INTERTWINED HISTORIES: Plants in their Social Contexts

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the nature of plants

how different scientific perspectives shape our understanding of what plants are

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prologue

There exists a perspective both in popular culture and in some scientific contexts that plants are inactive and insensitive organisms not capable of perceiving and responding to their environments. This perception of plants is based partly on the fact that the lives of plants are so profoundly and obviously different from our own, yet ample evidence exists demonstrating that plants are highly capable of responding to their environments. In part because of the social politics of publishing, even the use of terms such as "plant behaviour" was historically discouraged in the scientific literature. However, in the past 20–25 years there has been a marked shift in the language surrounding plant biology that has accompanied an analogous shift in our philosophical and empirical approaches to understanding plants. In science, sometimes it is challenging to move forward in a given field until the underlying philosophy of what we are trying to figure out is better understood. Until there were advances in our philosophical approach to studying plants, we were not properly equipped to understand which questions to ask. We believe that as a field, plant behaviour continues to be limited more by philosophy than the ability to do the natural science research, though there is much progress on both fronts.

In this essay, we discuss different scientific perspectives on plants and how this affects the questions and answers we come to in plant biological research. We also discuss some of the research being done in our lab[1] and why we can comfortably discuss plant behaviour based on the data rather than personal opinion. Finally, we end on some thoughts about where our current ideas and research may lead us.

on being a plant

There are multiple scientific perspectives about what a plant is. For example, if we were interested in understanding the plants in our home garden, one way we could think of the plants therein would be through the use of descriptive terms. We could describe the garden in terms of what species are present and in what quantities—cucumbers (*Cucumis sativus),* sunflowers (*Helianthus annuus),* and tomatoes (*Solanum lycopersicum*), for example. We could alternatively eschew species boundaries (which tend to be especially blurry for plants) and describe the plants in terms of the characteristics that they have: the different shapes of their body parts, for example. We could note that the fruits of our cucumber plants are a very different shape from those of our tomatoes, or that our sunflowers tend to be much taller than our cucumber plants, which might allow them to thrive under different circumstances. These are widely used and useful approaches to answering questions about plant ecology: For example, what characteristics in plants tend to be found in different environments, and why? But the information we obtain from understanding differences in species compositions and physical traits does not necessarily tell us about what individual plants are, or what they are capable of.

The more dominant perspective in research, and certainly in agriculture, is that a plant is a factory. Plants convert raw materials into usable products such as food and building materials. We can take this factory, put it in a specific location, give it supplies, and then collect the products. There is a great deal of funding available for researchers working in agroforestry to work toward "improvement" of plants in this context, where improvement does not mean making a better organism but making a better factory. In returning to our garden, we could predict that adding more nutrients into the soil would allow the plants to produce more product. However, we might not necessarily understand what individual plants are doing in response to the enrichment. If we broadcast nutrients across the entire system, we also would not have very much control over where those nutrients ended up. Conservation biologists sometimes also seem to consider a plant to be a kind of factory that gives us ecological goods and services. It stores our carbon, produces oxygen, and provides food and habitats for other organisms.

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Though the dominant paradigm in plant biology is the idea of maximizing the products we can attain from plants, we are beginning to show that this has been a problem for attaining a broader understanding of what plants are. We tend to describe plants in terms of the species that are present in a given location, and what these species tend to look like or could be used for. However, in a natural system, *species* do not interact with each other. *Species* may not even be real, since dividing organisms into species is an artificial construct that is useful only in certain contexts. Individual organisms, on the hand, are real, and these individuals do interact; individuals interact with each other, the natural world, resources, their enemies, and their allies. Many perspectives about what a plant is ignore the individuality of the organism; they are focused on plants as a whole but not as individuals who operate in their environment.

How can we learn about nature without knowing who is in nature? In our lab, we seek to ask questions so that we understand the natural world by understanding the individuals that live in it. To return to our garden, what if we shifted our focus to try to understand what individuals in this environment were doing? For example, will our cucumber plant grow differently if placed next to our tall sunflower? Or how will its roots respond if we change where we put the fertilizer? What will happen if it is presented with both of these changes? Our lab is moving more and more toward taking an approach to understanding plants based on what they are capable of and how they act under certain conditions. We are taking a very traditional scientific, experimental approach to a very non-traditional set of questions.

