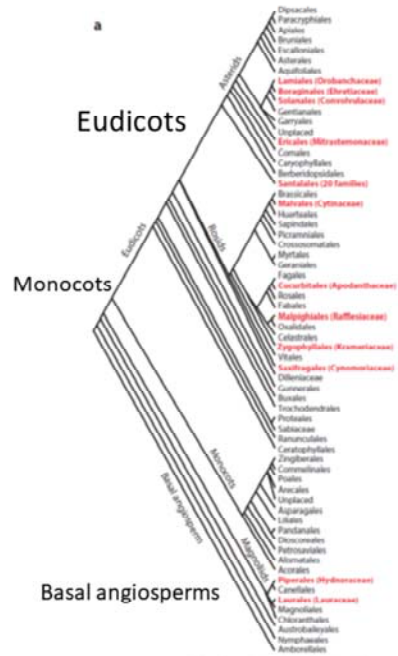
<https://www.britannica.com/plant/parasitic-plant>

<https://chatham.ces.ncsu.edu/2014/12/does-mistletoe-harm-trees-2/>

the haustorium, a specialized organ for host attachment, invasion, vasculature connection, and material transfer between the host and the parasite (Figure 1). The word haustorium comes from the Latin haustor or haurire, which means “water drawer.”

Diversity of parasitic plants

- Parasitism has evolved independently at least 12 times within the plant kingdom.
- Approximately 4,500 parasitic species in 28 families.
- Found in eudicots and basal angiosperms
 - 1% of the dicot angiosperm species
 - No monocot angiosperm species



Annu. Rev. Plant Biol. 2016.67:643-667

Approximately 4,500 parasitic species belonging to 28 families, representing 1% of the dicotyledonous angiosperm species, have been reported (53). These parasitic species derived from 12 or 13 independent evolutionary events (143) and therefore show taxonomic diversity and morphological variation (Figure 1).

True Parasitic Plants



<https://www.gettyimages.com/detail/news-photo/mistletoe-plant-with-haustoria-in-the-trunk-of-the-host-news-photo/857129812>



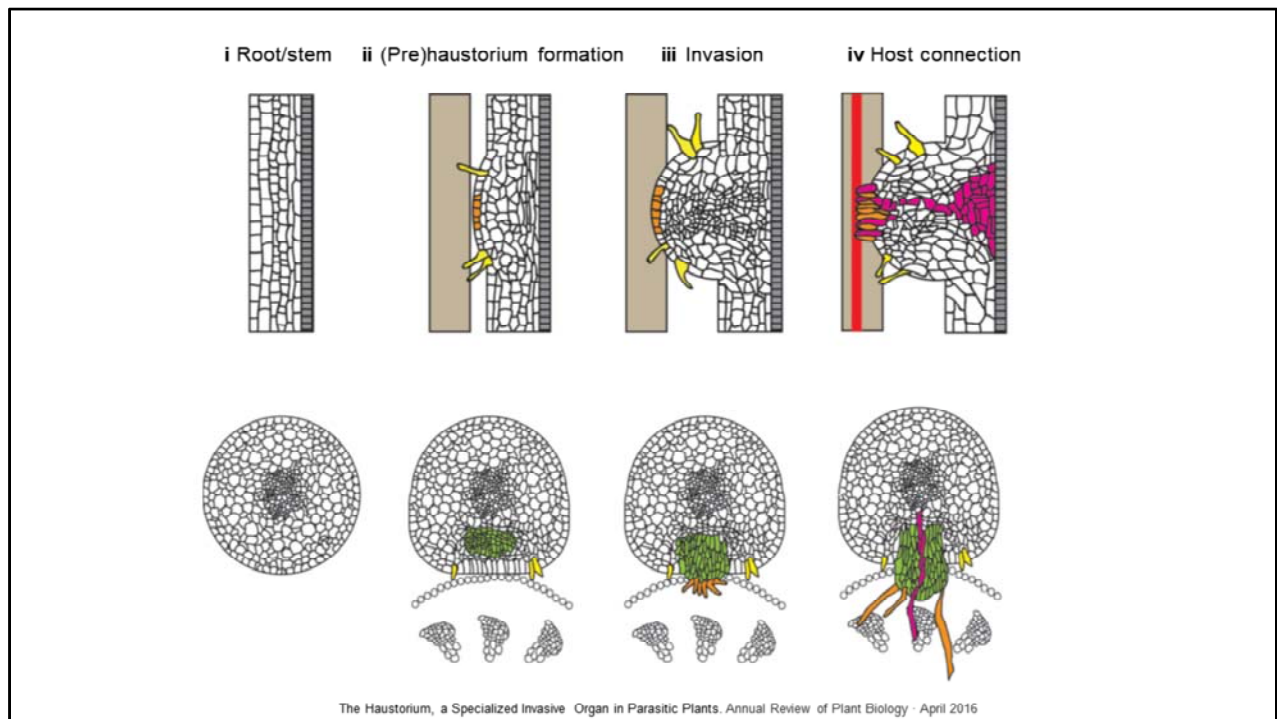
alamy stock photo

<https://www.alamy.com/parasitic-dodder-plant-cuscuta-showing-penetration-parasitic-haustor>

The defining structural feature of a parasitic plant is the haustorium.

<https://www.britannica.com/plant/parasitic-plant>

Haustoria are modified roots
the haustorium, a specialized organ for host attachment, invasion, vasculature connection, and material transfer between the host and the parasite (Figure 1). The word haustorium comes from the Latin haustor or haurire, which means “water drawer.”

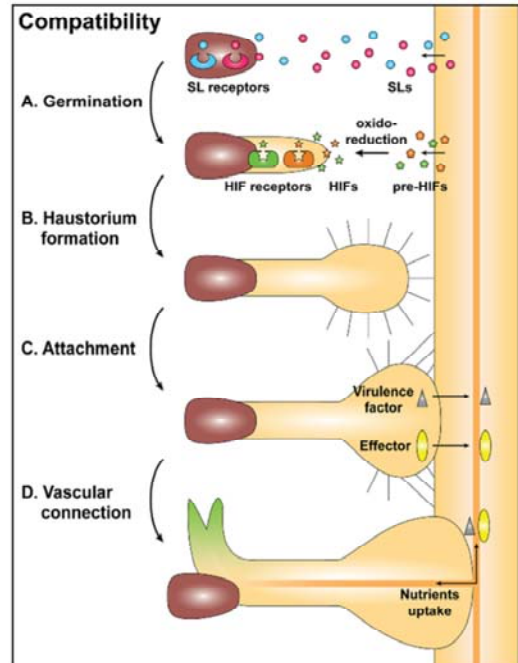


Haustorium forms upon detection of haustorium-inducing factors derived from the host plant. Specialized hairs in the parasite roots secrete adhesive glues to anchor their haustoria to the host roots and to assist in penetration by providing mechanical forces toward the host tissue.

This organ penetrates into the host stem or root and connects to its vasculature, allowing exchange of materials such as water, nutrients, proteins, nucleotides, pathogens, and retrotransposons between the host and the parasite.

