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Plant sentience?
Between romanticism and denial: Science

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Abstract: A growing number of non-human animal species are being seriously considered as candidates for sentience, but plants are either forgotten or explicitly excluded from these debates. In our view, this is based on the belief that plant behavior is hardwired and inflexible and on an underestimation of the role of plant electrophysiology. We weigh such assumptions against the evidence to suggest that it is time to take seriously the hypothesis that plants, too, might be sentient. We hope this target article will serve as an invitation to investigate sentience in plants with the same rigor as in non-human animals.

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1. Comparative cognition and the study of sentience in plants: An overview of the debate

'Sentience' refers to the capacity of an individual to have *felt states*, including sensory experiences, external or internal. Although the interest in studying sentience in non-human organisms is increasing, this research remains, in our view, remarkably

zoocentric (Calvo 2018a; Calvo and Lawrence, 2023). We hope to redress this tendency, inviting scientists and philosophers to address the question of whether plants, too, may be sentient. Our hope is to convince researchers that this possibility is worth exploring scientifically (Segundo-Ortin & Calvo, 2022; Raja & Segundo-Ortin, 2021).

Scientific study of non-human sentience (animal or non-animal) is particularly challenging because direct evidence is lacking. Pearce (2008, p. 221) questions the very possibility of determining whether a non-human animal is conscious because we cannot "observe directly the mental states of an animal." Echoing this view, Shettleworth (2010, p. 7) writes that "the point of most researchers studying animal cognition is that how animals process information can and should be analyzed without making any assumptions about what their private experiences are like."

Researchers must hence rely on indirect evidence, whether overt behavioral markers or correlated electrochemical activity. This "leap from observable behavior and physiological processes to conjectures about private conscious experiences" (Mazor et al., 2022, p. 3) requires some justification. Andrews (2020, Chapter 4) points out that most researchers rely on reasoning by analogy. If a behavior that occurs when humans experience pain is also observed in other species, we might infer that there too it is accompanied by the experience of pain.

We can never be sure that the analogous behavior is accompanied by a subjective experience. The response to a damaging stimulus, for example, could be caused by insentient *nociception* (damage-detection) rather than pain. Moreover, analogy might be convincing with members of the ape clade and some other non-hominid mammals but it loses its strength as the target species becomes more distant from our own. What kind of behavior should we take as indicative of sentience in fruit flies? "If there are conscious entities that do not behave like humans, and if there is consciousness that we cannot perceive, then those entities will be unjustly excluded. Quite different beings may fail to meet those criteria while still being conscious" (Andrews 2020, p. 93). The same rationale applies to neurophysiological evidence. There is no *principled* reason to deny that radically different neural structures could give rise to felt states (Chittka 2017; Pagàn 2019; Solé et al. 2019).

Sentience is nevertheless being increasingly recognized in many animal species, from apes, mammals, birds, reptiles and fishes, to octopuses and other invertebrates (Andrews, 2020; Crump et al., 2022; Mikhalevich & Powell, 2020). Based on behavioral and electrophysiological studies in invertebrates, Barron and Klein (2016; Klein & Barron, 2016) argue that some insects may have the capacity for sentience: Even though they are very different from the brain structures thought to support sentience in vertebrates, insects' cephalic ganglia produce integrated neural representations of the world. Barron & Klein suggest that such representations are indicative of sentience, akin to those produced in vertebrates' midbrains, with the cephalic ganglion of insects functionally equivalent to the midbrain.

More skepticism is found when we move beyond the animal kingdom to the possibility that non-animal organisms, such as plants, can feel. Some authors have tried to argue against this skepticism. The "Cellular Basis of Consciousness" (CBC) theory (Baluška,

Miller & Reber, 2021; Baluška & Reber, 2020, 2021; Reber & Baluška, 2020) proposes a bottom-up, evolutionary view of sentience. According to CBC, sentience emerged as an inherent feature of the first life-forms, including prokaryotes, and *all* biological taxa are equipped with some degree of feeling (Reber, 2019). "[A]ll adaptive functioning organisms, from the earliest on, must be sentient [...]. A non-sentient organism [...] would be an evolutionary dead-end" (Baluška & Reber, 2019, p. 1). According to CBC, sentience emerged to facilitate flexible adaptation to the environment; its complexity depends on the specific needs of each species and the characteristics of its ecological niche. Other researchers have argued that, contrary to CBC, current scientific knowledge does not provide serious support for investigating plant sentience (Mallatt et al., 2020; Taiz et al., 2019; we elaborate on these arguments in section 3).

We agree that there is still much to be discussed before it can be accepted that plants feel, but we would disagree with those who would rather deny the possibility of plant sentience altogether. Regarding plant cognition (rather than sentience) current empirical findings strongly suggest that plants can perform many putatively cognitive abilities once thought to be unique to animals (Segundo-Ortin & Calvo, 2019). These abilities include the capacity to communicate with the plant's biotic local environment (Arimura & Pearse, 2017; Karban, 2015); to distinguish kin from non-kin and modify behavior accordingly (Bilas et al., 2021); to make flexible decisions about multiple options and trade-offs (Karban & Orrock, 2018; Lee et al., Submitted); and even to learn from and remember past experiences (Baluška et al. 2018). Nevertheless, even if plants have surprising *cognitive abilities*, it remains debatable whether this is evidence that they *feel*, any more than similar abilities in robots and neural networks imply that they feel.

A series of striking functional analogies between the nervous system of animals and the non-neural vascular system of higher plants has also been reported (see section 3 below). These similarities have motivated some researchers to broaden the definition of a 'nervous' system to include plants for "a better understanding of how evolution has driven the features of signal generation, transmission and processing in multicellular beings" (Miguel-Tomé & Llinás, 2021). Calvo (2017) has argued that the emerging field of plant neurobiology (Baluška et al. 2006; Brenner et al. 2006) offers new ways to investigate how plants integrate information from different parameters.

In what follows we review the current evidence on plant cognitive activity and its electrophysiological substrate. Section 2 examines plant cognition. Section 3 reviews electrophysiological processes that may underlie plant cognition and sentience. We conclude with some general remarks about the implications of these findings.

