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**Exploring Movements in Pea Plants: Decision-Making in  
Support Selection**

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## Abstract

Choosing a support is a crucial aspect of the life journey of climbing plants. Those that can find a suitable support exhibit higher performance and fitness. While numerous studies on climbing plants have provided insights into the mechanistic details of support-searching behaviors, few have explored the purposeful nature of these movements and the decision-making processes involved. One crucial factor influencing plants' decisions is the diameter of the support. Once it exceeds a certain point, climbing plants struggle to maintain tensional forces and detach from the support. In this connection, the present study focuses on the decision-making processes underlying support-searching in pea plants (*Pisum sativum L.*). The plants were grown in two conditions: a single-support setting and an environment to choose between two supports of different diameters. As they developed, their movements were analyzed using time-lapse photography and 3D motion analysis. Consistently with previous research suggesting a preference for supports with smaller diameters, the results show an inclination among plants to choose the thinner support. The statistical analyses revealed disparities in the kinematic properties depending on the growth condition and the grasped support type. Plants that chose a thicker support differed significantly in their movement patterns from plants that grasped a thin support. Similarly, plants grown in the single-support condition varied from those in the decision-making condition. The current study elucidates the decision-making process of climbing plants in their search for support and presents evidence that plants adopt different plastic responses, choosing the one that optimally corresponds to environmental conditions.

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## Chapter I

### Vegetative Life in Science

Plants are the most common living organism on Earth, and outnumber even bacteria — a fact not so obvious to many. They constitute approximately 80% of the biomass, while the animal kingdom accounts only for 1% (Bar-On et al., 2018). Plants contribute to the balance of ecosystems and enrich the environment by reducing soil erosion and pollution, as well as providing sustenance and shelter for animals (Fernando, 2012). The relationship between plants and humans predates the emergence of *Homo sapiens*. Our species coevolved with the Plantae kingdom — hominids oriented themselves biochemically to ingest plants and rely on them for specific amino acid intake (Schaal, 2019). However, we became increasingly detached from nature as human civilization progressed. The natural world seems to have ceased being an essential contributor in the quest for survival but rather have become a blank existence to be dominated for humans to forge ahead (Hall, 2011). This is the cause and effect of the dominance of the anthropomorphic on Earth. Still, many pointed out that there is more to plants than meets the eye. Recent findings have revealed several complex cognitive abilities observed in plants, suggesting that they may be considered cognitive agents.

#### 1.1. Views on plants through eras

Humans' consistent portrayal of plants as inanimate objects (Mancuso & Viola, 2015) stems from the prevailing men-nature dualism (Hall, 2011). Western cultures' disregard for the existence of plants dates back to the thoughts of Plato and Aristotle, two Ancient Greek philosophers. According to them, plants possessed the lowest level of the soul; therefore, they were devoid of any intelligence or volition (Hall, 2011). The bulk of the world's religions overlooked the existence of plants as sentient beings deserving of respect and instead viewed them as the abiotic mass that served the interests of humans (Mancuso & Viola, 2015).

However, this anthropomorphic belief has not been the only one prevailing. Throughout history, voices have been raised in defense of plants' sentience, both in research and folk culture.

The personification of nature is a recurring theme in pagan myths. Pan, the deity of wilderness, was worshiped by the ancient Greeks, and his cult practices were held in subterranean spaces such as caves, and grottoes. Moreover, the Greek mythology, incorporated a significant number of nymphs - goddesses that resembled maidens and were believed to be associated with trees, rivers, and mountains. They were the personification of specific wildlife forms, recognizing the elegance and beauty of nature.

In Celtic tradition, Druids performed sacred rites with the use of plants (e.g., oak leaves; Hall, 2011), to which they credited the absolute healing power (von Pflugk-Harttung, 1893). The relationship between humans and plants could also be observed in the old Irish and Welsh names — Mac Cuil meant Son of Hazel, while Dergen meant Son of Oak (Hall, 2011). For Baltic tribes, plants — especially trees — were the sacred dwellings of deities and human souls, and as such, they were to be prayed to and respected (Šeškauskaitė, 2017). They were temporary vessels for the spirit and if the tree were to be felled, the soul would transfer to a newborn. This belief made trees an integral component of the reincarnation cycle (Šeškauskaitė, 2017).

Despite the influence of Plato and Aristotle, notable ancient Greek philosophers asserted that plants are intelligent and sentient beings. Empedoclean proposed that plants' thinking abilities were mostly related to food-searching, and failing to do so would result in nutrient deficiency, and consequently, in pain. He also suggested ceasing the usage of laurel as the prize, as to avoid harming the plant (Hall, 2011). Theophrastus, known to many as the "Father of Botany," preached against seeking exact correspondence to animals' functions in plants and recognized them as autonomous beings (Hall, 2011).

In the 19th century, the light on plants' behavior was shed by Charles Darwin himself. In his book *The Power of Movement in Plants* (Darwin, 1880), he exuberantly described not only the movements of plants (i.e., circumnutation) but also the sensory features of the root, naming it the "plant brain" (Barlow, 2006). In his experiments, Darwin (1875) placed the plants in between the glass plate and the stationary reference point, which he then used to mark the plant's movements throughout the day. He observed that plants repositioned themselves depending on the stimulus — they moved away from the harm or drew near the resources (Darwin, 1875). His finding paved the way for future research on plants' movements and behaviors.

## **1.2. The revival of plants' sentience**

The idea that plants might be cognitive beings, evincing intelligent behavior started its revival in recent years. Trewavas (2003) claimed that the discussion of intelligence should not be limited to human and animal studies, as we can find evidence of it in plants: in the forms of trial-and-error learning and memory. Research showing that plants are capable of complex behavior repertoires (Evans & Cain, 1995; Pfeffer, 1873; Takahashi & Scott, 1993) sparked an upsurge of interest in the hypothesis of plant sentience (Baluška et al., 2006; 2009; Baluška & Levin, 2016; Trewavas, 2003; 2016; 2017). Plants are able to forage for nutrients (Hutchings & De Kroon, 1994), defend themselves from herbivores (Dicke & van Loon, 2000; Karban & Myers, 1989), and respond to cues regarding their current and future environmental states (Karbon, 2008). Moreover, plants may be conditioned via experiences, suggesting that they possess the ability to learn and store the acquired information (Gagliano et al., 2016; Karban, 2008). It should not be feasible to display such a wide range of behaviors in an ever-changing environment unless some kind of cognition was at play.

### ***1.2.1. Defining cognitive behavior in plants***

How do we define intelligence in plants? According to Trewavas (2003), it is an “*adaptively variable growth and development during the lifetime of the individual.*” Trewavas (2016; 2017) alleges the intelligence definition created by Legg and Hutter (2007) and argues that plants fulfill the requirements to be described as intelligent beings. He reasons that (i) plants interact with the environment through responses to signals (behavior), (ii) their goal is to reproduce and the more fitness they exhibit the more profit they gain, (iii) they can adapt in order to survive (Trewavas, 2016) which can be observed in them dominating the eucaryotic life on Earth.

Most definitions of intelligence place a strong emphasis on the role of behavior. When an organism alters its behavior so its chances of survival increase in a threatening or competitive environment, it is considered to be intelligent (Calvo et al., 2020). This means, that from the beginning of their growth as seedlings, plants are exposed to predators, and so they have to perceive the threatening stimulus (e.g., chewing, saliva), store this information for future use, and change their behavior or generate a new protective method (Calvo et al., 2020) to prevail as an individual organism and species. Lyon and colleagues (2021) describe cognition in terms of adaptive behavior which plants certainly display. As an example, roots are able to sense soil structure, differentiate themselves from alien roots and even guide the reorganization of the physical composition of a plant as the result of competition for nutrients (Calvo Garzón & Keijzer, 2011).

Nevertheless, the most evident proof of intelligent behavior is the ability to move without restraint from place to place, which plants obviously lack. The objectors of attributing intelligence to plants, justify their view using this argument. However, they overlook the fact that most organisms developed the ability to move around in order to forage for food — something that plants do not require by virtue of photosynthesis (Trewavas, 2003).



Hence, this fact should not be used against the cognitive behavior in plants, especially since a wide variety of movements can be observed in the flora (see Chapter II). Furthermore, humans tend to think about the world in anthropocentric terms: if they can observe a similarity between their looks or behavior and those of an organism, they are more likely to consider it an intelligent being. As such, attributing intelligence to animals, specifically mammals, comes to us with relative ease, while plants due to their “in-place” nature are not commonly perceived as sentient.