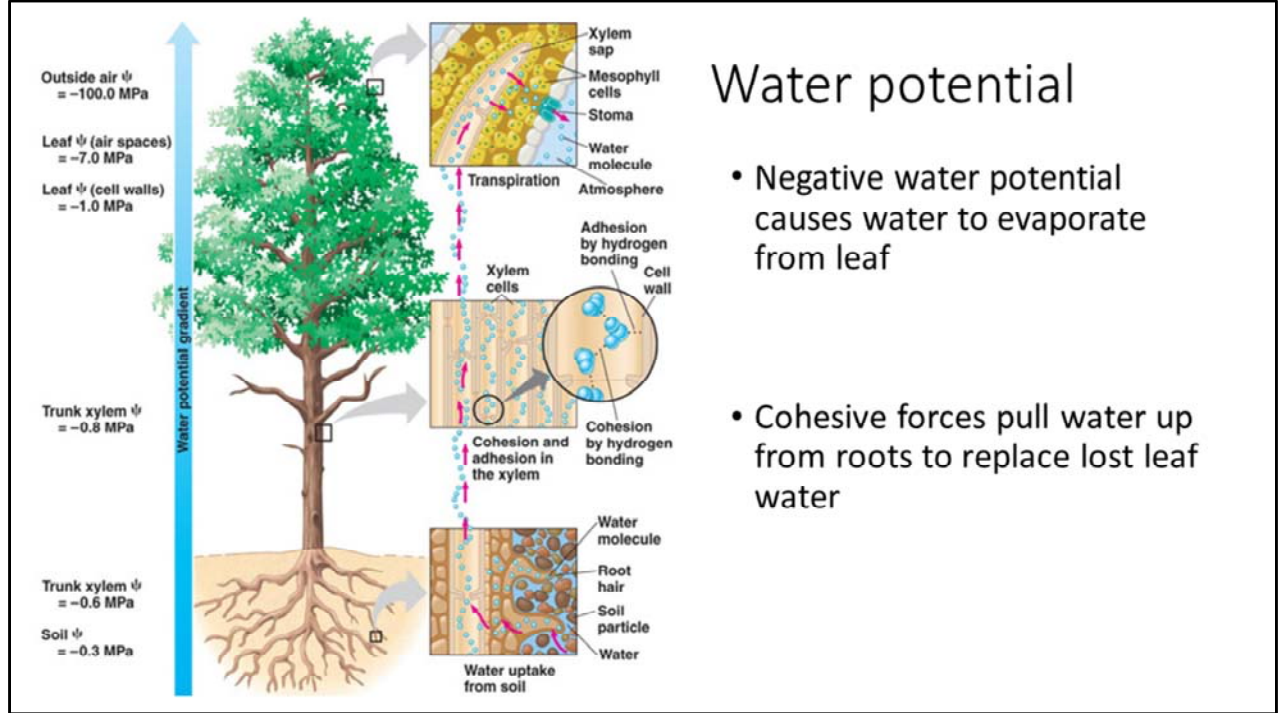
Haustorium formation

- Sense and attach to host
 - Recognize chemicals also used to attract symbiotic fungi and bacteria to plant roots
- Penetrate host tissues
 - Fragment and dissolve cell walls rather than crushing them
- Avoid host immunity system
 - Mimic pollen tube growth to avoid immunity activation
- Develop vascular connection
 - Lower water potential than host plant



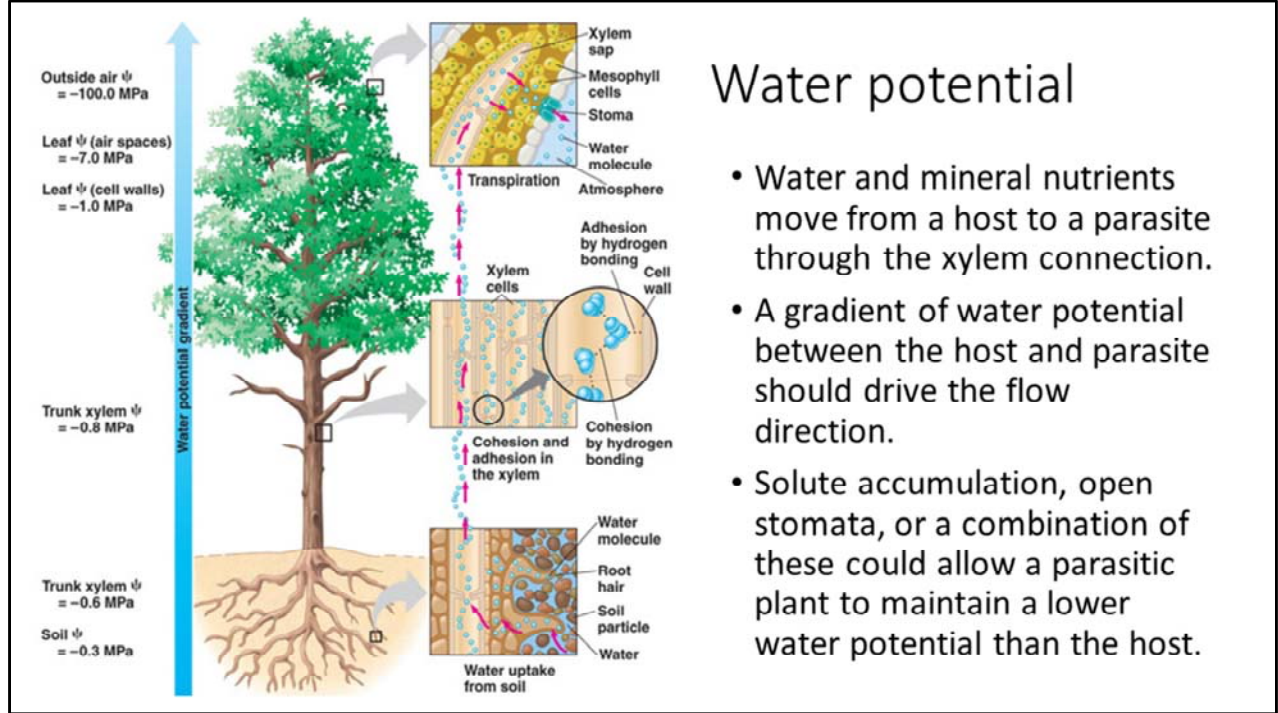
Saucet SB, Shirasu K (2016) Molecular Parasitic Plant-Host Interactions. *PLoS Pathog* 12(12): e1005978. <https://doi.org/10.1371/journal.ppat.1005978>

The haustorium has four main sequential functions: to attach to the host, to penetrate the host tissues, to avoid the host immunity system, and to develop a vascular connection between the host and parasite to absorb water and nutrients. Recent comparative transcriptome analysis using three Orobanchaceae species also revealed adaptive changes in genes recruited from pollen tube development in parasitic lineages



Water potential

- Negative water potential causes water to evaporate from leaf
- Cohesive forces pull water up from roots to replace lost leaf water



Water potential

- Water and mineral nutrients move from a host to a parasite through the xylem connection.
- A gradient of water potential between the host and parasite should drive the flow direction.
- Solute accumulation, open stomata, or a combination of these could allow a parasitic plant to maintain a lower water potential than the host.

Life forms

Witchweed (*Striga bilabiata*)



<https://www.britannica.com/plant/parasitic-plant>

Dodder (*Cuscuta gronovii*)



<https://www.britannica.com/plant/parasitic-plant>

European mistletoe (*Viscum album*)



CC BY-SA 2.0, <https://commons.wikimedia.org/w/index.php?curid=34475>

They occur in many life forms, including annual and perennial herbs (e.g. *Rhinanthus* spp. and *Bartsia* spp.), vines (e.g. *Cuscuta* spp. and *Cassytha* spp.), shrubs (e.g. *Oxalis* spp. and mistletoes) and trees (sandlewoods, e.g. *Okoubaka aubrevillei*, which grows up to 40 m tall; Veenendaal et al., 1996).

Life forms



O Roberts

Nuytsia floribunda
Western Australian Christmas Tree

<http://anpsa.org.au/n-flt.html>



Okoubaka aubrevillei
Death tree

© nidafoto - Fotolia

<https://www.netdoktor.de/homoeopathie/okoubaka/>



Rafflesia spp.
Corpse flower

<https://www.sciencefocus.com/nature/top-5-parasitic-plants/>

Nuytsia floribunda - It is a root hemiparasite, is photosynthetic and mainly obtains water and mineral nutrients from its hosts. The [haustoria](#) attach themselves to roots of many nearby plants and draw water and therefore nutrients from them. sandlewoods, *Okoubaka aubrevillei*, which grows up to 40 m tall – no other trees appear to grow in proximity to this tree. It also provides an explanation as to why, among other things, the locals believe the tree to possess magical powers. Powered bark is used to counteract ingested poisons. “in his own country it is customary to take some of this powder following a meal – particularly if one not is entirely certain of the host’s friendship”

Rafflesia spp. - The plant has no stems, leaves or roots. It is a [holoparasite](#) of vines in the genus [Tetrastigma](#) ([Vitaceae](#)), spreading its absorptive organ, the [haustorium](#), inside the tissue of the vine - In some species, such as [Rafflesia arnoldii](#), the flower may be over 100 centimetres (39 in) in diameter, and weigh up to 10 kilograms (22 lb). Even one of the smallest species, [R. bailei](#), has 12 cm diameter flowers.

