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(Re)claiming Plants in Comparative Psychology

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Up until the middle of the 19th century, some data about plant behavior could be found in books dealing with comparative psychology. The tendency gradually faded away, and the topic was almost exclusively treated in literature dealing with plant physiology. In recent years, however, there has been a revamping of psychological terminology and theorizing to describe, explain, and formulate hypotheses on the evidence that many of the sophisticated behaviors plants exhibit are an expression of cognitive competences that are generally attributed to human and nonhuman animals. In this work I shall discuss a selection of experimental studies supporting the idea that plants could be defined as cognitive agents. Experiments showing that the behavior of plants is controlled by a representation of its goal, episodic-like memory, and decision-making will be described. It is not, however, my intention to embrace any position as to whether or to what degree plants are conscious. Rather, I hope to (re)fuel the discussion within the psychological community that will point in the direction of integrating studies concerning adaptive plant behavior within the wider field of comparative psychology.

Keywords: comparative psychology, plants cognition, cognitive psychology, ecology, evolution

Including plant behavior within the domain of comparative psychology has been considered absurd by many (Adams, 2018; Alpi et al., 2007; Taiz et al., 2019). Nevertheless, in English-speaking universities, plant behavior was treated up until 1935 in comparative psychology texts (Applewhite, 1975; Warden, 1928; Warden, Jenkins, & Warner, 1935; Yerkes, 1913), and the contribution of plants to our understanding of behavior and cognition continues to be acknowledged (Baluška & Levin, 2016; Baluška & Mancuso, 2009; Calvo Garzón & Keijzer, 2011; Castiello, 2019; Cvrčková, Žárský, & Markoš, 2016; Gagliano, 2015; Garzón, 2007; Keijzer, 2017; Parise, Gagliano, & Souza, 2020; Segundo-Ortin & Calvo, 2019; Trewavas, 2014, 2016, 2017; van Duijn, 2017). A unitary view that does not separate plants from animals emerges from that body of works. Although the idea that plants may behave in a cognitive way may baffle the general public, many of us are genuinely amazed by the complexity of plant responses, that is, by plants' ability to adapt to an ever-changing environment. Also, evidence is accumulating supporting notions, formerly considered esoteric, that plants can communicate, remember, decide, and even count, all abilities that one would normally call cognitive if they were observed in animals.

Given these considerations, the intention behind this essay is that of proposing to (re)introduce aspects of plant behavior into the domain of comparative psychology in such a way as to permit us to examine how *aneural* systems may contribute to or increase our understanding of the processes at the origin of cognition. Of course, it would be a mistake to say that plants should be studied *instead* of animals when one is seeking to understand the functioning of the nervous system. The parallels nevertheless are quite intriguing, and ultimately many do admit that the behaviors of plants and animals complement one other rather nicely. Naturally, the dissimilarities between the anatomies of plants and animals could lead to bemusement, but there is surely a stronger case in favor of similarities because they allow generalizations to be made. Indeed, even at a very basic level, the structure and physiology of plants share many features with the neural networks of animals, such as electrical signaling, genetics and hormonology (Chamovitz, 2018). Having said all this, clearly, animal behavior cannot be compared to the ways plants function, and I would like to ask the reader up front to "forgive" me for using terminology throughout the paper that is usually specific to animal experience. Have no doubt that when I describe what a plant sees or what it smells, I am not claiming that it has eyes or a nose.

This article is not to be considered a comprehensive discussion on the subject, as I will be examining only selected examples from the growing literature examining the intriguing possibility of plant cognition (Baluška & Levin, 2016; Gagliano, 2015; Segundo-Ortin & Calvo, 2019). It does intend to look at this topic from outside the box and to ask (and to answer, if possible) some tricky questions such as the following: Does it make sense to use cognitive psychology vocabulary in reference to plants? Does saying that plants can communicate, learn, decide, or plan a movement intentionally necessarily mean something different from what we intend when we refer to similar processes put in place by human and nonhuman

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animals? Do plants respond in a hard-wired, inflexible, reflexive manner, or are they capable of cognitive activities?

This essay is divided into three main sections: The first one deals with the ongoing debate concerning the idea that processes outside of the central brain could contribute to cognition. The second section focuses on empirical evidence of plant communication, learning and memory, decision-making, and intentional action processes. In the final section I will attempt to file all this evidence under the "situated cognition" theoretical approach and refer to some schools of thought.

I shall argue that plants' cognitive abilities deserve to be taken seriously. As plants should be considered cognitive agents, as such, they offer us a unique opportunity for a comparative approach, which can potentially lead us to the "roots" of cognition.

Cognition Outside the Brain

Discussions on the limits of cognition across taxa are of course conditioned by how we define "cognition" and "cognitive." Cognitivism, or the classical conception of cognition, assumes that a large complex brain and neural systems are necessary to support cognitive capacities, but this is not always the case (Lyon, 2019). In insects, for example, miniature brains support a variety of complex behaviors facilitated by sophisticated cognitive abilities (Perry, Barron, & Chittka, 2017). Even remarkable decision-like behavior and information processing has been observed in some organisms, such as the slime mold *Physarum polycephalum* (Ray et al., 2019) that lack a neural architecture but nevertheless exhibit some forms of learning (Boisseau, Vogel, & Dussutour, 2016). With these examples in mind, I would like to examine the behavior of brainless organisms such as plants and review the theories of cognition. The ideas expressed here will be reexamined later on in this work to explain the experimental evidence reported in terms of existing theoretical frameworks.

The general class of nonmutually exclusive theories on cognition beyond the brain is generally termed *situated cognition* (Cheng, 2018). *Embodied cognition* is a kind of situated cognition that assigns cognition to parts of the body other than to the central nervous system (CNS). Embodied cognition emphasizes the importance of the role played by bodily states as well as action for cognition. At the heart of embodied cognition is the notion that cognition relies on the sensorimotor system (Gallese, 2008). To examine the question in more concrete terms, the arm movements of the *Octopus vulgaris* (Hochner, 2012, 2013) can give us an unexpected hand. In octopus, control over its eight arms presents challenges and it can prove quite challenging, as each limb has many degrees of freedom. With only one fixed point of reference connecting the limbs to the body, each can bend anywhere along its length. By using suction cups interspersed along the length of each limb, the octopus has the freedom to grab food anywhere along its arms. Primates differ significantly in this respect, as they almost always grab food with a hand/paw, the distal ends of a limb, or occasionally use a tool held in the hand/s. Furthermore, a primate's arm/s bend/s only at the elbow; the octopus has infinite degrees of freedom because it is not constrained by hard exo- or endoskeletons. With so many degrees of freedom, each limb becomes neurally complex. By reducing the number of degrees of freedom to a more manageable number, embodied cognition can solve such control problems.

Extended cognition is a second kind of situated cognition that refers to cognition that encompasses physical objects in the world (Clark & Chalmers, 1998; Kaplan, 2012). The principal idea is that cognition extends beyond the physical boundaries of the organism into its environment and is inclusive of objects that are not part of the body. This hypothesis posits that the environment plays an active role in cognitive processes that are not confined to the CNS or the body, as an organism can enhance its cognition by manipulating its environment. Consider the case of spider ecology (Japyassú & Laland, 2017). Web builder spiders adjust the tension of their thread by extending their cognition and adjusting the tension of the web threads. Tighter web threads lead to a lower threshold of disturbance needed to catch the spider's attention. Thread tension thus calibrates the threshold level for attention. When tight, tinier objects such as prey items are registered, the causal chain is satisfied in one direction. The spider in turn adjusts its web tension based on its state. In practice, a hungrier spider will tend to tighten the web, as hunger makes even smaller preys worth its attention. This demonstrates that the cognitive capacities of the spider also affect its environment (Japyassú & Laland, 2017). The spider intervenes in a component external to itself, and that intervention then affects the spider's cognition (Kaplan, 2012).

