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Understanding Plant Movement:

From Kinematics to Machine Learning

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To

the living beings

SYNOPSIS

Despite their seemingly immobile nature, plants can move, a fact that has often gone overlooked. Recent discoveries have begun to furnish compelling evidence that plants are not passive organisms. They are capable of harboring intentions and translating them into goal-directed actions. This emerging evidence has sparked a lively discussion regarding the cognitive potential of plants. One innovative perspective for the study of plant behavior lies in examining it through the theoretical framework of motor cognition, which posits that cognition is fundamentally intertwined with action. My thesis is focused on investigating motor cognition in plant behavior through a combination of kinematic analysis and machine learning techniques. In particular, I dedicated myself to understanding decision-making, which entails the evaluation of costs and benefits associated with actions carried out under different contexts.

I shall begin this path by providing an in-depth exploration of motor cognition, and following this concept, behavior will be discussed as intentional by analyzing its final goal. Recent evidence that demonstrates goal-directed behavior in plants will be presented, and the possibility of these actions being intentional will be discussed (Chapter 1). This discussion highlights the "goal-directedness" of plant movement and sets the stage for my

investigation of motor intentions in the plant domain. Given the absence of a designated structural basis for cognition in plants, this exploration offers an alternative perspective on how cognitive processes may manifest. In doing so, the thesis will provide alternative theoretical frameworks — post-cognitivist theories — for studying plants that move beyond neurocentric paradigms. All of these theories will be used to interpret the experimental findings and addressed in the final discussion.

The thesis will move forward to the topic of plant movement. In Chapter 2, I will introduce the physiological mechanisms that drive plant movement. Several types of plant movements will be discussed, which serve as the foundation for witnessing the presence of movements in plants. In particular, I shall focus on a universal movement exhibited by different organs in climbing plants — circumnutation.

The theoretical backdrop of motor intention and plant movements paves the way for a detailed examination of the experiments conducted. Given the relatively nascent nature of the study of plant movements, Chapter 3 will be dedicated to introducing common methods employed for this purpose, including time-lapse photography and 3D motion analysis. Additionally, the thesis will introduce the potential of machine learning for understanding plant movements, setting the stage for my subsequent experiments.

After providing the theoretical background, in Chapter 4, I will highlight the aim of my research, grounded in two goals: first, to examine the motor intentions underlying plant support-searching and their associated decision-making processes; second, to enrich our approaches to understanding plants through the innovative application of machine learning. Then, in Chapter 5, I will describe the general methods employed.

Starting from Chapter 6, the experiments will be presented. The first study focused on the adaptive behavior of pea plants when faced with the presence/absence of a potential support. The results demonstrated not only that plants can discern the presence or absence of a support in the environment, but also that they can program their movements accordingly.

In Chapters 7 and 8, I shall report on experiments explicitly designed to investigate the decision-making processes underlying plant support-searching. The results indicate that plants can make decisions when it comes to supports, and that they show preferences which may well stem from a careful evaluation of the environment. Moreover, I will demonstrate that the presence of alternatives determines a decisional complexity, that is played out in the kinematics of circumnutation.

From Chapters 9 to 11, I will use machine learning techniques to analyze the plant behavioral data I have collected. I employed models for unsupervised anomaly detection, supervised machine learning, and ensemble learning. In supervised machine learning, the classifiers showed the ability to identify the distinct patterns of circumnutation to make predictions regarding plants' growth across different conditions. Unlike traditional statistical analysis, which provides a general overview of the plant movement, the machine learning approach allows for the detection of subtle programming abilities nested in the kinematical patterning. For instance, I found that it is the movement of the "junction" below the "tendrils," rather than the tendrils, to be modulated during support-searching. Harnessing the predictive capabilities of machine learning, these findings provide valuable insights into how plants navigate their surroundings and make informed choices.

After presenting my experimental work I shall offer a discussion referring to several sensory mechanisms, including touch sensitivity and a form of primitive vision, both of which could be proposed as potential mechanisms to support plants during the decision-making process. In addition, I will introduce long-distance signaling pathways, shedding light on how plants assimilate information from diverse sensory inputs to make choices.

The last part of the thesis will examine plant movement through the lens of post-cognitivist theories that well-espouse the concept of motor cognition. Plants are open systems with a remarkable ability to deal with the complexities of an ever-changing environment, and they are capable of acquiring and integrating complex information in order to implement plastic responses. By nesting my findings within cognitive theories, I hope to develop a fresh perspective in understanding cognition and reveal its manifestations across taxa.

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PART I

THEORETICAL BACKGROUND

CHAPTER 1

MOTOR COGNITION

"Plants move to survive, to thrive, and to interact with the world in ways we are only beginning to understand."

Daniel Chamovitz

Motor cognition entails concepts that generally refer to the integration of cognitive processes with motor functions. It often encompasses the notion of action representation and the subsequent execution of the action (Jeannerod, 1994, 2006). Action, in the context of motor cognition, involves the movements that are generated to satisfy an intention directed towards a specific motor goal or as a response to something of significance in the physical and social environments. Therefore, it is fundamental that these notions possess the nature of being anticipatory, goal-directed, and undergo evolvement in terms of both pace and time across various levels of complexity.

Intention plays an indispensable role in the domain of action representations, as it pertains to states that are in close proximity to the execution of the action. Motor cognition, as showing intention in action, is commonly referred to as *motor intention* because this term more precisely conveys the profound connection between intention and its direct consequence, which is a goal-directed movement; also, it is typically used to describe the early stages of action generation (Jeannerod, 1994).

This chapter will focus on these concepts that serve to theoretically contextualize the kind of plant behaviors I have investigated. Motor cognition offers an ideal theoretical window to explain plant behavior because its core seizes the idea that cognition is embodied in action. Plant behavior can be discussed as intentional by analyzing its final goal. I shall discuss recent empirical evidence that demonstrates goal-directed behavior in plants, and consider the possibility of the action being intentional. As this chapter comes to a close, I shall introduce several cognitive frameworks that could provide theoretical shelters for the presence of cognition nested in plant behavior.

1.1. Motor Intention[1]

The term "intention" encompasses a multitude of concepts that pertain to various domains (Barresi & Moore, 1996; Bratman, 1987; Gallese & Goldman, 1998; Perner, 1991; Woodward & Guajardo, 2002). An individual can harbor and even voice an intention, a desire, an active striving or disposition to do something, just as they can refer to something that is purposeful or value-laden. Intention can also refer to beliefs and/or ideas (Searle & Willis, 1995), whereas intentionality, in the phenomenological sense, denotes a property of

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the mind of representing or standing for states of affairs and/or objects (Searle, 1983), it has also been defined as a pervasive feature of many mental states, beliefs, and ideas (Brentano, 1874; Husserl, 1891).

The majority of studies in the literature dealing with the role of motor intention suggest that the intention of carrying out a specific action is something that precedes its actual motor execution (Ansuini et al., 2014; Bonini et al., 2013; Llinás, 2002). Plants were excluded from this debate because of being sessile. This isn't the case though, as plants are actually very much in tune with their environment and are indeed capable of a variety of movements. Darwin and Darwin (1880), for example, observed that the tendrils of climbing plants tend to assume the shape of whatever surface they come into contact with; that is, they progressively learn the shape of potential support characteristics (Trewavas, 2017). The behavior described implies that the plants perceive the support and plan their movements appropriately. Climbing plants seem, in fact, to represent actions in terms of their perceivable consequences. To all appearances, the selecting, planning, and initiating of a movement is mediated by action-effect anticipations. In accordance with this theory, plants may possess a sort of intention that precedes their motoric behavior, that, as for animals, it becomes "visible" in the surface flow of an organism's motion (Ansuini et al., 2014).

The present section will focus on the theoretical framework pertaining to motor intention within a comparative study. Specifically, it will explore how intentions that lead to action are represented, as well as the signs of motor intentions observed in plants through modular growth and phenotypic plasticity.

1.1.1. Motor intentions in animals

According to Libet (1985), an act is regarded as intentional when (i) it arises endogenously, not in direct response to an external stimulus or cue; (ii) there are no externally imposed restrictions or compulsions that directly or immediately control subjects' initiation and performance of the act; and (iii) most important, subjects *feel* introspectively that they are performing the act on their own initiative and that they are *free* to start or not to start the act as they wish. The majority of studies dealing with the concept of motor intentions in animals espouse the view that motor intention is specified in advance of the actual movement execution (Ansuini et al., 2014; Bonini et al., 2013). It was Merleau-Ponty (1945) who first coined the term "motor intentionality," referring to a pattern of intentionality exemplified by purposive, goal-directed, unreflective bodily activities. According to this definition, there are two ways to explain motor intentions: one involving an intentional relation to the object that is essentially cognitive or can serve as the input to cognitive processes. Another involves a bodily set or preparation to deal with the object (Kelly, 2002).

According to one authoritative view (Searle, 1983), motor intentions can be considered at two distinct levels: *prior intention*, defined as an intention to act formed in advance of the action itself, and *intention-in-action*, which refers to the representation of the desire that causes the act. The intentional content of an intention-in-action consists of self-referential causality (Searle, 1980). While several theorists have embraced this dualistic approach (Brand, 1984; Bratman, 1987; Mele & William, 1992; Pacherie, 2018), nearly all theories focus on the motor goal, which — although at different levels of complexity —

constitutes the core of what intentions represent, that is, "*goals and the means to those goals*" (Pacherie, 2018).

1.1.2. Goal-directedness

The concept of *goal* is central to the literature dealing with the correlates of intentional actions. Generally speaking, the undertaking of an action is associated with a goal. Movements can be considered goal-directed if they are tuned to the task, and their execution is under voluntary control. According to this definition, the desired result of the movement, that is, the final goal of the action persists in the agent's phenomenological experience throughout the time the action is unfolding and until it has been completed. The goal entails a great deal of the environment around and the possible future events tied to it. Goals serve as a representation of the future, not only in a motivational nature, but also axiological, or deontic. That means not only about how the world is, but how the world should be, and how the organism would like the world to be (Pezzulo, 2008).

Research on goal-directedness has produced insightful findings revealing, for example, how specific kinematic landmarks in reach-to-grasp movements are modulated depending on the object's attributes, such as how far away it is, its size, shape, texture, fragility, and weight (Castiello, 2005, 2020, 2023). To attain a goal, an agent must organize a reaching-grasping action sequence, taking into account the structural features of the object and planning and executing the movement accordingly. A number of behavioral studies in humans have indicated that the first part of a complex action sequence (e.g., the arm reaching and the hand shaping to grasp an object) is influenced by the final goal and, more specifically, by the motor acts that follow the first part (e.g., lifting, placing; Ansuini et al., 2008; Ansuini et al., 2006; Armbrüster & Spijkers, 2006; Gentilucci et al., 1997; Marteniuk et al., 1987; Rosenbaum et al., 2012).

1.1.3. Motor intentions in plants

As pointed out by Marder (2012): "*When animals intend to do something, they enact their directedness-toward by moving their muscles; their intentionality is expressed in modular growth and phenotypic plasticity.*" Plants, instead, generate action potentials and synthesize the protein RHD3, which is responsible for the correct arrangement of root cell files underlying the direction of root growth (Baluška, 2010). This directionality, along with its deliberate regulation, is relevant to the quest for plant intentionality. Plant and animal behaviors are the outcomes of the goals underlying intentional comportments. In phenomenological terms, each type of plant perception expresses a mode of its intentionality: directedness toward the light in photosensitivity, directedness toward sources of heat in thermo-sensitivity, as well as toward (or away from) self and others in kin recognition. In each of these cases, it is not just a question of perceiving, but also of interpreting signals and making decisions in a non-automatic manner in the face of at times conflicting conditions. Intentionality here assumes the more colloquial sense of deliberate purposeful behavior, raising the questions: do plants intend to defend themselves against herbivores? Do they intend to resist the force of gravity and the common stresses they experience?

Studies reporting on individual root systems that are growing to limit the resources of their competitors seem to imply that there is some form of intention (Gruntman &

Novoplansky, 2004; Maina et al., 2002). The communication network of the cells and tissues making up an individual plant may be the mechanistic basis of intention in plant behavior. Just like human beings, plants seem to gather information about their surroundings, check it out with their internal and external network systems, and make decisions that reconcile their own well-being with that of the environment. Spacers, defined as the plant's underground root systems and above-ground stems or shoots that explore the environment in the quest for optimal patches of nutrient-rich soil (Bell, 1984), are relevant to this argument about plant intelligence and intentionality. As Marder (2012) suggested, spacers are another sign of plant intentionality and goal-directed behavior, and confirm that plants should not be considered organisms that are passive to their own needs and to what is going on in their environment.

Evidence of intentional actions in plants

Plants program their movements purposefully and in ways that are flexible and anticipatory (Bonato et al., 2023; Ceccarini et al., 2020a, 2020b; Guerra et al., 2022; Guerra et al., 2019; Raja et al., 2020; Wang et al., 2023a; Wang et al., 2023b). The tendrils of *Passiflora* exhibit an incredible flexible control of circumnutation while they are searching for supports (Baillaud, 1962). Circumnutating *Passiflora* tendrils can modify their direction in conformity with plant-made support that keeps moving from one place to another. The support was switched to a different position whenever the tendril approached it, and the tendril continued to change its circumnutating movement in pursuit of the support.

Researchers focusing on the kinematic signatures characterizing the movement of climbing plants have reported that pea plants (*Pisum sativum*) can program their movement in advance and can move their tendrils (i.e., specialized stems, leaves, or petioles used by climbing plants to seek, find and attach to a support) depending on the specific characteristics of the to-be-grasped support. When researchers studied the kinematic features of a pea plant's movements while it approached and grasped a thick or a thin support, they found that the plant perceived the support and modulated the kinematics of its tendrils' aperture depending on the support's thickness (Ceccarini et al., 2020a; Guerra et al., 2019). The peak of the average and the maximum velocity of the tendrils were higher for the thin supports than for the thicker ones. Moreover, the times at which the tendrils reached peak velocity and the tendrils reached the maximum aperture, both calculated as a percentage of the movement duration, were later for the thinner than for the thicker supports. Likewise, the maximum distance between the tendrils was significantly greater for the thinner support than for the thicker one (Guerra et al., 2019).

The movement of pea plants appears to comply with the speed–accuracy trade-off principle (SAT; Woodworth, 1899), which is the inclination or decision to choose speed over accuracy (Ceccarini et al., 2020b). While it has long been known that SATs are a key feature of animal movement, the idea that plants use SATs is coming into its own (Chittka et al., 2009). By studying the trajectories of the tips of the shoots of climbing pea plants leaning to reach a support, Ceccarini et al. (2020a) uncovered that the plants perceived the properties of the support even before they made contact with it. Additionally, similar to some animal species, the plants were able to modulate movement velocity strategically depending on the difficulty of the task. The average and the maximum velocities of the tendrils were, in fact, faster when the plants had to reach and grasp a thinner with respect to a thicker support (Ceccarini et al., 2020a). In a subsequent study, Ceccarini et al. (2020b) set out to investigate if climbing plants are able to improve the accuracy of their movement plan by correcting their secondary submovements. Their findings showed that the plants were, in fact, able to correct their movement plan and, just as humans (Meyer et al., 1988), they can strategically increase the production of secondary submovements when the task requires more precision. These findings support the hypothesis that the movement of plants is not a cause-effect mechanism but an appropriately planned, controlled, and, if necessary, corrected operation.

These findings are important because they demonstrate that plants exhibit forms of motor intentions that are similar to those of a variety of animal species (Castiello, 2005; Castiello & Dadda, 2019; Klein et al., 1985; Sustaita et al., 2013; Whishaw, 1996). They also contradict the scientific consensus that plants' movement is driven exclusively by cause-effect mechanisms and hard-wired inflexible reflexes. Ultimately, they have heralded a change in the way plant behavior is usually considered.

1.1.4. Decision-making in goal-directedness

The concept of goal-directedness is essentially intertwined with the ability to anticipate the future, wherein decision-making is inevitably involved. Anticipations generate goals, which are derived from the valuable information extracted from the environment. This means that the goals are anticipatory representations that can select and guide actions (Pezzulo, 2008). The act of selecting a comportment is a manifestation of the decision-making process. Therefore, an organism that exhibits anticipatory behavior must possess the capacity for decision-making.

In *On the Movements and Habits of Climbing Plants*, Charles Darwin (1875) coined the term *circumnutation* to describe the elliptical/spiral growth movement around the plant's central axis that could be modified for the good of the plant. He was of the opinion that the driving/regulating apparatus responsible for circumnutation was internal (i.e., Darwinian internal oscillatory model). This would explain climbing plants that are able to modify their circumnutation movement to reach and grasp a potential external support (e.g., a pole, a host plant) in the surrounding environment in an effort to grow vertically (Darwin, 1875; Gianoli, 2015; Guerra et al., 2019; Runyon et al., 2006; Tronchet, 1977).

Darwin also advanced the hypothesis that climbing plants are able to sense the properties of support structures and to make decisions on the basis of that information. Indeed, he was able to illustrate plants' purposeful behavior when he showed that climbing plants perceived a support that was objectively unsuitable because of its smoothness or thickness (Darwin, 1875; Gianoli, 2015). Commenting on his experiment with the *Bignonia capreolata* plant, he pointed out that the plant initially exhibited an oscillatory movement when an unclimbable smooth glass rod support was presented, but then began to show an irregular unwinding movement as if it were seeking to find a suitable support elsewhere. He provided in another experiment, the plant with a blackened zinc plate and noted that the tendrils initially bent themselves around the edges of the plate but soon recoiled and straightened themselves out, as if they were correcting an erroneous decision. In addition, he described experiments with the *Solanum dulcamara*, a plant that he found could twine around supports with a 3 mm diameter but not around one with a 5 or 6 mm diameter, which was perceived, evidently, as inappropriate (Darwin, 1875).

In recent years, a growing body of evidence has confirmed Darwin's observations, and there are numerous reports that plants are able to put in place some forms of decision-making. For instance, some have investigated the *Cuscuta pentagona* plant, which needs to find and attach itself to a host plant such as the cultivated tomato (*Lycopersicon esculentum*) in order to gain nutrient from it and survive. It has been demonstrated that the *Cuscuta pentagona* is able to locate a host plant via volatile compound cues and to direct its growing movement toward it (Runyon et al., 2006). Moreover, it is able to distinguish between different types of host plants such as the tomato and *Impatiens* plants (*Impatiens wallerana*), and to choose the one that is most appropriate for its needs (Runyon et al., 2006). Dener and colleagues (2016) investigated decision-making in the root development of the pea plant (*Pisum sativum*) using the risk sensitivity theory (RST). According to RST, the rational decision is the one that maximizes fitness (Mcnamara & Houston, 1992). In the study, root growth displayed both risk-prone and risk-averse behaviors, which better support the RST hypothesis than previous animal testing. It appears that pea plants make rational economic decisions in terms of risk sensitivity (Dener et al., 2016; Schmid, 2016). Plant decision-making is also explored in the context of the social environment. Gruntman and colleagues (2017) compared the responses of *Potentilla reptans*, centered on their ability to out-compete their neighbors for accessing light. Observed shifts in the responses between vertical growth, shade tolerance, and lateral growth suggest that plants can choose adaptively from several alternatives under light-competition scenarios (Gruntman et al., 2017).

A theoretical framework in resonance with these experimental findings has been proposed by Karban and Orrock (2018). They delineated a judgment and decision-making (JDM) model that is specifically targeted to plant behavior, demonstrating that plant behavior can be constructively modeled by identifying four distinct components: (i) a cue or stimulus that provides information, (ii) a judgment whereby the plant perceives and processes this informative cue, (iii) a decision whereby the plant chooses among several options based on their relative costs and benefits, and (iv) action.

Needless to say, this model entails a process leading to action starting from perception and passing through decision. To this end, I will now introduce the tenets of theories that challenge the necessity of attributing cognitive abilities only to the nervous system, as they emphasize the value of cognitive activities in all living systems, surpassing the limitations imposed by classic cognitive theories. These theories will serve as helpful lenses through which to interpret the experimental findings discussed in Chapter 12.

1.2. Post-Cognitivism: Eschewing Neuron-Based Ascriptions

Cognition, a concept often associated with refined mental processes, has traditionally been regarded as the hallmark of intelligent entities, predominantly humans and other mammals. It is often associated with the brain, implying that it requires a rationalization based on representations. For instance, Carey (2011) views the representations as *states of the nervous system that have content, that refer to concrete or abstract entities, properties, and events*.