Types of parasitic plants

- Attachment point
 - Stem or root
- Nutritional dependence
 - Hemiparasite or holoparasite
- Life cycle requirements
 - Obligate or facultative



MBP: American Mistletoe in Harford Co., Maryland (12/21)



<https://www.prairymoon.com/castilleja-coccinea-indian-paintbrush-prairie-moon-nursery.html>



https://commons.wikimedia.org/wiki/File:Conepeltis_america_Bear_Corn.jpg

Attachment Point

- Stem parasites

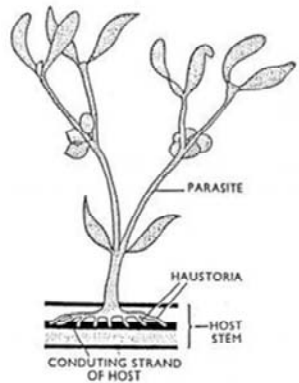


Fig. 12.2. *Viscum* (Mistletoe)

Mistletoe – *Phoradendron leucarpum* American/Eastern mistletoe



MBP: American Mistletoe in Harford Co., Maryland (12/16/2017). Photo by [Josh Kimm](#)



MBP: American Mistletoe fruiting in Harford Co., Maryland (12/16/2017). Photo by [Josh Kimm](#). (MBP 105)

Phoradendron, a name derived from two Greek words meaning "tree thief." One species in Maryland.

Mistletoe seeds are covered with a musilaginous, glue-like substance called viscin that sticks to the bills of birds. In fact, it resembles rubber cement when the seeds are rolled between your fingers. When birds try to clean their bills, the seeds adhere to the limbs of other trees and shrubs. The seeds also pass through the bird's digestive tract and are transported from one bush to another in the bird's droppings.

Mistletoe: from two Germanic words: mista (dung) and tan (twig); referring to bird droppings on a branch or stem.

<http://www.biologydiscussion.com/angiosperm/special-modes-of-nutrition-in-angiosperms-plant-physiology/23094>

Attachment Point

- Stem parasites



Fig. 12.1. *Cuscuta*.

Dodder (Witches' hair) – *Cuscuta* spp.



<https://commons.wikimedia.org/w/index.php?curid=209875>



Plant genetics: Gene transfer from parasitic to host plants. November 2004. Nature 432(7014):165-6

<http://www.biologydiscussion.com/angiosperm/special-modes-of-nutrition-in-angiosperms-plant-physiology/23094>

Morning glory family. Nine species in the Flora of Virginia and MPB. Germinates in soil, forms small terrestrial root system that soon degenerates.

Attachment Point

- Root parasites



https://www.123rf.com/photo_96361208_vintage-engraving-of-orobanche-alba-or-thyme-broomrape-parasitic-plant-with-stems-completely-lacking.html



<http://www.farmalierganes.com/Flora/Angiospermae/Orobanchaceae/Orobanchaceae/Orobanche-Grey.Glandulosae/Orobanche-alba/Orobanche-alba.htm>

Orobanche spp.
(Broomrape)

Orobanche uniflora



By Arieh Tal. Copyright © 2019 Arieh Tal. botphoto.com
<https://gobotany.newenglandwild.org/species/orobanche/uniflora/>

Most are in the Orobanchaceae (broomrape family). Hemiparasitic members used to be in the Scrophularaceae.

English name broomrape because they were thought to grow as tubers ("rapum") from brooms (the common name for the legume *Cytisus*).

Attachment Point

- Root parasites



<https://trekoho.com/2012/09/24/beechdrops-our-third-plant-without-chlorophyll/>

Beech drops
Epifagus virginiana



https://commons.wikimedia.org/wiki/File:Epifagus_virginiana.jpg

Family: [Orobanchaceae](#) Beechdrops are used to monitor forest health because of their dependence on their host and the sensitivity to its environment. The comparisons of the demographic histories of the host and the parasite strongly suggest that host density was the primary determinant in the parasite's range expansion and population genetics—not the host's own genetic patterns and migration routes.

Attachment Point

Conopholis americana (Squawroot, Bearcorn)

- Root parasites



https://commons.wikimedia.org/wiki/File:Conopholis_americana_-_Bear_Corn.jpg



<https://botanypphoto.botanicalgarden.ubc.ca/2005/05/conopholis-americana/>

When blooming, resembles a pine cone or cob of corn growing from the roots of mostly oak and beech trees.

It is usually found in dense clumps of several erect stems and growing in shady forested sites.

The scientific name comes from the appearance of the erect stems which have numerous scale like flowers that look a bit like a pinecone, with conos meaning 'cone' and pholos meaning 'scale' in ancient Greek (Black and Judziewicz, 2008).

This dense inflorescence comes to the surface only after the parasite's root system attaches to the oak root and forms a large woody gall and then builds up enough growth (about four years)

Attachment Point

- Root parasites



<https://www.prairiemoon.com/castilleja-coccinea-indian-paintbrush-prairie-moon-nursery.html>

Castilleja coccinea
Eastern Indian
Paintbrush



<https://shop.sussexconservation.org/products/castilleja-coccinea-indian-paintbrush>

[Orobanchaceae](#): Though it can survive on its own, studies indicate a forty-fold growth increase when its roots parasitize those of another plant for nutrients.^[5] It is primarily pollinated by [ruby-throated hummingbirds](#) who can transfer the pollen long distances between typically small and scattered populations of this plant.

Nutritional Dependence

Hemiparasite



MBP- American Mistletoe in Harford Co., Maryland (12/16/2017). Photo by [Josh Emm](#).

<https://shop.sussexconservation.org/products/castilleja-coccinea-indian-paintbrush>

Holoparasite



https://commons.wikimedia.org/wiki/File:Conopholis_america_-_Bear_Corn.jpg

<https://commons.wikimedia.org/w/index.php?curid=209875>

Epifagus virginiana | Beechdrops | Gene G. King Park, Bridgewater, 9/17/2012, Photo H. & M. Ling

By Arieh Tal. Copyright © 2019 Arieh Tal. botphoto.com <https://gbotany.newenglandwild.org/species/orbanchef/umbifera/>

20%–80% of hemiparasite biomass is derived from the host assimilates differing across species and developmental stages.

Numerous studies conducted in arid or semiarid conditions have thus demonstrated 50–80% proportion of host derived carbon in biomass of mistletoes.

The ability of hemiparasites to acquire organic carbon (largely in the form of xylem-mobile organic and amino acids)

In general, holoparasites tend to have leaves reduced to scales (or absent in Hydnoraceae), succulent stems, and a primary haustorium (derived from the seedling radicle). On the forest floor, little sunlight penetrates, hence nonphotosynthetic holoparasites such as Balanophoraceae and Rafflesiaceae can be found here.

Life cycle requirements

Obligate

- All holoparasites
- All stem parasites (holoparasites and hemiparasites)
- Some root hemiparasites

Facultative

- Some root hemiparasites



<https://parasiticplants.siu.edu/images/HoloHemiPars2.jpg>

Obligate Parasite. A plant that must attach to a host to complete its life cycle. All holoparasites are obligate whereas only some hemiparasites are obligate such as mistletoes and *Striga asiatica*.

Stem hemiparasites are attached to the host stem (usually trunk or branches) and are all obligate parasites, unable to survive without a host.

Facultative Parasite. A hemiparasitic plant that does not require a host to complete its life cycle. Note, however, that in nature, parasitism is nearly always observed. Many members of Orobanchaceae are facultative hemiparasites such as *Agalinis*, *Aureolaria*, and *Seymeria*. Some root parasites can complete life cycle without host but rarely do.

Generalists vs. specialists

Cuscuta spp. (dodder)

- Hundreds of hosts in diverse families



<https://commons.wikimedia.org/w/index.php?curid=209875>

Epifagus virginiana (beech drops)

- One host *Fagus grandifolia*



https://commons.wikimedia.org/wiki/File:Epifagus_virginiana.jpg

Evidence exists that the generalist strategy has the greatest chance for survival over evolutionary time.

Most parasitic plants are generalists

Intriguingly, despite the large host range of the majority of parasitic plants, many also show high levels of host preference, such that while many different plant species within a community can act as hosts, the majority of hosts are taken from just a subset of those available

Better host: longer lived (woody), high nitrogen (legume), accessible vascular system, low defenses, better access to limiting resources (deep water in drought)

Biting the hand that feeds you

An organism that lives in or on an organism of another species (its host) and benefits by deriving nutrients at the other's expense.

Symbiosis



all parasitic plant species have evolved under the constraint that they do not kill their hosts prior to successful reproduction.