Though the questions we are asking are non-traditional, there is a historical context to the study of plant behaviour dating at least as far back as Charles Darwin. Darwin published *The Power of Movement in Plants* in 1880. In it, he states that "it is hardly an exaggeration to say that the tip of the radicle, thus endowed [with sensitivity] and having the power of directing the movements of the adjoining parts, acts like the brain of one of the lower animals."[2] By making this comparison, Darwin recognized that plants could take in information about their environments and respond to it. Almost thirty years ago, the first paper synthesizing the concept of plant behaviour was published,[3] and the field is continuing to expand.

using behavioural ecology to understand plants

Although the amount of research being done in plant behaviour is small compared to other fields in plant biology, there have been many studies demonstrating interesting behaviour in plants, particularly in the last ten years. For the purposes of this essay, we want to focus on research done in our home lab because we can speak more intimately to the way that the research was done, but we would be remiss not to acknowledge that this work is part of a larger context, including scientists such as Stefano Mancuso at the University of Florence (plant communication), Monica Gagliano at the University of Western Australia (plant learning and memory), Suzanne Simard at the University of British Columbia (communication and resource sharing in plants), and Susan Dudley at McMaster University (kin recognition in plants).

One plant with a behavioural response unusually obvious to human eyes is *Mimosa pudica*, the sensitive plant. When touched, it responds by closing its leaves. This is widely thought to be a defensive strategy, a way of hiding from or otherwise deterring leaf herbivores such as insects and grazing mammals. However, this strategy has costs for the plant.

The plant's ability to photosynthesize and produce food is greatly reduced when the leaves are closed, since the plant is hiding from the sun as much as it is hiding from herbivores. We knew that the amount of time that individual *Mimosa* plants take to reopen their leaves varies, so we wanted to ask under what circumstances the leaves would stay hidden for longer. In studies of animal behaviour, we know that many animals frequently accept more risk of being eaten if they are starving. If an organism is starving, it will go where the predators are if the food is there. Conversely, organisms that are well fed will be more likely to avoid the risk of predation. If we view *Mimosa pudica* leaf-closing behaviour as avoiding predation risk, we can use theory from animal behavioural ecology to make predictions about when they should hide for longer. Since plants obtain energy from light, we could make the behavioural prediction that if a plant is very "well fed" under high light conditions, it will hide for longer. If the plant is "starving" in low light conditions, however, it would reopen quickly since it has greater energy requirements.

Besides the reduction in photosynthesis, there is another cost to the plant of this behaviour, which is that reopening the leaves after closure requires energy. A more conventional prediction based on plant physiology would be that since reopening the leaves

takes energy, plants would be able to reopen leaves faster under high light conditions because there is more energy available to do so. This illustrates an interesting case where using two different general approaches to understanding plants results in two very different, testable hypotheses.

To test this, we created high and low light environments and measured how long leaves took to reopen in these different environments. Our results showed that under high light, leaves reopened more slowly, therefore hiding for longer, as was predicted by behavioural theory.[4] Our findings were consistent with behavioural theory and inconsistent with more traditional understandings of plant biology. This is a prime example of why we, as plant scientists, are moving away from pure physiological predictions and approaches. This has led to a need for frameworks that allow us to incorporate both behaviour and physiology into our understandings of how plants work.

Most of the behavioural work we do in the lab looks at root systems. We want to understand what drives plants to place their roots in particular locations, because plants are capable of altering the distribution of their roots in response to their environments. Roots are essential for acquiring resources from the soil, so their placement has big consequences for plants, and there are obvious analogies to be made between how plants forage for resources and how animals search for food.

Studying root behaviour comes with a unique set of challenges: for one, dirt is dark, and it obscures the roots, so observing roots requires unique solutions. For another, a lot of behavioural theory is based on the idea of an organism with a single body and a single mouth. For plants, roots are the location of tens of thousands if not millions of root tips, all of which can acquire resources from their environments, and so act as "mouths" for the plant. They also serve as sensory organs, so while they are acquiring resources from the environment they are also detecting the environment. The roots also serve an essential structural purpose, anchoring the plant. The environments roots grow into are complex and contain other plant roots, enemies (such as predators and parasites), and potential allies (such as mycorrhizal fungi that may aid in nutrient uptake), as well as nutrients and other factors. Plants are unique organisms, and so we need to create new theories to understand them, but we can also borrow some pre-existing aspects of behavioural theory.

Many behavioural ecologists use the concept of "optimal foraging" as a framework for understanding animal foraging behaviour. The essential idea is that in acquiring food, animals make foraging decisions consistent with fitness outcomes. On a very basic level,

Sensitive plant, Mimosa pudica, native to central and south America. Handcoloured copperplate stipple engraving from Jussieu's *Dictionary of Natural Science*, Florence, Italy, 1837. Engraved by Corsi, drawn by Pierre Jean-Francois Turpin, and published by Batelli e Figli. Credit: Album / Florilegius.

we could predict that animals that are actively foraging should concentrate their efforts in areas where food is available, rather than where it is not. This concept also appears to hold true for how plants place their roots in soil. If we were to observe the roots of different individual plants in our garden and see how they responded to heterogeneity in nutrient concentrations in the soil, we would find a common thread: most plants put more of their roots where the food is (i.e., where nutrient concentrations are high) than in areas where nutrient concentrations are lower.[5] This makes sense from an evolutionary perspective, since plants that are better equipped to capture resources from their environment should be at an advantage. Like animals, given a choice, plants usually go where the resources are, although they usually accomplish this by changing the way they grow rather than by moving.

