Are plants cognitive? A reply to Adams

Miguel Segundo-Ortin[a], Paco Calvo[b],*

[a] *Faculty of Law, Humanities and the Arts, University of Wollongong, Australia*
[b] *Minimal Intelligence Lab (MINT Lab), Universidad de Murcia, Spain*

HIGHLIGHTS

- Offers an empirically informed philosophical discussion of plant intelligence.
- Discusses crucial aspects of the nervous-like vascular system of plants.
- Explores important analogies between plant and animal behavior.

ARTICLE INFO

ABSTRACT

According to F. Adams [this journal, vol. 68, 2018] cognition cannot be realized in plants or bacteria. In his view, plants and bacteria respond to the here-and-now in a hardwired, inflexible manner, and are therefore incapable of cognitive activity. This article takes issue with the pursuit of plant cognition from the perspective of an empirically informed philosophy of plant neurobiology. As we argue, empirical evidence shows, contra Adams, that plant behavior is in many ways analogous to animal behavior. This renders plants suitable to be described as cognitive agents in a non-metaphorical way. Sections two to four review the arguments offered by Adams in light of scientific evidence on plant adaptive behavior, decision-making, anticipation, as well as learning and memory. Section five introduces the 'phyto-nervous' system of plants. To conclude, section six resituates the quest for plant cognition into a broader approach in cognitive science, as represented by enactive and ecological schools of thought. Overall, we aim to motivate the idea that plants may be considered genuine cognitive agents. Our hope is to help propel public awareness and discussion of plant intelligence once appropriately stripped of anthropocentric preconceptions of the sort that Adams' position appears to exemplify.

1. Extra! Extra! A new war on cognition!

Fred Adams begins his recent *Cognition wars* [this journal, 2018, vol. 68] by announcing that "there is a war going on over what counts as cognition" (p. 20). The conflict has two main battlefields. The first, a long-standing one, pertains to the discussion between what he calls 'the traditional view' in cognitive science—that is, the view that equates cognition with brain-bound processes—, and the theories of embodied (Varela, Thompson, & Rosch, 1991) and extended (Clark & Chalmers, 1998) cognition. The second battlefield is relatively newer and has to do with the kinds of organisms across phyla we deem to be cognitive. As Adams advances, a number of plant scientists and bacteriologists have recently informed us that plants and bacteria do behave in a cognitive or intelligent way. He focuses on this second battlefield, promising to evaluate both the scope and plausibility of such claims.

After analyzing different instances of behavior in plants and

bacteria, Adams concludes that scientists that call such behaviors cognitive must mean something entirely different by 'cognition'. When scientists say that plants and bacteria 'learn', 'decide', or 'choose', they necessarily mean something different to what we mean when we say, for instance, that 'Anna chooses water instead of beer'. Plants and bacteria, he suggests, respond to the here-and-now in a hard-wired, inflexible manner, meaning that they are incapable of cognitive activity. Thus, attributing cognitive abilities to plants and bacteria is a profound mistake, unless such attributions are figurative or metaphorical:

> The use of cognitive terms by plant scientists and biologists who study plant and bacterial behavior, is likely being used because there is no better term for what these scientists have discovered, namely, that these organisms use informational exchanges with the environment and other cells in the organism to guide and control behavior. That is, they are systems whose behavior is

* Corresponding author. MINT Lab, Departamento de Filosofía, Edif. Luis Vives, Campus de Espinardo, Universidad de Murcia, 30100, Murcia, Spain.
E-mail address: fjcalvo@um.es (P. Calvo).

informationally driven. … It is for that reason that these scientists are taking what Dennett (1987) has called the "intentional stance" towards these organisms. Taking this stance is perfectly harmless if one is using it as a mere heuristic device or metaphor, but if one intends the cognitive ascriptions to be true, then it is not harmless. (p. 30)

In this Discussion, we aim to show that Adam's conclusions with regard to this matter are unfounded. [1]

To keep the record straight, we agree with Adams that inflexible, hard-wired reactions to current environmental stimuli are not interesting from a cognitive science perspective. Yet recent empirical discoveries suggest that the behavioral repertoire of plants (and bacteria, for that matter)[2] contains much more than hard-wired reflexes. Plants appear to behave in ways that are adaptive, flexible, anticipatory, and goal-directed (Calvo, 2018). Taking this into account, we argue that plant behavior is in many ways analogous to animal behavior, meaning that plants are suitable candidates to be described as cognitive agents in a non-metaphorical way.

Survival mandates that organisms must explore the environment and secure life-sustaining resources. Although sessile, plants are no exception. To accomplish this need, plants have evolved different foraging strategies, and sensitivity to a variety of environmental cues, that we can appreciate as part of their vast behavioral repertoire (Silvertown & Gordon, 1989). Put somewhat differently, plant behavior takes the idiosyncratic form of 'phenotypic plasticity', courtesy of cell elongation, among other tricks in their bag (Calvo, 2018; Trewavas, 2014, 2017).

Overall, we aim to motivate the idea that plants may be considered cognitive agents. To do so, our discussion is divided into five sections. The first three deal respectively with the notions of adaptive behavior and decision-making; anticipation; and learning and memory. In this first part, we discuss specific claims made by Adams regarding the alleged lack of cognitive abilities in plants. We shall move on then to introduce the interested reader to the 'nervous' system of plants in the context of the emerging field of Plant Neurobiology (Calvo, 2016). We end up by re-situating the quest for plant cognition into a broader approach in cognitive science, as represented by (post-cognitivist) embodied, enactive and ecological schools of thought.

2. On adaptive behavior and decision-making

Traditionally, plant behavior has been interpreted as purely reactive and mechanical; that is, as an overt manifestation of hardwired instincts triggered by environmental stimuli. Adams explicitly shares this view. As he suggests, plants are no more sophisticated than a garage door equipped with a presence detector. In the presence of a sufficiently large object, the sensor triggers, causing the mechanism that closes the door to stop automatically. This behavior, Adams argues, can be said to be informationally-driven, caused by the detection of a relevant environmental condition, but is not cognitive:

Some plants detect drops in temperature and this causes the leaves to fold, only to reopen when the temperature climbs. This is a kind of sensor, and it is coupled with processes that close and open the leaves (no less than closing the garage door). But the plant thinks

not, cognizes not (the same as the garage door). (p. 28)

Scientific evidence, however, calls doubts upon this received view. To begin with, plant behavior can be directional (e.g., phototropic sun-tracking) or non-directional (nastic responses such as the folding of some plant leaves, or the closing of the traps of some carnivorous species). Such responses can also be positive or negative. For instance, whereas roots are photophobic (Burbach, Markus, Zhang, Schlicht, & Baluška, 2012) and exhibit negative phototropic behavior, they are positively geotropic, growing downwards. Shoots, by contrast, generally grow away from the gravity vector, and towards light sources.

It does not mean, however, that plants react to gravity or light on a one-by-one basis—that is, by producing automatic responses to individual sources of stimulation. As a matter of fact, multiple experiments show that plants can sample and integrate over 20 diverse biotic and abiotic parameters. These parameters are continuously monitored by plants with an eye to deciding how to behave adaptively (Hodge, 2009; Baluška & Mancuso, 2009; Karban et al., 2014; Karban, 2015).

Plant roots, for example, are sensitive to many environmental cues, including gravity, water, minerals, chemicals and alien roots (Baluška et al., 2006; Yokawa & Baluška, 2018). It is by combining information from these multiple vectors that plants can maximize their fitness, eliding responses that involve structural changes at the level of their physiology, morphology, and phenotype.