### ***1.2.2. Plant perception***

Just like animals, plants are capable of perceiving the world around them. They do so thanks to over twenty senses. Certain sensory abilities are shared between the Animalia kingdom and plants — including touch, sight, hearing, smell, and taste — but some are unique just to plants, such as their ability to detect electromagnetic force (Mancuso & Viola, 2015). Sensory information is acquired from the environment through specialized receptors corresponding to distinct sensory modalities. As an example, light receptors react to the ratio of red to far-red light to adjust the growth and shade detection (Karban, 2021). Further, the climbing plants’ tendrils have been reported to possess greater proprioception sensitivity than humans (Karban, 2021). This touch sensitivity is possible thanks to many membrane ion channels involved in mechanoperception (Monshausen & Haswell, 2013).

Due to their advanced sensory capacities plants are capable of complex behaviors that allow them to interact with the environment. Plants can discriminate between themselves and other plants (self/non-self discrimination); they can identify the members of their own species (kin recognition) and communicate with other individuals in the face of danger. Since such behaviors can be considered cognitive, the following section of this chapter shall discuss them more in-depth, leading to the description of a complex process of decision-making.

### *Self vs Non-self discrimination*

All organisms, from bacteria to animals, possess a recognition system that allows them to distinguish between themselves and other life forms. Self-recognition is an essential ability for the survival of organisms — it allows individuals to protect themselves from attackers (Karban, 2021) and prevents self-fertilization (Vekemans & Castric, 2021). Via emitted chemicals, roots can differentiate between self and non-self and consequently respond differently depending on the encountered object — either by suppressing growth or aggressive competition towards alien plants (Calvo et al., 2020; Gruntman & Novoplansky, 2004; Karban, 2021). Self-discrimination can also take place aboveground. Fukano and Yamawo (2015) found out that the vines of *C. japonica* were more likely to attach to the non-self shoots using the tendrils as the recognition tool.

### *Kin recognition*

Kin recognition is the ability of an organism to differentiate close genetic relatives, such as offspring or siblings, from non-kin. Plants, too, can successfully distinguish between their conspecifics and interspecific. Crepy and Casal (2015) demonstrated that leaves of *Arabidopsis thaliana* altered their orientation to decrease the shading between their kin neighbors but failed to do so when growing with other plant species. Similarly, the defensive mechanism, activated by cues from neighboring plants, was more effective if the plants were related (Karban et al., 2013).

Furthermore, according to root allocation studies, plants compete for resources more belligerently if faced against another species (Segundo-Ortin & Calvo, 2022). This competitive stance may be related to the fact that organisms increase their chance for reproduction while collaborating with their kin (Karban, 2021), and prevailing against interspecific.

## *Communication*

The literature mentions two phenomena based on sending and receiving information in plants: eavesdropping and communication. Communication is the process in which the biotic signal is transferred to the receiving individual, either by another plant or from one tissue to another (Karban, 2021). The sender opts to share the information with the receiver, while the interaction in eavesdropping is unintentional (Karban, 2021).

Plant-to-plant interaction transpires by employing secreted chemical signals, either above or below the ground (Wang et al., 2021). Substances released by leaves, flowers, and fruits are called volatile organic compounds (VOCs), and they partake in airborne communication between plants (Segundo-Ortin & Calvo, 2022). This type of information relay is usually used in the situation of herbivore-attack (Wang et al., 2021) to warn neighboring individuals of the danger so they can fortify their defenses.

On the other hand, roots are the primary participants in the belowground communication between plants. They exude the secondary metabolites that signal to other roots, triggering responses such as root detection and recognition or behavioral change in shoots and leaves (Wang et al., 2021). Warning cues can be transferred through roots to multiple plants through a “grapevine.” The threatened plants signal to other unstressed specimens, which respond to the imminent danger and pass the information on by sharing their rooting volume (Novoplansky, 2019).

Another form of communication was revealed in a recent study by Khait et al. (2023), that demonstrated that under stress, plants emit a scream-like sound that can be detected by other organisms, informing them about the graveness of the injury and the plant’s state.

## *Learning and memory*

The term “learning” can be defined as the process of acquiring novel skills or knowledge, while “memory” refers to the process of encoding and storing information for

future use (Nečka et al., 2006). Although the traditional models often encompass the cognitive processing of information within a nervous system, it is acknowledged that some forms of learning and memory may exclusively depend on molecular and cellular processes. Amid them, we can distinguish immune responses, genetic heredity, or epigenetic modifications (Michmizos & Hilioti, 2019). Thuswise, it should be feasible to undertake an endeavor to discover the mechanisms underlying memory and learning in plants.

An example of habituation in *Mimosa pudica*, characterized by a reduction in leaf closer, was demonstrated by Pfeffer in 1873. Moreover, Gagliano and colleagues (2014) provided evidence for long-term memory in plants by showing that the effects of habituation can span up to 28 days. Their further studies (Gagliano et al., 2016) suggest that as the result of training, *Pisum sativum* can learn to associate the conditioned stimulus (i.e., presence of the fan) with the unconditioned stimulus (i.e., the onset of light). Priming a seed has been observed to impact the subsequent behavior of the plant following its germination (Bruce et al., 2007; Thellier et al., 2000), and short-term electrical memory can be seen in Venus flytraps (*Dionaea muscipula*) as they can store small subthreshold charges that accumulate over time and allow for the closing of the trap (Volkov et al., 2008). Additionally, plants can store information regarding past encounters with herbivores and pathogens, which enables them to respond quicker and more effectively to future attacks (Karban, 2008; 2021).

### ***1.2.3. Plant decision-making***

Decision-making can be defined as a cognitive process of picking an option from two or more alternatives (APA Dictionary of Psychology). According to Bechtel and Bich (2021) making a decision requires taking “*measurements and applying a norm to make a selection*” of which the simplest example is a selection of kinetic reaction. If we follow this line of thinking and assume that decision-making is the choice of alternative actions based on the sensory integration of internal and external information, we can concur that all living

organisms have this capacity. Indeed, plants or bacteria are not able to take into account as elaborate data as animals do, yet this does not void their abilities to make a decision beneficial to their survival. It only suggests that more complex decisions require more complex control mechanisms (Bechtel & Bich, 2021). The empirical findings seem to endorse this point of view.

To begin with, in their experiment with split-root plants, Dener et al. (2016) demonstrated that pea plants show risk-prone behavior when the average resource concentration is low, and opt to allocate their roots in the variant patch. On the other hand, if the constant nutrient aggregation is high, the pea plant chose to avoid the risk, and allocated resources to the roots in such a patch, rather than in the pot with a variable nutrient supply (Dener et al., 2016). This study was based on the risk sensitivity theory, which states that the agent switches between risk aversion and proneness, so its decision maximizes fitness, and according to Schmid (2016), it illustrates better rational decision-making than animal studies do. Furthermore, Gruntman et al. (2017) found that *Potentilla reptans* chooses different responses to light competition depending on the circumstances, and the possibility of overcoming its neighbors. The plant selected the optimal action that would allow it to thrive in its environment.

The findings of Wang and colleagues (2023) provide further evidence of plants being able to decide between two alternative options. When given a choice between thin and thick support, pea plants show a preference for the former, supporting the hypothesis that they choose the more beneficial option for themselves. The kinematics between pea plants differed significantly as well, depending on whether the plants were grown in the single-support condition or were in a position to choose between two supports of different diameters. For example, the circumnutation length was greater for plants grown in a double-support setting (Wang et al., 2023).

#### ***1.2.4. Nesting cognitive theories to plant behavior***

In cognitive sciences, the concept of cognition has been extensively contemplated as an outcome of the developed nervous systems in humans and other animals. Nevertheless, it should be noted that neurons do not constitute cognition per se. Rather, their development and existence can be attributed to the optimization of ancient mechanisms found in progenitor organisms (Baluška & Levin, 2016). For example, the bacteria *Escherichia coli* was shown to possess the learning capacity (Mitchel et al., 2009). In this study, *E. coli* was exposed to the lactose-maltose sequence first, and then to the sequence of reverse order during the subsequent test-trial. The bacteria exhibited a lack of metabolic readiness for the initial presence of maltose, indicating an anticipation of a certain event (Mitchel et al., 2009). Such an “unusual” discovery of cognitive behavior in organisms lacking a nervous system prompts researchers to ponder the potential existence of other cognitive behaviors in aneural organisms, thereby giving rise to the emergence of compelling theories of cognition.

Gibson’s theory of affordances (1977; 1979) has laid the groundwork for numerous theories, such as extended cognition theory, that branch off from the idea of brain-centered cognition. According to Gibson, the perception of the environment involves not only its attributes in terms of shapes, colors, and spatial relationships but also the potential for interaction with the object. The *affordances* are what the environment offers to an organism, which could be either beneficial or harmful. In other words, they are an action possibility that exists for a given agent in their specific environment. Gibson’s initial theory did not specifically address the affordances to the plants; however, it is possible to expand this concept to include flora. Plants, like other organisms, interact with their environment by using available opportunities to facilitate their continuous growth, making them a viable addition to the existing theory.

