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Final Dissertation

**Root-to-shoot Communication for the Coding of
Object Thickness in Pea Plants**

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Abstract

Plants characterized by a weak stem, such as climbing plants, need to find a potential support (i.e., a stick or a wooden trunk) to reach the greatest light exposure. Since Darwin's observation, several studies on the searching and attachment behaviors of climbing plants have reported the unique ability of climbing plants to process different support features as to modulate their movement accordingly. Nevertheless, the strategies underlying this ability have yet to be uncovered. The present research tries to fill this gap by investigating how the interaction between the above- (i.e., stem, tendril, ...) and below-ground (i.e., the root system) plant's organs is played out in the kinematics of the approach to grasp movement. The movement of pea plants (*Pisum sativum* L.) toward a stimulus characterized by different thicknesses with respect to the below- and above-ground part of it (i.e., perturbed conditions) was assessed by means of three-dimensional (3D) kinematical analysis. Control conditions, in which one-thickness stimulus (i.e., thin, or thick) was presented, were also considered. Results suggest the contribution of the root system in sensing, coding, and processing below-ground information and how such information is evaluated and eventually modified at the level of the aerial part of the plant to fulfill the end-goal of the movement. Results are discussed in terms of a functional equilibrium reached through a crosstalk between the grounded and the aerial components of the plant.

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Chapter 1. Introduction

1.1. Plant Intelligence & Cognition

What exactly qualifies an organism as intelligent? Why did organisms need to evolve intelligence as part of their evolutionary process? Answers to these questions can be found by considering the ultimate goal of every organism in life: survival. To survive, every organism must fit into its environment, which means that it must perceive relevant aspects of their environment, solve problems, make decisions, and learn from their mistakes in order to cope with the varying needs and challenges they face. These kinds of processes bring about the kind of intelligent behavior that is defined as cognition. Overall, every living creature must do its best to make it to the next day; survival is a universal task.

Normally in science, research should start with the simple systems and gradually progress to the more complex ones to better understand the concepts. However, we began to research intelligence and cognitive processes from the most complex system: humans. This has led us to see the world through an anthropocentric lens, ignoring the fact that other creatures can also display intelligent behavior. Nevertheless, every organism has its own way of displaying intelligent behavior through cognitive processes in order to survive. Plants are no exception to this; they have their own intelligent survival strategies. In this chapter, I shall talk about the perspectives of the great philosophers and scientists in history about plants, what they can do, and contemporary debates on plant cognition.

1.1.1. From Ancient Greece: An Odyssey to Discover Plant Cognition

Ancient Greece

Since ancient times, humans have always wondered if there are other intelligent beings in the universe, like themselves, and this quest still goes on. Although plants dominate the Earth, people do not associate them with intelligence and cognition. However, contrary to the view that plants lack intelligence or any cognitive ability, many philosophers, and scientists from

ancient times till the present have dared to think about plants' ability to perceive and respond to the surrounding environments. For example, according to Empedocles, who carried the traces of ancient animistic understanding in his philosophy, everything comes from four roots (i.e., earth, fire, water, and air), and in this respect, animals, and plants are essentially related to each other (Empedocles & Wright, 1981). In the Empedoclean philosophy, all beings have aspects of sensitivity, they can think, feel pleasure, and pain (Hall, 2011). Democritus of Abdera (460–360 BCE), the father of the atom, shared Empedocles' inclusive mindset and believed that everything is in motion, even if only at the atomic level. According to him, even plants that seemed immobile were moving. He went beyond this idea and compared trees with men upside down: the head under the ground, and the feet above the ground (Mancuso & Viola, 2015).

In the dialogues *Timaeus*, Plato (427–347 BCE) considered plants as living things with a limited capacity for sensation and pleasure, desire, and pain; his point of view was zoocentric. He claimed that plants were created particularly for the use of human beings (Plato & Zeyl, 2000). Plato's idea about plants was perpetuated by Aristotle's exclusionist hierarchical ordering of life, in which plants were placed at the bottom. Aristotle asserted that plants have a vegetative soul (i.e., only capable of nourishment and reproduction) that is inferior to humans and other animals (Aristotle & Hett, 1957).

Unlike Aristotle, his pupil Theophrastus (371–287 BCE) had ideas about plants that were more similar to Empedocles and ancient Greek mythology, his ideas were oriented toward inclusiveness rather than exclusiveness (Theophrastus & Hort, 1916). He attempted to look at the plants from their point of view and underlined the connection and relatedness between the plant kingdom and humanity. While his mentor, Aristotle, regarded plants as passive beings lacking sensation and intellect, Theophrastus viewed plants as volitional, minded, intentional beings that have their own autonomy and purpose in life. However (and unfortunately),

Aristotle's zoocentric philosophical approach had a greater impact than Theophrastus upon Western philosophers and scientists.

The great classifier, Swedish botanist Carl Nilsson Linnaeus (1707–1778), also accepted the Aristotelian point of view without question. Although Linnaeus (1755) claimed that plants sleep, he believed that plants live a passive life devoid of sensation and reason; besides, it was not known at the time that sleep is linked to the brain's most advanced processes. Furthermore, even though he witnessed that carnivorous plants eat animals, he was reluctant to accept that and attempted to develop alternative hypotheses about what he saw, like the animal staying inside the plant of its own will (Hall, 2011; Mancuso & Viola, 2015).

The zoocentric idea that depicts plants as inferior beings and nature as human-dominated remained unquestioned and eventually turned into dogma with the authorization of the West's dominant religion. The idea that plants' behavior is automatic and predetermined was further strengthened by Hegel in the 19th century. To Hegel, plants are not autonomous, find completion only in the inorganic “other” (e.g., sunlight or the minerals and water in the ground) in their environment. Even though we now know plants' ability to react to their ever-changing environmental circumstances explains their phenotypic plasticity; for a long time, scientists and philosophers ascribed these features to the deficient status of their subjectiveness in the grip of the inorganic world (Marder, 2012).

Charles Darwin and the plants

With the publication of Darwin's *Origin of Species* in the nineteenth century, the dogmatic idea of natural hierarchy, which portrays humans as superior to nature and as her master, took a hit. He proved that humans, other animals, and, implicitly plants, evolved from a common ancestor. Darwin was very passionate about plants and devoted most of his life to botanical studies. His particular interest in climbing plant species began when he read an article by his intellectual friend Asa Gray (1858) about the movement of wild cucumber tendrils. He then requested some

seeds from his friend to see it for himself. However, he did not settle for observing only one plant and studied the movements of many climbing plants via several experiments, compiling his findings in his book *On the Movements and Habits of Climbing Plants* (Darwin, 1875). He continued to conduct experiments on the growth processes and movements of many plant species by exposing them to various stimuli, and this led to yet another book, *The Power of Movement in Plants* (Darwin, 1897). To study plant movements, he developed a simple but time-consuming method: he grew the plants in pots that were either completely dark or had light from above or on one side and were covered above by a large horizontal sheet of glass, as well as another vertical sheet on one side. He visually lined up a bead of wax on a glass needle affixed to a plant organ (e.g., shoots, roots, leaves) with a stationary dot on a card and marked the glass. By repeatedly doing this every few minutes for several hours, Darwin connected the dots to map out plants' movements and discovered that the growing tips of all plant organs rotate around a central axis. He coined the term *circumnutation* to describe this oscillatory plant movement. His observations led him to the conclusion that all plant organs circumnutate, and that the various forms of the tropic movement were just modified versions of circumnutation. As a result of his many experiments, he was most impressed by the radicle tip's ability to sense dangerous objects (e.g., rocks, or toxic chemicals in the soil), water, and gravity and adjust its movements in response to the stimuli. Darwin (1875) expressed his admiration with these words:

“...It is hardly an exaggeration to say that the tip of the radicle thus endowed, and having the power of directing the movements of the adjoining parts, acts like the brain of one of the lower animals; the brain being seated within the anterior end of the body, receiving impressions from the sense-organs, and directing the several movements. (p. 573)”

Democritus's perspective on plants (i.e., comparing trees to the upside-down people) was scientifically brought back to life by Darwin with the root-brain hypothesis. The root-brain hypothesis, proposed by Darwin and his son Francis Darwin, states that the root apex functions as a diffuse brain, similar to the brains of lower animals, with its apex seated at the anterior pole of the plant body (Baluška et al., 2004; 2009; Darwin 1897). He was the first person of modern botany that acknowledge the plants' cognitive ability, and their behavior as intelligent and purposeful rather than automatic and predetermined. However, even Darwin could not entirely escape from the influence of the zoocentric dogmatic belief, by comparing plants with lower animals. Despite this, his long and devoted studies on plants paved the way for contemporary studies on plant intelligence and cognition.

1.1.2. Plant Cognition: The Modern Debate

Perceptual systems in plants

Despite all the accumulated scientific evidence that contradicts the notion that plants are insensitive and lack cognitive abilities, the dogmatic belief in the natural hierarchy still impacts even the scientific areas. However, despite all these dogmatic beliefs, in recent years, scientists have started to conceptualize the aspects of plant intelligence by taking into account plants' perspectives.

Plants have a wide range of perceptual modalities at their disposal, including vision, olfactory, tactile, hearing, and many more. Indeed, it has been suggested that due to their sessile nature, they may perceive their environment more and with greater sensitivity and discrimination than roaming animals (Trewavas, 2009). Light is more than just a source of energy for plants; for example, some plants determine the best time of year to flower based on the length of the day, which they can understand thanks to their ability to differentiate between colors (e.g., red light to measure the length of the night). Plants, of course, do not see in pictures the way we do, but they do have their own form of vision. Plants not only can perceive colors that we are not able

to see, such as UV and infrared light but also can perceive whether the light is coming from the left, right, or above them, whether it's midday or the sunset. They can realize if they are being overshadowed by another plant that is blocking their light, and they can understand how long the lights have been on (Chamovitz, 2013). Furthermore, several studies have suggested that the upper and subepidermal layers of the leaf contain cells that act as ocelli, or eye-like structures that allow plants to gather visual information about their environment (Baluška & Mancuso, 2016). This theory is supported by research on *Boquilla trifoliolata*, a climbing wood vine that is an expert at mimicry. *Boquilla trifoliolata* can perfectly mimic the host plant's leaf colors, shapes, sizes, orientations, and petiole lengths. Most importantly, they can imitate their host's appearance even when they are not in direct contact, which supports the idea that plants are capable not only of sensing but also of decoding visual inputs (Ceccarini et al., 2020a; Gianoli & Carrasco-Urra, 2014).

Plants can emit odors that animals and humans find appealing, but they can also perceive their own odors as well as the odors of neighboring plants. Plants use "smells," or molecules known as volatile organic compounds (VOCs), to gather information from their surroundings and communicate with one another and with insects. They can detect nearby danger by eavesdropping on when their neighbors are attacked by a caterpillar eating their leaves, and as a result, they boost their immunity before becoming the target of the danger (Rhoades, 1983). *Cuscuta pentagona* (dodder), a parasitic plant, uses volatiles to locate and choose its host (Runyon et al., 2006).

Plants can detect when they are being touched by using small sensory organs known as mechanosensitive channels, which are found in small numbers throughout the plant but most frequently on the epidermal cells that are in direct contact with the external environment. These unique receptors (i.e., mechanosensitive channels) are activated when the plant comes into contact with something or when vibrations reach it (Mancuso & Viola, 2015). Some of them

even respond to touch with visible immediate movements. To protect itself from potential herbivores, *Mimosa pudica*, for example, closes its leaves when touched. When an insect lands on the leaves of the Venus flytrap, the carnivorous plant closes its trap to feed itself. When climbing plants come into contact with a potential support, they begin coiling their tendrils. The burr cucumber (*Sicyos angulatus*), for example, can begin coiling at a weight of only a quarter of a microgram, making it ten times more sensitive than humans (Chamovitz, 2013).

