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Plants on the Move: Decision-Making Underlying Support-Searching in Pea Plants

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ABSTRACT

The process of finding a suitable support is crucial for the growth and development of climbing plants, as those that succeed in finding one tend to have better performance and fitness compared to those that do not. While there have been numerous studies that have investigated the details of how climbing plants seek and attach to supports, there has been relatively little research on the ecological importance of this behavior and the elements that influence it. One of the elements is the diameter of the support, which can affect its suitability for climbing plants. If the support diameter is too large, the plant may not be able to keep tensional forces and may lose its attachment to the support. To further explore this issue, we experimented with pea plants by giving them choices between supports of different diameters while tracking their movement using a three-dimensional motion analyzing software. Our results indicated that the way climbing plants move can vary depending on the number of potential supports available in the surroundings. In addition, when presented with a thin and a thick support, the plants tended to prefer the former over the latter. These findings elucidate how climbing plants make decisions about support searching and suggest that they are capable of adapting their behavior in response to different environmental conditions.

Table of Contents

| | |
|---|----|
| ABSTRACT | 1 |
| 1. INTRODUCTION | 3 |
| 1.1 The Development of Understandings towards Plants..... | 3 |
| 1.2 Plant cognition nowadays | 5 |
| 1.3 Plants on the move..... | 9 |
| 1.4 Physiological mechanisms underlying plants' movement..... | 11 |
| 2. OBJECTIVES..... | 14 |
| 3. MATERIALS AND METHODS | 16 |
| 3.1 Subjects..... | 16 |
| 3.2 Experimental conditions | 16 |
| 3.3 Experimental setup | 17 |
| 3.4 Kinematic acquisition and data processing | 19 |
| 3.5 Dependent measure..... | 20 |
| 4. RESULTS..... | 24 |
| 4.1 Qualitative results | 24 |
| 4.2 Kinematic results | 25 |
| DISCUSSION..... | 30 |
| REFERENCES | 34 |

1. INTRODUCTION

1.1 The Development of Understandings towards Plants

Humans' perception towards nature is constantly evolving through time. From a historical perspective, ancient Greeks built a hierarchy representing the view of nature, with humans at the top, followed by animals, then plants are at the bottom (Naddaf, 2014). From the dieting use in the gather-hunter era to the agricultural societies, the way we apply plants has a profound influence on our society. For instance, the earliest written evidence of the application of herbs could be traced back to 5000 years ago, in a Sumerian clay slab from Nagpur. 12 recipes for drug preparation referring to over 250 various plants were discovered (Kelly, 2009).

Although there is a significant benefit of plants for humans in various degrees, we are still lacking a conception of what else could plants do. In the classic work of *Peri psyches*, Aristotle classified all living things, plants, animals, and humans based on his analogy engine regarding souls. According to Aristotle, plants possess a vegetative soul which enables plants to reproduce and grow; animals in addition also possess a sensitive soul that allows them to sense surroundings and pursue movements; humans as a peculiar case, not only have both vegetable and sensitive souls but also encounter so-called rational soul which accredits to reasoning and reflection (Taylor, 1992).

Another ancient Greek philosopher Theophrastus wrote extensively about plants and their behavior in his book *Enquiry into Plants*, Theophrastus observed that plants exhibited certain behavior, such as growing towards light and water, and described the processes of pollination and seed dispersal. One of Theophrastus' most important contributions was his observation that plants exhibit different behaviors in response to

different stimuli. For example, he noted that some plants will grow towards sources of light, while others will grow away from it (Hughes, 1985).

In the 18th century, a concept called vitalism started to be discussed by many biologists. This theory held that living organisms possessed a unique quality that could not be explained by the laws of physics and chemistry alone. Proponents of vitalism believed that plants had a kind of consciousness or vitality that made them fundamentally different from non-living matter (TF Döring et al., 2012).

Until the 19th century, through ecological observations, a naturalist Charles Darwin proposed that there were similarities between the movements of plants and animals, and that both could be explained through the principles of natural selection. (Darwin, 1880). Darwin proposed an evolutionary point of view in his book *The Power of Movement in Plants* (1880). In the book, Charles Darwin introduced the concept of circumnutation, which refers to the regular, oscillatory movements exhibited by growing plant organs, such as stems and tendrils. He observed and analyzed these movements in detail and proposed that they are a result of the unequal growth rates of different parts of the organ. Darwin believes there is a behavioral change that exists based on the drive to survive in plants (Jørgensen et al., 2015).

Darwin's work also shed light on the mechanisms underlying plant movement, such as the role of light and gravity. He conducted experiments on the bending of plant shoots towards a light source and found that the tip of the shoot was responsible for the bending, which he called the "perception of light" (Darwin, 1880). In addition, in the book *Insectivorous Plants*, Darwin (1875) studied the behavior of plants that were able to capture and digest insects. He observed that these plants exhibited complex mechanisms for capturing and digesting their prey. This was considered as a form of adaptive behavior

in plants. According to Darwin, plant movement is not solely a passive effect in respect of surroundings, rather, it is a directive act responding to external stimuli (Darwin, 1880; Whippo et al., 2009). Furthermore, Darwin also proposed the hypothesis of “root-brain”, later imply the root of the plant may exhibit certain functions as an organ-like brain (Darwin, 1880; Kutschera et al., 2009).

Overall, Darwin’s work on plant behavior paved the way for future research in the field and contributed to our understanding of the complex and dynamic nature of plants.

1.2 Plant cognition nowadays

Recent studies have shown that some plants exhibit cognitive behavior that was once thought to be exclusive to animals. What hinders the understanding of plants is that they do not have a central nervous system. Some argue cognitive behaviors demand the nervous system since the nervous system plays an important role in controlling one’s body and commanding orders to the rest of the body base on sensory information given. For instance, animals are well-known for their cognitive abilities, such as decision-making, learning, and memory. They can use information from their environment to make decisions that improve their chances of survival.

Despite the phylogenetic point of view, current studies are making attempts to explore if plants are also able to demonstrate certain behaviors one would consider as cognitive. For example, one study shows that plants may respond to competition for light in different ways, including vertical growth, shade tolerance, and lateral growth (Gruntman et al., 2017). The scholars proposed the hypothesis that *Potentilla reptans* can "choose" which response to use based on their ability to compete with their neighbors. The results show that the plants exhibit different responses depending on the density and height of their neighbors, with the highest vertical growth under short-dense neighbors,

the highest specific leaf area under tall-dense neighbors, and an increase in total stolon length under tall-sparse neighbors (Gruntman et al., 2017).