For illustration, consider salt-avoidance behavior, as performed by the root apparatus. Because salinity is a major constraint for plant growth (a high concentration in the substrate below ground can disrupt rather dramatically cellular biochemistry), roots have evolved sensitivity to abnormal saline conditions, being able to adapt their growth accordingly. Li and Zhang (2008) tested this capability in *Arabidopsis thaliana*, the model lab plant *par excellence* (see also Sun et al., 2007; Yokawa, Derrien-Maze, Mancuso, & Baluška, 2014). Li and Zhang set up a two-layer medium in a growth bottle, putting a normal nutrient agar medium at the top, and a salt-stressed agar medium at the bottom. As expected, the roots of seedlings started to grow straight downwards exhibiting a positive gravitropic behavior. However, as soon as the level of NaCl became slightly higher, the roots of seedlings curved and grew upward toward the medium with lower levels of salt. Interestingly, roots started to bend upward even before contacting the high-salt medium (250 mM NaCl) of the bottom, which, according to Li and Zhang, indicates "that roots can sense ion gradients in the growing environment and … make decisions that enable roots to stay away from high salt" (2008, p. 352).

In a series of experiments with *Pisum sativum*, the garden pea, Dener, Kacelnik, and Shemesh (2016) have demonstrated that root growth can also vary with respect to temporal variance in nutrient availability. For their experiment, Dener and colleagues used split-root pea plants—that is, plants whose primary root tips are cut off, so that lateral roots can develop from the incision zone and grow in separate containers. One pot received constant and the other one variable nutrient concentration. What they found is that when the nutrient concentration in the first pot was sufficient for the plants to meet their metabolic needs, they grew more roots in this pot. However, when the concentration of nutrients was not enough for the plant to survive, plants allocated more biomass in the second pot—the one receiving the variable nutrient concentration. For Dener and colleagues, it suggests that plants "respond strategically to patches varying in their average of nutrient availability" (p. 1765), switching between risk-prone and risk-averse behavior as a function of resource availability. Commenting on this experiment, Schmid (2016) claims that it indicates that "theories of decision making and optimal behavior developed for animals and humans can be applied to plants" (p. R677).

Moreover, resources are often sparse, and organisms have to compete for them. To do so, plants have evolved the ability to detect the presence of others, developing different responses accordingly.

Cahill et al. (2010) measured patterns of root growth of *Abutilon*

---

[1] To build his argument, Adams relies on Ben-Jacob (2009), Calvo Garzón and Keijzer (2009), Calvo Garzón (2007), Lyon and Keijzer (2007), Trewavas (2003). In what follows we shall take issue with Adams' charges from an empirically informed philosophy of cognitive science perspective.

[2] For the sake of concision, our reply focuses exclusively upon plants, although the line of response to be rehearsed herewith applies, *mutatis mutandis*, to the case of bacterial cognition (see, for example, Baluška & Levin, 2016; Hung, 2017; Tagkopoulos, Liu, & Tavazoie, 2008; and; Westerhoff et al., 2014). For a review of the early history of intelligent behavior in bacteria, see Jennings (1906).

theoprasti, an annual plant from the Malvaceae family, while manipulating both competition and resource distribution. Exemplars of *A. theoprasti* were planted into six combinations of soil, depending on heterogeneity (uniform, patch-center, and patch-edge) and competition conditions (alone and with a competitor). In all treatments, individuals were planted on opposite sides of the pot. Cahill and colleagues reported different foraging behavior depending on the conditions. When plants grew alone, they displayed both maximum root distribution and maximum rooting breadth. This was so independently of how resources were distributed. When a competitor was present, by contrast, plants adopted restricted foraging strategies (different root distribution and breadth), depending on the allocation and distribution of resources. For Cahill and colleagues, these results suggest that root placement in *A. theoprasti* is determined by the non-additive combination of information regarding the neighbor presence and resource distribution.

Likewise, Trewavas (2014) reports that when young exemplars of *Calamagrostis canadiensis*, a species of wetland grass commonly known as 'bluejoint', are offered adjacent habitats to grow, they choose the habitat with the best conditions of competition, warmth, and light. Moreover, he mentions, *C. canadiensis* "also discriminate these conditions in combination … choosing light plus warm soil in preference to others" (p. 84).

Light foraging and competition also offer a good case study. Gruntman, Groß, Májeková, and Tielbörger (2017) conducted a series of experiments with *Potentilla reptans*, a clonal plant in the Rosaceae family. In clonal plants, light competition is well-known for eliciting three types of phenotypic responses: shade avoidance, shade tolerance, and competition-avoidance. Shade avoidance responses typically involve morphological adjustments that result in vertical growth, thereby allowing the plant to position its leaves in conditions of higher light exposure. Shade tolerance responses, instead, involve morphological changes that promote plant performance under limited light conditions. These morphological changes typically involve an increase in leaf area. Finally, competition-avoidance responses typically involve horizontal spread.

Gruntman et al. (2017) built an experimental setup that simulated three different light competition settings. The first one simulated similarly sized and dense neighbors, which can be outgrown vertically but offers limited advantages of horizontal growth. The second one simulated tall, dense neighbors, offering limited advantages of either vertical or horizontal growth. The third one simulated taller but sparse neighbors, which cannot be outgrown vertically but offers higher light availability in the horizontal direction.

They found that *P. reptans* can tailor its phenotype according to the relative stature and densities of their opponents. When subjected to the first setting, plants displayed the highest vertical inclination—viz., the highest height-per-diameter ratio. When subjected to the second setting, by contrast, plants exhibited a lower vertical inclination, but the highest leaf area. Finally, exemplars under tall and sparse neighbors displayed low levels of vertical inclination and leaf area, but longer stolons.

Taking stock, as the previous examples illustrate (but see Trewavas, 2014, 2017, and references therein, for many other examples), we can see that plants' interactions with the environment need not be automatic responses to single cues. Plants sample different informational vectors, and respond flexibly by adapting both their morphology and their phenotype to increase energy intake and efficiency. Crucially, to repeat, plants can respond not just to the particular magnitude (and direction) of a given environmental variable, but also to its temporal and relational profile with respect to other variables (Silvertown & Gordon, 1989). Bluntly put, this is anything but unsophisticated 'garage door' behavior.

A note of caution is needed, though. The possibility that plants combine information in a pairwise fashion (e.g., gravity vector vs. light; minerals vs. salt concentration; etc.) cannot be discarded beforehand. The fact that plant behaviors are not automatic responses to single cues

(e.g., salt concentration together with gravitation accounts for partly geotropic responses) is compatible with the alternative hypothesis that plants are able to separate the cues linearly and, in this case, simply allow salt, if present in high concentrations, to override the gravitational cue. If that were the case, the analogy between plant and animal behavior would appear unjustified. But, by the same token, it cannot be discarded that the stream of sensorial information is being integrated and assessed in a richer, contextual manner. Complex configurations of stimuli may need to be discriminated, if the flexible capacities of plants are to be accounted for.

In sum, more research is needed to distinguish those cases of plant behavior where we may resort to relatively simple rules from those that defy a linear separation of the problem space. Our point is simply that, considering what we know empirically, it is not clear that we can dismiss the hypothesis that plants behave in cognitive manners, as Adams does.

