



## Carnivory and parasitism in plants

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**Abstract.** Only a relatively small number of plant groups are capable of taking organic matter directly from other organisms. Plants that are capable of connecting to other plants and diverting nutrients from them using haustoria are known as parasitic plants. Plants that are capable of capturing animals and absorbing nutrients from them using traps are known as carnivorous plants. A comparison between these two syndromes is given in respect to mechanisms and classification, with reference to the difficulties in classifying the traps by mechanisms. The terms holo-carnivorous, hemi-carnivorous and pseudo-carnivorous are suggested for use in the discussion of carnivorous mechanisms. With parasitic plants it is clear that in natural habitats host and parasite coexist in an equilibrium that allows both of them to develop and to set seeds. An analogy between carnivorous and parasitic plants in this respect seems plausible once we consider the carnivorous plants as parasites of prey communities, not of individual prey. It is essential for the existence of any carnivorous plant species in natural habitats that the prey communities will co-exist with it in equilibrium. In addition, one should not rule out the possibility that in addition to the mutualistic relations that are known to exist between pitcher plants and insect communities that feed on them and serve as prey, mutualistic relations may also exist between insects and other carnivorous plants.

### Introduction

Most plants are autotrophic, producing their own organic substances thanks to their ability to photosynthesize sugars. Only a relatively small number of plant groups can take organic matter directly from other organisms. One important group is the carnivorous plants that can take animal matter; the other group is the parasitic plants that can take nutrients from other living plants. Both groups developed special organs that allow these capabilities.

The understanding of the mechanisms of parasitism and carnivory has reached some peaks in recent years, yet much is still to be studied in these two interesting plant groups. The aim of the present paper is to compare the two groups, which seem to have much in common.

### Definitions

*Parasitism* in plants is defined as the ability of a plant to divert water and nutrients from other living plants by a special organ, the **haustorium** (Kuijt, 1969). Plants that are capable of connecting to other plants and diverting nutrients from them using haustoria are known as parasitic plants (PP).

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**Carnivory** in plants is defined as the ability of a plant to capture animals and to use them for the plant nutrition, by a special organ, the *trap* (Juniper *et al.*, 1989). Plants that are capable of capturing animals and absorbing nutrients from them using traps are known as carnivorous plants (CP).

Both definitions are not satisfactory, having many exceptions. This is natural because any such definition is arbitrary, based on human perception of plants rather than on clear biological boundaries between plant groups. Such biological boundaries simply do not exist. Nevertheless, for our convenience, these general definitions allow to examine relatively small groups of plants that share some unique series of characters.

### Frequency of occurrence

Both carnivorous and parasitic plants are relatively rare in nature, but they are often domesticated either purposely as ornamentals, in the case of carnivorous plants (some of which are massively grown in culture), or accidentally as weeds, in the case of parasitic plants (some of which threaten agricultural productivity).

### Polyphyletic evolution

The carnivorous syndrome and also the parasitic syndrome are polyphyletic, each has developed independently in various non-related plant groups, nevertheless they show similar organs and seem to function in similar manners. For example, adhesive traps can be found in *Drosera* and *Pinguicula* that belong to two non-related plant families. Likewise, pitchers can be found in *Cephalotus*, *Sarracenia* and *Nepenthes*, and moving traps in the aquatic *Aldrovanda* and *Utricularia*, both latter cases showing a concurrent occurrence of similar trapping devices in non-related plant families.

With parasitic plants the situation is very similar. Root parasites developed in e.g. the Rafflesiaceae, Balanophoraceae, Hydnoraceae and Orobanchaceae that are non-related plant families. Likewise, twining leafless parasites can be found in the non-related genera *Cuscuta* (Convolvulaceae) and *Cassytha* (Lauraceae).

### The Scrophulariaceae in relation to CP and PP

An interesting link between CP and PP is provided in the Scrophulariaceae. This plant family that exhibits many autotrophic plants is also closely related to both Orobanchaceae and Lentibulariaceae. Whereas the latter is known as a family of carnivorous plants, (e.g. *Utricularia*, *Pinguicula*, and *Genlisea*) the former is a family of holoparasitic plants (e.g. *Orobanche*, *Cistanche*, and *Epifagus*). Parasitic plants in the Scrophulariaceae and Orobanchaceae families have been traditionally depicted as forming a linear evolutionary series beginning with hemi-parasitism (e.g. *Striga hermonthica*) and ending with holo-parasitism (e.g. *Cistanche spp.*). The Scrophulariaceae genera *Lathraea* and *Hyobanche* have been viewed as transitional links between the hemi-parasitic members of Scrophulariaceae and the strictly holo-parasitic habit of the Orobanchaceae (Young *et al.*, 1999). But it also seems that in the Scrophulariaceae parasitism and carnivory developed concomitantly. The extreme case in this respect is found in the genus *Lathraea*. Plants of this genus are holoparasitic, but they also carry special small utricles that may serve as traps. The function of these organs is not yet understood, yet it was suggested that *Lathraea* represents a plant that had both parasitic and carnivorous capabilities (Juniper *et al.*, 1989).