A third kind of situated cognition is *enactivism*. According to this theory, organisms selectively form their environments through interaction and engagement with the world; their dynamic relationship with their environment gives rise to cognition (Di Paolo, Buhrmann, & Barandiaran, 2017; Hutto & Myin, 2014, 2017; Thompson, 2007; Ward, Silverman, & Villalobos, 2017). According to the *enactivist* theory, a cognitive system is not merely an organization responding to external obstacles. Instead, cognitive systems are autonomous, open systems that meet needs and goals by exploring the environment and, in so doing, they regulate their sensorimotor coupling in context-specific circumstances. This theory emphasizes emergent cognitive structures that are self-organizing as a result of interactions between the organism and its environment. For example, during improvised dancing, although the maneuvers of the dancers are decidedly spontaneous, they are nevertheless recognizable as a dance and not merely a series of flailing-about movements of the limbs (Merritt, 2015). Yet, it would be difficult to classify the intelligence on display as deliberative, as those bodies are objects in motion. The engagement in the environment and the movement of the dancer exemplify enactivism. Where there is more than one dancer improvising on stage, intelligence includes extended social cognition in the form of immediate reactions to one another, which has been called participatory sense-making (De Jaegher & Di Paolo, 2007). Human–dog play may have something in common with improvised dance. Mitchell and Thompson (1991) have demonstrated that humans improvise and create variations on a theme just as their canine companions do. This research examined variations of a repetitive sequence of actions. For example, the common ball-retrieval game can be readily interrupted by a "fake" throw, whereby the ball does not leave the human's hand. The human player fake-throws the ball to see if the dog continues to proceed in the anticipated direction of the throw. Familiar dogs were observed to potentially invent a compatible project—avoid fake-out—whereby the goal is to react as little as possible to any fake throws the human might pose. Both improvised dance and human–dog play might also fit

under the extended cognition tent, as each subject in a dance or the play is causally influencing the other subject's cognition.

This brief classification of cognitive "species" provides us with a context that will help us interpret experimental studies in brainless organisms such as plants. I will now, in particular, consider the possibility of situated cognition in plants.

Signaling and Communication

Plants cannot speak, but communication channels are being reported at an increasing rate, with a growing number of recipient species found to tune in (Heil, 2014; Trewavas, 2016). We now know that plant chemical language based on volatile organic compounds (VOCs), for example, is capable of true semantic flexibility, in the sense that new meanings may be assigned to deep-rooted chemical words and used in novel interactions and new contexts (for review, see Gagliano & Grimonprez, 2015; Holopainen, 2004). The volatile "words" used by plants appear to be rather specific in what they convey (Kessler, Gase, & Baldwin, 2008). When a plant sends out volatile molecules indicating that it has been attacked by herbivorous insects, it is conveying a piece of public information to a number of parties, including not only other plants but also other herbivores and the predators of their attackers. This phenomenon is very similar to pheromonal communication in animals (Wyatt, 2017), the chemical communication of human beings that has recently been reported (Parma, Gordon, Cecchetto, Cavazzana, Lundstrom, et al., 2017), and signals across species (Lübke & Pause, 2015).

Peñuelas, Llusia, and Estiarte (1995) focused on terpenoids as chemical compounds present in plant-to-plant chemical messages. Terpenoids, the most diverse group of VOCs, are a large, diverse class of organic compounds produced by a variety of plants that are easily induced and emitted in response to abiotic and biotic stress factors. In the language of plants, each five-carbon isoprene unit (C5) of terpenoids forms a "syllable," and the sequential combination of these units forms a "word." Diverse terpenoid blends in the volatile plume emitted by a plant forms the "message," and the "dialects" of plant language depend upon the qualitative and quantitative characteristics of terpene composition in different plant species (Peñuelas et al., 1995).

It would seem that the chemical language of plants is more meaningful and effective among kin (i.e., genetically identical or related) than for strangers (Karban, Shiojiri, Ishizaki, Wetzel, & Evans, 2013). A number of plants are found to respond to volatile cues emitted by experimentally wounded neighbors by attempting to increase resistance to herbivory. It has been reported that *Artemisia tridentata* (big sagebrush; family: Asteraceae) plants that are more closely related have more effective communication (Karban et al., 2013). In an experiment by Karban et al. (2013), plants in the field experienced less leaf herbivory when they received cues from close relatives with respect to when they received them from more distantly related plants (Figure 1). That would mean that plants can react differently depending on relatedness, making it less probable that emitters will aid distant relatives and more probable that they will respond to close relatives. A more effective defense is probably the most important consequence of kin recognition in plants.

Other examples of kin recognition have been described. When Murphy and Dudley (2009; Dudley & File, 2007) tested a North American species, *Impatiens pallida* Nutt. (pale touch-me-not; family: Balsaminaceae) for the ability to recognize kin, they found strong responses to aboveground competition and a favorable reaction to growing with relatives. When the experimenters measured the plant's response to aboveground light quality cues of competition (low or high ratio of far-red to red light) and to the presence of neighbor roots, they found that the response depended on whether the neighbor was a sibling or a stranger. The study found that *I. pallida* plants were capable of kin recognition when they were in the presence of another plant's roots. There were several traits that showed response to relatedness in plants sharing pots. Some of these were increased stem elongation in response to the presence of a kin and an increased leaf-to-root allocation in the presence of a stranger, potentially indicating reduced interference (cooperation) for kin and increased competition for strangers. These plants simultaneously responded to both competition cues,

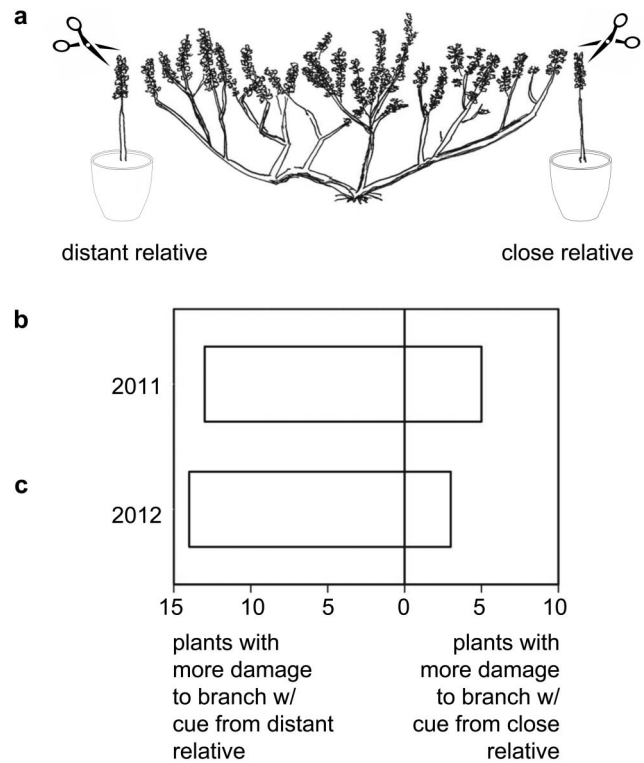

Figure 1. (a) Graphical depiction of the experimental setup displaying a rooted receiver plant with two potted volatile donor plants: One was closely related to the receiver and one was distantly related. At the start of the growing season (June 2011 or May 2012), the leaves of the potted donors were clipped with scissors. The natural levels of damage caused by herbivores for the two branches for each receiver plant were measured at the end of the season (b, c). The number of receiver plants with more herbivore damage on the branch near a donor that was either a distant or a close relative. In 2011, 13 out of 18 receiver plants experienced more damage on the branch near the clipped distant relative. In 2012, 14 out of 17 receiver plants experienced more leaf damage on the branch near the clipped distant relative. From "Kin recognition affects plant communication and defence" by R. Karban, K. Shiojiri, S. Ishizaki, W. C. Wetzel, and R. Y. Evans, 2013, *Proceedings of the Royal Society B Biological Science, 280*, 20123062. Copyright [2013] by The Royal Society. Adapted with permission.

with the effects of an aboveground cue depending on the presence of a belowground one.