To illustrate this, I shall quote the example of plant attunement to the surrounding

soundscape and its ability to produce its own clicking sounds and detect acoustic signals from other plants (Gagliano et al., 2012; Gagliano, 2015). This capability raises the possibility that plants, similar to echolocating bats, could emit sonic clicks and analyze the returning echoes. By doing so, they could gather information about their environment and the neighboring surroundings. Echolocation, which involves self-communication in the animal world, might serve as an efficient means for plants like twiners and tendril climbers to navigate through three-dimensional spaces (Gagliano, 2015). Additionally, it allows them to track moving objects, detect stationary obstacles, and most crucially, locate suitable host trees or other structures to climb or attach themselves to. When encountering different types of supports, such as those made of varying materials and possessing different structural qualities, the way incoming acoustic waves are reflected or absorbed would differ. This disparity influences the degree and clarity of the echoes bouncing back to the plant, providing information about the perceived suitability of a particular structure. Consequently, plants can make appropriate behavioral decisions based on this context-specific information, that is the affordances offered by the environment (Gagliano, 2015).

In the book *The embodied mind: Cognitive science and human experience*, Varela et al. (1991) challenged Gibson's work and proposed a novel theoretical framework known as enactivism. According to this perspective, cognition emerges and self-organizes through the dynamic interplay between the environment and the agent. Specifically, it is the sensorimotor patterns that perceptually guide actions that give rise to cognition. In the enactive approach, the agency can be considered if three requirements are met: (i) autonomy, (ii) interactional asymmetry, and (iii) normativity (Popova & Rączaszek-Leonardi, 2020). An organism can be considered autonomous if it is able to adjust to the changed conditions of the environment. Furthermore, it is imperative for the system to actively initiate and drive those interactions, rather than passively react to stimuli, thereby exhibiting interactional asymmetry. Moreover,

the system must achieve an optimal level of engagement with its surroundings (Popova & Rączaszek-Leonardi, 2020).

An experiment with *Passiflora* demonstrated that tendrils can alter their position and movements in pursuit of a support that is relocated from place to place just before the tendrils grasp it (Baillaud, 1962; Wang et al., 2021). Moreover, if a plant comes in contact with a very thick support, instead of choosing a maladaptive option of attaching itself to the unsuited support, it can twine around itself (Gianoli, 2015). These findings indicate that plants can actively interact with the environment and adjust their reactions accordingly, while their movements seem to guide the cognition, and thus meeting the conditions imposed by enactivism.

The extended cognition theory presents an alternative perspective that could be easily applied to plants. It states that cognitive processes extend beyond the brain or the body to the objects with which the agent interacts (Clark & Chalmers, 1998). Following this line of thinking, the environment is a part of the plant's cognitive system as long as it can be manipulated by it (Parise et al., 2020). This could be observed in the plant's communication system which influences the behavior of other representatives of the flora, thus making it an externalized form of the cognitive process of an agent. Additionally, plants are able to extend their cognitive processes to enhance the perception of the underground environment beyond the physical limitations of their roots. They achieve this by actively modifying both the rhizosphere and the roots' influence zone. One example of this enhanced perception is seen when plants encounter obstacles in the soil. The plant can sense the presence of obstacles through the accumulation of allelopathic exudates between the obstacle and the roots. These exudates hinder root growth in the direction where they accumulate (Parise et al., 2020). In an experiment conducted by Falik et al. (2005), when the exudates were removed from the soil around the obstacle, the plant lost its ability to perceive the obstacle, and its roots grew



toward it as if the obstacle was not there. The lack of the exudates hindered the perception of the plant, thus demonstrating their involvement in the flora's extended cognition system.

While the aforementioned classic theories expanded views on cognition beyond brain constraints to organism-environment interaction, more novel theories frame cognitive functions in the context of their evolutionary origins and how they developed in more complex organisms, like humans. According to basal cognition theory and minimal cognition theory, cognitive abilities can be observed at the level of prokaryotes (Lyon et al., 2021). Basal cognition describes the processes that allow organisms to explore and track the ever-changing environmental states to select a survival-appropriate action (Lyon et al., 2021). Those mechanisms involve capacities from response-orienting to more complex functions like decision-making and problem-solving. Basal cognition, thus, refers to basic cognitive processes that form building blocks for more complex cognitive abilities (Lyon et al., 2021). As mentioned before, plants have been shown to be able to learn by associations (Gagliano et al., 2016), and possess a short-term memory (Volkov et al., 2008). Moreover, tendrils of *Cayratia japonica* exhibit self-recognition behavior (Baluška & Mancuso, 2021). All the examples can be considered as basic forms of cognitive abilities that can be observed in animals or humans, ergo basal cognition theory could be applied to the flora.

Minimal cognition theory states that cognition is a purely biological phenomenon manifested as the capacity to modify the environment for one's benefit (Calvo Garzón & Keijzer, 2011). Of such behavior, plants are more than capable. For example, during a prolonged period of insufficient nutrition availability, plants can release their metabolites (i.e., flavonoids) into the soil where they bind the ions necessary for plant growth and as a result increase nutrient accessibility (Mierziak et al., 2014). One of the constraints of this approach lies in the assumption that for the organism to be cognitive it has to be free-moving. As such, bacteria, but not plants could be considered cognitive agents. To Jonas (1966; 1968), however,

this requirement could be fulfilled if we consider that plants possess sufficient motility in terms of their survival.

Matthew Sims (2021) proposed a theory that connects biogenic and anthropogenic approaches to cognition. His “continuum of intentionality” thesis suggests that intentionality is a graded construct, moving from less complex to more elaborated forms of cognition. Strong intentionality is what can be described by mental states, while weak intentionality drives anticipatory sensorimotor and biochemical behavior, making it phenotype-relative. If one assumes that intentionality and cognition can be considered a spectrum, then there is no reason why plants could not act with intentions. With less complex than those behind humans’ decisions, but with intentions nonetheless.

## **Chapter II**

### **Plants in Motion**

Plants are commonly regarded as immobile organisms that are constrained to just one place. This claim is not accurate as plants exhibit a wide range of movements. The time scale of the human perceptive system, accustomed to fast actions, has led to a lack of innate capacity to perceive and subsequently appreciate the movements exhibited by plants.

In general, plants move at a much slower pace than animals. Their movements are defined by the shortening or lengthening of the plant's anatomical structures, including leaves, roots, shoots, and tendrils, and as such they are connected to the plant's growth. Plants' tropic and nastic movements are commonly discussed in relation to their response to environmental stimuli. Moreover, it has been reported that plants can move autonomously, even without apparent stimuli that could potentially influence their actions (Stolarz, 2009). Such movements are referred to as nutations and are characterized by circular oscillatory movements.

In this chapter, the focus will be on elucidating the mechanisms underlying plant movement, exploring various types of movements that are relatively obscure, and eventually, gaining a deeper understanding of the inherent flexibility exhibited by plants.

#### **2.1. Physiological mechanisms behind plant movements**

The absence of musculature does not impede plants from exhibiting a variety of movements. Instead, water plays the role of a prime mover (Dumais & Forterre, 2012). The driving force of plant motions is hydrostatic pressure which is a pressure exerted by a fluid due to gravity. This is possible thanks to the presence of a wall surrounding plant cells, which protects them from bursting as the pressure increases (Mano & Hasebe, 2021).

To put it simply, plants move by pumping water into and from the cells. Due to the

osmotic gradient, water flows from the area with a high concentration of water molecules to the site of low concentration. Osmosis, in turn, leads to local changes in cell volume and tissue stiffness that result in large-scale deformations which ultimately allow for the motions to occur (Dumais & Forterre, 2012).

The mechanism responsible for the majority of plant movements is turgor pressure (Forterre, 2013). It is generated by the difference in water gradient inside and outside the cell. Turgor pressure is counteracted by external forces, such as gravity, so the balance between them is kept. The movement is produced when this equilibrium is broken off (Mano & Hasebe, 2021). Turgor pressure leads to elastic changes in the cell length, which can result in a gradual elongation of a plant organ (Dumais & Forterre, 2012).

Another mechanism worth mentioning is the mechanical instability responsible for rapid plant movements. Due to osmosis, elastic energy is stored in the cell walls, prevented by an energy barrier from being immediately released. Only after, a threshold is reached, the barrier can be overcome, and the accumulated energy is converted into kinetic energy (Dumais & Forterre, 2012; Forterre, 2013). Movements based on mechanical instability are majorly fast motions, which are generated due to two types of mechanisms: (i) snap-buckling instabilities and (ii) explosive fracture (Forterre, 2013).