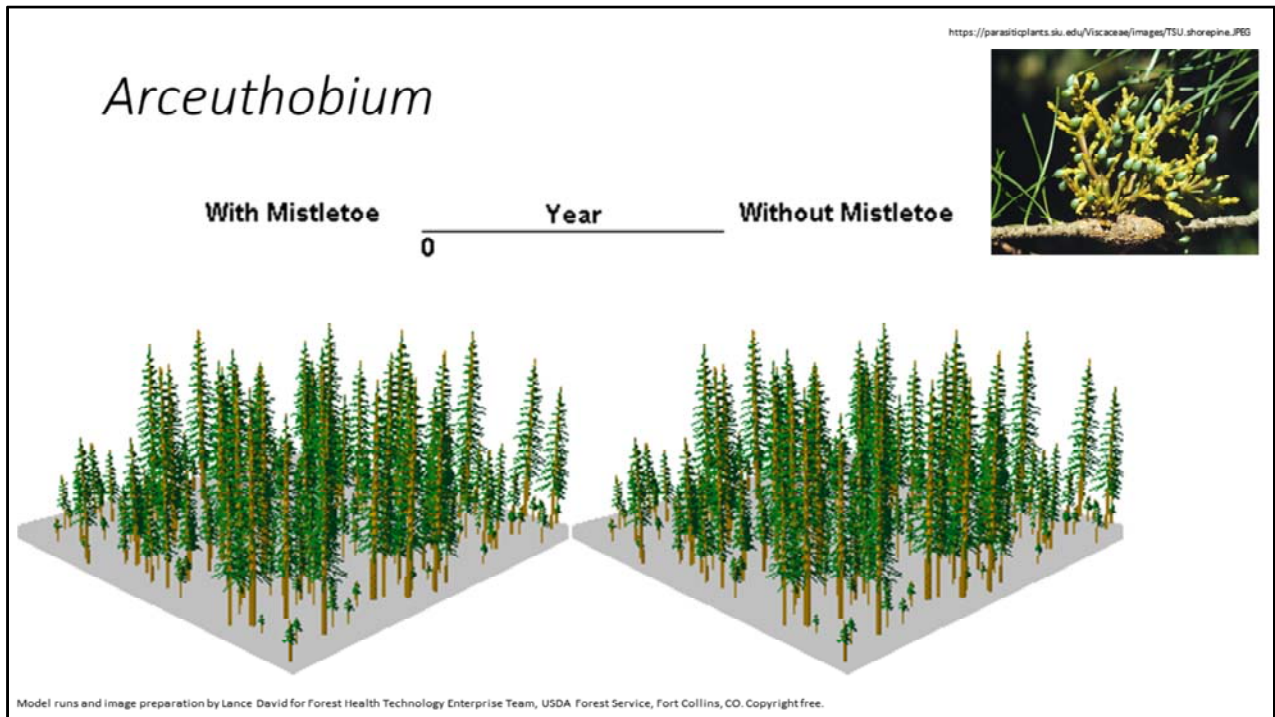


Several parasitic plants are among the most devastating agricultural weed pests worldwide.

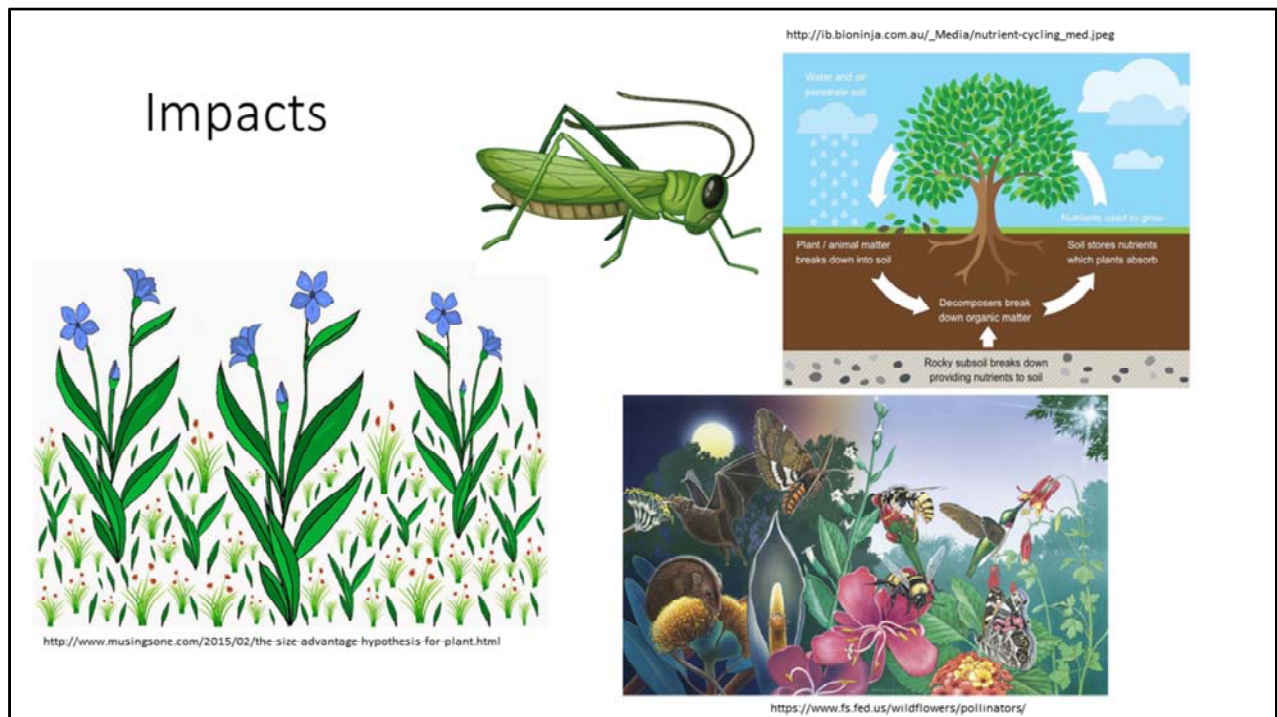
Most of the damage inflicted upon economically valuable hosts is caused by just four genera: *Cuscuta*, *Arceuthobium*, *Orobanche*, and *Striga*.

***Striga hermonthica* (L.) Benth. or witchweed is a parasitic weed that attacks maize, sorghum, and pearl millet.** The parasitic weed *Striga* causes yield losses of 30-80% on 2.5 million hectares of crops in Africa.

***Striga* infestations can become so severe in all major cereal producing regions of Africa that farmers will abandon their fields to cereal production and therefore large swathes of Africa will be precluded from becoming major cereal producing areas.**



Animation of effects of dwarf mistletoe over 100 years in a Douglas-fir stand.
 Gymnosperms
 11.3 million cubic meters of wood in the western U.S.
 \$1.4 billion dollars in losses
 1,000,000 homes per year!



Parasitism often severely reduces host performance, which leads to changes in competitive interactions between host and nonhost plants and a cascade of effects on community structure, diversity, vegetation cycling and zonation (Pennings & Callaway, 2002). the uptake of host solutes can have consequences for organisms of other trophic levels (such as herbivores and pollinators), and co-occurring organisms may also be affected by the impacts of parasitic plants on the abiotic environment, including impacts on nutrient cycling, soil water relations, local temperature and atmospheric CO₂ concentrations.

True parasites in Maryland

Bastard Toadflax *Comandra umbellata*



Bastard Toadflax blooming in Allegany Co., Maryland (5/19/2016). Photo by [Ed Boxel](#). (MBP list)

American Mistletoe
Phoradendron leucarpum



American Mistletoe growing on Red Maple in Somerset Co., Maryland (1/20/2013). Photo by [Bill Hubick](#). (MBP list)

Five-angled Dodder
Cuscuta campestris



Five-angled Dodder in Anne Arundel Co., Maryland (6/25/2011). Photo by [Bill Harms](#). (MBP list)

[Family Santalaceae](#) - Bastard Toadflax *Comandra umbellata*

[Order Santalales](#) > [Family Viscaceae](#) > [Genus Phoradendron](#) - American mistletoe

[Order Solanales](#) > [Family Convolvulaceae](#) > [Genus Cuscuta](#) - 9 species in MBP

True parasites in Maryland

Downy Yellow False Foxglove
Aureolaria virginica



Downy Yellow False Foxglove in Allegheny Co., Maryland
(6/30/2015). Photo by [Kimberly Booth](#). ([MBP list](#))

Scarlet Indian Paintbrush
Castilleja coccinea



Scarlet Indian Paintbrush in Garrett Co., Maryland
(5/28/2007). Photo by [Gary Van Velsir](#). ([MBP list](#))

Purple Gerardia *Agalinis purpurea*



Purple Gerardia blooming on Assateague Island,
Maryland (8/30/2013). Photo by [Bill Hubick](#). ([MBP list](#))

Orobanchaceae – hemiparasites used to be *Scrophulariaceae*
Aureolaria – 4 species in MBP
Scarlet Indian Paintbrush *Castilleja coccinea* – S1
Agalinis – 8 species in MBP. Several state rare or extirpated.