These classic cognitive approaches are founded on the notion that mental processes are computational processes that operate representations, and adhere to internalist and neuro-centric perspectives, positing that cognition is exclusively confined to the brain (Gallagher, 2005). However, recent studies present a counter-argument to the conventional viewpoint by revealing a captivating finding: cognition may surpass the boundaries of the neurons and is pervasive across an extensive spectrum of living organisms (Baluška, 2010; Baluška & Levin, 2016; Calvo & Keijzer, 2011; Castiello, 2023; Souza et al., 2018; Trewavas, 2017).

Cognitive phenomena such as associative learning, which have commonly been linked to cognitive manifestation in humans, have also been observed in other species including plants (Gagliano et al., 2016), insects (Faber et al., 1999), and unicellular organisms (Gershman et al., 2021; Pershin et al., 2009; Saigusa et al., 2008). Plants demonstrate a diverse range of behaviors that imply the presence of cognitive processes such as decision-making, memory, learning, and problem-solving abilities (Gagliano et al., 2016; Gruntman et al., 2017; Parise et al., 2021; Runyon et al., 2006), thereby challenging and transforming our understanding of cognition. In a similar vein, it has been observed that unicellular organisms possess remarkable problem-solving abilities and learning capabilities, shedding light on the intricacies of cognition at a microscopic scale (Nakagaki et al., 2004; Nakagaki et al., 2000; Saigusa et al., 2008).

After all, cognition is for *doing*, not for *thinking*, and accordingly, the basic concepts of cognitive science such as representations are being defined (Pezzulo, 2008). Post-cognitivist theories including 4E cognition, extended mind theory (Clark & Chalmers, 1998), ecological psychology (Gibson, 1979), active inference theory (Friston et al., 2017; Pezzulo et al., 2015) provide shelters to those "outsiders" in the realm of cognition. This array of approaches offloads cognitive processes onto the environment, and in certain cases, they may be regarded as integral components of the cognitive system or exert a causal influence on cognitive behavior. Post-cognitivism sprung up as a result of the paradigm shift in understanding mental representation as a cognitive process. The majority of the theories here dismiss the commitments to representations, and instead, prioritize the relevance of bodily processes and interactions with the environment.

The concepts of 4E cognition (embodied, embedded, extended, enactive) present transformative paradigms across the fields of cognitive psychology, molecular biology, neuroscience, and physiology. Unlike classic views that center exclusively on the brain as the primary locus of cognitive processes, the 4E cognition asserts that cognition is fundamentally influenced and dispersed throughout the entirety of the body, the environment around it, and the interaction between the organisms and the environment. The notion of body–environment coupling is a fundamental principle within these frameworks although its precise definition may vary.

Embodied cognition

Embodied cognition can be referred to by various definitions that place emphasis on different subsets of claims while sometimes dismissing others (Gallagher, 2005, 2023). In general, the embodied cognition theory posits that both the neural and extra-neural processes, along with their interaction with the environment constitute significant factors (Gallagher, 2023). This perspective highlights the integral connection between the mind and the body, establishing that cognitive processes are deeply shaped by bodily experiences, sensory-motor interactions, and emotional states. In this view, the body is not merely a passive container for the mind, but rather an engaged contributor that influences our thoughts, perceptions, and understanding of the world. Wilson (2002) put forth a six-view summarizing different perspectives in embodied cognition, and they are: *(i) cognition is situated that the environment in which it happens plays a significant role; (ii) cognition is time-pressured; (iii) we offload cognitive work onto the environment; (iv) the environment is part of the cognitive system; (v) cognition is for action; (vi) offline cognition is body-based.* It is argued that the fourth view to be the most problematic (Wilson, 2002), still, embodied cognition recognizes the reliance of organisms on environmental cues and signals to navigate their surroundings, locate resources, and respond to cues.

Embedded cognition

Embedded cognition expands upon the cognitive perspective by acknowledging that cognitive processes are not confined within the human mind but rather are deeply associated with the environment (Clark, 2008). The environment functions as an external repository of information and an extension of cognitive abilities, offering one to offload mental tasks onto the physical realm. Within the spectrum of organisms, embedded cognition points out that cognitive activities are deeply intertwined with the organism's ecological niche which is resources and *affordances* (Gibson, 1977) provided by its environment. An example of cognitive offloading within the framework of embedded cognition can be observed in the behavior of a spider, which utilizes its web as an external memory to monitor the whereabouts of its prey. This strategy effectively alleviates the cognitive load on the spider's nervous system. This particular viewpoint offers a comprehensive comprehension of the manner in which cognitive processes are situated and distributed throughout living systems.

Extended cognition

Clark and Chalmers (1998) put forward the extended cognition hypothesis, stating that cognition has the potential to extend beyond the physical boundary of an organism into its environment, becoming both embodied and embedded within its environment. This perspective suggests that cognitive processes can incorporate external objects that are not inherently a part of the organism. Given this view, it is proposed that the environment exerts an active role in facilitating cognitive processes, and these processes extend beyond the central nervous system and the physical body, spanning the organism's ability to engage actively with and manipulate the environment to optimize its cognitive abilities. Such as the case of extended spider cognition, which involves the outsourcing of information processing to the body or the environment (Japyassú & Laland, 2017). It has been demonstrated that web builder spiders adjust the tension of their thread by extending their cognition and adjusting the tension of the web threads. Tighter web threads lead to a lower threshold of disturbance needed to catch the spider's attention. Thread tension thus calibrates the threshold level for attention. When tight, tinier objects such as prey items are registered, the causal chain is satisfied in one direction. The spider, in turn, adjusts its web tension based on its hunger state. In practice, a hungrier spider will tend to tighten the web as even smaller prey is worth its attention. This demonstrates that the cognitive capacities of the spider also affect its environment (Japyassú & Laland, 2017).

Enactive cognition

Enactive cognition focuses on the active and dynamic features that define cognition, advocating that cognitive processes arise from an organism's continuous interactions with the environment (Schlicht & Starzak, 2021). Cognition rather than seen solely as a passive representation of the external world, is conceptualized as a fluid process of sense-making and meaning construction enabled by embodied action and perception. There are several enactive proposals including the autopoietic (Thompson, 2010), the radical (Hutto & Myin, 2012), and the sensorimotor approach (O'regan & Noë, 2001). Regardless of their differences, all of these approaches share the common view on cognition, that is the enactive approach depicted (Varela et al., 1991): "*Perception consists in perceptually guided action, and cognitive structures emerge from the recurrent sensorimotor patterns that enable action to be perceptually guided.*" Radical enactivists claim that experiencing organisms are set up to be set off by certain *worldly offerings* — that they respond to such offerings in distinctive sensorimotor ways that exhibit a certain minimal kind of directedness and phenomenality (Hutto & Myin, 2012). The feature of the worldly offering are often identified with what Gibson (1979) called *affordances*, that is what the environment offers the organisms, and what it provides or furnishes, either for good or ill. The enactivistic theories rely heavily on Gibson's ecological approach to perception. The idea of coupling and affordance are important conceptual tools in the accounts of perception (Hutto & Myin, 2012; O'regan & Noë, 2001; Schlicht & Starzak, 2021).

1.2.1. 4E: Implications for the explanation of plant behavior

Recent findings suggest that plants interact with objects in the environment in an intentional manner (Ceccarini et al., 2020a, 2020b; Guerra et al., 2019; Raja et al., 2020). It has been demonstrated, for example, that they perceive a support and modulate their kinematics depending on its thickness. It has also been reported that the biological and behavioral dynamic nutation patterns of bean plants are influenced by the presence of a support in their vicinity (Raja et al., 2020). These findings are in line with some theories regarding motor intention. Merleau-Ponty's definition of motor intention as purposive, unreflective goal-directed activities is a pretty accurate description of a climbing plant leaning toward a support. Further, as said above, according to Libet (1985), an act is intentional when (i) it arises endogenously, not in direct response to an external stimulus or cue; (ii) there are no externally imposed restrictions or compulsions that directly or immediately control subjects' initiation and performance of the act; and (iii) subjects feel introspectively that they are performing the act on their own initiative and that they are free to start or not to start the act as they wish. The behavioral manifestations of climbing plants reported here seem to agree with Libet's definition of intentional actions. In fact: (i) climbing plants can move and choose a support on the basis of their endogenous need to seek the sun. An unsuitable or no support fails to satisfy their intention; (ii) climbing plants control their circumnutation movement and interact with their surroundings without any externally imposed compulsions; it is a behavior that arises from their very nature; (iii) climbing plants act freely and are able to terminate the process when the support is not suitable or when there is no support.

Some may say that this conceptual framework does not work for plants because, in order to act in a goal-directed manner, they need to be able to construct a representation of the environment, including potential supports. And it goes without saying that many argue a priori that cognition is impossible in plants (Adams, 2018). In classical views, mental representations are created by a number of neurophysiological mechanisms in the brain that are activated after perceptual processing occurs. The events activating mental representations take place, according to this view, in the following order: physical signals are received through the perceptual systems and transmitted to the brain, then the physical signals are translated into mental representations (e.g., concepts, intentions) with the mind in charge of processing them, finally the motor system operationalizes the mind's will.

This explanation of mental representations does not take plants as cognitive agents into consideration since they lack a brain and a centralized nervous system (CNS) where mental states and representations can be localized. Scholars favoring the 4E cognition are challenging the notion of representational content by taking into consideration extra-neural bodily structures and the environment (Clark, 2008; Clark & Chalmers, 1998; Di Paolo et al., 2017; Gallagher, 2005, 2023; Gibson, 1977; Hutto & Myin, 2012, 2017; Noë & Noë, 2004; Schlicht, 2018; Thomasson, 2007; Thompson, 2010; Varela et al., 1991). According to Gibson (1979), for example, cognitive activities do not necessarily depend on mental representations but on affordances. What an organism perceives of an object is not only its physical properties but also its affordances, in other words, what it can do with them (Gibson, 1979). The key to understanding affordance is that it is relational and characterizes the suitability of the environment to the organism, which means that it depends on their current intentions and capabilities. The notion of intention is crucial here because the same environment can provide various affordances to different organisms or to the same organism at different times. For instance, the defensive leaf-folding behavior of the *Mimosa pudica* plant in response to repeated physical disturbances exemplifies how affordances can be adjusted by the same organism (Gagliano et al., 2014).

In the extended cognition theory, the environment plays an active role in cognitive processes that are not confined to the CNS or to the body (Clark, 2008). Plants too can extend their cognitive processing into their environment by actively modifying the rhizosphere and the soil directly influenced by root secretions, as well as shaping the root microbiome to the microbial community of the roots (Parise et al., 2020; Parise & Marder, 2023). This process allows plants to extend their sensorial apparatus and externalize a part of their information-processing system. As a result, seeing plants as isolated organisms distinct from their surroundings becomes inadequate (Parise & Marder, 2023). It has been seen, for example, that the accumulation of exudates between obstacles and the roots is related to the plant perception of obstacles in the soil, causing inhibited root growth in the direction of the accumulated exudates (Falik et al., 2005).

The enactivist approach to cognition is another alternative one that would allow us to consider plants as cognitive agents and circumvent some of the challenges linked to the mental representation theory (Calvo & Keijzer, 2011; Carello et al., 2012; Castiello, 2020; Maher, 2017). De Carvalho and Rolla (2020) proposed an enactivist–ecological approach according to which complex cognitive capacities such as ones involving representations are deeply rooted in the basic processes that enable biological organisms to survive and maintain their integrity in a dynamic environment. The approach offers a base upon which the theory of cognition in single-cell organisms, plants, animals, and humans can be constructed.

The 4E cognition theories allow cognition to be not-just-in-the-head and extend beyond the constraints of the body. Putting aside a representational approach, plant behavior can be interpreted under a different light. The experiments on pea tendrils reported that they acted in an intentional goal-directed manner in an embodied form of cognition in which the plant and the stimulus (i.e., the support) interacted as a single unit (Guerra et al., 2019). The environment, in this case, could be considered part of the plants' intention as it approached the support it intended to grasp.

Contemporary theories aligned with the classic post-cognitivist theories by placing more emphasis on ascribing cognition to the entirety of mechanisms and processes that underlie information acquisition, storage, processing, and use, at any level of organization (Baluška & Levin, 2016; Lyon, 2015). The debate has also seen active involvement from various theories, including the anticipatory approach (Pezzulo, 2008; Sims, 2023), biosemiotics (Barbieri, 2008), information integration theory (IIT; Tononi, 2004), quantum-based approaches (Barlow, 2015), free-energy principle (Friston, 2010, 2013; Sims, 2021b), and predictive-processing (Calvo & Friston, 2017; Hohwy, 2013; Sims, 2019). The shift in our understanding of cognition, transitioned from the question "whether the brain is a prerequisite for cognitive abilities" to the acknowledgment that "all biological systems possess some form of cognitive potential." Plant behavior, in this context, requires no justification for being cognitive, as it is essential for all living systems to exhibit cognitive abilities to be adaptive to the environment. At its core, cognition refers to the ability to acquire, process, and interpret information to interact with the environment effectively. The differences in cognitive processes and manifestations in the species of life are clear, yet a common thread can be found in the remarkable adaptive behaviors and responses exhibited by these living systems (Levin, 2023; Lyon et al., 2021; Sims, 2021a).

All in all, the post-cognitivism provides compelling arguments against the anthropocentric perspective on cognition. By acknowledging cognitive abilities in a broader spectrum of organisms and accepting the inseparable connection between cognitive agents and their environments.

CHAPTER 2

PLANT ON THE MOVE

"The more I study nature, the more I become impressed with ever-increasing force, that the contrivances and beautiful adaptations slowly acquired through each part occasionally varying in a slight degree but in many ways, with the preservation of those variations which were beneficial to the organism under complex and ever-varying conditions of life, transcend in an incomparable manner the contrivances and adaptations in which the most fertile imagination of [hu]man could invent."

Charles Darwin

The understanding of plant movements has developed over time, stemming from the realization that plants are not as immobile as thought. This journey departs with Jean-Baptiste Lamarck (1744 – 1829) who studied the touch-sensitive mechanisms of *Mimosa pudica*. Later on, René Desfontaines (1750 – 1833) asked his students to observe the behavior of *Mimosa pudica* by putting them in a hackney cab for a nonstop tour on the road of Paris (Mancuso, 2018).

Then it was with Charles Darwin that plants movement was given the necessary attention and was comprehensively examined. In the seminal work *On the Movements and Habits of Climbing Plants*, he extensively analyzed the behavior and physiology of climbing plants, and described how they interact with the environment by exhibiting movements in their growth patterns. In a subsequent book entitled *The Power of Movement in Plants* (1880), he and his son Francis explored various aspects of plant movements, encompassing the examination of phototropism and geotropism, the influence of music on plant growth in mimosa plants, the co-evolutionary relationship between plants and their pollinators, the nature of circumnutation in climbing plant organs, and most importantly, the recognition of the importance of external factors in shaping plant movements. The emergence of scientific investigation spearheaded by Darwin regarding the behavior and response of plants has resulted in significant changes in the comprehension of plant behavior.

This chapter covers the many different domains of plant movement, starting with a comprehensive look at the hydraulic and mechanical instability processes that underpin these movements. Then moving forward to the realm of the movement types exhibited by plants. A pivotal focus of this investigation on plant movement lies in the enigmatic world of climbing plants, renowned for their unique ability to interact with and ascend preferred supports. The phenomenon of circumnutation movement and its mechanisms, which add a layer of complexity, will be introduced.

2.1. Plant Movements: The Mechanisms

Within the tranquil landscapes of the botanical sphere resides a realm characterized by hidden intricacies, whereby plant movements occur with precision and intentionality

(Castiello, 2020, 2023; Wang et al., 2021). Ever since Darwin's pioneering work, it has been shown that plants display systematic movements as a means to compensate for their inability to move from their stationary position (Darwin, 1875; Darwin & Darwin, 1880). The diversity and extent of the mechanisms governing the movement of plants is broad. Unlike animals who rely on muscular coordination, plants have evolved specialized fluid-driven mechanisms to generate movements. Hydraulic processes are the primary engine of plant movements, with the majority of these movements occurring over extended periods of time. Nevertheless, a rapid motion might be facilitated in plants by means of mechanical instability, upon reaching a certain pressure threshold in the cell walls.

Throughout all stages of growth, from shoot to root development, plants demonstrate both slow-motion movements driven by hydraulic principles and rapid motion facilitated by mechanical instability. In the long run, these mechanisms support plants to perform various adaptive movements for dealing with changes in their environment.

2.1.1. Hydraulicity

Plants deploy a hydraulic process that facilitates the flow of water in and out of their cells, via their semipermeable membranes. *Turgor pressure* and *osmosis* are the primary sources for generating movements in the modulation of cellular volume and tissue stiffness. Turgor pressure in plants arises from the osmotic flow of water, which is a force produced by the plasma membrane and the cell wall when they push against each other. An elevation in turgor pressure causes swelling in cellular volume, whereas a drop in turgor induces shrinkage. The range of turgor pressures fluctuates as small as 0.1 – 0.4 MPa in plant cells, and up to 4 MPa in the stomata (Franks et al., 2001; Taiz & Zeiger, 2002). Plants can be resilient by adjusting their internal pressure values through the process of osmosis. One feature that distinguishes plants from the majority of organisms is the presence of a cell wall that encloses their cells. This stiff cell wall, composed of cellulose microfibrils, is used to sustain a broad range of pressures, which is embedded inside a matrix of polysaccharides (Carpita & Gibeaut, 1993). The maintenance of pressure in cells is achieved through the continuous adjustment and equilibrium of an osmotic gradient between the cytoplasm of the cells and their surrounding environment. A high turgor pressure can induce a mechanical force, resulting in cellular deformation and observable macroscopic motion in plants.

In addition to the basic water exchange, there exists another type of hydraulic movement known as small reversible changes in cell volume. This can be altered within the elastic range, a phenomenon often influenced by the transportation of ions through specific pumps. The opening and closing of stomata are the most widely recognized reversible movements observed in plants (Meidner & Mansfield, 1968).

Hydraulic movements are widely observed in various plant species, and they operate as vital mechanisms in various fundamental processes involved in growth and development (Beauzamy et al., 2014; Cosgrove, 1987; Dodd, 2013; Fricke & Flowers, 1998; Steudle, 2000; Zimmermann et al., 2013). Growth, which manifests as the elongation of the stems, is the most pervasive phenomenon driven by hydraulicity.

The movements in plants can be attributed to a specific organ known as the *pulvinus*, which is located at the junction between the leaf and stem. According to Hill and Findlay

(1981), the angle of motion in the pulvinus can be altered due to a discrepancy in osmotic swelling or shrinking between its opposing sides. The pulvinus movement usually takes time; however, in unusual cases such as *Mimosa pudica*, it can occur within a matter of seconds. The foliage of mimosa plant has a double pinnate structure, with the leaves positioned at an angle of 60 degrees in reference to the stem. When they encounter a mechanical stimulation such as touch, shaking, or blowing, this stimulus triggers an action potential that propagates from the stimulated leaflet to the pulvinus. Following that, the action potential spreads from the pulvinus to other parts of the mimosa along the petiole, which is a structure that attaches the leaf blade to the stem. The mimosa plant exhibits an interesting movement whereby its leaflets move in pairs, ascending and closing along their upper surfaces, while simultaneously bending towards the apex of the scion. The scion, which refers to the part of the grafted plant responsible for developing shoots, exhibits a concurrent downward bending.

In addition to the hydraulic mechanisms driven by osmotic gradients, several events have demonstrated that osmotic gradients do not solely govern the processes of water exchange between cells and their external environment. *Passive actuation*, driven by humidity gradients, is one of the processes observed among others. When plants are exposed to a dry environment, they initiate passive movements that are influenced by the processes of hydration and dehydration. Plant species, including pollen grains, are consistently challenged by an uncomfortable osmotic environment (Katifori et al., 2010). When confronted with such a challenge, the phenomenon of evaporation occurs as cells are subjected to a dry environment characterized by a reduced partial hydraulic pressure, causing alterations in cellular volume. *Hygromorphs*, which are a different kind of humidity-induced movements, are observed within the sclerenchyma tissue in dead cells (Jost & Gibson, 1907). A degree of asymmetry in the orientation of the fibrils within the sclerenchymal cell wall reforms the local swelling/shrinking at the cellular level into a perceptible bend movement (Reyssat & Mahadevan, 2009).

2.1.2. Mechanical instability

Plant cells and tissues permit the flow of water between the cell membrane and plant tissue in order to support growth and expansion. Therefore, the speed of water-driven movements is constrained by the maximum transportation velocity in the organ body (Skotheim & Mahadevan, 2005). Some plant species have evolved several mechanical instabilities to generate rapid movements, surpassing the capabilities of basic water-driven mechanisms. These strategies operate by taking advantage of the water flow, propelled by osmotic or humidity gradients, to gradually store elastic energy within the cell walls. Once the pressure surpasses a critical threshold, it causes the overcoming of the energy barrier, leading to the abrupt release of elastic stress (Dumais & Forterre, 2012). Landau and Lifshits (1986) described the concept of geometric frustration as a mechanism to empower a movement like snap-buckling instabilities. This phenomenon is predicated upon a deformation mode in terms of elastic energy. In carnivorous plants, a thin shell can be structured in a certain configuration when the maximum energy barrier is not surpassed. However, accumulating elastic energy with increasing pressure can trigger the shell to surpass the energy barrier. Then, the stored energy is discharged as the system snaps into the minimal elastic energy configuration.