A concept of intelligence that includes plants

Starting from Stenhouse's (1974) definition of intelligence as adaptive variable behaviors throughout the life of the individual, Anthony Trewavas (2002) pointed out that intelligence can be seen through behavioral plasticity in the plant kingdom. Even though the word intelligence has many definitions, it is derived from the Latin *interlegere*, which means to choose between. Every living being needs to make numerous decisions concerning possible activities in order to survive in a complex, dynamic, and competitive environment (Baluška & Levin, 2016).

While studying intelligence, we expect that intelligent behavior can be seen only in movements that happen in a time frame that we are familiar with. Unlike animals, plants do not possess the ability to locomote, however, they can exhibit movements generally induced by growth, and their growth process is adaptively variable. Due to their sessile nature, plants are extremely sensitive to their surroundings in order to increase their fitness. Nowadays, the misbelief that plants lack cognitive abilities emerges from brain-chauvinism, a presumption that to display intelligent behavior, one organism must have a nervous system (Schull, 1990; Vertosick, 2002). However, research shows that even single-celled organisms such as slime mold, *Dictyostelium*, *Paramecium* exhibit intelligent behaviors; naturally, the idea that also plants can exhibit intelligent behaviors should not come as a surprise (Trewavas, 2014). Plants are very in tune with their environment, actively sampling at least 22 different biotic and abiotic environmental

signals and integrating this data with their internal state to decide what is good or bad for them (Calvo Garzón & Keijzer, 2011). Indeed, recent research on plants demonstrates that they are highly sensitive cognitive organisms that perceive, assess, learn, remember, solve problems, make decisions, and communicate with one another by actively gathering information from their environment.

Gagliano and her colleagues (2014) investigated the acquisition and expression of a long-lasting memory for a learned behavior in *Mimosa pudica*. The potted plants were placed in a custom-made apparatus that enabled plants to be dropped from a height of 15 cm regularly by sliding along the rail. To prevent bouncing, the apparatus was secured with a shallow depression in the foam base. Initially, when the plants dropped, they closed their leaves. After training, the plants learned that closing themselves off is unnecessary in response to this repetitive but harmless stimulus, so they kept their leaves open to forage light. Not only did the plants learn to ignore the stimulus, but they also remembered it even after 28 days. Researchers ruled out the alternative explanation for a decrease in re-opening response due to exhaustion of energy or other resources by showing that plants opened their leaves when they were shaken at a different rate. Another groundbreaking study on garden peas focused on Pavlovian learning. The garden pea seedlings were placed at the bottom of a Y-shaped maze, the pea plants were conditioned to associate light (i.e., unconditioned stimulus) with the air (i.e., conditioned stimulus) from a fan. The results have indicated that plants can learn that after wind, the light will appear (Gagliano et al., 2016).

Some plants have also the ability to count. For example, a carnivorous plant, the Venus flytrap, can count how often it has been touched by a potential prey visiting its trap, to avoid false alarms or determine whether the caught animal is big enough and nutritious or not. Thanks to this counting ability, the Venus flytrap can balance the cost and benefit of its energy-consuming snap buckling movement (Böhm et al., 2016).

Plants' behaviour nested in ecological psychology, enactivism & extended cognition

Recent studies have shown that plants program their movements purposefully and in ways that are flexible and anticipatory (Guerra et al., 2019; Raja et al., 2020). Climbing plants, for example, can sense the properties of support structures and "make decisions" based on this data. Darwin (1875) demonstrated that climbing plants can distinguish between suitable and unsuitable supports based on their smoothness or thickness, implying that climbing plants can act purposefully. He illustrated this concept by exposing the crossvine, *Bignonia capreolata*, to an unclimbable smooth glass rod support; initially, the plant displayed an oscillatory movement, but then began to exhibit an irregular unwinding movement, as if it intended to find a suitable support (Gianoli, 2015). In light of Darwin's findings, recent research focusing on the kinematic features of pea plant movements while approaching and grasping a thick or thin support reported that pea plants (*Pisum sativum* L.) can program their movements in advance and can move their tendrils depending on the thickness of the support (Guerra et al., 2019; 2021). These findings, by implying motor intentions in plants, contradict the scientific consensus that plant movement is solely driven by cause-effect mechanisms and hard-wired inflexible reflexes. Finally, they have signaled a shift in the way plant behavior is typically regarded (Wang et al., 2021).

So, how do neuron-less creatures, such as plants, have all the cognitive abilities that have been attributed to humans and other animals by traditional cognitive sciences, which view brain processes as the only basis of the cognitive process? On the contrary to the traditional cognitive view, several new scientific approaches such as extended and enactivist cognition present more open-ended explanations of cognition and intelligence that do not exclude neuron-less organisms, simply by acknowledging the importance of the extracranial processes related to the body and the environment of the cognitive agents.

For example, ecological psychology considers cognition as affordance-based, rather than mental representation-based. James Gibson (1977) coined the term "*affordance*" which refers to the features of the environment perceived by the cognizing agent directly, rather than representatively, and allows the cognizing agent to act upon the things in its environment in a certain way, based on the organism's bodily structure, intentions, and capabilities. Affordance theory is similar to embodied cognition, both of the approaches defend that the anatomy of a cognizing subject affects its perception of the external world, certain body types will entail certain types of cognitions (Carvalho & Rolla, 2020).

Affordances are always relational between the cognizing subject and the possibilities offered by some entity or complex entities in its environment, these possibilities can be either harmful or beneficial. The entities can be anything, a physical part of the environment, another organism sharing information, or even an abstract concept that offers some opportunities to the cognizing agent (Newen, 2018). For example, a wooden stick can be a playable object for dogs, a flammable object for a person having a barbecue, or a climbable support for climbing plants. The environment invites organisms to act and behave by continuous offers of possible opportunities that give rise to making decisions and acting. Put it differently, the relationship between cognitive agents and their environment is bidirectional. So according to ecological psychology, the cognitive processes of the organisms cannot be fully understood without taking into consideration their environment, in this sense organism and its environment are an inseparable unit that forms its cognition.

For example, plants are sensitive to sounds in their surroundings and can produce their own clicking sounds as well as to detect acoustic signals from other plants. They could send out acoustic clicks and 'listen' for the echoes, allowing them to gather information about their surroundings and the neighborhood within them. Twiners and tendril climbers, for example, could use echolocation as a form of self-communication to navigate 3D space, track moving

objects, detect stationary obstacles, and, most importantly, find appropriate host trees or other scaffolds to climb up to or attach to. In the latter case, supports of various materials and structural qualities are expected to reflect or absorb an incoming acoustic wave in different ways, defining the degree and clarity of echoes bouncing back and the perceived affordance a given structure offers to the plant. Naturally, this would enable the plant to make the best behavioral and/or physiological decision possible in the given circumstances (Gagliano, 2015). Similar to ecological psychology, extended cognition recognizes that cognitive processes can extend to the affordances provided by the environment. A cognitive agent might use the opportunities afforded by its environment to solve a problem or to memorize information. A smartphone or even a piece of paper can be an example of a cognitive extension to the environment. In this case, the cognitive processes take place both within the organism's body and in its surroundings. In other words, some piece of cognition of cognitive agents is offloaded to their environment, expanded beyond their bodies (Clark & Chalmers, 1998; Parise et al., 2020). The extended cognition hypothesis has been exemplified by Japyassú and Laland (2017) with their study on the behavioral complexity of the spiders and the relationship with their webs. Since the spiders' web acts as a filter of the information that reaches the spider, the more vibrated web areas will attract the spiders' attention more, which results in the maximization of the chances of foraging. Studies have shown that with manipulation of the tension on the web, spiders' attention can be drawn even in formerly unfruitful areas of the web. These findings demonstrated that manipulation of the web as well as the spider's central nervous system alters the cognitive process. The findings also show that extended cognition is not exclusive to humans as other organisms, particularly those with niche construction abilities, can extend their cognition to their environment as well.

In a recent study, primarily two ways in which the plants may extend their cognition to their environment have been proposed: by favors of their root exudates and by favors of the

microorganisms that live associated with the roots (Parise et al., 2020). The root exudates are fluids secreted by the root that maintain the plants' perception of their underground environment, the distribution and aggregation of root exudates assist plants to prevent growth towards the inanimate objects, process the features of those objects. The root exudates have also an important role in interactions between plant roots and other plants, microbes, and nematodes present in the rhizosphere. It has been empirically established that removing exudates from the substrate hinders the plant from perceiving obstacles and even causes it to grow toward them as if they were not there at all (Falik et al., 2005). By actively modifying the rhizosphere and the influence zone of the roots, the collaboration between a plant and its exudates constructs a cognitive system.

Similar to the communication between gut bacteria and the central nervous system that influences animal behavior, plant cognition is extended to the environment via microorganisms such as bacterial communities that live along with the roots (Castiello, 2021). The abundance and diversity of the microbiotic community in the rhizosphere are actively manipulated by the plants for their own benefit via the many different substances exuded by the roots. In a study conducted by Huang et al. (2019), it has been demonstrated that *Arabidopsis* has specific pathways for synthesizing triterpenes that regulate *Arabidopsis*-specific bacterial community. The composition of this specific microbial community can act as a kind of memory bank beyond the plants' body and moreover, this information can be handed down to the next generations that grow in the same soil. Another study on *Arabidopsis* examined the role of root exudates in the establishment of soil memory followed by infection. The plants have altered the substrate microbiota by secreting several different substances that modulated the bacterial community. The results indicated that thanks to the soil memory passed down from previous generations, the next generations can resist the pathogen attack significantly better (Yuan et al., 2018).

The enactivism is another alternative approach to cognition that challenges standard cognitivist understanding of cognition as the processing of representations, by providing a framework for the theory of cognition in single-cell organisms, plants, animals. According to the enactivist approach, the cognitive activities are constituted in the dynamic interaction between the cognitive agents and their environment, by the organism's exploration and manipulation of what its environment affords. From the enactivist perspective, the cognitive system is not merely a passive being reacting to external impediments, but an open, autonomous system that explores its environment to meet needs and goals through controlling sensorimotor coupling in a variety of circumstances. Pea plants, for example, are known to be extremely adaptable climbing plants and not just react to the surroundings in a single, fixed way. They move with the intention of finding support, and when they detect suitable support, they start to approach the support and climb around it. The three-dimensional (3D) kinematic analysis of pea plants has provided the first empirical evidence on the plant not only perceives the support but also considers the structure of the support they intend to grasp and plan their movement accordingly ahead of time (Guerra et al., 2019).

From a general point of view, all these approaches meet in the middle, they agree that cognition cannot be limited to the brain and goes beyond the body, overflowing to the environment. Cognitive agents are actively engaged with their surroundings and cognitive processes are dynamic interactions between the cognitive agents and their surroundings. All these approaches to cognition pave the way for studies on the cognition of neuron-less organisms simply by acknowledging the importance of extracranial processes and the environment.

