Title
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Why are Carnivorous Plants the “Most Wonderful Plants in the World”?

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Abstract

Carnivorous plants have evolved convergently around five times in evolutionary history. These plants are found in poor-soil environments and adapt their leaves to form mechanisms to trap prey, in order to outsource nutrients missing from the soil. New developments in digestive enzymes and leaf modification into traps have been found recently. Carnivorous plants shed an important light in the relationship between ecology and evolution and how changes in environment can lead to changes in form and function. Concerns about climate change's potential effect on carnivorous plants have also been of great discussion recently, with pushes to conserve the carnivorous plants.

Origins and Environment

Charles Darwin was among the first to classify carnivorous plants on a phylogenetic tree in 1875. Carnivorous plants are known to have evolved convergently many times throughout evolutionary history. Carnivorous plants need to be able to obtain nutrients from dead organisms in its environment, which will give it advantages in growth or reproduction; they must also be able to digest, attract, and capture their prey (1). These plants are found on every continent except Antarctica (2). Their preferred environments happen to be those that have water-logged and nutrient depleted soil (3). Nitrogen and phosphorus are limiting nutrients that cause the plant to have to outsource them (1). Poor soil nutrition has led carnivorous plants to obtain nitrogen and phosphorus elsewhere, so they have evolved to kill and digest insects in order to outsource their nutrients. Carnivorous plants also have high rates of mutations, which can explain their high adaptation rates (4).

Carnivorous plants have been used as a model to show the relationship between ecological factors and evolution, as the adaptations for carnivorous plants are marked by poor ecological conditions. Using carnivorous plants as a model organism has allowed an understanding of the trade-offs in a carnivorous organism, through its photosynthetic rate, the formation of trapping mechanisms via leaves, and the energy cost of the trapping mechanism by digestive enzymes.

Cost-benefit model in Carnivorous plants

There is a trade-off between a plant being carnivorous, where the energy gain of the trap has to be greater than energy loss from trap production. This trade-off of energy gain or loss is described in a cost-benefit model. The cost-benefit model explains why carnivorous plants are confined to areas with poor-soil and bright light (5). Since the soil often has low levels of nitrogen and phosphorus, these are limiters of the plant's growth. In the poor soil, there are also lower rates of photosynthesis and poor nutrient absorption by the roots of the plant (6). These have caused carnivorous plants to adapt and form trapping mechanisms. The conditions that must be met for the adaption to possibly occur are low levels of nutrients in the soil, but enough light that it isn't considered a limiting factor on the plant’s growth. The cost-benefit model is founded on the hypothesis that there will be an increase in photosynthesis due to carnivory, offsetting the energy loss by creating the trapping mechanisms (1).Since the carnivorous traps are inexpensive for the plant to create and the energy gain from the plant is very high, there does not need to be substantial photosynthetic gain for a benefit from the trap (7). The purpose of a carnivorous trap is to capture nitrogen for the plant, which is needed by chloroplasts to undergo photosynthesis. Because the level of nitrogen the traps uptake is very high, the plant does not need that much of a substantial photosynthetic gain to favor carnivory.

However, the rate of photosynthesis is dramatically lower than non-carnivorous plants. The trade-off between carnivory and light and water capture also makes carnivorous plants poor competitors (8). Depending on environmental conditions, carnivorous plants have been able to have phenotypic plasticity to adapt to environmental changes (8). The idea of phenotypic plasticity in pitcher plants is presented in Figure 1 where a pitcher plant is able to revert to flat leaves in rich-soil, with their function to be photosynthesis only. The ability for some carnivorous plants to revert to a purely photosynthetic plant can allow for the plants to be long-lived and survive in different conditions. The ability for phenotypic plasticity can allow for an understanding of environmental change and how it affects plants, as well as an insight on how climate change can affect plants. In environments with high-nutrient soil, carnivorous plants can completely lose their ability to be carnivorous, as the plant will not need to input the energy gain to create mechanisms of trapping if the roots are able to obtain adequate levels of nutrients (3). This means that there is a relationship between the plant's ability to uptake nutrients from its environment through roots and the adaption to become carnivorous. If the plant is in an area where its roots functions are not limited, then the plant will not adapt to become carnivorous.