2. Cognition[1]

The interest in plant sentience emerges from observations of cognitive capacities in plants. Cognition in plants can be inferred from changes in their behaviors that improve their chances of survival (Calvo et al., 2020; Calvo & Trewavas, 2020). Cognitive processes are sometimes the best explanation of their behavioral repertoire (Karban, 2008; Silvertown & Gordon, 1989), with "behavior" meaning the "observable consequences of the choices a living entity makes in response to external or internal stimuli" (Cvrčková et al., 2016, p. 3).

Plant cognition involves "the manipulation of the environment in order to enable metabolic functioning" (Calvo, 2018b), but not all plant behavior is cognitive. Plant cognition is inferred from behavioral patterns that are adaptive, flexible, anticipatory, and goal-directed (Calvo, 2016; Calvo and Lawrence, 2023). The evidence can take many forms (Baluška et al., 2006), including time-lapse photography (Brenner, 2017; Stolarz, 2009; Stolarz et al., 2014) and specialized electrophysiological techniques (Volkov, 2012; Volkov, 2017) to identify complex morphological and physiological responses (Karban, 2008) during ontogeny that would otherwise be missed (Calvo & Trewavas, 2020). These techniques reveal that plants are highly flexible, being able to do more than simply react to the here-and-now in a fixed, hardwired manner (Raja et al., 2020; Segundo-Ortin & Calvo, 2019; Trewavas, 2017; Trewavas, 2014).

Rooted in the Aristotelian distinction between motion and self-motion (Linson & Calvo, 2020), one of the reasons plants have not been considered cognizers is that they were thought to be unable to control their own movement endogenously. [Recent research on the patterns of growth of common bean shoots (*Phaseolus vulgaris*) has shown that the bending of its vine is influenced by the presence of a nearby climbable pole (Raja et al., 2020)](#) **[click to view]**. If the bean vine's attempt to reach the pole fails, it straightens out and tries again. The fact that the vine's movements are continuously reconfigured in the attempts to reach the pole suggests that they are not ballistic but endogenously controlled by the plant to attain a specific goal.

2.1 Communication. One of the ways intra-plant and inter-plant communication take place is via airborne volatile organic compounds (VOCs). VOCs are primary and secondary metabolites that plants exude through their leaves, flowers, fruits and the rest of their plant bodies (Baldwin, 2010; Baldwin et al., 2006; Meents et al., 2019). The release of VOCs into the air is not a physiologically recycled byproduct of the assimilated carbon. Instead, many adaptive interactions are mediated by VOCs (He et al., 2019) operating as informational cues among conspecifics and members of different species alike, and among both mutualists and competitors (Novoplansky, 2019).

VOCs may be emitted after a herbivore attack, permitting plants to adjust their phenotypes and trigger adaptive defense mechanisms. Receiving VOCs allows plants to protect themselves against a wide variety of sources of stress. Behavioral responses

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[1] Sections 2 and 3 have been adapted, with substantive changes, from Segundo-Ortin and Calvo (2021).

include (1) attracting the natural predators of herbivores or pathogens and (2) priming the plant's own defenses to deter future damage (Caruso & Parachnowitsch, 2016; Dicke et al., 2003; Dicke & Baldwin, 2010; Heil & Karban, 2010; Holopainen, 2004; Kalske et al., 2019; Ninkovic et al., 2016; Šimpraga et al., 2016). A well-known illustration of the role that VOCs can play in non-kin relations is provided by *Cuscuta* spp. (dodder), a genus of parasitic vines that lack chlorophyll to photosynthesize their own food. [They exploit the VOCs being emitted by potential hosts such as tomatoes (*Lycopersicon esculentum*) and wheat (*Triticum aestivum*) to locate them (Runyon, 2006)](#) **[click to view]**. Dodders can combine chemical and light cues to discern both the nutritional quality of potential plant–hosts, and their distance and shape (Smith et al., 2021).

Other unexpected forms of communication include sensitivity to sound vibrations in plant–invertebrate acoustic interactions (Gagliano et al., 2012). The model plant *Arabidopsis thaliana* can detect, through epidermal outgrowths (hairs called "trichomes"), the specific vibrations produced by the munching of caterpillars; it can then respond to the caterpillars by synthesizing toxins (Appel & Cocroft, 2014). Remarkably, *Arabidopsis* can discriminate the trichome frequencies caused by chewing from those caused by wind or insect songs. Trichomes thus act as "mechanical antennae" (Liu et al., 2017), enabling *Arabidopsis* to respond in a selective and ecologically meaningful way. Similarly, Veits et al. (2019) report that *Oenothera drummondii* flowers exposed to sounds of the same frequency as those produced by flying bees produce sweeter nectar, increasing the chances of cross-pollination.

Communication also takes place underground, thanks to the interactions of roots with the mycelial networks of mycorrhizal fungi (Johnson & Gilbert, 2015; Simard, 2018; Simard et al., 2012). The symbiotic exchange of information between fungi and plant roots results in flexible and adaptive changes on the plant's side, including rapid changes in physiology, gene regulation, and defense responses (Gorzelak et al., 2015; Song et al., 2015). Similar communication-based symbiotic interactions have been reported between plants and insects (Heil, 2016; Mittelbach et al., 2019), with plants able to control the behavior of their insect partners via chemical compounds (Grasso et al., 2015).

2.2 Kin and species recognition. Evidence of the capacity to discriminate kin from non-kin, and to distinguish between conspecifics and members of different species has been found in plants (Bilas et al., 2021). Studies focusing on root allocation and interaction show that *Impatiens pallida* specimens fight for resources more aggressively if competing with non-kin or strangers (Murphy & Dudley, 2009), that is, with unrelated conspecifics belonging to the same population. Similarly, root allocation in *Cakile edentula* increases when a group of strangers shares a pot, but not when groups of kin members do it (Dudley & File, 2007). These findings suggest that root interaction and root-derived chemical exudates play a crucial role as cues for kin recognition and competitive kin discrimination, triggering adaptive behavioral changes (Biedrzycki et al., 2010; Novoplansky, 2019; Semchenko et al., 2014).

Further studies point out the importance of photoreceptors in kin recognition. Crepy and Casal (2015; Bais, 2015) report that *Arabidopsis* recognize kin neighbors by detecting red to far-red light ratios and blue light profiles. *Arabidopsis* interacting with kin produce

more seeds than when they interact with non-kin. This is interpreted as evidence for cooperative behavior in plants.