True parasites in Maryland

Canadian Lousewort *Pedicularis canadensis*



Canadian Lousewort blooming in Garrett Co., Maryland (5/28/2007). Photo by [Wayne Longbottom](#). ([MBP list](#))

Narrow-leaved Cow-wheat *Melampyrum lineare*



Narrow leaved Cow-wheat blooming in Frederick Co., Maryland (7/8/2013). Photo by [Bonnie Ott](#). ([MBP list](#))
By Keir Morse. Copyright © 2019 Keir Morse. [www.keiriosity.com](#)

Melampyrum – 3 varieties of one species in MBP

Pedicularis – 2 species in MBP *P. lanceolata* is state rare

True parasites in Maryland

Squawroot *Conopholis americana*



Squawroot in Garrett Co., Maryland (5/22/2016). Photo by [Robert Ferraro](#). ([MBP list](#))

Beechdrops *Epifagus virginiana*



Beechdrops in bloom in Howard Co., Maryland (10/2/2014). Photo by [Nancy Magnusson](#). ([MBP list](#))

One-flowered Broomrape
Aphyllon (Orobanche) uniflorum



One-flowered Broomrape blooming in Cecil Co., Maryland (4/29/2017). Photo by [Ashley Bradford](#). ([MBP list](#))

Conopholis – 1 species in MBP – parasite on *Quercus*

Epifagus virginiana – monotypic genus – common

Orobanche - One-flowered Broomrape *Aphyllon uniflorum* - native; *Orobanche minor* – invasive.

Heterotrophs (“different feeding”)

- True parasites: obtain carbon compounds from host plants through haustoria.
- Myco-heterotrophs: obtain carbon compounds from host plants via mycorrhizal fungal connection.
- Carnivorous plants (not parasitic): obtain nutrients (phosphorus, nitrogen) from trapped insects.



Image Credit: Flickr User wackybadger, via CC

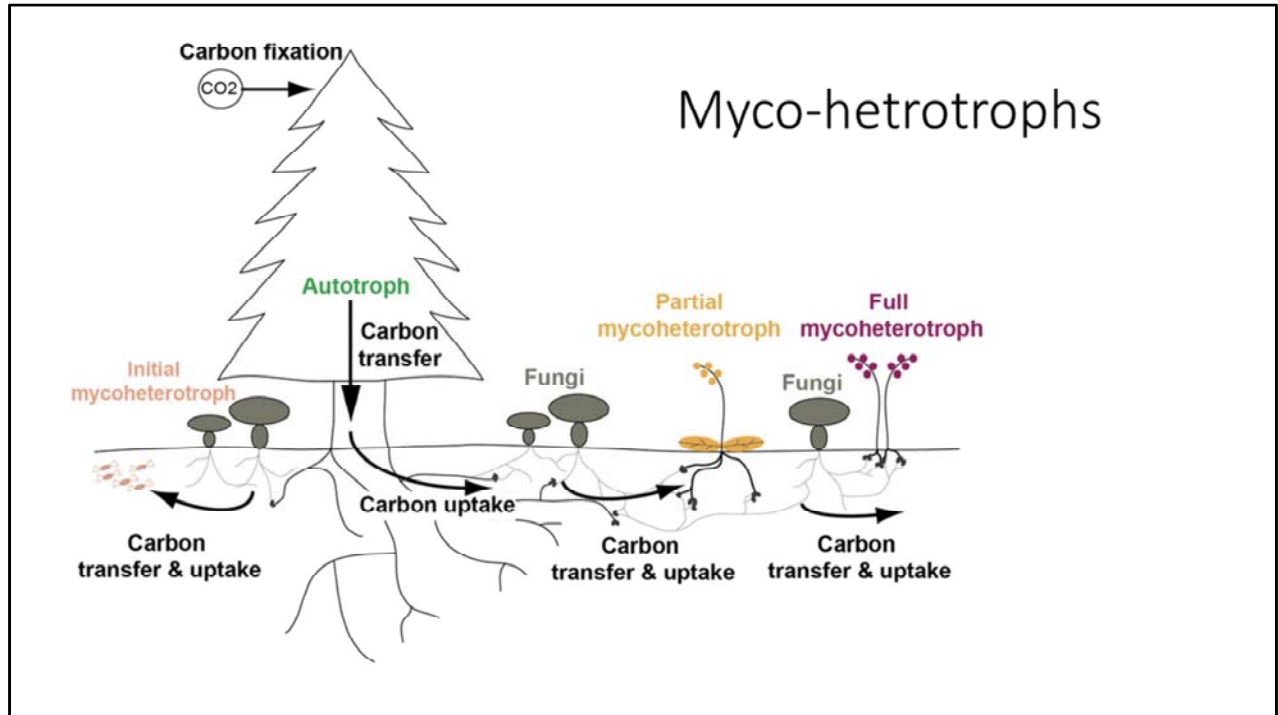


https://commons.wikimedia.org/wiki/File:Pink_indian_pipes.jpg



<http://www.welivealot.com/venus-flytrap-facts-for-kids/>

Parasite is from the Greek para (beside) and sitos (grain or food) which literally means “beside the food”. If a plant also induces disease symptoms in a host, then it is a pathogen as well as parasite. A general term that refers to both parasites and mycotrophs that derive carbon from sources other than their own photosynthesis is heterotrophic, which simply means “different feeding.”



<https://3c1703fe8d.site.internapcdn.net/newman/gfx/news/2018/1-partialmycoh.jpg>
 mycoheterotrophs obtain their nutrition indirectly from the plant via a mycorrhizal fungus. Finally, mycoheterotrophs are sometimes mistakenly called **saprophytes**. There are no true saprophytes in the angiosperms. Only fungi can directly utilize dead organic material.

Mycorrhizal Fungi

- Mycorrhiza means “fungus root” and was first used in 1885
- 95% of all plant species belong to a genera that characteristically form mycorrhizae.
- Thought to have evolved with the first land plants
- More prevalent in perennial plants than in annual plants



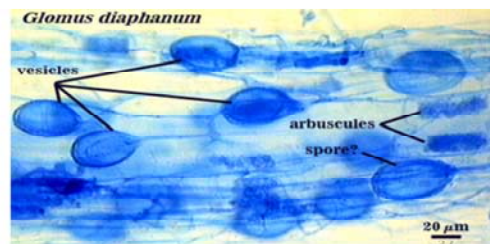
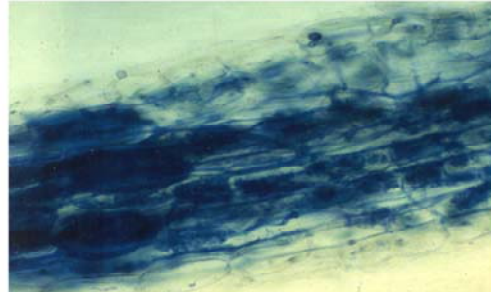
Ectomycorrhizae