Figure 1: Phenotypic Plasticity in Pitcher Plants

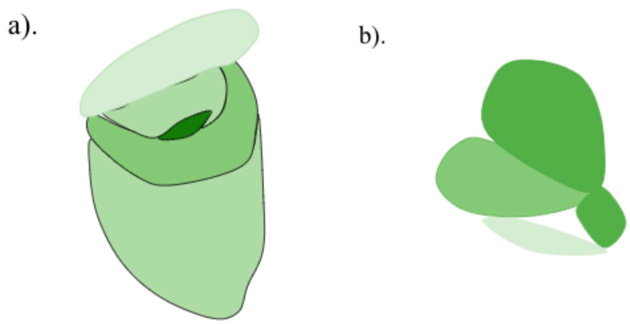


Figure 1: Phenotypic Plasticity in Pitcher Plants. A). depicts a pitcher plant in poor soil environment, which has a clear pitcher morphology. B). depicts a pitcher plant in an environment with rich-soil nutrition, as a result it has reverted to have flat leaves, with their function solely photosynthetic.

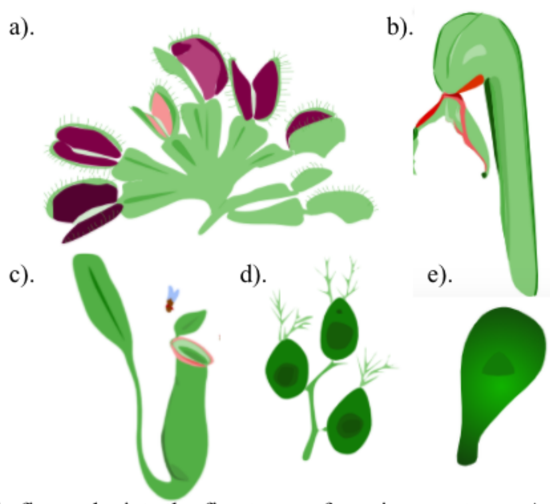
Although the idea of phenotypic plasticity seems to go against the cost-benefit model, since it states that carnivory is favored. Instead, phenotypic plasticity supports the cost-benefit model as it shows that the environment is the reason for the adaptation to carnivory and the traps only benefit is to outsource and obtain nitrogen for photosynthesis when in poor conditions. When conditions revert to being in well-draining nutrient-rich soil, carnivory traps are not needed and it will be a waste of energy to create the traps.

Trapping mechanisms and digestive properties

There are five known trapping mechanisms in carnivorous plants, which are snap traps, lobster traps, pitfall traps, bladder traps, and sticky traps as shown in figure 2 (9). These trapping mechanisms can be categorized as either active or passive (10). An active trap relies on movements to capture prey, while a passive trap depends on its morphology and shape of the traps. An example of an active trap is a snap trap, like a Venus flytrap, and a passive trap would be a pitfall trap, such as that of a pitcher plant. Trapping mechanisms are formed by specialized leaves. The adaptation of leaves to become trapping mechanisms has occurred by small-scale gene duplication events over time. It has been suggested that these gene duplication events have transitioned pectin or chitin to form trapping mechanisms (11). The plant does not allocate every leaf to become a trap though, the traps have been restricted to the upper leaf domain on the plant (9). This is necessary as it allows a developing plant to have designated areas to form traps and allows the plant to form radialized leaves early on. The exact method that carnivorous plants use to create their traps is not yet known; however, there is insight that variation in the growth rate along dorsal midlines leads to the specialization of the traps (12). Further specialization on the dorsal midline and differing growth rates allows for the different types of traps as seen in figure

2. The traps also need to be able to attract prey. A carnivorous plant uses several methods to attract prey, such as olfactory, visual, or acoustic attractants (13).

Figure 2: Five Types of Carnivorous Traps



This figure depicts the five types of carnivorous traps. A shows a snap trap, which is an active trap that catches a prey when they brush on their trigger hairs. B is a lobster-pot trap, which is passive and traps the prey inside it, and the prey cannot leave. C is a passive pitfall trap that the prey goes in and gets trapped in the digestive fluid. D is a bladder trap which pulls prey in like a vacuum. E is a passive sticky trap, where the prey gets stuck on hairs on the traps surface.

Once the traps are formed, the plant needs to create digestive enzymes in order to break down its prey and obtain nutrients. In pitcher plants, within the pitchers, there are digestive glands that secrete enzymes upon contact with a prey. The digestive enzymes are only secreted when the prey is in contact, as there is a cost-benefit ratio, as the production of these enzymes cause energetic costs (10). Different types of carnivorous plants create their own type of digestive enzymes. Protease has been found to be the main enzyme in pitcher plants (10). This readily available enzyme in the plant, allows for a cost-beneficial digestive enzyme as pitcher plants are subject to their digestive enzymes getting diluted from rainwater due to the morphology of the traps. The use of protease allows the plant to be able to secrete enzymes in contact with the prey inside of the pitcher.

