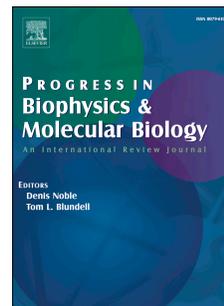


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## Do plants pay attention? A possible phenomenological-empirical approach

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### Abstract

Attention is the important ability of flexibly controlling limited cognitive resources. It ensures that organisms engage with the activities and stimuli that are relevant to their survival. Despite the cognitive capabilities of plants and their complex behavioural repertoire, the study of attention in plants has been largely neglected. In this article, we advance the hypothesis that plants are endowed with the ability of attaining attentive states. We depart from a transdisciplinary basis of philosophy, psychology, physics and plant ecophysiology to propose a framework that seeks to explain how plant attention might operate and how it could be studied empirically. In particular, the phenomenological approach seems particularly important to explain plant attention theoretically, and plant electrophysiology seems particularly suited to study it empirically. We propose the use of electrophysiological techniques as a viable way for studying it, and we revisit previous work to support our hypothesis. We conclude this essay with some remarks on future directions for the study of plant attention and its implications to botany.

**Keywords: Plant cognition; cognitive psychology; phenomenology; electrome; consciousness; complex systems**

### 1 Introduction

Broadly speaking, cognition can be defined as the process by which organisms perceive, process, value, store, and use environmental cues to increase their chances of survival (Calvo Garzón 2007; Shettleworth 2010; Souza et al. 2018; Lyon 2020). Once, it was believed that only organisms endowed with a central nervous system (CNS) and brains could be considered cognitive agents. However, cognition seems to be a far more widespread phenomenon. Indeed, many authors currently understand cognition as a *sine*

1 *qua non* phenomenon supporting life (Trewavas and Baluška 2011; Gagliano 2015;  
2 Varela et al. 2016; Lyon et al. 2021; Reber and Baluška 2021). This means that all  
3 organisms are, in essence, cognitive (Gagliano 2015; Baluška and Levin 2016; Varela et  
4 al. 2016; Cazalis et al. 2017; Lyon et al. 2021; Reber and Baluška 2021; Shapiro 2021).  
5 Indeed, amazing cognitive capabilities have been recognised even in non-neural  
6 organisms such as bacteria (Shapiro 2007; 2021), slime moulds (Latty and Beekman  
7 2011; Boussard et al. 2021), amoebae (Schaap 2021), fungi (Alekklett and Boddy 2021),  
8 and plants (Brenner et al. 2006; Trewavas 2003, Marder 2012, Calvo et al. 2020; Baluška  
9 and Mancuso 2021; Castiello 2021).

10 In this connection, many questions regarding the nature of non-neural cognition have  
11 been raised. For example, (1) *what* constitutes cognition in non-neural organisms; (2)  
12 *when* and *how* it is behaviourally expressed in these systems; and (3) whether  
13 investigating cognition in non-neural systems raises important evolutionary questions  
14 such as, are there limits to *where* and *when* cognition can evolve?

15 To address these questions, we need both a solid philosophical and epistemological basis  
16 as well as empirical data. To stay on the subject of plants—the focus of this work—it has  
17 been demonstrated that they are aware of their environment (Novoplansky 1991; Cahill  
18 Jr and McNickle 2011; Gagliano et al. 2017; Guerra et al. 2019; 2021a; White and  
19 Yamashita 2022); that they project future situations and act upon expectations in goal-  
20 oriented manners (Novoplansky 1991; Runyon et al. 2006; Shemesh et al. 2010; Gagliano  
21 et al. 2016; Gruntman et al. 2017); that they are able to make decisions (Runyon et al.  
22 2006; Gagliano et al. 2016; Gruntman et al. 2017; Née et al. 2017; Elhakeem et al. 2018);  
23 that they communicate with each other and with other organisms (Oldroyd 2013; Karban  
24 2015; Gilbert and Johnson 2017); and that they are able to store memories and learn  
25 (Amador-Vargas et al. 2014; Gagliano et al. 2014; Crisp et al. 2016; Souza et al. 2018;  
26 Galviz et al. 2020). There is even evidence of higher forms of learning in plants, such as  
27 learning by anticipation and association (Gagliano et al. 2016; Latzel and Münzbergová  
28 2018).

29 This is only the beginning, and many new scientific questions are yet to be addressed.  
30 One of these questions deals with the possibility that plants can be attentive toward certain  
31 environmental cues (Marder 2012, 2013; Parise et al. 2021). In other words, could a plant  
32 focus on specific environmental cues relevant to the accomplishment of a cognitive task,  
33 to the exclusion of other cues?

34 With this question in mind, we reviewed available literature and evaluated whether there  
35 is evidence supporting the hypothesis that plants are capable of attaining attentive states.  
36 We propose that this claim can be supported by studies on plant electrophysiology, at  
37 least at the level of plant organs. Electrophysiology is particularly important in this  
38 process because electrical signalling is one of the main routes for rapid information  
39 integration in the plant body when plants face environmental changes (Brenner et al.  
40 2006; Fromm and Lautner 2007; Baluška and Mancuso 2009a, b; Choi et al. 2016b; Huber  
41 and Bauerle 2016; de Toledo et al. 2019; Miguel-Tomé and Llinás 2021). Attention here  
42 is intended as a cognitive process that allows organisms to handle a selected piece of all  
43 the relevant information in the environment at the time (Grondin 2016). The main idea is  
44 that, by focusing on the most important environmental cues at the moment, the amount

1 of information to be dealt with is reduced so that the behavioural outcome is optimised  
2 (Castiello and Umiltà 1990). In this view, attention allows a more efficient investment of  
3 energy.

4 In this work, based on fields as diverse as psychology, philosophy, physics, and plant  
5 ecophysiology, we develop this hypothesis and propose an empirical approach to study  
6 the phenomenon of attention in plants. At the outset, we shall briefly outline the varieties  
7 of attention and how they are currently operationalised, focusing on how they could be  
8 applied to plants. Naturally, we cannot equate human attention to how plants function in  
9 their worlds, but we ask the reader to indulge us in using a terminology usually reserved  
10 for human experience throughout the review. In section 3, we approach the concept of  
11 attention within the phenomenological tradition and explore how it might be important to  
12 plant biology. Then, in sections 4 and 5, we shall discuss how studies on the electrome of  
13 plants could be useful to study attention in plants. We conclude our essay by discussing  
14 the potential implications of our hypothesis for botany and the life sciences in general.

15

## 16 **2 What is attention**

17 Attention is a topic widely discussed publicly and studied scientifically. It has  
18 many definitions within and across multiple fields including philosophy, psychology,  
19 neuroscience, and biology (Chun et al. 2011). As William James (1890) wrote at the dawn  
20 of experimental psychology, “Everyone knows what attention is. It is the taking  
21 possession by the mind, in clear, and vivid form, of one out of what seems several  
22 simultaneously possible objects or trains of thought.” Since James wrote this, many  
23 attempts have been made to more precisely define and quantify this process while also  
24 identifying the underlying biological architectures that give rise to it.

25 Attention is certainly far from a clear or unified concept. Yet, despite its many, vague,  
26 and sometimes conflicting definitions, there is a core quality of attention that is  
27 demonstrably of high importance to information processing in biological systems.  
28 Attention allows for the flexible control of limited cognitive resources (Kahneman 1973).  
29 Why those resources are limited and how they can best be controlled will vary across the  
30 cases, but the ability to dynamically alter and route the flow of information has clear  
31 benefits for the adaptiveness of any system.

32

### 33 **2.1 Varieties of attention**

34 The scientific study of attention began in psychology, where careful behavioural  
35 experimentation gave rise to precise demonstrations of the tendencies and abilities of  
36 attention in different circumstances (Driver 2001). Below, the broad classes of attention  
37 which could be operationalised in plants will be introduced.

38

#### 39 **2.1.1 Arousal, alertness, or vigilance**

40 In its most generic form, attention could be described as merely an overall level  
41 of alertness or ability to engage with surroundings. In this way, it partly overlaps with

1 arousal and the sleep-wake spectrum (Oken et al. 2006). In psychology, vigilance refers  
2 to the ability to sustain attention and is therefore related to it as well.

3 Studying organisms in different phases of the sleep-wake cycle or while on sedatives  
4 offers a view of how this form of attention can vary and what the behavioural  
5 consequences are. By giving subjects repetitive tasks that require a level of sustained  
6 attention—such as keeping a ball within a certain region on a screen—researchers have  
7 observed extended periods of poor performance in drowsy patients that correlate with  
8 changes in EEG signals (Makeig et al. 2000). Yet, there are ways in which tasks can be  
9 made more engaging that can lead to higher performance even in drowsy or sedated states.  
10 This includes increasing the promise of reward for performing the task, adding novelty  
11 or irregularity, or introducing stress (Oken et al. 2006). Therefore, general attention  
12 appears to have limited reserves that will not be deployed in the case of a mundane or  
13 insufficiently rewarding task but can be called upon for more promising or interesting  
14 work (Oken et al. 2006).