2.3 Decision-making. Huang et al. (2021) write that "[o]ne reason many theorists resist applying cognitive vocabulary to simpler organisms, especially those without neurons, is that their behavior is thought to be just the product of reflexes" (p. 1057). Plant researchers are no exception to this tendency. Yet the current evidence suggests that this view of plant behavior as purely reactive and mechanical is mistaken (see Baluška & Mancuso, 2009; Segundo-Ortin & Calvo, 2019).

When a target system selects an option from a set of alternatives, and when this choice displays a level of reliability and repeatability that is greater than chance, we agree with Reid et al. (2015) that it should be interpreted as decision-making. Because plants inhabit complex environments, behavioral decision-making (e.g., choosing between alternative courses of action such as direction and rate of growth) is imperative for them (Trewavas, 2017). Like animals, plants must decide about where best to forage for light and nutrients (among other resources patchily distributed in different qualities and concentrations), and about repellents to grow away from. VOCs mediate decision-making in *Cuscuta*. Although both tomato plants and wheat elicit the directed growth response of this parasite vine, experiments have shown that it prefers the former to the latter when both options are presented in tandem (Runyon, 2006). Results indicate that although *Cuscuta* exemplars are sensitive to a variety of VOCs, they respond preferentially to those produced by the most nutritious host. Likewise, Trewavas (2014) reports that when exemplars of *Calamagrostis canadiensis* are offered adjacent habitats to grow, they choose the habitat with the best conditions of competition, warmth, and light. However, *C. canadiensis* can also "discriminate these conditions in combination [...] choosing light plus warm soil in preference to others" (p. 84).

Decision-making also takes place in the root apparatus (Hodge, 2009). Because high concentrations of salinity can disrupt plants' cellular biochemistry, roots have evolved sensitivity to abnormal saline conditions, adapting their growth accordingly. Li and Zhang (2008) studied salt-avoidance behavior by growing exemplars of *A. thaliana* in a medium with increasing levels of salinity. They found that roots started to bend upward, inverting their natural gravitropic behavior, before reaching the high-salt agar (250 mM NaCl) at the bottom. This indicates that "roots can sense ion gradients [and] make decisions that enable roots to stay away from high salt" (p. 352).

This kind of behavior represents a sort of basic "go/no-go" decision also referred to as "global inhibition" (Tomasello 2020). Similar studies concern avoidance behavior and competition in individuals of the same species. In a series of experiments, Cahill and colleagues (2010) measured root growth in *Abutilon theophrasti* while manipulating both competition (alone and with a competitor) and resource distribution in the soil (homogeneous, patch-centered, and patch-edge). As the authors explain, their goal was "to determine whether root foraging behavior was an additive response to multiple forms of environmental information or whether plants used novel behaviors under different combinations of conditions" (p. 1).

The reports indicate a striking level of flexibility. For example, when plants grew alone they displayed maximum root distribution, independently of how the resources were distributed. Root foraging behavior changed when a competitor was present, however. Although their root systems strongly avoided each other when growing into a soil with homogeneous nutrient availability, if a nutrient-rich patch was placed between the two exemplars, plants grew roots in the high-quality soil, overriding their usual avoidance tendencies. For the authors, this clearly indicates that plants integrate and combine information about nutrient availability and neighbors when making decisions concerning foraging, and that "root placement for this species is determined by a hierarchical set of decision rules" (p. 1).

There has traditionally been some resistance to describing the behavior of plants as decision-making. One argument that supports this resistance is that decision-making requires a single individual evaluating the costs and benefits of different courses of action. This is point is raised by Firn (2004), for whom "the concept of the individual, to which intelligence and behavior are intimately linked, cannot usefully be applied to plants" (p. 345). For him, because plants do not have a central controller (something equivalent to a brain), plants cannot be considered as individuals in the proper sense of the term. Instead, plants must be understood as aggregates or collections of cells; their behavior is the sum of the adaptive responses of the cells. Hence, because so-called decisions of plants are "not determined centrally […] There is no choice made by 'the plant'; rather, events occur within the plant that dramatically change the balance within the economic union, with consequent changes to the fate of some members of the union" (pp. 347-348). Firn concludes that applying cognitive terms such as decision-making to plants is both unproductive and unjustified because it would call for a level of individuality and centralization that cannot be found in plants (for similar arguments see Taiz et al., 2020, pp. 679–680).

The view that decision-making requires an individual, and most particularly a central controller, is contested in the contemporary literature, however. For example, Reid et al. (2015) propose a more encompassing definition of decision as "the action by an entity (individual organism or group) of selecting an option from a set of alternatives, based on characteristics of the alternatives that the entity can perceive;" These authors add that such a definition "makes possible the comparison of the decision-making capabilities of different entities regardless of their nature or level of complexity" (p. 44). Similarly, a series of papers co-authored by Bechtel, Huang and Bich (Huang et al., 2021; Bich & Bechtel, 2022; Bechtel & Bich, 2021) examine the evidence about decision-making from a phylogenetic perspective and conclude that many decisions in nature, including some performed by mammals and human beings, are controlled by heterarchically distributed mechanisms. If these authors are right, then there is no reason to exclude plants from making decisions because they lack a central controller, as Firn (2004) does.

2.4   Risk sensitivity.   Decision-making in comparative cognition is studied from economic and biological perspectives. Whereas economic models of decision-making focus on logical processes that maximize expected utility, biology-inspired models adopt an evolutionary perspective and assume that individuals seek to maximize fitness. As Petrillo and Rosati explain, "[o]ne fundamental way in which biological ideas about rationality differ from those in economics is that the context of decision is assumed to

have a major impact on its fitness consequences […] animals may show context effects that appear "irrational" from an economic perspective, but which in fact maximize their fitness" (2021, p. 772). For example, it is expected that an organism will take more risks in foraging when it is in a poor energetic state. In contrast, it is more rational to behave in a risk-averse way if satiated. Likewise, organisms are expected to prefer low quality food if the risk of predation involved in acquiring a better-quality food is too high. For many researchers, these decision-making processes provide evidence of cognitive sophistication, for they require that different parameters be integrated and compared in order to make a decision as to how to act (see Reid et al., 2015; Tomasello, 2022).