1.2. Plants on the Move

Plants are frequently thought of as immobile organisms, but they are not. They exhibit both endogenous and exogenous movements. Endogenous movements refer to autonomous motoric behavior that is not related to any external stimuli, it is a manifestation of plants' internal states. Exogenous movements are the reactions to environmental factors (e.g., light, gravity, temperature, water, touch, and chemical substances). Thanks to their own subjective sense of internal and external awareness, plants can exhibit a wide range of movements in line with their needs. However, we know that plants do not have muscles, so how come they can display a diverse range of movements? Many scientists, such as Burdon Sanderson (1882), Sir Jagdish Chandra Bose (Tandon, 2019), and Charles Darwin (1897), devoted a large part of their lives to understanding what kinds of mechanisms drive plant movements. In the following chapter, I shall introduce known mechanisms driving plant movements (e.g., turgor pressure, osmosis, snap-buckling) as well as different types of movements in plants (e.g., circumnutation, tropic, and nastic movements).

1.2.1. Mechanisms Underlying Plant Movements

Plants can display various movements, while most of them are slower and cannot be easily perceivable such as the movement of the shoots towards the sun (i.e., phototropic movements), some plant species can move as rapidly as animals. For example, most of the carnivorous plants show rapid movements to catch preys, other plant species exhibit rapid movements for reproduction via the explosive fruits, pollen, and spore catapults, or as the *Mimosa pudica* that folds its leaves rapidly when mechanically stimulated to defend itself against predators (Forterre et al., 2016; Hagihara & Toyota, 2020; Hayashi et al., 2009). This means that plant motion can be very slow and invisible to the naked eye, or it can be as fast as the blinking of an eye. Despite their ability to perform a wide range of movements, plants lack a central nervous system or muscles to produce movements as animals do. Furthermore, the plant tissues are neither soft

nor can they be easily deformed, in contrast to the animal tissues (Dumais & Forterre, 2011; Hill & Findlay, 1981). Despite all of this, in their evolutionary journey, plants have found different ways to generate various movements.

The mechanisms underlying plant movements can be classified into hydraulic (i.e., fluid-driven) movements and mechanical instabilities. The hydraulic plant movements rely on water transport across cells and tissues, so these movements' speed can only go high as fast as the water can move across the plant body (Skotheim & Mahadevan, 2005). The fluid-driven plant movements consist of irreversible movements and reversible movements. During the growth process of immature plant cells, their cell walls irreversibly extend, and cell volumes are increased due to the water influx; since the growth cannot be reversed, the movements of these immature plant cells are classified as irreversible water-driven movements (Lockhart, 1965). Reversible movements occur in the mature cells. They are caused by swelling and shrinking of the cell volume due to the water transport between the cell and its environment, these movements are limited by the elasticity of the cell wall. Water movements might occur according to the osmotic and humidity gradients (Dumais & Forterre, 2011; Reyssat & Mahadevan, 2009). The most important reversible fluid-driven plant movements are the opening and closing of stomata (i.e., microscopic pores on the surface of aerial plant organs) since they control the photosynthetic gas change between the plant shoot and the atmosphere and the leaf transpiration. A pair of curved, tubular guard cells control the stomatal formation by using a driving force known as turgor pressure. Turgor pressure refers to the hydrostatic pressure generated by the osmotically driven inflow of water in response to the cellular concentration of ions, sugars, and other solutes, into cells across a selectively permeable membrane against the cell wall of a plant, fungi, or bacteria cells. Turgor pressure, in addition to the stomatal formation, plays numerous other important roles in the lives of plants, including cell enlargement, growth and shape maintenance, signaling, and seed dispersal. Also, the

dynamic variations in turgor pressure form the basis of plants' movements (Beauzamy et al., 2014; Harrison et al., 2019; Kollist et al., 2014; Sussmilch et al., 2018).

Although it is extraordinary what plants can do with osmosis and turgor pressure, some plants need more energy to be able to break the limits of fluid-driven movements to move rapidly, especially as the size of the moving tissue gets bigger. So even though the turgor pressure and water potential still matter for the fastest species of the plant kingdom, the maximum speed of water is not rapid enough to explain their speed (Skotheim & Mahadevan, 2005; Dumais & Forterre, 2011). Some plants use mechanical instabilities to go beyond the hydraulic limitation to move much faster, such as the trapping mechanisms of Venus flytrap and bladderwort (Hill & Findlay, 1981), explosive seed dispersal of dwarf mistletoe, which is a parasitic plant that infects Pinaceae and Cupressaceae (deBruyn et al., 2015). Another example is the leptosporangiate ferns' catapult mechanism, triggered by cavitation (i.e., a gas bubble formed by the rupture of water) and is used by their specialized cells, the annulus, which is located on the outer side of the sporangium. The mechanism is named after its resemblance to medieval catapult weapons (Noblin et al., 2012; Ritman & Milburn, 1990). The essence of plants' strategy for exhibiting fast movements is simple: instead of immediately using the energy induced by water movement, they save it for their big moment. In other words, they do not rely solely on the speed of the water, but rather gradually store elastic energy in their cell walls, which they then release when an energy barrier is crossed.

Hydraulic mechanisms in plants

The power of the water lies in its tendency to move freely from one area to another in a particular environment or system which is called water potential. The water potential is of vital importance to the plants because they need to transport the water and minerals from their roots to the shoots against gravity to photosynthesize. Water molecules move via a special version of diffusion called osmosis, the net movement of water molecules through a semi-permeable

membrane from the hypotonic (i.e., less soluted) solution to the hypertonic (i.e., high soluted) solution. Water movements can be indirectly affected by the change of the differential osmotic potential across the cell boundary. Plants by their very nature, are made of pressure bombs due to the change of water content in the plant cell. Plant cells change the volume of the cytosolic and vacuolar concentration of osmotically active molecules (i.e., ions, sugars, amino acids) for osmoregulation which is the osmotic adjustment of the cell to control its water content (Beauzamy et al., 2014). The spectrum of water pressures that plants can sustain is spectacular, the highest pressure they reach can keep up with the man-made hydraulic machines. This large range in pressure values is resulting from the exchange of water between the plant cell and its environment via osmosis or evaporation (Forterre, 2013). Plants exhibit turgor pressure when their cells are turgid due to the internal hydrostatic pressure against the cell wall. Plant cells alternate between turgor and the flaccid state as the amount of water in the cell changes, and these alterations provide the power to change cell volume and form the basis of many plant movements (Dumais & Forterre, 2011; Forterre, 2013). For example, two guard cells must swell and become turgid as a result of the water influx caused by the K^+ influx to form the stoma. When K^+ leaves the cells, the guard cells become flaccid and close the stoma, causing water efflux.

To understand how plants can manipulate water to exhibit movements, we need to take a much closer look at them, the secrets hidden in their cell structures. Plants have some specific cell structures that other eukaryotes do not have such as the cell wall and vacuole, and these structures enable them to alter the water volume inside the cells (Chamovitz, 2013). The vacuole is a vesicle that can contain water, organic or inorganic molecules. While vacuole acts as a warehouse, inside the plant cells, water moves through aquaporins (i.e., water channels embedded in the plasma membrane) and plasmodesmata (i.e., intracellular cytoplasmic connections) due to the gradient in water potential. Thanks to the stiff structure of the cell wall,

plant cells can sustain a large pressure so when a high amount of water goes into the cell, first into the vacuole, the plant cells do not burst (i.e., cell lysis) contrary to animal cells (Dumais & Forterre, 2011). In fact, plants need turgor pressure during their growth which is very important for their structural rigidity and integrity (Beauzamy et al., 2014), stomates formation (Woolfenden et al., 2018), nyctinastic movements (Bhatla & Lal, 2018). While many leguminous species can fold their leaflets at sunset and unfold them again at sunrise which is a relatively slow, circadian movement named nyctinastic movement (i.e., sleep movement), in addition to this movement, *Mimosa pudica*, and its close relatives have evolved to rapidly fold inward and droop to protect itself from potential herbivores. This seismonastic movement is hundreds of times faster than the nyctinastic movement and can occur within seconds of being stimulated by wind, touch, vibration, or heat. It can also be stimulated electrically (Mano & Hasebe, 2021; Volkov et al., 2010). The seismonastic movement is the fastest possible water-driven plant movement. However, there are still debates about whether *Mimosa pudica* uses only a hydraulic mechanism or yet-to-be-discovered mechanisms. *Mimosa pudica* gives rise to these questions about its mechanism because its speed is very close to the upper limit that the water-driven plant movements can reach, considering the size of the pulvini (Dumais & Forterre, 2011; Forterre, 2013; Mano & Hasebe, 2021). Pulvini are joint-like thickened motor organs that are responsible for both the nyctinastic and seismonastic movements. Pulvini are located at the base of each leaflet, rachilla, and petiole, have extensor (upper side) and flexor (lower side) halves (Hagihara & Toyota, 2020). When there is no stimulation, both halves are turgid, pushing each other, and this makes leaflets stay open. When *Mimosa pudica* is stimulated the turgor pressure in pulvini cells decreases, and the plant's mechanosensory response varies in strength and speed according to the degree of stimulation. After the plant is stimulated, an action potential occurs which results in translocation of ions (i.e., K^+ , Cl^-) from the extensor side to the flexor side that leads to the water exchange between the extensor and

flexor sides of the pulvini. When the stimulation is stronger these electrical, chemical, hydraulic signals carry the long-range information even in unstimulated leaves, the demonstration of a strong stimulation involves also drooping movement (Baluška et al., 2006).

Beyond hydraulicity: Mechanical instability

Even though many plants have the ability of sensation of touch, not many can display a visible immediate response as *Mimosa pudica* and what is more, many carnivorous plants such as the Venus flytrap and Bladderwort can move fast enough to catch insects. Although the whole mechanism of *Mimosa pudica*'s rapid seismonastic movement is still undetermined, the main power is still the changes in the turgor pressure of plant cells. However, the snap buckling movement of the Venus flytrap is 10 times faster than the rapid seismonastic movement of the *Mimosa pudica*. Given the size of its trap, the Venus flytrap cannot move so quickly using only water transport. Indeed, it exceeds the limit of the poroelastic timescale for water diffusion. The poroelastic time refers to the time required for the pressure to equilibrate by diffusion through fluid transport in soft, wet tissues (Forterre, 2013; Skotheim & Mahadevan, 2005; Volkov et al., 2010). Based on this poroelastic time, Skotheim and Mahadevan (2005) classified all naturally occurring movements into two types: water-driven movements (swelling/growth) and rapid movements based on elastic/mechanical instabilities (buckling, fracture). Water-driven movements are slow and limited by the maximum speed of water transport in the plant body; on the other hand, rapid movements based on mechanical instabilities can overcome this poroelastic boundary. There are two broad types of mechanical instability mechanisms that are used by various plant species: snap buckling and explosive fracture, both mechanisms are underlined by the rapid geometrical changes. The explosive fractures damage the tissue so those movements are single-time events, whereas snap buckling movements can be repeated because the tissue is not damaged (Dumais & Forterre, 2011; Forterre, 2013).