15 This variety of attention may be seen in plants when they must keep track of a number of  
16 environmental features throughout days or months in order to regulate its growth and  
17 development. For example, many tropical and subtropical tree species from  
18 semideciduous forests rely on the increasing daylight to trigger blossoming, in spite of  
19 the variation of other environmental factors like rain and temperature (Rivera et al. 2002).  
20 On the other hand, in temperate regions, trees rely on the photoperiod and also other  
21 factors like temperature to regulate seasonal growth (Maurya and Bhalerao 2017). The  
22 study of plant dormancy and photoperiodism could be fruitful to investigate this kind of  
23 attention in plants, because plants must keep ‘focused’ on the gradual variations of certain  
24 environmental features over time to trigger certain behaviours.

25

### 26 **2.1.2 Selective attention and the control of action**

27 Most of research on attention has viewed selection as essentially a perceptual  
28 problem, with attentional mechanisms required to protect the senses from overload. While  
29 this may indeed be one of several functions that attention serves, the need for selection  
30 also arises when one considers the requirement of actions rather than perception. In fact,  
31 some theories of attention, such as the pre-motor theory of attention (Rizzolatti et al.  
32 1987), posit that attention can be operationalised through action (Rizzolatti et al. 1987).

33 Allport (1987) defined this aspect of the selective integration problem as “selection-for-  
34 action”. For example, when choosing a piece of fruit from a bowl, many fruits are visible  
35 and within the reaching space, but only the one that we desire governs the particular  
36 pattern and direction of movement. How is the motor output for reaching and grasping  
37 that particular fruit selected? Where is the locus of this selection? Do the other fruits,  
38 different in size, shape, colour and weight, produce interference? Overall, this theory  
39 suggests a predominant role for attention in shaping behaviour through influencing motor  
40 output (Castiello 1999).

41 Yet, not all actions involve movement, especially in the case of plants. Acclimation,  
42 variations in the transpiration rate, adjustments in photosynthetic rate and other metabolic  
43 adjustments are typical plant actions that do not require movement, while other actions  
44 like climbing, blooming, sun-tracking and capturing prey (in the case of carnivorous

1 plants) obviously do. Climbing plants growing in a complex environment like a tree  
2 crown or a fence, for example, need to select among many different possible supports and  
3 organise their movements and growth to secure the correct reaching and grasping  
4 behaviours to accomplish their goals. The study of the behaviour of climbing species can  
5 be useful for understanding whether this kind of attention happens in plants. For example,  
6 Guerra et al. (2019) demonstrated that the garden pea plant (*Pisum sativum* L.) can  
7 perceive a support nearby and modulate the kinematics and aperture of its tendrils  
8 depending on the supports' thickness. Thicker supports elicit a kinematical pattern  
9 suggestive of a more demanding processing than thinner supports. This phenomenon can  
10 be explained in attentional terms given that deploying attention for the processing of a  
11 greater area might be more energy-consuming than deploying attention on a smaller  
12 surface (Castiello and Umiltà 1992). In the case of climbers, the extra processing might  
13 be needed to scan a thicker support so as to select with greater precision the contact points  
14 for efficiently establishing a firm hold of the support.

15

### 16 **2.1.3 Feature attention**

17 Feature attention is another form of selective attention. In the study of feature  
18 attention, instead of being cued to attend to a particular location, subjects are cued in each  
19 trial to attend to a particular feature such as a specific colour, a particular shape, or a  
20 certain orientation (Rossi and Paradiso 1995). The goal of the task may be to detect the  
21 cued feature presented on the screen, or readout another one of its qualities (e.g., to answer  
22 'what colour is the square?' should result in attention firstly deployed to squares).

23 A closely related topic to feature attention is object attention (Chen 2012). Here, attention  
24 is not deployed to an abstract feature in advance of a visual stimulus, but rather it is  
25 applied to a particular object in the visual scene. The initial feedforward pass of activity  
26 through the visual hierarchy is able to pre-attentively segregate objects from their  
27 backgrounds in parallel across the visual field, provided these objects have stark and  
28 salient differences from the background. In more crowded or complex visual scenes,  
29 recurrent and serial processing is needed in order to identify different objects. Serial  
30 processing involves moving limited attentional resources from one location in the image  
31 to another. The question of how it is possible to perform perceptual grouping of low-level  
32 features into a coherent object identity. It is believed that attention may be required for  
33 grouping, particularly for novel or complex objects. In the case of plants, this may be  
34 especially important for the detection of obstacles by the roots, which require locating an  
35 object that is defined by a conjunction of several features present in the soil (e.g., a small  
36 rock surrounded by soft soil).

37

### 38 **2.1.4 Attention in other sensory modalities**

39 A famous example of the need for selective attention in audition is the "cocktail  
40 party problem": the difficulty of focusing on the speech from one speaker in a crowded  
41 room of multiple speakers and other noises (Cherry 1953). Solving the problem is  
42 believed to involve 'early' selection wherein low-level features of a voice such as pitch  
43 are used to determine which auditory information is passed on for further linguistic

1 processing. Interestingly, selective auditory attention has the ability to control neural  
2 activity even at the earliest level of auditory processing, the cochlea. Obviously, plants  
3 do not have such organ, but they have a rich sensorial system that detects a multitude of  
4 different stimuli at the same time (Karban 2015) and they need to be able to prioritise  
5 some stimuli over others depending on what they are experiencing.

6

### 7 **2.1.5 Attention and memory**

8 Attention and memory have many possible forms of interaction. If memory has a  
9 limited capacity, for example, it makes sense to be selective about which information is  
10 allowed to be stored. For plants, in particular, storing memories has high metabolic costs  
11 because all the plant tissues are constantly being renewed and therefore memories should  
12 be actively maintained and transferred from the decaying tissues to the new ones, which  
13 limits its capacity of storing information in the long run (Thellier and Lüttge 2012; Galviz  
14 et al. 2020). In this way, the ability of attention to dynamically select a subset of total  
15 information is well-matched to the needs of the memory systems. In the other direction,  
16 deciding to recall a specific memory is a choice about how to deploy limited resources.  
17 Therefore, both memory encoding and retrieval can rely on attention. Many behavioural  
18 studies have explored the extent to which attention is needed for memory retrieval (Lozito  
19 and Mulligan 2006).

20 Even if memory retrieval does not pull from shared attentional resources, it is still clear  
21 that some memories are selected for more vivid retrieval at any given moment than others.  
22 Therefore, a selection process must occur (Wagner et al. 2005). Adaptation can also be  
23 considered as implicitly requiring memory. Here, responses may decrease or increase  
24 after repeated exposure to the same stimulus. Attention by increasing the response to  
25 attended stimuli would have effects on adaptation. We will discuss this further in Section  
26 6.

27

## 28 **3 A phenomenological theory of attention**

29 Philosophers have studied attention since the turn of the last century within the  
30 phenomenological tradition pioneered by Husserl (1913[1983]). For Husserl, attention in  
31 the human cognitive realm coincides with intentionality, that is, with the dynamic  
32 directedness of the awareness toward its object. Importantly, in the early  
33 phenomenological framework, consciousness or awareness is already understood as  
34 selectivity (Marder 2013), as the uneven and shifting focus on some stimuli at the expense  
35 of others that recede to a vague background of living experience but that can stand out in  
36 the sphere of attention in light of the changing circumstances and needs. That is to say,  
37 phenomenology understands awareness as attention and attention as awareness in an  
38 organism's real-time engagements with the surrounding world.

39 An important implication of the phenomenological theory of attention, developed later  
40 on by Gurwitsch (1966), Arvidson (2006), and Marder (2009, 2011), is that all modes of  
41 awareness are necessarily attentive. But the specificity of attention also needs to be  
42 established in order not to conflate its concept with that of awareness, on the one hand,  
43 and sensitivity, on the other. While the dynamic phenomenological theory of awareness

1 comprehends it as a tending of intentionality to the intended object, attention, within  
2 multiple and potentially mutually contradictory tendencies of intentionality, is the focus,  
3 capable of undergoing modulations and characterised by uneven investments of energy  
4 at the expense of backgrounded stimuli. The focus of attention implies a prior decision,  
5 which may not itself rise to the level of conscious representation and which singles out a  
6 stimulus or a set of stimuli among many competing ones that is worth attending to. As  
7 such, it implies a disproportionately greater investment of energy compared to other such  
8 stimuli. Crucially, attention is the foundation for future-oriented anticipation and  
9 decision-making (projection), as much as for the past-oriented memory (retention). It is,  
10 therefore, the basis of psychical life (Husserl 1913[1983]).