Plants may also be capable of associative learning and can modify their behavior based on past experiences. For instance, studies show that the pea plant (*Pisum sativum* L.) was able to learn to associate a sound with the presence of a nearby nitrogen source. The plants were exposed to a clicking sound before being given nitrogen, and after a few repetitions, they began to grow more toward the sound even in the absence of nitrogen (Gagliano et al., 2016). This indicates that the plants were able to remember the association between sound and the presence of nitrogen and modify their growth pattern accordingly. This is a fascinating discovery that challenges our understanding of plant cognition and behavior.

One of the most astonishing discoveries arguing whether plants encounter memories. For example, during the investigation of the electrical memory of the Venus flytrap (*Dionaea muscipula*), scholars found that the plant can distinguish between two and five stimuli, and that the memory lasts for about 30 seconds, which is based on the changes in the electrical potential across the membrane of the plant cells (Volkov et al., 2008). Another study on *Arabidopsis thaliana* demonstrated that the plants are capable of encoding and remembering information about their environment, allowing them to adapt and respond to changing conditions, such as adjusting their internal circadian clocks to optimize their photosynthesis and growth (O'Neill et al., 2011).

Although plants do not produce vocal languages, there may exist a method for plants to communicate. A study found that sagebrush plants release chemicals in response to insect damage that not only attract predators of the insects, but also warn nearby sagebrush plants to produce their own chemical defenses (Karban, 2013). Furthermore,

Hirokazu Toju and colleagues (2014) discovered that the interactions between plants and fungi were not random, but rather formed specific patterns and communities through a plant-fungal network. These communities were driven by factors such as soil type, climate, and geographic location, which influenced the health and productivity of the plants in the ecosystem (Hirokazu et al., 2014).

In 1990, studies described a particular region of the root apex of maize, which is interpolated between the elongation area and the apical meristem as the most sensitive spot of the plant. This may correspond to what Darwin inferred as the 1.0-1.5 mm from the tip of the root. This part of the root apex has been named “basal meristem”. The function of this area could reproduce cells rapidly for elongation starting from the basal border of the root apex. Some scholars argue this shall be renamed as the command center of the plant, or even, the cognitive center (Baluška et al., 1990).

The emergence of the idea of collective intelligence in the 20th century claims that complex behaviors may appear from the collective actions of many simple and relatively unintelligent entities, such as cells, organisms, or even groups of individuals (Bloom, 2013). In the context of plants, this theory suggests that plant behavior and cognition arise from the collective actions of cells and organs working together, rather than being controlled by a centralized brain or nervous system (Mancuso, 2018).

Another idea such as embodied cognition is a theory that suggests that cognitive processes are deeply influenced by the body and the surrounding environment (Wilson 2002). It proposes that the mind and body are intertwined and that they work together to create our experiences and perceptions of the world. In other words, the body is not just a passive organ that carries the mind around, but an active participant in the cognitive process (Barsalou, 2010).

Similarly, Enactivism is a paradigm that also emphasizes the active role of the environment in shaping the behavior and cognition of an organism (Reid, 1996). As for plants, Enactivism suggests that the physical and chemical properties of the environment actively shape plant behavior and cognition (Reid, 1996). For instance, a recent study aimed to investigate the changes in the temporal dynamics of low-voltage electrical signals in soybean seedlings under different environmental conditions (cold, low light, and low osmotic potential), and the results showed that the temporal dynamic of the electrical signaling displayed a complex non-linear behavior with long-range persistence, and under low light and osmotic stress conditions, the system exhibited spikes with power law distribution. Indicate that plants, can respond and adapt to changing environmental conditions in a dynamic and self-organized manner (Souza et al., 2017).

On top of an ecological point of view, psychologists argue that perception and action are closely intertwined and that organisms actively engage with their environment to gather information and accomplish goals (Gibson et al., 1966). In recent years, this approach has been applied to the study of plant behavior and cognition. By studying the circumnutation of climbing bean stems, Calvo and his colleagues believed that plants may perceive and guide their movements ecologically, picking up invariant information in their environment through specific variables (Calvo et al., 2015).

The emerging theories of collective intelligence, embodied cognition, and Enactivism suggest that plant behavior and cognition may arise from the complex interactions of cells, organs, and the environment. As we continue to uncover the mysteries of plant cognition, we may discover even more surprising and fascinating ways in which plants interact with their environment and exhibit complex behaviors.

1.3 Plants on the move

One of the misunderstandings of plants in general is that plants are static, rooted in a certain place and immobile. Nonetheless, within centuries of investigations, plants express abundant movements for different purposes. For instance, as written in the book of Darwin *the Power of Movement in Plants*, Darwin analyzed various types of plant movements, from the twisting of tendrils to the opening and the closing of flowers (Darwin, 1880).

One of the most well-known examples of plant movement is *phototropism*, or the ability of plants to grow toward a source of light. This phenomenon was first described by Charles Darwin in the 19th century, who observed that seedlings bend towards a light source even when it is positioned at an angle to the vertical axis of the plant (Darwin, 1880). More recent research has revealed that this process is mediated by the hormone auxin, which accumulates on the shaded side of the plant and promotes growth in that region (Pickard, 1985).

Other plant growth responses include *gravitropism*, or the ability of plants to orient their growth in response to gravity (Gilroy, 2008). One classic example of *gravitropism* can be observed in the growth of roots and shoots. In roots, the cells on the lower side of the root elongate faster than the cells on the upper side, causing the root to bend downward and grow deeper into the soil. Conversely, in shoots, the cells on the upper side elongate faster, causing the shoot to bend upward and grow toward the light (Chen et al., 1999).

Nastic movements in plants are rapid, reversible, and non-directional movements in response to environmental stimuli such as light, temperature, humidity, touch, and chemicals (Lalit, 2002). One example of nastic movements is the closing of the leaves of the Venus flytrap (*Dionaea muscipula*) in response to the touch of an insect. This

movement is triggered by the stimulation of sensitive trigger hairs on the inner surface of the leaves, which leads to the rapid release of stored elastic energy in the leaf blades, causing them to fold and trap the prey (Forterre et al., 2005)

Over a century ago, researchers in plant physiology observed that plant organs, such as roots, shoots, flower stalks, and branches, do not grow in a single direction but rather oscillate slowly around a mean growth direction which is named circumnutation by Charles Darwin (Darwin, 1875). This oscillatory growth pattern is a result of the asymmetric growth rate that is typical of elongating plant organs (Brown, 1993).