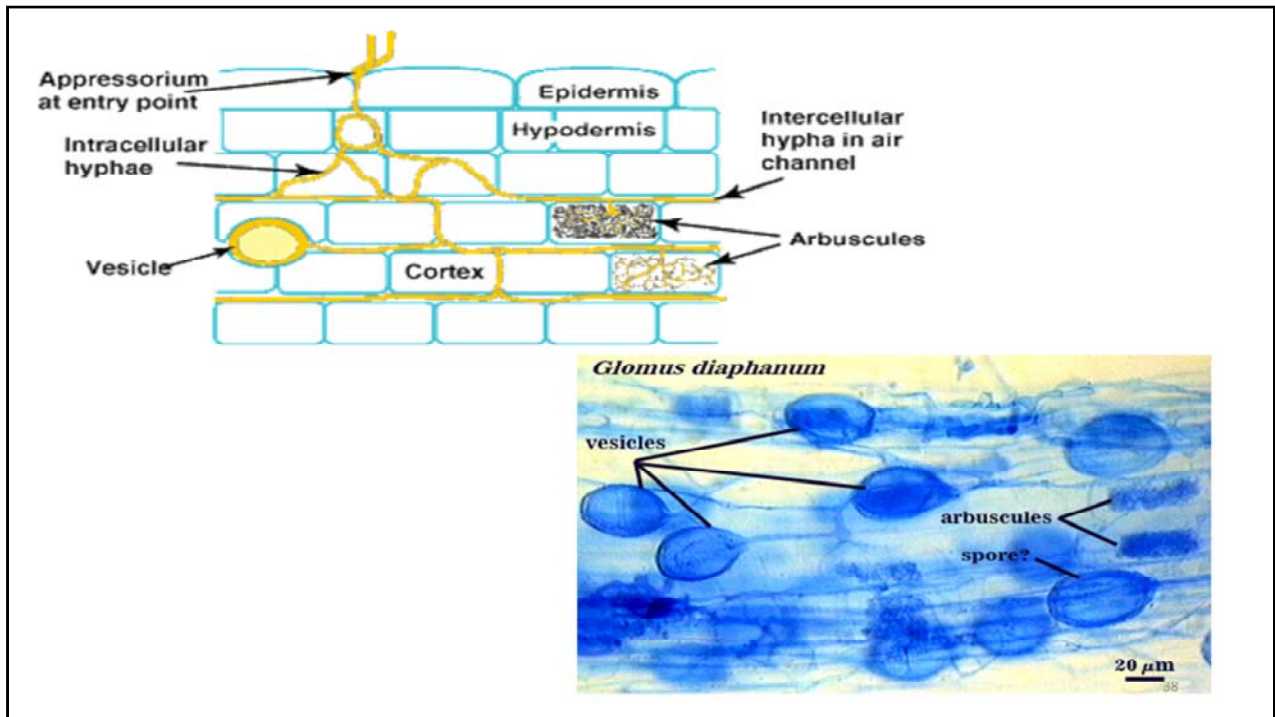
- Found in northern forests where decomposition is slow and nitrogen remains locked up in organic matter
- Forms structures on the outside of plant roots (ecto)
- Can often be seen with the naked eye
- Reproduce by mushrooms
- Oaks, Pines and Eucalyptus
- Little specificity (either way)
 - Douglas-fir reported to be associated with some 2,000 fungal species across its range



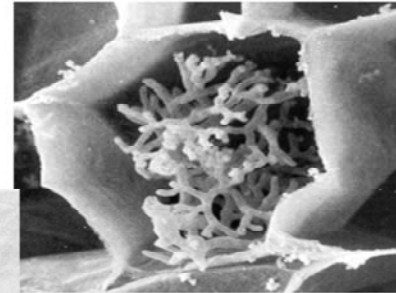
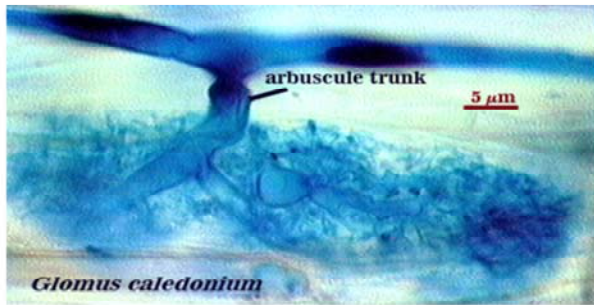
Endomycorrhizae (Arbuscular mycorrhizae)

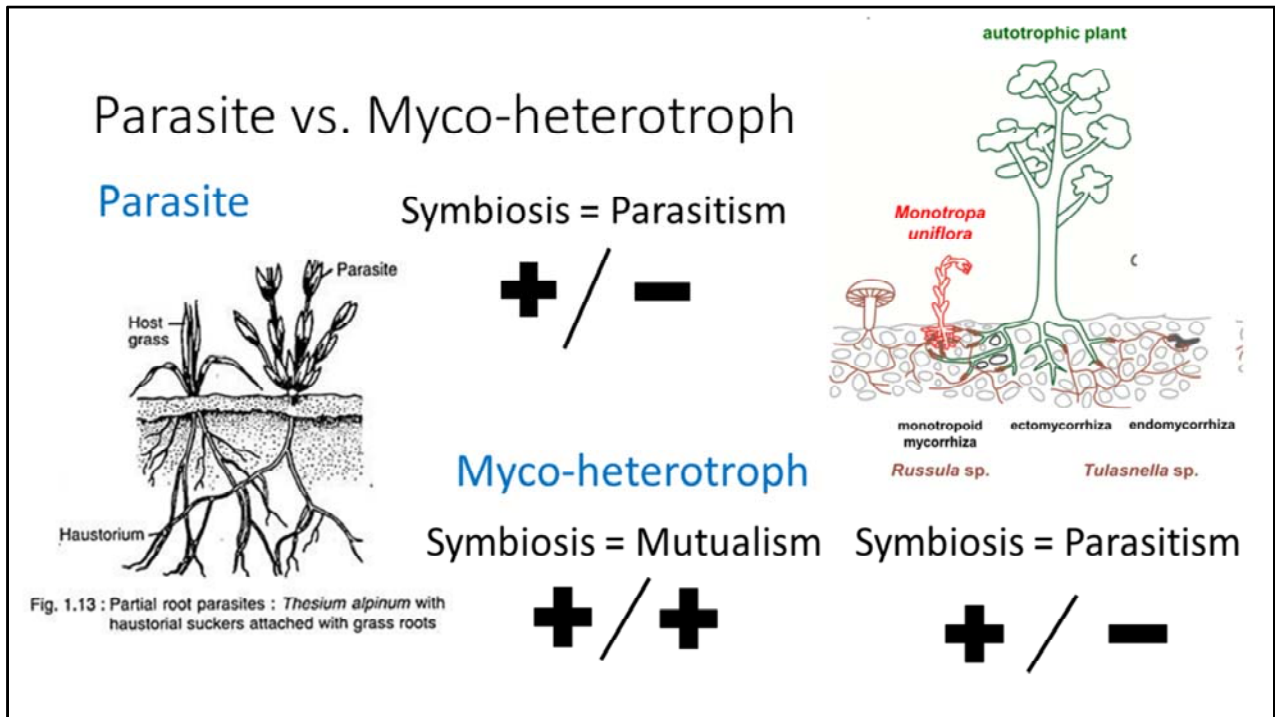
- Found in southern forests and grasslands where fast decomposition doesn't limit nitrogen
- Important for transferring phosphorus that binds to mineral soil particles
- Forms structures on the inside of plant roots (endo)
- Roots need to be stained to observe fungi
- Reproduce by forming spores in the soil
- Ancient association
- Little specificity (either way)





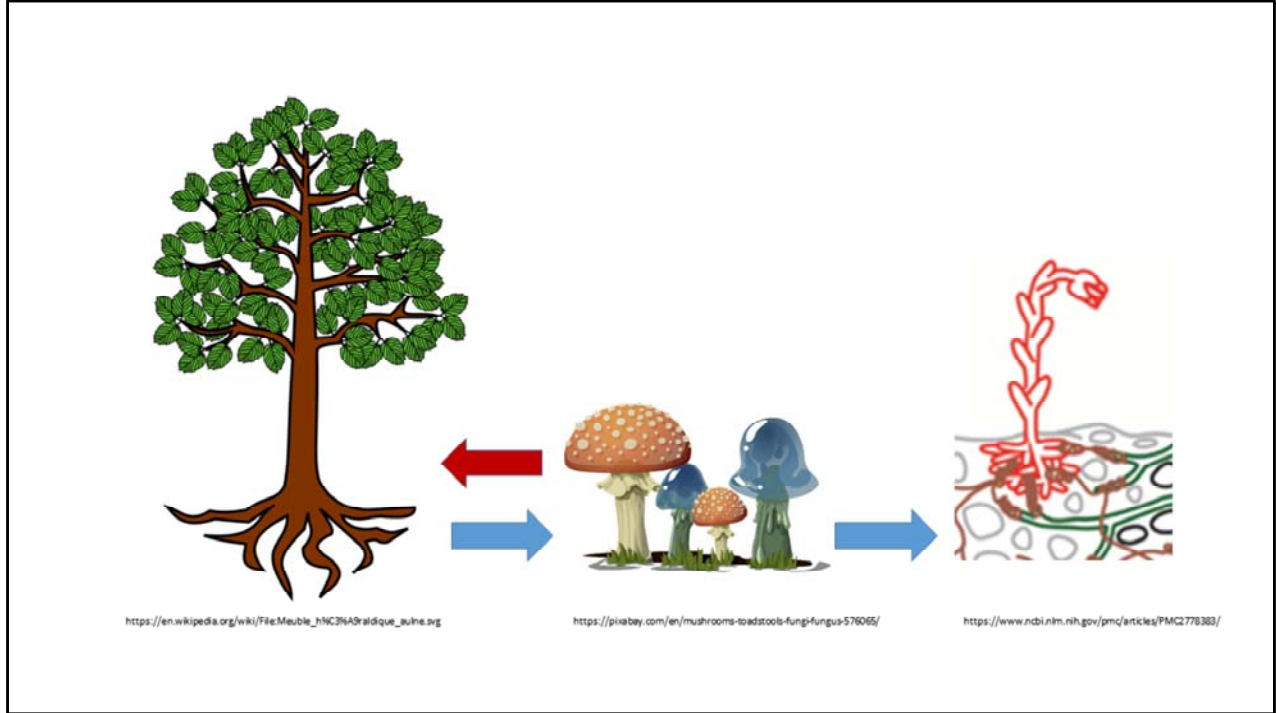
Arbuscules





With few exceptions, myco-heterotrophic Aneuraceae, Orchidaceae and Ericaceae exploit ectomycorrhizal networks while myco-heterotrophic Burmanniaceae, Corsiaceae, Gentianaceae, Thismiaceae and Triuridaceae exploit arbuscular mycorrhizal networks

The majority of fully myco-heterotrophic flowering plants are restricted to the tropics, but myco-heterotrophic Ericaceae and some Orchidaceae occur in temperate forests.