Plants thus seem to interact with their own kin and multiple other species below ground in complex ways (Amzallag, 1999; de Kroon, Visser, Huber, Mommer, & Hutchings, 2009). Some of the most likely sources of interaction cues are root exudates (Chen, During, & Anten, 2012; Peñuelas et al., 2014), which may act as a cue when there are competitive neighbors (Bais, Weir, Perry, Gilroy, & Vivanco, 2006). Root exudates may indicate the relative extent or nature of neighboring plants, be they kin or strangers, allowing responding plants to adjust their patterns of biomass allocation accordingly (Chen et al., 2012).

Learning and Memory

If plants are capable of associative learning, the capacity may be linked to phenotypic plasticity. Naturally, we wonder if this sort of learning is similar to what we find in human and nonhuman animals. Evidence is accumulating that the answer is "yes." A recent study focusing on the *Mimosa pudica* L. (shameplant; family: Mimosaceae) plant, the most studied model for habituation, found that it exhibits a form of nonassociative learning. The plant learns to tolerate certain kinds of shocks, such as those experienced when they are dropped on the floor, without activating their widely known leaf-folding response (Gagliano, Renton, Depczynski, & Mancuso, 2014). After it has been dropped a number of times, the plant "realizes" that being dropped is normal, although it continues to be sensitive to other unexpected events, such as being touched or shaken. More astonishingly, this habituated reflex lasts up to a month, which demonstrates the acquisition and expression of a long-lasting memory (Figure 2).

Plants also exhibit evidence of a short-term memory. The Venus flytrap (*Dionea muscipula* J. Ellis; family: Droseraceae) contains two sensitive hairs that must be touched within 20 s of each other for the trap to close. Visitors searching for food eventually touch the trigger hairs, leading to the electric excitation of the trap; the mechanical stimulus is converted into an all-or-nothing action potential (conveyed to motor cells at the base of the trap) that controls closure and engenders a decaying short-term memory (Trewavas, 2017). Two hairs are used to avoid erroneous closure induced by stimuli coming from a nontarget source (e.g., raindrops or a fallen leaf; Böhm et al., 2016). If the hairs are touched more than twice, the plant "assumes" that an insect has been caught. This phenomenon might be considered a form of sensitization. It takes more than one stimulus to trigger a response, or, put another way, one stimulus sensitizes the plant to a second stimulus. A similar phenomenon of sequential events when a stimulus strikes sensors can be found in the sting release of sea anemones (Watson & Hessinger, 1989).

Returning to learning, recent research has tested the ability of the garden pea (*Pisum sativum* L.; family: Fabacee) to learn by associating relevant cues. Gagliano, Vyazovskiy, Borbély, Grimonprez, and Depczynski (2016) carried out a classical conditioning experiment in which the airflow created by a fan (the conditioned stimulus) was followed by the occurrence of blue light (the unconditioned stimulus). Training took place inside a custom-designed Y maze so that the growth pattern of the pea plants could

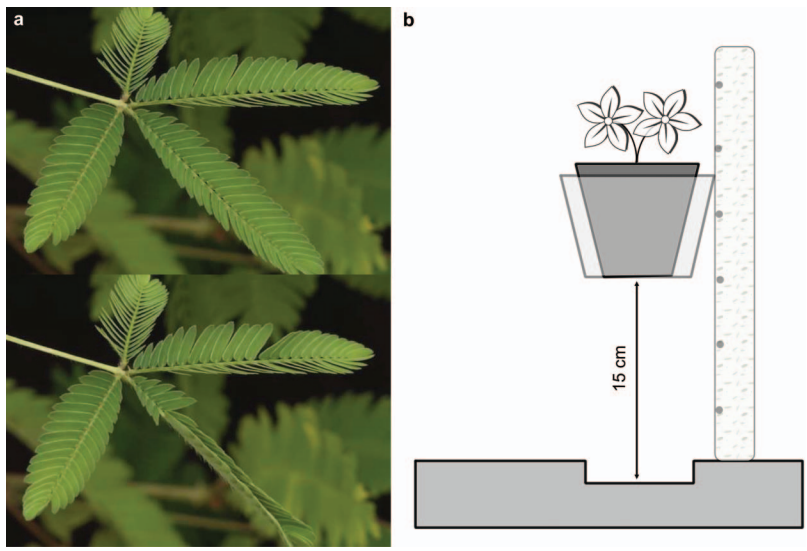

Figure 2. (a) The sensitive *Mimosa pudica* plant was considered the ideal model for this study because of its capacity to rapidly fold its leaves in response to physical disturbance. The maximum leaf breadth before and after training was carefully measured tip-to-tip. (b) The setup consisted of a plastic vessel mounted with hangers onto a marked steel rail, which was, in turn, secured to a foam base. Tightly fitted into the host vessel, individual potted plants were manually elevated to the 15-cm height mark and allowed to drop by sliding along the rail. The shallow depression in the foam base at the landing point of the vessel prevented it from bouncing at impact. A standard level of disturbance sufficient to force the closure of all leaves was administered to all the plants. From "Experience teaches plants to learn faster and forget slower in environments where it matters" by M. Gagliano, M. Renton, M. Depczynski, and S. Mancuso, 2014, *Oecologia, 175*, 63–72. Copyright [2014] by Springer Nature. Adapted with permission. See the online article for the color version of this figure.

be studied as they approached the Y-bifurcation, and the plants started growing into one of the two arms. Their results showed that the seedlings not only anticipated the unconditioned stimulus: They adapted their phototropic behavior by associating the neutral stimulus, the presence and position of a fan, with the occurrence of light (Gagliano et al., 2016). These results show that associative learning is an essential component of plant behavior. Associative learning, therefore, may represent a universal adaptive mechanism shared by both animals and plants (Figure 3).

Making Decisions

Plants can make decisions, and fairly complex ones at that. One major decision in the life cycle of plants is when to commence flowering (Angel, Song, Dean, & Howard, 2011; Boss, Bastow, Mylne, & Dean, 2004). The other major decision is when to initiate a new plant (Finch-Savage & Leubner-Metzger, 2006). But competition and a dynamic environment are the main determinants that really push plant decision-making to its limits. In one experiment, whenever plants were presented with tall competitors, they fell into shade-tolerance mode. Conversely, when *Potentilla reptans* L. (creeping cinquefoil; family: Rosaceae) plants were surrounded by small, dense vegetation, they attempted to grow vertically (Gruntman, Groß, Májeková, & Tielbörger, 2017). There are also subtler decisions that plants tend to make. For instance, plants "decide" to enter into a shade-tolerance mode that makes their leaves thinner and wider (to capture as much light as possible) depending on the level of their competition. Choosing one out of several different responses dependent on their circumstances could be particularly important in heterogeneous environments where plants may find themselves growing near neighbors with different sizes, ages, and density, and the decision could be a life-or-death one (Figure 4).

Plants can also demonstrate sensitivity to risk; namely, they can make adaptive decisions that take into account environmental variance, an ability previously ascribed only to the animal kingdom. For instance, during one study, the roots of pea plants were split between two pots, hence facing the decision of which pot to prioritize (Dener, Kacelnik, & Shemesh, 2016; Schmid, 2016). The results indicated that the plants grew more roots in the pot with higher levels of nutrients, showing an adaptive response similar to that exhibited by animals assigning superior foraging effort to richer food patches.