11 Formulated as such, the concept of attention allows us to understand it as a wider  
12 phenomenon that encompasses all and every living organism, or even part of it, regardless  
13 of the presence of a CNS. Therefore, one is free to explore empirically the phenomenon  
14 in whatever organism one decides to study. Since this essay explores plants, we will focus  
15 on them, but this approach could be useful to explore the concept of attention in other  
16 organisms as well, particularly those that live without a CNS, like fungi, sea sponges, and  
17 the like, or even in subsystems within an organism, such as the immune system.

18 The topic of plant attention has not been much discussed in the literature until Marder  
19 (2013). He used a phenomenological approach to provide a non-zoocentric definition of  
20 attention. According to him, attention is “a disproportionate investment of physical or  
21 mental energy by an organism, tissue, or cell, into a particular activity or into the reception  
22 of a singled-out stimulus or set of stimuli” (Marder 2013). Therefore, plant attention  
23 would be equivalent to the singling out of stimuli among those that are already meaningful  
24 to plants (for example, humidity gradients, red/far-red light, and so on) in keeping with  
25 (1) the changing environmental conditions, (2) the plants’ physiological states and goals,  
26 and (3) the interaction of (1) and (2).

27 In this perspective, the concept of plant attention is conceivable when considering the  
28 cognitive capabilities of plants. For example, studies with climbing plants suggest that  
29 these plants actively search for a support with their aboveground organs and tendrils  
30 (Runyon et al. 2006; Guerra et al. 2019; Ceccarini et al. 2020). An active search singles  
31 out what is being searched in keeping with an attentive energy investment. The goal-  
32 oriented behaviour of some plants, which involves *en route* trials and correction of errors,  
33 can also be seen as requiring attention (Schwartz and Koller 1986; Elhakeem et al. 2018;  
34 Raja et al. 2020; White and Yamashita 2022). At minimum, the orientation to a goal  
35 implies attention to the goal itself and to the means for accomplishing it. The Venus  
36 flytrap, (*Dionaea muscipula* J.Ellis), counts the number of times an insect hits the  
37 trichomes of its lobes to know whether it needs to close its traps and when to do it (Böhm  
38 et al. 2016). The first time the trichome is triggered requires attention to the following  
39 stimulus (as well as the memory of the preceding one), which must occur within a limited  
40 amount of time to fire the trap (Hodick and Sievers 1988; Volkov et al. 2008; Böhm et al.  
41 2016). Keeping high intracellular levels of calcium seems to be involved in the process  
42 (Hodick and Sievers 1988; Suda et al. 2020). Even phototropism towards white/blue light  
43 observed in many plants requires attention. Despite the fluctuating conditions of the  
44 environment (including day-night alternations), the plant keeps growing towards the  
45 source of light, which is the singled-out stimulus in its sphere of attention. The positive

1 and negative tropisms of roots can also be accounted for as good examples of processes  
2 that require attention because in spite of other stimuli like touch or light being present,  
3 the plant organ follows the gravity gradient to direct its growth.

4 Due to the intrinsic modularity of plants, attention could be deployed even by plant organs  
5 or modules. For instance, root apices following gradients of or cues for minerals,  
6 nutrients, and water could be interpreted as examples of behaviours that require attention.  
7 Roots receive a plethora of stimuli such as low-light gradients, touch by small animals,  
8 interactions with pathogens and symbiotic microorganisms, sounds etc. Still, they are not  
9 ‘distracted’ from their main goal, which is finding one or another resource (Robinson et  
10 al. 1999; Baluška et al. 2009; Giehl and von Wirén 2014; Gagliano et al. 2017; Baluška  
11 et al. 2021). The ability of root apices to follow environmental cues and direct the  
12 movements of the root were recognised by Darwin already in the 19<sup>th</sup> century (Darwin  
13 and Darwin 1880); and also here, the involvement of electrical signalling seems to be  
14 critical to these behaviours (Masi et al. 2009, 2015; Baluška and Mancuso 2013b).

15 However, as interesting as they may seem, none of the examples mentioned above allow  
16 an experimental inference of the attentional processes in plants. We have observed the  
17 external behaviour of these organisms, but not what is going on inside them in cognitive  
18 terms. How do the shifts of plant attention happen? What does an attentive state in a plant  
19 entail? Besides, the kind of attentional behaviour plants display is completely different  
20 from the one that humans and animals display, not least because behaviour is defined and  
21 expressed differently in plants than it is in humans and non-sessile animals. A plant-  
22 specific method to verify plant attention is needed if we want to progress in this  
23 discussion. Along these lines, a possible and promising path is to investigate the  
24 phenomenon of plant attention through the study of the overall bioelectrical activity of  
25 plants, named plant electrome, which we shall detail below. Such an investigation will  
26 begin to provide an answer to the question of how to investigate the attention of plants  
27 empirically.

28

#### 29 **4 Plant electrome: “the electrical dimension of plant life”**

30 The phrase quoted above is from the title of de Toledo et al.’s (2019) review on  
31 plant electrome and it reflects the fundamental importance of this phenomenon to the life  
32 of plants. The term “electrome” was coined by De Loof (2016) to refer to the totality of  
33 electrical activity that happens in an organism or a part of it in a stretch of time. This is  
34 the sum of all electrical processes, including cell membrane depolarisations, ion fluxes,  
35 electrical transport chains in mitochondria and chloroplasts, among others. All these  
36 electrical activities interact constantly leading to the emergence of patterns, which are  
37 observable at higher scales. A very familiar example of electromic measurements in  
38 humans is the electroencephalograms (EEGs).

39 In EEGs, despite the noisy and complex characteristic of the signals, there are well-known  
40 recognisable patterns and features related with different processes. External stimuli,  
41 including the physical, chemical, social, and emotional varieties, together with many  
42 drugs and anaesthetics, are responsible for specific traits on human and non-human EEGs.  
43 The EEGs also reflect diverse emotional states and states of consciousness, and they

1 change depending on the cognitive tasks performed by the subjects, such as learning and  
2 attention (Lehmann et al. 2001; Chialvo 2010; Rubinov et al. 2011; He 2014; Meisel et  
3 al. 2012).

4 Among the stimuli/state-dependent features observed in EEGs, there are brain waves,  
5 described by a band of frequencies (Berthouze et al. 2010; Chialvo 2010). Attention in  
6 humans is commonly associated with gamma waves, which range from 25 to 140 Hz.  
7 These waves are considered the highest band-frequency and are credited as the most  
8 powerful in brain information processing, since they are also associated with problem-  
9 solving, learning, and mindfulness meditation (de Arcangelis and Herrmann 2010). The  
10 electrical signals of plants do not have such high frequencies because plant cells cannot  
11 produce APs with such frequencies (Volkov 2006). Nevertheless, different plant electrical  
12 signals combined also result in waves with varied frequencies that usually reflect the  
13 plant's states under the influence of external stimuli (de Toledo et al. 2019).

14 The combination of the entire electrical activity of plants generates their electrome (De  
15 Loof 2016; Souza et al. 2017). Plants can produce electrical signals by the same  
16 mechanisms as animals do, i.e., transient variations of membrane potential due to uneven  
17 concentration of ions in both sides of cell membranes. In plants, however, the main ion  
18 involved in membrane variations of potential is calcium ( $\text{Ca}^{2+}$ ). When plant cells are at a  
19 resting state,  $\text{Ca}^{2+}$  ions concentrate mainly in the apoplast, while the cytoplasm is  
20 negatively charged. This creates an electrical tension in the cell membrane. Different  
21 stimuli may trigger the opening of stimulus-specific calcium channels in cell membrane,  
22 allowing the influx of  $\text{Ca}^{2+}$  to the cytoplasm. There are hundreds of such channels in  
23 plants, which are sensitive to a panoply of stimuli like stretching, mechanical pressure,  
24 variations of electric potential, neurotransmitters (e.g., glutamate), light stimuli and  
25 chemicals (Hedrich 2012; Canales et al. 2018; Cuin et al. 2018). These channels are  
26 expressed differently depending on the tissue and the age of the cells, and are sorted and  
27 transported to the membranes by specific proteins (Canales et al. 2018; Wudick et al.  
28 2018).

29 Depending on the  $\text{Ca}^{2+}$  channels stimulated, different electrical signals are triggered. In  
30 contrast to animal cells, which normally produce solely action potentials (APs)—a rapid  
31 and transient self-propagable depolarisation event that depends on a critical threshold to  
32 be fired following an all-or-nothing principle, and that has a fixed size—, plants produce  
33 at least three others beyond APs: (1) Variation potentials (VPs), which are similar to APs,  
34 but do not depend on a threshold, are not self-propagable, and involve the temporary  
35 inactivation of the  $\text{H}^+$ -ATPase pumps that otherwise would rapidly restore the membrane  
36 potential (Stahlberg et al. 2006; Yan et al. 2009; Vodenev et al. 2016); (2) systemic  
37 potentials (SPs), which are self-propagable but do not follow the all-or-nothing principle,  
38 and are characterised by a hyperpolarisation of the cell membrane, instead of a  
39 depolarisation (Zimmermann et al. 2009; 2016); and, finally, (3) local electrical potentials  
40 (LEPs), which are triggered when there is a brief inactivation of the  $\text{H}^+$ -ATPases and the  
41 amplitude of which depends on the intensity of the stimulus (Yan et al. 2009; Sukhova et  
42 al. 2017).