The basic idea behind these mechanisms is to use an energy barrier to accumulate elastic

potential energy and rapidly convert it to kinetic energy once the threshold is crossed. The energy barrier is originated from the geometrical structures of plants. Furthermore, because some plants have a relatively smaller size and a more ready-to-move structure, they do not require such mechanisms to induce rapid movement; they can move quickly simply by transporting water across their body (e.g., waterwheel plant). For these reasons, understanding the geometrical structures of plants is critical in order to fully comprehend the mechanisms underlying their movements. The importance of understanding plants' geometrical structures comes to the light with the comparison of movements of the Venus flytrap and its sister species the aquatic waterwheel plant, *Aldrovanda vesiculosa*, which are both carnivorous plants that can display rapid movements for nutritional purposes. While *Aldrovanda* catch preys only with hydraulic mechanism, Venus flytrap needs to cross the hydraulic limit by using the mechanical instability mechanism. The leaves are already curved inward in *Aldrovanda* at the resting state so when it's stimulated by a potential prey, its leaf does not produce a snap, also the size of the *Aldrovanda* leaves are ten times smaller than Venus flytrap which means the movement can be actuated 100 times faster by simply using only the water-driven mechanism. On the contrary, the Venus flytrap shuts in a few tenths of a second, which is too fast to be actuated by solely water transport across its leaves, so it needs a mechanical instability mechanism to be able to faster than its prey, both because of its larger size and its trap lobes close by inverting its curvature (Dumais & Forterre, 2011; Forterre et al., 2005; Poppinga et al., 2013; Skotheim & Mahadevan, 2005).

Venus flytrap has a lower leaf (i.e., petiole) for photosynthesis and an upper leaf (i.e., leaf lamina) which acts as a trap to catch prey. The trap has two lobes connected by a midrib, and at the center of each lobe, there are three or more trigger hairs that have the ability of mechanosensation. Trigger hairs are as picky as they are sensitive, this is because the Venus flytrap needs to catch an ideal size of the prey, it would be a waste of energy to close the trap

for a too small prey. Within 20 seconds at least two hair needs to be touched, even when those hairs are on different lobes, an action potential is triggered to close the trap (Burdon-Sanderson, 1873; Volkov et al., 2007). When a prey land on Venus flytrap's leaves, mechanically sensitive ion channels generate receptor potentials which eventually cross a threshold and induce an action potential that then spreads all over to the leaf lobe. Venus flytrap's signaling network is based in part on mechanisms similar to those of animals, with anion channels with voltage-dependent properties similar to neuronal channels. The outer edges of the trap lobes then start to inwardly bend, but the double curvature architecture of the Venus flytrap makes a mechanical boundary (i.e., threshold energy) that needs to be overcome in order to display snap-buckling movements. During the slow initial active bending, the lobes store elastic energy that is suddenly released if the threshold energy is exceeded and the lobes change their overall curvature from concave to convex the trap abruptly close then, on the edges of the leaves, long small spines called cilia are interlocked and form a prison-like structure to keep prey inside the trap. The trap is then not completely closed, and the mechanical stimuli exerted by the caught prey trying to escape require a slow and complete closure, thus allowing the so-called "external stomach formation" of the closed lobes for the digestion of prey (Dumais & Forterre, 2011; Poppinga et al., 2013; Forterre, 2013).

1.2.2. Types of Plant Movements

The environment is in constant change, and like every other organism, plants need to sense, respond to these changes. So, even though plants cannot change their location, they can reorient their organs to gather and integrate various information from their environment to optimize their growth, survival, and reproduction. A simple example of this is that any plant grows in the direction of the light, or the roots are elongated towards the direction of water and food or growing away from toxic chemicals. Another example is the petal motions seen in *Tulipa* (Liliaceae) and *Crocus* (Iridaceae) flowers that open and close in response to temperature

differences. Flowers open in response to a small increase in ambient temperature and close in response to lowering the temperature (Koller & Van Volkenburgh, 2011).

As shown in these examples, plants exhibit movements in response to external stimuli such as light, gravity, temperature, or touch. Some plant movements are directional, called tropic movements, while others are non-directional, called nastic movements. Among all the movements performed by plants, circumnutation is one of the most researched nastic movements, which refers to oscillatory movement around a central axis (Srivastava, 2002). Circumnutation is ubiquitous among all plants but very exaggerated in climbing plants. In the following part, I shall define and exemplify tropic and nastic movements. In addition, I will explain the circumnutation movement with some examples, specifically the circumnutation movement of pea plants.

Tropic movements

Tropic movements are caused by the differential, asymmetrical growth between the opposite sides of the plants' organ and strongly depend on the direction of the stimulus they perceive (Barlow et al., 1989). Tropic movements are present on all plants' organs with radial symmetry such as root and stem, and relatively slower compared to nastic movements. The plant organs may bend towards the stimulus (i.e., positive tropic movement) or away from the stimulus (i.e., negative tropic movements). The main types of stimuli that induce tropical growth movements are gravity and light. Let's say you try to grow a plant horizontally; you'll see that the shoot of the plant does not grow horizontally but turns upward (i.e., away from gravitational force and towards the light source) and similarly roots will grow towards the gravitational force and away from the light.

Plants have evolved to get most of their energy from sunlight, through photosynthesis, so light is vital for them, and in a roundabout way, for all life on Earth. Light is one of the most versatile environmental signals, varying in four parameters: quality (wavelength), quantity (fluence, i.e.,

photons m^{-2}), direction, and duration (photoperiod). Phototropism allows plants to forage for light more efficiently. The phototropic movements are bending towards or away from a blue-light stimulation which activates the phototropins (i.e., blue light receptor). Darwin (1897) discovered that the tips of plant shoots were sensitive to light. This observation contributed to the discovery of the first plant hormone, auxin (i.e., a growth hormone that tells plant cells to increase their length), which is produced in the shoot tip but moves down the stems to regulate growth and development (Karban, 2015; Went, 1926). Stems display positive phototropism, while roots display negative phototropism due to the uneven distribution of the auxin hormone. Unilateral light causes the accumulation of auxin on the dark side, causing the stem to elongate only on the dark side, so the stem curves toward the light. Auxin appears on the upper side of roots in response to gravitational force, causing roots to grow downward, and on the "downside" of stems and leaves, causing them to grow upward (Bhatla & Lal, 2018; Chamovitz, 2013, Esmon et al., 2005). Additionally, studies on *Arabidopsis thaliana* showed that root phototropism was the trait coupled to fitness, and only under high light conditions (Galen et al., 2004). In a subsequent study, Galen and colleagues (2007) found that negative root phototropism (i.e., bending away from directional blue light) improves the ability of the plant to access water, which under high light conditions is more abundant deeper in the soil due to increased evaporation near the surface (Holland et al., 2009).

Gravitropism is the slow reorientation of plant growth in response to gravity, and a key determinant of the form and posture of land plants (Bastien et al., 2012). In both shoots and roots, gravity is sensed by statocyte cells located in the columella of the root tip and the endodermis of the shoot. These cells contain amyloplasts, starch-storing plastids that sediment in the direction of gravity when the plant is tilted, triggering differential growth. In experiments using a centrifugal device, Chauvet and colleagues (2016) demonstrated that the shoot bending response is independent of gravity intensity; additionally, there is no angular threshold of

response when plants are subjected to sustained inclination. These findings imply that plants respond to organ and statocyte inclination directly rather than by measuring the force exerted by statoliths upon cellular components. Within minutes, gravity stimulates lateral redistribution of auxin towards the lower side of the organ in both roots and shoots, resulting in directional growth. Roots exhibit positive gravitropic movements, while shoots exhibit negative gravitropic movements (Žádníková et al., 2015). Notably, a recent study has revealed that auxin redistribution is also responsible for the gravitropic responses of woody stems, which cannot undergo elongation growth and instead rely upon asymmetric radial growth to grow away from gravity (Gerttula et al., 2015; Harmer & Brooks, 2018).

Plants had to give up unlimited access to water and deal with the compressive effects of gravity when they colonized the land (Niklas, 1997). However, they have evolved to be able to sense differences in water potential in the local environment and regulate their growth accordingly, a process known as hydrotropism, which begins in the root cap with moisture gradient sensing. The ability of the root cap to detect moisture gradients appears to produce a dominant signal that lessens the gravity response (Eapen et al., 2005). One of the first modern papers to demonstrate the existence of hydrotropism in roots used a pea mutant lacking both gravitropism and phototropism in roots (Jaffe et al., 1985). According to these authors, the early-perception phase of hydrotropism occurs in the root cap because roots grow normally but do not respond to moisture gradients once the cap is removed. Recently, Takahashi and his colleagues (2003) have proposed that reduced responsiveness to gravity in hydrotropically responsive roots is, at least in part, caused by the simultaneous degradation of amyloplasts in columella cells of *Arabidopsis* and radish (Kiss, 2007).

Thigmotropism is the response of a plant organ to mechanical stimulation. One can easily imagine that the gravitropic and thigmotropic responses of roots might be intimately related. In fact, according to a recent study done by Massa and Gilroy (2003), proper root tip growth

requires the integration of both a gravity response and a touch response (Esmon et al., 2005). Root thigmotropism, like gravitropism, is an important process that allows plants to deal with impenetrable obstacles in their environment, such as rocks in the soil, by allowing roots to bend quickly away from the obstacles and find their edge (Braam, 2004). The combination of root obstacle avoidance and root gravitropism allows roots to grow downward into deep soil in search of water and nutrients (Zhang et al., 2019). Thigmotropism is also important in the coiling movement of climbing plant tendrils in the direction of an object that they touch. Climbing plants circumnutate until they find an appropriate support, at which point they begin to bend toward the support (Scorza & Dornelas, 2011). Touch stimulation causes a rapid onset of tip coiling, often within seconds, allowing for a secure attachment to an object. However, the application of water droplets causes no coiling response; thus, tendrils avoid nonproductive coiling in rainstorms. Furthermore, coiling that occurs in response to transient stimulation is frequently reversed by uncoiling (Braam, 2004; Jaffe & Galston, 1968).

Nastic movements

Nastic movements occur in response to external stimuli, but unlike tropic movements, they are not dependent on the location of the stimulus because the direction of the movements is predetermined by the plant such as nyctinastic movements (i.e., in response to the onset of darkness) or epinastic (i.e., downward growth) or hyponastic (i.e., upward growth) movements. The nastic movements can be caused by either unidirectional or diffused stimuli, which affect their quality. A strong vibration, for example, will induce a faster and more distributed seismonastic response in *Mimosa pudica*. Nastic movements are driven by growth or turgor changes. Internally directed autonomic nastic movements include those displayed by developing buds as they swell and open. Induced nastic movements are externally directed for instance the reaction of the leaves and flowers in responses to changing light (i.e., photonastic movement) and temperature (i.e., thermonastic movement). While photonastic movements are

synchronized by the dark to light transition, the skotonastic movements are synchronized by the light to dark transition. Chemonastic movements such as opening and closing of guard cells form stomata in response to the carbon dioxide. Nastic movements are more rapid, specialized than tropic movements. Indeed, some plant movements are so fast that they can even be detectable by the human eye, for example, the thigmonastic movements exhibited in response to touch by some carnivorous plants (e.g., the Venus flytrap, bladderwort, waterwheel plant) and the seismonastic movement (i.e., a special version of the thigmonastic movements induced by vibration) displayed by *Mimosa pudica* (Guo et al., 2015).

In a study on Loasoideae, a subfamily of Loasaceae, it was shown that they exhibit thigmonastic stamen (i.e., the male reproductive part of a flower) movements to control their pollen release. It has been demonstrated that both abiotic (e.g., light and temperature) and biotic stimuli (e.g., pollinator availability and visitation frequency) influence the stamen movement (Henning & Weigend, 2013). According to another study, flowers of *Nasa poissoniana* are able to perceive, record, and memorize these visitation rates and adjust their flower behavior based on previous experience when subjected to constant, regular visitation rates. Thigmonastic stamen movement is critical for these plants because it allows them to optimize the balance between pollen provision and pollen protection (viability loss), make the best use of the pollinator, and increase the likelihood of successful outbreeding (Mittelbach et al., 2019).