3. On anticipatory behavior

Anticipation is another relevant feature of cognition, according to Adams (2018), and we cannot but concur. As he writes, "[i]f a system has the capacity to anticipate what is going to happen in its environment, that sounds like the right kind of capacity to be a cognitive capacity" (p. 26). He doubts, however, that plants are capable of doing so, and we cannot but disagree. Considering (metabolically speaking) how costly mismatches can be for organisms whose decisions take the form of development and growth over long periods of time, and whose changes can be flexible but sometimes also irreversible, plants cannot afford *not* to be able to anticipate the future.

Although one of us (PC) has recently discussed plant anticipatory behavior at length elsewhere (Calvo & Friston, 2017), in his treatment, Adams borrows a previous example from [Calvo] Calvo Garzón (2007), and so we shall get started with Adams' preferred example before we submit to the reader's consideration some of the more recent literature.

Echoing Schwartz and Koller (1986), Calvo Garzón and Keijzer (2009) reported that leaf laminas of *Lavatera cretica*, a species of flowering plant in the Mallow family, reorient during the night in order to face the direction of sunrise ahead of time.[3] Heliotropic nocturnal reorientation constitutes a complex off-line response, and shows that *L. cretica* "can, not only anticipate the direction of the sunrise, but also allows for this anticipatory behavior to be retained for a number of days in the absence of solar-tracking" (Calvo Garzón and Keijzer (2009), p. 210).

For Adams (2018), however, it is misguided to interpret heliotropic nocturnal reorientation as a complex off-line (cognitive) response. In his own words: "I fail to see why [this behavior] would constitute *the right sort* of "anticipation" … to be within the domain of the cognitive" (p. 26, emphasis added).

But, why isn't the offline nocturnal reorienting behavior of *L. cretica* leaves an instance of cognitive anticipation? Adams offers no clear answer to this question. Instead, he shifts the focus from the behavior itself to its underlying causes. As he asserts, whether leaf orientation is cognitive "will depend on what kind of mechanism is involved in the so-called "anticipation", and how it is processing information" (p. 26). As he argues, there is a form of anticipation that is full-blown cognitive, and this is so because it involves future-oriented representations (p. 26). Since *L. cretica* don't have, presumably, these kinds of representations, it follows that its anticipatory behavior is not cognitive.

---

[3] This allows *L. cretica* to optimize sunlight intake whilst avoiding devoting metabolic resources that are needed for other physiological processes that take place before dawn (Kreps & Kay, 1997). Although Adams only cites [Calvo] Calvo Garzón (2007) in this regard, the interested reader may care to consult a somewhat more recent elaboration of the *L. cretica* example in García Rodríguez and Calvo Garzón (2010).

Yet we must be cautious here. On the one hand, we have the question of whether plants can anticipate what is about to happen in the environment. The issue here is whether the empirical evidence we have supports this view. On the other hand, we have the question for the mechanisms that underlie such anticipations. This is an entirely different issue, as it pertains to what best explains the anticipatory capabilities of plants, if any.

In his analysis, Adams conflates both issues, and infers that plants' anticipatory behavior is not cognitive because it does not involve cognitive representations.[4] By doing so, however, Adams is conflating *explanandum* and *explanans*, begging the question against non-representational theories of cognition; theories that have been proposed in the past together with representational ones (Calvo, 2016; Calvo, Baluška, & Sims, 2016).

To avoid this fallacy, we recommend addressing both issues separately. In what follows, we explore the first issue. Our goal here is to motivate the view that plants do indeed behave in an anticipatory manner.[5]

Anticipatory capabilities have been tested more recently at the root level with pea plants. As reported by Novoplansky (2016), young pea plants grow different roots if subjected to variable, temporally dynamic, and static homogeneous and heterogeneous nutrient regimes. When given a choice, plants not only develop bigger biomasses in roots located in richer patches; in fact, they discriminately allocate more resources to roots that develop in patches with *increasing* nutrient levels. More strikingly, they do so even if these patches are poorer in absolute terms than the others. According to Novoplansky, "[t]hese findings demonstrate that rather than responding to absolute resource availabilities, plants are able to perceive and integrate information regarding dynamic changes in resource levels and utilize it to anticipate growth conditions in ways that maximize their long-term performance" (p. 63). Pea plant roots, so the evidence suggests, do not grow in a blind, hardwired way. Instead, their growth is sensitive to relative values of resource availability, and is conditioned by the *future* availability of nutrients.

This and other examples have led some theorists to conceive of plants as proactive, 'anticipatory engines' (Calvo et al., 2016; Calvo & Friston, 2017). According to this view, plants are constantly monitoring gradients and *guessing* ahead of time what the world is like. These predictions enable them to minimize surprise in pretty much the same way as animals do, and to adapt to the local conditions via phenotypic plasticity.

It goes without saying that the interpretation of plants as anticipatory engines is still a long shot from equating their behaviors with, for instance, the *planning* of the western scrub-jay corvid (*Aphelocoma californica*). With an eye to provisioning itself for future needs, this corvid can even store away types of foods in hiding places where they can be retrieved at will as it becomes hungry the following day (Raby, Alexis, Dickinson, & Clayton, 2007). Again, more research is needed before we can conclude that, for example, the dynamic foraging behavior of pea plants—whose roots would anticipate growth conditions and develop bigger root biomasses in patches with an increasing amount of nutrients (Novoplansky, 2016)—can be interpreted along similar lines, as opposed to being explained by appealing to chemotactic signal integration, as has been done in bacteria (Khan, Spudich, McCray, & Trentham, 1995).

We advocate that those interested in the debate over plant cognition take into serious consideration the need to inform theoretical discussion with tools, such as time-lapse photography, that have the potential to unearth *patterns* of behavior. Generally speaking, plants' responses are markedly slower than those of animals. From this, we run the risk of concluding that plants cannot stand up to animal comparison (e.g., "reflexes, escape, arousal, attack, and recognition"—Silvertown & Gordon, 1989, p. 362), only to find out that the methodologies and tools of observation were inappropriate for the model organism in question, provided the very idiosyncratic nature of their responses.

4. On learning and memory

Relying on Firn (2004) and [Calvo] Calvo Garzón (2007), Adams advocates for a skeptical position toward the possibility of learning in plants. As he argues, "the term 'learn' cannot mean the same thing in the mouth of a plant scientist as it means when used by the animal-learning theorist" (p. 21). For him, what plant scientists call 'learning' is more accurately described in terms of mutations—viz., changes in the genotype of the plant. This sort of learning, he adds, is not of the same kind as the one we find in human and non-human animals, "who learn in their lifetime and not at the level of the genome" (p. 22).[6]

Recent empirical evidence, however, contradicts this view, suggesting that plants enhance their chance of survival by modifying their behavioral repertoire through learning and memory processes.

The sensitive plant *Mimosa pudica*—a species that is well-known for its capacity to fold its leaves when disturbed—is the best-studied model for habituation, a form of non-associative learning. Experimental results date back to Pfeffer (1873) and Bose (1906). The former showed how the leaflets would diminish their folding response to a frequently repeated mechanical stimulus. Bose, in turn, extended Pfeffer's insights to electrical stimuli, showing that the leaflet folding response could be likewise triggered electrically, and not just mechanically (for a review of the history of learning in plants, see Abramson & Chicas-Mosier, 2016).