43 All of these signals can be produced at the same time in the same or different tissues,  
44 depending on the stimulus received; they can be combined and integrated by the plant;

1 and they travel throughout the plant from cell to cell through the plasmodesmata and,  
2 especially, the long sieve tubes of the phloem (van Bel et al. 2013; Choi et al. 2016a, b;  
3 Hedrich et al. 2016). In exceptional cases, VPs presumably can also travel through the  
4 vases of the xylem (see Vodeneev et al. 2016). However, this whole-plant intense  
5 signalling does not need to be triggered by an external stimulus or set of stimuli. It is  
6 known that plants have a basal, non-evoked electrical signalling that occurs all the time  
7 and is characteristic of each individual plant (Bose 1926; Sheperd 2005, 2012; Debono  
8 2013). This is the plant electrome. The electrome emerges from the interaction of all the  
9 electrical activity of plants, and it changes its dynamics depending on what the plant is  
10 experiencing or doing (Souza et al. 2017; de Toledo et al. 2019). Therefore, shifts in light  
11 intensity, irrigation or drought, cold, osmotic stresses, infection by pathogens, and  
12 virtually everything a plant perceives, even the detection of other plants nearby, alter the  
13 dynamic of its internal electrical signalling (Fromm and Lautner 2007; Gil et al. 2008;  
14 Asai et al. 2009; Gallé et al. 2015; Saraiva et al. 2017; Souza et al. 2017; Szechyńska-  
15 Hebda et al. 2017; de Toledo et al. 2019; Simmi et al. 2020; Parise et al. 2021).

16 The connection of the electrome with the plant's sensorial world, its behaviour, and eco-  
17 physiological activities, is supposed to be so tight that Debono and Souza (2019),  
18 following a mesological approach, proposed it as an interface between the plant's internal  
19 processes and the world. With the available evidence, it seems that everything a plant  
20 does in the world alters its electrome, and every stimulus from the world does the same.  
21 Indeed, changes in the electrome are not random and are related to each specific stimulus.  
22 Thus, the electrome has stimuli-dependent patterns, and these patterns in the electrical  
23 activity can be recognised and classified by machine learning algorithms (Pereira et al.  
24 2018; Simmi et al. 2020; Parise et al. 2021; Najdenovska et al. 2021; Reissig et al. 2021).  
25 Consequently, the analysis of the electrome is an excellent tool for observing the effects  
26 of the different physiological activities of a plant and the impact of environmental  
27 fluctuations on it.

28 The movement of charges inside the plant generates an electrical field. Since plants are  
29 three-dimensional, they cannot be described as an electrical circuit, and the vectorial  
30 characteristic of its electrical field cannot be ignored. However, the vectorial function that  
31 describes an electrical field ( $\vec{E}$ ) is very special because its rotational is always null.  
32 According to the Stokes' theorem, the electrical field can be described as:

33 
$$\vec{E} = -\vec{\nabla}V$$

34 Where the electrical field (vector) is equal to minus one gradient (vector,  $\vec{\nabla}$ ) of the scalar  
35 potential (number,  $V$ ), which is called electrical potential. In other words, we can work  
36 with numbers and not vectors. In the end, calculating its gradient suffices to return to the  
37 real result of the electrical field. The electrical potential is a mathematical construct  
38 created to aid the characterisation of an electrical field. The electrical potential is not real;  
39 the electrical field is.

40 When we analyse the electrical field in biological studies, we normally intend to observe  
41 the frequency with which electrical fields oscillate. All the movements of charged  
42 particles within a cell or tissue create an electrical field that shifts from positive to  
43 negative, depending, e.g., on the frequency with which ion channels in the membranes

1 open or close. This, aligned with many other activities that generate electrodynamics  
2 inside the cells (like the electron transport chain in the membranes of the thylakoids, the  
3 transport of protons, and so forth), results in an electrical field that can run long distances  
4 in plants, oscillating in specific frequencies that may contain information (Baluška and  
5 Mancuso 2013a, b; De Loof 2016; de Toledo 2019).

6 Therefore, the electrophotographic technique is used to study the electrical field of plant  
7 tissues, which corresponds to its electrome. The electrodes interact with this field and  
8 allow the observation of its dynamics. Since it is not easy to measure the electrical field  
9 of a three-dimensional structure, the use of its electrical potential ( $V$ ) is a necessary  
10 mathematical interface for this analysis.

11 To record the plant electrome, conversely, is quite simple. It requires, for example, needle  
12 electrodes that are inserted in a particular part of the plant, a device to amplify and clear  
13 the signals recorded, and a specific software for the analysis of the time series obtained.  
14 The time series ( $\Delta V$ ) are composed by numerous measurements of potential variation  
15 ( $\Delta V$ ) by a pair of electrodes during a stretch of time. Therefore,  $\Delta V = \{\Delta V_1, \Delta V_2, \dots, \Delta V_N\}$ ,  
16 where  $\Delta V_i$  is the difference of potential between the electrodes and  $N$  is the length of the  
17 time series (Saraiva et al. 2017).

18 Beyond machine-learning algorithms, time series can be analysed by many other  
19 techniques to uncover the traits of the plant electrome, some of them classical in  
20 electrophysiology in general. In this essay, by way of concision, we will explore only  
21 those we believe are useful for inferring the phenomenon of attention in plants. For a  
22 more detailed account on the plant electrome, please see de Toledo et al. (2019) and  
23 references therein.

24 Some quantitative techniques commonly used to analyse the plant electrome are  
25 presented below.

26

#### 27 **4.1 Mean of the variation of potential**

28 The mean of the variation of electrical potential ( $\Delta V$ ) between electrodes is a quite  
29 simplistic measurement. However, it can provide some information on the general  
30 behaviour of a time series. For example, an increase in the activity of the ion channels  
31 can result in higher use of energy, for the repolarisation of the cell membrane requires  
32 ATP consumption. Bioelectrically, it may be reflected in wider  $\Delta V$  events due to the  
33 increased occurrence of  $\Delta V$  spikes, which may appear as an increase in its mean value (de  
34 Toledo et al. 2019; Parise et al. 2021). This, in turn, aligned with the other analyses  
35 described below, may suggest that more attention is being paid, if we keep to our  
36 definition of attention as the dynamic simplification, selectivity, and disproportionate  
37 investment of energy in response to some stimuli but not others.

38 It is important to note, though, that the absence of an increase in the mean of  $\Delta V$  does not  
39 necessarily reflect the absence of an increase in energy expenditure. The ion channels can  
40 intensify its activity without causing high spikes of  $\Delta V$ , but rather increasing the  
41 frequency with which the  $\Delta V$  events occur, which is also suggestive of higher energy  
42 consumption. The increase in the frequencies can be assessed by techniques such as the

1 Fast Fourier Transform (FFT). In the studies presented here, the FFT was not used as a  
 2 measure to compare the plant's electrome before and after some stimulus, but it was  
 3 incorporated into other analyses such as the Power Spectrum Density (PSD). However, it  
 4 has potential to infer higher energy expenditure in the cases mentioned.

5

## 6 **4.2 Autocorrelation and Power Spectral Density function**

7 Electrophysiological time series are not homogeneous, but rather composed of  
 8 many different frequencies with diverse signal amplitudes, which result in very complex  
 9 dynamics. In order to analyse these signals, one strategy is to “cut” the time series in  
 10 “pieces” and compare each piece with the piece before it, which allows us to disclose  
 11 patterns in the time series and helps to understand its dynamics. This method is called  
 12 autocorrelation.