Circumnutations are complex, rhythmic movements exhibited by many plants, which are influenced by internal and external factors, including light, gravity, and water availability. For example, stimuli such as light, with plants exhibiting phototropism by adjusting the direction of their circumnutation in response to the light direction (Darwin, 1875). Darwin also noticed that the tendrils of climbing plants via circumnutation can investigate surroundings for resources and supports (Brown, 1993). Speaking of supports of the climbing plants, the velocity of circumnutation has been found to be determined by the thickness of the supports. When plants needed to grasp a thinner support, both the average and maximum velocity of their tendrils tended to be faster. This is likely due to the increased difficulty of interacting with a thicker support, which requires more precise movement control to accurately ascend (Ceccarini et al., 2020). The ability to adjust the movement of a plant based on the properties of the support it is reaching for underlie the possibility of cognitive agents in plants, that are capable of controlling their movements through anticipatory processes (Ceccarini et al., 2021).

Plants have been shown to exhibit responses to their environment that go beyond simple physiological reactions, and circumnutation may be an example of this. Another

research bases on the circumnutation of plant roots and found that the movement was not simply a response to gravity or touch, but also seemed to be purposeful in searching for nutrients and water in the soil (Yokawa et al., 2018).

In the field of plant cognition, plant movement and behaviors have gained an extensive interest. Some scholars believe that the movement of plants are not solely mechanical, but rather intentional. One study suggests that lima bean plants were able to learn and remember the presence of herbivores in their environment through the release of volatile chemicals. The plants then produced more defensive chemicals to deter the herbivores, indicating an intentional response to their surroundings (Arimura et al., 2000).

In conclusion, the idea that plants are static and passive organisms has been challenged by numerous studies that have revealed the diverse and intentional movements of plants. These movements are not only for survival, but also for growth and adaptation. The emerging field of plant cognition has shed light on the complex sensory and signaling mechanisms underlying plant movement and behavior. With further research, we may uncover more evidence of the intentional nature of plant movements and broaden our understanding on the non-human organisms.

1.4 Physiological mechanisms underlying plants' movement

Plants are known for their ability to move in a variety of ways, from bending toward the light to curling their leaves when touched. These movements are not driven by muscle contractions, as is the case in animals, but instead by physiological mechanisms that allow plants to respond to environmental cues.

One of the signs underlying plant movements is a hydraulic mechanism, which involves the regulation of water flow in the plant cells. This refers to a plant's ability to maintain turgor pressure within its cells. Turgor pressure is the force exerted by water

inside the plant cell against the cell wall. By maintaining high turgor pressure, plants can support their leaves and stems, and generate movements. For example, the Venus flytrap (*Dionaea muscipula*) uses turgor pressure to snap shut its leaves when triggered by the presence of an insect (Hodick et al., 1989). The researchers found that the closure of the trap is the result of a snap-buckling instability, which is actively controlled by the plant. This instability is responsible for the fast closure of the trap, which takes only about 100 ms to complete (Forterre et al., 2005).

Regarding climbing plants, hydraulic pressure plays an important role in supporting the plant's growth and survival. In a recent study of the liana *Hedera helix*, researchers found that it requires special strategies to maintain the integrity of water transport and ensure supply to large crown areas (Ganthaler et al., 2019).

In addition to hydraulic mechanisms, there are other physiological mechanisms that allow plants to move and respond to their environment. One such mechanism is the electrical signaling within plants. Botany research from modern aspects illustrates that there exists electrical signaling in many plants from different regions of the plant body which corresponds to certain stimuli from the environment (Volkov et al., 2010). For example, The Venus flytrap (*Dionaea muscipula*) is a carnivorous plant that uses electrical signals to trigger its trap. When an insect touches the trigger hairs on the leaf surface, it creates a small electrical signal that travels through the leaf and triggers the trap to close. The electrical signal is generated by ion channels in the leaf cells, which allow charged ions to flow in and out of the cell, creating a voltage difference. This voltage difference then triggers the release of calcium ions, which causes the trap to close (Volkov et al., 2009).

To summarize, these examples demonstrate the diverse and sophisticated physiological mechanisms that plants use to move and respond to their environment. By better understanding these mechanisms, we can look in-depth into the fascinating and complex lives of plants and explore the further possibility of their potential cognition.

2. OBJECTIVES

The concept of plants being static and unresponsive has been refuted by various studies that have uncovered the intentional and diverse movements of plants. Plants exhibit phototropism, gravitropism, nastic movements, and circumnutation, which are not only for survival but also for growth and adaptation. The field of plant cognition has gained immense interest in recent years, revealing the complex sensory and signaling mechanisms underlying plant movement and behavior. This emerging field may provide more evidence of the intentional nature of plant movements and broaden our understanding of non-human organisms.

Based on previous research, climbing plants have long been a fascinating subject due to their specialized adaptations that enable them to compete for resources (Niklas, 2011). However, little is known about how these plants make decisions regarding stimulus searching and attachment behaviors. Climbing plants are an ideal model system for studying decision-making in plants because they respond rapidly to environmental cues and finding a suitable support is crucial for their growth and development (Gianoli, 2015).

Charles Darwin made initial observations on the oscillatory movements of exploring stems and tendrils performing circumnutation and noted that vines could locate potential supports and even show aversion towards them (Darwin, 1875). Recent studies using kinematic analysis of pea plants have demonstrated that plants can perceive a support and modify the kinematics of the tendrils' aperture depending on its thickness (Ceccarini et al., 2020). For climbing plants, thinner and thicker supports differ, with thicker supports being more difficult to grasp and requiring more energy to wrap around (Castiello, 2020).

The aim of the current study is twofold. First, to investigate how pea plants respond when confronted with differently sized supports. Second, to determine whether the decision-making process affects the circumnutations of the tendrils. The study hypothesizes that pea plants prefer thinner supports and that differences in movement kinematics will be evident across conditions, despite the plants still considering the thicker support as a potential option for an ever-changing environment.