As plant organs (e.g., leaves, petals, and sepals) develop, they may exhibit unequal growth expansion on the two sides, resulting in hyponastic or epinastic growth movement. For example, the leaves of tomato plants growing in soil flooded with water exhibit epinastic movement of leaves. These are under endogenous control, and though the growth is irreversible, the bending of the organ is reversible (Bhatla & Lal, 2018). It has now been proven that the differential distribution of auxin and ethylene controls hyponastic and epinastic movements (Hayes, 1981; Tieman et al., 2000). The lowermost leaves change from hyponastic to epinastic growth as the

growth progresses. Poppy flowers also exhibit a shift between hyponasty and epinasty at various stages of development. When poppy flower buds are immature, they exhibit epinastic growth. When the plant is mature enough for pollination, the flower begins to open, and growth is reversed, resulting in hyponastic movement, and straightening of the flower. Interestingly, the poppy flower responds to rain by bending the peduncle downward and losing petal turgor, causing the flower to close and thus prevent pollen loss (Bhatla & Lal, 2018).

Leguminous plants, for example, exhibit nyctinastic movements in which they open their leaves during the daytime and fold them at night to "sleep." For centuries, scientists have been fascinated by this movement, with the earliest records dating back to Alexander the Great's reign (Schildknecht, 1983). The nyctinastic movement is caused by the asymmetric volume change of cells in the pulvini between the adaxial (upper) and abaxial (lower) sides of the leaflet. This leaf movement shows circadian rhythmic patterns and is regulated by a biological clock with a cycle of about 24 hours (Baluška & Vivanco, 2009). From observations of nyctinasty, Bünning (1936) proposed the first hypothesis on the mechanism of the circadian clock. Inspired by these achievements, Satter & Galston (1973) compared nyctinasty to the "Rosetta Stone" for the circadian clock, suggesting that a molecular understanding of nyctinasty would lead to a similarly detailed understanding of the circadian clock (Ueda et al., 2019).

Plants are constantly subjected to temperature fluctuations and must respond appropriately to a variety of cues ranging from freezing to heat stress (Penfield, 2008; Van Zanten et al., 2014; Casal & Balasubramanian, 2019; Ding et al., 2020). For example, the thermonasty of the rosette (i.e., the circular arrangement of leaves or leaf-like structures) leaves is considered primarily a heat stress avoidance strategy, induced to avoid overheating by direct solar heat flux on the leaves. Furthermore, thermonasty improves leaf cooling capacity by increasing evaporation (Crawford et al., 2012; Bridge et al., 2013). Indeed, the clever use of infrared thermography and *Arabidopsis* mutants in Phytochrome Interacting Factor 4 (*pif4-2*), which is disrupted in

temperature responsiveness, revealed that thermonastic leaves are cooler in warm environments compared to their horizontally oriented counterparts (Park et al., 2019; van Zanten et al., 2021).

Circumnutation

Circumnutation is seen in all plants as well as in fungi (*Basidiomycetes*), algae (*Spirogyra*), bryophytes (*Ceratodon purpureus*). Darwin (1897) studied the movements of hundreds of plant species, and he gathered this data in his book called *The Power of Plant Movements*. Darwin demonstrated that the growing tips of the organs of all plants exhibit a circular motion by sequentially bending and twisting in different directions, and he coined this movement as *circumnutation*. Charles Darwin and his son Francis Darwin suggested the internal oscillator model, which is related to the biological clock mechanism, circumnutation movements are depending on the internal state of the plants, mediated by an internal oscillator. So circumnutatory movements are considered endogenous movements. Darwin indicated that every growing part of every plant is continually circumnutating, even though generally on a small scale. Moreover, Darwin (1897) demonstrated that the other movements such as epinasty, hyponasty, the nyctitropic movements (i.e., sleep movements of leaves and cotyledons), light-related, and gravitation-related, or alternation of all these factors are just modified versions of circumnutatory movements. If we observe a rotation of the oscillatory patterns of a circumnutating stem, we will see after revolving towards to north, it will bend gradually easterly, and when it focuses to the east it will bend to the south, then to the west, and back again to the north. During this slow dance of the plants, if its movement is regular the apex would describe a circle, or since the stem is always growing upwards, its shape will be a circular spiral. However, generally, these oscillatory movements are not quite regular so most of the time plant organs describe irregular elliptical or oval shapes (Darwin, 1897). Thanks to these movements plants can explore their surroundings systematically to compensate for their sessile nature. So, while their oscillatory movements, they do not return along the same line rather

change their rotation to explore different parts of their environment. The period, shape, the amplitude of the circumnutation movements can change across plant species, or the different organs of the same plant, and between the different developmental stages of growth in the same plant (Kitazawa et al. 2005). These oscillatory movements can occur in circular, elliptical, and irregular zigzags, triangle-like shapes, and the direction of movement can be clockwise or counter-clockwise (Stolarz, 2009).

The difference in the growth rates of the opposite sides of the plants causes bending and twisting which results in circumnutating movements. What happens in the cell level of a nutating plant organ is that the turgor pressure on the convex side becomes 10% bigger than on the concave side (Vanden Driessche 2000). Since these movements are related to growth, anything that might affect the growth process of a plant will also affect the circumnutatory movements.

Even though circumnutation movements are ubiquitous among all plants, more apparent and regular in climbing plants that have evolved to find another support to save energy rather than forming self-supporting branches to reach sunlight. While the aim of these circular movements is obvious in climbing plants, we do not know why it's happening on non-climbing plants yet (Mancuso & Shabala, 2007).

Climbing plants use several ways to attach their external supports and according to this, Darwin (1875) categorized climbing plants into five classes (i.e., twining plants, leaf-climbers, tendril-bearers, root-climbers, hook-climbers). In this paper, I shall give an example of circumnutation movements of tendril-bearers pea plants (*Pisum sativum*).

Tendrils are irritable, long, slender organs derived from stems, leaves, or flower peduncles. Tendril-bearers circumnutate more quickly and exhibit irregular ellipsoidal shapes. Even within the same individual, the direction of circumnutation of tendril-bearers varies (Isnard & Silk, 2009). Pea plants' nutational trajectory is elliptical to circular from above, with the long axis in the plane parallel to the axis of leaf placement (Galston et al., 1964). Additionally, Jaffe (1972)

demonstrated that tendrils of pea plants that have not yet been mechanically stimulated are circumnutating rapidly suggesting that plants try to find a support as quickly as possible and have a lower potential to coil. When a tendril detects a potential support, it begins to circumnutate slowly, indicating that the energy spent on the circumnutations is preferentially diverted into contact coiling, increasing the coiling ability. Reduced circumnutations speed during the approach phase may also allow plants to extend the time window in which tendrils determine the contact points with the support, allowing them to correct their trajectories and select more accurate contact points to twin more firmly on the support (Ceccarini et al., 2020a).

1.3. Background to the Present Study

Almost all plant shoots are constantly growing and circumnutating in search of light. Their mass and weight increase as they grow. Plant shoots typically support the weight of their aerial shoots by investing a large proportion of their resources in tissues dedicated exclusively to mechanical resistance to gravity and wind. Climbing plants have evolved alternative strategies for supporting the weight of their upper parts while using far fewer precious resources and reducing the amount of weight that must be supported. Rather than developing their own tissues for mechanical supports, they focus their efforts on developing motor organs (e.g., tendrils) that specialize in locating and utilizing external supports (i.e., a stick or a wooden trunk) with high efficiency so they can save energy. Tendrils are typically long, thin, and extremely flexible, allowing them to perform exaggerated circumnutations to locate external support, grasp it, and climb to gain height (Kim et al., 2016; Vidoni et al., 2015). The organ becomes convex where its cells elongate, and its apex constantly circumnutates to seek an appropriate support from the aerial environment. The distance between the apex and the moving zone of elongation determines the amount of space explored in each cycle, which varies between different plants. The space explored by the hop (*Humulus*) can reach a diameter of 50 cm. It can reach to 150

cm in the porcelain flower (*Hoya carnos*a; Koller & Van Volkenburgh, 2011).

The impact of support accessibility on the diversity of climbing plants has been demonstrated by observations in controlled environments (Puntieri & Pyšek, 1993; Schweitzer & Larson, 1999), but also in forests (Putz, 1984; Stansbury et al., 2007), and open habitats (Gianoli, 2002; González-Teuber & Gianoli, 2007; Price & Wilcut, 2007). Climbing plants that are unable to find a support receive insufficient light, limiting their growth and/or reproduction in comparison to those that have successfully climbed onto a support (Garbin et al., 2012). Finding appropriate support optimizes fitness and gives rise to changes in growth form, biomass allocation, morphology, and physiology (den Dubbelden & Oosterbeek, 1995; Gianoli, 2001; 2003; 2004; Jaffe, 1979; Jaffe & Galston, 1968; Puntieri & Pyšek, 1993; Strong & Ray, 1975). Because climbing plants rely on external supports for a variety of reasons, it is not an exaggeration to say that finding the right support is critical to their survival.

Since Darwin's seminal studies on climbing plants (Darwin, 1875), numerous studies have been conducted to investigate the underlying mechanisms of the support searching and attachment behaviors of climbing plants at the anatomical, biomechanical, physiological, and cellular levels (e.g., Gerbode et al., 2012; Putz & Holbrook, 1992; Bauer et al., 2011; Jaffe, 1979; Jaffe & Galston, 1968; Raja et al., 2020; Stolarz, 2009; Bowling & Vaughn, 2009; Weiler et al., 1993). Darwin (1875) observed that when the *Bignonia capreolata* L. tendrils touch a too thick or too smooth stimulus, first they bend towards it and started to curl around it but since the support is not appropriate, the tendrils change their decision and stop attaching to that support. Herbaceous twining vines behave similarly in that when they come into contact with a very thick trunk, they wind around themselves rather than around the tree trunk. Without mentioning diameter restrictions, Darwin (1875) also stated that wrapping around thick-stemmed trees would not be suitable for annual vines, because they would not be able to reach better light levels until the end of the growing season.

The aforementioned cases lend considerable support to speculative claims that some climbing plants can regulate their circumnutation patterns more or less depending on features of the support targets, for instance, the thickness (i.e., diameter), with respect to what would be expected by chance movement (Gianoli, 2015). Indeed, both theoretical and empirical approaches show that when the diameter of the support exceeds a certain point, twining plants are unable to maintain tensional forces and thus lose attachment to the support (Carrasco-Urra & Gianoli, 2009; Goriely & Neukirch, 2006; Putz, 1984; Putz & Holbrook, 1992).

Laboratory settings further provide evidence to the claims of stimulus-thickness effects with kinematical analysis of the characteristics of the pea plants' movements. The tendrils' average and maximum velocity were found to be higher for thinner stimuli than for thicker stimuli. The tendrils took longer to reach peak velocity and maximum aperture when the stimuli were thinner, as measured by percentages of movement duration. Similarly, the maximum distance between the tendrils was significantly greater for the thinner stimuli (Guerra et al., 2019). These pea plant behaviors are understandable considering that reaching and grasping thicker supports takes more energy than reaching and grasping thinner ones. Plants that grasp a thick support must lengthen their tendrils to efficiently coil the stimulus (Rowe et al., 2006), as well as strengthen the tensional forces to resist gravity (Gianoli, 2015). Because these processes are characterized by a high Adenosine triphosphate (ATP) consumption, coiling around a thicker support requires more energy (Putz and Holbrook, 1992).

Moreover, it has been observed that pea plants are capable of processing the properties of a support and adjusting their velocity and aperture according to the thickness level of support, even before any above-ground organ of the plant (e.g., tendrils, apex) makes mechanical contact with the stimulus (Guerra et al., 2019). This observation raised the question of the role of pea plant roots in sensing the thickness of a support.