13 Autocorrelation is a measure of the correlation of an event with this same event with a  
 14 lag of time. The higher the autocorrelation value, the higher the amount of time between  
 15 two correlated events in a time series. Therefore, it indicates how long into the future the  
 16 influence of an event lasts. In the case of the electrome, it indicates how much an event  
 17 of variation of tension influences other events further in the time series. It is calculated  
 18 using Pearson's correlation:

$$19 \quad \rho(\tau) = \frac{\langle (x - \langle x \rangle) \cdot (y_{\tau+i} - \langle y_{\tau} \rangle) \rangle}{\sigma x \cdot \sigma y}$$

20 Where  $-1 \leq \rho(\tau) \leq 1$ ,  $\tau$  is the time lag,  $\langle \dots \rangle$  represents a mean,  $\langle x \rangle = \frac{1}{N} \sum_{i=1}^N x_i$ ,

$$21 \quad \langle y \rangle = \frac{1}{N-t+1} \sum_{i=1}^N y_i, \quad \sigma x = \sqrt{\frac{1}{N} \sum_{i=1}^N (x_i - \langle x \rangle)^2}, \quad \text{and} \quad \sigma y =$$

$$22 \quad \sqrt{\frac{1}{N-\tau+N} \sum_{i=\tau}^N (y_i - \langle y_{\tau} \rangle)^2}. \text{ When } \rho(\tau) > 0, \text{ the variables are positively correlated, and}$$

23 when  $\rho(\tau) < 0$ , they are negatively correlated. If  $\rho(\tau) = 0$ , the variables are not linearly  
 24 correlated. To obtain the autocorrelation function, we consider  $x = \Delta V$ , and  $y = \Delta V_{(\tau)}$ .

25 Therefore, we have a function to the same variable  $\Delta V$  lagged in  $\tau$  (Saraiva et al. 2017).

26 The Power Spectral Density (PSD) Function is used to study how the power of the  $\Delta V$   
 27 events is distributed in each unit of time of the time series. The PSD,  $S_x(f)$ , is defined  
 28 as:

$$29 \quad S_x(f) = F[R_x(\tau)] = \int_{-\infty}^{\infty} R_x(\tau) e^{-2j\pi f \tau} d\tau$$

30 Where  $j = \sqrt{-1}$ , being  $X(t)$  a random stationary signal with an autocorrelation given by  
 31 the function  $R_x(\tau)$ . The equation above conveys that the PSD function can be described  
 32 as the Fourier Transform of its autocorrelation  $R_x(\tau)$ . This is the formal definition of PSD  
 33 (Howard 2002). As a measure of the power contained in the signals, the PSD can be used  
 34 to understand how the power of the signals vary through time.

35 Previous studies on the characteristics of the plant electrome have yielded the conclusion  
 36 that the function that describes the probability of the occurrence of spike-like  $\Delta V$  events,

1 with their different amplitudes, is a power law (Saraiva et al. 2017; Souza et al. 2018;  
 2 Simmi et al. 2020; Parise et al. 2021). This means that these events have no typical size  
 3 or frequency of occurrence, and they cannot be predicted. Phenomena described by power  
 4 laws typically show scale-invariance and fractality, and are widespread in nature. For  
 5 example, the number of neuron synapses, the occurrence and magnitude of earthquakes,  
 6 the outbreak of epidemics, the occurrence of solar flares, the size and distribution of  
 7 burned patches and tree gaps in a forest, and so on, are described by power laws (Bak  
 8 1996; Gisier 2001; Filotas et al. 2014; Souza et al. 2017). Power laws are indicative of  
 9 self-organised systems in critical states, for they are more likely to appear when a system  
 10 is close to the critical point of changing its state (Bak et al. 1996). This means that the  
 11 spike-like  $\Delta V$  events of a plant electrome display a highly complex dynamics, present  
 12 fractality in their organisation (i.e., are scale invariant), and bear information (Saraiva et  
 13 al. 2017; Souza et al. 2017). When we analyse the electrome as noise, we observe that the  
 14 PSD can be described by a power law given by the equation:

$$15 \quad S_x(f) = \frac{1}{f^\beta}$$

16 In the time series observed in nature, the value of the exponent  $\beta$  typically varies between  
 17 0 and 3. Exponent  $\beta = 0$  indicates random, stochastic dynamics. It is called ‘white noise’  
 18 in reference to white light because all the segments of the spectrum are equally mixed. If  
 19 the exponent is 3, it indicates absolute regularity and predictability of the signals. Values  
 20 close to this exponent are found in fairly regular events such as the Nile River minima  
 21 and the annual precipitation regime at St Lawrence Estuary, Canada (Mandelbrot and  
 22 Wallis 1969; Cuddington and Yodzis 1999). When  $\beta = 3$ , the resultant noise is called  
 23 black. Both white and black noise have little capacity to convey information because  
 24 either they are absolutely random or strictly regular. When the exponent approaches 1, it  
 25 indicates the most complex dynamics, with long-range correlations in the signals, and  
 26 highest scale invariance, i.e., new information can be found at all the levels of  
 27 organisation of the signals (Gisier 2001). It is traditionally called pink noise (because of  
 28 the spectral similarity with red/pink light), or 1/f noise.  $\beta = 2$  is called brown noise  
 29 because of the similarity with Brownian movement that the function with this exponent  
 30 describes.

31 We have observed that the range of the plant electromes we have studied normally lies  
 32 around 1 and 2 (Saraiva et al. 2017; Souza et al. 2017; Simmi et al. 2020; Parise et al.  
 33 2021), between complete regularity and absolute randomness, “between crystal and  
 34 smoke”, in the words of Henri Atlan (1979), which characterises phenomena with high  
 35 complexity. Besides, the electrome dynamics are variable and, depending on what the  
 36 plant is experiencing or doing, they may change, becoming more complex or more  
 37 regular. Consequently, these alterations are reflected in the exponent  $\beta$  of the PSD. It has  
 38 been observed that plants under stress show an increase in the value of the exponent  $\beta$ ,  
 39 distancing the noise from 1/f, which had been previously identified as an indication of a  
 40 compromised system (Saraiva et al. 2017; Souza et al. 2017). This may not be the only  
 41 explanation for the increase, as we will see below.

42 Furthermore, 1/f-like behaviour in EEG from human brains can be a signature of learning  
 43 process (de Arcangelis and Herrmann 2010), which is also an insightful hypothesis for

1 plants, taking into account the evidence mentioned above for SOC behaviour in the plant  
 2 electrome. It is even more interesting since it is expected that a previous state of attention  
 3 would be necessary for efficient learning acquisition.

#### 4 4.3 Approximate Entropy as a measure of complexity

6 Considering the behaviour and the complexity of chaotic systems like the  
 7 electrome, Pincus (1991, 1995) developed the Approximate Entropy (*ApEn*) analysis  
 8 which is, in a few words, a measure of the complexity of time series dynamics. The *ApEn*  
 9 was developed with the assumption that time series possess repetitive patterns that make  
 10 them predictable. It calculates the probability of similar patterns to appear along a time  
 11 series, which provides information on the predictability, or regularity, of its dynamics. In  
 12 other words, repetitive time series (less complex) earn low values of *ApEn*, and more  
 13 random time series return higher values. More specifically, deterministic time series  
 14 result in a value of  $ApEn = 0$ , and the higher the *ApEn* value, the more random the time  
 15 series is, until reaching its maximum values, which indicate total randomness and  
 16 consequently absence of complexity. The most complex time series are situated between  
 17 the two extremes.

18 The *ApEn* has been used in medicine to analyse electroencephalograms and  
 19 electrocardiograms (Costa et al. 2005), and is also useful for the analysis of  
 20 electrophytograms (e.g., Saraiva et al. 2017; Souza et al. 2017; Simmi et al. 2020; Parise  
 21 et al. 2021). One problem that may arise from this analysis is that the measurement of the  
 22 time series in only one scale can provide misleading information on the complexity of the  
 23 system, for example, indicating an increase in complexity when it should be less complex  
 24 (Costa et al. 2005). This problem can be overcome when we analyse the *ApEn* of the same  
 25 time series on many different scales. In this case, Multiscale Approximate Entropy  
 26 ( $ApEn(s)$ ) is employed. With this technique, the time series is divided into different blocks  
 27 of increasing size  $s$ , then the arithmetic mean of the values within each block is calculated,  
 28 and the *ApEn* of each time series is obtained. For example, the original time series  $\Delta V =$   
 29  $\{\Delta V_1, \Delta V_2, \dots, \Delta V_N\}$  is  $s = 1$ . For  $s = 2$ , we calculate the *ApEn* of:

$$30 \quad \Delta V_{s=2} = \{(\Delta V_1 + \Delta V_2)/2, (\Delta V_3 + \Delta V_4)/2, (\Delta V_5 + \Delta V_6)/2, \dots, (\Delta V_{N-1} + \Delta V_N)/2\}$$

31 For  $s = 3$ , we calculate the *ApEn* of:

$$32 \quad \Delta V_{s=3} = \{(\Delta V_1 + \Delta V_2 + \Delta V_3)/3, (\Delta V_4 + \Delta V_5 + \Delta V_6)/3, \dots, (\Delta V_{N-2} + \Delta V_{N-1} + \Delta V_N)/3\}$$

33 And so forth, obtaining the *ApEn* of different ‘granulometries’ of the same time series  
 34 until  $s = N$ . The values for each  $ApEn(s)$  are plotted in a graph and analysed as an  
 35 ensemble. The decay or increase of the  $ApEn(s)$  values in each scale indicate whether  
 36 there is new information and levels of complexity in each scale. For an application of this  
 37 technique to the analysis of plant electrome, see Simmi et al. (2020) and Parise et al.  
 38 (2021).