Experiments that involve trade-offs are designed precisely to measure the adaptability and flexibility of decision-making processes. Some non-animal species, such as *Physarum polycephalum*, aka "slime mould," display such flexible decision-making under risk conditions (Latty & Beekman, 2010), and so do plants. For example, in a series of experiments with *P. sativum*, Dener et al. (2016) demonstrated that root growth can show risk sensitivity. They framed their experiment in relation to Risk sensitivity theory. This theory predicts that there is an inflection point at which the switch between risk-averse and risk-prone behavior maximizes fitness. Risk sensitivity theory is commonly used to study rational decision-making in human and non-human animals from a biological perspective. For their experiment, Dener et al. used split-root pea plants— plants whose root tips grow in separate containers—and allocated different nutrient regimes to both pots: one pot received a constant concentration of nutrient while the other one received a variable one. Experimenters found that if the nutrient concentration in the first pot was enough for the plants to meet their metabolic needs, they grew roots in this pot. However, if the concentration of nutrients was insufficient, plants allocated more roots to the pot that receives the variable nutrient concentration, a behavior that is interpreted as risk-prone given the context of the experiment. For Dener et al., these findings suggest that plants "respond strategically to patches varying in their average of nutrient availability" (p. 1765), and that they can switch between risk-prone and risk-averse behavior as a function of resource availability. Commenting on these findings, Schmid (2016) goes as far as to claim that they indicate that when faced with choices concerning different environmental conditions, plants make rational decisions in favor of the option that maximizes their fitness. For him, this implies that "theories of decision making and optimal behavior developed for animals and humans can be applied to plants" (p. R677). Similar experiments involve trade-offs concerning the expression of defensive traits against herbivores at the cost of other plant functions, such as growth or reproduction (Züst & Agrawal, 2017).

Taken together these findings suggest that plants can engage in complex decision-making, integrating and weighting information from different parameters and trade-offs, and prioritizing responses to improve the chance of survival. In other words, plants do not select courses of action randomly, but seem to evaluate available alternatives in a context-sensitive and flexible manner. As Moulton et al. (2020) explicate, "even within a simple plant, multiple environmental cues will combine and overlap in effecting mechanotransducive signals, hormonal response, differential growth, and ultimate change in shape" (p. 32227). As we will see in the following section, the complexity of plant decision-making and multiscale stimulus integration is further exemplified in experiments that involve anticipation and assessment of future states of affairs. We hold

that these kinds of behaviors cannot be understood as individual responses to single stimuli.

2.5 Anticipatory behavior. Getting things wrong can be rather costly when it comes to fitness. Only those organisms that have the ability to "act ahead of time" can survive in a dynamical, ever-changing environment. Furthermore, if we consider that plant behavior takes place across very slow timescales in comparison to animal behaviors, and that changes are often irreversible, we can see why plants cannot afford *not* to be able to anticipate the future (Calvo & Friston, 2017).

For a basic example of anticipatory behavior, consider the leaf laminas of *Lavatera cretica* that reorient during the night in order to face the direction of the sunrise (Garcia Rodriguez & Calvo Garzon, 2010). Heliotropic nocturnal reorientation can be retained for a number of days in the absence of solar-tracking (Schwartz & Koller, 1986). Anticipatory behavior has also been observed at the root level. Consistently with the findings of Dener et al. (2016), Novoplansky (2016; Shemesh et al., 2010) reports that young exemplars of *Pisum sativum* grow different roots if subjected to variable, temporally dynamic, and static nutrient regimes. For example, when given a choice, plants allocate more root biomass in patches with increasing nutrient levels. The striking fact, however, is that they do so even in the cases when "dynamic" patches were poorer in absolute terms than the "static" ones. For Novoplansky, this indicates 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). This result further reinforces the idea that plants switch between risk-averse and risk-prone behavior depending on context.

Motivated by these findings, plants have been characterized as "anticipatory engines" (Calvo et al., 2016; Calvo & Friston, 2017). Accordingly, plants are constantly monitoring gradients in order to "guess" what the world is like. These predictions allow plants to "minimize surprise," and to adapt to the yet-to-come environmental conditions via phenotypic plasticity (see chapter 5 in Calvo and Lawrence, 2023).

2.6 Learning and memory. The literature on plant learning and memory can be traced back to the 19th Century (Abramson & Chicas-Mosier, 2016). Consider habituation, for example: Habituation occurs when the response to a repeated stimulus decreases and this decrease is not due to, say, sensory adaptation or motor fatigue. An early study on habituation was conducted by Pfeffer (1873) on *Mimosa pudica*,[2] demonstrating that repeated mechanical stimulation led to a decrease in leaflet closure (see also Bose, 1906).

More recently, Gagliano et al. (2014) have studied habituation in *Mimosa* in the context of light foraging and risk predation. Rather than simply confirming Pfeffer's discoveries,

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[2] In the interests of historical accuracy: The first careful observations of *Mimosa* leaf-folding behavior were reported in Hooke's *Micrographia* (1665) (Roblin, 1979), and in the eighteenth century by Desfontaines (Hiernaux, 2019). Only later, in 1873, did Pfeffer performed his *Mimosa* experiments.

two striking facts about this phenomenon were reported. First, leaf-folding habituation was more persistent for *Mimosa* exemplars growing in energetically costly environments (e.g., environments where light is scarce). This indicates that habituation is responsive to environmental conditions. Second, the habituated reflex could last for up to 28 days. This suggests the acquisition of long-lasting memory in *Mimosa*.

Subsequent studies have sought more sophisticated forms of learning, such as classical conditioning. This takes place when a conditioned stimulus (CS) is paired with an unconditioned stimulus (UC) that elicits a reflex. After a number of CS–US pairings, the response previously elicited by the US is now elicited by the CS. Recent research by Gagliano et al. (2016) has shown that, after training, pea plant (*P. sativum*) specimens associated the presence of a fan (CS) with the onset of light (US). Besides, measuring expressional changes in heat-responsive genes, Bhandawat et al. (2020) have reported the occurrence of aversive conditioning in *A. thaliana*. Last, [*Nasa poissoniana* adjust the timing of their pollen presentation based on previously experienced pollinator visitation intervals (Mittelbach et al. 2019)](#) **[click to view]**.