3. MATERIALS AND METHODS

3.1 Subjects

The experimental sample comprised a total of 16 snow peas (*Pisum sativum* var. *saccharum* cv Carouby de Maussane) were chosen as study plants. Seeds were potted at 8 cm from the pot's border and sowed at a depth of 2.5 cm.

Two types of wooden support were considered: a 'thin' support of 13 mm in diameter (Koto -13 mm) and a 'thick' support of 40 mm in diameter (Koto - 40 mm; [Figure 1a](#)). Both supports were 54 cm in height. The supports were inserted 7 cm below the soil surface ([Figure 1b](#)).

3.2 Experimental conditions

The subjects were randomly assigned to two experimental conditions termed single (SS) and double support (DS) conditions. For the SS condition, 8 plants were raised individually in the presence of the 'thin' support ([Figure 1c](#)). For the DS condition ([Figure 1d](#)), 8 plants were raised individually in the presence of both the 'thin' and the 'thick' support. The location of the differently sized supports was counterbalanced across subjects to avoid a potential bias due to the direction of circumnutation (clockwise or counterclockwise). The supports were positioned so that the first leaf developed by a sprout faced the midpoint between the two supports. This was done to prevent a growing bias in favor of either one or the other support.

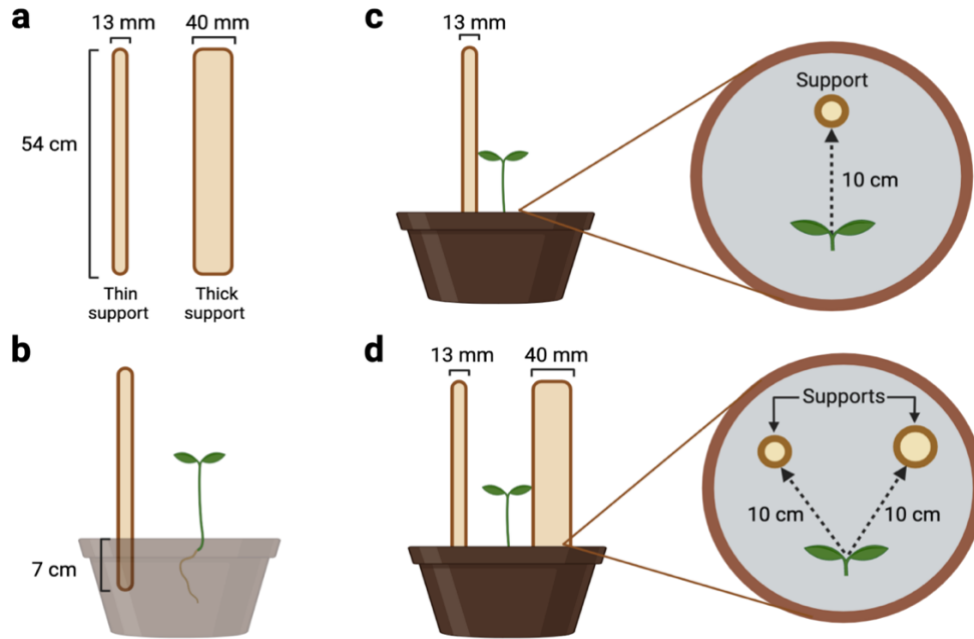


Figure 1: (a) Graphical depiction of the “thin” and the “thick” support; (b) the location of the support in the pot, and how it was inserted in the soil. The single-support and the double-support condition are represented in panels c and d, respectively.

3.3 Experimental setup

Plants grew individually in a thermo-light-controlled growth chamber (Cultibox SG combi 80×80×160 cm; [Figure 2](#)). The temperature was set at 26 °C by means of an extractor fan equipped with a thermo-regulator (TT125 vents; 125 mm-diameter; max 280 mc/h) and an input-ventilation fan (Blauberg Tubo 100 - 102 m³/h).

The two-fan combination allowed for a steady air flow rate into the growth chamber with a mean air residence time of 60 seconds. The fan was carefully placed so that air circulation did not affect the plants' movements.

Cylindrical pots (40cm in diameter, 20cm in depth) were filled with river sand (type 16SS, dimension 0.8/1.2 mm, weight 1.4) and positioned at the center of the growth chamber. Each plant was exposed for 12 hours (6 a.m. to 6 p.m.) to a cool white

led lamp (V-TAC innovative LED lighting, VT-911-100W, Des Moines, IA, USA) that was positioned 50 cm above each seedling. Photosynthetic Photon Flux Density at 50 cm under the lamp in correspondence with the seedling was $350 \mu\text{mol}_{\text{ph}}/(\text{m}^2\text{s})$ (quantum sensor LI-190R, Lincoln, Nebraska, USA).

At the beginning of each experiment, the pots were fertilized using a half-strength solution culture (Murashige and Skoog Basal Salt Micronutrient Solution; [see components & organics](#)). The pots were watered three times a week using distilled water (Sai Acqua Demineralizzata, Parma, Italy).

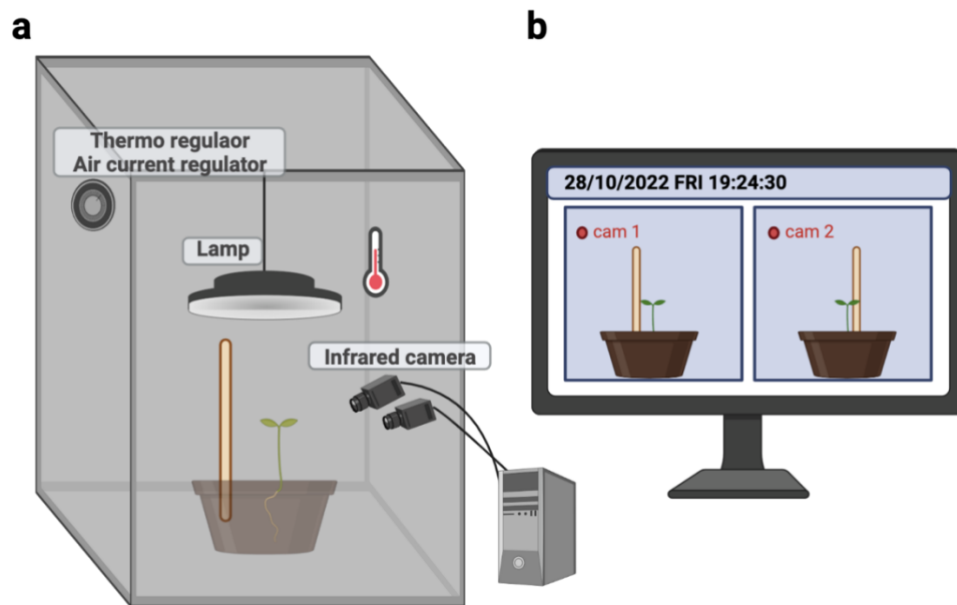


Figure 2: Graphical illustration of the experimental setup (a). Panel b represents how the plants were ‘seen’ by the infrared cameras.