Snap-buckling instability is a phenomenon observed in elastic structures when they undergo a sudden and rapid transition from one stable configuration to another, typically due to the accumulation and release of elastic energy. This instability occurs when the structure is subjected to an external force or deformation. The phenomenon is particularly prominent when a geometric constraint is present, which introduces an energy barrier during the transition between stable states. When the barrier is overcome the motion occurs (Forterre, 2013). The closing of the trap of Venus flytrap is an example of a rapid movement caused by snap-buckling instability. Two lobes attached at the midrib create the trap, which acts as the

geometric constraint that accumulates elastic energy. As more energy is stored, the energy becomes significant enough that each lobe undergoes a rapid and sudden buckling from the inside out, resulting in the trap snapping shut (Forterre et al., 2005; Forterre, 2013).

Explosive fracture is a mechanism used by certain plants (e.g., *Erodium cicutarium*; Evangelista et al., 2011) to disperse their seeds, spores and aid their reproduction. This movement is called “explosive” because it involves a rapid and forceful release of stored mechanical energy, which is done by breaking molecular bonds (Forterre, 2013).

## **2.2. The variety of plant movements**

Plants, as sessile organisms, do not seem to move as much as animals do. To the naked eye, the plentitude of plant movements remains clandestine, however, careful observations and the use of advanced recording methods reveal the wide range of kinetic abilities of the flora. Charles Darwin (1865; 1875; 1880) was among the first to extensively describe the movements of plants, with particular distinction to endogenous, helical motions: namely circumnutations. During his experiments (Darwin, 1875), he noted that plants can differentiate between surface features and act upon them using the internal force that guides circumnutations. He has also focused on touch and light sensitivity in plants. Darwin (1880) observed that the tips of radicles in nearly all plants are sensitive to contact and transmit an influence upwards. He tested his ideas by affixing little squares of stiff card stock to radicle tips and observed the root’s response. The researcher also studied phototropism and found that light is not acting directly on the responding cells or their cell walls, but rather as a stimulus, in the same way as light acts on the nervous systems of animals. He concluded that light sensitivity was nearly the same between plants and animals. Even though his findings and theory of plant movements were first regarded as controversial, Darwin undeniably, inspired many scientists to pursue this area of research.

Plants’ movements are generally divided into nastic and tropic movements (or

tropism). Both refer to the movements induced by external stimuli, however, tropic movements follow the direction of the stimulus, while nastic movements are objectless. What is more, among all the fascinating movements, one particular type of movement called “nutations,” has attracted great attention in recent research due to its role in climbing plants’ survival.

### ***2.2.1. Nastic and tropic movements***

Nastic movements pertain to non-directional, reversible movements produced as a response to the external stimulus. They are independent of the direction of the trigger and the movement orientation is marked by the structure of the plant organ (*4th International Conference for Biodigital Architecture & Genetics*, 2020). There are many types of nastic movements: plants can respond to stress (hydronasty), light (photonasty), temperature (thermonasty), and more. The rapid closure of Venus flytrap leaves in order to entrap the insect is an example of thigmonasty — a movement in response to touch. If two consecutive sensitive hairs located on the inner side of the leaf are triggered, the trap closes immediately. Similarly, leaves of *Mimosa pudica* fold when touched, showcasing the defensive mechanisms against mechanical damage (Guo et al., 2015). Change of the leaves’ position during the night (Kiss, 2006) and their curling and rolling (Wang et al., 2020) are examples of nyctinasty and thermonasty respectively.

Plant tropism, on the other hand, is the differential growth response to an external event, which reorients the plant’s organs depending on the direction of the stimulus (Esmon et al., 2005). The growth response can be positive — towards the resources, or negative — away from harm (Gilroy, 2008). Contrary to nastic motions, tropism tends to be a slower movement (Guo et al., 2015). Tropism is generally discussed in terms of gravitropism (gravity-directed growth) and phototropism (response to blue light), but there are many types of stimuli triggering a reaction, such as water and moisture (hydrotropism), touch

(thigmotropism; Cassab, 2007; Esmon et al., 2005; Schrank, 1950), electric fields (electrotropism), or temperature (thermotropism; Cassab, 2007).

Tropic movements enable plants to adjust to the changing environment in order to optimize resource intake. If a plant falls it can “get up” thanks to the gravitropic growth; if it is shaded too much, tropic movements can “move it” back towards the light (Hart, 1990). However, realistically, plants are exposed to multiple stimuli at the same time, imposing on them the ability to integrate simultaneous information from different sources. In regards to this, Moulton et al. (2020) created a computational model which demonstrated that the competing tropic signals result in complex plant behaviors. To balance the multiple stimuli so a task can be performed, plants increase or decrease the elected tropism response. The proposed model suggests that plants actively solve the problems presented by the environment and that there might be more to plant tropism than just a simple stimulus-response growth.

### ***2.2.2. Circumnutations***

Nutation is the general terminology for the bending movements resulting from the unequal growth rates on the sides of the organ (Migliaccio et al., 2013). Plant nutation refer to the rhythmic, oscillatory movements of plant stems, leaves, or roots that can occur even in the absence of external stimuli. The tips of these organs move laterally through arcs, instead of linearly, as they grow (Hart, 1990), and can do so in a clockwise or counter-clockwise direction (Mugnai et al., 2007). These movements are typically slow and transpire over hours to days. Among them, circumnutations have been discussed most, thanks to their in-depth analysis by Darwin (1880).

Circumnutations are the elliptical movements of plant organs, in which tips outline a circular shape due to the elongation of an organ. The motion was first referred to as “revolving nutation” by Sachs et al. (1875), but the present-day term was coined by Darwin

(1880). In climbing plants their role is to seek mechanical support, while in roots they allow for soil exploration and nutrient forage (Darwin, 1880; Stolarz, 2009).

In his research endeavors, Darwin (1880) conducted a series of experiments with a view to comprehend the circumnutating movements exhibited by plants. By recording the positional changes of plant organs, he discovered that, by undergoing changes in the shape and physical positions, plants display behaviors similar to animals, albeit at a slower pace. He noted that circumnutations could be observed in multiple seedling organs like radicles, hypocotyls, and cotyledons across different plant species, making it a universal phenomenon. His presuppositions were confirmed later on when he observed that mature plants also circumnutate. These discoveries, together with his knowledge of animal observations, led him to posit that circumnutations arose as a form of “habits” aimed at facilitating the emergence of a seedling from the soil and encouraging the growth of the roots in search of nutrients. Furthermore, Darwin (1880) suggested that tropic movements represent a modified form of circumnutations and that plants perceive environmental cues through the tip of their roots or shoots.

Circumnutations are indeed universal movements of plants, yet their patterns and forms vary from plant to plant, and organ to organ. They are usually discussed in terms of four parameters: amplitude, period, shape, and direction (Stolarz, 2009).

The amplitude of circumnutations can vary greatly even in the same plant (Migliaccio et al., 2013). They can change due to external stimuli such as light/darkness or the administration of plant hormones, which can influence the circular movements of the sunflowers (*Helianthus annuus*) and wild beans (*Phaseolus*) respectively (Stolarz, 2009). The period of oscillations depends on the morphological features of a plant and external conditions like temperature or light (Stolarz, 2009). The rhythm of circumnutations can last for less than 60 minutes, a few hours, or follow the ultradian cycle (Migliaccio et al., 2013).



What is more, Johnsson and Heathcote (1973) distinguished two periods of movements: a relatively large one called macronutations, and micronutations overlapping the former.

### *The circumnutations models*

Even though extensive research has been conducted on circumnutations following Darwin's proposals, a lack of consensus regarding the underlying mechanisms that govern them remains. Over the past years, researchers fluctuated between two primary theoretical frameworks: the "Internal Oscillator" Model (Heathcote & Aston, 1970) and the "Gravitotropic Overshoot" Model (Mugnai et al., 2007). However, there appears to be a prevailing trend toward the integration of these two schools (Agostinelli et al., 2021; Migliaccio et al., 2013; Stolarz, 2009).

Darwin (1880) was the one who proposed that plant circumnutations are endogenous in nature, meaning that they are driven and regulated by the internal oscillator. According to Brown (1993), this theory has stood firm, so there must be something fundamental in the growth process that creates this universal movement in plants. Arnal (1953) proposed that circumnutations could be attributed to the periodical outflow of auxins from the tip to the growing zone that subsequently triggers a flux in the growth rate. Furthermore, in favor of this approach, Brown and Chapman (1988) reported that in the conditions with a removed gravitational stimulus, sunflower shoots continued to circumnutate, albeit with a decreased frequency.