More recently, Gagliano, Renton, Depczynski, and Mancuso (2014) have studied habituation in *Mimosa* in the context of light foraging and risk predation. Applying the theory and methodology of animal learning research, Gagliano and colleagues subjected exemplars of *Mimosa* to repeated 15 cm falls. Although harmless, these stimuli were enough to cause leaves to fold. The goal of the experiment was to test whether *Mimosa* plants can detect that a repeated stimulus is harmless, ignoring it in subsequent interactions. Like Pfeffer had done a century earlier, Gagliano and colleagues demonstrated that leaf-folding behavior exhibits habituation, and this habituation is responsive to environmental conditions. Their research appears to confirm that *Mimosa* can learn from past interactions; indicating, in addition, that the studied exemplars developed more efficient responses—responses for the sake of minimizing energy waste and optimizing light foraging. Leaf-folding habituation, the study shows, is more pronounced and persistent for exemplars growing in energetically costly environments.[7] Finally, and more shockingly, they found out that this habituated reflex lasted for up to 28 days, which demonstrates the acquisition

---

[4] Adams is particularly clear on this matter. As he argues, commenting on Lyon (2006), "if she has in mind the kind of mechanism in plants and other organisms that drive their behavior but in ways that don't involve cognitive level representations, then I wonder why the term "cognition" is being used literally, not metaphorically" (p. 26).

[5] Reasons of space prevent us from exploring the second issue—'Is the anticipatory behavior of plants best explained by positing cognitive representations?'—, but see García Rodríguez and Calvo Garzón (2010) for an elaboration of the idea that architectural constraints *per se* do not entail that cognition is a matter of representations.

[6] Other philosophers have shown similar skepticism on this matter. Tye (1997), for example, asserts that "[t]he behavior of plants is inflexible. It is genetically determined and, therefore, not modifiable by learning. Plants do not learn from experience" (p. 302). In a similar vein, Sterelny (2005) argues that changes in the behavior of plants are best explained as the results of mutation at the level of lineage. If that is the case, there is nothing such as learning at the level of the individual—that is, learning as consequence of past interactions with the environment.

[7] For the experiments, exemplars of *Mimosa* were randomly assigned to one of the two environments, one with high light (HL) and the other with low-light (LL) conditions. After seeing that a single drop did not elicit any behavior at change, experimenters subjected both groups of plants to a series of seven consecutive trains of 60 drops, each at either 5 or 10 second intervals. They discovered that leaves started to re-open even before the first train of drops was delivered entirely, and that leaves had stopped closing by the end of the first train. They also discovered that the leaf-folding reflex habituated more rapidly under LL, suggesting that leaf-folding reflex habituation is sensitive to the environmental conditions.

and expression of a long-lasting memory in *Mimosa*.

And yet, however intriguing the behavior of *Mimosa* happens to be—the possibility to study its behavior to the naked eye, as in the case of the Venus flytrap and other carnivorous species, has certainly contributed to its dissemination— plant learning is not limited to simple habituation. More sophisticated forms of learning, including Pavlovian classical conditioning, have been reported in *Mimosa* exemplars (Holmes & Gruenberg, 1965), as well as in other less *flashy* species.

Although in the case of the *Mimosa* studies researchers were unable to confirm the presence of classical conditioning (Holmes & Yost, 1966), recent research on the garden pea (*Pisum sativum*) has tested, successfully, the ability to learn by associating significant cues.

Gagliano, Vyazovskiy, Borbély, Grimonprez, and Depczynski (2016) employed a classical conditioning paradigm where the airflow produced by a fan (the conditioned stimulus) was predicted by the occurrence of blue light (the unconditioned stimulus). Training took place inside a custom-designed Y-maze such that the pattern of growth of pea seedlings could be studied as the exemplars approached the Y-bifurcation, and grew either toward one arm or the other. Their results show not only that *P. sativum* can anticipate the occurrence of a biologically significant event by relying on related environmental cues, but also that they can adapt their phototropic behavior by associating a neutral factor—the presence and position of the fan—with the occurrence of light.

In particular, plants were randomly assigned to two different groups. In one group, exposure to light (L) and fan airflow (F) was on the same arm of the maze (L + F), whereas in the other group L and F were on opposite arms (L v F). The experiment tested for both a positive association of F with L, resulting in the plant seeking out F as a predictor of L, and a negative association, resulting in the plant avoiding F. They found out that the majority of seedlings exhibited a conditioned response to the fan. In the F + L group, 62% of the seedlings grew towards the fan, whereas in the F v L group, 69% of the seedlings grew in the direction opposite to the fan.

This empirical data appears to contradict Adams' (2018) views on plant learning.[8] As we have seen, plants can learn in their lifetime, and they can modify their behavioral repertoire on the basis of past events and interactions. Both associative and non-associative forms of learning are ubiquitous in the animal kingdom, and the fact that plants are capable of both reinforces our thesis that plants ought to be considered as cognitive agents (see Baluška et al., 2018, for the most recent review of plant learning and memory).

With that being said, one could argue that it is premature to assume that Gagliano's experiments on associative learning in pea plants are to be interpreted alongside conditioning experiments in the animal literature. For one thing, typically, classical Pavlovian conditioning is the one and only behaviorist perspective that the plant science community takes into account. But other forms of behaviorism could well bring new light to the discussion of plant learning. Some neobehaviorists make use of intervening variables (see Abramson & Calvo, 2018 and references therein). In fact, altering the meaning of stimulus and response can result in the merging of cognitive and neobehaviorist approaches (Denny, 1986).

One way or another, closer attention to ecological conditions and experimental replication (a commodity nowadays, Grice, Barrett, Schlimgen, & Abramson, 2012) will certainly shed light upon the dispute. As Affifi (2018) observes:

> If Gagliano et al. (2016) experiment is replicated and associative learning by pea plants triangulated in laboratory settings, we should

take these conditioning experiments out to field settings. […] Where and how conditioning breaks down (if it breaks down) would provide important insights into the nature of plant intelligence. (p. 30)

Next, we would like to call into question one more aspect of Adam's analysis. As he warns us, "if one attributes cognition […] to plants, one must be prepared to find the mechanisms to support such attributions. But I would add that those mechanisms as well must share some similarities, if only in the ways in which they process information or the levels of information processed" (p. 21). In what follows, we take issue with the all too thorny issue of the 'nervous' system of plants.[9]

5. The 'nervous' system of plants

As we saw, plants can navigate multiple vectors, producing flexible and context-dependent responses. This ability, Trewavas (2005) argues, calls for the integration of information among the different plant structures. Finding the signaling mechanisms that underlie such cognitive abilities is the target of the emerging field of Plant Neurobiology (Baluška, Hlavacka, Mancuso, & Barlow, 2006; Calvo, 2016).

We are well aware that speaking of plant *neuro*biology can, and indeed has generated a good deal of controversy in the past (Alpi et al., 2007; Brenner, Stahlberg, Mancuso, Baluška, & Van Volkenburgh, 2007; Trewavas, 2007). Although it is undoubtedly true that plants do not have neurons (and synapses) that could give rise to a 'brain' or a 'nervous' system, they respond electrically to many different environmental factors. Plants possess cells capable of electrical signaling and transmission; that is, cells that are functionally equivalent to animal neurons. Plant neurobiologists refer to these cells as "phytoneurones," and to the research area as "phytoneurology" (Calvo, Sahi, & Trewavas, 2017).