The rapid closure of the Venus flytrap (*Dionaea muscipula*) is one of the most well-known plant movements, which is marked by a snap buckling instability. The closure movements observed in Venus flytrap can be attributed to three phases: a slow initial phase lasting 1/3 second, followed by a rapid intermediate phase lasting 1/10 second, and finally a second slow phase lasting 1/3 second (Forterre et al., 2005). Upon the stimulation of the touch, the trap begins to operate, leading to the onset of a slow initial phase. During this phase, elastic energy is gradually stored until the energy storage reaches a critical threshold, at which point the open curvature of the trap becomes unsustainable. Then, the two lobes undergo a process of inward curvature during the phase of rapid intermediation. Lastly, a second slow snapping phase ensues to complete the motion. The closure process takes an extended period of time and exhibits a higher level of hydration compared to simply inertial snapping.

2.2. Types of Plant Movements

Plants demonstrate a remarkable assortment of movements that can often escape from our perception. They exhibit a remarkable ability to move, ranging from the curvature of their stems towards sunlight to the rapid folding of their leaves in reaction to tactile stimulation. The fascinating world of plant movements reveals complex dynamics that shape their interactions with the surrounding environment and bring out their ability to adapt. Among the plant movements, tropic and nastic movements emerge as captivating chapters in this narrative of botanical mobility (Darwin & Darwin, 1880).

2.2.1. Tropic movements

Plant tropisms refer to the phenomenon of plants undergoing a reorientation process in reaction to environmental stimuli, such as light and touch. Tropic movements are characterized by their relatively slow pace and extended duration. Each tropic response consists of its own assemblage of chemicals/hormones that play essential roles in perceiving signals, amplifying and attenuating signals, and facilitating the development of the growth response (Esmon et al., 2004). Positive tropism is an expression used to describe the behavior in which a stem exhibits bending towards a light stimulus, whereas negative tropism relates to the behavior wherein a stem moves away from it. Tropism covers a wide range of movements, including phototropism (i.e., response to light), gravitropism (i.e., response to gravity), thigmotropism (i.e., response to touch), heliotropism (i.e., the sun-tracking movement), chemotropism (i.e., response to chemicals), and hydrotropism (i.e., response to moisture). Below, I will present a review of the main tropic movements.

Phototropism

Undoubtedly, the phenomenon of plants exhibiting positive phototropic growth towards light has been a subject of considerable scientific interest. However, the underlying mechanism that governs this light-responsive behavior remained unclear until the reports by Darwin (Darwin, 1875; Darwin & Darwin, 1880). Darwin's observations focused on the phenomenon in which the tip of an oat coleoptile displayed a curvature towards the light source when exposed to lateral illumination. He hypothesized the existence of a light-sensing receptor located at the tip of the shoot. Following Darwin's pioneering insights, Went (1928;

1935) made significant advancements in identifying *auxin* (indole-3-acetic acid; IAA) as a substance that fosters growth. The redistribution of auxin within plants may potentially serve as the driving force behind their phototropic response. Auxin synthesis takes place within the shoot tip and is subsequently transported in a downward direction from the apex, this process is known as the basipetal movement (Goldsmith, 1966). The coordinated action of this process produces a discernible disparity in auxin distribution within the plant. The highest concentration of auxin is found at the tip of the shoot and gradually decreases as it is transported throughout the plant. The fluctuation in auxin concentration also gives rise to contrasting sensitivities, with the shoot tip exhibiting decreased sensitivity while the root exhibits increased sensitivity.

The Cholodny–Went theory elucidates the mechanistic underpinning of phototropic response, particularly in cases where the incident light does not exactly coincide with the apex of the shoot but instead arrives at an oblique angle (Trewavas, 1992). The arrival of imbalanced light input leads to varying amounts of illumination on opposite sides of the shoot tip. As a result, a greater influx of auxin is directed towards the less illuminated side, instigating cell expansion in that region, thereby inducing the curvature of the shoot towards the direction of the light source.

While positive phototropism is a commonly observed phenomenon in plants, it is important to note that plant behavior also includes instances of negative phototropism. It is worth noting that certain climbing plants demonstrate a preference for growing in the direction of shaded areas. In a similar vein, Ruppel et al. (2001) determined that red light photoreceptors induce a reorientation of root tips away from the source of light in

Arabidopsis. These intriguing instances underscore the nuanced and diverse nature of plant responses to light stimuli.

Thigmotropism

Thigmotropism, a phenomenon that refers to directional response caused by the induction of differential growth upon physical touch. The core principle of thigmotropism is based on the phenomenon of unilateral growth inhibition, where the rate of growth on the side of the stem that is touched is suppressed compared to the opposing side. The development of elaborate growth patterns can be observed in flowering plants, fungi, tendrils, and twining plants. Darwin's work (1875) contributed to the understanding of the tactile perception displayed by climbing plant species, something they employ to identify the most suitable structure. The circumnutation movements shown by the shoot enable them to come into close proximity with a surrounding support, then they bend towards and finally, they encircle around it. The thigmotropic modality enables climbing plants to efficiently look for and capitalize on vertical supports. The case of pea plants is noteworthy, as their tendrils embody the thigmotropic reaction. The tendrils engage in oscillatory movements until they come into contact with a sufficient support structure, at which point they securely attach themselves to the neighboring substrate. Nevertheless, in cases where the attempt proves unsuccessful, many outcomes may arise, including rigidity, coiling initiation, or withering away (Darwin, 1875).

The interplay between thigmotropic movements and gravitropic responses reveals an intriguing dynamic (Massa & Gilroy, 2003). Root tip growth is an exquisite example of this "symbiotic" relationship, as its ideal development requires the integration of both tactile and gravitational inputs. When faced with obstacles, roots clearly demonstrate an evident negative thigmotropic reaction, which is coupled by a simultaneous suppression of the gravitropic response. This allows the roots to effectively avoid obstacles.

2.2.2. Nastic movements

In parallel with tropism, nastic movements are directional responses that occur irrespective of the stimulus's position. They are rapid, reversible, and non-directional movements exhibited by plants in response to various external stimuli. Nastic movements in plants allow rapid responses to environmental fluctuations, enhancing their prospects for survival and reproductive success. Some carnivorous plants, for instance, *Dionaea trap*, use orientational nastic movements in response to direction-independent stimuli. The initiation of these movements can be attributed to several causes, including temperature, mechanical stimulation, and circadian rhythms. It frequently arises from changes in the water content, ion concentration, or hormone distribution inside cells, leading to alterations to turgor pressure and the shape of cells. A range of nastic movements can be observed in plants, including nyctinasty (i.e., sleep movements), seismonasty (i.e., movements in response to mechanical stimulations), thermonasty (i.e., temperature response), epinasty (i.e., downward curvature), hyponasty (i.e., upward curvature), and circumnutation.

Epinasty & Hyponasty

Plants have developed intricate systems of movement in order to effectively respond and adapt to the ever-changing conditions in their environments. This adaptive reaction allows them not only to survive but also thrive in their environment. These responsive mechanisms frequently originate from changes in turgor pressure or growth patterns, wherein epinasty and hyponasty emerge as prominent examples of these responses.

Epinasty is featured as a downward curvature, driven by an augmented rate of cell expansion on the upper adaxial side of the organ compared to the lower abaxial side. It is jointly regulated by gravity, ethylene, and auxin. This movement is commonly observed in monocotyledons when the entire leaves show a curving response, or in dicotyledonous plant species where the upper side of the leaf petiole shows growth. Epinasty can also be observed in orthotropic structures, such as stems or pedicels. Notably, the region where the curvature is initially discernible undergoes subsequent acceleration in elongation, eventually culminating in an apical orientation, leading the organ's tip to form an angle with the vertical stem (Palmer, 1985). This response is frequently triggered in the presence of unfavorable environmental conditions, such as drought, waterlogging, salinity stress, or pathogenic invasion.

Hyponasty produces an upward bending curvature, contrasting with epinasty. This movement is frequently encountered in leaf clades of both monocotyledons and dicotyledons, as well as in leaf petioles (Voesenek & Blom, 1989). Notably observed among rosette species, hyponasty often emerges as a response to environmental challenges such as flooding, proximity to neighboring plants, or elevated ambient temperatures (Polko et al., 2011). The coordination of hyponastic responses is supported by an intricate link between ethylene and auxin. An example of this can be seen in semiaquatic plants such as *Rumex palustris*, where younger petioles display an upward curvature as a reaction to being fully submerged (Polko et al., 2011). In this scenario, auxin and gibberellins (GAs) function as downstream targets for ethylene, regulating specific stages of submersion-induced hyponasty. The onset of petiole hyponasty is primarily dependent on the transportation of auxin, but the initiation of hyponastic growth and the maintenance of maximal petiole angles are regulated by ethylene and gibberellins (Polko et al., 2011). The movement of hyponasty, when combined with increased linear elongation, enables plants to regain contact with the atmosphere, thereby facilitating the restoration of efficient gas exchange (Voesenek & Blom, 1989).

2.3. The Case of Climbing Plants

Climbing plants, a unique class of species, survive and thrive by finding potential host/support in the environment through hydraulic mechanisms. They have evolved specialized anatomical structures and physiological mechanisms to climb, attach, and cline onto physical objects. These plants exhibit fascinating growth patterns and adaptive responses that enable them to ascend vertical surfaces and enhance light acquisition and other vital resources.

Darwin (1875) described how he monitored the slow growth/movement of climbing plants that were visible to the human eye or carefully measured them at regular intervals. On the basis of these records, he was able to conclude that the leaves, stems, and roots of plants move in circles over long periods of time, coined as circumnutation (Darwin, 1875; Darwin & Darwin, 1880). He categorized climbing plants based on their climbing mechanisms into five main classes (see also Isnard & Silk, 2009):

i. Twining plants: This category includes plants that exhibit a helical movement trajectory with extensive arcs during the exploration of the potential support. Typical twining plants such as *Dioscorea spp.* and *Ipomoea spp.* adopt the movements of circumnutation in its growing organs.
ii. Leaf-climbers and irritable organs: Darwin described leaf-climbers as climbing with the help of a sensitive petiole that curves and grasps the support after contact. Leaf-climbers are commonly seen in tropical lianas and are known for their rapid circumnutating movements and sensitivity to touch (Treub, 1883).
iii. Tendril-bearers: Circumnutation movement is also found in tendril-bearers, most evidently at the tendrils. Tendrils are long, delicate, specialized organs with a threadlike shape derived from stems, leaves, or peduncles. Plants like *Pisum sativum* use tendrils as a means of finding a support and securing an attachment. Jaffe and Galston (1968) have delineated the three main movements observed in tendrils. The initial movement, circumnutation, involves a winding movement around a stimulus, enhancing the likelihood of contact with support. Following by the second movement which is known as contact coiling, wherein the tendrils exhibit a coiling behavior around the support. The third movement observed is referred to as free coiling, which occurs autonomously regardless of the type of stimulation. In this case, the tendrils exhibit a helical tube structure that wraps around its own axis.
iv. Root-climbers: Also known as clinging-climbers, are a class of climbing plants that uses their adventitious roots to attach and anchor themselves to vertical

surfaces. Root-climbing plants commonly have very little adhesive structures known as holdfasts or adhesive pads on their roots. These anatomical features are responsible for the secretion of substances that help with the adhesion of roots to surfaces, offering stability and support to the plant throughout its vertical growth. Some examples of plant species that fall under this category are Parthenocissus species and Hedera species.

v. Hook-climbers: The class of hook-climbers encompasses plants that use passive means such as recurved spines, hooks, or thorns to ease their climbing behavior. *Uncaria spp.* and *Rubiaceae* are considered to be the most exemplary. According to Darwin (1875) and Putz (1984), hook-climbers may not display spontaneous circular movements and have a lower level of adaptability for climbing. Hook-climbers use distinctive anatomical features in the form of unique hook-shaped structures that enable them to firmly adhere to various surfaces providing support.

After providing an overview of plant movements and specifically discussing climbing plants, it becomes evident that the movements exhibited by plants hold a wealth of scientific inquiry. My research is primarily centered on the phenomenon of circumnutation, the forthcoming sections will further introduce circumnutation and its underlying mechanisms, elucidating the physiological, cellular, and molecular processes involved in it. I shall also present some evidence from previous observations that shed light on climbing plants' preference toward supports characterized by specific features.

2.3.1. Circumnutation in climbing plants

Darwin (1875) described circumnutation as "*a continuous self-bowing of the whole shoot, successively directed to all points of the compass.*" Derived through careful observation, he defined circumnutation as a helical movement of organs, exhibiting morphological variations. Circumnutations can be observed across the plant kingdom, as they occur from the roots to the shoots in different plant species. The tips of the shoots, the leaves, and the roots, all execute a similar movement trajectory as sway in circles as they grow.

With circumnutations, shoots explore the outer world for finding a potential support while roots conquer the belowground to secure essential nutrient intake. Darwin's investigative focus was directed toward twining plants, as these species exhibit pronounced circumnutation in their twining stems. The heightened circumnutation in twining plants serves to increase the likelihood of encountering a suitable support structure. Some twining plants, such as *Dioscorea* species and *Ipomoea* species, showcase an enlarged radius during circumnutation. In these instances, the circumnutating stem assumes a distinctive configuration: it maintains a vertical orientation at its base, transitions to a straight and horizontal alignment around the apex, and then curves within a plane in the central portion of the stem (Isnard & Silk, 2009). During circumnutation, the stem conducts an intricate rhythmic dance to undulate upward around the vertical support. Soon after, the coil surrounds the supporting pole and tightens basally in a helical shape. The rhythmic pattern is altered when the stem encounters vertical support and the duration varies from approximately 2 to more than 9 hours (Darwin, 1875). Circumnutation occurs only during the process of growing, it determines an oscillation either clockwise or counterclockwise.

Most oscillation frequencies are around 50 µHz, therefore special methods such as time-lapse techniques are needed to estimate the trajectories.

In an examination presented by Stolarz (2009), a comprehensive assessment was put forth regarding circumnutation as a movement, focusing on its physiological, cellular, and molecular underpinnings. When quantifying and qualifying circumnutation, four parameters are commonly considered for measuring circumnutation, they are (i) the amplitude of circumnutations; (ii) the period of circumnutations — ultradian rhythm; (iii) the shape of circumnutations; (iv) the direction of circumnutations.

Circumnutation possesses a multifarious nature, which can be attributed to the convergence of many different factors such as hormone gradients, development patterns, and external stimuli. The mechanisms driving circumnutation involve a number of physiological aspects such as changes in cell volume, alterations in turgor pressure, fluctuations in ion concentrations, and interplay of hormones (Johnsson, 1997; Stolarz, 2009). These mechanisms are underpinned by distinct cellular events, including irreversible volume changes leading to elongation or contraction phenomena, or a combination thereof (Stolarz, 2009). To generate circumnutation, the coordinated and phase-synchronized cooperation of cells surrounding the circumnutating organ is essential. This collaborative effort involves key components such as the epidermis (Hejnowicz & Sievers, 1995), the endodermal cells (Hatakeda et al., 2003) and the interconnected plasmodesmata, facilitating intercellular communication (Stolarz, 2009). Ion channels that regulate ion and water fluxes also play a pivotal role. The distribution of ions, including Ca^{2+}, K^{+}, Cl^{-}, and proton pumps, intricately modulates circumnutation by influencing parameters like bending, amplitude, and period (Millet & Badot, 1996; Shabala & Newman, 1997a, 1997b; Zachariassen & Johnsson, 1988). This ion-mediated oscillation system contributes to the contraction/expansion model within the motor cells of organisms such as *Desmodium motorium* pulvinus (Engelmann, 1998).

Hormones, particularly auxin, are also significant contributors to the process. Asymmetrical auxin distribution within the organ fosters differential growth rates and curvature (Trewavas, 1992), thus facilitating circumnutation. This uneven auxin distribution is further influenced by external factors such as light, gravity, and mechanical forces (Went, 1935).

The initial exploration into circumnutation's regulatory mechanisms was made by Darwin, he described its endogenous nature (Darwin, 1875). He posited it as an inherent oscillator engendering a growth wave circumventing the elongating stem. Conversely, Israelsson and Johnsson (1967) proposed an exogenous model, attributing circumnutation generation to external stimuli such as gravity. They interpreted circumnutation as a gravity-mediated tropic movement. Subsequent investigations on *Helianthus annuus* affirmed that alterations in gravitational forces impact circumnutation's amplitude, period, and intensity (Andersen & Johnsson, 1972; Johnsson & Israelsson, 1968). Synthesizing these perspectives, an amalgamative view emerged, suggesting that circumnutation arises from the interplay between endogenous and exogenous influences. Brown's work (1993) indicated that circumnutation arises from both intrinsic oscillation and gravitational effects, offering empirical evidence that gravity, while influential, is not an exclusive determinant. Through meticulous experimentation, Brown effectively invalidated gravity's indispensability and delineated a model involving growth-sensitive symplastic communication control.

2.3.2. Host preference in climbing plants

Scientists have long been intrigued by the specialized adaptations of climbing plants that enable them to compete for necessary resources, such as sunlight (Niklas, 2011). However, despite this prolonged fascination, we know surprisingly little about how climbing plants make decisions with regard to stimulus searching and attachment behaviors. In fact, climbing plants can be an ideal model system for studying the decision-making in plants because they show rapid changes in response to environmental cues (Gianoli, 2015). For them, finding a suitable support upon which they can climb is among the most important factors affecting their growth and development (Gianoli & Gonzalez-Teuber, 2005). Among the myriad aspects of support-searching behavior, one particularly fascinating phenomenon has garnered considerable attention: their distinct preference for supports of varying diameters. This distinctive preference has been widely documented across a spectrum of climbing plant species, prompting an extensive inquiry into the intricate interplay of underlying physiological, biomechanical, and ecological factors that underpin this remarkable behavior (Gianoli, 2015; Putz, 1984).

Darwin (1875) noted that vines are not only able to locate potential supports and grow towards them, but they can even show an aversive response. He first described this effect with regard to the *Bignonia capreolata* tendrils that initially seized and then let go of sticks that were inappropriate in terms of size. If, because of its thickness, a stimulus was perceived as inadequate, after initially seizing it, the tendrils let go of it (Darwin, 1875). This case provides a degree of support to speculative claims that some climbing plants can judge the thickness of potential supports and modify their circumnutation patterns to a greater or lesser extent, depending on the features of potential supports with respect to what would be expected by chance movement.

Recent investigations conducted in forest settings have revealed a proclivity among climbing plants often display preferences for smaller supports over larger ones, owing to various factors including mechanical stability, resource allocation, and growth strategies (Gianoli, 2015; Givnish, 1995). Climbing plants, such as lianas, tend to flourish in early successional habitats where supports in smaller diameters prevail (Dewalt et al., 2000; Ladwig & Meiners, 2010; Putz, 1984), underpinning their augmented suitability for liana recruitment (Leicht-Young et al., 2010). In the scenario where fewer small diameter supports endure in the understory during the progression of forest successions, lianas in old-growth forests have typically established themselves during early succession or possess mechanisms like root-climbing that facilitate ascent onto larger diameter trees (Morrissey et al., 2009; Putz, 1984; Schnitzler, 1995). The abundance of liana species that use different climbing mechanisms is also predicted to change with succession. Stem twiners and tendril climbers, reliant on small diameter supports, dominate early successional stages, whereas root climbers, adhering to trunks instead of encircling them, are primed for ascending larger diameter trees in later stages of succession (Hegarty & Caballé, 1991; Putz & Holbrook, 1992).

CHAPTER 3

APPROACHES TO STUDY PLANT MOVEMENT

"The wonder is that we can see these trees and not wonder more."

Ralph Waldo Emerson

Over time, a wide range of approaches have been devised to gain a deeper understanding of plant behavior. I shall start the chapter by presenting a preliminary method to track plant movement, then move to outline cutting-edge methods — time-lapse photography and motion analysis — that enable us to observe and track plant movements with greater precision. Later, I will focus on the forefront of methodological advancement in current research, that is, the use of machine learning techniques and how they might contribute to the field of plant behavior. This new approach allows us to automatically identify diseases, stress, and electrophysiological signals in plants. At last, I will discuss the promise that machine learning holds in decoding plant movement. By combining classic approaches with computational capabilities current research is on the verge of uncovering novel aspects of plant behavior.