### Classification of traps

The carnivorous plants are basically classified according to their taxonomic status. In addition we often classify them by their trapping mechanism, which may vary even in a

single plant family. Thus, flypaper traps can be found in both Droseraceae and Lentibulariaceae, but these two families also exhibit other trapping mechanisms, such as snap-traps in the Droseraceae and suction traps in the Lentibulariaceae (Lloyd, 1942). Classifying the traps on the basis of their functional principle is difficult. In Sarraceniaceae, for example, some *Sarracenia* species secrete a digestive fluid and are fully carnivorous, other species depend on external sources of water and on digestive enzymes secreted by microorganisms or by insect inquilines for prey breakdown and digestion (Hepburn *et al.*, 1927; Joel and Heide-Jorgensen, 1985), and some *Heliophora* species seem not to benefit at all from their traps in terms of digested animal matter (Juniper *et al.*, 1989). More so, plants like *Roridula* do not have any digestive capabilities, nor do they have digestive gland, but they developed mutualistic relations with a hemipteran insect that helps in transmitting nutrients from the prey to the plant. This insect consumes the prey that is captured by the secretion on the stalked glands of *Roridula*'s leaves, and the faecal nitrogen of the insect is then taken up by the leaves (Ellis and Midgley, 1996). We can see that in spite of the lack of a digestive system in *Roridula*, it can still be considered carnivorous because it fits into the CP definition, i.e. capable of capturing animals and absorbing nutrients from them in traps.

### Similarity between parasitic and carnivorous plants

Are there any similarities between these two plant groups? Indeed both have alternative feeding organs, the trap and the haustorium, and both are able to use organic substances from other organisms. All carnivorous plants are photosynthetic, i.e. they are green plants, able to produce organic substances of their own through photosynthesis. This is also true for many parasitic plants.

Nevertheless, some highly specialized parasitic plants are devoid of any photosynthetic capability. In fact, parts of the photosynthetic genome in these plants are missing or altered (Young *et al.*, 1999). As a consequence, these obligatory parasitic plants are classified as *holo-parasites*, since they are totally dependent on their hosts for organic matter. On the other hand, parasitic plants that are able to supply themselves with at least some organic matter through photosynthesis, having a functional photosynthetic genome, are classified as *hemi-parasites* (Kuijt, 1969). This nomenclature is very convenient, though sometimes controversial.

In a similar manner one may also classify the carnivorous plants according to their carnivorous status. Carnivorous plants that trap animals, digest them using their own digestive glands, and absorb nutrients from the prey may be classified as *holo-carnivorous*. Clear examples for this group are *Dionaea muscipula* and *Drosera rotundifolia*. Carnivorous plants that have traps and are capable of absorbing digested animal matter, but do not secrete digestive enzyme by themselves, may be classified as *hemi-carnivorous*. An example for this group is *Roridula* spp. And those plants that do not exploit animal matter for their nutrition but have organs that are homologous to known traps, may be classified as *pseudo-carnivorous*.

Parasitic plants can also be classified as obligatory if their development is fully dependent on nutrient supply from a host. A similar classification is irrelevant for carnivorous plants simply because there is no single carnivorous species that is known to fully depend on the supply of animal matter. Nevertheless there are some carnivorous plants that are known to benefit a lot from carnivory, in term of growth rates and seed set (Darwin, 1875), while for other species the contribution of animal matter is not significant.

### Specific organs

As stated above, carnivorous plants have digestive surfaces, and parasitic plants have haustoria. Both organs allow the transfer of nutrients from other organisms that serve as sources of nutrients. The digestive glands in carnivorous plants vary from a small organ containing a few cells (in *Utricularia* and *Cephalotus*) to a multicellular

multilayered gland (in *Drosophyllum*, *Triphyophyllum* and some species of *Nepenthes*). Despite the differences, the digestive glands and also other digestive surfaces, like the pitcher epithelium of *Sarracenia*, show a common architecture that is composed of the same components in almost all carnivorous plants: glandular cells on top, and endodermoid cells mediating between the glandular cells and the leaf tissues (Joel, 1986). Usually conductive elements are also present, allowing the transport of digestion products from the glands to other plant organs.

Similarity can also be found in haustoria structure in the different parasitic plant groups. Haustoria are principally composed of the same components in almost all parasitic plants (Kuijt, 1969), and develop in similar manners: intrusive cells penetrate host tissues, and then the intrusive body develops conductive tissues that connect directly to the conductive tissues of the host (Joel *et al.*, 1998). This is true for root parasites, twining parasites, and mistletoes.

Clearly, the digestive surface in CP, which is usually composed of numerous digestive glands, serves as an active transport organ that absorbs animal matter from the trap cavity (or from the digestive pool). This structure actively controls the transfer of digested substances to the plant conductive system. The haustorium in parasitic plants is likewise capable of absorbing water and nutrients from neighboring host tissues during its early development. However, it seems that once the haustorium matures, it usually serves as a passive bridge rather than as an active sucking organ (Joel *et al.*, 1998). This difference between haustoria and digestive glands is intrinsic in the basic nature of these two syndromes. While the parasitic plants divert nutrient supply from a living organism to which they connect, the carnivorous plants digest and absorb organic matter from non-living organisms. In the former case the parasitic strategy is based on the formation of a strong 'sink' that drives nutrients from the host. In the latter case the carnivorous plant cannot manipulate the animal to supply it with nutrients; it simply takes the nutrients that build the body of the prey by external digestion and active absorption.