3.4 Kinematic acquisition and data processing

For each growth chamber, a pair of RGB-infrared cameras (IP 2.1 Mpx outdoor varifocal IR 1080P) were placed 110 cm above the ground, spaced at 45 cm to record stereo images of the plant ([Figure 2](#)).

The cameras were connected via Ethernet cables to a 10-port wireless router (D-link Dsr-250n) connected via Wi-Fi to a PC. The frame acquisition and saving process were controlled by CamRecorder software (Ab. Acus s.r.l., Milan, Italy; see [Figure 2](#)). Each camera's intrinsic, extrinsic, and lens distortion parameters were estimated using a Matlab Camera Calibrator App. Depth extraction from the single images was carried out by taking 20 pictures of a chessboard (squares' size 18×18 mm, 10 columns \times 7 rows) from multiple angles and distances in natural non-direct light conditions. For stereo calibration, the same chessboard used for the single-camera calibration process was placed in the middle of the growth chamber. The two cameras synchronously acquired the frame every 180 seconds (frequency 0.0056 Hz). RGB images were acquired during the daylight cycle and infrared images during the night cycle. The anatomical landmarks of interest were the tendrils developing from the considered leaf. We considered the initial frame as the one corresponding to the appearance of the tendrils for the considered leaf. The end frame was defined as the frame in which the tendrils start to coil the support. Images from both left and right cameras were used in order to reconstruct 3D trajectories. An ad hoc software (Ab. Acus s.r.l., Milan, Italy) developed in Matlab was used to identify anatomical points to be investigated by means of markers, and to track their position frame-by-frame on the images acquired by the two cameras to reconstruct the 3D trajectory of each marker.

The markers on the anatomical landmarks of interest (i.e., the tendrils) were inserted post-hoc. The tracking procedures were at first performed automatically throughout the time course of the movement sequence using the Kanade-Lucas-Tomasi (KLT) algorithm on the frames acquired by each camera, after distortion removal. The tracking was manually verified by the experimenter, who checked the position of the markers frame-by-frame. The 3-D trajectory of each tracked marker was computed by triangulating the 2-D trajectories obtained from the two cameras. Finally, the trajectory was reconstructed with a series of coordinates in 3D (x, y, z), where the x - z plane is the horizontal plane, and the x - y plane and z - y plane as the vertical planes perpendicular to each other.

3.5 Dependent measure

The considered dependent measures were the following (Simonetti et al., 2021):

- (i) Number of circumnutations: the number of circumnutations performed by a plant from the time it was potted to the time it grasped the support.
- (ii) Circumnutation duration: the time taken by a plant to complete a single circumnutation.
- (iii) Distance from the center of circumnutation to the origin ([Figure 3](#), segment a): The distance between the circumnutation center and the plant origin.
- (iv) Length of the circumnutation major axis ([Figure 3](#), segment b): the maximum distance between two points of the circumnutation trajectory.
- (v) Circumnutation length ([Figure 3](#), segment c): the length of the overall path computed as the sum of all the Euclidean distances between subsequent points during a single circumnutation.

(vi) Circumnutation area ([Figure 3](#), segment d): the sum of pixels with a value equal to 1 obtained from the binarization of the circumnutation trajectory.

(vii) Amplitude of peak velocity: values for the average of maximum velocity.

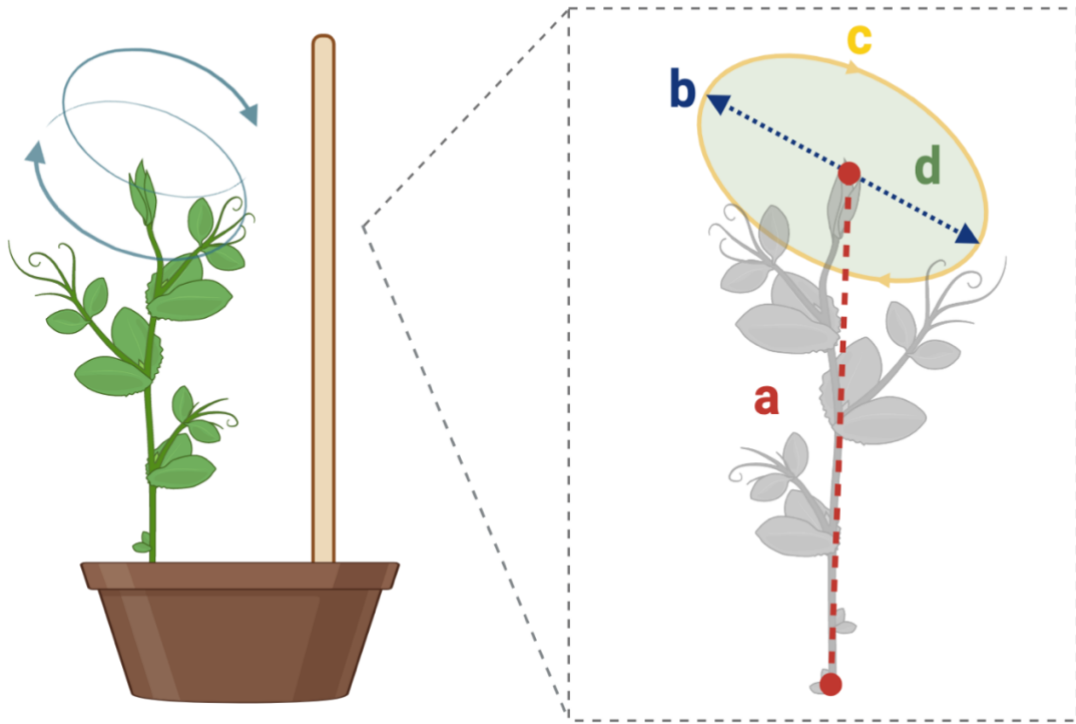


Figure 3: Graphical illustration of the dependent measure. (a) The distance from the center of circumnutation to the origin is represented as red/dash line; (b) the length of the circumnutation major axis is represented as blue/dash line; (c) the circumnutation length is represented as yellow/solid line; (d) the circumnutation area is represented in green.