39 In summary, the analyses presented above are very effective tools to understand what is  
 40 happening to a plant, in terms of its bioelectrical activity, and how the plant is dealing  
 41 with the world. And, in fact, it so happens that the electrome of plants was observed to  
 42 change under a variety of physiological and ecological stimuli. In particular, stressful

1 events were correlated with a decrease in the complexity of the signals (Saraiva et al.  
2 2017; Souza et al. 2017), while subtle events, with an increase (Simmi et al. 2020). The  
3 lesser complexity of stressed plant signals was hypothesised to be an effect of the  
4 degradation of such systems. However, we propose another possibility to explain these  
5 results: the plant is paying attention.

6

## 7 **5 A possible framework for plant attention**

8 In a recent work, Parise et al. (2021) studied the parasitic dodder plant, *Cuscuta*  
9 *racemosa* Mart., interacting from a distance with different species of potential hosts. The  
10 researchers placed twigs of dodders inside a box with either bean or wheat plants inside,  
11 which respectively represent a viable and a non-viable host to the dodder. They measured  
12 the electrome of the dodder two hours before the presentation to a host, as a control, and  
13 two hours after the host was placed inside the box. The researchers observed that the  
14 dodder's electrome had a likely higher variation of energy, became more regular and  
15 predictable, and presented a higher autocorrelation of signals, especially when plants  
16 were presented to a viable host. These results indicated that, even from a distance, the  
17 dodder was capable of detecting the presence of a host and altered its electrome dynamics  
18 accordingly. Such electrome changes towards a more organised state suggested that  
19 dodder plants not only distinguished the more promising host, but also, they might have  
20 'focused' their electrome activity, suggesting a likely process of attention towards their  
21 hosts (Parise et al. 2021).

22 Attention as a phenomenon that engages the whole plant may be considerably rare. Since  
23 plants are modular organisms composed of many semiautonomous units (each one  
24 capable of individually processing and using information locally; Lüttge 2021), there  
25 wouldn't be many occasions when the attention of the whole plant would be required. A  
26 root normally does not need to deal with the problems and stimuli a leaf receives, and  
27 vice versa. They have local problems that likely require the attention of the modules  
28 involved and no more than those modules. Physiological integration, or lack thereof, and  
29 cognitive integration go together.

30 From a bioelectrical point of view, each plant tissue has different bioelectrical properties  
31 due to the different expression of ion channels and sorting proteins in these tissues  
32 (Canales et al. 2018; Wudick et al. 2018; Cuin et al. 2018). Besides, parenchymatic cells  
33 of the leaves are excited with lower thresholds than the sieve tubes of the phloem, the  
34 main highway by which long-distance electrical signals travel (Sukhov et al. 2011; Huber  
35 and Bauerle 2016; Vodeneev et al. 2016). This can allow some modulating or sorting of  
36 the signals, where weak signals will remain local and only strong signals that must be  
37 communicated to the rest of the plant will be propagated systemically (de Toledo et al.  
38 2019). Additionally, plants may have 'checkpoints' for filtering these signals. For  
39 example, the parenchymal cells of the hypocotyl of *Arabidopsis* are electrically  
40 uncoupled, meaning that the only pathway for the exchange of electrical signals between  
41 root and shoot are vascular bundles (Canales et al. 2018; de Toledo et al. 2019).

42 Nevertheless, sometimes, the whole plant faces a problem that requires coordinated  
43 activity of the entire organism. In the case of the dodders in Parise et al. (2021), when the

1 plants were alone inside the boxes, every stimulus could be relevant to each cell or tissue  
2 that perceived it. Once the host was placed inside the box, strong and important  
3 environmental cues presumably required the coordination of all the dodder's cells to  
4 respond to it, since the dodder's goal is to reach its host and parasitise it. It requires a  
5 reorganisation of the dodder internal state, including at the cognitive level, to respond to  
6 the cue as a whole. Therefore, if there was a process of attention occurring in the dodder,  
7 it likely was dispersed before the stimulus, and subsequently focused on the host and the  
8 actions needed to secure it.

9 In autotrophic plants, where food resources come from multiple sources at the same time,  
10 it may be even tougher to observe whole-plant attention. However, in most of plant  
11 species, there are occasions when a plant needs to act not as a bunch of modules, but as a  
12 single unit. For example, when roots detect that little water is available in the soil, they  
13 send electrical and hydraulic signals to the shoot to stimulate the closure of stomata to  
14 prevent loss of water (Gil et al. 2008; Brunner et al. 2015). Then, they release ABA  
15 hormones that stimulate the stomata to stay closed at the same time that the whole plant  
16 begins to synthesise drought-related proteins and increase the levels of sugars and other  
17 solutes within all the tissues so as to increase the plant osmotic potential (Seo and Koshiha  
18 2011; Brunner et al. 2015; Jain et al. 2019). Even the leaves of the mesophyll, after  
19 receiving electrical and hydraulic signals indicating drought, synthesise ABA on their  
20 own (Seo and Koshiha 2011). This all requires a joint effort from all the modules, working  
21 synchronously for the common good. Using the analogy of a plant as a democratic  
22 confederation (Trewavas 2003), a healthy plant is like a nation where each citizen deals  
23 with its own business and communicates to others when necessary. The citizens know  
24 they belong to the same country because they have the documents that prove this, they  
25 have a shared language and a shared culture, but it is a loose, dispersed belonging. On the  
26 other hand, a stressed plant, or a plant engaged in an activity that requires integration of  
27 most of or all its parts, is like a nation at the World Cup, where citizens get an increased  
28 feeling of belonging to their country, more than in normal times. When their team is  
29 playing, everybody gathers in front of their televisions to watch the game. The nation is  
30 paying attention, synchronically mourning each penalty and cheering each goal. While  
31 political analogies may project a human bias onto plants, this bias is mitigated if we  
32 remember that politics is not an exclusively human affair, but is, at the extreme, a  
33 cosmopolitics, embracing the entire cosmos (Strengers 2010).

34 Bioelectrically speaking, the examples above suggest that when a stimulus is important  
35 enough to require the response of the whole plant, minor, local stimuli will be ignored in  
36 favour of the main stimulus in question. There could be a stronger firing of systemic  
37 electrical signals which will travel throughout the plant stimulating the modules in the  
38 same way and synchronising the functioning of them all. There will probably be an  
39 increase in the energy invested in these signals, as well as in the response to them, and  
40 these signals will be more correlated among them. In some sense, like awareness that  
41 comes into being, according to Husserl, each time anew with a different attentional or  
42 intentional tendency, so the whole plant "comes into being" on the exceptional basis of  
43 an environmental emergency when attention to the most significant stimulus is required  
44 from all plant organs, tissues, and cells. That is, despite certain level of integration  
45 between all the modules, whole plant awareness does not happen all the time, but only  
46 during the exertions of whole-plant attention.