### Perception of chemical stimuli

Unlike almost all other higher plants, seed germination in obligate root parasites depends on receipt of a chemical signal from the roots of host plants. These parasitic plants are totally dependent on a specific association with a host that provides them with nutrients and water, so the chemical recognition system ensures that germination starts only when suitable host roots are available in the immediate vicinity of the parasite seed. A similar dependence of seed germination on an external chemical stimulus does not exist for carnivorous plants. However, the onset of digestive activity is often triggered by a chemical stimulus that originates in the captured prey (Juniper *et al.*, 1989). In both cases, very low stimulant concentrations are needed. In *Dionaea* a chemical stimulus leads first to the development of cuticular gaps in the digestive glands (Joel *et al.*, 1983), and then it also elicits the secretion of the digestive fluid into the trap cavity (Robins, 1976). The chemical recognition of a prey inside the trap ensures that the plant spends its digestive resources only when suitable prey is available in the immediate vicinity of the digestive surface.

### Attachment to the alternative source of nutrition

The first step both in a parasitic activity and in a carnivorous trapping of prey is the attachment of a specialized plant organ to the source of alternative food. In the parasitic plants this is done by the attachment organ, a unique structure that adheres to the surface of the host plant, usually with the aid of a special anchoring secreted substance. This strong anchoring allows the parasite to push the intrusive cells into host tissues without disconnecting from the host (Joel and Losner-Goshen, 1994). In the carnivorous plants the attachment is done by the trap that captures the prey and retains it, usually with the aid of a liquid that allows retention and close contact for later digestive

activities. However, while the parasites take nutrients from living organisms, the carnivorous plants kill their prey before nutrients can be taken. Thus, enzymatic activities in carnivorous plants are responsible for the digestion of prey tissues (Juniper *et al.* 1989), whereas enzymatic activities of parasitic plants allow the intrusion into living host tissues (Losner-Goshen *et al.*, 1998).

### Nutrient transfer

In both carnivorous and parasitic plants the taken nutrients are transferred to the plant sinks, *i.e.* to the developing leaves, roots, flowers, etc. While it is known that the incoming nutrients are first metabolized in the traps and only then transferred to the vegetative or reproductive apices in carnivorous plants (Juniper *et al.*, 1989), it is not yet clear whether the nutrients absorbed by parasitic plants are first metabolized in the haustoria, or, as it may also be the case, the two mature organisms, the parasite and its host, co-exist connected to each other. In this case the parasite serves, in physiological terms, just as an additional sink in the "united organism".

### CP-prey and PP-host relations

The above discussion brings us to some basic characteristics of parasitism in plants. There are two important stages in plant parasitism. The first is characterized by intrusion of the young parasitic haustorium into host tissues, bypassing or neutralizing the host defense mechanisms of the host (Joel and Portnoy, 1998). This is the intrusive developmental stage. Then the haustorium matures, and the host and parasite coordinate their growth in such a manner that leads to precise alignment of the conductive tissues of the parasite with those of the host (Joel, 2000). This is the coordinated developmental stage. The parasite clearly benefits from these relations, being nourished by its host. This is essential at least for holo-parasites. Though nothing is known on possible benefits for the host from these relations, it is clear that the two partners eventually coexist in an equilibrium that allows both of them to develop and to set seeds. Damage is caused to the host only in disturbed systems (like agricultural fields) where this equilibrium is broken, not in undisturbed natural habitats. Clearly the parasite does not impose any threat on the existence of natural host species communities.

With carnivorous plants the situation looks different; nevertheless one can make some analogy between carnivorous plants and parasitic plants in this respect, once we consider the carnivorous plants as parasites of prey communities. Although prey capture is usually fatal for any individual prey, the community of any particular animal species is never endangered by carnivorous plants. Whatever number of individuals the animal community loses, it is essential for the existence of the carnivorous plant species that the prey community will co-exist with it in equilibrium.

The relations between a carnivorous plant and its prey community may differ, though, in different systems.

With some pitcher plants it is now clear that their relations with some prey communities are mutualistic rather than parasitic. Insects benefit from pitcher nectar that serves for their nutrition in habitats where sources of floral nectar might be uncommon. At the same time the insects pay the plants in a small portion of their community which is 'sacrificed' as prey and consumed by the plants, which grow in nutrient-poor soils (Joel, 1988). It seems that nobody has ever looked into the influence of insect trapping by non-pitched CP on the insect community in natural habitats. Other mutualistic relations may be discovered. In any case one may put forward the hypothesis that carnivorous plants can reduce the size of an insect community to the extent that reduces intra-specific competition within this community. By this, the CP would probably not differ from other predators in a balanced habitat.

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