Moreover, it is important to note that although plant excitable cells lack axons-like structures, they are capable of producing and supporting action potentials (APs), akin to animal ones (Baluška & Mancuso, 2009) as well as variation potentials (VPs)—this time, specific of plant cells—among other sorts of electric, as well as hydraulic and chemical, signals that have been unearthed only in recent years (Huber et al., 2016; Souza, Ferreira, Saraiva, & Toledo, 2017).[10] These electric potentials are propagated in the membranes of plant cells, being transmitted along vascular conduits distributed throughout the whole plant body, courtesy of a complex network of bundles of phloem, xylem and cambium (Fromm & Lautner, 2007; Trebacz, Dziubinska, & Krol, 2006). Overall, this electrical transmission is crucial for plants, as it underlies their ability to respond in a fast and yet coordinated manner to environmental contingencies (Baluška, Mancuso, Volkmann, & Barlow, 2010; Trewavas, 2014).

An important debate, in relation to one of Adams' lines of resistance, pertains to the form that a plant's phyto-nervous system can take. Remarkably, plant anatomy and electrophysiology reveal that phytoneurones are highly cross-linked, forming complex stacks of interconnected bundles akin to the cellular networks we find in the nervous sytems of invertebrates (Volkov, 2012, 2013).

Consider the *Papaya* tree, to take an illustration from Indian physicist,

---

[8] The careful reader will have noted that "the majority of seedlings exhibited a conditioned response" could be interpreted as a bit of an overstatement. After all, the number of seedlings that responded to F in the absence of L is only slightly more than half. However, as Gagliano explains (personal communication), it should be noted that an expectation of 50:50 (random choice) is not the baseline of reference, as the natural behavior of pea seedlings is to grow in the direction in which L was experienced for the last time. When provided an *ecological* baseline, the results are consistent with the associative learning hypothesis.

[9] Thorny to the extent that even Gagliano, a firm advocate of plant cognition, comments: "To insist on using [neuro-talk] for plants is like to insist that plants must fit in the animal-like model. So, it seems a little contradictory to then say that plants do their thing their way […] plants and animals are indeed very different in structures but functionally may not be so different. Applying such a word to plants is to rob them of their own unique way of doing their thing" (personal communication).

[10] APs and VPs relate to non-damaging and to damaging stimuli, respectively. In the case of APs, and despite the lack of axonal projections in plant cells, information is transmitted electrically in a wavelike manner (Choi, Hilleary, Swanson, Kim, & Gilroy, 2016). The initiating signals known to induce the spread of waves of depolarization include physical damage, leaf and fruit removal, rapid and stressful variations in temperature, changes in light, or mechanical stress from bending, to name but a few. In the case of VPs, these can be induced by herbivore predation, heat or wounding, for instance.

Fig. 1. Distribution and network of vascular tissue in a single stem layer of Papaya. According to the text in the script, there are 20 such layers of vascular tissue, one inside the other (like Russian dolls) and surrounding the whole trunk. The bundles are connected through enormous numbers of tangential connections and perhaps anastomoses to form a complex excitable structure. "The existence of a system of nerves enables the plant to act as a single organized whole" - a requirement perhaps for selection on fitness (From Calvo, Sahi and Trewavas 2017b - Figure and quote taken from Fig. 54, page 121,; Bose, 1926).

and father of the field of plant electrophysiology, J.C. Bose. From his (unfortunately) largely ignored *The Nervous Mechanism of Plants*, a book that dates back to 1926, we learn that the vascular system (Fig. 1) of the *Papaya* tree consists of vascular elements cross-linked by numerous, irregularly distributed, tangential connections. In mature stems and trunks, this vascular architecture becomes very complex, showing tangential connections and anastomoses (cross-links) between numerous bundles, forming a complex, *reticulated* system. This vascular system, originally thought to mediate exclusively the transport of water and nutrients, allows plants to coordinate their behavior, with electric signaling occurring over long distances through the vascular bundles (see Calvo et al., 2017).

Gagliano et al. (2016) speculate as to the physiological and molecular mechanisms that underlie associative learning, as exemplified by pea plants; epigenetic reprogramming, being one key factor (Thellier & Lüttge, 2013). Understood, as in the Papaya case, as a neural-like network for the sake of information-processing, we can easily see how to move on from plant physiology to plant 'psychology'. For illustration, consider the case of learning.

It is well known that synaptic modifiability underlies animal learning (Hebb, 1949). Interestingly, despite the lack of neurons, it is easy to see how the same functional principles apply to the information-processing network of Papaya, again under epigenetic principles of the sort deployed by non-neural systems, more generally (Ginsburg & Jablonka, 2009). To cut a long story short, plant learning can take place courtesy of a phyto-neural network in which 'plant synapses' can be modified as a result of experience.[11] Information can thus flow selectively throughout the vascular system of plants (for a clear-cut parallelism between plants and neural networks in learning, see Trewavas, 1999). As Trewavas (2014) puts it:

> Just as the process of learning in a brain could be represented as a time series, a set of snapshots of developing brain connections, in plants, each snapshot may possibly be represented by developing plasmodesmatal connections or equally, successive new tissues. So, instead of changing dendrite connections, plants form new networks by creating new tissues, a series of developing brains as it were (p. 14).

---

[11] Baluška et al. (2004) consider "acting-based asymmetric adhesion domains specialized for rapid cell-to-cell communication which is accomplished by vesicle trafficking" (p. 9) to be the functional equivalent of the animal synapse. For a survey of many other functional similarities between plant cells and animal neurons, see Baluška (2010).

Having a substrate that is functionally equivalent to a nervous system of animals, and in line with the aforementioned considerations, we submit to the readers' consideration the working hypothesis that plant cognition could possibly be realized, at least in part, in such a phyto-nervous system. We say "at least in part" because, following recent post-cognitivist trends in cognitive science (Calvo and Gomila 2008; Robbins and Aydede 2009), we do not think that (animal) cognition is realized in the nervous system *alone*. Instead, we think that cognition occurs across the brain-body-environment triplet. Applying the same rationality, we hypothesize that plant cognition happens across their own green triplet: phyto-neuronal structures, plant body, and environment.

6. Resituating cognition

Why is the quest for plant cognition relevant? Throughout his article, Adams (2018) repeats that there is no adequate, unified notion of cognition that fits both the behavior of humans and the one of plants (and bacteria). In his own words: "I fail to see that there is such a common core or that the explanation of these 'basic behaviors' will yield a unified account of cognition that will cover equally the behavior of bacteria [and plants] and humans" (p. 29). If so, accepting that plants are cognitive implies using the word 'cognition' in equivocal ways—we must mean one thing for humans, and other for plants.

To bypass this problem, and in the absence of this unifying account, Adams suggests to restrict the use of the term, distinguishing between information-driven behavior and cognition, proper.

But, how does information-driven behavior differ from cognitive behavior? The difference, Adams argues, relies on the kind of cognitive mechanisms involved in both. For him, cognition only comes into play when the system is able to exploit representations—that is, mental states that are subjected to semantic evaluation, namely, that can be true or false, accurate or inaccurate, veridical or non-veridical, and so on. Such representational states, he argues, take the form of propositional attitudes—e.g., beliefs, desires, thoughts, hopes, etc.—, and require the mastery of concepts. In light of this, he concludes, "since [plants and bacteria] lack beliefs or concepts—the higher-level, discriminating representations associated with genuine knowledge—what they do isn't really cognition" (p. 23).

This position is nonetheless problematic. To begin with, there is no reason to suppose that cognition depends on having conceptual-level, semantically evaluable representations. To do so, we argued before, is simply to beg the question against non-representational theories of cognition.