Indeed, Guerra and colleagues (2021) conducted a series of experiments to investigate the role

of the root system in the coding of stimulus thickness in pea plants (*Pisum sativum*). In one experiment, the stimulus was placed in the soil, allowing the root system to detect it; in another experiment, the stimulus was lifted to the ground, preventing the root system from detecting it. They compared the tendril circumnutation movements of pea plants under these conditions. The findings confirmed that stimulus thickness affects movement patterns when the stimulus is accessible to the root system, but not when it is not. When the stimulus was lifted to the ground, the plants continued to circumnutate but as if they were blindfolded, they could not localize it and fell down. These findings support the hypothesis that the root system is involved in sensing the presence and the thickness of a stimulus and that the information perceived influences the planning and the execution of the climbing plants' approach-to-grasp movements. They imply, at the very least, that plants are unable to code for the thickness of the stimulus solely based on information provided by the aerial components of the plants (i.e., stem and tendrils).

1.4. My Research

In the light of all the evaluations mentioned above, the present study aims to look further into the root system's contribution to the coding of stimulus thickness by examining the interaction between the root system and the shoot growth (Brouwer, 1963). To test this, the movement of pea plants toward a stimulus that differs in thickness above and below ground was measured (i.e., perturbed conditions). A group of plants was subjected to a stimulus in which the below-ground portion was thin, and the above-ground portion was thick (the 'Thin-Below' condition; see Figure 1a). Another group of plants was exposed to a stimulus in which the below-ground portion was thick, and the above-ground portion was thin ('Thick-Below' condition; see Figure 1b). Movements during perturbed trials were compared to one-thickness stimuli, which could be thin or thick (i.e., control conditions). Specifically, trials for the 'Thin-Below' perturbed condition were compared with trials for the 'Control-Thick' condition (Figure 1a and d), and movements for the 'Thick-Below' condition were compared with movements for the 'Control-

Thin' condition (Figure 1b and c).

We hypothesized that if the root system plays a significant role in sensing stimulus thickness, then the kinematical parameterization would be oriented by the thickness of the below-ground part of the stimulus. We expect differences between the perturbed and control conditions since the thickness of the below part of the stimuli used for the perturbed conditions differs from the thickness of the stimulus used for the control conditions. Keep in mind that previous research with pea plants has revealed that their movements are characterized by specific kinematic signatures for stimuli of different thicknesses (Ceccarini et al., 2020a, b; Guerra et al., 2019; 2021).

On the other hand, if the aerial parts of the plant are involved in the detection of the thickness of the stimulus, no significant difference should be observed between the perturbed and control conditions. Because the upper part of the stimuli used in the perturbed conditions has the same thickness as the stimuli used in the control conditions.

The third hypothesis proposes a crosstalk between the plant's roots and aerial parts, which will inevitably be influenced by the stimulus's inconsistency between below- and above-ground components. If the below-ground information contradicts the movement's end-goal, the above-ground organs (i.e., stem, tendrils...) readjust their movement accordingly.

Chapter 2. Methods

2.1. Subjects

Forty snow peas (*P. sativum* var. *saccharatum* cv Carouby de Maussane) were chosen as the study plants (see Table 1). Healthy-looking pea seeds were selected, potted, and kept at the conditions outlined below. The plants were randomly assigned to the experimental conditions.

Table 1. Sample description

Control-Thick vs Thin-Below		
Stimulus	Control-Thick	Thin-Below
N°	10	10
Distance	12 cm	12 cm
Germination period	6 d (± 0.5 ; Range 4 - 10)	5 d (± 1.22 ; Range 5 - 12)
Age	21 d (± 3.1 ; Range 14 - 26)	16.5 d (± 1.7 ; Range 14 - 19)
Control-Thin vs Thick-Below		
Stimulus	Control-Thin	Thick-Below
N°	10	10
Distance	12 cm	12 cm
Germination period	5.5 d (± 0.6 ; Range 4 - 7)	5 d (± 1.5 ; Range 3 - 10)
Age	14 d (± 2 ; Range 10 - 20)	21.5 d (± 5.6 ; Range 9 - 26)

Note: Germination period and age, which are expressed in days, refer to the median, while median absolute deviation is noted in parentheses.

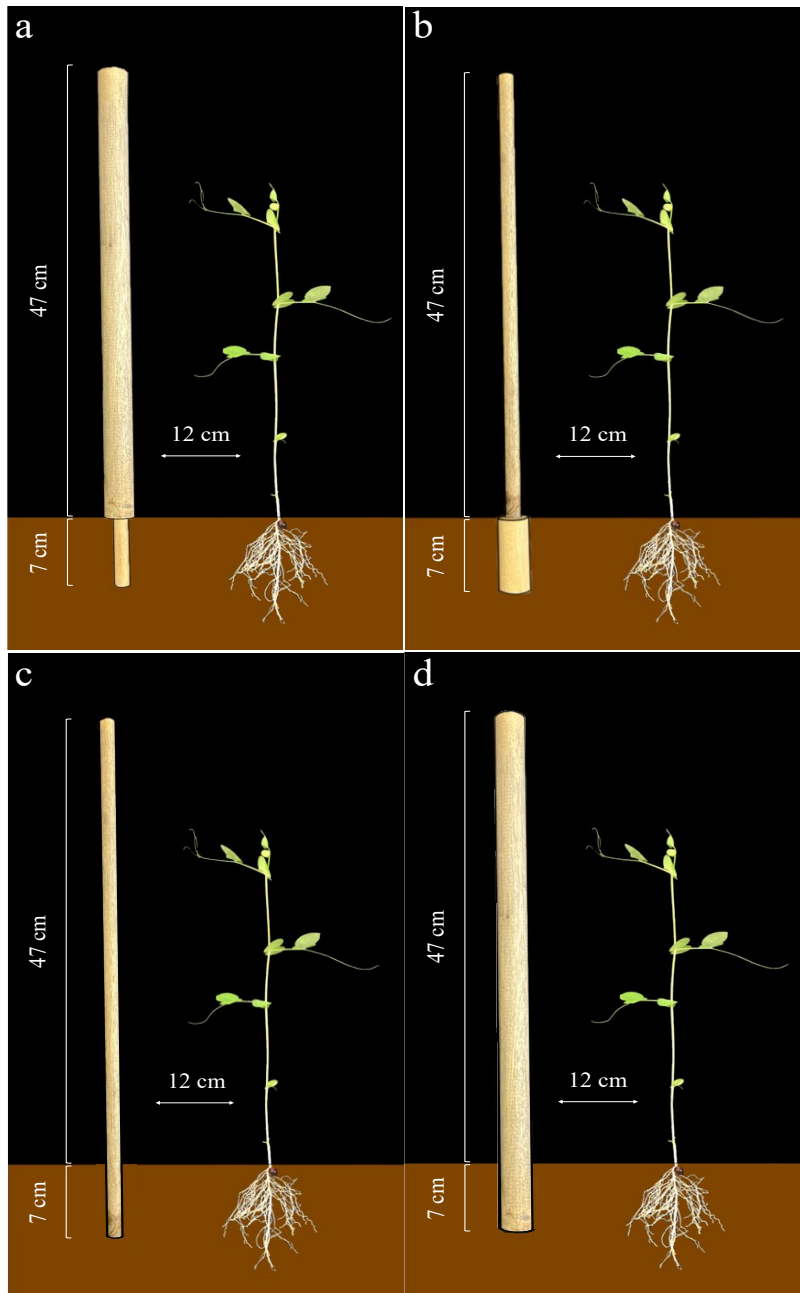


Figure 1: **Schematics for the supports used.** Condition (a), the ‘Thick-Below’ condition (b), the ‘Control-Thin’ condition (c), and the ‘Control-Thick’ condition (d). The support was positioned in front of the first plant’s leaf at a distance of 12 cm.

2.2. Stimuli

The stimuli were 54 cm in height wooden poles (i.e., the below-ground part of the stimulus was 7 cm in height, while the above-ground part of the stimulus was 47 cm in height) positioned at 12 cm from the plant's first unifoliate leaf (Figure 2). The stimulus varied in diameter depending on experimental conditions (see Figure 1). For the (i) 'Thin-below' perturbation (Figure 1a) the below-ground part of the stimulus was 1.2 cm in diameter, whereas the above-ground part of the stimulus was 3 cm in diameter; (ii) 'Thick-below' perturbation (Figure 1b), the below-ground part of the stimulus was 3 cm in diameter, whereas the above-ground of the stimulus was 1.2 cm, (iii) 'Control-Thin' condition (Figure 1c) the diameter was 1.2 cm; (iv) 'Control-Thick' condition (Figure 1d) the diameter was 3 cm in diameter.

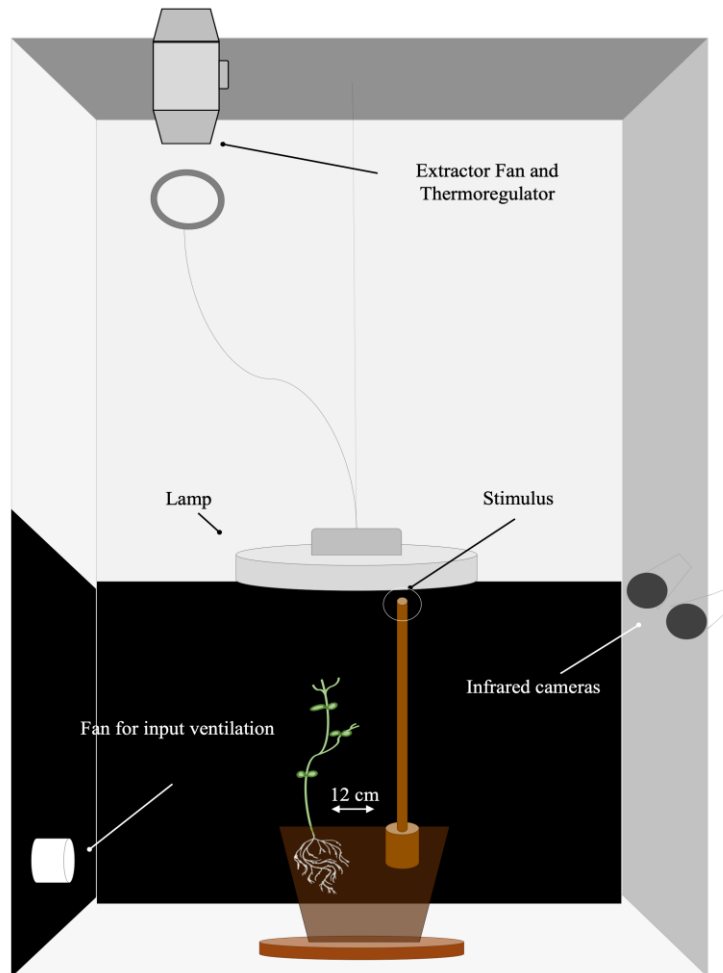


Figure 2: **Graphical Representation of the Experimental Set-Up.** The represented example is for the 'Thick-Below' condition.