Statistical analysis

The descriptive statistics including median, interquartile range (IQR), range, quartiles have been calculated. Statistical analyses were conducted using the Bayesian approach. The objective of Bayesian estimation is to allocate credibility to a distribution of alternative parameter values (posterior distribution) that is consistent with the observed

data, by generating many samples using the Markov chain Monte Carlo approach (MCMC). In this study, we adopt the two-sided Bayesian Mann-Whitney U test since the dependent variables are not normally distributed. Mann-Whitney U test is a non-parametric test that does not require the assumption of normality. The analysis was performed using JASP (JASP Team, 2023) nested within the environment R (see used packages: <https://jasp-stats.org/r-package-list/>; R Team, 2010). We choose the default prior defined by a Cauchy distribution centered on a zero-effect size (δ) and a scale of 0.707 because prior knowledge regarding the exposition of plants to a double-support condition is absent (van Doorn et al 2021; Ly et al., 2016).

Data augmentation is generated with 5 chains of 1000 iterations that allows for simpler and more feasible simulation from a posterior distribution. In the analysis, W is calculated in the Mann-Whitney U test as the smaller of the rank total between the two conditions. Bayes factor (BF) is obtained to quantify the relative predictive performance of two hypotheses (van Doorn et al., 2021). In our study, BF quantifies evidence for the presence or absence of the difference between the DS condition and the SS condition. The null hypothesis (H_0) here is that there is no difference in kinematics between the DS and the SS condition. The alternative hypothesis (H_1) is that there is a difference. The BF_{10} value is the likelihood of data given H_1 divided by H_0 . The BF_{01} value is calculated as H_0 divided by H_1 . The results are reported based on Jeffery's scheme that proposes a series of labels for which specific Bayes factor values can be considered either "no evidence", "anecdotal (1 – 3)", "moderate (3 – 10)", "strong (10 – 30)", "very strong (30 – 100)", or "decisive (> 100)" relative evidence for alternative hypothesis (Jeffreys, 1998). R-hat is also reported to check the degree of convergence of MCMC algorithms based on outcomes stability. The closer the value of R-hat is to 1, the better

convergence to the underlying distribution. Credible intervals (CI) are set as 95%, which is simply the central portion of the posterior distribution that contains 95% of the values.

4. RESULTS

4.1 Qualitative results

For all plants and in both experimental conditions (i.e., SS and DS), the tendrils displayed a circumnutating growing pattern. As soon as a plant sensed the support it strategically altered the tendril's movement trajectory, so to bend towards the support ([Figure 4a, b](#)).

For the DS condition, plants exhibited a very strong preference for the thin support and grew less than the plants for the SS condition by the time they grasped the support ([Figure 4c, d](#)). Eight of the nine plants for the DS condition began to grow and move toward the thin support relatively early, even while they were too tiny to reach out for any support.

These plants were able to aim precisely toward the thin support and grasp it by modulating/twisting the angles of the new petiole, and this is visible to the naked eye. Only one plant tried to cling onto the thick support, but ultimately failed and fell.

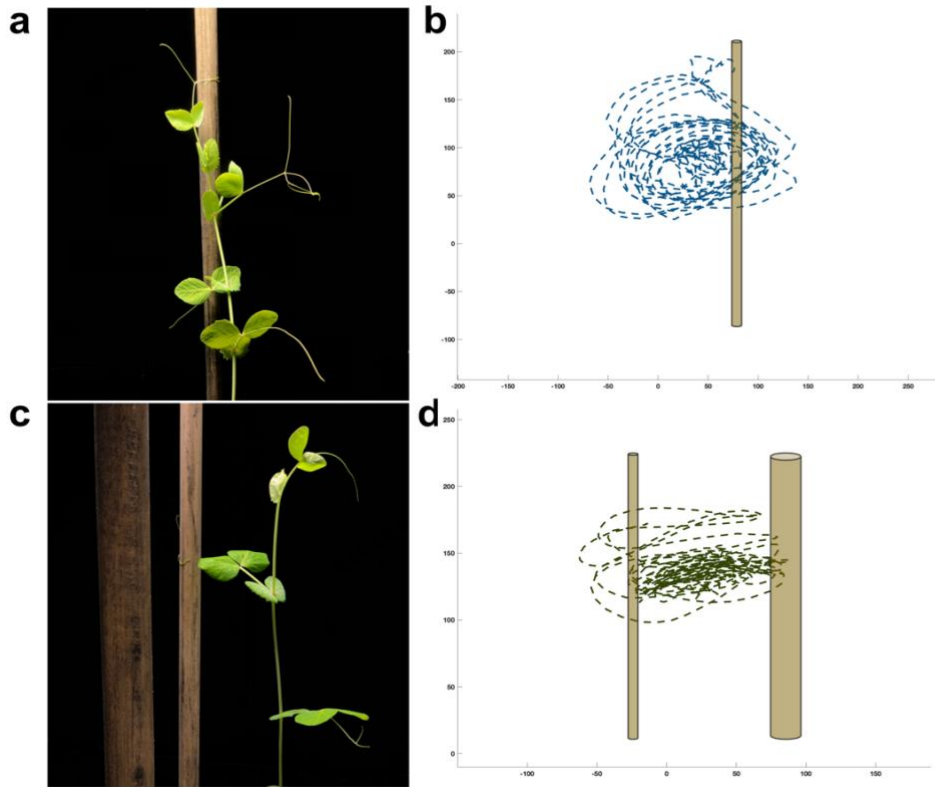


Figure 4: (a) The frame representing an exemplar plant grasping the support for the single-support (SS) condition and the graphical representation of its trajectory (b). (c) A plant grasping the thinner support for the double-support (DS) condition and the graphical representation of its trajectory (d).

4.2 Kinematic results

The descriptive statistics and kinematic results when comparing the DS with the SS conditions are provided below (Tables 1 and 2). Please remember that here the comparison is between the thin support for the SS condition and the thin support for the DS condition. This is because for the DS condition plants always choose the thinner support.