Secondly, this approach to cognition seems overly demanding, for even if we assume that human beings are capable of conceptual competence, we can rationally wonder whether this capability spans to non-human animals. Thus, by positing conceptual representations as the *hallmark* of cognition as Adams does (p. 25), we run the risk of advancing important (and undue) limitations to our cognitive science, leaving out of consideration all forms of sophisticated behavior that we find in the animal and plant kingdoms, and restricting the domain of the cognitive to human beings exclusively.

Adams appears effectively to fall prey to Morgan's canon; an appeal to parsimony in comparative psychology that, although once upon a time a commandment, is increasingly being called into question from all quarters of the cognitive science community. In fact, we can say that Adams is swimming against the stream of contemporary research in comparative cognition in this respect (Allen, 2017; Andrews, 2015; Buckner, 2017; Calvo, 2017; Figdor, 2018).

Contra Adams, we propose to go a step further and call into question, not only anthropocentrism, but also zoocentrism. To do so, we suggest the adoption of an approach along the lines of enactivism (Di Paolo, Buhrmann, & Barandiaran, 2017; Thompson, 2007; Hutto & Myin, 2013, 2017) and ecological psychology (Gibson, 1979/2015;

Chemero, 2009). Going this direction, we put the emphasis on agency and adaptivity instead of conceptual competence, and we conceive of cognition primarily as intelligent behavior—that is, as the capability of organisms to actively interact with the environment in adaptive, flexible and sophisticated ways so as to maintain their systemic autonomy.

From this perspective, a cognitive system is an autonomous, open system that explores the environment to meet its own needs and goals, instead of simply reacting to the external impingements, and that is capable of actively regulating its sensorimotor coupling in context-sensitive ways. Complex intelligent behavior, according to this view, needs not complex forms of cognition such as the ones posited by Adams (2018).

Importantly, the ecological-enactive approach invites us to think of complex cognitive capacities such as the ones that involve representations as being deeply rooted in the more basic processes that enable biological organisms to survive and maintain their integrity in a dynamical environment. It thus offers valuable resources to construct a theory of cognition that reaches all the way from single cell organisms to human beings, including plants.

Perhaps surprisingly, however, some enactivists have expressed doubts about the cognitive status of plants. According to Froese and Di Paolo (2011), for instance, "a plant does not have the same kind of relationship with its environment as does an animal which has to move and perceive in order to sustain itself" (p. 9). For them, because plants need not actively regulate their interaction with the environment as animals (and even bacteria!) do, it is not clear that they have evolved cognitive resources.

In a similar vein, Barrett (2015) compares plants with *Portia* spiders and asserts that:

[T]he behavior of *Portia* spiders is very flexible—one could almost say inventive—and they don't just respond to the world in a singular, fixed manner. This is true of all animals, from amoebas to armadillos. All show at least some variability in how they act and regulate their behavior in the world. They do so because they are animals, and not plants. (p. 71)

Thus, although committed to an ecological-enactive approach to cognition, both Barrett (2015) and Froese and Di Paolo (2011) align themselves with a long-standing tradition in philosophy, a tradition that has consistently and continuously seen plants as being fundamentally different from animals in their relationship with the environment. Patricia Churchland (1989) nicely captures this view as follows: "If you root yourself in the ground, you can afford to be stupid. But if you move, you must have mechanisms for moving, and mechanisms to ensure that the movement is not utterly arbitrary and independent of what is going on outside" (p. 13). [12]

Theoretical prejudices aside, in light of the scientific evidence outlined earlier, we hope to have shown that such a plant-blind view, whichever quarter it comes from, is unmotivated. From our previous discussion we conclude that there are no empirical or theoretical reasons to discard beforehand that certain patterns of plant behavior call for some form of cognitive agency. Indeed, we think that considering plants as cognitive agents would enable us to develop a more comprehensive account of cognition, one that sheds light on how cognitive abilities could have evolved, perhaps differently, across phyla.

---

[12] Perhaps, somewhat symptomatically, it is worth noting that even researchers such as Harry Heft, whose work has helped lay the theoretical foundations of the ecological approach, observed in his *Ecological Psychology in Context* (2001): "Categorical boundaries are rarely sharp. Where do plants fit into this conceptual division [animate-inanimate]? Admittedly, they do not fit into either category, but because they lack agency, for the purposes of an ecological psychology they fit into the inanimate category" (p. xxiii, fn. 1).

References

Abramson, C. I., & Calvo, P. (2018). General issues in the cognitive analysis of plant learning and intelligence. In F. Baluska, M. Gagliano, & G. Witzany (Eds.). *Memory and learning in plants* (pp. 35–49). New York, NY: Springer.

Abramson, C. I., & Chicas-Mosier, A. M. (2016). Learning in plants: Lessons from Mimosa pudica. *Frontiers in Psychology, 7*https://doi.org/10.3389/fpsyg.2016.00417.

Adams, F. (2018). Cognition wars. *Studies In History and Philosophy of Science Part A, 68*, 20–30. https://doi.org/10.1016/j.shpsa.2017.11.007.

Affifi, R. (2018). Deweyan psychology in plant intelligence research: Transforming stimulus and response. In F. Baluška, M. Gagliano, & G. Witzany (Eds.). *Memory and learning in plants* (pp. 17–33). Cham: Springer International Publishing. https://doi.org/10.1007/978-3-319-75596-0_2.

Allen, C. (2017). On (not) defining cognition. *Synthese, 194*, 4233–4249. https://doi.org/10.1007/s11229-017-1454-4.

Alpi, A., Amrhein, N., Bertl, A., Blatt, M. R., Blumwald, E., Cervone, F., et al. (2007). Plant neurobiology: No brain, no gain? *Trends in Plant Science, 12*(4), 135–136. https://doi.org/10.1016/j.tplants.2007.03.002.

Andrews, K. (2015). *The animal mind: An introduction to the philosophy of animal cognition.* Abingdon, Oxon: Routledge.

Baluška, F. (2010). Recent surprising similarities between plant cells and neurons. *Plant Signaling & Behavior, 5*, 1–3.

Baluška, F., Gagliano, M., & Witzany, G. (Eds.). (2018). *Memory and learning in plants.* New York, NY: Springer.

Baluška, F., & Levin, M. (2016). On having no head: Cognition throughout biological Systems. *Frontiers in Psychology, 7*https://doi.org/10.3389/fpsyg.2016.00902.

Baluška, F., & Mancuso, S. (2009). Plants and animals: Convergent evolution in action? In F. Baluška (Ed.). *Plant-environment interactions* (pp. 285–301). Berlin: Springer. https://doi.org/10.1007/978-3-540-89230-4_15.

Baluška, F., Mancuso, S., Volkmann, D., & Barlow, P. W. (2010). Root apex transition zone: A signalling–response nexus in the root. *Trends in Plant Science, 15*(7), 402–408. https://doi.org/10.1016/j.tplants.2010.04.007.

Baluška, F., Hlavacka, A., Mancuso, S., & Barlow, P. W. (2006). Neurobiological view of plants and their body plan. In F. Baluška, S. Mancuso, & D. Volkmann (Eds.). *Communication in plants: Neuronal aspects of plant life* (pp. 19–35). New York, NY: Springer.

Barrett, L. (2015). *Beyond the brain: How body and environment shape animal and human minds.* Princeton: Princeton University Press.

Ben-Jacob, E. (2009). Learning from bacteria about natural information processing. *Annals of the New York Academy of Sciences, 1178*, 78–90. https://doi.org/10.1111/j.1749-6632.2009.05022.x.