2.3. Germination and Growth Conditions

Cylindrical pots (D 20 cm height 20 cm) were filled with silica sand (type 16SS, dimension 0.8/1.2 mm, weight 1.4). At the beginning of each experiment, the pots were watered and fertilized using a half-strength solution culture (Murashige and Skoog Basal Salt Micronutrient Solution; 10x, liquid, plant cell culture tested; SIGMA Life Science). The pots were then watered with tap water as needed three times a week. One seed per pot was placed at 6 cm from the pot's border and sowed at a depth of 2.5 cm. Each pot was then enclosed in a growth chamber (Cultibox SG combi 80x80x160 cm; Figure 2) so that the seeds could germinate and grow in controlled environmental conditions. The chamber air temperature was set at 26 °C; the extractor fan was equipped with a thermo-regulator (TT125; 125 mm-diameter; max 280 MC/H vents) and there was an input-ventilation fan (Blauberg Tubo 100 - 102m³/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 placed so that air movement did not affect the plants' movements. Plants were grown with an 11.25- hour photoperiod (5.45 am to 5 pm) under 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 of the seedling was 350 $\mu\text{mol}_{\text{ph}}/(\text{m}^2\text{s})$ (quantum sensor LI-190R, Lincoln, Nebraska USA). Reflective Mylar® film of chamber walls allowed for better uniformity in light distribution. The experimental methodology was applied to the single plants which were grown individually in a growing chamber.

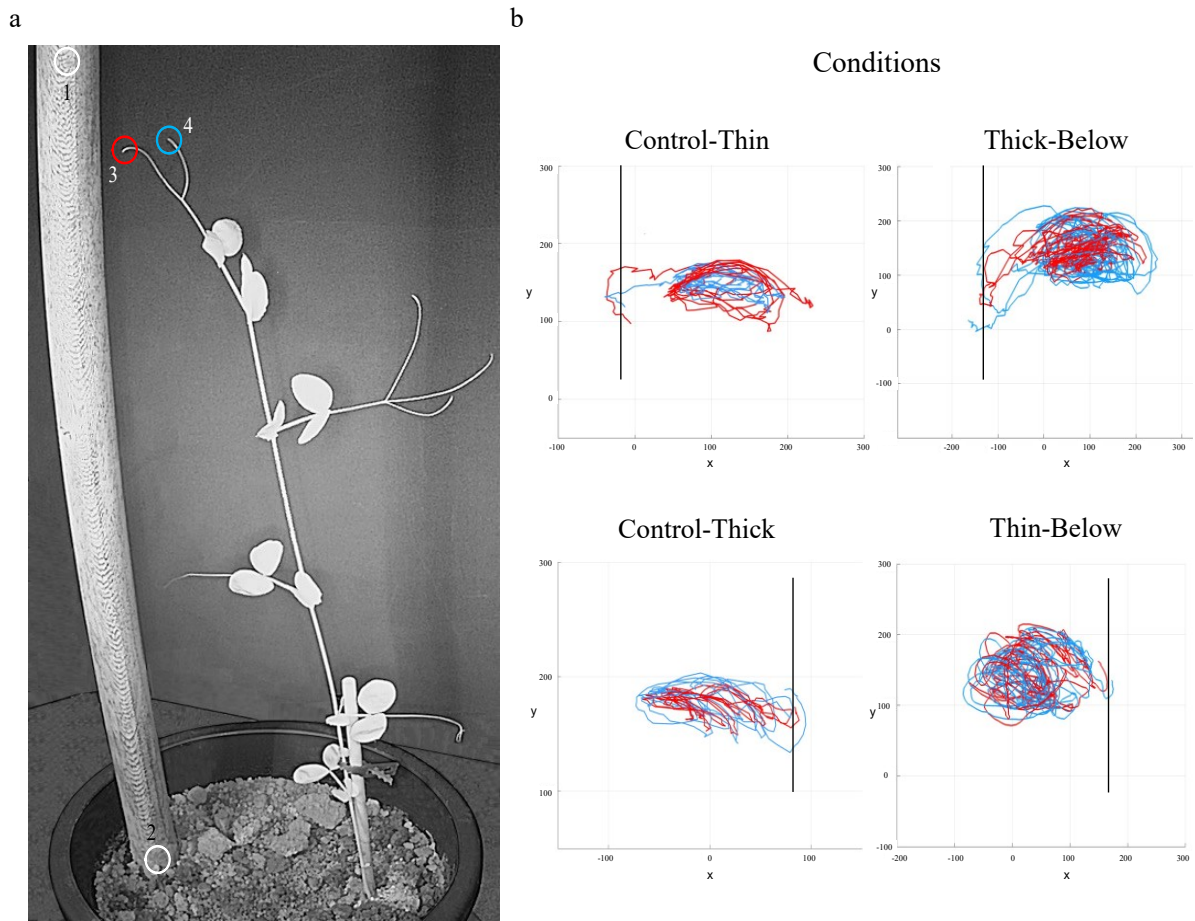


Figure 3: The Landmarks Considered and Examples of the Spatial Trajectories. (a) The landmarks considered were the stimulus (1,2) and the tip of the tendrils (3,4). The colours of the circles correspond to the colours of the trajectories shown in the right-side panel. Panel ‘b’ represents the trajectories for the tip of the tendrils for the ‘Control-Thin’, ‘Thin-Below’, ‘Control-Thick’ and ‘Thick-Below’ stimulus conditions. The stimulus is represented by the solid vertical line. The axis x and y refer to the sagittal and vertical axis in mm, respectively.

2.4. Video Recording and Data Analysis

For each growth chamber, a pair of RGB-infrared cameras (i.e., 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. The cameras were connected via Ethernet cables to a 10-port wireless router (i.e., D-link Dsr-250n) connected via Wi-Fi to a PC, and the frame acquisition and saving process were controlled by CamRecorder software (Ab.Acus s.r.l., Milan, Italy). To maximize the contrast between the peas' anatomical landmarks (e.g., the tendrils) and the background, black felt velvet was fixed on some sectors of the walls of the boxes and the wooden stimuli were darkened with charcoal. The intrinsic, extrinsic, and the lens distortion parameters of each camera 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' side 18mm, 10 columns, 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 photos were then taken by the two cameras to extract the stereo calibration parameters. In accordance with the experimental protocol, a frame was synchronously acquired every 3 minutes (frequency 0.0056 Hz) by the cameras. An ad hoc software (Ab.Acus s.r.l., Milan, Italy) developed by Matlab was used to position the markers, track their position frame-by-frame on the images acquired by the two cameras to reconstruct the 3D trajectory of each marker.

The tendrils developing from the considered node were studied. In those cases, in which the plant grasped the stimulus, the coiled leaf was analysed. When no grasping occurred, the first node, counting from the bottom of the plant, characterized by two or three tendrils was examined. The initial frame was defined as the frame in which the tendrils of the considered leaf were visible from the apex. The end of plant movement was defined as the frame in which the tendrils of the leaf started to coil around the stimulus or a frame in which the tendrils

remained apart. The markers on the anatomical landmarks of interest, namely the tips of the tendrils were inserted post-hoc (Figure 3 a). The markers were also positioned on the stimulus (i.e., on both the lowest and the highest point of the stimulus) as reference points.

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 3D trajectory of each tracked marker was computed by triangulating the 2D trajectories obtained from the two cameras (Figure 3 b). The dependent variables specifically tailored to test our experimental hypothesis on the basis of previous evidence (e.g., Guerra et al., 2019; 2021) were: (i) the movement time; (ii) the spatial trajectories of the landmarks considered; (iii) the maximum velocity of the tendrils during *circumnutation*; (iv) the time it took for maximum tendril velocity to be reached as a percentage of movement duration; (v) the maximum aperture of the tendrils corresponding to the maximum distance reached by the tip of the tendrils during the approach phase; (vi) the time it took for the maximum aperture of the tendrils to be reached as a percentage of movement duration.

Statistical tests were carried out to compare the median values for each of the dependent measures considered across all the conditions using the Wilcoxon rank-sum test (one-tailed). In addition to W -statistic and the p -value, we report the effect's size calculated as $r = z/\sqrt{N}$, in which z is the z-score and N is the total number of observations (Rosenthal, 1991). All statistical analyses were carried out using the computing environment R (R Core Team, 2013) software and the function *wilcox.test*.

Chapter 3. Results

3.1. Qualitative Results

For all the experimental conditions, the tip of the tendrils showed a growing movement pattern characterized as circumnutation (Figure 3a and b), which aims to find a potential support in the environment. Once the plant detected and perceived the support, strategically modified the trajectory of its tendrils that started to bend toward the support to approach and clasp it. Importantly, plants directed their movement toward the support and shaped the choreography of the tendrils depending on support thickness before any physical contact with it (Ceccarini et al., 2020a; Guerra et al., 2019; 2021).

3.2. Kinematical Results

3.2.1. Control Conditions

The pattern of results obtained for the control conditions mirror those reported in previous studies in which one-sized ‘thick’ and ‘thin’ supports were compared (see Table 2; Ceccarini et al., 2020a; Guerra et al., 2019; 2021). Movement time was longer for the ‘Control-Thick’ than the ‘Control-Thin’ condition (Figure 4). The maximum tendrils velocity was lower, and the peak of maximum tendrils velocity occurred earlier for the thicker than the thinner support (Table 2). The maximum tendrils aperture was wider and the time at which it occurred was later for the thinner than the thicker support (Table 2). This aspect is important because it provides a confirmation that *P. sativum* plants exhibit a different kinematical pattern for thick and thin supports (Ceccarini et al., 2020a; Guerra et al., 2019; 2021). And therefore, they provide the ideal comparison for investigating the effects determined by the perturbed conditions.

Table 2. Kinematical Values

Control-Thick vs Control-Thin		Median	
	Control-Thick	Control-Thin	
Maximum tendrils velocity (mm/min)	11.86	13.04	
Time of maximum tendrils velocity (%)	76.78	79.93	
Maximum tendrils aperture (mm)	30.80	38.52	
Time of maximum tendrils aperture (%)	81.9	87.22	

Control-Thick vs Thin-below		Median	
	Control-Thick	Thin-Below	
Maximum tendrils velocity (mm/min)	11.86	15.05	
Time of maximum tendrils velocity (%)	76.78	46.09	
Maximum tendrils aperture (mm)	30.80	53.40	
Time of maximum tendrils aperture (%)	81.9	68.72	

Control-Thin vs Thick-below		Median	
	Control-Thin	Thick-Below	
Maximum tendrils velocity (mm/min)	13.04	14.36	
Time of maximum tendrils velocity (%)	79.93	55.37	
Maximum tendrils aperture (mm)	30.80	42.66	
Time of maximum tendrils aperture (%)	87.22	84.56	

Note: mm = millimeters; min = minutes; % = percentage of movement duration.

3.2.2. 'Thin-Below' vs 'Control-Thick'

Movement time was longer for the perturbed than for the control condition ($W=297$; $p=.024$; $r=.29$; Figure 4). The maximum tendrils velocity was higher for the perturbed than for the control condition ($W= 192$; $p=.001$; $r= .41$; Table 2). The time at which the maximum velocity of the tendrils occurred was earlier for the perturbed than for the control conditions ($W= 540$; $p=.006$; $r= .35$; Table 2). The maximum aperture of the tendrils was greater for the perturbed than for the control condition ($W= 134$; $p<.001$; $r= .46$; Table 2). Further, the time at which the maximum aperture of the tendrils occurred was earlier for the perturbed than for the control trials ($W= 460$; $p=.004$; $r= .37$; Table 2).

3.2.3. 'Thick-Below' vs 'Control-Thin'

Movement time was longer for the perturbed than for the control condition ($W=238.5$; $p=.001$; $r=.40$; Figure 4). Similarly, the peak of maximum velocity of the tendrils occurred earlier for the perturbed than for the control trials ($W= 483$; $p=.037$; $r= .27$; Table 2).

