The Hidden Army of Pitcher Plants

Imagine that you work in a flower shop. One day, you come across an unusual plant and decide to buy it. However, you soon discover that this plant needs blood to thrive.

I've given you sunlight.

I've given you rain.

Looks like you're not happy,

'Less I open a vein.

I'll give you a few drops

If that'll appease.

Now please-oh please-grow for me!

(Howard & Alan, 1986)

Just as you think that things cannot get worse, your plant soon gains the ability to speak, continually demanding to be fed. You are then manipulated by her, getting convinced to murder to feed her, achieve success as well as win a girl's heart. As you likely would have anticipated, the ending to this is unlikely to be good. More people find out about your plant and a mad scientist makes clones of her. Owning one of these plants becomes trendy, and as expected, the plants soon grow into an army and take over the world, growing in size with every human they eat.

This is similar to the events that took place in the classic 1960 horror musical comedy, 'The Little Shop of Horrors'. While we have yet to find plants that are able speak, there is some truth in this piece of science fiction. The idea of a carnivorous plant seems counterintuitive, as we often consider plants to be passive life forms that produce their own food through the process of photosynthesis. However, we also know that some plants are predators and can feed on animals.

The fact that dead insects are found on certain plants has been known for a very long time. However, before Darwin's book on insectivorous plants was published in 1875, it was common belief that insects merely drowned in the water collected in these plants or became stuck on the sticky parts of these plants. Animals eat plants, and it was outrageous to think that the opposite could be true – that plants can feed on animals! In fact, one author had written that the creator (i.e. God) had designed these plants to kill insects to control the population of insects (Anonymous, 1852). But, as always, Darwin was not satisfied with this explanation and instead set out to find a naturalistic explanation for this phenomenon. He thought that the capture of insects had to be beneficial for plants also. In his experiments, he found that plants excreted substances that were extremely similar to the digestive juices one can find in an animal stomach (Darwin, 1875).

It has almost become common knowledge that bacteria live in our guts, with wide-ranging connections to the human condition. Companies pump out multitudes of probiotic products that claim to benefit our health by improving the number and diversity of 'good' bacteria that live in our gut. In fact, we are also hosts of a plethora of other microscopic organisms such as archaea, fungi, and viruses unseen to the human eye. Together, these form the human microbiome (Dethlefsen et al., 2007; Hoffmann et al., 2013; Minot et al., 2012). Knowing this made me wonder if the "gut" of carnivorous plants contain a microbiome just as animal guts do. Well, it turns out that I am not the first to make this connection. Especially in recent years, ecologists have set out to find out more about the plant "gut" microbiome, though there is still surprisingly little known about the associations between carnivorous plants and their hidden army of microbes (Sickel et al., 2016).

The killer plant gut

Just like in the 'The Little Shop of Horrors', carnivorous plants in the real world not only photosynthesise, but have also evolved the ability to kill and consume animals in order to thrive. This is an alternative way for them to obtain nitrogen while living in nutrient-poor soils (Juniper et al., 1989). While some plants may produce digestive juices to digest their prey (Juniper et al., 1989; Gallie & Chang 1997), nitrogen is often made available for absorption by bacteria living on the plant (Mouquet et al., 2008).

Carnivorous plants can be categorised according to the way they trap their victims, including adhesive traps like the butterwort, pitfall traps like those of the pitcher plants, and snap traps such as the venus flytrap. Among the different types of carnivorous plants, pitchers in particular have often been compared to the animal gut (Bittleston et al., 2018; Darwin, 1875). This is unsurprising as both contain an abundance of nutrients in an acidic environment and hence have similar microbiomes that aid in food digestion (Koopman & Carstens, 2011; Lam et al., 2017; Takeuchi et al., 2015). The most prevalent phyla of bacteria in the human gut –Firmicutes, Bacteroidetes, and Proteobacteria–are also the dominant phyla found in the *Sarracenia alata* pitcher plant species (Koopman & Carstens, 2011). In addition to bacteria, other microbes such as fungi, algae, protozoa, and possibly even archaea can be found in pitchers as well as the human gut (Boynton, 2012; Buckley et al., 2003; Cochran-Stafira & von Ende, 1998; Krieger & Kourtev, 2012). Besides this, many types of insect larvae and even frogs have been found living in pitchers (Tropical Pitcher Plant, 2020)!

Assembling the microbial army

There are almost 200 known species of pitcher plant, which ecologists have placed into 5 groups – the *Nepenthes*, *Sarracenia*, *Cephalotus*, *Heliamphora*, and *Darlingtonia*. The tropical pitcher plant (*Nepenthes*) has cups that form from the ends of its tendrils (Tropical Pitcher Plant, 2020). On the other hand, in trumpet pitchers (*Sarracenia*), the entire leaf folds to form a pitcher. While *Nepenthes* pitchers likely contain microbes even before opening (Chou, 2014), *Sarracenia* pitchers are sterile and do not contain any bacteria (Peterson et al., 2008). It is only after they open that rainwater collects and its army of microbes and invertebrates are recruited (Young et al., 2018). As such, the factors that shape the microbiome of *Nepenthes* and *Sarracenia* pitchers are likely to differ. These factors include the plant itself, its environment, food availability and even the other organisms living in pitchers.