3.1. Classic Approach

Darwin designed several methods to track and document the movements of plants (Darwin, 1875; Darwin & Darwin, 1880). Through methods that may appear limited, he characterized phototropism, geotropism, and circumnutation. Darwin made detailed documentation of plant growth and movement, such as the direction, rate of growth, the curvature of plant organs, and the patterns of movement observed over time.

Darwin and his son Francis Darwin (1880), long before time-lapse photography came into play, they studied plant movements using a very time-consuming, low-tech procedure: they suspended a glass plate above a plant and marked on the glass the position of the tip of the plant every few minutes for several hours. By connecting the dots, they mapped out the exact movements of their subject. And they concluded that when comparing plant movements to animal movements, plant movements had "*at least the ghosts of similar qualities*" (Darwin, 1901). Following this path, in the early 20th century, Sir Jagadish Chandra Bose invented a device known as the "crescograph," which uses a collection of mechanical gears and a smoked glass plate to register the movement of both the shoots and roots of the plants (Bose & Das, 1919). The precision of the apparatus enables to magnify negligible movements up to 10,000 times.

Time-lapse photography/videography involves shooting a sequence of photos or frames of a plant at a regular interval, it generates videos where the frame rate is much lower than the rate used to view the sequence of the frames. When these frames are played in rapid succession, they form a video sequence that visually reveals changes and movements that take place slowly over time. This technique is widely used to study plant movements and growth dynamics because of its ability to accentuate processes and motions that are typically imperceptible to the human eye.

Wilhelm Pfeffer was inspired by the stop-motion gallop of a racehorse filmed by Eadweard Muybridge. Between the years 1898 and 1900, he created the first time-lapse videos for the purpose of scientific examination of plant movement. Videos were created to reveal the sleep movements of *Desmodium gyrans* and *Mimosa spegazzinii*, the root network development in *Vicia faba*, and the curving movement of gravitropism in *Impatiens glandulifera*. Pfeffer acknowledged the prospective value of imaging techniques, expressing his opinion that "*Photographic registration will probably be largely employed in the future, for series of pictures may be obtained which when placed in a kinematograph show the phases of several days' or weeks' growth in a minute or so*" (Pfeffer, 1900).

The use of time-lapse photography has proven to be highly valuable for the study of plant movements, in particular, circumnutation/nutation (Caré et al., 1998; Guerra et al., 2019; Head, 1965; Raja et al., 2020). By capturing frames at regular intervals, researchers can examine the patterns of circumnutation, revealing details about its amplitude, frequency, and symmetry. This examination and analysis of movements exhibited by plants usually requires the implementation of several techniques and methodologies. Time-lapse photography is usually combined with motion analysis to augment the findings through the quantitative study of the movements and behaviors in a two-dimensional (2D) plane or three-dimensional (3D) space. Motion analysis can be autonomous and semi-autonomous, both involve the tracking of targeted movement within a given plane or space. Within these techniques, 3D motion analysis stands out as an effective tool for reconstructing the trajectory of moving objects in space by the complete inclusion of movements in all three dimensions. Typically, it follows the path taken over time and space by a recognizable part of the observed plant organ (Fiorello et al., 2020). Motion analysis further enables the examination of kinematics and extraction of relevant features for motor control. The integrated approach provides the opportunity to understand plants' patterns of behavior, and can boost our understanding on the biomechanics that govern plant behaviors.

Although morphologies in circumnutation vary among different climbing species, several parameters (e.g., amplitude, period, shape, and direction) are typically estimated by tailoring them to individual experimental models. To investigate the mechanism responsible for circumnutation, which could be driven by changes in cell volume, the researchers analyzed the epidermal cells of *Phaseolus vulgaris* during the processes of cell elongation and oscillatory movement (Caré et al., 1998). Throughout the course of the experiment, a series of photographs were captured at ten-minute intervals using time-lapse photography. This methodology was employed to document the morphological changes of the epidermal cells and to concurrently record the movement of the shoot. Reversible changes in cell length were revealed in the bending area and were responsible for circumnutation.

The integration of kinematic analysis obtained through time-lapse photography and motion analysis holds significant value not only in its present application for comprehending the features of organism behavior, but also in its potential to enhance the field by inspiring the development of artificial intelligence systems aimed at simulating plant-inspired robots (e.g., Plantoid robot) and constructing distributed cognitive process (Laschi et al., 2016; Wooten et al., 2018).

3.2. Machine Learning Approach

The horizon of plant behavior research continues broadening through the integration of machine learning (ML) techniques. ML itself is a multidisciplinary approach to data analysis that embraces probability theory, statistics, decision theory, visualization, and optimization (Singh et al., 2016). ML is applied to achieve a higher degree of automation and reduce the need for manual intervention and subjective judgment in the process of data collection and analysis. Through learning, ML algorithms strive to produce results that are more objective and accurate. By efficiently learning from a substantial amount of data in a short time, it enables us to draw conclusions and make inferences, especially when faced with unstructured data that poses challenges in determining the appropriate dimensions. Therefore, in a transformative shift, ML algorithms may offer a novel lens through which to explore plant behaviors. Several ML approaches have recently achieved impressive performance on a variety of predictive tasks, such as species identification (Carranza-Rojas et al., 2017; Unger et al., 2020), plant distribution modeling (Botella et al., 2018; Zhang & Li, 2017), weed detection (Yu et al., 2019), stomatal classification (Aono et al., 2021), and forest monitoring (Jodas et al., 2022). They are also being applied to questions of comparative genomics (Xu & Jackson, 2019), gene expression (Mochida et al., 2018), and conducting high-throughput phenotyping (Singh et al., 2016; Ubbens & Stavness, 2017) for agricultural and ecological research.

Taking the context of plant behavior, ML has been implemented and proved to be reliable in the detection and identification of plant disease and stress, mainly through phenotyping (Lowe et al., 2017; Rumpf et al., 2010; Singh et al., 2016; Singh et al., 2018), and electrophysiology (Najdenovska et al., 2021; Parise et al., 2021). The standard approach to disease and stress detection/identification relies on checking the observable signs and symptoms that frequently manifest at the middle to late stages of infection. The procedure to identify the causal agent is through either manual detection or diagnostic tests, both of which require a lot of time and labor in the field. That said, the application of ML techniques for high throughput phenotyping which entails training models on large datasets of healthy and stressed plant parts, would enable researchers to obtain rapid disease diagnosis and stress detection. For instance, employing deep learning models such as convolutional neural networks (CNN) to process hyperspectral image analysis techniques for the detection and classification of plant disease and stress were tested and demonstrated the capacity in qualifying the disease and quantifying the severity (Lowe et al., 2017).

ML algorithms can serve as a valuable tool for conducting phenotyping tasks that are time-consuming and demanding. More so, these algorithms have the capacity to detect and identify subtle phenotypic changes associated with disease or stress, leading to a pre-symptomatic diagnosis even before the onset of the disease (Rumpf et al., 2010; Singh et al., 2016). For instance, Rumpf et al. (2010) employed machine learning techniques based on Support Vector Machine and spectral vegetation indices to study the early detection and classification of sugar beet disease before it is visible. The potential of pre-symptomatic detection of the plant diseases was demonstrated, depending on the type and stage of disease the classification accuracy was between 65% and 90%.

ML can be used to analyze electrophysiological signals emitted by plants under stress, as plants show the capacity of generating and propagating electrical signals (Trebacz et al., 2006; Volkov et al., 2000; Zimmermann et al., 2009), including action potentials (APs), variation potentials (VPs), also called slow wave potentials (SWPs), local electrical potentials (LEPs), and system potential (SP). Automated monitoring of plant development is becoming a key enabler for optimized agricultural production (Navarro et al., 2020), plant electrical signals as an early event in the plant–stimulus interaction (Li et al., 2021) could be highly informative. The application of ML techniques has been employed to investigate the electrical response of tomato plants cultivated in a conventional production setting (Najdenovska et al., 2021). This work aims to examine the plant's electrical reaction to various stress factors, including drought, nutritional deficits, and infestation by spider mites. The classification has been shown to be effective in automating the monitoring of plant development and accurately classifying different types of stress in plants.

A recent electrophysiological study used machine learning techniques to analyze data and revealed that dodder (*Cuscuta racemosa*) exhibits host-directed attention through electromic dynamics. Parise et al. (2021) provided clear evidence indicating a significant alteration in the electrical signaling of dodders when they perceive the presence of a nearby host. This observation suggests that dodders possess the ability to discern various host species even from a distance.

Drawing inspiration from the above-mentioned studies, the potential to harness machine learning in the study of plant movements opens a promising avenue. While this application remains largely unexplored, it holds the potential to provide insights into cognitive behavior in plants and might be an alternative method of facilitating our understanding in plant movements and enabling predictive behavior in plants.

Predicting plant behavior through their movement is important for several reasons. Realistic predictions could aid in the formation of conservation strategies to combat the decline in biodiversity. For example, predicting movement might be important in the context of understanding the spread of infectious diseases through plant species. Many diseases are spread through different means of communication between individuals. Realistic predictions of the movement of infected individuals can suggest interventions that will optimally alleviate the further spread of diseases. Moreover, ML can catalyze advancements in modeling plant growth and development, along with the simulation of robotic plants (Fiorello et al., 2020; Laschi et al., 2016). Computational plant models or "virtual plants" are increasingly seen as useful tools for comprehending complex relationships between gene function, plant physiology, plant development, and the resulting plant form (Prusinkiewicz, 2004).

We have seen great development, extending from Charles Darwin's preliminary approaches to machine learning techniques. The study of plant behavior has evolved to encompass a broad spectrum of methodologies. Time-lapse analysis continues to provide sound and valuable insights into the movements of plants. Meanwhile, the integration of machine learning is expanding our understanding of plant responses, enabling disease identification, stress detection, and possibly, movement analysis. Hopefully, the potential convergence of traditional methodologies and machine learning holds promise for enhancing our understanding of plant behaviors and their interactions with the environment.

CHAPTER 4

MY RESEARCH

Understanding behavior in climbing plants is a continuous and evolving endeavor. The investigation of climbing plants has been approached from various perspectives, including phylogenetic, morphologic (Rowe et al., 2004; Rowe & Speck, 1996) as well as chemical composition and ultrastructural organization (Hoffmann et al., 2003). Little thought has been given to the organization of their movements as they show rapid changes in response to environmental cues such as a suitable support. Although the exploration of plant movements can be traced back to Darwin's work (Darwin, 1875; Darwin & Darwin, 1880), our knowledge of plant movements remains in its nascent stage. A reason behind this lack of interest is the fact that plants movements are so slow as to be imperceptible to the naked eye.

Time-lapse photography may be used to speed up plant movements to a human perceptual level, allowing us to appreciate it. This methodological approach aims to accentuate the behavior of plants rather than artificially simulating animal movement. We can use this strategy to observe the real nature of plants' behavior. Just as watching videos of animals in slow motion to observe hidden details, we can view time-lapse videos of plants exposing meaningful variations.

Since climbing plants require external hosts/supports for their growth, the characteristics of the support such as size, material, color, and shape also play a pivotal role (Darwin, 1875; Gianoli, 2015; Guerra et al., 2021; Guerra et al., 2019; Price & Wilcut, 2007; Runyon et al., 2006; Wang et al., 2023a). Finding, approaching, and grasping a potential support is crucial for climbing plants, potentially impacting upon the overall wellness of the plants. Although numerous studies conducted on the behavior of climbing plants have provided insights into the mechanisms involved in support-searching and attachment, far fewer studies have addressed the ecological significance of support-searching behavior and the factors that affect it. Among these, the diameter of supports influences their suitability. Climbing plants often display preferences for smaller supports over larger ones. However, the extent of our knowledge regarding the decision-making processes of climbing plants in relation to support-searching and attachment behaviors is rather limited.

Another matter of concern is the predominant reliance on field observations that document morphological and physiological responses (Putz & Holbrook, 1992), as well as laboratory studies that focus on the characterization of movement patterning through the use of time-lapse photography (Guerra et al., 2021; Raja et al., 2020; Stolarz & Dziubińska, 2017). Whilst this body of research provides quantitative data, the process might be admittedly subjective and rather preliminary. Machine learning approaches could potentially serve as an objective alternative to facilitate a precise phenotypic characterization. The application of machine learning in addressing questions related to plant biology is still in its infancy, yet the applicability of these methods to a broad range of problems is evident

(Botella et al., 2018; Carranza-Rojas et al., 2017; Mochida et al., 2018; Schuettpelz et al., 2017; Singh et al., 2016; Unger et al., 2020). To date, employing machine learning approaches for the purpose of modeling or predicting plant movements remains unexplored. The ability to predict plant behavior on the basis of their movement is of great significance for both ecological purposes and agricultural applications. Realistic predictions could aid in the formation of conservation strategies to combat the decline in biodiversity.

Therefore, the main objective of my research is twofold: firstly, to scrutinize the movements of pea plants through the combination of time-lapse photography and 3D motion analysis; secondly, to examine plant movement, specifically circumnutation, by exploiting the potential of machine learning techniques.

PART II

METHODOLOGY

CHAPTER 5

GENERAL METHODS

In this chapter, I will describe the methodologies and procedures that are common to all experiments. Instances that deviate from what is included in this chapter will be reported within the *Materials and Methods* section for each specific experiment.

5.1. Sample Description

Pea plants (*Pisum sativum* var. saccharum cv Carouby de Maussane; from now on *P. sativum*) were chosen as the plant model. They are annual climbing plants with tendrils, modified leaves used by the plants to approach and grasp a suitable support in the environment (Figure 5.1). Healthy-looking *P. sativum* seeds were selected, potted, and kept under different experimental conditions. For each experiment, plants were randomly assigned to the experimental conditions.

5.2. Type of Support

The supports were wooden cylindrical poles of 54 cm in height varying in diameter (13, 30, and 40 mm) positioned at 10 cm in front of the plant.

Figure 5.1. A photograph representing a *P. sativum* plant grasping a wooden pole.

5.3. Growth Setup

Plants grew individually in a thermo-light-controlled growth chamber (Cultibox SG combi 80 × 80 × 160 cm; Figure 5.2a). The temperature was set at 26 °C by means of an extractor fan equipped with a thermo-regulator (TT125 vents; 125 mm-diameter; max 280 mc/h) and an input-ventilation fan (Blauberg Tubo 100 – 102 m^3/h). The two-fan combination allowed for a steady air flow rate into the growth chamber with a mean air residence time of 60 seconds. The fan was carefully placed so that air circulation did not affect the plants movements. Cylindrical pots (40cm in diameter, 20cm in depth) were filled with river sand (type 16SS, dimension 0.8/1.2 mm, weight 1.4) and positioned at the center of the growth chamber. Each plant was exposed for 12 hours (6 a.m. to 6 p.m.) to a cool white led lamp (V-TAC innovative LED lighting, VT-911-100W, Des Moines, IA, USA) that was positioned 50 cm above each seedling. Photosynthetic Photon Flux Density at 50 cm under the lamp in correspondence with the seedling was 350 $\mu mol_{ph}/(m^2 s)$ (quantum sensor LI-190R, Lincoln, Nebraska, USA). At the beginning of each experiment, the pots were fertilized using a half-strength solution culture (Murashige and Skoog Basal Salt Micronutrient Solution; see components & organics). The pots were watered three times a week using distilled water (Sai Acqua Demineralizzata, Parma, Italy).

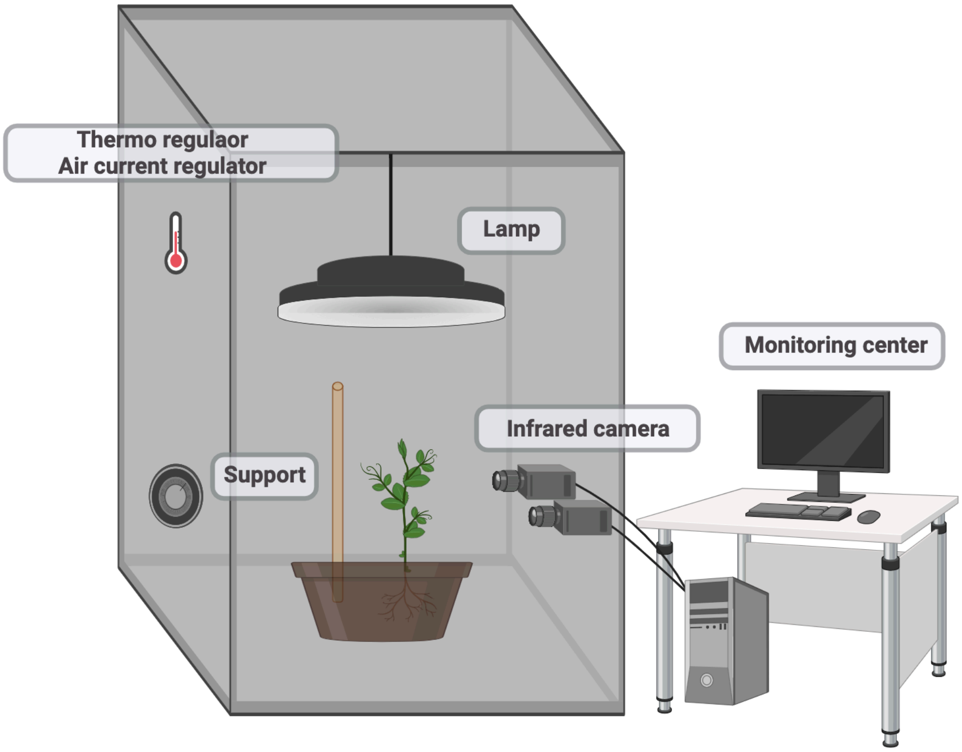

Figure 5.2. Graphical illustration of experimental setup and demonstration of how plants were captured by the infrared cameras.

5.4. Kinematics

5.4.1. Data acquisition and processing

For each growth chamber, a pair of RGB-infrared cameras (IP 2.1 Mpx outdoor varifocal IR 1080P) were placed 110 cm above the ground, spaced at 45 cm to record stereo images of the plant. The cameras were connected via Ethernet cables to a 10-port wireless router (D-link Dsr-250n) connected via Wi-Fi to a PC. The frame acquisition and saving process were controlled by CamRecorder software (Ab.Acus s.r.l., Milan, Italy; Figure 5.2b). Each camera's intrinsic, extrinsic, and lens distortion parameters were estimated using a Matlab Camera Calibrator App. Depth extraction from the single images was carried out by taking 20 pictures of a chessboard (squares size 18 × 18 mm, 10 columns × 7 rows) from multiple angles and distances in natural non-direct light conditions. For stereo calibration, the same chessboard used for the single-camera calibration process was placed in the middle of the growth chamber. The two cameras synchronously acquired the frame every 180 seconds (frequency 0.0056 Hz). RGB images were acquired during the daylight cycle and infrared images during the night cycle.

The main anatomical landmarks of interest were the tendrils developing from the studied leaf. I considered the initial frame as the one corresponding to the appearance of the tendrils for the considered leaf. The end frame was defined as the frame in which the tendrils start to coil the support or before the plant falls, depending on the experimental conditions. Images from both left and right cameras in order to reconstruct 3D trajectories were used. An ad hoc software (Ab.Acus s.r.l., Milan, Italy) developed in Matlab was used to identify anatomical points to be investigated by means of markers, and to track their positions frame-by-frame on the images acquired by the two cameras to reconstruct the 3D trajectory of each marker. The markers on the anatomical landmarks of interest (i.e., the tendrils) were inserted post-hoc. The tracking procedures were at first performed automatically throughout the time course of the movement sequence using the Kanade-Lucas-Tomasi (KLT) algorithm on the frames acquired by each camera, after distortion removal. The tracking was manually verified by the experimenter, who checked the position of the markers frame-by-frame. The 3D trajectory of each tracked marker was computed by triangulating the 2D trajectories obtained from the two cameras. Finally, the trajectory was reconstructed in 3D (x, y, z), where the x-z plane is the horizontal plane, and the x-y plane and z-y plane as the vertical planes perpendicular to each other.

5.5. Machine Learning Approach

Machine Learning algorithms are a collection of algorithms that possess the unique characteristic of not being entirely determined by programmers. They iteratively learn the target function through the manipulation of data. In essence, data serves as the fuel behind the functioning of machine learning algorithms. The primary methodology employed for my experiments was the supervised machine learning classifiers. Anomaly detection was also employed as a novel exploratory technique.

5.5.1. Supervised machine learning classification

In the context of the supervised machine learning adopted in Chapters 10 and 11, the algorithms require a set of sample data in order to learn how to accurately predict the growth conditions of plants. This entails the development of functions that can effectively capture the relationship between the input variables and the target variable. These samples were represented in a matrix by means of two primary vectors: x, and y. The vector x denotes a set of characteristics that the algorithms can use to distinguish between plants.