Israelsson and Johnsson (1967) put forth a model that advocates for the exogenous nature of circumnutations. This gravity-dependent theory credits the nutational oscillations to a sequence of gravitropic responses with overshoots (Brown, 1993), which were thought to serve as correcting movements of an erroneously aligned plant organ (Heathcote & Aston, 1970). Many experiments have shown that a change in gravity force affects the parameters of circumnutations (Hatakeda et al., 2003; Israelsson & Johnsson, 1967; Kiss,

2006; Zachariassen et al., 1987).

Finally, a model that integrated both theories emerged (Johnsson et al., 1999), wherein gravitropic response functions as the externally driven feedback of oscillation, while endogenous oscillator transfers the rhythmic signals (Mugnai et al., 2007). In this view, the inner oscillator plays a key role in the production of circumnutations, while gravity and tropic reaction modulate the movements (Stolarz, 2009).

## Chapter III

### My Research

In order to grow thrive, climbing plants need to attach themselves to a support. Plants that fail to achieve this goal show a reduced growth rate (Gianoli, 2015) or end up falling. Young climbing plants exhibit large-radius circular movements serving as exploratory motions (Isnard & Silk, 2009). After a support is encountered the pattern of circumnutation changes, and the period of the movements increases so the plant can coil around it (Isnard & Silk, 2009).

In hindsight, however, not much attention has been directed toward the decision-making behind the support-selection movements of climbing plants. Kinematic studies, focusing on decision-making process behind circumnutations, found the difference between plant movements depending on the presence or absence of a support (Guerra et al., 2019; Raja et al., 2020), and the diameter thickness of a support (Guerra et al., 2022). As an example, one can allege the study done by Guerra and colleagues (2019), who, through the kinematic recording, found that the kinematics of circumnutations in a growing pea plant (*Pisum sativum L.*) differed depending on the presence/absence of a support in the environment. The average and the maximum tendril velocity were higher for the support condition, but the timing it took to reach them was quicker for the plants without a support to grasp. More recently, Wang et al. (2023) have found that just like in their natural habitat (Carrasco-Urra & Gianoli, 2009; Putz, 1984), climbing plants showed a preference for thin support compared to thick one. Such results may stem from the fact that grasping a thicker support is more metabolically demanding for plants, and the tensional forces required to twine around the support are too costly to maintain (Carrasco-Urra & Gianoli, 2009; Goriely & Neukirch, 2006). Thus, the observed preference for thin supports might be a manifestation of a decision-making process that allows plants to choose the most beneficial option for their

survival.

Based on the findings of Wang et al. (2023) it has been deduced that the absence of instances where a plant would interact with and attach itself to the thicker support (i.e., 40 mm in diameter) indicated that the thickness of this support posed both mechanical and metabolic challenges for the plants. This research investigated further, how the diameter thickness of a potential support influenced the behavior of a pea plant and at which point it can be deemed unsuitable by a growing plant.

To explore this, pea plants were divided and randomly assigned to one of the three experimental conditions: (i) a “single” condition in which a group of plants was raised in the presence of a thinner (*S-thin*) support; (ii) a “single” condition where a group of plants was grown alongside a thicker support (*S-thick*); (iii) a “decision-making” (*DM*) condition, in which plants vegetated in the presence of two supports — both thinner and thicker. Plants that eventually grasped the thinner support were categorized as *DM-thin*, while those that gripped the thicker support were categorized as *DM-thick*. The plants were expected to exhibit different kinematic patterns depending on whether they grew in the vicinity of a single or two supports. Furthermore, since the support of 40 mm in diameter was too big to be considered an adequate support by pea plants (Wang et al., 2023), it was hypothesized, that reducing the size of the thick support to 30 mm in diameter might turn it into a potential support. The change should be visible in distinctive kinematic patterns.

## Chapter IV

### Methods and Materials

#### 4.1. Subjects

A total number of 38 snow peas (*Pisum sativum* var. *saccharum* cv Carouby de Maussane) were used as study plants. The seeds were potted at an 8 cm radius width and 2.5 cm depth.

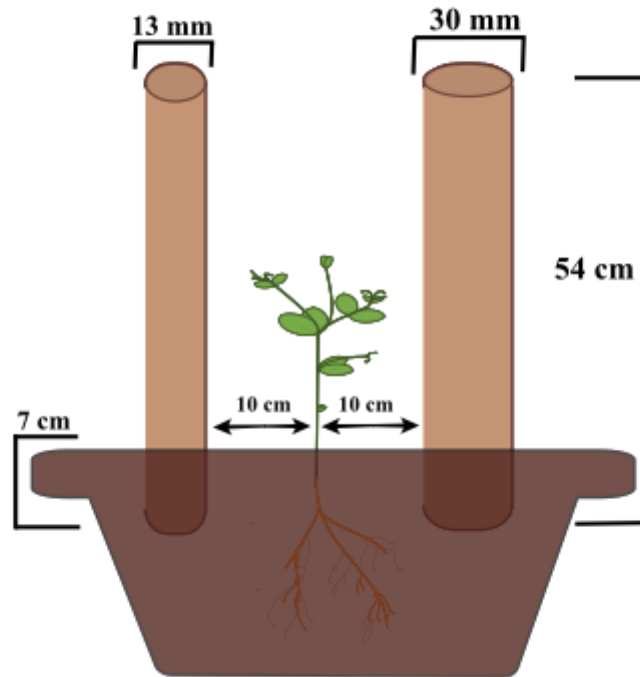
#### 4.2. Support type

Two types of wooden supports, both 54 cm in height, were applied: (i) a *thin* support of 13 mm diameter (Koto -13 mm), and (ii) a *thick* support of 30 mm diameter (Koto - 30 mm). The supports were installed 7 cm below the soil surface and 10 cm from the pea plant (Figure 1).

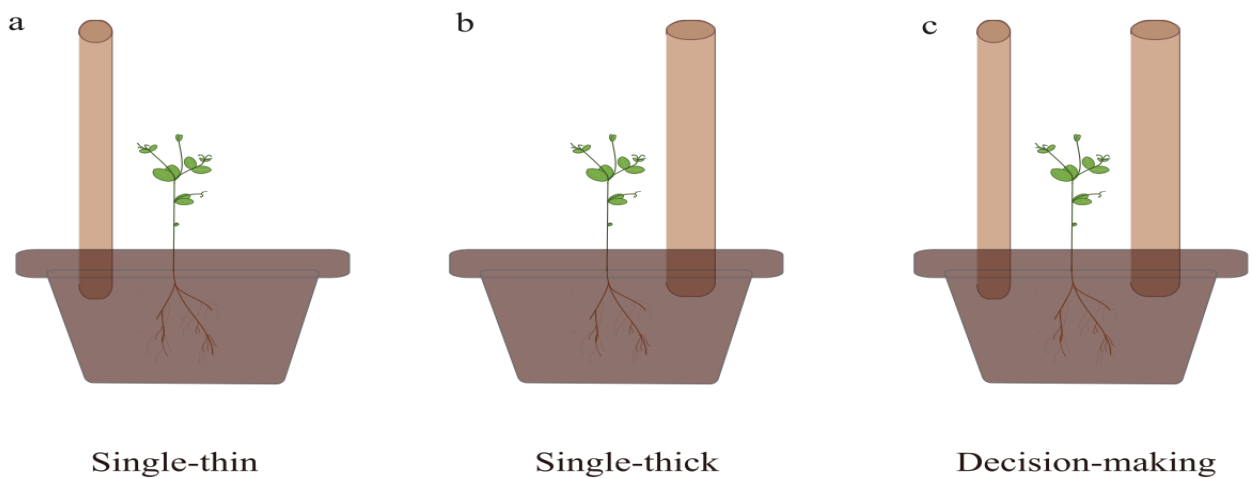
#### 4.3. Experimental conditions

The plants were grown individually in the presence of a single thinner support (*S-thin* condition); a single thicker support (*S-thick* condition) or with both thin and thick supports present (decision-making condition; Figure 2 a-c). The plants which chose the thin support were classified as *DM-thin*, while those that grasped the thick support were categorized as *DM-thick*.

As the circumnutation could have been either clock- or counter-clockwise, the location between support types was reversed across subjects to avoid any potential bias in the results. Furthermore, the supports were placed at an equal distance from the plant cotyledon. In this manner, the first leaf developed by a sprout faced the precise midpoint of the two supports, and a growing bias in favor of either support was prevented.



**Figure 1.** Experimental setup of a seedling and supports in a pot. Illustration of thin (13 mm) and thick (30 mm) supports placed 10 cm from a seedling and 7 cm below-ground.



**Figure 2.** Graphical depiction of the three experimental conditions: (a) “S-thin,” (b) “S-thick,” and (c) “decision-making.”

#### 4.4. Growth setup

To ensure an even growth of all plants, they were grown individually in the thermo-light-controlled growth chambers (Cultibox SG combi 80 × 80 × 160 cm) with the temperature set to 26 °C. The two-fan combination 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 m<sup>3</sup>/h) guaranteed a steady air flow rate into the growth chamber with a mean air residence time of 60 seconds. The fan's placement was adjusted so the air circulation did not affect the plants' movements.