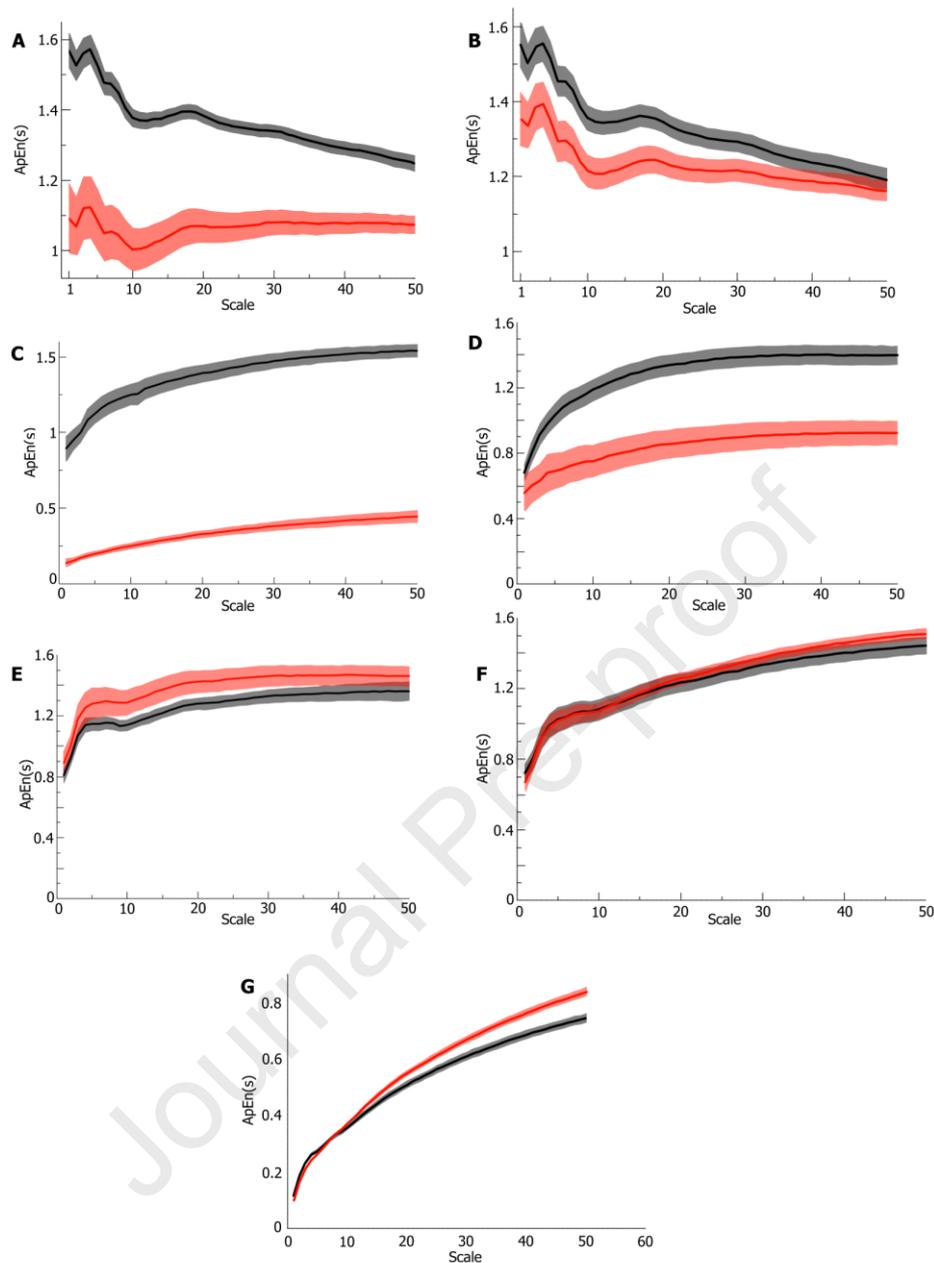
1 Consequently, we support the hypothesis that the electrical activity of a plant in a state of  
2 attention will decrease its complexity, the signals becoming more regular, predictable and  
3 organised, and the autocorrelation of these signals will increase. This could be observed  
4 empirically by recording the electrome of a plant before and during a stimulus that is  
5 likely to require whole-plant attention and then conducting the analyses described above.  
6 We hypothesise that during an attentional process, the value of the exponent  $\beta$  of PSD  
7 would increase, and the  $ApEn$  and  $ApEn(s)$  would decrease (in the case of  $ApEn(s)$ , the  
8 decrease would be observed in most of the scales), indicating more regularity of the  
9 signals. At the same time, the autocorrelation of the signals is likely to increase. This  
10 combination of increased autocorrelation with decreased complexity is important to  
11 distinguish from situations where the system as whole begins to fail, suggesting an added  
12 cognitive component that refers to the plant's attentional state. In the case of a pure system  
13 failure, there would not be an increase in the autocorrelation, because the plant's vital  
14 functions would be failing too.

15 Seeking a preliminary corroboration of our hypothesis, we have looked for evidence in  
16 the literature of the phenomena described above. As a result of a meta-analysis, we  
17 present the values of the mean of  $\Delta V$  events, the exponent  $\beta$  of PSD, the  $ApEn$  and  
18 autocorrelation function of different works with different species in Table 1, and the  
19 values of  $ApEn(s)$  in Figure 1. The values presented in Table 1 must be analysed with the  
20 greatest caution because it is an oversimplification of the results found in the studies  
21 referenced. The studies involve different methodologies, such as different time-recording  
22 of the time series and different frequencies in the acquisition of the signals. Consequently,  
23 they are not directly comparable among themselves. Nevertheless, the analysis of Table  
24 1 shows a pattern in the plants' response: under stressful situations, most plants increased  
25 the mean of the  $\Delta V$ , the value of the exponent  $\beta$  of PSD, and the autocorrelation, and  
26 decreased the values of the  $ApEn$ .

27 Interestingly, infection by a biotrophic fungus caused an increase in the complexity of  
28 signals, perhaps because these stimuli do not require a strong whole-plant response  
29 (Simmi et al. 2020). In fact, this type of fungus deceives plant defences to ensure the  
30 infection of living tissues (Gebrie 2016; Simmi et al. 2020). Consequently, signals related  
31 to the fungal infection do not stand out in the sphere of a plant's attention but are only  
32 registered by modules that do not succeed to pass on a large amount of information to  
33 more distal parts of the plant. On the other hand, sudden osmotic stress induced by a low  
34 water potential solution with polyethylene glycol (PEG) caused an increase in the  
35 exponent  $\beta$  of PSD, suggesting more regularity in the signals but, at the same time,  
36 presented a decrease in the autocorrelation. It is possible that this is not an example of  
37 attention only, but rather a general failure of the system.

38 Regarding the  $ApEn(s)$  (Figure 1), subtle and beneficial stimuli such as irrigation with  
39  $H_2O$  and nutrient solution (de Toledo et al. unpublished results), and infection with a  
40 biotrophic fungus (Simmi et al. 2020), increased the  $ApEn$  at almost all the scales. On the  
41 other hand, destructive stimuli to autotrophic plants or the presentation of a host to a  
42 parasitic plant decreased the  $ApEn$  at almost all the scales, suggesting increased regularity  
43 and less complexity in the signals of plants under attention-demanding tasks.

44



1

2 **Figure 1:** *ApEn(s)* for different plant species before (black) and after (red) different stimuli.  
 3 Shaded areas around the lines represent standard error. **A:** dodder plants (*Cuscuta racemosa*  
 4 Mart.) before and after being presented to bean plant. **B:** dodder plants before and after being  
 5 presented to wheat plant. **C:** bean plants (*Phaseolus vulgaris* L.) before and after being subject  
 6 to osmotic stress with PEG. **D:** bean plants before and after being subjected to osmotic stress  
 7 with NaCl. **E:** bean plants before and after being irrigated with nutrient solution. **F:** bean plant  
 8 before and after being irrigated with distilled water. **G:** tomato plants (*Solanum lycopersicum*  
 9 L.) before and after being infected by a biotrophic fungus. Figures modified from Parise et al.  
 10 (2021) (A-B), de Toledo et al. (unpublished results) (C-F), and Simmi et al. (2020) (G).

11

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Species	Stimulus	$\Delta V$ ( $\mu V$ )	$\Delta V$ ( $\mu V$ )	PSD ( $\beta$ )	PSD ( $\beta$ )	ApEn	ApEn	Autocorr.	Autocorr.	Reference
<i>G. max</i>	Osmotic Mannitol	?	?	$1.5 \pm 0.3$	<b><math>2.6 \pm 0.2</math></b>	$1.12 \pm 0.21$	<b><math>0.67 \pm 0.39</math></b>	?	?	Saraiva et al. (2017)
<i>G. max</i>	Cold	-0.3	<b>0.3</b>	$1.51 \pm 0.21$	<b><math>2.85 \pm 0.69</math></b>	*	*	?	?	Saraiva (2017); Souza et al. (2017)
<i>G. max</i>	Low light	-0.14	<b>-0.14</b>	$1.51 \pm 0.22$	<b><math>1.96 \pm 0.30</math></b>	*	*	?	?	Saraiva (2017); Souza et al. (2017)
<i>G. max</i>	Osmotic Mannitol	-0.1	<b>-0.07</b>	$1.51 \pm 0.23$	<b><math>2.58 \pm 0.34</math></b>	*	*	?	?	Saraiva (2017); Souza et al. (2017)
<i>C. racemosa</i>	Host (bean)	-148.0	<b>457.0</b>	$1.19 \pm 0.23$	<b><math>1.24 \pm 0.26</math></b>	15.68	<b>0.90</b>	36.03	<b>196.92</b>	Parise et al. (2021)
<i>C. racemosa</i>	Host (wheat)	138.0	<b>697.0</b>	$1.28 \pm 0.30$	<b><math>1.41 \pm 0.26</math></b>	16.06	<b>11.83</b>	36.5	<b>127.19</b>	Parise et al. (2021)
<i>P. vulgaris</i>	Osmotic PEG	?	?	1.65	<b>2.13</b>	0.86	<b>0.15</b>	46.81	<b>30.67</b>	de Toledo et al. (unpublished results)
<i>P. vulgaris</i>	Osmotic NaCl	?	?	1.9	<b>1.94</b>	0.68	<b>0.55</b>	30.66	<b>84.27</b>	de Toledo et al. (unpublished results)
<i>P. vulgaris</i>	Irrigation H <sub>2</sub> O	?	?	1.76	<b>1.75</b>	0.73	<b>0.67</b>	46.84	<b>54.08</b>	de Toledo et al. (unpublished results)
<i>P. vulgaris</i>	Nutrient Sol.	?	?	1.75	<b>1.76</b>	0.81	<b>0.89</b>	30.036	<b>27.62</b>	de Toledo et al. (unpublished results)
<i>S. lycopersicum</i>	Pathogen	?	?	2.13	<b>1.95</b>	?	<b>20% higher</b>	?	?	Simmi et al. (2020)