Bose, J. C. (1906). *Plant response.* London: Longmans.

Bose, J. C. (1926). *The nervous mechanism of plants.* London: Longmans, Green.

Brenner, E. D., Stahlberg, R., Mancuso, S., Baluška, F., & Van Volkenburgh, E. (2007). Plant neurobiology: The gain is more than the name. *Trends in Plant Science, 12*(7), 285–286. https://doi.org/10.1016/j.tplants.2007.06.005.

Buckner, C. (2017). Understanding associative and cognitive explanations in comparative psychology. In K. Andrews, & J. Beck (Eds.). *The routledge handbook of philosophy of animal minds*Abingdon: Routledgehttps://doi.org/10.4324/9781315742250.ch39.

Burbach, C., Markus, K., Zhang, Y., Schlicht, M., & Baluška, F. (2012). Photophobic behavior of maize roots. *Plant Signaling & Behavior, 7*(7), 874–878. https://doi.org/10.4161/psb.21012.

Cahill, J. F., McNickle, G. G., Haag, J. J., Lamb, E. G., Nyanumba, S. M., & Clair, C. C. S. (2010). Plants integrate information about nutrients and neighbors. *Science, 328*(5986), 1657–1657 https://doi.org/10.1126/science.1189736.

Calvo, P. (2016). The philosophy of plant neurobiology: A manifesto. *Synthese, 193*(5), 1323–1343. https://doi.org/10.1007/s11229-016-1040-1.

Calvo, P. (2017). What is it like to be a plant? *Journal of Consciousness Studies, 24*(9–10), 205–227.

Calvo, P. (2018). Plantae. In J. Vonk, & T. K. Shackelford (Eds.). *Encyclopedia of animal cognition and behavior.* New York, NY: Springer.

Calvo Garzón, P. (2007). The quest for cognition in Plant Neurobiology. *Plant Signaling & Behavior, 2*(4), 208–211.

Calvo Garzón, P., & Keijzer, F. (2009). Cognition in plants. In F. Baluška (Ed.). *Plant-environment interactions* (pp. 247–266). Berlin: Springer.

Calvo, P., Baluška, F., & Sims, A. (2016). "Feature detection" vs. "predictive coding." Models of plant behavior. *Frontiers in Psychology, 7*https://doi.org/10.3389/fpsyg.2016.01505.

Calvo, P., & Friston, K. (2017). Predicting green: Really radical (plant) predictive processing. *Journal of The Royal Society Interface, 14*(131), 20170096. https://doi.org/10.1098/rsif.2017.0096.

Calvo, P., & Gomila, A. (Eds.). (2008). *Handbook of cognitive science: An embodied approach.* Amsterdam: Elsevier.

Calvo, P., Sahi, V. P., & Trewavas, A. (2017). Are plants sentient? *Plant. Cell &*

Environment, 40(11), 2858–2869. https://doi.org/10.1111/pce.13065.

Chemero, A. (2009). *Radical embodied cognitive science.* Cambridge, Mass: MIT Press.

Choi, W.-G., Hilleary, R., Swanson, S. J., Kim, S.-H., & Gilroy, S. (2016). Rapid, long-distance electrical and calcium signaling in plants. *Annual Review of Plant Biology, 67*(1), 287–307. https://doi.org/10.1146/annurev-arplant-043015-112130.

Churchland, P. S. (1989). *Neurophilosophy: Toward a unified science of the mind-brain.* Cambridge, Mass: MIT Press.

Clark, A., & Chalmers, D. (1998). The extended mind. *Analysis, 58*(1), 7–19. https://doi.org/10.1093/analys/58.1.7.

Dener, E., Kacelnik, A., & Shemesh, H. (2016). Pea plants show risk sensitivity. *Current Biology, 26*(13), 1763–1767. https://doi.org/10.1016/j.cub.2016.05.008.

Dennett, D. C. (1987). *The intentional stance.* Cambridge, Mass: MIT Press.

Denny, M. R. (1986). Retention of s-r in the midst of the cognitive invasion. In D. F. Kendrick, M. E. Rilling, & M. R. Denny (Eds.). *Theories of animal memory.* Hillsdale, NJ: Lawrence Erlbaum Associates.

Di Paolo, E., Buhrmann, T., & Barandiaran, X. (2017). *Sensorimotor life: An enactive proposal.* Oxford, New York: Oxford University Press.

Figdor, C. (2018). *Pieces of mind: The proper domain of psychological predicates.* Oxford, New York: Oxford University Press.

Firn, R. (2004). Plant intelligence: An alternative point of view. *Annals of Botany, 93*(4), 345–351. https://doi.org/10.1093/aob/mch058.

Froese, T., & Di Paolo, E. A. (2011). The enactive approach: Theoretical sketches from cell to society. *Pragmatics and Cognition, 19*(1), 1–36. https://doi.org/10.1075/pc.19.1.01fro.

Fromm, J., & Lautner, S. (2007). Electrical signals and their physiological significance in plants. *Plant, Cell and Environment, 30*(3), 249–257. https://doi.org/10.1111/j.1365-3040.2006.01614.x.

Gagliano, M., Renton, M., Depczynski, M., & Mancuso, S. (2014). Experience teaches plants to learn faster and forget slower in environments where it matters. *Oecologia, 175*(1), 63–72. https://doi.org/10.1007/s00442-013-2873-7.

Gagliano, M., Vyazovskiy, V. V., Borbély, A. A., Grimonprez, M., & Depczynski, M. (2016). Learning by association in plants. *Scientific Reports, 6*(1)https://doi.org/10.1038/srep38427.

García Rodríguez, A., & Calvo Garzón, P. (2010). Is cognition a matter of representations? Emulation, teleology, and time-keeping in biological systems. *Adaptive Behavior, 18*(5), 400–415. https://doi.org/10.1177/1059712310385479.

Gibson, J. J. (1979/2015). *The ecological approach to visual perception.* New York, NY: Psychology Press.

Ginsburg, S., & Jablonka, E. (2009). Epigenetic learning in non-neural organisms. *Journal of Biosciences, 34*(4), 633–646.

Grice, J. W., Barrett, P. T., Schlimgen, L. A., & Abramson, C. I. (2012). Toward a brighter future for psychology as an observation oriented science. *Behavioral Sciences, 2*(1), 1–22. https://doi.org/10.3390/bs2010001.

Gruntman, M., Groß, D., Májeková, M., & Tielbörger, K. (2017). Decision-making in plants under competition. *Nature Communications, 8*(1), 2235. https://doi.org/10.1038/s41467-017-02147-2.

Hebb, D. O. (1949). *The organization of behavior: A neuropsychological theory.* New York, NY: Wiley.

Hodge, A. (2009). Root decisions. *Plant, Cell and Environment, 32*(6), 628–640. https://doi.org/10.1111/j.1365-3040.2008.01891.x.

Holmes, E., & Gruenberg, G. (1965). Learning in plants. *Worm Runner's Dig. 7,* 9–12.

Holmes, E., & Yost, M. (1966). "Behavioral" studies in the sensitive plant. *Worm Runner's Dig. 8,* 38–40.

Huber, A. E., & Bauerle, T. L. (2016). Long-distance plant signaling pathways in response to multiple stressors: The gap in knowledge. *Journal of Experimental Botany, 67*(7), 2063–2079. https://doi.org/10.1093/jxb/erw099.