All these experiments suggest that plants can learn from past experience, eliciting changes at the level of behavior and phenotype for the sake of maximizing fitness. Needless to say, the research on plant learning and memory is just flowering, and further independent replications are needed before we can claim confidently that plants are able to learn (Abramson & Chicas-Mosier, 2016). In fact, the literature yields a mixed bag of negative (Holmes & Gruenberg, 1965; Holmes & Yost, 1966), positive (Armus, 1970), and unclear results (Haney, 1969; Levy et al., 1970). Adelman (2018) reviews these results and Gagliano et al., (2016) and Markel (2020a, 2020b) discuss the evidence, or lack thereof, for associative learning in plants.

In light of the inconsistent results being reported, at the Minimal Intelligence Lab, we are currently attempting to replicate Gagliano et al.'s (2016) results independently (Ponkshe et al., submitted). We have identified eleven methodological factors that must be addressed, from germination and transplantation of seedlings to experimental design and apparatus issues. We have proposed a number of ways to overcome these hurdles, such as incorporating non-invasive time-lapse photography for finer control in the administration of stimuli, monitoring plant growth throughout the experiment, and increasing statistical power. (Opaque Y mazes prevent direct observation of plant behavior throughout experiments and make it impossible to either accept or reject the possibility of associative learning in the current experimental setup). We are as yet unable to report conclusive evidence for or against associative learning in plants. To draw ecologically meaningful conclusions it will also be important to extend these experiments beyond the lab (Abramson & Calvo, 2018; Affifi, 2018).

2.7 Foraging and competition. The capacity of plants to integrate information from different variables plays an essential role in their ability to develop different strategies for nutrient foraging (De Kroon et al., 2009). Latzel and Münzbergová (2018) report that clones of *Fragaria vesca* can associate locations of soil nutrients with particular light intensities and that they can use this previous experience to anticipate the presence of nutrients in a new environment. This experiment confirms previous evidence that

epigenetic memory of previous interactions provides clonal plants with an advantage for foraging in not yet occupied environments (González et al., 2016, 2017).

Foraging is also affected by competition. Cahill et al. (2010) measured patterns of root growth in *Abutilon theoprasti* while manipulating both competition and resource allocation. They reported different foraging behaviors depending on the conditions. When plants grew alone, they displayed maximum root distribution as well as breadth, independent of resource distribution. However, when competitors were present, plants adopted different foraging strategies depending on the allocation of resources. Similarly, Gruntman et al. (2017) conducted a series of experiments with *Potentilla reptans* where they simulated different light competition settings. They found that *P. reptans* can tailor its phenotype—namely, induce changes in the vertical inclination, leaf area, and so on— according to the relative stature and densities of their opponents. The studies of Gruntman et al. demonstrate that plants "pick up" information from their competitors in order to make decisions about appropriate foraging strategies (Novoplansky, 2009).

Recent studies have been performed at the level of root interaction. For example, Cabal et al. (2020) have successfully applied game theoretical models—models originally designed to predict strategic interactions between decision-makers in zero-sum competition games—to predict the behavior of *Capsicuum annum* competing for soil resources.

2.8 Mimicry. Mimicry refers to the adaptive similarity or resemblance between a mimic organism and its model. Whereas mimicry is a well-known phenomenon in the animal kingdom, examples of true plant mimicry are less frequent, with documented cases in the plant literature being scarce (Niu et al., 2018; Lev-Yadun, 2016). An illustration nonetheless is provided by Gianoli and Carrasco-Urra (2014), who report that the leaves of *Boquila trifoliolata* can mimic the leaves of its supporting host, including size, shape, orientation, color, and petiole length, among other features. Moreover, the same individual can mimic two different hosts in a series. According to Gianoli and Carrasco-Urra, mimicry in *B. trifoliolata* is related to predation avoidance; they gain protection against herbivores by climbing onto trees whose leaves they mimic.

Mimicry by *B. trifoliolata* has also been observed with a complete lack of tactile contact. Mimicry had previously been observed in other species, such as Australian mistletoes, but in the case of *B. trifoliolata*, the absence of any (physiological) connection between vine and support, together with the impressive serial mimicry, counters some rival hypotheses as to the underlying mechanism (cf. Pannell, 2014).

Two rival hypotheses are airborne VOC communication and horizontal gene transfer (Gianoli & Carrasco-Urra, 2014). However, taking into account that physical contact is not needed for mimicry to take place, a more radical hypothesis has recently been advanced: a plant-specific form of proto-vision akin to the ocelloid-based vision found in cyanobacteria and some dinoflagellates (cf. Gianoli, 2017). This hypothesis finds preliminary support in a recent study conducted by White and Yamashita (2022). The authors placed artificial plastic vine models above the *Boquila* exemplars and found that as the plants grew toward the artificial plants, the leaves adopted a very different shape (in terms of area, perimeter, length, and width) compared to the controls. White and

Yamashita interpreted these morphological alterations as attempts to mimic the plastic leaves.[3]

Finally, Schaefer and Ruxton (2009) studied deception by orchids *Ophrys exaltata* and *Epipactis helleborine*, and distinguished between plants relying on mimicry to achieve pollination and those relying on the exploitation of perceptual biases of animals. According to the researchers, since the exploitation of perceptual biases is a less restrictive strategy than mimicry, the former could be a precursor for the evolution of the latter. As they explain, "if distinct plants exploit similar sensory biases, they can be "within reach" in animals' perceptual world for mimicry to evolve gradually" (p. 682).

Note that we are focusing exclusively on mimicry as occurring within one lifetime, not over evolutionary time. As we see it, what makes these instances of mimicry cognitively interesting is that they involve adaptations to the current contingencies of the environment. That the same exemplar of *Boquila* can tailor its phenotype to mimic different hosts (from different taxa) consecutively (Gianoli & Carrasco-Urra, 2014) invites explanations that *prima facie* resemble those invoked to account for the behaviors of some animal species (Lev-Yadun, 2016).

2.9 Numerosity. As research in animal cognition shows, numerical competence, the ability to estimate and process discrete magnitudes such as the number of times an event occurs (Anobile et al., 2021), is shared across a wide variety of phyla. Number-space mapping in chicks (Rugani et al., 2017) and numerosity in honeybees (Howard et al., 2019a, 2019b) first come to light in non-mammalian species. As Rapp et al. (2020) observe, insects can use action potentials to encode basic numerical concepts non-symbolically. Yet, if insects can help themselves to the number of action potentials to solve numerosity-related tasks, the roots of "numerical competence" can be traced further down the tree of life.