Firstly, larvae of the *Wyeomyia smithii* mosquito is a key predator in pitchers, and its presence increases the number and type of bacteria (Peterson et al., 2008). This could be a direct influence, with mosquito faeces feeding bacteria (Peterson et al., 2008). However, it is more likely that this relationship is indirect, with larvae negatively affecting protozoa, which predate on bacteria (Cochran-Stafira and von Ende, 1998; Kneitel, 2007).

Habitat and environment may also influence the pitcher microbiome. As an example, the *Kiloniellaceae* family of bacteria is found only in pitcher plants living in the Sapa Bog of Wisconsin, USA (Grothjan & Young, 2019). This is likely because *Kiloniellaceae* bacteria prefer areas of high acidity such as the groundwater in the Sapa Bog (Bott et al., 2008; Wiese et al., 2009). Additionally, especially in *Sarracenia* pitchers that are sterile before opening, microbes on prey likely contribute to the pitcher microbiome. Therefore, the prey available to the plant can shape the resulting microbiome (Stasulli et al., 2020). On a more global scale, the microbiome of Southeast Asian *Nepenthes* and the North American *Sarracenia* are also distinctly different (Bittleston et al., 2018).

With this said, the influence of habitat seems to be secondary to the pitcher plant itself in shaping its army of microbes. Species of bacteria found in pitchers are actually quite different from those found in the soil they grow in. Additionally, while they start out different in each plant, pitcher microbiomes in plants of the same species become increasingly similar over time (Koopman et al., 2010; Koopman & Carstens, 2011). This is due to the unique features of each species of pitcher plant. A study of two species of *Sarracenia*, *Sarracenia minor* and *Sarracenia ava*, has found that they have different bacterial compositions (Stasulli et al., 2020). While further research is underway to find out the reason for this, it could possibly be attributed to the lid of the *Sarracenia minor* folding in a way that closes off much of its opening to the environment, while the lid of the *Sarracenia ava* is raised such that its opening is more exposed (Stasulli et al., 2020).

Mobilisation of the microbial army

Although some pitcher plants feed on animal dung or the occasional tree shrew, most have an insect diet and attract their prey by secreting sweet-smelling nectar (Tropical Pitcher Plant, 2020). While trying to reach the nectar, unsuspecting insects soon find themselves slipping and falling into the death traps, then drowning in the deadly fluid (Tropical Pitcher Plant, 2020). These insects are then physically broken into smaller pieces by other insects (Heard, 1994). This increases the surface area available for enzymes to chemically break down the pieces of animal matter, releasing carbon, nitrogen, phosphorus, and other nutrients (Schulze et al., 1997). Mainly, chitinases digest the exoskeleton of insects and proteases break down proteins to release carbon and nitrogen, while phosphatases cut phosphates from organic molecules (An et al., 2002; Young et al., 2018). Some pitcher plants like the *Nepenthes* produce their own digestive enzymes (Luciano & Newell, 2017), however others like the *Sarracenia* rely more on bacteria, algae, and fungi for digestion (Adlassnig et al., 2011; Young et al., 2018). Nonetheless, pitcher plants all rely on their microbes to some extent for their enzymatic activities to unlock nutrients otherwise trapped in prey.

Not only do they have digestive capabilities, the bacteria army of the California pitcher plant (*Danthonia californica*) may even alter the composition of pitcher fluid to make it deadlier (Armitage, 2016). As early as 1927, scientists have noticed that the fluid in some pitchers is quite different from water, with abnormally low surface tensions (Hepburn et al., 1927). This means that insects that are usually able to walk on water with ease, suddenly find themselves sinking into this deadly pitcher fluid. More recently, ecologist Dave Armitage isolated bacteria from pitcher fluids, adding them to water along with ground-up crickets as food. After a month, he dropped ants into these concoctions and observed that ants were less likely to escape with higher concentrations of bacteria added (Armitage, 2016). While these bacteria have yet to be identified, *Pseudomonas*, *Pedobacter*, and *Serratia* are likely candidates (Guerra-Santos et al., 1984; Marqués et al., 2012; Matsuyama et al., 2011). However, it remains possible that the lower surface tensions observed was a consequence of fatty oils being released during prey digestion (Armitage, 2016).