3

4 **Table 1.** Values for electronic analyses before (regular text) and after (**bold text**) different stimuli. Orange-filled cells indicate an increase in the values after  
5 the stimulus. Green-filled cells indicate a decrease in the value of the stimulus, and non-coloured cells indicate no significant variation.  $\Delta V$ : mean variation of  
6 electrical potential in  $\mu V$ . **PSD ( $\beta$ )**: value of the exponent  $\beta$  of the Power Spectral Density analysis. Higher values mean a decrease in signal complexity. **ApEn**:  
7 approximate entropy. Higher values indicate increased complexity. **Autocorr.**: autocorrelation values. The species studied were soybean (*Glicine max* (L.)  
8 Merr.), tomato (*Solanum lycopersicum* L.), dodder (*Cuscuta racemosa* Mart.), and bean plants (*Phaseolus vulgaris* L.). \*The values of *ApEn* available at Saraiva  
9 (2017) were informed in a graph, which makes impossible to provide an exact value. The question mark (?) indicates that the value was not provided in the  
10 original study.

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## 2 **6 Are we paying attention to plant attention?**

3 According to the data available, the existing evidence supports the hypothesis that  
4 plants are capable of attaining attentive states. It seems that when a task requires the  
5 coordinated behaviour of the entire plant, signals apparently become more regular and  
6 correlated. It is conceivable, also, that there is more energy being expended with these  
7 signals because of the increase in the mean  $\Delta V$  in most cases. This is an encouraging  
8 factor as far as the viability of our hypothesis is concerned, but some caveats must be  
9 mentioned before we proceed to the discussion.

10 Despite the potentially general applicability of our hypothesis, for most land plants have  
11 the same modular structure, there is no reason to think that attentive behaviour will work  
12 equally in all the species. We do propose that the electrome of plants under a state of  
13 attention will likely behave as we described, but it will probably vary depending on plant  
14 species, the individuality of each plant, its age, and the kind of stimulus it is receiving. In  
15 addition, the studies mentioned above considered the mean of all the time series (with  
16 their different lengths), which eliminates the influence of time in the process. The process  
17 of attention is likely to last for different time lengths depending on plant species and the  
18 individuality of each plant. It might last only until the problem or task that the whole plant  
19 faces is solved. This was not the case in most of the studies presented in Table 1 and  
20 Figure 1 because stimuli lasted for the entire time series recordings, and this is why we  
21 believe the values presented there are reliable. However, in the future, it will be desirable  
22 to monitor the value variations of the proposed parameters through time in order to  
23 understand its dynamics.

24 In the study of Simmi et al. (2020), for example, plants were infected by the biotrophic  
25 fungus *Oidium neolycopersici* L. Kiss, 2001, which deceives the plant's immune system  
26 by making itself undetectable to the plant. Accordingly, alterations in the tomato plants'  
27 electrome were only detectable on the first day of the infection, when the fungus was  
28 penetrating the plant cells, and four days before the first visible symptoms of the disease.  
29 This could justify the increase in the overall complexity of signals as presumably some  
30 modules were working differently, so that richer information was running throughout the  
31 plant. If the process of whole-plant attention had occurred, it was likely to have happened  
32 only in the first 24 h post-infection or less. Without observing these developments through  
33 time, information on this transient attentive state is lost.

34 The studies by Gagliano et al. (2014, 2016) on plant learning also suggest that a transient  
35 process of attention might have occurred, but in opposite directions. Learning by  
36 habituation means that a harmless stimulus causes a reaction by the organism, but as the  
37 organism is repeatedly stimulated, it learns to ignore it (Eisenstein et al. 2001). This  
38 suggests that a harmless stimulus initially triggers an attentive state towards it, but  
39 through the habituation process, the organism gradually pays less attention to the stimulus  
40 until not perceiving it anymore. This is likely what happened with the *Mimosa pudica* L.  
41 plants when the fall they were repeatedly subjected to did not trigger the closing of the  
42 leaves (Gagliano et al. 2014). In contrast, sensitisation, the opposite of habituation, could  
43 require more and more attention as the organism becomes more sensitive to the stimulus  
44 (Eisenstein et al. 2001; Conrath et al. 2006).

1 Similarly to sensitisation, associative learning presumably causes the opposite effect of  
2 habituation on attention: a cue that was originally neutral, i.e., not worthy of attention,  
3 increasingly becomes more significant to the point where the plant cannot help but  
4 respond to that cue (Gagliano et al. 2016). It learns to pay attention to it as a prerequisite  
5 to associative learning. These studies illustrate the importance of time in the process of  
6 attention, which should not be neglected in future studies.

7 Overall, the phenomenon of attention in plants seems to be transient and context-  
8 dependent, much as it is in other living organisms. Modules or groups of modules are  
9 attentive to the relevant cues and signals they perceive, and whole-plant attention may  
10 only emerge rarely, occasionally, and depending on the plant's needs. There is always a  
11 basal communication between the modules, and they all 'know' (in a strictly  
12 physiological sense) that they belong to a higher unity. This is what enables plants to  
13 recognise self, to distinguish self from nonself, and also to understand their physical  
14 boundaries (Falik et al. 2003; Hamant and Mouliat 2016; Bertoli et al. 2020).  
15 Physiological integration is extremely important for the modules to recognise themselves  
16 as part of the plant (Holzapfel and Alpert 2003; Falik et al. 2006; Fukano and Yamawo  
17 2015), but this recognition mechanism can be reinforced when whole-plant attention is  
18 required, presumably provoking the bioelectrical effects described above.

19 We could, therefore, say that a plant oscillates between distraction and awareness,  
20 between "not being" and "coming into being" (Husserl 1913[1983]). This transient and  
21 distributed nature of plant attention can provide insights into new hypotheses about how  
22 this phenomenon occurs and its implications for plant growth, adaptability, and ecological  
23 relationships. We discussed attention broadly, as the phenomenon of selecting a piece of  
24 all the relevant information in the environment to direct action. However, as mentioned  
25 in Section 2, there are many varieties of attention, though most of these studies were  
26 performed in human subjects. To understand which are the varieties of attention present  
27 in plants is a goal for the future. We already suggested some of the situations in which  
28 different kinds of attention could be necessary to plants, which can provide ideas for new  
29 hypotheses and experiments to test them.

30 Finally, due to the close relation between attention and awareness/consciousness,  
31 especially in the phenomenological tradition, we indulge ourselves to go a little further in  
32 the possible outcomes of empirical studies on plant attention. Lately, some authors have  
33 been discussing the possibility of consciousness in plants, a highly controversial topic  
34 (Trewavas and Baluška 2011; Taiz et al. 2019; Mallatt 2020; Trewavas et al. 2020; Calvo  
35 et al. 2021; Trewavas 2021). In human brains, empirical evidence for consciousness has  
36 been considered in terms of changes in electrical activity that are triggered by some  
37 stimulus. A subject is only conscious or aware of a stimulus if it is strong enough to recruit  
38 the attention of a great part of the cortex (Sergent et al. 2005; Tononi et al. 2016).  
39 Although we avoid any kind of anthropomorphism, an analogous functioning of putative  
40 plant consciousness, i.e., recruitment of bioelectrical activity to deal with some stimulus  
41 or set of stimuli, is not impossible. When all the modules coordinate their behaviour to  
42 attend to a cue, could we say the plant as a whole became conscious of that cue, or  
43 conscious of itself as a whole organism? This is an intriguing question to be investigated  
44 in the future.

1 In conclusion, we have proposed a phenomenological-empirical approach to address plant  
2 attention, a very neglected aspect in current studies of plant cognition. If our hypothesis  
3 is correct, it opens vast possibilities to study attention not only in plants, but also in other  
4 modular organisms, like fungi and sea sponges. However, there is much work to be done.  
5 The hypothesis needs to be corroborated with careful experiments specifically designed  
6 to test it, and herein we provided some of the tools to do it. To all the experimental  
7 scientists reading this, we hope it sounds as an invitation.

8

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## **Highlights**

Plants could present attention to certain actions and environmental cues.

Plant attention would allow the processing of information when cognitive capabilities are limited.

Plant attention is proposed to happen through synchronisation of the electrical signalling of plant modules.

Methods to observe plant attention empirically through electrophysiological analyses are proposed.

Journal Pre-proof

### **Declaration of Interest**

The authors declare that they have no competing financial interests or personal relationships that could be perceived to have influenced the work reported in this paper.

Journal Pre-proof