Specifically, these characteristics correspond to the features extracted from plant movements. Hence, it is crucial to ascertain the salient features associated with the definition of vector x. The vector y represents the target variable (i.e., the growth condition of a plant), that is associated with the target function when considering the corresponding vector x. The sample in this way, was referred to as a vector x and its corresponding vector y, which are represented as follows:

$$\left\{\begin{pmatrix} x_1^1 & x_2^1 & x_3^1 & \cdots & x_m^1 \\ x_1^2 & x_2^2 & x_3^2 & \cdots & x_m^2 \\ x_1^3 & x_2^3 & x_2^3 & \cdots & x_m^3 \\ x_1^4 & x_2^4 & x_3^4 & \cdots & x_m^4 \\ \cdots & \cdots & \cdots & \cdots & \cdots \\ x_1^n & x_2^n & x_3^n & \cdots & x_m^n \end{pmatrix}\right\} f(p) \left\{\begin{pmatrix} y^1 \\ y^2 \\ y^3 \\ y^4 \\ \cdots \\ y^n \end{pmatrix}\right\}$$

n: number of samples available in the dataset (i.e., plants);

m: number of features that are used to represent a sample (i.e., extracted features);

p: the number of dimensions used to describe the target (unknown) function;

$x \in \mathbb{R}^{n,x,m}$: the matrix of features where each row in this matrix is associated with the feature description of a single plant, and each column represents a single feature;

$y \in \mathbb{R}^{n,x,p}$: the target matrix, where the "ground truth" associated to the features matrix x.

The matrices x, y are the most important within the machine learning framework. These matrices enable the algorithms to acquire knowledge regarding a generalized function based solely on the samples present in the input dataset. Supervised learning requires making use of labeled data, wherein each input sample is paired with a matching answer. The labels serve as indicators of accurate results. After the classifiers have undergone training with supervision, they will be tasked with performing classification on unlabeled datasets. The process of standard classification consisted of several sequential phases.

Data preprocessing is a fundamental step in data analysis, involving various transformations done to raw data in order to obtain a refined and clean dataset. At this stage, the process of feature extraction is undertaken. This involves transforming the input data into a set of features that effectively capture pertinent characteristics or information related to the samples. These features serve as the foundation for the algorithm to identify and assimilate patterns.

The selection of the machine learning model is determined by the characteristics of the dataset. The data are partitioned into a training set and a test set in order to reduce potential biases while addressing concerns related to overfitting. During the training process, the model develops the ability to establish a mapping between the input features and their associated output labels by iteratively modifying its internal parameters.

The loss function, which evaluates the degree of concordance between the model's predictions and the true labels, is established. Consequently, the disparity between the predicted and real values is measured (Hastie et al., 2009). In this particular scenario, a commonly utilized zero-one loss function L was employed to evaluate the performance of a hypothesis function by quantifying the number of errors it generates on the training dataset.

$$L(\hat{y}, y) = [\hat{y} \neq y]$$

After undergoing training, the phase of generalization and prediction was initiated. The model became capable of making predictions or classifying novel input data by employing a developed function that relates features to labels. The performance of the models was evaluated using accuracy as the metric for classification.

5.5.2. Unsupervised anomaly detection

Unsupervised anomaly detection is a methodology employed to identify uncommon and atypical occurrences within a dataset, obviating the necessity of assigning labels to individual samples. The assumption of normality in the model posits that the majority of data points conform to regular distribution, whereas anomalies or outliers represent cases that vary from this presumed regular pattern.

The anomaly score was determined by calculating the similarity score using various learning techniques, including clustering, density-based methods, dimension reduction, ensemble approaches, or by modeling typical patterns of behavior. After mode assignment, a list of anomalous points was generated based on a predetermined threshold or gradient.

PART III

THE KINEMATICAL EXPERIMENTS

CHAPTER 6

A KINEMATICAL STUDY ON PEA PLANT MOVEMENT

6.1. Introduction

Experimental evidence demonstrates that some climbing plants are able to orient their movement towards a potential support (Raja et al., 2020). Based on prior kinematic findings (Ceccarini et al., 2020a, 2020b; Guerra et al., 2019), it can be inferred that the movement of pea plants is goal-directed and anticipatory. At the time the potential support is perceived trajectory for stem and tendrils start to veer towards it and the kinematic patterning differs with respect to when a plant moves in the absence of a potential support in the environment. Although the use of kinematic presents some limitations it remains the gold-standard approach to study movement in a variety of species and domains (Castiello, 2005; Castiello & Dadda, 2019). And, therefore, it has the potential to unravel the nature of plants movements.

The aim of this experiment is twofold. First, to validate the previously reported kinematical differences observed in pea plants depending on the presence or absence of a potential support. Second, to acquire data for the first implementation of machine learning classifiers based on the kinematics of plants movements (Chapters 9 & 10).

6.2. Materials and Methods

6.2.1. Subjects

A total of 32 snow peas (*P. sativum*) were chosen as study plants. Once germinated, one healthy-looking sprout was selected and randomly assigned to the experimental conditions.

6.2.2. Type of support

Wooden support of 13 mm in diameter was used. Support was 54 cm in height. The supports were inserted 7 cm below the soil surface, and were made available to the plants immediately after germination.

6.2.3. Experimental conditions

19 plants were grown individually in chambers without the presence of a support ("no support" condition; Figure 6.1a); 13 plants were grown individually in chambers where a potential support was present ("support" condition; Figure 6.1b).

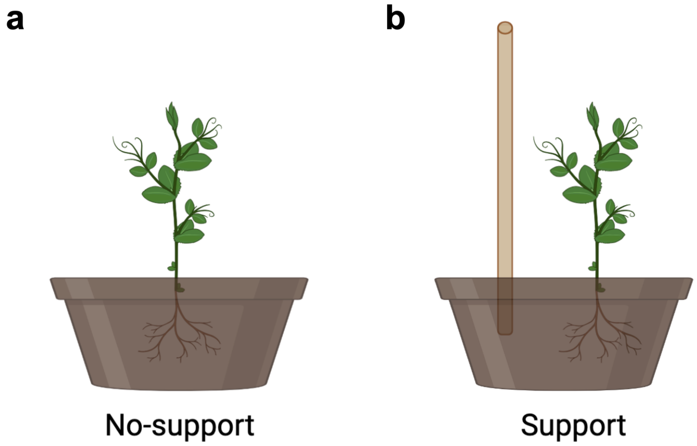

Figure 6.1. Graphical representation of the experimental conditions: (a) "no support" condition, and (b) "support" condition.

6.2.4. Dependent measures

The anatomical landmarks of interest were the "tendrils" and the "junction" (Figure 6.2), developing from the considered leaf. Kinematic features were analyzed to ascertain whether they differed for the "no support" and the "support" conditions. This aspect is fundamental to verify the ability of machine learning tools to discriminate between conditions.

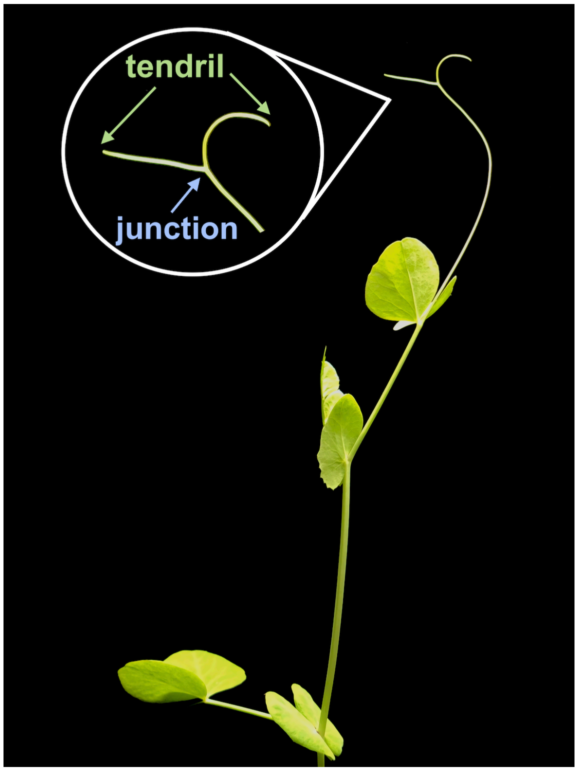

Figure 6.2. The anatomical landmarks of interest were the "tendrils" and the "junction" developing from the considered leaf. The "tendrils" refers to the tip of the shoot, and the "junction" refers to the point where the tendrils tie together.

The considered dependent measures were:

i. <u>The junction and the tendrils velocity</u> (Figure 6.3): 3D trajectories for the junction and the tendrils were acquired in Cartesian coordinates (*x*, *y*, *z*), where the x and y axis form the vertical dimension, and the x and z form the horizontal dimension. The coordinates for the tendrils are termed as (x_t, y_t, z_t), and those for the junction as (x_n, y_n, z_n). The velocity of the junction was calculated by computing the absolute value between the difference with n_i frames and n_{i+1} frames (i: 1, 2, 3, …, n). The velocity of the tendrils and the junction for each axis (v_x, v_y, v_z) and for each frame were acquired.

ii. The junction and the tendrils acceleration: acceleration for the junction and the tendrils were calculated as a velocity derivative.

iii. Tendrils aperture: relative vectors from the junction to the tip of the tendrils were extracted by calculating the mean of the tendrils ($\overline{X}_t$, $\overline{Y}_t$, $\overline{Z}_t$), minus the coordinates of the junction (x_n, y_n, z_n). Depending on the number of tendrils that one plant possesses, the tendril number could be either two or three. The standard deviation of the tendrils (σ_x, σ_y, σ_z), indicates the variability of the tendrils' aperture.

iv. Overall movement duration: the total amount of time in minutes that plant used to circumnutate.

v. Movement duration for single circumnutation: the amount of time in minutes that plant used to circumnutate once.

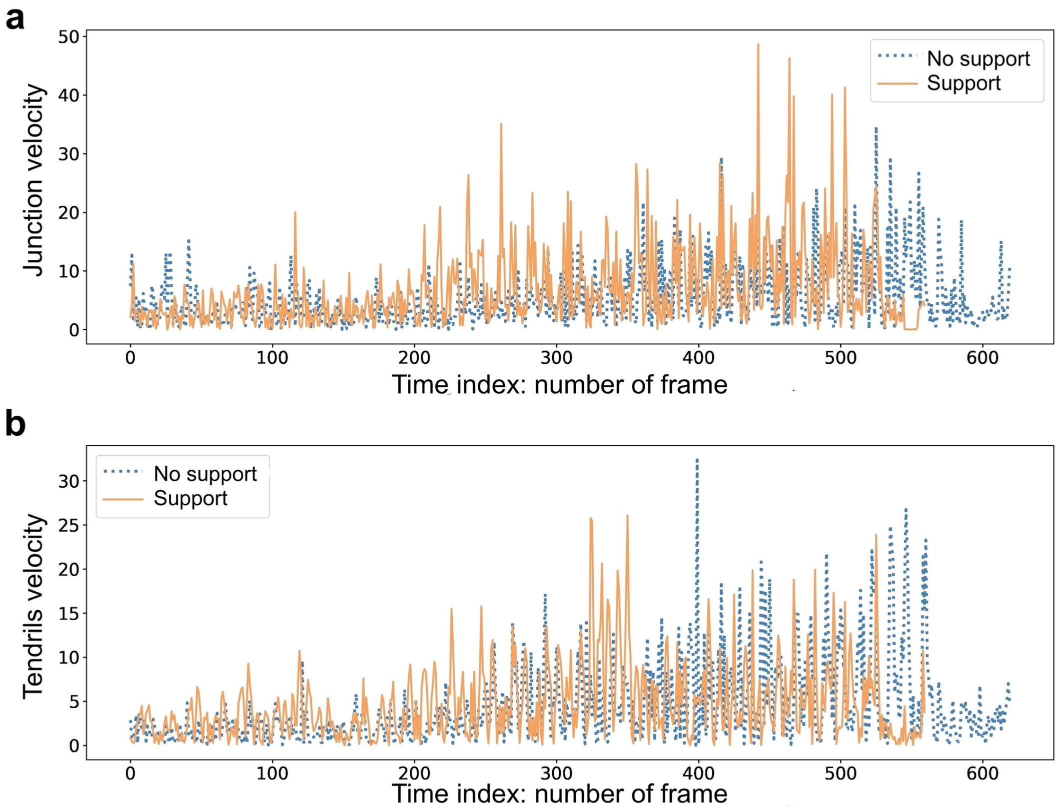

Figure 6.3. Graphical examples for (a) the junction velocity and (b) the tendrils velocity for the "no support" and the "support" conditions in time.

6.2.5. Statistical analysis

The Mann–Whitney U test as a non-parametric test was adopted. In this analysis, W is calculated as the smaller of the rank total between the two groups, and the size of the effect calculated as $r = z\sqrt{N}$ where z is the z-score and N is the total number of observations was also considered.

6.3. Results

6.3.1. Qualitative results

For all plants and for both the experimental conditions (i.e., "no support" and "support"), the tendrils and junctions displayed a circumnutating growing pattern. The plants that grew in the absence of the support continued to circumnutate toward the light source and then fell. For the plants that grew in the presence of the support, as soon as they sensed it, they strategically altered the movement trajectory so to bend towards it and prepare for grasping.

6.3.2. Kinematical results

The overall picture of the results mirrors what was reported in previous studies in which plants exhibit a significant difference with respect to dependent measures (Table 6.1; Guerra et al., 2019). The "junction velocity" and the "tendril velocity" were faster for the plants that grew in the presence of the support compared to the plants that grew in the absence of a potential support. For what concerns acceleration, plants with no support tend to exhibit a higher acceleration. Also, the tendrils tend to present a wider aperture for the no support than for the support condition. Finally, the duration of circumnutations was longer for the "no support" than the "support" condition.

Table 6.1. Kinematical values comparing the considered dependent measures for the "no support" and "support" conditions. Statistical values are also reported.

	Median				
	No Support	**Support**	*W*	*p*	*r*
Junction velocity (mm/min)	1.7488	3.5035	166.000	0.007	0.299
Junction acceleration (mm/min)	0.0006	−0.0001	51.000	0.021	0.257
Tendril velocity (mm/min)	2.5289	4.4670	1242.000	0.000	0.510
Tendril acceleration(mm/min)	0.0008	−0.0001	361.000	0.000	0.439
Tendrils aperture (mm)	25.2039	14.7132	245.000	0.000	0.394
Overall movement duration (min)	3744.000	1683.000	59.000	0.013	0.545
Circumnutation movement duration (min)	201.0857	217.000	143.000	0.103	0.181

Note. mm = millimeters; mm/min = millimeters by minutes.

6.4. Discussion

The results of the present study showed kinematic differences depending on the presence/absence of the support. For example, the “junction” and “tendrils velocity” were higher for the “support” than for the “no support” condition. And the tendency for plants exposed to the “no support” condition is to accelerate more quickly and have a greater tendrils aperture than those exposed to the “support” condition. These findings confirm the findings reported in previous literature and show how flexible and anticipatory these movements are (Guerra et al., 2019). Therefore, they provide the necessary information to instruct machine learning models and explore further issues concerned with anticipatory behavior. For instance, are all types of support the very same for a pea plants? Do they choose based on support features such as size? This is what I explored in the following chapters.

CHAPTER 7

DECISION-MAKING UNDERLYING SUPPORT-SEARCHING IN PEA PLANT: STUDY 1[2]

7.1. Introduction

Darwin's observations (1875) and more recent findings (Carrasco-Urra & Gianoli, 2009; Goriely & Neukirch, 2006; Putz & Holbrook, 1992; Saito, 2022) suggest that the size of a potential support make a difference for climbing plants. Grasping a thicker support being considered more difficult with respect to grasping a thinner one because of energy demands. In the former case, the plant not only needs to increase the length of its tendrils in order to wrap the support efficiently (Rowe et al., 2006), but also strengthen its tensional forces to counteract gravity and kinematics (Gianoli, 2015; Sousa-Baena et al., 2021). But how did they make this choice?

In light of these considerations, the aim of the current experiment is twofold. First, to ascertain what pea plants do when confronted with differently sized supports. To test this, pea plants were exposed to both a thin and thick support. If pea plants inevitably prefer thin

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[2] *Published*: Wang, Q., Guerra, S., Bonato, B., Simonetti, V., Bulgheroni, M., & Castiello, U. (2023). Decision-making underlying support-searching in pea plants. *Plants, 12*(8), 1597. https://doi.org/10.3390/plants12081597

supports, then a significantly higher frequency of movements directed toward them should be observed. Second, to ascertain whether such a decisional process impacts on the kinematics of the tendrils' circumnutations. A choice condition termed the "double-support" (DS) condition, in which thin and thick supports were both present in the environment, and a "single-support" (SS) condition, where only a thin support was present in the environment, were compared. Differences between conditions were expected to be evident at the level of movement kinematics. Further, I also predict that the plants may keep into account both supports in response to an ever-changing environment. If so, I expect a hybrid kinematical patterning accounting for differently sized supports.

7.2. Materials and Methods

7.2.1. Subjects

A total of 16 snow peas (*P. sativum*) were chosen as study plants.

7.2.2. Type of support

Two types of wooden support were considered: a "thin" support of 13 mm in diameter (Koto – 13 mm) and a "thick" support of 40 mm in diameter (Koto – 40 mm; Figure 7.1a). Both supports were 54 cm in height. The supports were inserted 7 cm below the soil surface (Figure 7.1b). The supports were made available to the plants immediately after germination.

7.2.3. Experimental conditions

The subjects were randomly assigned to two experimental conditions termed single-support (SS) and double-support (DS) conditions. For the SS condition, eight plants were raised individually in the presence of the "thin" support (Figure 7.1c). For the DS condition (Figure 7.1d), eight plants were raised individually in the presence of both the "thin" and the "thick" support. The location of the differently sized supports was counterbalanced across subjects to avoid a potential bias due to the direction of circumnutation (clockwise or counter-clockwise). The supports were positioned so that the first leaf developed by a sprout faced the midpoint between the two supports. This was done to prevent a growing bias in favor of either one or the other support. It should be noted that here, a "thick" single-support condition was not included. This decision was based on the observation that, during data acquisition for the DS condition, none of the plants successfully touched or grasped the thick support — they all went for the thin support. Consequently, it would be impossible to compare trials for a potentially thick SS condition with trials for the DS condition. Moreover, the differences between the thin and thick supports have been previously reported (Ceccarini et al., 2020a, 2020b; Guerra et al., 2019), and it has been established that the thicker support is not the best option for climbing plants (Carrasco-Urra & Gianoli, 2009; Darwin, 1875; Goriely & Neukirch, 2006; Putz & Holbrook, 1992; Rowe et al., 2006; Sousa-Baena et al., 2021). Therefore, a comparison to plants that achieved the same outcome of touching and grasping the thin support under the DS and SS conditions was confined.

In addition, the setting considered an equal distance between the plant and the surface of the supports and not necessarily the center of the support (Figure 7.1c,d). This appears to be a suitable positioning solution, given that I am focusing on the approaching phase preceding the grasping of the support and not on the coiling phase of the support.

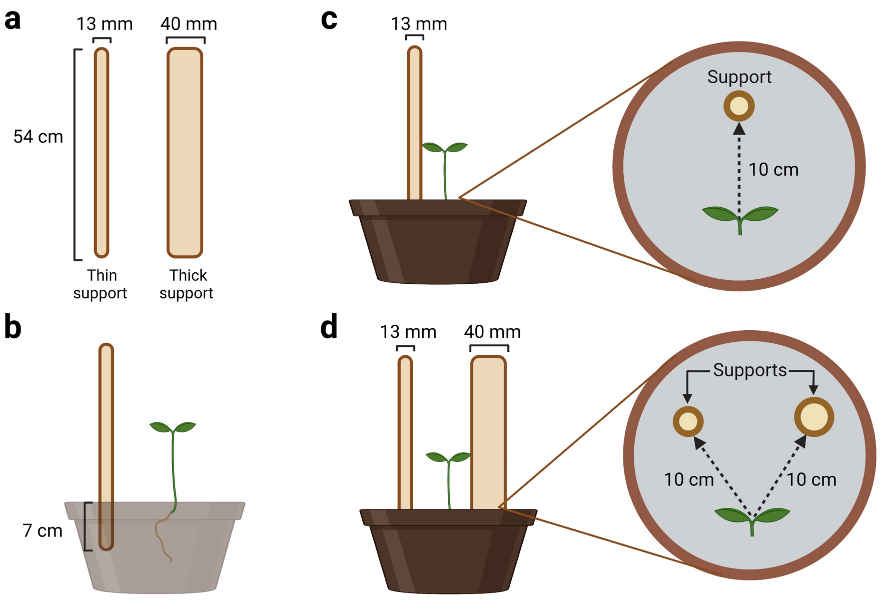


Figure 7.1. Graphical depiction of the (a) "thin" and "thick" supports; (b) the location of the support in the pot and how it was inserted in the soil. The single-support and double-support conditions are represented in panels (c) and (d), respectively.