In another experiment, the researchers split the roots of each plant between two pots with equal average nutrient concentrations, but one pot had a constant level and the other a variable one (Dener et al., 2016). The researchers were interested in ascertaining if the plants would "prefer" growing more roots in one or the other. Based on theories on how human and animal decision-makers respond to similar choices, they predicted that the plants would prefer the more variable, risk prone pot when the average nutrient level was low and refer the less variable pot when the average nutrient level was high. Because the average nutrient level was below what was required for the plant to prosper, the variable option offered the chance to "gamble" on a run of good luck. Instead, when the average conditions were good, it made sense to

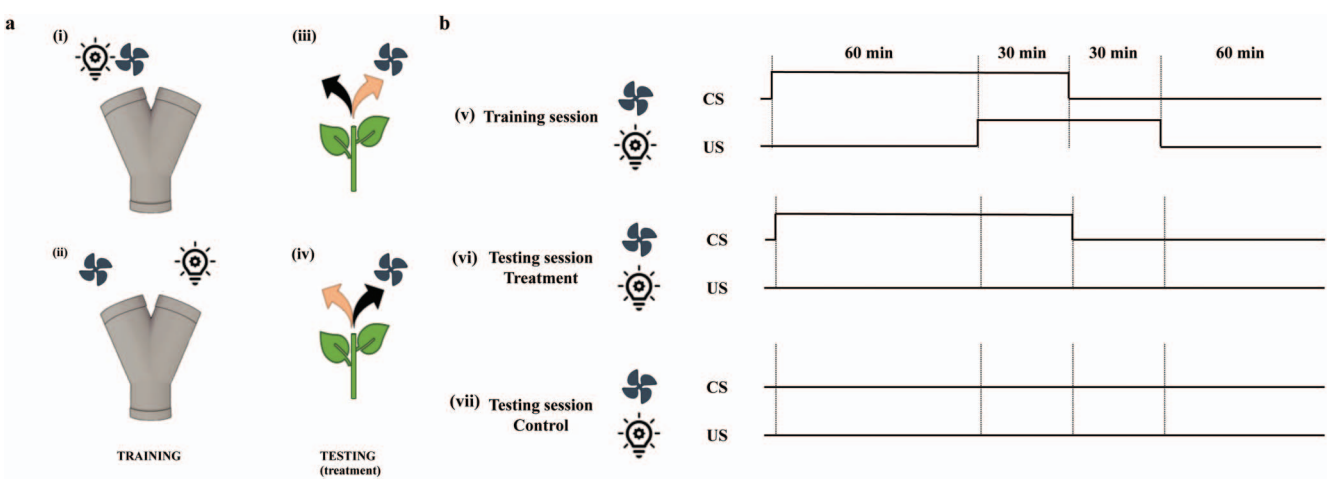

Figure 3. (a) The protocol used to evaluate associative learning of pea seedlings. During training the seedlings were exposed to the fan and light on either the same arm (i) or on the opposite arm (ii) of a Y maze. The fan served as the conditioned stimulus (CS) and light as the unconditioned stimulus (US). Two types of response were distinguished during testing with exposure to the fan alone. Correct response (CS): Seedlings growing into the arm of the maze where the light was "predicted" by the fan to occur (black arrow; iii [corresponding to Scenario i] and iv [corresponding to scenario ii]); incorrect response: Seedlings growing into the arm of the maze where the light was not "predicted" by the fan to occur (orange arrow; iii and iv). (b) The seedlings were trained during sessions separated by 1-h intervals. The 90-min CS preceded the 60-min US by 60 min so that there was a 30-min overlap (v). During the 1-day testing session, the seedlings were exposed to the fan alone for three 90-min sessions (vi). The seedlings of the control group were left undisturbed (vii; no fan, no light). From "Learning by association in plants" by M. Gagliano, V. V. Vyazovskiy, A. A. Borbély, M. Grimonprez, and M. Depczynski, 2016, *Scientific Reports, 6*, 38427. Copyright [2016] by Springer Nature. Adapted with permission. See the online article for the color version of this figure.

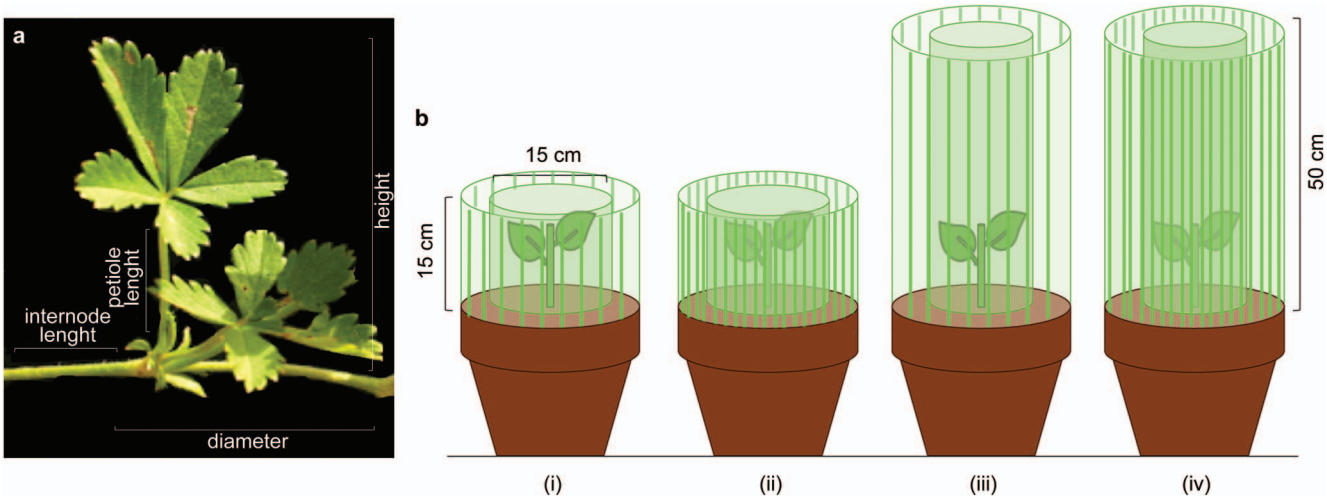

Figure 4. (a) A photograph of *Potentilla reptans* and a description of some of the measured variables. (b) A graphic representation of the experimental design. The experiment included treatments that simulated (i) short-sparse, (ii) short-dense, (iii) tall-sparse, and (iv) tall-dense neighboring vegetation. From "Decision-making in plants under competition" by M. Gruntman, D. Groß, M. Májeková, and K. Tielbörger, 2017, *Communications, 8*, 2235. Copyright [2017] by Springer Nature. Adapted with permission. See the online article for the color version of this figure.

go for the safe option. This is precisely what the pea plants did (Figure 5). The complex behavior these seedlings showed supports an idea, known as the risk sensitivity theory (Kacelnik & Bateson, 1997), that scientists have had trouble testing in insects and animals. According to this theory, when people have to choose between stable and uncertain outcomes, they will play it safe when things are going well, and they will take risks when times are rough. The experiment showed that plants are able to respond to risk and to switch to risk-prone or risk-averse behavior depending on resource availability. This indicates that those theories developed for animals and humans to explain decision-making and ideal behavior can also be applied to plants, which may at times serve as more suitable models.

Self and Others: A Matter of Games

Numerous experiments have shown that plants exhibit self-recognition. Approximately half of all angiosperms use self-incompatibility in reproduction. The individual discriminates against its own pollen arriving on the stigma, ensuring that even if it germinates, it is killed in favor of pollen from other individuals of the same species (Wilson & Burley, 1983). As another example, Falik and colleagues (Falik, de Kroon, & Novoplansky, 2006; Gruntman & Novoplansky, 2004) grew combinations of two ramets of *Trifolium repens* (white clover; family: Fabaceae) that were either intact, disconnected for varying amounts of time, or of a different genotype that were grown in a single pot altogether (Figure 6). As the interconnected ramets showed lower root length and mass with respect to the other combinations of ramets, this supports the notion that self/nonself discrimination was not based on biochemical recognition but on physiological coordination between different roots developing on the same plant. These results were consistent with the eight field-collected samples of genotypes and further support the idea that self/nonself discrimination is clearly present.