While much research has focused on the bacterial community of pitcher plants, scientists have also found that fungi are also important for pitchers. Not only do they contribute digestive enzymes, they also produce plant hormones that promote growth such as indole-3-acetic acid (Tan & Zou, 2001). This may account for increases in the size of pitchers (Glenn & Bodri, 2012). In addition to this, fungi also produce antimicrobial compounds to protect the plant against pathogens that cause disease. This includes the more common *Colletotrichum* species, as well as more unique species like *Lasiodiplodia*, *Isaria*, and *Meyerozyma guilliermondii* (Lee et al., 2014). Clearly, microbes are not only important for digestion in pitcher plants, but are likely to do whatever they can to increase the amount of food available to them and their host plant. Their strategies include preventing prey from making their escape, increasing the size of pitchers, or even protecting the plant from disease-causing pathogens.

The pitcher plant, however, is definitely not a freeloader in this microbe-plant relationship. In fact, pitchers are as important for the survival of its microbiome as the microbiome is for the survival of its host plant. Microbes find a suitable home in pitchers which also provides a source of food for them (Mouquet et al., 2008). Digestive enzymes produced by some pitcher plants may even help to increase the rate at which bacteria digests prey (Gallie & Chang 1997)! Furthermore, bacteria in pitchers are carbon-limited and their growth is constrained by the amount of carbon available to them (Gray et al., 2006). This carbon could be made available to them by their host plant, perhaps in the nectar produced, though further research has yet to be done (Gray et al., 2006). If true, this may even feedback to the plant as the increase in carbon will result in greater bacterial growth, leading to more digestion, hence increasing the amount of nitrogen released. Clearly, the fates of the pitcher plant and its microbiome are closely intertwined.

The microbial army and its significance

While this is all very intriguing, if you are anything like me, you may be wondering what the relevance of this is to you and I. Why are ecologists so invested in finding out more about these plants? Before embarking on my further research into this topic, I had merely found it interesting and did not see any way of applying this knowledge into my life. I had certainly not expected that research in this area would be relevant to so many aspects of our lives, from human health to the health of our planet.

A more direct application of this research would be that compounds produced by the fungi living in the pitchers of various species of pitcher plants can potentially be exploited for a large variety of uses. Although 60% of the enzymes produced for industrial uses originate from fungi (Østergaard & Olsen, 2011), fungi that live in plant tissues and organs are largely untapped, not to mention fungi in pitchers. Enzymes produced by these fungi have wide-ranging functions, such as asparaginase which is used as an anti-cancer drug in the treatment of leukaemia

(Appel et al., 2007; Lee et al., 2014). To add on, in the face of the looming threat of antibacterial resistance taking the lives of over 35,000 Americans annually (Centers for Disease Control and Prevention [CDC], 2019; Wernli et al., 2017), these fungi that have the potential to become novel sources of antimicrobial compounds are of undeniable value. In particular, pitcher fluids of the *Nepenthes hookeriana* and *Nepenthes sanguinea* have been found to exhibit antimicrobial activities against many species of bacteria (Stratton, 2019). Knowing this, it is evident that much more experimentation in this area is needed to tap on this largely untouched pool of resources in pitcher plants.

Looking beyond individual microbes, an entire ecosystem is contained within each individual pitcher. Even if from the same plant, each pitcher has their own distinct life history. These natural systems provide a unique opportunity to answer crucial questions regarding microbes, the factors that determine the composition of a microbial community and how this composition can change over time, as well as the contributions of each member to the community (Stasulli et al., 2020). The pitcher is an ideal model to study the associations between microbes and their hosts. Hence, there is potential for investigative work in this area to influence and steer research relating to the relationship between the human microbiome and its impact on human health.

Beyond the benefits to humans, the pitcher has also been used to model food webs. Scientists can easily manipulate these miniature and isolated ecosystems to study the effects of different changes on the microbial community and its pitcher environment. Furthermore, there is a comprehensive understanding of almost every element of the pitcher food web, including the pitcher microbiome. This is important because the microbes in many food webs remain largely unknown due to the difficulties in studying them (Peterson et al., 2008). This knowledge can also provide insight into the fluctuations of global systems, hence guiding the management of phenomena like climate change, loss of biodiversity, and ocean acidification (Brooks, 2011).

With industrialisation and urbanisation, more and more people are living in concrete jungles. On top of this, with our fast-paced lives as we strive for more wealth, more power, and more achievements, we also often forget to slow down and appreciate the wonders and beauty of nature around us. In my exploration into this topic, I am again reminded why I chose to study life science at university – to learn about how everything comes together in the natural world to work in harmony. Even the tiniest of creatures normally hidden from the naked eye can have such an enormous effect for us, for pitcher plants, and for the entire planet. The world cannot survive without microbes, and pitchers could offer the amazing opportunity to glean some understanding into the relationship between our planet Earth and her smallest inhabitants. There is still so much of nature to explore, and my journey into the world of pitcher plants and their army of microbes has made me realise what a wonderfully complex world it is that we live in, be it the seen or the unseen. It is truly amazing how all things work together to make the world go round!

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