7.2.4. Dependent measures

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

i. The number of circumnutations: the number of circumnutations performed by a plant from the time it was potted to the time it touched the support.

ii. The circumnutation duration (min): the time taken by a plant to complete a single circumnutation.

iii. Distance from the circumnutation gravity center to the origin (cm; Figure 7.2. Segment a): the distance between the circumnutation gravity center and the plant origin.

iv. <u>The length of the circumnutation major axis</u> (mm; Figure 7.2. Segment b): the maximum distance between two points of the circumnutation trajectory.

v. <u>The circumnutation length</u> (mm; Figure 7.2. Segment c): the length of the overall path computed as the sum of all the Euclidean distances between the subsequent points during a single circumnutation.

vi. <u>The circumnutation area</u> (mm^2; Figure 7.2. Segment d): the sum of pixels with a value equal to 1, obtained from the binarization of the circumnutation trajectory.

vii. <u>The amplitude of peak velocity</u> (mm/min): the values for the average of the maximum velocity.

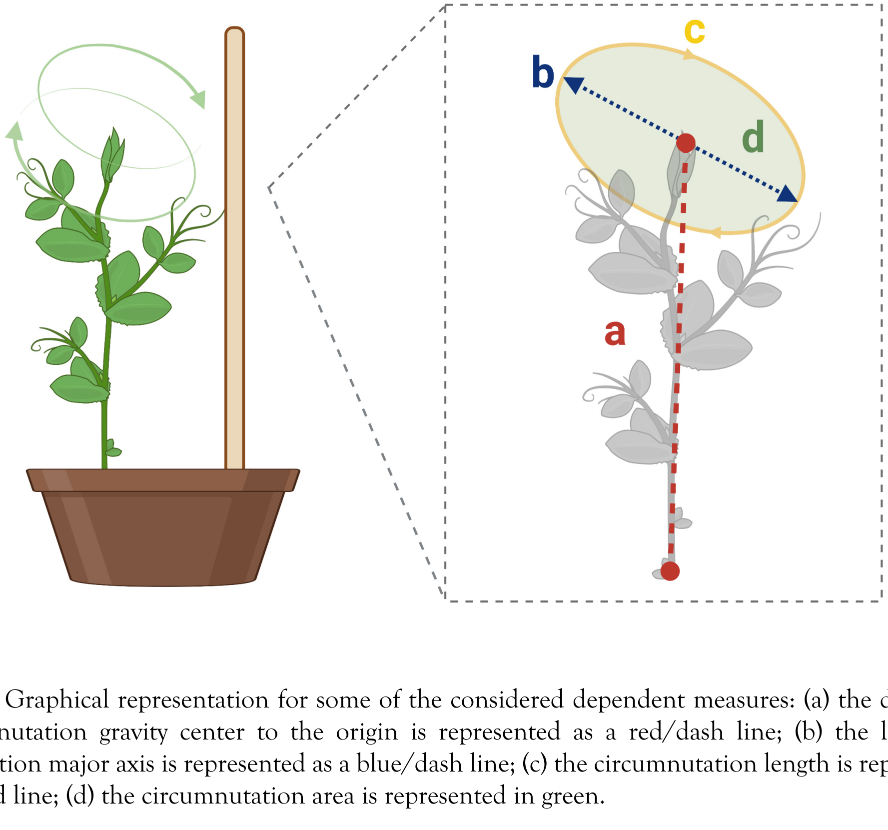


Figure 7.2. Graphical representation for some of the considered dependent measures: (a) the distance from the circumnutation gravity center to the origin is represented as a red/dash line; (b) the length of the circumnutation major axis is represented as a blue/dash line; (c) the circumnutation length is represented as a yellow/solid line; (d) the circumnutation area is represented in green.

7.2.5. Statistical analysis

The descriptive statistics, including the median, interquartile range (IQR), range, quartiles (Q_1 and Q_3) were calculated. Statistical analyses were conducted using the Bayesian approach. The objective of Bayesian estimation is to allocate credibility to a distribution of alternative parameter values (posterior distribution) that is consistent with the observed data by generating a large number of samples using the Markov chain Monte Carlo approach (MCMC). In this study, I adopted the two-sided Bayesian Mann–Whitney U test, given that the dependent variables were not normally distributed. The Mann–Whitney U test is a non-parametric test that does not require the assumption of normality. The analysis was performed using JASP (Jasp, 2023), which was nested within the environment R (R, 2010). I chose the default that was prior defined by a Cauchy distribution, which was centered on a zero-effect size (δ) and a scale of 0.707 because prior knowledge regarding the exposition of plants to a double-support condition was absent (Ly et al., 2016; Van Doorn et al., 2021). Data augmentation was generated with five chains of 1000 iterations, allowing for a simpler and more feasible simulation from a posterior distribution. In the analysis, W was calculated in the Mann–Whitney U test as the smaller of the rank total between the two conditions.

The Bayes factor (BF) was obtained to quantify the relative predictive performance of two hypotheses (Van Doorn et al., 2021). The BF quantifies evidence for the presence or absence of the difference between the DS and SS conditions. Here, the null hypothesis (H_0) was that there was no difference in kinematics between the DS and SS conditions. The alternative hypothesis (H_1) was that there was a difference. The BF_{10} value was the likelihood given H_1 divided by H_0. The BF_{01} value was calculated as H_0 divided by H_1. The results were reported based on Jeffery's scheme, which proposed a series of labels for which specific Bayes factor values could be considered as either "no evidence (0 – 1)," "anecdotal (1 – 3)," "moderate (3 – 10)," "strong (10 – 30)," "very strong (30 – 100)," or "decisive (> 100)" relative evidence for alternative hypotheses (Jeffreys, 1998). R-hat was also reported to check the degree of convergence of the MCMC algorithms based on outcome stability. The closer the value of R-hat is to 1, the better convergence to the underlying distribution. Credible intervals (CI) were set as 95%, which was simply the central portion of the posterior distribution that contains 95% of the values.

7.3. Results

7.3.1. Qualitative results

For all plants and in both experimental conditions (i.e., DS and SS), the tendrils displayed a circumnutating growing pattern. As soon as a plant sensed the support, it strategically altered the tendril's movement trajectory to bend towards the support (Figure 7.3a,b). For the DS condition, plants exhibited a very strong preference for the thin support and grew less than the plants for the SS condition by the time they touched the support (Figure 7.3c,d). Eight of the nine plants for the DS condition began to grow and move toward the thin support relatively early, even though they were too tiny to reach out for any support. These plants were able to aim precisely toward the thin support and touch it by modulating/twisting the angles of the new petiole, and this is visible to the naked eye. Only one plant tried to cling onto the thick support but ultimately failed and fell. The data for this plant have not been analyzed further. Among the eight plants for the SS condition: two circumnutated clockwise and two circumnutated counterclockwise. The remaining four exhibited both a clockwise and counterclockwise circumnutating pattern during the entire movement. As for the DS condition, four plants circumnutated clockwise, one plant circumnutated counterclockwise, and three circumnutated in a mixed manner.

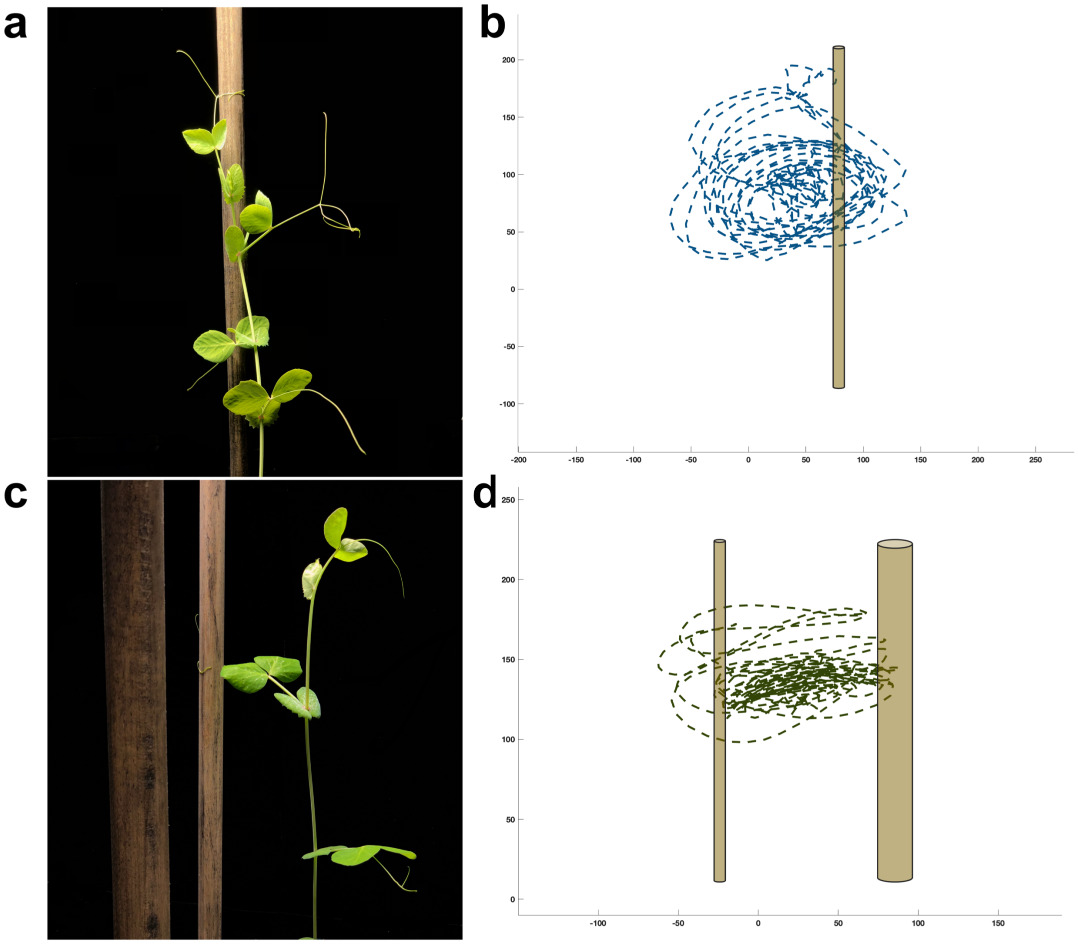


Figure 7.3. A frame representing an exemplar plant approaching the support for (a) the single-support (SS) condition with (b) a graphical representation of its trajectory. A plant approaching the thin support for (c) the double-support (DS) condition with (d) a graphical representation of its trajectory.

7.3.2. Kinematical results

The descriptive statistics and the kinematic results, when comparing the DS with the SS conditions, are provided below (Table 7.1).

Table 7.1. Descriptive statistics for the considered dependent measures for the two conditions considered.

	Condition	Median	IQR	Range	Q_1	Q_3
Number of circumnutations	DS	26.000	5.000	28.000	24.000	29.000
	SS	28.000	9.000	21.000	22.000	31.000
Circumnutation duration (min)	DS	63.000	18.000	84.000	57.000	75.000
	SS	69.000	15.000	114.000	60.000	75.000
Distance from the circumnutation gravity center to the origin (cm)	DS	13.055	14.361	62.527	8.212	22.573
	SS	16.017	32.062	96.865	9.394	41.456
Length of circumnutation major axis (mm)	DS	88.867	54.434	169.439	60.080	114.513
	SS	65.036	69.147	187.973	36.176	105.323
Circumnutation length (mm)	DS	221.764	172.506	643.428	147.370	319.876
	SS	166.488	196.104	503.609	85.797	281.900
Circumnutation area (mm^2)	DS	3580.500	6572.125	22965.250	1165.750	7737.875
	SS	1943.688	5298.375	14870.563	199.438	5497.813
Amplitude of the maximum peak velocity (mm/min)	DS	6.042	4.895	71.556	3.494	8.390
	SS	4.038	3.813	14.054	2.499	6.313

Note. DS = double-support condition; SS = single-support condition; IQR = interquartile range; Q_1 = 25th percentage, Q_3 = 75th percentage.

Number of Circumnutations

The Bayesian Mann–Whitney U analysis revealed a Bayes factor (BF_{10}) of 314.656, suggesting that there is a decisive difference between the SS and the DS conditions with respect to the number of circumnutations (BF_{10} = 314.656, BF_{01} = 0.003, W = 14220, R-hat = 1.008, 95% CI: [−0.657, −0.229]).

Circumnutation Duration

The Bayesian Mann–Whitney U analysis revealed a Bayes factor (BF_{10}) of 0.387, suggesting that there is no difference between the SS and the DS conditions with respect to the circumnutation duration (BF_{10} = 0.387, BF_{01} = 2.584, W = 17083, R-hat = 1.000, 95% CI: [−0.354, 0.029]).

Distance from the Circumnutation Gravity Center to the Origin

The Bayesian Mann–Whitney U analysis revealed a Bayes factor (BF_{10}) of 136.096, suggesting that there is a decisive difference between the SS and the DS conditions with respect to the distance from the circumnutation gravity center to the origin (BF_{10} = 136.096, BF_{01} = 0.007, W = 15132, R-hat = 1.031, 95% CI: [−0.575, −0.169].

Length of the Circumnutation Major Axis

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

Circumnutation Length

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

Circumnutation Area

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

Amplitude of Maximum Peak Velocity

The Bayesian Mann–Whitney U analysis revealed a Bayes factor (BF_{10}) of 4137.588, suggesting that there is a decisive difference between the SS and DS conditions with respect to the amplitude of maximum peak velocity (BF_{10} = 4137.588, BF_{01} = 0.0002, W = 25438, R-hat = 1.014, 95% CI: [0.380, 0.780]).

Correlational Analyses

A non-significant difference was found for the circumnutation duration across conditions, while the amplitude of peak velocity increased for the DS with respect to the SS condition. This might indicate the plants put in place a sort of isochrony principle (Viviani & Mccollum, 1983). The isochrony principle refers to a spontaneous tendency to increase the velocity of a movement depending on the linear extent of its trajectory to maintain the execution time as approximately constant (Sartori et al., 2013). To test this, I performed Pearson's correlation analysis (Cohen et al., 2009) between the circumnutation length and the amplitude of peak velocity (Van Rossum & Drake Jr, 2009). The results indicate a significant correlation between these measures (Pearson's r = 0.715, p-value = 0.000, 95% CI: [0.663, 0.760]; Figure 7.4).

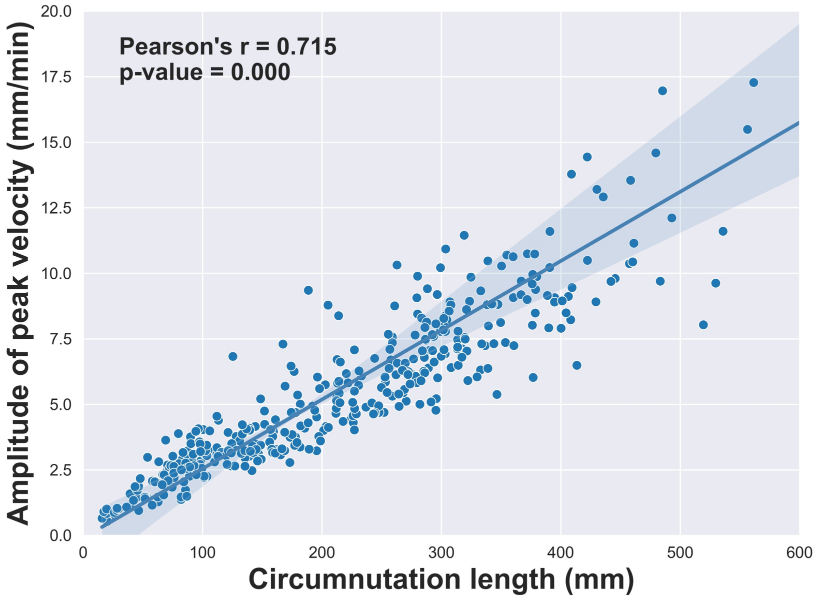


Figure 7.4. Pearson's correlation coefficient between the "circumnutation length" and the "amplitude of peak velocity."

7.4. Discussion

In this study, the kinematics of tendrils' circumnutation were examined from germination until the plants touched and grasped the support. The findings show that most of the considered dependent measures differed markedly between the DS and SS conditions. For instance, plants perform fewer and larger circumnutations, as evidenced by a lower "number of circumnutations," a longer "length of circumnutation major axis," and a longer "circumnutation length" for the DS than the SS condition. Further, the "circumnutation area" is greater for the DS than the SS condition. To achieve all this, plants increased the "amplitude of maximum peak velocity" for the DS condition. Altogether, this pattern of results might imply a more active and exploratory patterning for the plants facing a "choice" scenario. The "circumnutation duration," on the other hand, remains the same for both conditions. In this respect, the correlational analysis indicates that the "circumnutation length" and the "amplitude of the peak velocity" are strongly correlated. This suggests that the pea plants movement is based on the isochrony principle (Viviani & Mccollum, 1983). In these circumstances, plants maintain constant movement duration and scale velocity in order to cover longer distances, as witnessed by the longer circumnutation lengths. This appears to be an easy and appropriate organizational option adopted by the plant to program the patterning of circumnutation when a decision based on alternatives must be taken.

At this stage, the question is more about how climbing plants avoid an unsuitable host and choose a suitable one. A common belief is that the physiological mechanisms underlying behavioral responses in plants tend to be caused by simple, local reactions (Karban, 2008). As proposed by Saito (2022), these reactions might also be at the basis of the decision-making processes related to support diameter. In this view, changes in the coiling responses may be caused by local reactions in the tendrils. For instance, in many climbing plants, the coiling of tendrils is thought to be caused by the contraction of the gelatinous fibers (G fibers) after support has been contacted (Bowling & Vaughn, 2009; Saito, 2022). That is to say, when a suitable support is detected and recognized, the tendril shows a reflex behavior and rapidly bends in the stimulated direction (Vidoni et al., 2013). Put simply, at the basis of plants' support selection, there might be a mechanism that makes it possible to select a support with an appropriate diameter.

The emerging picture from the "choice" that the plants made might suggest a trade-off in terms of metabolic use. Touching and grasping a thick support would imply the growth of longer tendrils, which, in turn, would be more demanding in terms of energy exploitation.

This metabolically based decision would also reflect on movement kinematics. The movement towards thicker supports is much slower than for thinner supports (Guerra et al., 2019) and shows a great deal of online adjustments, visible as submovements along the velocity profiles (Ceccarini et al., 2020a). Therefore, plants might have the ability to monitor, detect, and process information that determines the preference for a thin support. These aspects are particularly evident when comparing circumnutation between the thin support for the DS and the SS conditions. Plants move faster and execute less but larger circumnutations for the latter than for the former. This signifies that despite that the plants are aiming at supports of the same size, being exposed to an alternative (the thick support for the DS condition) determines a decisional complexity that is played out in the kinematics of circumnutation. Therefore, it appears that circumnutation is not only affected by a complex occurrence of factors, such as light, gravity, touch, and hormonal signals (Stolarz, 2009), but also by the presence of alternative supports in the environment.

A caveat of the present results at the observational level is that the direction of the circular movements could be either clockwise or counterclockwise, and it could change within the same plant. Whether climbing plants are right- or left-handers is an aspect tackled in previous literature (Schuster & Engelmann, 1997), and that may be pursued in connection with decision-making. Further research is required to establish such a link.

In conclusion, the results of this study offer a contextual framework for the different well-known responses of climbing plants when searching for a support. More importantly, a decision-making ability in plants has been demonstrated, which allows them to adaptively choose between responses according to the diameter of the available supports. Overall, the results of the study suggest that plants can acquire and integrate complex information about the environment in order to modify the extent of their plastic responses adaptively. Such complex decision-making could have important implications for the understanding of the processes that govern plant behavior. This is why I decided to further explore this issue in a second study described in the ensuing chapter.

CHAPTER 8

DECISION-MAKING UNDERLYING SUPPORT-SEARCHING IN PEA PLANT: STUDY 2

8.1. Introduction

As shown in Chapter 7, climbing plants display preferences for smaller supports over larger ones, owing to various factors including mechanical stability, resource allocation, and growth strategies (Gianoli, 2015; Givnish, 1995).

Based on these findings, it has been inferred that the absence of any instances of plants approaching and grasping the thick support (i.e., 40 mm in diameter) was an indication that the diameter of the thick support was both mechanically and metabolically demanding for the plants. Here I further investigated this issue to understand up to which point a potential support could be considered unsuitable in terms of size by pea plants.