Self-recognition of individuals is crucial to competitive games and, indeed, competition between plants can be described by various versions of game theory. For instance, competition via root systems enables kinds of tit-for-tat strategies (Axelrod & Hamilton, 1981). An agent using this strategy will at first cooperate with an opponent, and then he or she/it will replicate the opponent's previous action. If the opponent was previously cooperative, the agent will behave cooperatively. If not, he or she/it will be uncooperative. In this context, cooperation between participants produces a more favorable outcome than a noncooperative strategy. So how, you may ask, does this apply to plants? We know that plants proliferate their own root systems to monopolize soil resources at the expense of their competitors (Gersani, Brown, O'Brien, Maina, & Abramsky, 2001). But intriguingly, we also know that a plant experiencing water-stressful conditions (leading to a reduction in growth) can convey that information to numerous conspecifics growing nearby via a root-to-root relay network. The forewarned plants immediately adopt the same water-saving strategies of the forewarner even before water stress sets in (Falik, Mordoch, Ben-Natan, Vanunu, Goldstein, et al., 2012). Admittedly, we would be expecting to see plants using competitive strategies to gain limited resources. From a different viewpoint, although warnings by plants experiencing water-stressful conditions might appear altruistic, they could be an intelligent strategy to induce their competitors to adopt a water-saving behavior that would, at the end of the day, benefit both.

The Social Side of Plants

It may seem farfetched to speak of the social psychology of plants, yet when writing about the relations between plants, Cle-

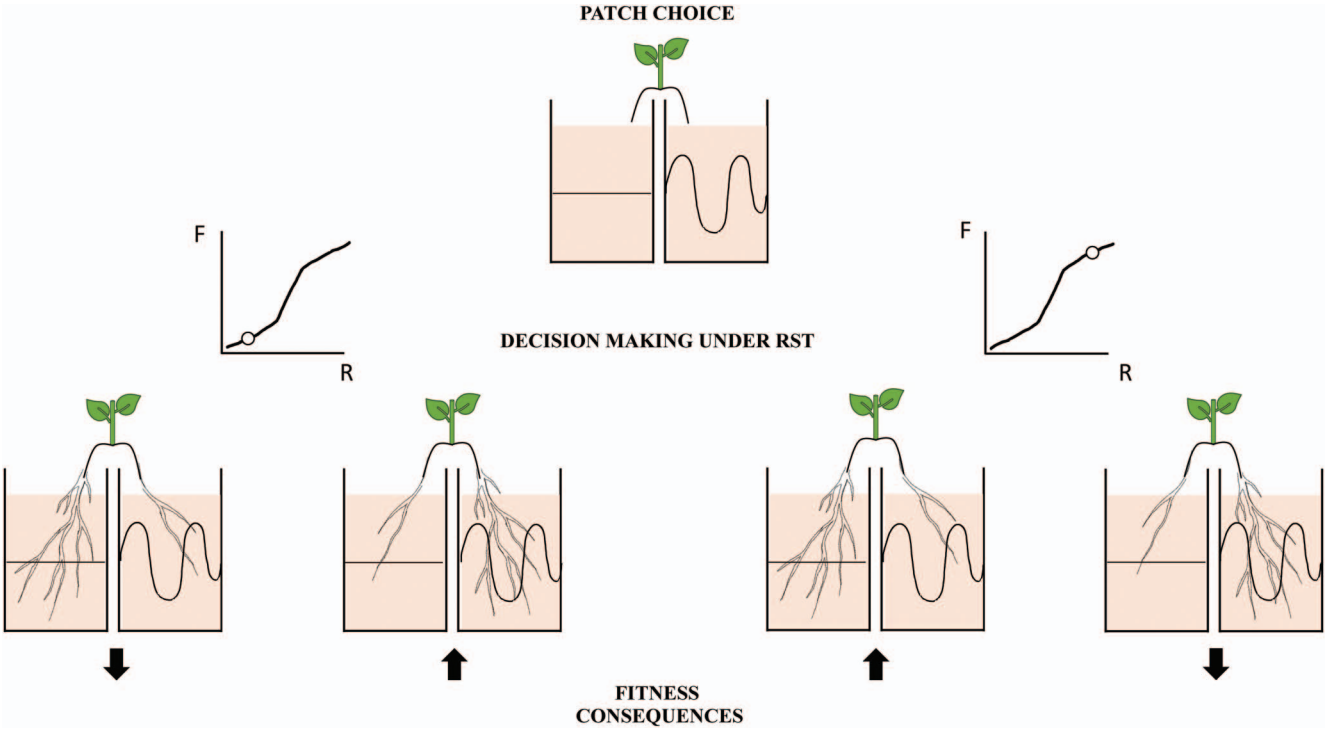

Figure 5. A plant with a split-root system preferentially allocates biomass to roots in a pot with variable levels of resources when the average resource concentration is low and fitness returns (F) are accelerating with increasing resource (R) level (circle in the left plot relating F to R). In contrast, the plant shows a risk-averse behavior when average resource concentration is high and fitness gains are decelerating with increasing resource level (right side). From "Decision-making: Are plants more rational than animals?" by B. Schmid, 2016, *Current Biology, 26*, R675–R678. Copyright [2016] by Elsevier Ltd. Adapted with permission. See the online article for the color version of this figure.

ments (1935) referred to behaviors that can be termed competitive or cooperative, as well as patterns of dominance, integration, or subordination going on in the families and even clans of plant communities. Some of the social behaviors mentioned here have been discussed earlier in this work (e.g., competition, cooperation, kin recognition, and families) and are reminiscent of the kind of social organization exhibited by animals (Whitehead, 1997).

Clements (1935) claimed that the first definite families were formed by unicellular algae, who reproduce by multiplying by fission or by the production of mucilage that serves a similar purpose. Although these families may be temporary, they are characterized by a division of labor as special cells take over the tasks of dividing the thread of apical growth and of spore production. Examples of living beings working together to their mutual advantage as well as all grades of parasitism and antagonism can also be found among bacteria (Buchanan, 1935; Jennings, 1906).

In some cases, plants may even exhibit rudimentary signs of parenting functions. Multicellular green alga, *Volvox carteri*, for example, produce small daughter colonies that are eventually released from the parent as they mature. Simard et al. (1997), whose research demonstrates that trees can exchange information, communicate their needs, and send one other nutrients via a network of latticed fungi buried in the soil, have greatly contributed to our understanding of how plants collaborate and help one another. For the most part, this is carried out through the mycorrhizal network, which is a kind of an underground pipeline connecting tree root systems so that nutrients, carbon and water can be exchanged. The researchers set out to study the Paper birch and Douglas fir growing together in early successional forest communities in British Columbia. They found that that the two types of trees do indeed compete with one other, but they also cooperate by sending nutrients and carbon back and forth through their mycorrhizal networks (Simard et al., 1997). Those researchers designed an experiment showing that the trees were aware when one of them was in need of help and readily gave it (Simard et al., 1997; Simard, 2009). Their study demonstrated that as the Douglas fir became shaded in the summertime, its excess carbon was transmitted to the birch. Then, in the fall, when the birch was losing its leaves and the fir had excess carbon because it was still photosynthesizing, it returned the favor. In evolutionary terms, the mycorrhizal networks seem to be the key to this relationship as they direct the transfer of carbon to ensure that they and the other members of the community receive the food that they need.