Plants may well benefit from numerical competence during "hunting." The carnivorous plant *Dionaea muscipula* (Venus flytrap) can keep track of the number of times that the trigger hairs located in the inner side of the snap trap are stimulated (Böhm et al., 2016; Hedrich et al., 2016). When an insect lands on the trap and tilts the mechanoreceptors in the hairs, it induces the firing of action potentials (APs) responsible for the closing of the trap (see section 3). Yet, for the trap to close, a second stimulation must be repeated within 20s-30s of the first one. Otherwise, the cycle resets. Besides, it appears that *Dionaea* can store information bio-electrically for short periods of time, discriminating the number of stored signals even further. When trapped, panicking insects repeatedly touch the trigger hairs, inducing the release of acidic enzymes that decompose them. However, once the trap has been shut and the prey is

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[3] As with the associative learning experiments, there are methodological concerns related to the experimental design that prevent us from discussing this result more thoroughly until independent replications are available.

trapped, *Dionaea* keeps counting episodes of mechanical stimulation, only releasing its digestive enzymes once it has reached five (Böhm et al., 2016) **[click to view]**.

Further studies are needed before we can claim that plants exhibit numerosity-related abilities, and before we can tell how sophisticated such abilities are in relation to those exhibited by animals. Nieder (2020) hypothesizes, however, that plant sensitivity to numerical quantity, even if rudimentary, may play a role in enhancing adaptive decision-making in various ecologically meaningful contexts. Burri et al. (2020 *[see accompanying images]*) have reported that the Venus flytrap has the plasticity to adapt its carnivorous skills to different prey; it can snap its trap shut after one single stimulation that would serve to elicit two consecutive action potentials.

2.10 Swarm intelligence. Swarm intelligence—the collective adaptive behavior of a decentralized group of individuals in response to sensory input in the vicinity—is common in bird flocking, ant colonies, fish schooling, bacterial colonies, and even human communities (Krause et al., 2010). Recent evidence suggests it could be present in plants as well.

As mentioned earlier, growing root apices exhibit complex behavior and decision-making about where to grow. Ciszak et al. (2012) report that complex root systems deploy coordinated growing for resource optimization and competition too. Individual roots can induce a change in the direction of growth in the roots of their vicinity, giving rise to episodic patterns of coordinated activity among individual root apices. Swarm behavior of this kind is crucial for adaptive success, for it helps maize roots scan the soil structure collectively, enhancing their ability to detect nutrient patches. Elaborating on this, Baluška, Lev-Yadun, and Mancuso (2010) speculate that information transmission between individual root apices can take place via the combination of different mechanisms, including internal, neuron-like electrical activity, segregated chemical volatiles, and, finally, electric fields generated by each individual root (see section 3). Apart from whatever mechanisms enable swarm behavior in plants, the study of root behavior seems to indicate that roots can solve problems collectively.

3. Plant Neurobiology (PN): A Scientific Framework for the Study of Plant Intelligence and Sentience

Plant neurobiology (PN) studies plant signaling with the aim of providing an explanation of how plants, as information-processing systems, perceive, and act in an integrated and purposeful manner (Baluška et al., 2006; Brenner et al., 2006; Calvo, 2016). The rationale that underlies this scientific endeavor is that intelligent behavior requires information to be integrated with an eye to coordinating physiological needs among the different plant structures.

Decision making, kin recognition, learning, and the rest of the competences reviewed in section 2, call for the informational integration of the plant body as a whole (Cahill et al., 2010; Souza et al., 2017; Costa et al., 2023). To alter traits in the phenotype and achieve flexible global behavior, plants cannot rely on a single source of information. To make foraging decisions, for example, plants must process incoming information concerning many parameters simultaneously (Novoplansky, 2016). These include both biotic and abiotic parameters, ranging from light, temperature, mechanical or vibrational cues to variations in supply of water and humidity, the distribution of resources in the soil, the presence of volatile and non-volatile chemicals, and many parameters (Calvo & Trewavas, 2020). All these informational resources get combined to maximize fitness and decision-making efficiency (van Loon, 2016).

The goal of Plant Neurobiology (PN) is to understand how the information signaling mechanisms across the root and shoot systems that give rise to intelligent behavior in plants integrated and fine-tuned. Several disciplines are called upon, including molecular biology, electrophysiology, biochemistry, evolutionary and developmental psychology, and plant ecology (Heras-Escribano & Calvo, 2020; Stahlberg 2006).

As the reader may have surmised, the very idea of plant *neuro*biology is not free of controversy. Since the term was first coined by Brenner and colleagues (2006), different authors have reacted against it. Alpi et al. (2007) and Struik et al. (2008) have argued that the concept is based on vague analogies and adds nothing to our current understanding of plant physiology, ecology, and metabolism. Brenner et al. (2007) then responded that PN "creates an important and yet unfilled niche for plant biology," and that "the use of neurobiological terms and our understanding of plant behavior [has] generated ideas about how to understand the broader picture of plant signaling" (p. 286). Similarly, Trewavas (2007) has argued that neurobiology concepts are "an essential adjunct to the imaginative scientific mind in confronting some of the most recalcitrant problems in plant biology" (p. 232). These disputes are far from settled yet (chapter 4 in Calvo & Lawrence, 2023; see also Baluška & Reber, 2019; Calvo & Trewavas, 2021; Mallatt et al., 2020; Taiz et al., 2019, 2020).

We do not believe it is useful to debate whether 'neurobiology' is the most appropriate term for organisms that lack neurons and synapses (Calvo & Lawrence, 2023). We agree that it is important to be cautious and critical with metaphors and analogies. The concept of 'neurobiology' might prove useful in understanding the physiology of chemicals and

electrical activity in plant cells. What justifies using concepts from animal neurobiology to characterize plant signaling and behavior? Even though plants do not have neurons and synapses that could give rise to a nervous system, restricting the term 'neurobiology' too tightly to neurons risks missing many molecular-level functional similarities between animal and plant signaling systems and substrates (Baluška and Mancuso, 2009a; 2009b; Baluška 2010).