The seeds were sowed in cylindrical pots (40cm in diameter, 20cm in depth), which 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. A led lamp (V-TAC innovative LED lighting, VT-911-100W, Des Moines, IA, USA) was positioned 50 cm above each seedling to expose them to the cool white light for 12 hours (from 6 a.m. to 6 p.m.). The light fell onto plants 50 cm under the lamp in correspondence with seedling allocation, and the Photosynthetic Photon Flux Density 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 plants were watered three times a week using distilled water (Sai Acqua Demineralizzata, Parma, Italy).

#### 4.5. Kinematic recording and data processing

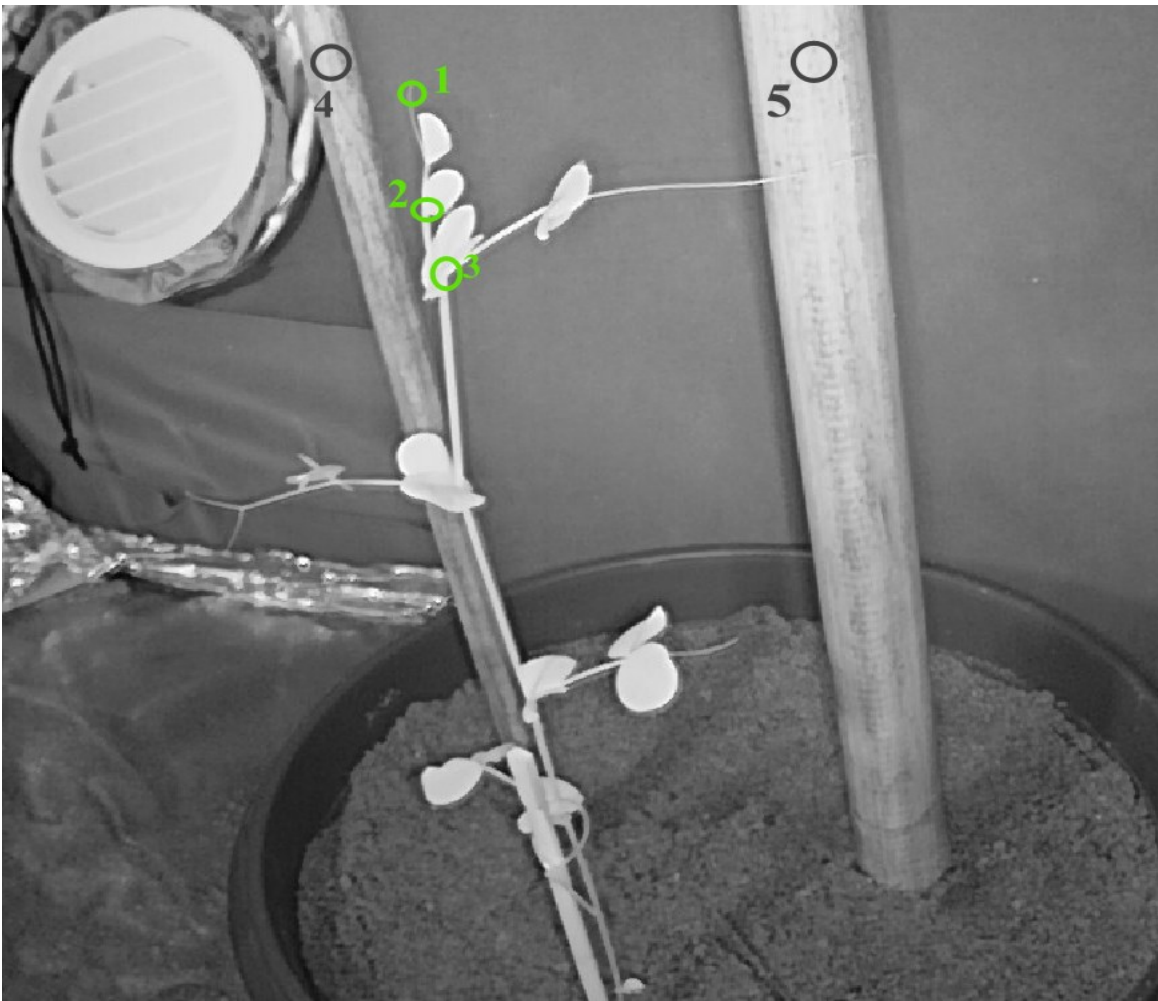
Each growth chamber was equipped with a pair of RGB-infrared cameras, specifically IP 2.1 Mpx outdoor varifocal IR 1080P cameras. They were positioned 110 cm above the ground, spaced 45 cm apart, in order to capture stereo images of the plants. To establish connectivity, the cameras were linked to a 10-port wireless router (D-link Dsr-250n) via Ethernet cables, which, in turn, connected to a PC through Wi-Fi. The CamRecorder software

(developed by Ab. Acus s.r.l., Milan, Italy) was responsible for controlling the process of capturing and saving frames. The intrinsic, extrinsic, and lens distortion parameters for each camera were determined using the Matlab Camera Calibrator App. Depth information from individual images was obtained by capturing 20 pictures of a chessboard (squares' size  $18 \times 18$  mm, 10 columns  $\times$  7 rows) from different angles and distances under natural, indirect lighting conditions. For stereo calibration, the same chessboard was positioned at the center of the growth chamber. The two cameras synchronized every 180 seconds to capture a frame, resulting in a frequency of 0.0056 Hz. RGB images were acquired during the day cycle, while infrared images were obtained during the night cycle.

The analysis focused on the tendrils developing from the specified leaf, which served as the anatomical landmarks of interest. The initial frame corresponded to the moment when the tendrils first appeared, while the end frame was defined by the tendrils' coiling around the support. Both the left and right camera images were used to reconstruct three-dimensional trajectories for every marker. A software program, developed in Matlab (Ab. Acus s.r.l., Milan, Italy) was used to identify anatomical points of interest (Figure 3) and track their position frame by frame in the images captured by the two cameras. The insertion of markers on the anatomical landmarks (i.e., the tendrils) was performed after the initial recording. Initially, the tracking process was automated using the Kanade-Lucas-Tomasi (KLT) algorithm on the undistorted frames from each camera. The experimenter manually verified the tracking by checking the marker positions frame by frame.

The 2D trajectories obtained from the two cameras were then used to triangulate and calculate the 3D trajectory for each tracked marker. Ultimately, the trajectory was reconstructed in a series of coordinates in three-dimensional space ( $x, y, z$ ), where the  $x$ - $z$  plane represents the horizontal plane, and the  $x$ - $y$  and  $z$ - $y$  planes represent the vertical planes perpendicular to each other.





**Figure 3.** The considered anatomical landmarks for kinematic recording. The tracked landmarks included: (1) the tendril(s); (2) the apex; (3) the internode. Markers were also positioned on the supports (4, 5) to serve as reference points.

#### **4.6. Dependent measure**

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

- i. Total movement duration (min): the time it takes from the moment tendrils developed from the apex to the time they approach the support and start coiling around it.
- ii. Circumnutation duration (min): the time taken by a plant to complete a single circumnutation.

- iii. Number of circumnutations: the number of circumnutations performed by a plant from the time when tendrils developed from the apex till the time they approached the support.
- iv. Length of the circumnutations major axis (mm): the maximum distance between the two points characterizing the maximum axis for the circumnutations trajectory.
- v. Circumnutations length (mm): the sum of all the Euclidean distances between subsequent points during a single circumnutations.
- vi. Circumnutations area (mm<sup>2</sup>): the sum of pixels with a value equal to 1 obtained from the binarization of the circumnutations trajectory.
- vii. Amplitude of average velocity (mm/min): the average velocity during the entire movement.
- viii. Amplitude of the maximum peak velocity (mm/min): the maximum peak velocity reached during the entire movement.
- ix. Maximum aperture (mm): the maximum distance between the tendrils.
- x. Direction switching: the times at which the plant switched the direction of circumnutations.

#### **4.7. Statistical analysis**

The analysis was carried out using the JASP software (Team., 2023), which was nested within the environment R (see used packages: <https://jasp-stats.org/r-package-list/>) (Team., 2010). First, the descriptive statistics of the median (Med), range, interquartile range (IQR), and quartiles (Q<sub>1</sub> and Q<sub>3</sub>) were calculated (Table 1). The assumption of normal distribution was tested with the Shapiro-Wilk test, which revealed that for most of the dependent variables, the normal distribution requirement was not met ( $p < .001$ ). Thus, the non-parametric Maan-Whitney U test (Table 2) was used to compare the groups, where the

$W$ -value was calculated as the smaller of the rank total between the two research groups. The adopted significance level was  $\alpha = 0.05$ .