Molecular tools have also been used to uncover another disconcerting phenomenon, the "mother trees" (Beiler, Durall, Simard, Maxwell, & Kretzer, 2010). By examining the short sequences of DNA, researchers were able to map the mycorrhizal fungi networks linking Douglas fir trees in a natural forest (Beiler et al., 2010). Their investigation showed that with only a few exceptions, all of the trees were linked. Importantly, the tallest, oldest trees of

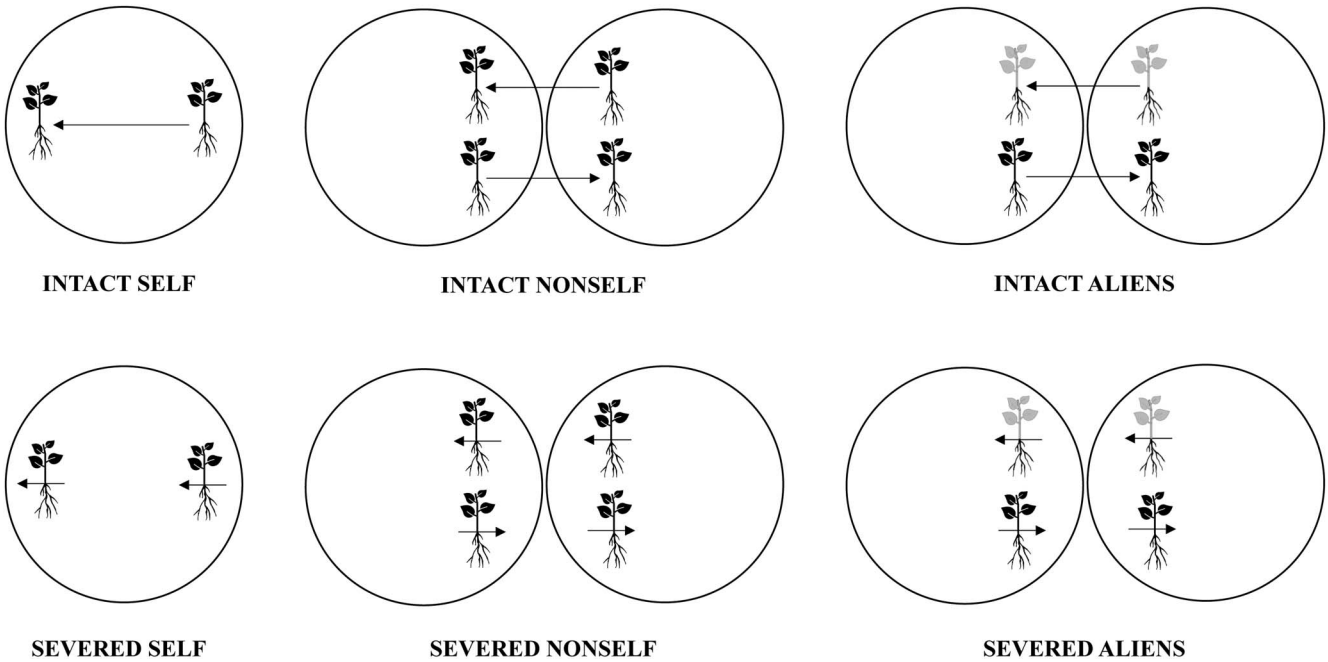

Figure 6. *Trifolium repens* ramet pairs with roots and shoots of similar size were grown, so each of their roots was confronted with another root that belonged to either the same (SELF) or to another physiological individual of the same (NON-SELF) or of a different genotype (ALIEN). The ramet connections were either left INTACT or SEVERED shortly before the experiment. The arrow represents the growth direction of the stolon. By reversing the growth direction, a younger ramet always competes with an older ramet in a single pot. Different shades represent different genotypes. From "Physiologicallymediated self/non-self root discrimination in Trifolium repens has mixed effects on plant performance" by O. Falik, H. de Kroon, and A. Novoplansky, 2006, *Plant Signaling and Behavior, 1*, 116–121. Copyright [2006] by Taylor & Francis. Adapted with permission.

the network had the most highly developed root systems and mycorrhizal networks. They also had more carbon flowing into the network and more root tips and were more connected to the other trees around them. Even more unexpectedly, they were able to recognize kin and to favor them.

According to recent reports, mycorrhiza-mediated nutrient transfer between trees can also help to keep even tree remnants alive (Bader & Leuzinger, 2019). When Bader and Leuzinger (2019) set out to investigate how nearby trees were able to keep a tree stump alive, they measured the water flow in the stump and the surrounding trees belonging to the same species and found that the water movement in the tree stump negatively correlated with that in the other trees, suggesting that the roots of the stump were grafted to those of the surrounding trees. Root grafts can form between genetically different trees if they are similar enough to permit an exchange of resources. Normally, this is not how trees operate as the water flow is driven by the water potential of the atmosphere. In this case, the stump has to follow what the rest of the trees are doing, as without transpiring leaves, it escapes the atmospheric pull. But although root grafts are common between living trees of the same species, why would a living kauri tree want to keep a nearby stump alive? The advantages are obvious for the stump: With no green tissue of its own, it would be dead without the grafts. But why would the host trees keep the useless stump alive? What is in it for them? The hypothesis posited by the researchers was that the graftage was formed before the tree lost its leaves and became a stump. The wider root system provided greater access to resources such as water and nutrients and increased their stability on a steep forest slope. The fact that one of the trees stopped providing carbohydrates may have gone unnoticed, so the old stump continues to live through its attachment to other living trees. This has far-reaching consequences for our perception of trees, as it would seem that we are not dealing with trees as individuals, but with the forest as a superorganism. During a drought, for example, trees with less access to water might be connected to others with a greater one; sharing limited resources increases their chances of survival.

These results are all pointing in the same direction toward an underground, invisible "wood-wide web" (Sen, 2000) that supports the social life of tree and other plant communities. Over 2 centuries ago, explorer-naturalist von Humboldt coined the term "socially organized plant life," and we are becoming ever more aware of its many implications (von Humboldt & Bonpland, 1807). It is time now to start thinking about the sort of unit the study of social vegetation should be based on and how it can be characterized and distinguished from other living communities.

Plants' Relationships with Other Organisms

Just as animals, plants are responsive to their environment and the organisms that populate it (Witzany & Baluška, 2012). They rely on complex interactions with birds and insects to complete

sexual reproduction. Plants reward these pollinators with nectar and other compounds necessary to the diet of obliging birds and insects (Cozzolino & Widmer, 2005). Complex interactions between insect pheromones and plant volatile semiochemicals have also been recorded (Reddy & Guerrero, 2004). Consider, for example, the case of *Arum* spp. (family: Araceae); many species of this flowering plant attract insects to animal dung where they would otherwise gather and reproduce (Kite et al., 1998). It is not common knowledge that some plants and ants appear to cooperate mutually to protect plants from herbivores, pathogens, and other competing plants (Brouat, Garcia, Andary, & McKey, 2001; Dejean, Solano, Ayroles, Corbara, & Orivel, 2005). As a reward for the ants' efforts, the plant secretes nectar (Heil, Rattke, & Boland, 2005) and constructive specialist food bodies (Solano, Belin-Depoux, & Dejean, 2005). In some cases, when the plant recognizes an enemy, it can recruit them to its cause (Arimura, Kost, & Boland, 2005). Take plant roots attacked by insects; these roots secrete volatiles when attacked, attracting nematodes to attack the predators (Rasmann et al., 2005). Plants can release these volatiles in aerial environments, informing surrounding plants of pathogens, allowing them to increase their immunity (Paré & Tumlinson, 1999; Reddy & Guerrero, 2004). Interestingly, the signature of released volatiles in cases of herbivore damage is different from the volatiles released for general wound reactions (Arimura et al., 2005). This phenomenon has been analyzed in field conditions for perennials, including beech and ash trees, as well as under greenhouse conditions for many herbaceous annuals, including brussels sprouts and cucumbers (Paré & Tumlinson, 1999).

Plants on the Move

Although plants are unable to move from one place to another, they are very much in tune with their environment and are very capable of a variety of movements. Some plant responses do involve physical movement and are remarkably animal-like in effect, though not in scale. Plants may not move as far or as quickly as animals, but some are hardly immobile. The important issue here is that some plants' movements achieve many of the same functional ends as those of animals (Huey et al., 2002). For instance, a part of the life cycle of many plants and animals implies relocation to a new site (Croteau, 2010). A common form for such relocation is dispersal, an ecological process that involves the movement of an individual (or multiple individuals) away from the population in which they were born to another location, or population, where they will settle and reproduce. Dispersal can be active or passive. The former is common in both adult and juvenile animals and involves movement of the entire organism through its own ability. Passive dispersal is evident in both plants and animals unable to move that uses dispersal units called *disseminules* to aid in reproduction or the exploitation of new environments. Many disseminules are adapted for movement by specific dispersal agents such as wind, water, or another animal capable of active dispersal. Among the sessile adult animals that utilize passive dispersal are invertebrates such as sponges and corals. Their disseminules are typically specialized buds or cells used in reproduction. In plants, seeds, spores, and fruits are the most common disseminules. All of them have modifications for movement away from the parent plant via available environmental kinetic energy. Some disseminules are explosively released over short distances, whereas others fall to the ground at the base of the parent plant. Seeds and fruits are scattered by invertebrates, mammals, and birds during feeding and distributed in feces after ingestion. Water currents, winds, and flying animals are among the most successful agents of long-distance passive dispersal. Seeds and fruits that have wings, hairs, or inflated processes are carried efficiently by wind. In addition, some plants have sticky seeds or fruits that adhere to the feathers or fur of mobile animals.