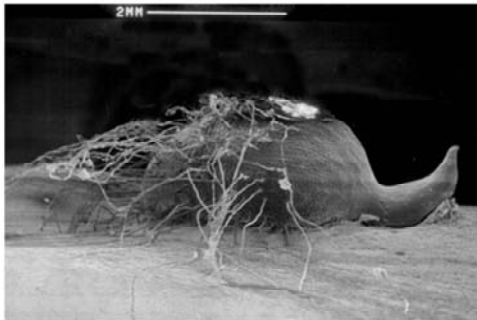


physiological continuity is established among a photosynthetic mycorrhizal plant, a mycorrhizal fungus and a nonphotosynthetic mycorrhizal plant. photosynthetic plant interacts only indirectly with the epiparasitic plant and the photosynthetic plant cannot select against the epiparasitic plant without selecting against a fungal mutualist.

Diversity of myco-heterotrophs

Facultative myco-heterotrophs

- Only during establishment phase



<https://www.kings.co.nz/userfiles/Editorial/orchids/orchid-seed-germinating.jpg>

Obligate myco-heterotrophs

- Dependent throughout lifetime

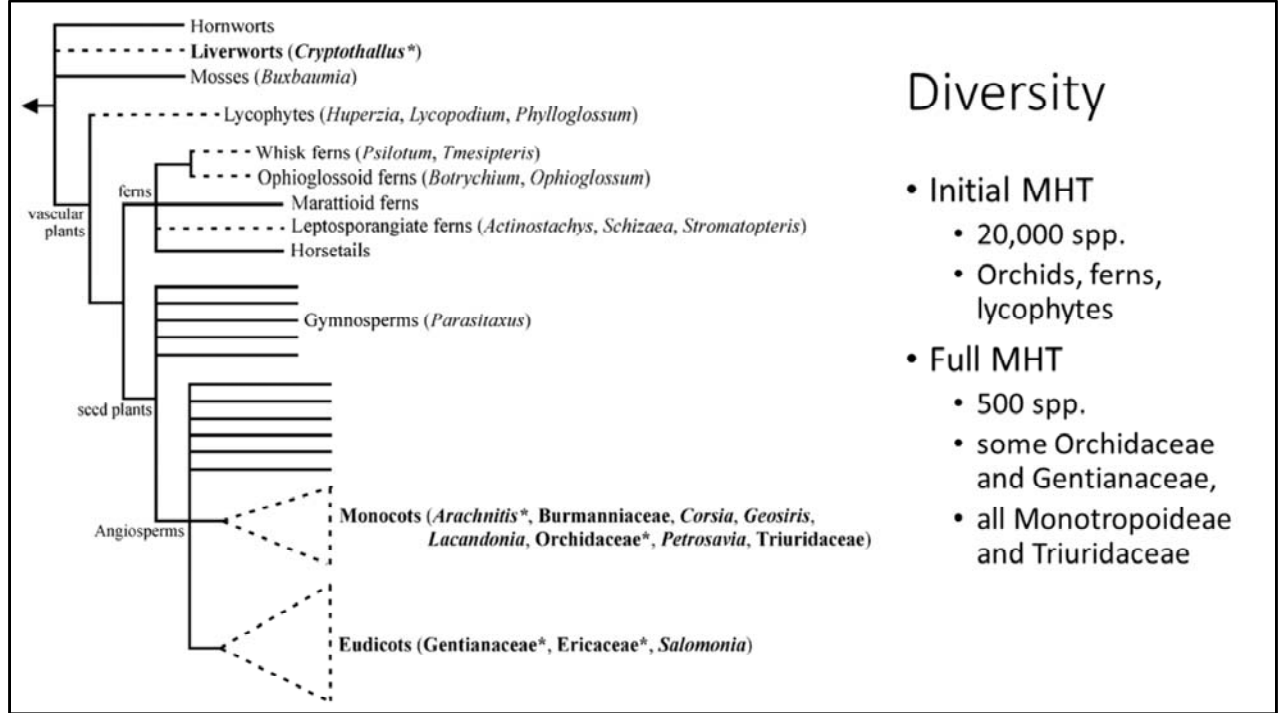


•Mycoheterotrophy: The Biology of Plants Living on Fungi

New Phytologist (2005) **167** : 335–352

A further distinction is made between plants that are myco-heterotrophic only during their establishment phase (e.g. most, if not all, Orchidaceae, many ferns and lycophytes), and those that are obligately myco-heterotrophic throughout their lifetime (e.g. some Orchidaceae and Gentianaceae, all Monotropoideae and Triuridaceae).

(a) *Voyria clavata* (Gentianaceae). (b) A large clump of *Epirixathes* plants (Polygalaceae) from Malaysian Borneo. (c) *Voyria tenuiflora* (Gentianaceae) photographed in French Guiana by Heiko Hentrich. (d) *Allotropia virgata* (Ericaceae) in Umqua Forest, Oregon, USA. (e) *Sarcodes sanguinea* (Ericaceae) at Lassen Volcanic National Park in California, USA



Full myco-heterotrophy evolved independently over 40 times within plant lineages and it has been confirmed in liverworts, monocots and eudicots.

Lineages of plants that have evolved myco-heterotrophy (dashed branches).

Lineages with full myco-heterotrophs are shown in bold (c. 500 spp.). The rest contain initially myco-heterotrophic plants only (c. 20 000 spp.).

Asterisks indicate lineages for which some molecular identification of mycorrhizal fungi has been carried out.

extant obligate plant cheaters of mycorrhizas have evolved independently multiple times (at least once in liverworts, perhaps once in ferns and in gymnosperms, probably tens of times in monocots and at least four times in dicots).

(ii) mycorrhizas have been investigated in very few of the putative myco-heterotrophic plants; and

(iii) myco-heterotrophic plants spend most of their life cycle underground, many are ephemeral and small, and new lineages are still being discovered.

Parasitaxus usta



<https://www.flickr.com/photos/tim-waters/349306324/in/photolist-wShAQ-4esgmy/>



<http://stanohepa-passion.over-blog.com/>

Forests of New Caledonia - *P. usta* utilized a fungal intermediary to parasitize the roots of its only known host, another member of the Podocarpaceae family, *Falcatifolium taxoides*. It is a very difficult plant to locate in the wild and, because it can be killed simply by stepping on the delicate shoots that are often concealed beneath forest litter, The transfer of carbon (sugars) from the host plant is achieved mainly through a fungal intermediary, as in the case of mycoheterotrophs such as the nonphotosynthetic ericads pinesap (*Hypopitys*) and indian-pipe (*Monotropa*), but a direct xylem connection with the host may also occur and may facilitate nitrogen transfer from the host. The plant also has a high stomatal conductance and low water potential, like the mistletoes. Thus it has a unique form of parasitism unlike any other known plant.