A case in point is the capacity of plant cells to produce and support action potentials (APs) when exposed to different stimuli (Favre & Agosti, 2007; Felle & Zimmermann, 2007; Zimmermann et al., 2009). Lee and Calvo (2022) argue that even though textbook characterizations of APs focus primarily, and often uniquely, on those produced by neurons, the AP of plants "closely resembles those action potentials in animals" (p. 11). This is so despite the differences in their molecular components, resting potentials and speed of propagation. Plant APs exhibit the standard three-fold phase of depolarization, repolarization, and hyperpolarization. The APs play a role in several critical functions of plants, including respiration, photosynthesis and the movement of organs. This is illustrated in the well-studied examples of *Mimosa Pudica* and *Dionaea muscipula* (Venus flytrap) (Li et al., 2021; Volkov, 2006, 2012; Yokawa et al., 2018; 2019). In *D. muscipula*, APs are not only involved in shutting the trap, but also in initiating digestion, stopping the whole process if the prey is unsuitable (i.e., it is too small, or not food). This suggests that APs are important in the Venus flytrap's ability to count the episodes of hair mechanical stimulation continuously (see section 2.9) so as to avoid unnecessary expenditure of energy.

Damaging and non-damaging stimuli can evoke the generation and transmission of different types of electric signals. Apart from APs, plants also produce, through different molecular mechanisms of generation and transmission, short-distance electrical signals (local electrical potentials - LEPs) and long-distance ones such as variation potentials (VPs) and system potentials (SPs) (Debono & Souza, 2019; Gilroy et al., 2016; Vodeneev et al., 2015). Transmission properties of different types of electrical signals can differ significantly. LEPs, induced by environmental changes in the soil structure (watering, fertility, etc.), or above ground in light, temperature or relative humidity, can only be transmitted locally, between adjacent cells, due to high resistance. In such cases, propagation takes place via plasmodesmata channels along the cell membrane. When resistance is low, electrical signals can travel over longer distances, from sensor to effector sites, along vascular conduits distributed throughout the whole plant body via a complex network of bundles of phloem. This acts as the primary carrier, together with xylem and cambium pathways, depending on the type of signal in question (Baluška & Mancuso, 2009a, 2009b; Brenner et al., 2006; Huber & Bauerle, 2016; Souza et al., 2017; Trebacz et al., 2006). The vascular system composed of such bundles of phloem, xylem and cambium thus acts effectively as a long-distance inter-organ communication system (Calvo et al., 2020; Lucas et al., 2013).

VPs and SPs differ from APs in several ways. VPs contravene the all-or-none principle that characterizes APs, moving at a slower speed, with a shape that can vary depending on the intensity of the evoking stimuli. SPs and VPs also vary in their amplitude, decreasing as the signals spread away from the site of induction (Yan et al., 2009). Unlike APs, VPs and SPs are related to the regulation of the plasma membrane H+-ATPase. Inhibition of the

H+-ATPase initiates VPs, triggering membrane potential depolarization (Choi et al., 2017). Whereas VPs consist of depolarization events, SPs are long-distance hyperpolarization events (Zimmermann et al., 2016) that can propagate from leaf to leaf (Lee and Calvo, 2022). Irrespective of the variations in electrophysiological profiles, electrical signals have a significant and direct bearing on physiological activities underlying plant behavior, such as elongation, growth or reduction of turgor pressure. They also influence the rate of photosynthesis and transpiration, pollination and fertilization, and gene expression (Yan et al., 2009).

Chemicals known to play a role as neurotransmitters in animals, such as acetylcholine, glutamate, dopamine, histamine, noradrenalin, serotonin, and g-aminobutyric acid (GABA), are also found in plants (Volkov, 2017; Žárský, 2015). This is no surprise, as a vast array of molecular mechanisms (including ion channels) evolved prior to the emergence of animal nervous systems (Baluška & Levin, 2016). Some of these neurotransmitters, such as GABA, may be viewed as not merely metabolite but as a signalling molecule proper (Bouché et al., 2003; Bouché and Fromm, 2004).

[Glutamate too serves to increase calcium ion concentration, assisting in the propagation of the electrical signal throughout the plant after wounding (Toyota et al., 2018)](#) **[click to view].** This may well have implications our understanding the phylogenetic development of plant neurotransmitters (see Lee and Calvo, 2022).

As noted in the introduction, all this evidence has led Miguel-Tomé and Llinás (2021) to support the broadening of the scientific definition of "nervous system" so as to include plants, defining our target systems by what they do, and not by what types of tissues carry out the functions of interest. Using the same neurological terminology could help reveal what is going on when plants carry out the various cognitive functions that have been reported (Calvo and Lawrence, 2023).

Searching the vascular bases of natural behavior provides the opportunity to correlate plants' behavior and phyto-neural activity. Even though a thorough understanding of plant signaling is yet to be achieved, the current working hypothesis is that cells' electrical excitability and its propagation are partially responsible for the capacity of plants to respond to changing environmental conditions as coherent, globally organized units, rather than an amalgam of stimulus–response mechanisms. For more complete knowledge of how electrical conduction takes place in vascular cells, we must determine how electrical, hydraulic and chemical signaling pathways interact, triggering integrated and synergistic responses at the level of the plant system (Huber & Bauerle, 2016).

Producing such an integrated approach to plant signaling and behavior is the ultimate goal of PN. Some authors (Baluška, 2016; Calvo, 2017; Trewavas et al., 2020) have argued that the emerging field of PN can also provide a new way to approaching plant *sentience* scientifically. According to Calvo et al. (2017), aside from the obvious differences between the nervous systems of animals and the vascular systems of plants, "plants lack none of the functional structures that are supposedly needed [to be sentient]" (p. 205). Trewavas et al. (2020) hypothesize that "changes in levels of plant sentience will be consistently linked to changes in long-distance electrical signaling and vascular complexities" (p. 217). These authors propose time-lapse observations of plant behavior,

electrophysiological recordings, and phytohormone secretion as potential indicators of sentience in plants (see Calvo et al., 2017, 2021; Mediano et al., 2021).