Table 1. Descriptive statistics for the considered dependent measures.

| | Group | Median | IQR | Range | 25th percentile | 50th percentile | 75th percentile |
|---|--------------|---------------|------------|--------------|------------------------|------------------------|------------------------|
| Number of circumutation | DS | 26.000 | 5.000 | 28.000 | 24.000 | 26.000 | 29.000 |
| | SS | 28.000 | 9.000 | 21.000 | 22.000 | 28.000 | 31.000 |
| Circumutations duration (min) | DS | 63.000 | 18.000 | 84.000 | 57.000 | 63.000 | 75.000 |
| | SS | 69.000 | 15.000 | 114.000 | 60.000 | 69.000 | 75.000 |
| Distance from the gravity center to the origin (cm) | DS | 13.055 | 14.361 | 62.527 | 8.212 | 13.055 | 22.573 |
| | SS | 16.017 | 32.062 | 96.865 | 9.394 | 16.017 | 41.456 |
| Length of circumnutation major axis (mm) | DS | 88.867 | 54.434 | 169.439 | 60.080 | 88.867 | 114.513 |
| | SS | 65.036 | 69.147 | 187.973 | 36.176 | 65.036 | 105.323 |
| Circumnutation length (mm) | DS | 221.764 | 172.506 | 643.428 | 147.370 | 221.764 | 319.876 |
| | SS | 166.488 | 196.104 | 503.609 | 85.797 | 166.488 | 281.900 |
| Circumnutation area (mm ²) | DS | 3580.500 | 6572.125 | 22965.250 | 1165.750 | 3580.500 | 7737.875 |
| | SS | 1943.688 | 5298.375 | 14870.563 | 199.438 | 1943.688 | 5497.813 |
| Amplitude of the maximum peak velocity (mm/min) | DS | 6.042 | 4.895 | 71.556 | 3.494 | 6.042 | 8.390 |
| | SS | 4.038 | 3.813 | 14.054 | 2.499 | 4.038 | 6.313 |

Note. DS=double-support condition; SS=single support condition

Table 2. Two-sided Bayesian Mann-Whitney U test for the DS and the SS conditions.

| | BF₁₀ | W | R-hat |
|---|------------------------|-----------|--------------|
| Number of circumnutation | 314.656 | 14220.000 | 1.008 |
| Circumnutation duration | 0.387 | 17083.000 | 1.000 |
| Distance from the circumnutation center to the origin | 43.665 | 15057.000 | 1.007 |
| Length of the circumnutation major axis | 734.705 | 24455.000 | 1.016 |
| Circumnutation length | 980.421 | 24433.000 | 1.015 |
| Circumnutation area | 1267.886 | 24611.500 | 1.008 |
| Amplitude of maximum peak velocity | 4137.588 | 24538.000 | 1.014 |

Note. Result based on data augmentation algorithm with 5 chains of 1000 iterations.

Number of circumnutation

The Bayesian Mann-Whitney U analysis revealed a Bayes factor (BF₁₀) of 314.656, suggesting that there is a decisive difference between the SS and the DS conditions with respect to the number of circumnutations (BF₁₀ = 314.656, BF₀₁ = 0.003, W = 14220, R-hat = 1.008, 95% CI: [-0.657, -0.229]).

Circumnutation duration

The Bayesian Mann-Whitney U analysis revealed a Bayes factor (BF₁₀) of 0.387, suggesting anecdotal evidence that there is no difference between the SS and the DS conditions with respect to circumnutation duration (BF₁₀ = 0.387, BF₀₁ = 2.584, W = 17083, R-hat = 1.000, 95% CI: [-0.354, 0.029]).

Distance from the circumnutation center to the origin

The Bayesian Mann-Whitney U analysis revealed a Bayes factor (BF₁₀) of 43.665, suggesting that there is a decisive difference between the SS and the DS with respect to

the center distance from origin for the plants' conditions ($BF_{10} = 43.665$, $BF_{01} = 0.023$, $W = 15057$, $R\text{-hat} = 1.007$, 95% CI: $[-0.596, -0.192]$).

Length of the circumnutation major axis

The Bayesian Mann-Whitney U analysis revealed a Bayes factor (BF_{10}) of 734.705, suggesting that there is a decisive difference between the SS and the DS conditions with respect to the length of circumnutation major axis ($BF_{10} = 734.705$, $BF_{01} = 0.001$, $W = 24455$, $R\text{-hat} = 1.016$, 95% CI: $[0.275, 0.676]$).

Circumnutation length

The Bayesian Mann-Whitney U analysis revealed a Bayes factor (BF_{10}) of 980.421, suggesting that there is a decisive difference between the SS and the DS condition with respect to circumnutation length ($BF_{10} = 980.421$, $BF_{01} = 0.001$, $W = 24433$, $R\text{-hat} = 1.015$, 95% CI: $[0.290, 0.693]$).

Circumnutation area

The Bayesian Mann-Whitney U analysis revealed a Bayes factor (BF_{10}) of 1267.886, suggesting that there is a decisive difference between the SS and the DS condition with respect to the area of circumnutation ($BF_{10} = 1267.886$, $BF_{01} = 0.0008$, $W = 24611.5$, $R\text{-hat} = 1.008$, 95% CI: $[0.299, 0.697]$).

Amplitude of maximum peak velocity

The Bayesian Mann-Whitney U analysis revealed a Bayes factor (BF_{10}) of 4137.588, suggesting that there is a decisive difference between the SS and the DS condition with

respect to amplitude of maximum peak velocity ($BF_{10} = 4137.588$, $BF_{01} = 0.0002$, $W = 25438$, $R\text{-hat} = 1.014$, 95% CI: [0.380, 0.780]).