Hung, T.-W. (2017). Rationality and Escherichia coli. In T.-W. Hung, & T. J. Lane (Eds.). *Rationality constraints and contexts* (pp. 227–240). San Diego: Academic Press. https://doi.org/10.1016/B978-0-12-804600-5.00012-X.

Hutto, D. D., & Myin, E. (2013). *Radicalizing Enactivism: Basic minds without content.* Cambridge, Mass: MIT Press.

Hutto, D. D., & Myin, E. (2017). *Evolving enactivism: Basic minds meet content.* Cambridge, Mass: MIT Press.

Jennings, H. S. (1906). *Behavior of the lower organisms.* New York, NY: Columbia University Press.

Karban, R. (2015). *Plant sensing and communication.* Chicago: The University of Chicago Press.

Karban, R., Wetzel, W. C., Shiojiri, K., Ishizaki, S., Ramirez, S. R., & Blande, J. D. (2014). Deciphering the language of plant communication: Volatile chemotypes of sagebrush. *New Phytologist, 204*(2), 380–385. https://doi.org/10.1111/nph.12887.

Khan, S., Spudich, J. L., McCray, J. A., & Trentham, D. R. (1995). Chemotactic signal integration in bacteria. *Proceedings of the National Academy of Sciences, 92*(21), 9757–9761. https://doi.org/10.1073/pnas.92.21.9757.

Kreps, J., & Kay, S. (1997). Coordination of plant metabolism and development by the circadian clock. *The Plant Cell Online, 9*(7), 1235–1244.

Li, X., & Zhang, W. (2008). Salt-avoidance tropism in Arabidopsis thaliana. *Plant Signaling & Behavior, 3*(5), 351–353. https://doi.org/10.4161/psb.3.5.5371.

Lyon, P. (2006). The biogenic approach to cognition. *Cognitive Processing, 7*(1), 11–29. https://doi.org/10.1007/s10339-005-0016-8.

Lyon, P., & Keijzer, F. A. (2007). The human stain: Why cognitivism can't tell us what cognition is & what it does. In B. Wallace, A. Ross, J. Davies, & T. Anderson (Eds.). *The mind, the body and the world. Psychology after cognitivism?* (pp. 132–165). Exeter, UK: Imprint Academic.

Novoplansky, A. (2016). Future perception in plants. In N. Mihai (Ed.). *Anticipation across disciplines* (pp. 57–70). New York, NY: Springer. https://doi.org/10.1007/978-3-319-22599-9_5.

Pfeffer, W. (1873). *Physiologische untersuchungen.* Leipzig: Springer.

Raby, C. R., Alexis, D. M., Dickinson, A., & Clayton, N. S. (2007). Planning for the future by western scrub-jays. *Nature, 445*(7130), 919–921. https://doi.org/10.1038/nature05575.

Robbins, P., & Aydede, M. (Eds.). (2009). *The cambridge handbook of situated cognition.* Cambridge, Mass: Cambridge University Press.

Schmid, B. (2016). Decision-making: Are plants more rational than animals? *Current Biology, 26*(14), R675–R678. https://doi.org/10.1016/j.cub.2016.05.073.

Schwartz, A., & Koller, D. (1986). Diurnal phototropism in solar tracking Leaves of Lavatera cretica. *Plant Physiology, 80*(3), 778–781.

Silvertown, J., & Gordon, D. M. (1989). A framework for plant behavior. *Annual Review of Ecology and Systematics, 20*(1), 349–366. https://doi.org/10.1146/annurev.es.20.110189.002025.

Souza, G. M., Ferreira, A. S., Saraiva, G. F. R., & Toledo, G. R. A. (2017). Plant "electrome" can be pushed toward a self-organized critical state by external cues: Evidences from a study with soybean seedlings subject to different environmental conditions. *Plant Signaling & Behavior, 12*(3), e1290040. https://doi.org/10.1080/15592324.2017.1290040.

Sterelny, K. (2005). Made by each other: Organisms and their environment. *Biology and Philosophy, 20*(1), 21–36. https://doi.org/10.1007/s10539-004-0759-0.

Sun, F., Zhang, W., Hu, H., Li, B., Wang, Y., Zhao, Y., et al. (2007). Salt modulates gravity signaling pathway to regulate growth direction of primary roots in Arabidopsis. *Plant Physiology, 146*(1), 178–188. https://doi.org/10.1104/pp.107.109413.

Tagkopoulos, I., Liu, Y.-C., & Tavazoie, S. (2008). Predictive behavior within microbial genetic networks. *Science, 320*(5881), 1313–1317.

Thellier, M., & Lüttge, U. (2013). Plant memory: A tentative model. *Plant Biology, 15*(1), 1–12. https://doi.org/10.1111/j.1438-8677.2012.00674.x.

Thompson, E. (2007). *Mind in life: Biology, phenomenology, and the sciences of mind.* Harvard: Harvard University Press.

Trebacz, K., Dziubinska, H., & Krol, E. (2006). Electrical signals in long-distance communication in plants. In F. Baluška, S. Mancuso, & D. Volkmann (Eds.). *Communication in plants: Neuronal aspects of plant life* (pp. 277–290). New York, NY: Springer. https://doi.org/10.1007/978-3-540-28516-8_19.

Trewavas, A. (1999). Le Calcium, c'est la vie: Calcium makes waves. *Plant Physiology, 120*(1), 1–6. https://doi.org/10.1104/pp.120.1.1.

Trewavas, A. (2003). Aspects of plant intelligence. *Annals of Botany, 92*(1), 1–20. https://doi.org/10.1093/aob/mcg101.

Trewavas, A. (2005). Green plants as intelligent organisms. *Trends in Plant Science, 10*(9), 413–419. https://doi.org/10.1016/j.tplants.2005.07.005.

Trewavas, A. (2007). Plant neurobiology – all metaphors have value. *Trends in Plant Science, 12*(6), 231–233. https://doi.org/10.1016/j.tplants.2007.04.006.

Trewavas, A. (2014). *Plant behaviour and intelligence.* Oxford: Oxford University Press.

Trewavas, A. (2017). The foundations of plant intelligence. *Interface Focus, 7*(3), 20160098. https://doi.org/10.1098/rsfs.2016.0098.

Tye, M. (1997). The problem of simple minds: Is there anything it is like to be a honey bee? *Philosophical Studies, 88,* 189–317.

Varela, F. J., Thompson, E., & Rosch, E. (1991). *The embodied Mind: Cognitive science and human experience.* Cambridge, Mass: MIT Press.

Volkov, A. (Ed.). (2012). *Plant electrophysiology: Signaling and responses.* New York, NY: Springer.

Volkov, A. (Ed.). (2013). *Plant electrophysiology.* New York, NY: Springer.

Westerhoff, H. V., Brooks, A. N., Simeonidis, E., García-Contreras, R., He, F., Boogerd, F. C., ... Kolodkin, A. (2014). Macromolecular networks and intelligence in microorganisms. *Frontiers in Microbiology, 5*https://doi.org/10.3389/fmicb.2014.00379.

Yokawa, K., & Baluška, F. (2018). Sense of space: Tactile sense for exploratory behavior of roots. *Communicative & Integrative Biology, 11*(2), 1–5. https://doi.org/10.1080/19420889.2018.1440881.

Yokawa, K., Derrien-Maze, N., Mancuso, S., & Baluška, F. (2014). Binary decisions in maize root behavior: Y-maze system as tool for unconventional computation in plants. *International Journal of Unconventional Computing, 10*(5/6), 381–390.