One promising way to investigate plant sentience involves the use of anesthetics (Baluška & Yokawa, 2021; Baluška et al., 2016; Grémiaux et al., 2014; Jakšová et al., 2021; Tsuchiya, 2017; Yokawa et al., 2018). Not only do plants endogenously produce anesthetic compounds such as ethanol, ethylene and divinyl ether in their tissues when stressed (Grémiaux et al., 2014; Tsuchiya, 2017) but they respond to exogenously administered anesthetic treatments too. Venus flytrap (D. *muscipula*) snap-shutting behavior ceases under general anesthesia; the same occurs with the leaf-folding response of *M. pudica* after mechanical stimulation (Yokawa et al., 2018).[4]

The current working hypothesis is that anesthesia compromises the integrity of the plasma membrane by dissolving in the lipid bilayer, thereby altering key membrane properties (Jakšová et al., 2021; Pavlovič et al., 2022). According to this theory, anesthesia would affect plants similarly to the way it affects animals, namely, by disrupting the firing of APs (Lee and Calvo, 2022). In particular, anesthesia would act on the action-potential-inducing glutamate and on GABA (which are otherwise "animal" neurotransmitters) to inhibit the production of electrical signals. An alternative to this lipid (membrane) theory is the protein (receptor) theory (Pawson & Forsyth, 2008), according to which the membrane changes interfere somehow with receptor proteins.

Even though the mechanisms and biomolecular functions underlying how anesthetics disrupt plant behavior and responsiveness are not yet understood, Baluška and Yokawa (2021) suggest that since "[a]nesthesia in humans induces a loss of awareness" this "could also be hypothesized to occur for plants" (p. 2). It is possible that anesthetics not only disrupt plant behavior but shut down plant sentience or awareness altogether (Baluška et al., 2016; Calvo & Lawrence, 2023).

The idea of plant sentience has recently been contested by Taiz et al. (2019, 2020; Mallatt et al., 2020). Their argument is two-fold. They argue that "the capacity to process environmental information for adaptive behavior and subjective awareness of the environment are two different things" (Mallatt et al., 2020, p. 219); the latter depends on complex nervous systems and brains. Consequently, vertebrates (including fish), arthropods, and cephalopods are probably sentient, but plants are not (Mallatt et

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[4] "Effects of a volatile anaesthetic agent, diethyl ether, on plant movements. (A) The leaf-closing movement of Mimosa pudica under 15 % diethyl ether. After 1 h of treatment, leaves completely lost the response to touch stimuli. All leaves gradually recovered closure movement after 7 h following the removal of diethyl ether. (B) The rapid trap movement of Dionaea muscipula disappeared after 1 h of 15 % diethyl ether treatment." (Yokawa et al. 2018, p. 750)

Six direct links to the clips from Yokawa et al. (2018) on Mimosa *pudica* (MP) and Dionaea muscipula (Venus flytrap) (DM), before, during and after anesthesia **(click to view)**:
MPbefore MPduring MPafter DMbefore DMduring DMafter

al., 2020, p. 684). These authors also argue that plants do not need sentience, for their behavior is purely reactive and hardwired: "Instead of subjective consciousness, plants evolved adaptive behavior that is genetically determined by natural selection and epigenetically determined by environmental factors" (Mallatt et al., 2020, p. 218).

Two caveats are in order. First, as shown in section 2 of our target article, the view that plant behavior is completely determined either by genetic or environmental factors is highly debatable in face of the evidence. Second, even if we cannot rule out the possibility that sentience emerges from the activity of a sophisticated nervous system, we have no empirical reasons to exclude the possibility that other forms of life have evolved different structures for sentience, along lines such as the functional equivalence between the mammalian midbrain and insects cephalic ganglion (Barron & Klein, 2016). Hence, even if we agree that ascribing sentience to plants may be premature, inasmuch as there is no consensus on what biological features are required for it (Godfrey-Smith, 2017), concluding that plants are not sentient because they lack brains (or neurons, for that matter) is just an assumption and begs the very question we are trying to address.

4. Concluding remarks

More and more animal species are being considered as serious candidates for cognition and sentience, but plants still appear to be either excluded or forgotten in these conisderations. We agree that the consequences of ascribing cognitive capacities (and especially sentience) to plants must be very carefully weighed. Whether the object of scientific study is fellow humans, laboratory rodents or plants, we need to bear in mind that in all three cases cognitive capacities can only be inferred, and primarily from behavior. In human and nonhuman animal studies, behavioral inferences can be complemented by cognitive neuroimaging methods, such as frequency-modulated magnetic resonance imaging (fMRI) and positron-emission tomography (PET-scanning). In studies on humans and other animals these complementary methods have helped to test hypotheses not only about their cognitive abilities, but also about their sentient states. The study of cognition and sentience in plants likewise stands to benefit from future use of functional analogues of neuroimaging techniques (Mediano et al., 2021). The potential toolkit for this includes MRI in intact plants (Van As, 2007; Van As et al., 2009; Borisjuk et al., 2012), plant PET-scanning (Hubeau & Steppe, 2015) and protoneuronal surface imaging techniques (Debono, 2013).

We are aware of the extra burden of proof that research on plant sentience entails, and that more detailed knowledge of plant behaviors is needed before we can make any confident claims about whether they are sentient. But, irrespective of how much weight we put on the cognitive and sentient capacities of plants, the overall epistemic situation is not unlike the one that animal researchers face. As reviewed in section 2, the current evidence suggests that plants can adapt to their environments in flexible, context-sensitive and risk-sensitive ways. They are able to anticipate future contingencies and can perhaps even learn and remember. Thus, since plants turn out to exhibit many of the cognitive abilities formerly assumed to be exclusive to animals, there is no reason to assume that they are incapable of sentience too. Not only does list of potential cognitive

abilities to be investigated include decision-making, learning, memory, anticipation and communication; it includes 'valence' too -- the "organism's capacity to assign a value (advantage/good, harm/bad) to a particular stimulus or the summary of information about its surroundings relative to its own current state." (Lyon et al., 2021). Plants have evolved their own means of behaving adaptively, through phenotypic plasticity instead of locomotion, as in the case of animals. In escape tropisms, for example, plants are aided instead by their own endogenously generated electric signals in assigning a negative value to aversive stimuli (Yan et al., 2022; Yokawa et al., 2013). Hence there is no reason to suppose they could not have evolved their own physical structures for sentience too (Calvo et al., 2017).

Considerable caution is needed before reaching any conclusion, but, should the growing literature on plants' behavioral repertoires (section 2) and underlying electrochemical activity (section 3) yield compelling enough evidence of plant sentience, then the ethical implications for our treatment of plants will need to be considered too (Kallhoff et al., 2018). We hope that plant-related ethical decisions will be on the agenda in the future, or at least that the research findings reviewed in this target article are taken into account in the measures adopted for the protection of flora. In the study of plant sentience, we urge, between the romanticism and the denial, doing the science. Caring for plants can only benefit us all in the long run.

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