Correlational analyses

We noticed a non-significant difference for circumnutation duration across conditions while the amplitude of peak velocity increased for the DS with respect to the SS condition. We felt that this may indicate the put in place of a sort of isochrony principle (Viviani et al., 1983) by the plants. To test this, we performed Pearson's correlation analysis (Cohen et al., 2009) between circumnutation length and the amplitude of peak velocity (Van Rossum et al., 1995). The results indicate a significant correlation between these measures (Pearson's $r = 0.715$, $p\text{-value} = .000$, 95% CI: [0.663, 0.760];

[Figure 5](#))

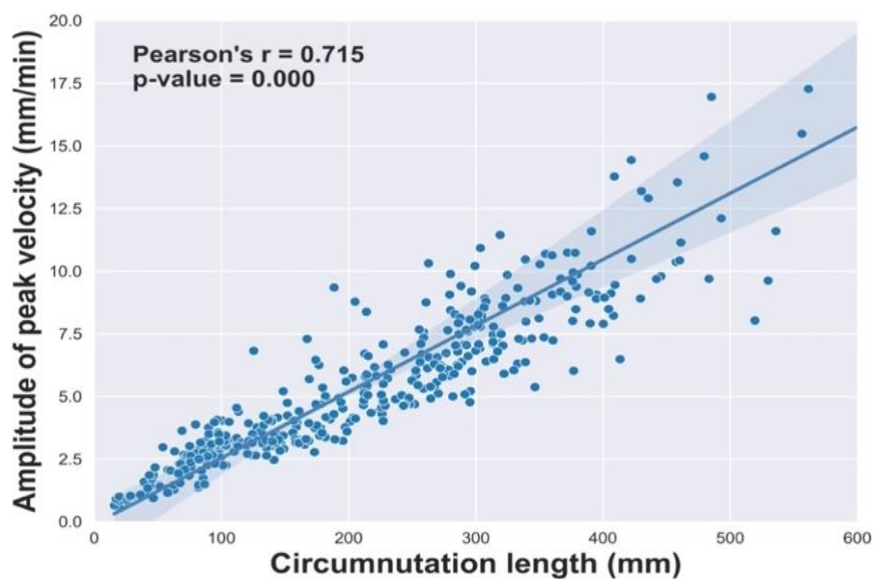


Figure 5: Pearson's correlation coefficient between the “circumnutation length” and the “amplitude of peak velocity”.

DISCUSSION

As we examined in the context of behaviors of pea plants in conditioned supports with various sizing, we could evidently doubt if there is a kinematic pattern based on whether the plants were shown in single or dual supports. The models in the experiment suggested an obvious tendency towards the thinner supports in decision-making of the pea plants in compared to the thicker ones. The results we obtained aligned with the previous research relevant in this topic, such as Darwin (1875) in the book *the Movement and Habits of Climbing Plants*, which described the adaptive behavior of the pea plants reaching the supports. Moreover, the results also support contemporary discoveries such as the mechanisms of climbing plants (Goriely et al., 2006). Within the increasing thickness of the support, when it reaches a specific threshold, the pea plants fail to sustain the tensional forces necessary for coiling around and reaching to the support, which make the thicker support desirable for attachment.

Furthermore, the study also explores the mechanisms behind the decision-making in pea plants as well as the selection of the various supports. It advocates the certain response may be due to the local reactions and physiological mechanisms such as the contraction of gelatinous fibers in the tendrils (Bowling et al., 2009). This suggests that there might be some sort of automatic mechanism for matching the desirable stimuli in the environment given based on the diameters of the potential supports.

However, the existing research focuses primarily on the final coiling of the pea plants and pays less attention to the composition of the action taken by the tendrils in the approaching stage (Guerra et al., 2019, 2021, 2022). To address this void, we documented the entire procedure of the pea plants reaching toward the supports, from the initial growth to the end of the grasping stage. We discovered the possible act as a trade-off regarding

metabolic expenditure. For example, thicker supports may require longer tendrils to be extended in order to grasp them, leading to increased energy consumption. This metabolic-dependent act may also affect the kinematic movement, suggesting the difference in speed for choosing various supports. More specifically, the speed in grasping thinner supports is relatively faster (Guerra et al., 2019). Hence, a certain level of information processing is necessary to integrate, interpret, and calculate the dependent information which arbitrates a preference for thinner supports. This raises questions about the internal processes and signaling pathways that underlie this decision-making. Understanding the molecular and physiological mechanisms involved in support selection and energy allocation could provide valuable insights into plant behavior and plant cognition.

These observations become particularly noticeable when correlating the kinematics of plants exposed to one or dual supports in the present studying, suggesting that the plants are able to perceive the environment and perform circumnutation respectively. Circumnutation patterns in thin support condition and dual support condition are different, the latter one appears to be faster, fewer but larger circumnutation. This kinematic difference suggests a higher level of tensional complexity. Interestingly, we observed the movement of pea plants seems to follow the principle of isochrony (Sartori et al., 2013). This pertains to the inherent inclination to adjust movement velocity based on the linear distance traveled, ensuring a relatively consistent execution time. In the case of pea plants, they maintain a consistent duration of movement while scaling the velocity for longer distances. This adaptive strategy seems to be the preferred and simplest organizational approach employed by plants when making decisions that involve alternative courses of action.

Traditionally, decision-making is considered to be solely human-associated behavior. However, numerous studies have shown the possibility of extending such cognitive acts to various organisms, including plants. Recent biologists proposed a constructive model for plant behavior, explaining the judgment process where plants perceive stimulus and execute actions based on costs and benefits (Karban et al., 2018). For example, the study by Dener and colleagues investigated the decision-making in the root development of pea plants using the risk sensitivity theory (Dener et al., 2019). The study found that pea plants displayed both risk-prone and risk-averse behaviors, suggesting that they tend to make rational economic decisions on risk sensitivity. Along with another study suggesting a light-dependent phenomenon of leaf inclination in *Arabidopsis thaliana* when subjected to shading by neighboring leaves, low light levels, or darkness. The plant responds by raising its leaves to more vertical orientations to avoid being overtopped.

The accumulating studies align with our experiment provide an atmosphere for researchers to discuss the probability of plants making various complex behaviors that are neither rigid nor mechanical (Calvo, 2016). One of the mechanisms is light acquisition at the level of stomata, which may allow plants to distinguish different light reflections from supports (Sharkey et al., 1981). Another hypothesis is called ‘plant electrome’ introduced by Souza and others, which refers to the ionic dynamics at different scales of plant organization (Debono et al., 2019). Souza believed that the role of the electrome in plant reactivity and found that it could be a unifying factor in understanding the flexible behavior of plants (Debono et al., 2019).

Within the exploration of numerous subjects, we believe our study renders a support for understanding the responses of climbing plants when searching for support and

demonstrate the presence of decision-making abilities in plants. It promotes the idea of plants being able to acquire and integrate complex information about their surroundings to modify the upcoming responses. Plants may have the potential to be far more complicated than we thought, thus we need further research to solidify our point of view.

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