## Chapter V

### Results

#### 5.1. Qualitative results

In all 38 pea plants the circumnutating pattern was visible for the shoots (i.e., tendrils), which bent and altered their movements in the direction of the sensed support.

In the single-support conditions eight plants grasped the thin support (*S-thin* condition) and 10 plants coiled around the thick support (*S-thick* condition). In the decision-making condition plants displayed a relative preference towards the thin support compared to the thick one. A total of 19 plants grasped and coiled around one of the supports: six plants chose the thick support (*DM-thick* condition) while 13 grasped the thin support (*DM-thin* condition). Only one plant failed to grasp a support and fell as a result, nonetheless, it showed an inclination towards the thick support. All plants were able to locate and aim with comparative precision for their chosen support.

#### 5.2. Kinematical results

Descriptive statistics (Table 1) for the comparisons across conditions for all dependent measures (Table 2) are provided below.

##### 5.2.1. *S-thin* vs. *S-thick*

The comparison between control conditions allows to confirm the kinematical differences regarding the size of a potential support, which were previously documented by Guerra et al. (2019). It is crucial to verify these differences in order to draw correct conclusions about the DM conditions. The statistical analysis done with the Mann–Whitney U test (Table 2) indicates that there is a significant difference between *S-thin* and *S-thick* conditions in terms of *circumnutation duration* ( $W = 32994.000$ ;  $p < .001$ ), *number of circumnutations* ( $W = 17115.000$ ;  $p < .001$ ), *circumnutation area* ( $W = 18967.000$ ;  $p =$

0.048), *amplitude of average velocity* ( $W = 14025.000$ ;  $p < .001$ ), and the *amplitude of the maximum peak velocity* ( $W = 14433.000$ ;  $p < .001$ ).

On the other hand, no significant results were found for the dependent measures: *total movement duration* ( $W = 59.000$ ;  $p = 0.101$ ), *circumnutation length* ( $W = 19283.000$ ;  $p = 0.085$ ), *length of circumnutation major axis* ( $W = 19361.000$ ;  $p = 0.098$ ), *direction switching* ( $W = 28.500$ ;  $p = 0.314$ ). Thus, plants in control conditions did not differ in terms of the mentioned parameters. Furthermore, unlike the formed hypothesis that plants in *S-thick* condition would show a greater *maximum aperture* ( $W = 206.000$ ;  $p = 0.140$ ) between tendrils than plants growing in the vicinity of thin support, the statistical analysis did not reveal any significant differences between groups.

### **5.2.2. DM-thin vs. S-thin**

This comparison allows for validation of the previous results suggesting differences in kinematic patterns between plants grown with single thin support in their proximity and plants seeded in an environment of choice between two supports of varying diameter thickness (Wang et al., 2023). The Mann–Whitney U test indicates that there is a significant difference between *DM-thin* and *S-thin* conditions in terms of *number of circumnutations* ( $W = 15972.000$ ;  $p < .001$ ), *length of circumnutation major axis* ( $W = 34937.000$ ;  $p < .001$ ), *circumnutation length* ( $W = 35616.000$ ;  $p < .001$ ), *circumnutation area* ( $W = 34687.000$ ;  $p < .001$ ), *amplitude of average velocity* ( $W = 33921.000$ ;  $p = 0.001$ ), and *amplitude of maximum peak velocity* ( $W = 35322.000$ ;  $p < .001$ ). Unlike the aforementioned study, however, our findings reveal the differences between groups regarding *circumnutation duration* ( $W = 34263.500$ ;  $p < .001$ ).

**Table 1. Descriptive statistics for kinematics in all groups**

	<b>Group</b>	<b>Median</b>	<b>IQR</b>	<b>Range</b>	<b>Q<sub>1</sub></b>	<b>Q<sub>3</sub></b>
Total movement duration (min)	DM-thick	2091.000	296.250	1332.000	1872.000	2168.250
	DM-thin	1764.000	552.000	1479.000	1551.000	2103.000
	S-thick	2592.000	790.500	4005.000	2191.500	2982.000
	S-thin	1828.500	693.750	1920.000	1638.000	2331.750
Circumnutation duration (min)	DM-thick	69.000	20.250	90.000	60.000	80.250
	DM-thin	72.000	26.250	102.000	60.750	87.000
	S-thick	93.000	42.000	186.000	72.000	114.000
	S-thin	69.000	15.000	114.000	60.000	75.000
Number of circumnutations	DM-thick	26.000	6.250	20.000	22.750	29.000
	DM-thin	25.000	7.000	11.000	20.000	27.000
	S-thick	23.000	10.000	26.000	20.000	30.000
	S-thin	28.000	9.000	21.000	22.000	31.000
Circumnutation major axis (mm)	DM-thick	79.420	59.586	174.967	48.565	108.151
	DM-thin	85.445	62.411	187.541	52.736	115.148
	S-thick	59.085	48.122	173.508	37.754	85.875
	S-thin	65.036	69.147	187.973	36.176	105.323
Circumnutation length (mm)	DM-thick	181.838	154.001	520.083	106.952	260.954
	DM-thin	230.532	181.438	548.856	134.550	315.988
	S-thick	151.862	147.475	465.898	85.154	232.629
	S-thin	166.488	196.104	503.609	85.797	281.900
Circumnutation area (mm <sup>2</sup> )	DM-thick	1226.906	3775.906	18244.750	362.047	4137.953
	DM-thin	2828.375	5518.469	19844.688	819.672	6338.141
	S-thick	966.813	3256.500	17338.500	280.688	3537.188
	S-thin	1943.688	5298.375	14870.563	199.438	5497.813
Amplitude of average velocity (mm <sup>2</sup> /min)	DM-thick	2.914	2.477	5.873	1.551	4.028
	DM-thin	3.164	2.269	6.023	2.016	4.284
	S-thick	1.789	1.403	4.543	1.159	2.562
	S-thin	2.738	2.647	6.271	1.430	4.077
Amplitude of the maximum peak velocity (mm <sup>2</sup> /min)	DM-thick	4.653	4.374	18.271	2.906	7.280
	DM-thin	5.324	4.212	16.558	3.437	7.649
	S-thick	2.817	2.031	11.041	1.813	3.844
	S-thin	4.038	3.813	14.054	2.499	6.313
Maximum aperture (mm)	DM-thick	65.213	30.179	54.930	46.174	76.353
	DM-thin	43.465	20.443	82.395	37.345	57.788
	S-thick	53.400	29.349	208.128	36.932	66.281
	S-thin	40.202	9.058	34.360	38.419	47.477
Direction switching	DM-thick	2.5000	1.000	6.000	2.000	3.000
	DM-thin	1.000	1.000	3.000	1.000	2.000
	S-thick	0.500	2.000	4.000	0.000	2.000
	S-thin	1.500	1.250	6.000	1.000	2.250

*Note.* IQR = interquartile range; Range = the difference between the maximum and minimum values; Q<sub>1</sub> = first quartile (25%); Q<sub>3</sub> = third quartile (75%).

**Table 2. Statistical analysis for all comparisons**

Dependent measures	S-thin vs. S-thick		DM-thin vs. S-thin		DM-thick vs. S-thick		DM-thin vs. DM-thick	
	W	<i>p</i>	W	<i>p</i>	W	<i>p</i>	W	<i>p</i>
Total movement duration	59.000	0.101	45.000	0.645	16.000	0.147	50.000	0.368
Circumnutation duration	32994.000	< .001	34263.500	< .001	8662.000	< .001	20375.000	0.031
Number of circumnutations	17115.000	< .001	15972.000	< .001	21069.000	< .001	31302.000	< .001
Length of circumnutation major axis	19361.000	0.098	34937.000	< .001	20899.000	< .001	20981.000	0.090
Circumnutation length	19283.000	0.085	35616.000	< .001	19817.000	0.010	18840.000	< .001
Circumnutation area	18967.000	0.048	34687.000	< .001	18853.000	0.099	17703.000	< .001
Amplitude of average velocity	14025.000	< .001	33921.000	0.001	23962.000	< .001	20211.000	0.023
Amplitude of maximum peak velocity	14433.000	< .001	35322.000	< .001	24676.000	< .001	20679.000	0.054
Maximum aperture	206.000	0.140	75.000	0.865	212.000	0.081	96.000	0.034
Direction switching	28.500	0.314	48.000	0.792	43.500	0.143	54.000	0.191

*Note.* The comparisons “S-thin vs. S-thick,” and “DM-thin vs. DM-thick” hypothesize that the maximum aperture is greater for the thick support than the thin one on the basis of previous findings in pea plants.