Some plants have responses that achieve much the same ends as the locomotor adjustments of animals. Plants can effectively choose where to live by growing toward the needed resources or away from environmental stressors (Bazzaz, 1991). Neotropical stilt palms (*Socratea exorrhiza*) move on their stilts toward light gaps (Leopold, Jaffe, Brokaw, & Goebel, 2000). Others such as climbing and clonal plants can crawl across the environment in search of appropriate habitats as animals do. In fact, such movements are sometimes called "foraging" (Harper, 1977). Similar to the orientation movements of animals (Stevenson, 1985), plants can orient their leaves and flowers toward or away from the sun (Stanton & Galen, 1989). Leaves of many plants change their orientation during the day, maintaining a perpendicular orientation to the sun's rays, and thereby enhance photosynthesis (rather than modulate body temperature as in lizards; Ehleringer & Forseth, 1980). Other movements such as the solar tracking by flowers of alpine buttercups (*Ranunculus*) provide a heat reward to insect pollinators as well as to increase seed set (Stanton & Galen, 1989).

Charles Darwin during his multifaceted career manifested a strong interest in plants' movement. He and his son Francis wrote a book on movement of plants (Darwin, 1875; Darwin & Darwin, 1880) in which they reported that plants have the capacity to move directionally as well as to exhibit tropic responses in response to directional environmental cues (Darwin & Darwin, 1880; Loeb, 1890). Darwin and Darwin (1880) in fact observed that the tendrils of climbing plants tend to assume the shape of the surfaces they have already come into contact with; that is, they learn progressively the shape of potential support characteristics (Darwin, 1875; Trewavas, 2017). This implicitly signifies that they perceive the support system, and they plan their movements accordingly. According to this view, climbing plants represent actions in terms of their perceivable consequences: Selecting, planning, and initiating an action is mediated by action-effect anticipations. This is a surprising notion, as interactions between organisms and objects have until now implicated the CNS. What Darwin's observations are suggesting is that there may be other options that do not require the CNS for adaptive perceptuomotor transformations to occur. A recent study seems to confirm this view (Guerra et al., 2019). The 3-D kinematic analysis of a climbing plant (*Pisum sativum* L.) demonstrated that the plant perceives a potential support and modulates the kinematics of the tendrils' aperture depending on the thickness of the support. One group of plants was tested with a "thick" support (3 cm diameter), and another was tested with a "thin" one (1.2 cm diameter). The results indicated that the plants not only acknowledged the presence of the support but that they scaled the kinematics of the tendrils' aperture depending on the support's thickness (Figure 7). The peak of the average and maximum velocity of the tendrils was higher for the thin support than the thicker ones. In temporal terms, the time at which the tendrils reached peak velocity and the time at which the tendrils reached the maximum aperture, both calculated as a percentage of move-

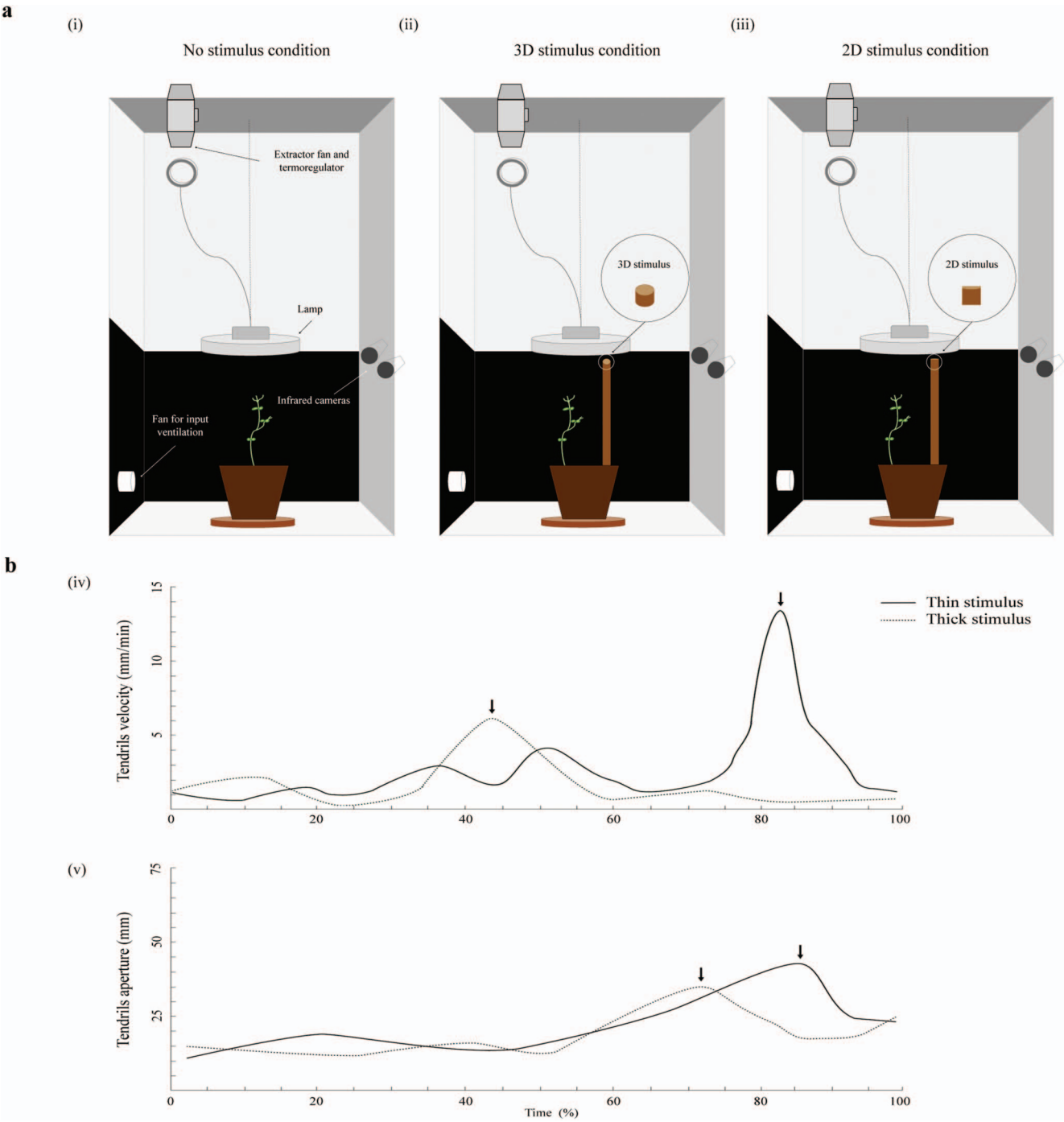

Figure 7. (a) Graphical depiction of the experimental set up and the experimental conditions considered in the study. (i) "No stimulus" condition; (ii) "3D Stimulus" condition in which a wooden pole (i.e., the 3-D stimulus) 60 cm high with a diameter of either 1.2 cm (thin stimulus) or of 3 cm (thick stimulus) was positioned at a distance of 12 cm in front of the first unifoliate leaf of each plant; (iii) "2D Stimulus" condition in which the 2-D representation (picture) of the 3-D stimuli was attached to one of the walls of the growth chamber. (b) The tendrils' kinematics was scaled with respect to the size of the supports. Velocity (iv) and tendrils aperture (v) profiles for the movements performed toward either the thick or the thin supports. Arrows indicate the occurrence of maximum peak velocity and maximum grip aperture depending on the thickness of the supports. Please note that when the support is thicker, the peak velocity is anticipated and the maximum aperture of the tendrils is reached earlier for the thicker with respect to the thinner support. From "Flexible control of movement in plants" by S. Guerra, A. Peressotti, F. Peressotti, M. Bulgheroni, W. Baccinelli, E. D'Amico, . . . U. Castiello, 2019, *Scientific Reports, 9*, 16570. Copyright [2019] by Springer Nature. Adapted with permission. See the online article for the color version of this figure.