Hypopitys monotropa
yellow pine-sap

1821
Is *M. hypopithys*
'parasitic on the
roots of other
plants?'

<https://gobotany.newenglandwild.org/species/hypopithys/monotropa/>

1881 Kamienski *Monotropa* is nourished by a fungus linked to tree roots.

1885 Frank Definition of mycorrhizas.

1892 Frank *Monotropa* is parasitic upon the fungus attached to its roots.

1894 Frank Mycorrhizal fungi benefit *Pinus* growth.

1934 Francke Fungi penetrate epidermal cells of *Monotropa*. Successful germination of *Monotropa* seeds.

1960 Björkman *Monotropa* is an epiparasite on the ectomycorrhizas of trees.

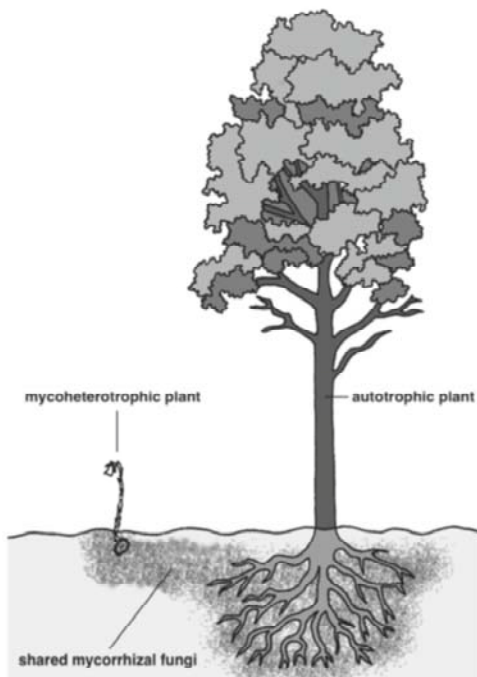
Physical separation from tree roots showed a marked reduction in *M. hypopithys* growth, and radioactive isotope labeling revealed greater translocation of carbon and phosphorus from *Picea* to *Monotropa* than to any other neighboring plants.



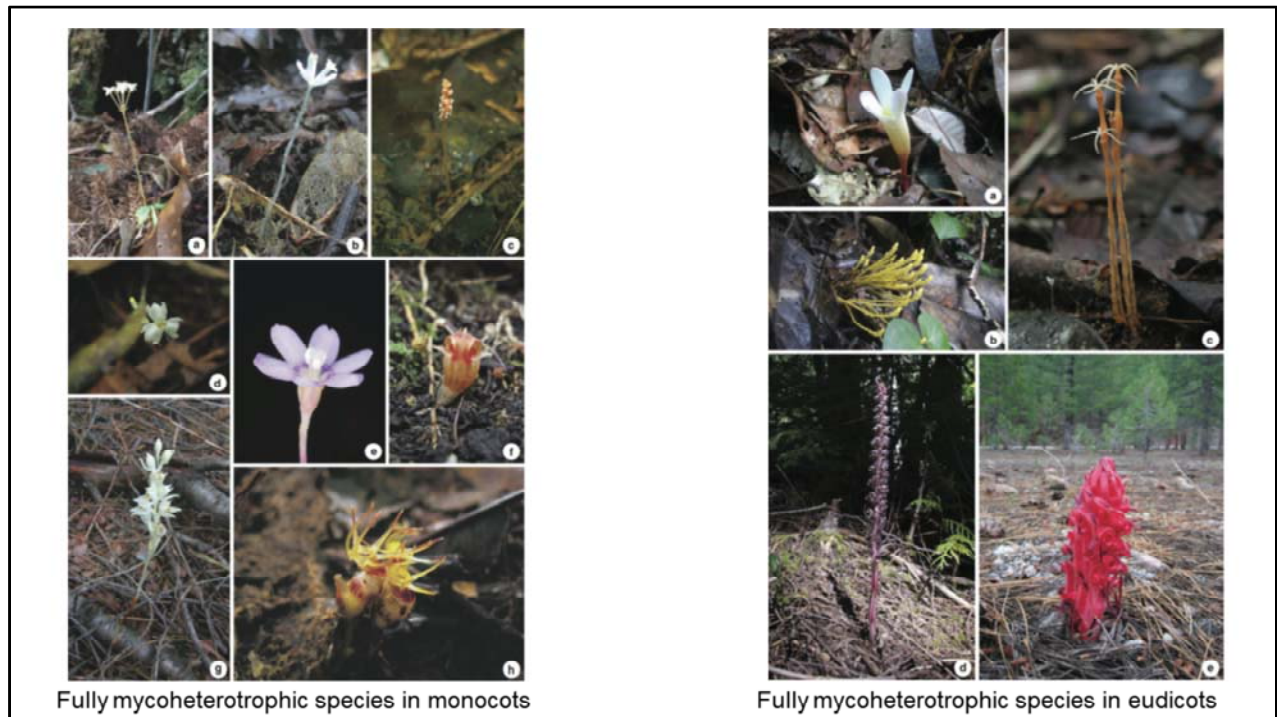
Monotropa uniflora
(Ghost plant, Indian pipe)

- A. Mature plants in the field
- B. Root system showing the typical cluster of mycorrhizas.
- C. Individual mycorrhizal root tip.
- D. Transversal section of a mycorrhiza showing a pseudoparenchymatous mantle, brown tannin layer, Hartig net surrounding epidermal cells, and the hyphal peg (arrow head) penetrating an epidermal cell.

Russulaceae Associated with Mycoheterotroph *Monotropa uniflora* (Ericaceae) in Tlaxcala, Mexico: A Phylogenetic Approach December 2015. Cryptogamie Mycologie 36(4):479-512



- Successful exploiters of the ectomycorrhizal symbiosis ultimately evolved from mutualists via defection.
- Exceptionally high specificity of myco-heterotrophic plants towards narrow clades of ecto- and arbuscular mycorrhizal fungi relative to autotrophic plants.
- Are nonphotosynthetic mycorrhizal plants parasitic?
 - If they supply nutrients, then no.



myco-heterotrophy makes it possible to succeed in the low-light conditions of understory habitats. In fact, most, if not all, nonphotosynthetic mycorrhizal plants are understory woodland inhabitants and, at least in the Ericaceae (Cullings *et al.*, 1996), they most likely evolved from photosynthetic mycorrhizal plants that inhabited understory woodland habitats.

Myco-heterotrophs in Maryland

Spotted Coralroot *Corallorhiza maculata*



Spotted Coralroot flowers in Iron Co., Wisconsin (8/1/2008). Photo by [Corey Raumont](#). (MBP list)

Spotted Wintergreen
Chimaphila maculata



Spotted Wintergreen in Frederick Co., Maryland (6/28/2015). Photo by [Bob Cammarata](#). (MBP list)

American Wintergreen *Pyrola americana*



American Wintergreen blooming in Montgomery Co., Maryland (6/15/2016). Photo by [Robert Ferraro](#). (MBP list)

[Family Orchidaceae](#) > [Genus Corallorhiza](#) - 4 in MBP – some rare
[Ericaceae](#) - *Chimaphila* – 2 species – partially mycoheterotrophic
[Ericaceae](#) - American Wintergreen *Pyrola americana*

Myco-heterotrophs in Maryland

Pinesap *Monotropa hypopithys*



Pinesap in St. Mary's Co., Maryland (6/30/2018).
Photo by [Bill Hubick \(MBP list\)](#)

Indian Pipe *Monotropa uniflora*



Indian Pipe in Cecil Co., Maryland (9/21/2014). Photo by
[Beth Johnson \(MBP list\)](#)

Virginia Pennywort
Obolaria virginica



Virginia Pennywort in Montgomery Co., Maryland
(4/26/2015). Photo by [Mike Ostrowski \(MBP list\)](#)



Pygmy Pipes
Monotropsis odorata

All Ericaceae

Pygmy Pipes *Monotropsis odorata* Schweinitz ex Elliott Endangered (MD) - S1 (Highly state rare) - Vulnerable Southeast US, Maryland at northern end of range. Specimens in Smithsonian from Baltimore and Anne Arundel Counties.

Gentianaceae: Virginia Pennywort - It is native to the eastern United States,^[2] where it is found in nutrient-rich forests. It is believed to be mycoheterotrophic, getting much of its nutrients through a symbiotic relationship with fungi, instead of through its small purplish-green leaves.¹

On Going Unnoticed by Robert Frost

As vain to raise a voice as a sigh
In the tumult of free leaves on high.
What are you in the shadow of trees
Engaged up there with the light and breeze?

Less than the coral-root you know
That is content with the daylight low,
And has no leaves at all of its own;
Whose spotted flowers hang meanly down.

You grasp the bark by a rugged pleat,
And look up small from the forest's feet.
The only leaf it drops goes wide,
Your name not written on either side.

You linger your little hour and are gone,
And still the wood sweep leafily on,
Not even missing the coral-root flower
You took as a trophy of the hour.

Western Spotted Coralroot - *Corallorhiza maculata*



http://www.digitalnaturalhistory.com/genus_corallorhiza_index.htm