Pea plants were randomly assigned to three experimental conditions: (i) a “single” condition in which a group of plants was raised in the presence of a thin support (S-thin); (ii) a “single” condition in which a group of plants was raised in the presence of a thick support (S-thick); (iii) a “decision-making” (DM) condition, in which plants grew in the presence of both a thin and a thick support. Note that for the sake of the analyses, plants that eventually grasped the thin support were termed as “DM-thin,” while those that grasped the thick support were termed as “DM-thick.” I predicted that plants would show differences at the level of kinematics between the single and the DM conditions. For the S conditions, I expected a kinematic patterning mirroring what was found in Chapter 7. For the DM condition, I hypothesized that reducing the size of the support to 30 mm in diameter would be preferable by the plant. If this might be the case, then I would expect that the choice among two supports equally acceptable by the plant would determine a distinctive kinematic patterning.

8.2. Materials and Methods

8.2.1. Subjects

38 snow peas (*P. sativum*) were chosen as study plants.

8.2.2. Type of support

The supports were wooden poles of 13 mm (“thin” support; Koto – 13 mm) and 30 mm (“thick” support; Koto – 30 mm) in diameter. Both supports were 54 cm in height. The supports were inserted 7 cm below the soil surface.

8.2.3. Experimental conditions

The experimental conditions were the following (Figure 8.1a-c):

i. S-thin: the growth of individual plants in the presence of a single thin support.
ii. S-thick: the growth of individual plants in the presence of a single thick support.
iii. DM: a “decision-making” (DM) condition in which plants grew in the presence

of both the thin and the thick supports. The plants were split into two groups: plants that choose the thin support were categorized as "DM-thin," plants that choose the thick support were categorized as "DM-thick."

For the DM condition, the location of the differently sized supports was counterbalanced across subjects as to avoid a potential bias in the results depending on whether the circumnutation was clockwise or counterclockwise. The supports were positioned at an equal side from the plant cotyledon so that the first leaf developed by a sprout faced the precise midpoint of the two supports. This was done to prevent a growing bias in favor of either support.

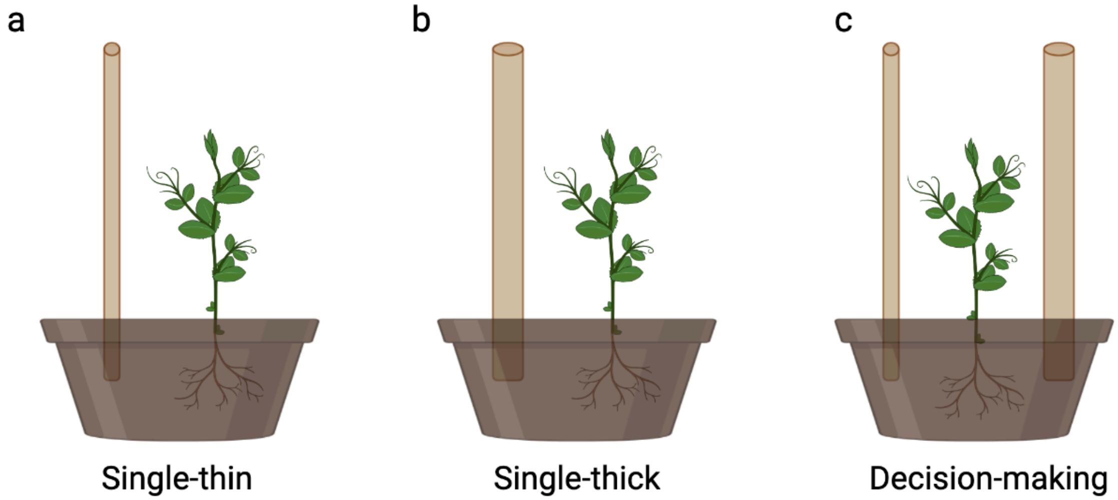


Figure 8.1. Graphical depiction of the three experimental conditions: (a) S-thin, (b) S-thick, and (c) decision-making.

8.2.4. Dependent measures

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

i. Total movement duration (min): the time it takes from the moment tendrils developed from the apex to the time they approach the support and start coiling around it.

ii. Circumnutation duration (min): the time taken by a plant to complete a single circumnutation.

iii. Number of circumnutations: the number of circumnutations performed by a plant from the time when tendrils developed from the apex till the time they approached the support.

iv. Length of the circumnutation major axis (mm): the maximum distance between the two points characterizing the maximum axis for the circumnutation trajectory.

v. Circumnutation length (mm): the sum of all the Euclidean distances between subsequent points during a single circumnutation.

vi. Circumnutation area (mm^2): the sum of pixels with a value equal to 1 obtained from the binarization of the circumnutation trajectory.

vii. Amplitude of average velocity (mm/min): the average velocity during the entire movement.

viii. Amplitude of the maximum peak velocity (mm/min): the maximum peak velocity reached during the entire movement.

ix. Maximum aperture (mm): the maximum distance between the tendrils.

x. Direction switching: the times at which the plant switched the direction of circumnutation.

8.2.5. Statistical analysis

The descriptive statistics including median (Med), range, interquartile range (IQR), and quartiles (Q_1 and Q_3) were calculated. In this study, I adopted the Mann–Whitney U test since the dependent variables were not normally distributed. Assumption checks have been done to test the normality (Shapiro–Wilk), and results suggested a significant deviation from normality ($p < 0.001$) for the majority of dependent measures. Mann–Whitney U test is a non-parametric test that does not require the assumption of normality. The analysis was performed using JASP (Jasp, 2023) nested within the environment R (R, 2010). In the analysis, *W* was calculated in the Mann–Whitney U test as the smaller of the rank total between the two groups.

8.3. Results

8.3.1. Qualitative results

For all 38 plants, the tendrils displayed a circumnutating growing pattern. Once plants sensed the support, they altered their movement to bend towards it. For the single conditions, eight plants grasped the thin support (S-thin) and 10 plants grasped the thick support (S-thick). For the decision-making condition, plants show a relative preference towards the thin support over the thick one. Out of 20 plants, six grasped the thick support (DM-thick), while 13 grasped the thin support (DM-thin). One plant preferred the thick support but failed to grasp it; therefore, it was not taken into account for the further steps of the analyses. Plants belonging to the DM-thin group developed relatively shorter tendrils compared to the DM-thick group.

8.3.2. Kinematical results

Statistical descriptive for the comparisons across conditions and groups for all dependent measures are provided below (Figure 8.2; Table 8.1; Appendix I Table 1).

Table 8.1. Statistical analysis for all comparisons.

	S-thin vs. S-thick		**DM-thin vs. S-thin**		**DM-thick vs. S-thick**		**DM-thin vs. DM-thick**	
Dependent measures	**W**	***p***	**W**	***p***	**W**	***p***	**W**	***p***
Total movement duration (min)	59.000	0.101	45.000	0.645	16.000	0.147	50.000	0.368
Circumnutation duration (min)	32994.000	< .001	34263.500	< .001	8662.000	< .001	20375.000	0.031
Number of circumnutations	17115.000	< .001	15972.000	< .001	21069.000	< .001	31302.000	< .001
Length of circumnutation major axis (mm)	19361.000	0.098	34937.000	< .001	20899.000	< .001	20981.000	0.090
Circumnutation length (mm)	19283.000	0.085	35616.000	< .001	19817.000	0.010	18840.000	< .001
Circumnutation area (mm^2)	18967.000	0.048	34687.000	< .001	18853.000	0.099	17703.000	< .001
Amplitude of average velocity (mm/min)	14025.000	< .001	33921.000	0.001	23962.000	< .001	20211.000	0.023
Amplitude of maximum peak velocity (mm/min)	14433.000	< .001	35322.000	< .001	24676.000	< .001	20679.000	0.054
Maximum aperture (mm)	206.000	0.140	75.000	0.865	212.000	0.081	96.000	0.034
Direction switching	28.500	0.314	48.000	0.792	43.500	0.143	54.000	0.191

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

S-thin vs. S-thick

This comparison aims to confirm the kinematical differences previously documented with respect to the size of a potential support (Guerra et al., 2019). Confirming these differences is fundamental in order to draw firm conclusions regarding the DM condition. As shown in Table 8.1 the Mann–Whitney U test reveals that there is a significant difference in terms of "circumnutation duration," "number of circumnutations," "circumnutation area," "amplitude of average velocity," and "amplitude of the maximum peak velocity" between the S-thin and the S-thick conditions.

DM-thin vs. S-thin

This comparison allows to validate the results reported in Chapter 7 (Wang et al., 2023b). The Mann–Whitney U test reveals that there is a significant difference between the DM-thin and the S-thin in terms of "circumnutation duration," "number of circumnutations," "circumnutation major axis," "circumnutation length," "circumnutation area," and "amplitude of average velocity."

DM-thick vs. S-thick

This comparison allows for the detection of hypothetical kinematic differences in plants when exposed to a decision-making condition compared to a single condition, specifically in relation to the thick support. An aspect that was not considered in Chapter 7. As shown in Table 8.1, the Mann–Whitney U test reveals that there is a significant difference between the DM-thick and S-thick in terms of "circumnutation duration," "number of circumnutations," "circumnutation major axis," "circumnutation length," "amplitude of average velocity," and "amplitude of the maximum peak velocity."

DM-thin vs. DM-thick

This comparison was made to compare the kinematics of plants experiencing a decision-making environment in which a thin and a thick support were both present and exhibited a preference for either the thin or the thick support. As shown in Table 8.1, the

Mann–Whitney U test reveals that there is a significant difference in terms of "circumnutation duration," "number of circumnutations," "circumnutation length," "circumnutation area," and the "amplitude of average velocity" between the DM-thin and the DM-thick. Moreover, the "maximum aperture" is significantly greater for the DM-thick than for the DM-thin.

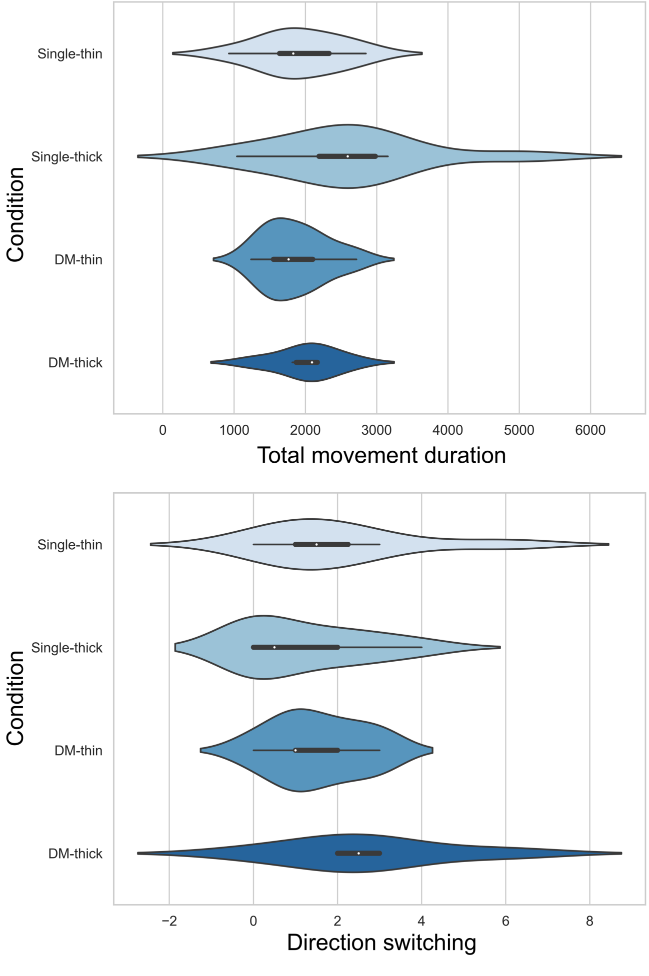


Figure 8.2. The kernel density estimate (KDE) plots of dependent measurements "total movement duration" and "direction switching" for each group S-thin, S-thick, DM-thin, and DM-thick, respectively. The white dot within each plot represents the median; the bolded line indicates the interquartile range (IQR) between Q_1 and Q_3, and the black line extending from the bolded bar reflects the range of the dataset between the minimum and maximum values. The width of the shape denotes the frequency of the data points. Note that the negative values where the plots may extend to are an artifact of KDEs, which means that the data contains values close to negative, namely 0.

8.4. Discussion

The present experiment offers a more thorough investigation of the decision process underlying support-searching in pea plants. Plants, overall, exhibit inherent variations in kinematics and temporal dynamics in response to environmental fluctuations. Plants move faster, circumnutate less, and their circumnutations cover a broader area for the DM condition with respect to the S conditions. Furthermore, plants exhibited kinematic variations when targeting supports of identical size for the "DM-thin vs. S-thin" and "DM-thick vs. S-thick" comparisons. This signifies that despite the plants oriented their movement toward supports of the same size, the presence of alternatives determines a decisional complexity that is played out in the kinematics of circumnutation. The presence of a relatively constant "total movement duration" across all conditions suggests that plants exhibit a tendency to maintain constant movement time while adjusting other features during circumnutations in order to accomplish their goals. Certain plants display the ability to change their direction of circumnutations multiple times prior to reaching a support. However, the frequency of direction switching does not differ significantly across conditions.

In addition, plants also show kinematical differences depending on the size of the support, as evidenced when considering the comparisons "S-thin vs. S-thick," and "DM-thin vs. DM-thick." The behavior of plants growing in the presence of a single support display variations confirming the previously documented findings regarding the ability of plants to adjust their movements and growth in response to the size of the support (Guerra et al., 2022; Guerra et al., 2019). However, plants appear to employ different strategies for supports of a similar size but nested within the DM condition. This implies that plants do not solely program their movements based on the size information, but rather exhibit dependence on other sorts of environmental factors, such as the number of supports present.

When looking at the plants exposed to the decision-making condition, kinematical differences between the "DM-thin vs. DM-thick" indicate that plants do not choose the support randomly. Rather, they seem to plan a purposeful goal-directed movement. The tendrils' "maximum aperture" is smaller when comparing the thin than the thick support group, which is in accordance with previous findings (Guerra et al., 2019). This finding demonstrates that the perception and modulation of size information are contingent upon the diverse environmental conditions, pushing the degree of flexibility involved in the regulation of movement to a higher level of sophistication.

The findings reported in Chapter 7 show that plants did not choose to grasp the thick support, which had a diameter of 40 mm, this was attributed to the higher energy demands and morphological expenses associated with such a support. Here it is revealed that a 30 mm diameter support is a viable option. A possible explanation is that this support may not disrupt homeostasis. It has been reported that the characteristics of a host can exert an impact on the liana distribution in forests (Leicht-Young et al., 2010). The phenomenon of "failsafe" properties has been observed in climbing plants, that is, if the tensile forces exceed a certain threshold, the hooks on the rachis will be detached and falls from trees with larger diameter (Isnard & Rowe, 2008; Rowe & Isnard, 2009; Rowe & Speck, 2014). However, some studies have identified a correlation between the tree size and the presence and abundance of lianas (Dewalt et al., 2000; Ladwig & Meiners, 2010; Pérez-Salicrup & De Meijere, 2005; Putz, 1984). It is possible that larger trees in mature forests are more likely to support lianas owing to their ability to bear greater biomass. This, in turn, may result in increased canopy cover and improved light acquisition, eventually leading to greater liana abundance. In the current experimental scenario, it is conceivable that this subset of plants might be the “ambitious” ones, as they exhibit a tendency to actively pursue a sturdy attachment that can withstand greater weight, thereby facilitating their potential for future growth.

Altogether, the above-mentioned findings indicate that plants possess the ability to engage in decision-making processes to adjust their behavior in response to their surroundings. The environmental distinctions provide open questions to the study of plants behavior. For instance, how did the plant acquire the support information and start to make these decisions? What is the most decision-sensitive anatomical landmarks? Which kinematical measures is more valuable and indicative for our understanding of plant movements and decisions? To answer these questions, I adopted explorative machine learning methods like anomaly detection via unsupervised machine learning (Chapter 9), and supervised machine learning classification (Chapter 10) by using the kinematical data collected in the above behavioral studies.

PART IV

THE MACHINE LEARNING EXPERIMENTS

CHAPTER 9

ANOMALY DETECTION: A MACHINE LEARNING METHOD TO INVESTIGATE PLANT BEHAVIOR

9.1. Introduction

Machine learning techniques are extensively used for uncovering movement features that go beyond what can be predicted on the basis of custom kinematical analyses. These features, if any, would allow for a better comprehension of already known behavioral patterns.

Unsupervised anomaly detection (AD) is an unsupervised machine learning technique used to identify uncommon items or observations that exhibit a high degree of rarity by deviating significantly from the remaining data. Therefore, it is often used to identify patterns and deviations that do not adhere to the standard behavior of a given model. The models are trained on unlabeled data without the presence of any explicit designations by assuming that the majority of points within the dataset are representative of normal behavior. The decision to make use of this particular method is frequently employed in the context of exploratory data analysis. Therefore, it may be advantageous to investigate the atypicality in plant movements, which can be interpreted as a distinct deviation from the typical circumnutation pattern. This deviation could potentially indicate varying executive decision-making processes in response to the environment. In contrast to classical kinematics, unsupervised AD offers particular benefits in identifying complex patterns that might not be readily discernible, and it can provide valuable insights into the timing of a plant's decision-making process regarding the movement toward a potential support.

The aim of this study is to provide a starting point in the application of machine learning techniques to plant behavioral data. An exploratory unsupervised AD was employed to investigate plants growing in the presence or absence of a potential support. The employed method allows for a more in-depth, but still preliminary, analysis of individual plants to identify potential variations in the movement patterning hidden within latent information processing and the decision-making dictated by an ever-changing environment. I anticipate that due to its exploratory nature, the insights obtained from the application of this method may not provide conclusive evidence.

9.2. Materials and Methods

9.2.1. Experimental conditions

A pair of plants were chosen from the dataset reported in Chapter 6. One plant, designated as plant "N," grew in a chamber without a potential support ("no support" condition), while the other one, designated as plant "S," grew in a chamber with a potential support ("support" condition).

9.2.2. Data preprocessing

The PyCaret anomaly detection is a Python-based library (Van Rossum & Drake Jr,

2009) that utilizes unsupervised machine learning models to effectively identify rare observations (i.e., outliers) that deviate significantly from the majority of the data (Pycaret.Org, 2020). The dataset pertaining to the trajectories of plants N and S were imported, subjected to a thorough data report examination and subsequently visualized through the use of Kernel Density Plot, as depicted in Figure 9.1. Then, the environment was configured in order to facilitate the utilization of unsupervised machine learning models. The time windows of movements were selected to encompass only the circumnutations. Therefore, the final frame was defined as either the frame just before the plant fell on the ground for plant N in the "no support" condition (number of selected frames: 622, time window: 1866 mins; Figure 9.1a), or the frame in which the tendrils start to coil for plant S in the "support" condition (number of selected frames: 561; time window: 1683 mins; Figure 9.1b). The dataset of each plant consists of 3 features: axis_x, axis_y, and axis_z. The dataset was normalized using the *z*-score method, without any clustering and threshold set for data filtering.

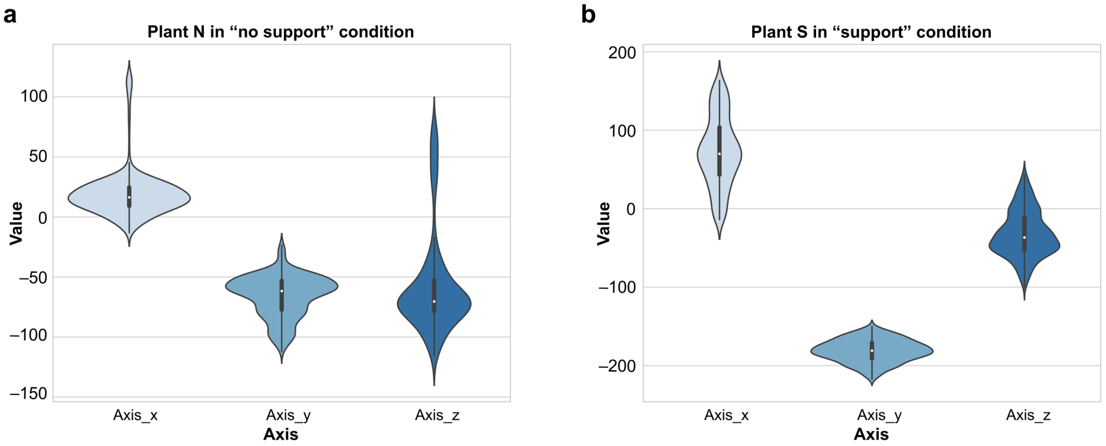


Figure 9.1. Distribution of values of the plants' movement trajectories in axis_x, axis_y, and axis_z: (a) plant N and (b) plant S.