ment duration, were later for the thinner support than the thicker support. The maximum distance between the tendrils was significantly greater for the thinner support than the thicker one. In another experiment, one group of plants was exposed to the photo of a thin support and another group to a photo of a thick one. Importantly, no quantitative differences in the dependent measures were detected across the two stimuli. This is particularly important because it signifies that the plants extracted the "graspable" properties of the stimulus to determine how to engage motor modules to produce suitable behavioral outputs. Another aspect concerned with the motor control of plants is that their movement obeys the speed–accuracy trade-off (Woodworth, 1899), a tendency for decision speed to covary with decision accuracy. The speed–accuracy trade-off is an inescapable property of aimed movements being present in a wide range of species, from insects to primates (Chittka, Skorupski, & Raine, 2009). By examining the swaying in circles of the tips of shoots exhibited by climbing plants (*Pisum sativum* L.) as they approach to grasp a potential support, Ceccarini et al. (in press) found that plants were able to process the properties of the support before contact and, similar to animal species, to modulate movement velocity strategically according to task difficulty. Altogether, these findings suggest that these plants are capable of flexible, goal-directed behavior, which is achieved through a sensorial analysis of the environment.

Nesting Plants' Cognition in Available Theories

In view of the abovementioned considerations, the question should no longer be *if* plants are cognitive organisms but *how* plants make use of their cognitive capacities. From the perspective of situated cognition (Cheng, 2018), and in particular with reference to embodied, extended and enactive cognition, plants can indeed be called cognitive agents. Historically speaking, plants have been excluded from the wider cognitive domain of embodied cognition, as it was thought that they lacked the sensorimotor organization that characterizes the embodied cognition theory (Gallese, 2008; Varela, Rosch, & Thompson, 1991). Unlike animals, plants do not have freedom of movement within their environment, which means that they lack the precondition for cognitively guided behavior proposed by these theorists. Embodied cognition emphasizes that free-moving, adaptive, flexible organisms organize their behavior and operate coherently. But it may not be necessary to link cognition to free movement within an environment. Although plants are stuck in the ground, they are nevertheless able to manipulate their environment by beginning new metabolic processes and modulating old ones. Furthermore, they can integrate internal and external signals displaying complex behaviors (some of which have been listed earlier). Embodied cognition has also been defined as some features of cognition that are shaped by aspects of the organism and not by the CNS (Calvo Garzón & Keijzer, 2011). Using this definition, all behavior demonstrated by plants is embodied, as they have no CNS. The fact that plants are capable of complex behaviors meets this modified definition of embodied cognition. Although different from that of animals, the behavior of plants is no less complex or adaptive (Di Paolo, 2005; Garzón, 2007). Other organisms without a CNS, such as slime molds, also exhibit behaviors that are considered cognitive. Similar to plants, the molds display sensory integration, decision-making, and memory (Boisseau et al., 2016; Reid, Latty, Dussutour, & Beekman, 2012).

Extended cognition posits that cognition may go beyond the mere physical bounds of an organism expanding into the environment and involving objects that do not form part of its morphology. There are two ways in which plants extend their cognition beyond their physical structures (Parise et al., 2020): through root exudates and through the microorganisms that live in association with the roots. As far as the first is concerned, it is possible that plants can modify their rhizosphere and the influence zone of their roots to expand their cognitive processes so that they can enhance their understanding of their underground environment beyond the physical boundary of their roots. For example, the accumulation of exudates between obstacles and roots is related to the plant's perception of obstacles in the soil, causing inhibited root growth in the direction of the accumulated exudates (Falik, Reides, Gersani, & Novoplansky, 2005). It has been experimentally proven that the plant is prevented from perceiving obstacles and even grows toward the obstacle as if they were not there, if exudates have been removed from the substrate (Falik et al., 2005). The relationship between plants and its exudates is similar to that of the spider with its web mentioned above; the plant, plus its exudates, forms the same cognitive system.

As far as microorganisms are concerned, plant cognition could be extended to the bacterial community that is associated with its roots. Animals too are now considered to be extended to microorganisms, in that gut bacteria "talk" to the CNS and are thought to influence behavior. For their own sake, plants actively manipulate their rhizosphere microbiome. An example can be found in *Arabidopsis*, in that it creates an *Arabidopsis*-specific bacterial community by synthesizing triterpenes through specific pathways to modulate the bacterial community that are associated with its rhizosphere (Huang et al., 2019). Through root exudates, the plant can modify the diversity and abundance of this bacterial community, and, in turn, the composition of the community can encode memories in the soil outside the plant's physical body. In addition to this, a plant can also extend its cognitive processes through the mycorrhizal fungi with which they are associated. Through root colonization, fungi can penetrate a plant's roots and interface to exchange signals and molecules (Müller & Harrison, 2019). The fungi amplify the absorptive area of the roots, thus helping the plant absorb water and nutrients such as phosphorus. Plants repay the fungi with photoassimilates (Simard, 2018). This association allows plants to perceive items outside of their own reach. For example, depending on what mycorrhizae perceive and absorb in a particular area, a plant may decide to grow its roots in one direction or another, depending on its need for nutrients and the water and resources that are available. As such, this association promotes a plant's perception and facilitates communication, learning, and memory in plants—all cognitive processes. As this evidence leads to the suggestion that plants extend their cognition beyond their physical bodies, it encourages us to reconsider where plant and environment overlap.

Connected to these observations, the capacity of organisms to adaptively, flexibly, and sophisticatedly interact with an environment to maintain their systematic autonomy forms the basis of enactivism (Di Paolo et al., 2017; Hutto & Myin, 2014, 2017; Thompson, 2007). Enactivism posits that it is the organisms' dynamic interaction between one another and their environment

that gives rise to cognition. According to this theory, an organism can selectively create its environments by engaging and interacting with the world around it. In other words, a cognitive system is not just a passive being reacting to external obstacles, but an open, autonomous system that explores an environment to meet goals and needs by regulating its sensorimotor coupling in a variety of context-specific circumstances. Enactivism is a particularly valuable theory with regard to cognition involving plants. Pea plants, for example, are known to be very flexible and not merely reactive to the world in a fixed, singular manner. The intrinsic kinematics of the tendrils' approach-to-grasp movements are programmed and controlled through their perception of the features of their surrounding environment (Guerra et al., 2019). In this regard, plants are similar to animals in their relationship with their environment, at least in terms of the cognitive control in action.

Conclusion

If plants can apparently communicate, learn, and move intentionally, should we consider these abilities as cognitive processes even in the absence of a CNS? If we do so, there is the risk of reviving old controversies over esoteric claims regarding plant consciousness. Recent findings attained using the most advanced techniques and rigorous experimental designs suggest nevertheless that the cognitive abilities of plants are not just wacky ideas. They show that complex centralized cerebral processes are not necessary for the implementation of cognitive behavior (Trewavas, 2014) and that simpler physiological mechanisms facilitating networks between different organs in an individual (Novoplansky, 1996; Shemesh, Arbiv, Gersani, Ovadia, & Novoplansky, 2010) or between individuals (Karban, 2015) can produce a form of cognition with complex adaptive behavioral outcomes. Despite more than 1.5 billion years of independent evolution, plants and animals show similarities in important behavioral patterns that are based on entirely different mechanisms. Psychologists have at their disposal an array of state-of-the-art instruments and techniques to study plant behavior, and, depending on the results of their experiments, they are in an ideal position to theorize about the mechanisms that underlie them. Importantly, they have a decisive contribution to make if we want to agree on a terminology and theories that can accommodate both animal and plants' relations with their environments.

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