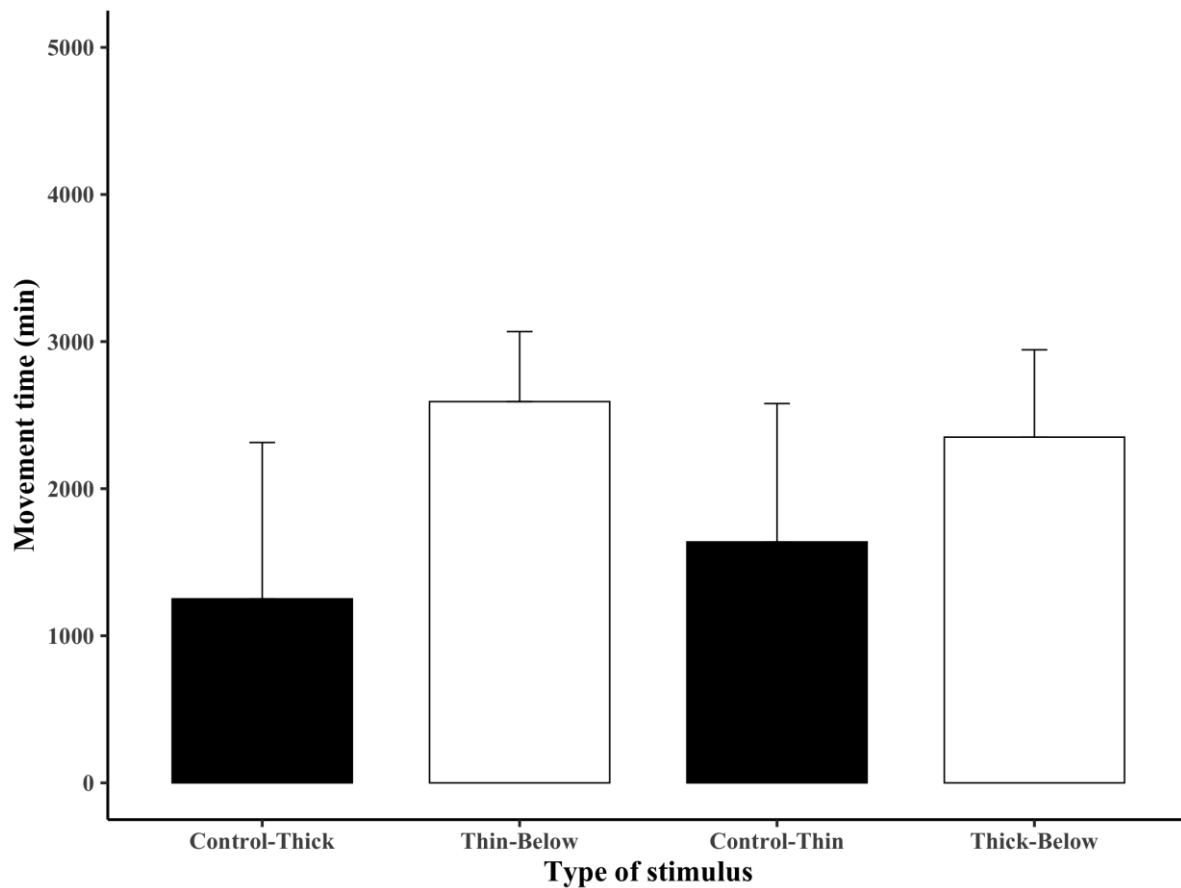


Figure 4: **Bar Plots Representing the Kinematical Values.** Bar plots representing the kinematical values for the comparisons between the Control-Thick and Thin-Below stimulus conditions and between the Control-Thin and Thick-Below stimulus conditions for the Movement time. Bars refer to the median, while error bars refer to the absolute deviation (MAD).

Chapter 4. Discussion

We set out on a journey to investigate the interaction between the shoot and root systems of pea plants for the coding of stimulus thickness by examining the kinematics of the approach to grasp movement. The results demonstrate differences in kinematical patterning when comparing perturbed and control trials. First and foremost, movement duration is longer in both perturbed conditions than in control trials, indicating that the thickness incongruity between above and below-ground parts in perturbed trials causes interference that prolongs movement duration. In control conditions, stimuli are one-thickness both under and above the ground. However, in perturbed conditions, the stimuli thicknesses are different in underground and aboveground. As a result, pea plants need to evaluate more information and determine which information is more reliable to follow in perturbed conditions. This could explain why plants require more time to exhibit movements in perturbed conditions.

When comparing the ‘Thin-Below’ with the ‘Control-Thick’ conditions, a differential pattern of results depending on the considered kinematical measures is observed. The amplitude of maximum velocity and the aperture of the tendrils suggest that pea plants modify the kinematical pattern of the movement based on the below-ground (i.e., thin) part of the stimulus. That is to say, the maximum tendrils velocity was higher, and the maximum tendrils aperture was wider in the perturbed condition than in the control-thick condition. Previous observations showed the same pattern for one-size thinner stimuli (Ceccarini et al., 2020a; Guerra et al., 2019; 2021). Therefore, in terms of amplitudes, the movement pattern appears to be based on information provided by the root system. On the contrary, when we consider the temporal parameters, such as the time at which the maximum peak velocity and grip aperture occur, pea plants arrange the kinematical pattern of the movement based on the above-ground (i.e., thick) part of the support. That is to say, for the perturbed condition, the peaks of the maximum velocity and the maximum aperture of the tendrils occurred earlier than for the control

condition. Previous findings are consistent with the current study, as the same pattern for one-sized thicker stimuli is observed (Ceccarini et al., 2020a; Guerra et al., 2019; 2021). As a result, it appears that the temporal pattern of the movement is based on the information provided by the aerial parts of the plant.

Overall, these findings suggest that the root system and the aerial parts of the plant are in communication. In order to balance the functionality between the roots and the shoot, the higher velocities determined by the processing of the 'thin' part of the stimulus need to be compensated by an earlier emergence of key kinematical parameters. To clarify, the time of maximum tendrils velocity and aperture are critical landmarks because they reflect the time when the tendrils begin to slow down and close upon the stimulus during the approaching phase, respectively. The importance stems from the fact that these movements are growth-related therefore irreversible, so they must be accomplished efficiently. Thus, plants need to reduce the metabolic and computational costs of irreversible but idle movements. However, ambiguity regarding these critical time windows may endanger the grasping of the stimulus. For this reason, if the information coming from the root system of the plant is inappropriate to optimize the chances of attachment, then the aerial parts of the plant need to make some modifications.

When we compared the 'Thick-Below' and the 'Control-Thin' conditions, we found no evidence of such crosstalk, and no kinematical effects were observed as a result of the perturbation. Apparently, what has been programmed based on the lower part of the stimulus (i.e., thick) fulfills the requirements for grasping the upper part of it (i.e., thin). Previous research on pea plants (Ceccarini et al., 2020a, b; Guerra et al., 2019; 2021) and climbing plants in general (Gianoli, 2015; Putz and Holbrook, 1992) has shown that grasping a thicker support is more difficult and requires more energy than grasping a thinner support. As a result, these findings can be interpreted as follows: it may be easier to customize a movement pattern associated with a thicker, more demanding stimulus for grasping a thinner, less demanding

stimulus. In such cases, the effects of the perturbation are minimized, and no differences from the control condition occur.

All these findings suggest that the root system transmits information to the shoots and thanks to this, can regulate the growth and behavior of the plant accordingly. This points to a functional balance between the roots and shoots based on a signaling interactive process (Aiken & Smucker, 1996; Turner, 1986; Brouwer, 1963). It is well established that such signals can determine an indirect root system effect on shoot characteristics, such as leaf size and the ability to orient leaves (Aiken & Smucker, 1996) and, possibly, the dynamics of the tendrils for adapting to thickness (Ceccarini et al., 2020a, b; Guerra et al., 2019; 2021).

The first question that comes to mind at this point is: how do plants integrate information from aboveground and underground organs to meet functional requirements? Although we are aware that our data reveals very little about possible physiological mechanisms underlying such effects, some speculative thoughts can be advanced.

The first possibility I would like to mention is the transmission of electric signals between the root system and the shoot (van Bel et al. 2014). Electrical signals can be generated both in the root system and in the aerial parts of the plant (e.g., stems and leaves). These signals can be propagated between the root and the shoot, ensuring that the physiological functions of the entire plant are coordinated. So far, four different types of electrical signal transduction have been reported in plants: the wound potentials (Volkov & Brown, 2006), the action potentials (AP; Hille, 1992), the slow-wave potentials (SWP; Stahlberg & Cosgrove, 1992; 1996; 1997), and the systemic potentials (SP; Zimmermann et al., 2009; 2016). The wound potential is limited to a short distance, whereas the AP, SWP, and SP can cover greater distances and potentially spread throughout the entire plant. Thus, the AP, the SWP play critical roles in root-to-shoot signaling, enabling two-way communication between roots and shoots.

Another possibility is related to the propagation of chemical signals such as the growth

hormones (i.e., auxin, cytokinin - CK, brassinosteroids - BRs, gibberellins - GA, and strigolactones - SLs). These hormones play a crucial part in coordinating many growth and behavioral processes in every stage of plants' lives by mutual interactions between them (Wang & Irving, 2011). They are essential for the development and growth of the new organs in both the upper and lower components of the plant (Durbak et al., 2012; Heil & Ton, 2008; Pieterse et al., 2012; Vanstraelen & Benkova, 2012; Torrey, 1976). Hormones have also been shown to move quickly from the roots to the shoot and vice versa via the xylem and phloem, respectively (Notaguchi & Okamoto, 2015; Symons & Reid, 2004). For instance, cytokinins such as trans-zeatin synthesized in the root have been detected in the xylem sap and they play a role in shoot growth (Takei et al., 2001; 2004). The shoot regulates cytokinin export from the root to the shoot, and this depends on the feedback signal generated by the branching regulator RMS4 (RAMOSUS4) acting in the shoot in pea plants (Beveridge et al., 1997). Moreover, cytokinin export to the shoot is sensitive to nitrogen, resulting in changes in the root and architecture of shoots (e.g., leaf expansion; Alvarez et al., 2012; Dodd et al., 2004; Forde, 2002). Both miRNAs (Vidal et al., 2010) and auxins are potential candidates for the shoot-to-root signals that mediate systemic nitrogen responses. For instance, in *Arabidopsis thaliana* L., it has been shown that the nitrate supply to roots is linked to lateral root responses via the modulation of shoot-to-root auxin transport (Guo et al., 2005).

It is also worth noting that the propagation of electrical signaling and the propagation of chemical signals are not mutually exclusive. In fact, it has been shown that when extracellular auxin hits the outside leaflet of the plasma membrane, it induces electric responses based on the ABP1 auxin-binding protein (Felle et al., 1991; Steffens et al., 2001; Baluška et al., 2004). This suggests that, in addition to hormone and morphogen-like properties, auxin also has neurotransmitter-like properties (Baluška & Mancuso, 2008).

The current results point to a possible interaction between the above- and the belowground parts of *Pisum sativum* plants for the processing of the thickness characterizing a potential support. The integration of the information from both above- and belowground plant organs may provide the plant with a complete reconstruction of its surroundings, resulting in a flexible adaptation of its behavior to ever-changing circumstances. Future research focusing on both kinematics and physiological measures is required to further investigate the functional equilibrium and interactivity of aboveground and belowground plant organs. The integrated analysis of plant growth responses at the kinematical and physiological levels may provide a new set of investigative tools to help us better understand plant behavior and ecophysiology.

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