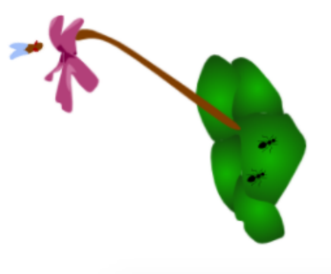
However, not every carnivorous plant has digestive enzymes. One pitcher plant, Nepenthes bicalcarata, has symbiosis with ants which allows for the breakdown and disposal of waste (5). The ants aid with both the capture and the disposal of the prey and they allow for the plants to obtain more nitrogen, which promotes growth in the plant (5). The differences in the types of digestion systems across carnivorous plants suggests that they are very well adapted to their environment and create cost-effective systems to obtain nutrients.

Pollination and Capture

Carnivorous plants are angiosperms, so they create flowers and need insects to be able to promote gene flow and pollination. Therefore, they need a way to reduce the probability that their pollinator will become their prey. The location of the carnivorous tissues or mechanisms on the plants is highly specific for the type of plant, this helps for the pollinators to not be subject to the traps. Carnivorous plants are also specialists, they prefer one type of prey over another. The type of insects that a carnivorous plant captures and digest depends on its morphology of the traps (7). In cases when there are multiple species of carnivorous plants in the same area, even further specialization has occurred as carnivorous plants are bad competitors (7). The specialization of prey for carnivorous plants is important because it allows for the plants to obtain the prey that are best fit for their traps and that will give them substantial nutrients. Insects account for the majority of a carnivorous plant's nitrogen uptake, which allows for the plants to thrive in low nitrogen environments (14). However, it has been found that insects are not the only prey carnivorous plants capture, but instead they are the most favorable. Carnivorous plants are also found to prey on rats, mice, and several small insects. Insects however, account for over seventy percent of the nitrogen uptake for carnivorous plants (14).

The reliance on insects for nitrogen promotes a need for the carnivorous plants to be able to decipher between the insects for prey and those for pollination. A way these plants are able to do that is in their morphology, the larger distance between the flower and the trap, the lower the probability that a pollinator will be mistaken for food (14). Figure 3 depicts the distance between the flower and the trap of a butterwort and the likelihood of the pollinator becoming prey. In general, the larger the distance between flower and trap, the less likely the pollinator will interact with the trap.

Figure 3: Pollination in Butterwort



This figure depicts a butterwort, which has a sticky trap on the ground and a flower off-shooting from the center of the trap. The distance between the trap and the flower decreases the likelihood the pollinator will be trapped and become prey.

Climate Change and Carnivory

Carnivorous plants are adapted to specific environments. The current rate of climate change poses challenges to carnivorous plants. Although carnivorous plants have a high rate of mutation and are able to go through phenotypic plasticity, the plants most likely will not be able to adapt to the changes in the climate (15). A majority of carnivorous plants reside in coastal areas that are susceptible to rising sea levels and storms due to climate change (15). The rising rate of climate change can cause habitat loss or declines in fitness in the habitat among carnivorous plants, potentially causing the extinction of several species of carnivorous plants. The loss of carnivorous plants can cause a wide gap in scientific knowledge on how plants are able to adapt and can cause a wide set back in the knowledge we have on carnivorous plants.

Conclusion

Carnivorous plants have been an interest for botanists for several decades, however a lot is still unknown. They have convergently evolved several times from angiosperms, with poor-soil being a catalyst for the adaptation to carnivory (3). Carnivorous plants have been used as a model for ecological and evolutionary relationships, showing how deeply related the two are. They also show how specialized plants can become as they have adapted to different niches, through the type of trap, the digestive system, and pollination. The formation of the trapping mechanisms is a wide field in the study of carnivorous plants and much is still left unknown. In the future, more studies regarding leaf modification for different types of carnivorous plants will need to be done to shed more insight into how these novel features arose. The effect of climate change on the population of carnivorous plants is also of great interest. Conservation efforts should be placed on carnivorous plants so as these plants do not become extinct as the climate gets warmer.

Glossary

Carnivorous plant	A plant that has the ability to attract, capture, and digest nutrients from animals or protozoans in order to gain nutrients.
Convergent evolution	Evolution that occurs in organisms not closely related, that results in similar traits as a result of similar environmental factors.
Protease	An enzyme that catalyzes the breakdown of

	proteins and peptides.
Phenotypic plasticity	Ability of an organism to change its morphology in response to an environment.

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