Behavioural theory also makes predictions about how animals should move around in an environment with patches of food. One prediction that comes from behavioural theory is that animals should spend more time in good patches with more resources than in lower-quality patches with fewer resources. This allows the animal to fully exploit the patch before moving on. This prediction is based on a mathematical model called the marginal value theorem,[6] but it also makes intuitive sense. We wanted to apply this concept to plants and ask what happens when a plant encounters a good-quality patch belowground: Do plants, like animals and humans, stop "looking" once they have found something?

We grew plants (a species named *Achillea millefolium*, or yarrow, which can be found distributed across the northern hemisphere) next to either a high-quality patch of soil or a low-quality patch. When we looked at how the roots grew over time, we found that plants in these two environments behaved consistently with animal behavioural theory. Plants grown next to high-quality patches did not grow their roots very far, while plants grown next to low-quality patches grew roots that extended far past the patch. In other words, plants that found food stopped exploring.[7] A more traditional concept of how plants grow would have predicted the opposite responses: with more resources, plants should have been able to grow more. As in the case with the leaf-closing behaviour in *Mimosa pudica*, this behavioural approach lent a different perspective that allowed us to better understand what was happening in these different environments. The animal-derived behavioural models are useful because they assume a rational player: natural selection. And natural selection has shaped plants as much as it has shaped the organisms that are more traditionally considered in the framework of behavioural ecology.

So far, we have discussed how plants behave when they are grown alone in the soil, but if our goal is to better understand the individuals in our garden, it is essential to understand the interactions between individuals—the social context that the plants make decisions in. Like us, plants can take multiple factors into account when they make decisions, and as with us, social interactions dictate much of their behaviour. This can be demonstrated by the way plants use information about both nutrients and neighbours to decide where to place their roots in the soil.[8]

In another experiment, we grew plants (*Abutilon theophrasti*, or velvetleaf, a common agricultural weed) in environments that either had a high-quality patch or homogenous soil, and with or without another plant in this soil. We found that this species did not respond to the high-quality patch in the same way as the yarrow plants did in the previous experiment. When grown alone, they grew their roots to the same spatial extent regardless of whether their roots encountered a good patch, effectively ignoring the patch. When we added a second plant to the homogenous soil environment, the plants responded by shortening the breadth of the root system and avoiding the other plant. What was striking was what happened when the plants were grown in environments with a high-quality patch *and* a neighbour. They displayed an entirely new foraging strategy wherein they grew roots into the patch and no longer avoided their neighbours to the same extent as when there was no patch between the two plants. We found that plants can integrate information about different aspects of their environment into new strategies, which implies a level of complexity in how plants perceive their environment and make decisions.

We conceptualize the way that plants place their roots in soil as the result of a decision-making process, which does not imply any cognitive abilities, but rather the ability to take in information about the environment and respond accordingly. We know that in human psychology and animal behaviour stressful events disrupt the ability to make good decisions—something most of us have learned from personal experience. Right now, we are asking whether this is true for plants too: Can stress disrupt the ability to make decisions in plants? We are using a stressful event (clipping the leaves of plants to simulate herbivory, which is a common stressor encountered by plants in nature) and observing the foraging behaviour of plants afterward to determine how stress affects these decisions. The results thus far indicate that these stressful events impact plants much like they do other organisms, including ourselves. Early evidence is suggesting that stress negatively affects the ability to make good foraging decisions in plants, a finding difficult to explain within the framework of traditional plant biology but with obvious parallels to animal psychology that should be explored further.

epilogue

What happens if we understand plants as individual organisms rather than factories? If we could understand how they find their food, could we modify our agricultural approach to take advantage of this knowledge? Could we be smarter in our fertilizer application so that there are less wasted resources, less run-off, less cost? Could we better understand how these behaviours impact larger patterns in biodiversity and other aspects of natural systems that we are interested in preserving?

And when we adjust our preconceptions about what plants are capable of, can we come to better understand these organisms that are so ubiquitous and so essential to our own success on this planet?

notes

1. Cahill Lab of Experimental Plant Ecology: https://grad.biology.ualberta.ca/labs/cahill/. James F. Cahill Jr. is a professor at the University of Alberta. Megan K. Ljubotina and Habba F. Mahal are graduate students in his lab.

2. Darwin, *Power of Movement in Plants,* 573.

3. Silvertown and Gordon, "Framework for Plant Behavior."

4. Jensen, Dill, and Cahill, "Applying Behavioral-Ecological Theory to Plant Defense."

5. Kembel and Cahill, "Plant Phenotypic Plasticity Belowground."

6. Charnov, "Optimal Foraging."

7. McNickle and Cahill, "Plant Root Growth and the Marginal Value Theorem."

8. Cahill et al., "Plants Integrate Information."

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