### 5.2.3. *DM-thick vs. S-thick*

Similar to the preceding comparison, this analysis enables the detection of hypothetical kinematic differences in plants grown in a decision-making condition when compared to a single condition; specifically in relation to the thicker support. The Mann–Whitney U test reveals that there is a significant difference between the *DM-thick* and *S-thick* conditions in terms of the following dependent measures: *circumnutation duration* ( $W = 8662.000$ ;  $p < .001$ ), *number of circumnutations* ( $W = 21069.000$ ;  $p < .001$ ), *length of circumnutation major axis* ( $W = 20899.000$ ;  $p < .001$ ), *circumnutation length* ( $W = 19817.000$ ;  $p = 0.010$ ), *amplitude of average velocity* ( $W = 23962.000$ ;  $p < .001$ ), and *amplitude of the maximum peak velocity* ( $W = 24676.000$ ;  $p < .001$ ). With the exception of no differences found in the size of the movements area, the results are in accordance with the

preceding comparison, further presenting kinematic differences between plants grown in a single support environment and those in decision-making setting.

#### 5.2.4. *DM-thin vs. DM-thick*

This comparison contrasted the kinematics of plants sowed in the presence of both thick and thin supports, that is in the decision-making setting, but ultimately showed a preference for either a thin or a thick support.

According to the analysis done with the Mann–Whitney U test, there is a significant difference in terms of parameters: *circumnutation duration* ( $W = 20375.000$ ;  $p = 0.031$ ), *number of circumnutations* ( $W = 31302.000$ ;  $p < .001$ ), *circumnutation length* ( $W = 18840.000$ ;  $p < .001$ ), *circumnutation area* ( $W = 17703.000$ ;  $p < .001$ ), and the *amplitude of average velocity* ( $W = 20211.000$ ;  $p = 0.023$ ) between the *DM-thin* and the *DM-thick* conditions. Moreover, as hypothesized, the *maximum aperture* between tendrils was significantly greater for plants that grasped the thick support ( $W = 96.000$ ;  $p = 0.034$ ) compared to the group that preferred the thin support.

On the other hand, no significant result was found for the dependent measures: *total movement duration* ( $W = 50.000$ ;  $p = 0.368$ ), *length of circumnutation major axis* ( $W = 20981.000$ ;  $p = 0.090$ ), *amplitude of maximum peak velocity* ( $W = 20679.000$ ;  $p = 0.054$ ), or *direction switching* ( $W = 54.000$ ;  $p = 0.191$ ). Thus, plants that showed a preference for the thin support didn't differ significantly from the *DM-thick* condition in terms of the mentioned parameters.



## Chapter VI

### Discussion

The present study has examined the behaviors of pea plants in different growth environments. The plants were placed in three experimental conditions: (i) in the presence of two supports of distinguishable diameter thickness; (ii) in a setting with a thin single-support; or (iii) with a thick single-support. This venture aimed to investigate whether the climbing plants, when placed in a situation of choice between two options would show a preference towards the more beneficial alternative. The second objective was to compare this behavior with plants growing in a single-support environment. As the results indicate, the pea plants majorly grasped the thinner support, thus demonstrating a preference for this particular support diameter. Moreover, kinematic patterns differed significantly depending on the preferred support type. Differences in behaviors were also observed between plants grown in an environment with a single-support and those exposed to two supports, specifically when it came to the number of performed movements, their duration, length, and velocity. Similar results were obtained when comparing conditions with a single support. Pea plants that were seeded in the presence of a single thin support exhibited different movement patterns from those grown with a single thick support.

The findings seem to be in accordance with the previous results that thicker supports are more demanding for tendrils to coil around than thin ones (Gianolli, 2015). What is more, a plant may need more energy to successfully attach to the thicker support (Guerra et al., 2019). Thus, to accumulate the necessary grasping power the plant may need to slow down the movements and perform more circumnutations before approaching the thick support and coiling around it. This action may further require developing longer tendrils which would allow for a greater aperture between them so that the grasping of the support is facilitated.

The results indicate significant differences between plants that preferred thin and those that preferred thick support in terms of kinematic features, regardless of the condition type. Plants can perceive their environment and integrate the information regarding different parameters (e.g., light, gravity, and humidity; Calvo Garzón, 2007) so they should be able to register the features of the available supports. Trewavas (2017) mentions that tendrils progressively learn the shape and characteristics of a support they come in contact with and subsequently assume a similar shape. This would indicate that the support perception takes place after the contact with it has been made. However, according to the present findings, the pea plant kinematic patterns were affected before the tendrils approached the support. The decision, which support to grasp in the decision-making condition, must have been made beforehand as a result of active processes of receiving and integrating external information.

Moreover, as this experiment reduced the size of a thick support from 40 mm (Wang et al., 2023) to 30 mm in diameter (Guerra et al., 2019; 2022), making it feasible for plants to actually grasp the thicker support, the results seem to further confirm observations that after a certain diameter thickness is reached the tensional forces necessary for attaching and twining around the support cannot be maintained by climbing plants (Darwin, 1875; Goriely & Neukirch, 2006; Putz, 1984;). Decreasing the diameter of a thick support was enough for plants to consider it as a suitable alternative. Since unknown variables (Severino, 2021) may be at play, perhaps, the thicker support might have been perceived as a more sturdy and enduring option — more beneficial for future gains. The plants that twined around the thick support might have been seeking a more secure alternative, thus choosing to trade the energy-saving growth towards the thinner support with potentially more certain survival in the future. In this regard, Karban and Orrock's (2018) propose to integrate the judgment and decision-making framework into plant studies. In their view, judgment refers to the way an organism processes information following its detection. The information can be gathered by perceiving

the current surroundings or by recalling previous sensory experiences (i.e., memory). Thus, judgment can be described as the assessment of perceived stimuli and the deduction of the individual's present conditions. This process of judgment differs from decision-making, which involves utilizing the information to select a course of action. Consequently, decision-making is often swayed by trade-offs among different potential outcomes and comparisons of alternate actions (Orrock et al., 2015). The outcome of decision-making can be described as a plant expressing preference or making a choice. The judgment ought to be molded through precise recognition of the environment, whereas decision-making should be influenced by the proportional advantages and disadvantages of specific actions (taking into account the precision of the judgment process) and the extent to which past and present signals anticipate future circumstances (Karban & Orrock, 2018).

The ecological-psychology-inspired view suggests that plants identify invariant structures in the changing environment, and the received information specifies the available ways to interact with an object in the vicinity of the climbing plant (Calvo et al., 2017). For information pick-up to happen, it's essential that there is an accessible perceptual medium to which the organism is sensitive, that is, necessary for survival. Furthermore, this medium must possess a structured nature (Sims, 2019). This also refers to the Gibsonian theory of affordances (1977; 1979) where a wooden support (i.e., medium of structured nature) can be perceived by a plant as an opportunity for twining and climbing. As affordances are occasions for actions they should be observed and decided upon before the grasping is initiated. This neatly enters into the plant predictive processing (PPP) hypothesis (Calvo & Friston, 2017; Sims, 2019), which proposes that plants can actively anticipate the states of their vicinity and adapt to local conditions. If a plant can perceive the features of the potential support in its proximity it can then adjust its growth and movements in such a way that the chances of grasping support are maximized, hence the difference in kinematic patterns

between plants that grasped thick or thin support. In essence, plant behaviors change depending on the surrounding they are in — whether they have an affordance of coiling around one single support or an opportunity to choose between two available options, among which one can potentially be more beneficial than the other. A similar explanation could be provided to clarify why the movements varied in non-decision-making conditions depending on the support thickness. As those plants were presented with only one affordance — to grow towards a single support — there was less information to detect. Thus, the judgement process and its consequent selection of action were focused on the features of the available support so that a plant could start growing and moving in such a way that increased its chances of grasping an available support. By contrast, in the decision-making setting, plant behavior had to be adjusted, taking into the account the characteristics of both available supports and the selection of the better affordance for climbing. The more complex the situation is, the more information to register and influence the behavior, which is reflected in the disparity of kinematic patterns. Thus, this explanation also illustrates how the interplay between the environment (i.e., experimental conditions) and stimuli features (i.e., support diameter) influences the behavior of pea plants.

To conclude, this research offers additional evidence of the plants' decision-making abilities in the kinematic pattern framework. The decisions have been demonstrated by preference in grasping the more adaptive support among two options, suggesting that the plant movements have to be underlain by complex processes of information integration. This view is reinforced by differences found in plant movements depending on their environment (decision-making or single-support setting) and the support thickness. The study provided further evidence for the utility of time-lapse photography and 3D motion analysis of plant movements in investigating their behaviors and decision-making abilities. Future research

may continue to borrow from comparative psychology (Castiello, 2023) to investigate in-depth the plant responses to stimuli and mechanisms behind support selection.

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