9.2.3. Anomaly detection

Once the dataset had been prepared, the subsequent steps were carried out, which involved the selection and assignment of models to the respective tasks. Three unsupervised machine-learning models were employed: Isolation Forest, *k*-Nearest neighbor, and one-class Support Vector Machine. These were chosen based on their robustness and wide applicability across diverse domains (Cortes & Vapnik, 1995; Parise et al., 2021).

i. Isolation forests (IF) are generated on the basis of binary decision trees. The algorithm as proposed by Liu et al. (2008), is designed to identify anomalies by segregating anomalous data points from normal ones by means of an ensemble of isolation trees (iTrees). Every iTree is trained using a subset of training observations that are sampled without replacement. The algorithm constructs an isolation tree by randomly selecting a split variable and split position iteratively, until each observation within a subset is assigned to a single leaf node. The occurrence of anomalies is infrequent and distinct, resulting in their placement in distinct leaf nodes that are closer to the root node. The anomaly scores in IF are determined by averaging the path lengths across all isolation trees to identify anomalies.

ii. The *k*-Nearest Neighbor algorithm (KNN) is a non-parametric machine learning technique employed for data classification, relying on similarities and diverse distance metrics (Cover & Hart, 1967). The underlying premise of the KNN algorithm is that points with similar attributes tend to be located in closer proximity to one another, while outliers are typically isolated points. The algorithm relies solely on the threshold values, so that the distance to the *kth* nearest neighbor can be interpreted as a local density estimate. According to Ramaswamy et al. (2000), the local density decreases as the distance to the *k* neighbors increases, thereby increasing the likelihood of the point being recognized as an outlier.

iii. Support Vector Machines (SVMs) are considered one of the most resilient statistical algorithms for classification (Cortes & Vapnik, 1995). One-class SVM (OCSVM) is a model used in the field of AD. Its purpose is to develop the capability to distinguish between anomaly points from a given dataset (Moya & Hush, 1996). The algorithm operated on the fundamental principle of reducing the volume of the hypersphere encompassing the instances belonging to a specific class. It considers all the remaining data points lying outside this hypersphere as outliers. The mathematical formula (Noumir et al., 2012) for computing the volume of a hypersphere with center c and radius r is as follows:

$$\min_{r,c} r^2 \ subject\ to, \|\phi(x_i) - c\|^2 \leq \ r^2 \ \forall i = 1, 2, \ldots, n$$

The dataset of Plants N and S were allocated to each model separately. The determination of an anomaly threshold occurs during the process of fitting the decision function, specifically it was set to a value of 0.05. This implies that 5% of points within the dataset were identified as anomalies or outliers. The function within assigned models was designed to generate a dataset that contains the detection of anomalies, and the presence of outliers was denoted by the value 1 while non-outliers was denoted by the value 0.

Additionally, the models included anomaly scores which served to quantify the level of significance of the anomaly in relation to previously observed anomalies (as illustrated in the *Results* section). Once the AD was completed for each model for both plants, the anomaly points were presented with relevant information such as “frame number,” “anomaly score,” “progress rate,” and “progress rate interval.” This was done to enable the interpretation of anomalies within the specific context of each plant. The term “frame number” referred to the numerical designation assigned to a specific frame outlined as anomaly. And the “anomaly score” denoted the score generated by each model that corresponded to the identified frame. The term “progress rate” represented at which percentage of movement, the plant movement pattern deviated from the norm. It was calculated by dividing the “frame number” by the total number of selected frames for each plant. The “progress rate interval” was used to quantify the temporal distance between successive anomaly frames. The Seaborn Pair Plot (Waskom, 2021) was adopted in matrix format to visually represent the pairwise relationships between axes within trajectories in each plant. The diagonal plots showed a univariate distribution plot that represented the marginal distribution of anomaly data points and the majority of data points in each column.

9.3. Results

There were 32 anomaly points out of the 622 outlined in plant N, and 28 anomaly points out of 561 outlined in plant S, which accounted for 5% of the total amount of frames. The majority of the anomaly points manifested during a rather late phase of the development for both plants. In the case of plant N, the movement appeared to be at a greater degree of random distribution and irregularity. In contrast, for plant S, the movements displayed a more consistent, rhythmic pattern that was comparable across all models. These patterns are depicted in Figures 9.2 to 9.4.

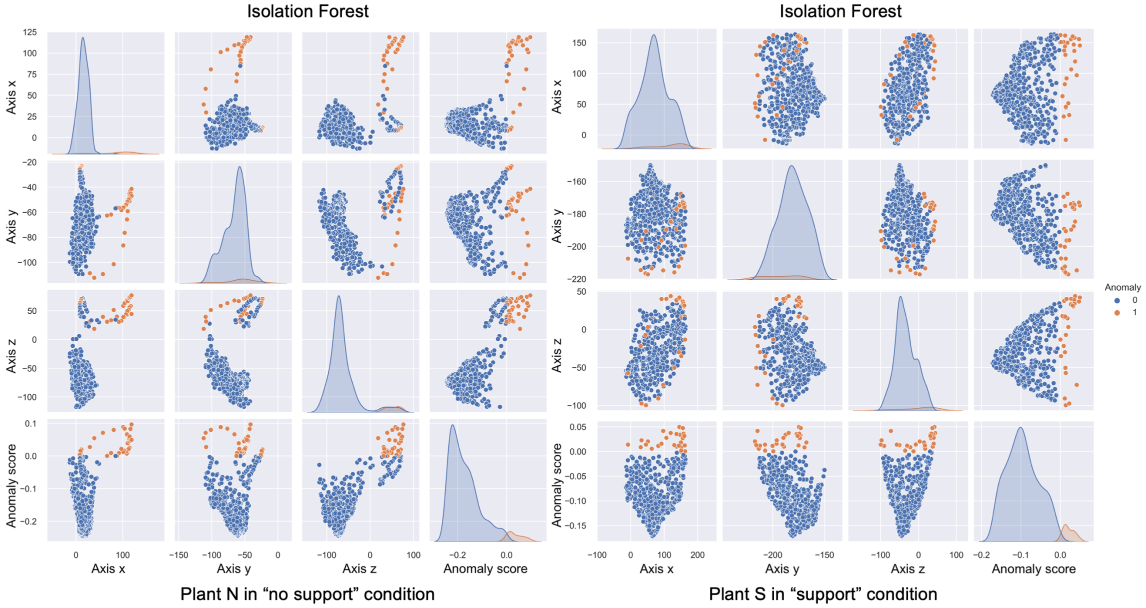


Figure 9.2. Pair plots of anomaly distribution for the IF model with comparison to the general trajectory distribution for plants N and S. The anomaly points are marked in color “orange,” and the rest of the points are marked in color “blue.” The diagonal plots show a univariate distribution plot that represents the marginal distribution of anomaly data points and the majority of data points for each column.

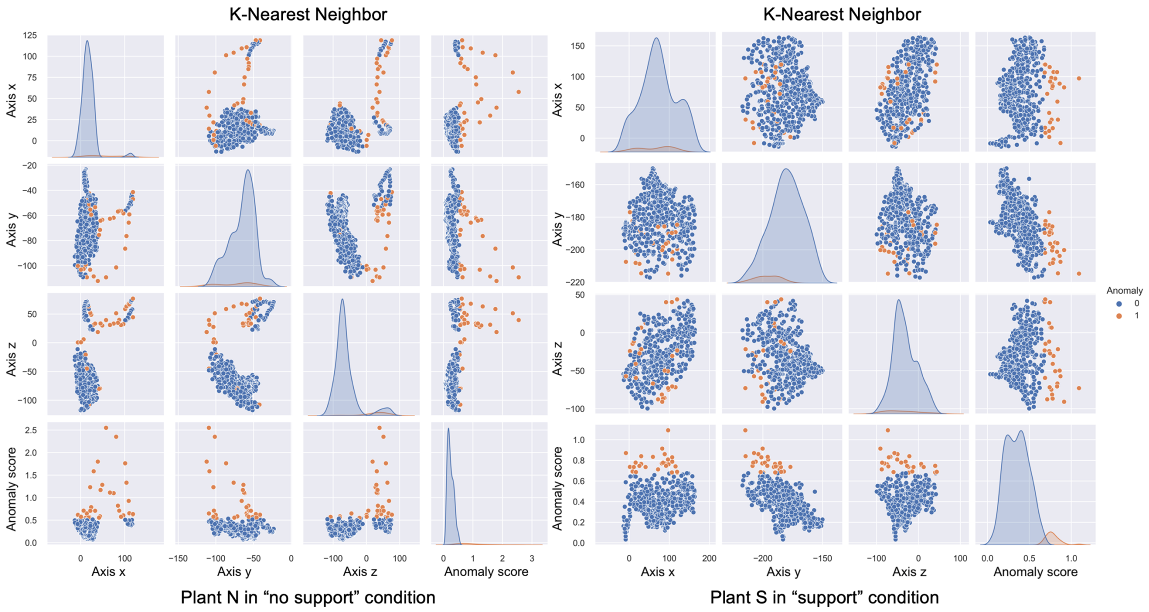
Plant N exhibited a notable departure from the previous pattern of movement at a relatively late stage. Furthermore, the plant movement pattern underwent an intensified change, particularly demonstrated by significant alterations in behavior during the final stages of the movement, just before it was about to fall. Plant S exhibited earlier and consistent progress in its movement, the pattern of the movement changed as it neared the end, particularly when it was in close proximity to the support.

9.3.1. Isolation Forest

The performance of IF is presented in Figure 9.2 (see also Appendix II Table 1). The plant N (progress rate: 89.694%) initiated to move later than plant S (progress rate: 68.036%). The progress rate interval is larger in plant S than in plant N, and the anomaly score is higher and varies more in plant N (IF: mean = 0.036, SD = 0.030) compared with plant S (IF: mean = 0.022, SD = 0.014). Nevertheless, the overall anomaly score does not exhibit a significant deviation from the remaining data points, indicating that the overall movement pattern remains relatively consistent when the IF model was employed.

9.3.2. K-Nearest Neighbor

The performance of KNN is presented in Figure 9.3 (see also Appendix II Table 2). The plant N (progress rate: 60.064%) started to move distinctively later than plant S (progress rate: 55.357%). The progress rate interval is larger in plant S than in plant N. The anomaly score is higher and varies more in plant N (KNN: mean = 0.967, SD = 0.533) compared with plant S (KNN: mean = 0.779, SD = 0.086). The overall movement pattern is relatively similar from one to another.



K-Nearest Neighbor

K-Nearest Neighbor

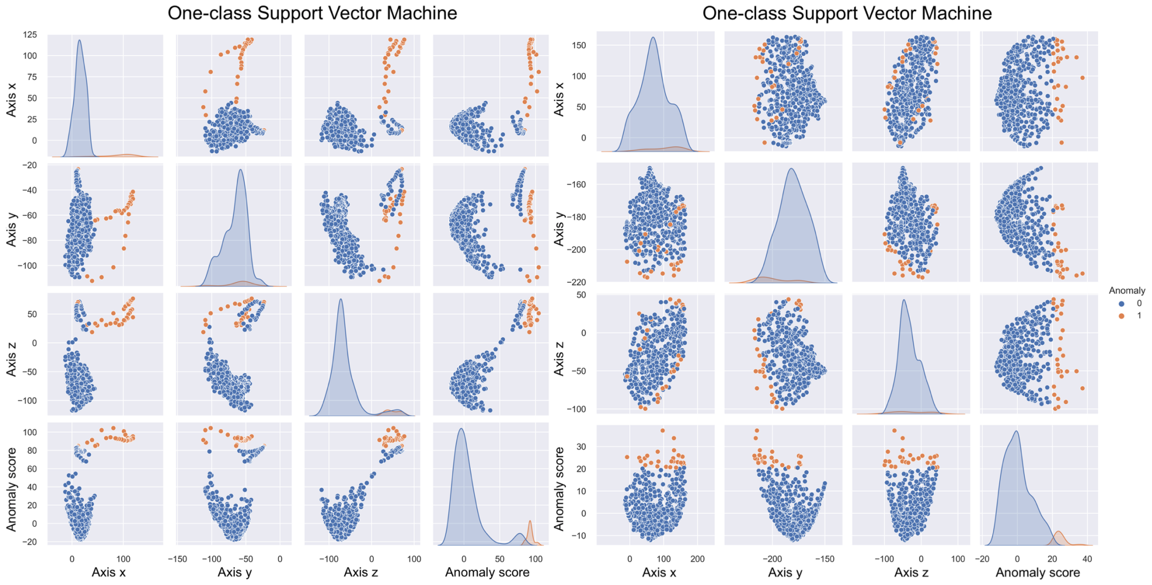
Plant N in “no support” condition

Plant S in “support” condition

Figure 9.3. Pair plots of anomaly distribution in the KNN model with respect to the general trajectory distribution for plants N and S. The anomaly points are colored in “orange.” The remaining points are colored in “blue.”

9.3.3. One-class Support Vector Machine

The performance of OCSVM is shown in Figure 9.4 (see also Appendix II Table 3). The plant N (progress rate: 89.694%) started to move distinctively later than plant S (progress rate: 74.643%). The progress rate interval is larger in plant S than in plant N. The anomaly score is much higher and varies more in plant N (OCSVM: mean = 92.466, SD = 4.444) compared with plant S (OCSVM: mean = 24.575, SD = 3.717).



Plant N in “no support” condition

Plant S in “support” condition

Figure 9.4. Pair plots of anomaly distribution in the OCSVM model with respect to the general trajectory distribution for plants N and S. The anomaly points are colored in “orange.” The remaining points are colored in “blue.”

9.4. Discussion

The present study examined the movement of pea plants using an exploratory unsupervised AD method. Overall, a consistent pattern of outliers was detected for all three models, indicating a degree of uniformity in the atypical behavior exhibited by each plant. The models also demonstrated that plants N and S exhibited distinct behaviors, with plant N showing an intensified change in motion under the “no support” condition in contrast to plant S under the “support” condition. The anomaly score is different with respect to different models, this could be attributed to variations in the underlying principles of the algorithms. However, it can be noticed that the scoring pattern is mostly consistent across models, suggesting that plant N tends to exhibit more erratic movement, while plant S tends to perform movement in a more regular manner.

One thing worth noticing is that the occurrence of anomaly points appeared subsequent to the completion of half of the entire sequence of circumnutations. This observation suggests that the appearance of anomaly points cannot be attributed to the oscillatory nature inherent in circumnutation. In turn, this could suggest that the behavioral differences are expressed when circumnutations are well-developed in the corresponding tendrils.

The finding that plant S showed more regularity in its movement suggests that the sensory input it receives from the environment is translated into controlled and steady movements towards its final goal, which is to grasp the support. The plant N increased irregularity during the final stage of movement indicating that it is moving in a relatively dysregulated manner, potentially resulting from the lack of a support in the environment. However, it is not possible to firmly demonstrate whether the detected differences between the plants are due to individual differences or the presence/absence of the support.

In general, the utilization of machine learning methods can enhance the classic kinematical approach by leveraging computational power to recognize intricate patterns. Further investigation is necessary to validate novel methods used in implementing machine learning, and a more comprehensive understanding of plant behavior is required in order to accurately interpret anomalies. Additionally, the development of model explainers specifically tailored to the context at hand is essential. Further attempts in the use of machine learning for the classification in plants movements are provided in the next experimental chapters.

CHAPTER 10

CLASSIFYING CIRCUMNUTATION IN PEA PLANT VIA MACHINE LEARNING[3]

10.1. Introduction

As stated in Chapter 3, machine learning may have a great, yet unexplored potential, for analyzing the movement of plants. In this experiment, machine learning methods were employed to classify plants movement, and to predict movement patterns which will enable us to build stochastic movement generators, useful in scenarios where collecting actual movement data is laborious.

Given that predicting plant movement is important when building simulators, I aimed to test whether machine learning methods could capture the movement patterns nested in actual kinematical data. Several machine learning classifiers were compared to model plants movement with the goal of generating models that, based on a binary labeled dataset, learn to discriminate between the presence/absence of a support in the environment to formulate precise predictions based on an unlabeled dataset. A difference might be found

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[3] *Published*: Wang, Q., Barbariol, T., Susto, G. A., Bonato, B., Guerra, S., & Castiello, U. (2023). Classifying circumnutation in pea plants via supervised machine learning. *Plants, 12*(4), 965. https://doi.org/10.3390/plants12040965

in the pattern of circumnutation that can be learned and classified rather accurately depending on the presence or absence of the support. If so, the most distinctive kinematic features that contribute to the classification tasks would be identified to provide additional information for driving future studies on the matter. Overall, this first attempt was to test whether machine learning might be a valid tool for studying the movement of plants.

10.2. Materials and Methods

10.2.1. Experimental conditions

The experimental conditions were described in Chapter 6. A total of 32 snow peas: 19 plants were grown individually in chambers without the presence of a support ("no support" condition; Figure 10.1a), while 13 plants were grown individually in chambers where a potential support was present ("support" condition; Figure 10.1b).

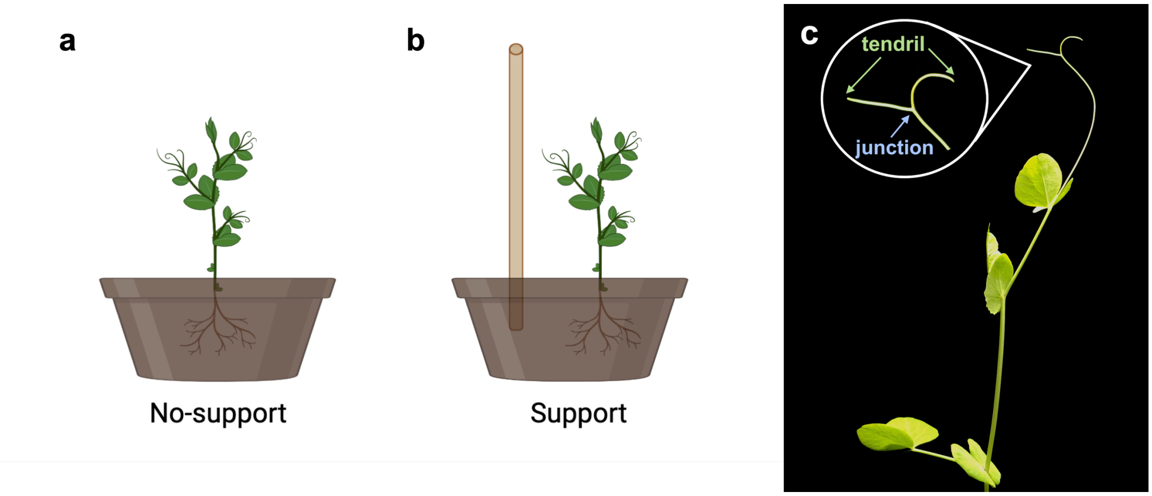

Figure 10.1. Experimental conditions and anatomical landmarks. (a) "No support" condition. (b) "Support" condition. (c) The anatomical landmarks of interest were the "tendrils" and the "junction" developing from the considered leaf. The "tendrils" refers to the tip of the shoot, and the "junction" refers to the point where the tendrils tie together.

10.2.2. Data processing

The anatomical landmarks of interest were the “tendril” and the “junction” (Figure 10.1c), developing from the considered leaf. The initial frame was the one corresponding to the appearance of the tendrils and the junction. The final frame was defined as either the frame in which the tendrils start to coil for the “support” condition (number of selected images: 699.62, SD = 379.28), or the frame just before the plant fell on the ground for the “no support” condition (number of selected images: 1617.11, SD = 1112.82). The 3D coordinates were obtained up to 15 digits after the decimal. The frames corresponding to the time at which the plants grasped the support or touched the ground in the absence of the support were removed from the data set. This was done to prevent classifiers from using these final frames to distinguish between the two conditions. Therefore, the classifiers were only fed with helical organ movements (i.e., circumnutation). Moreover, since each plant has its own starting position, the first frame was set as the origin (0, 0, 0) for all plants in order to prevent a location bias that could affect learning by the classification models (Figure 10.2a-c).

10.2.3. Derived features

Kinematic features were analyzed to ascertain whether they differed for the “support” and the “no support” conditions mirroring what reported in Chapter 6. This aspect is fundamental in order to verify the ability of machine learning tools to discriminate across conditions.

On this basis, the features considered for model classifications were the following:

"junction trajectory," "tendril trajectory," "junction velocity," "tendril velocity," "junction acceleration," "tendril acceleration," "tendrils aperture," "overall movement duration," "movement duration for each circumnutation," and "all features" (i.e., full kinematics).

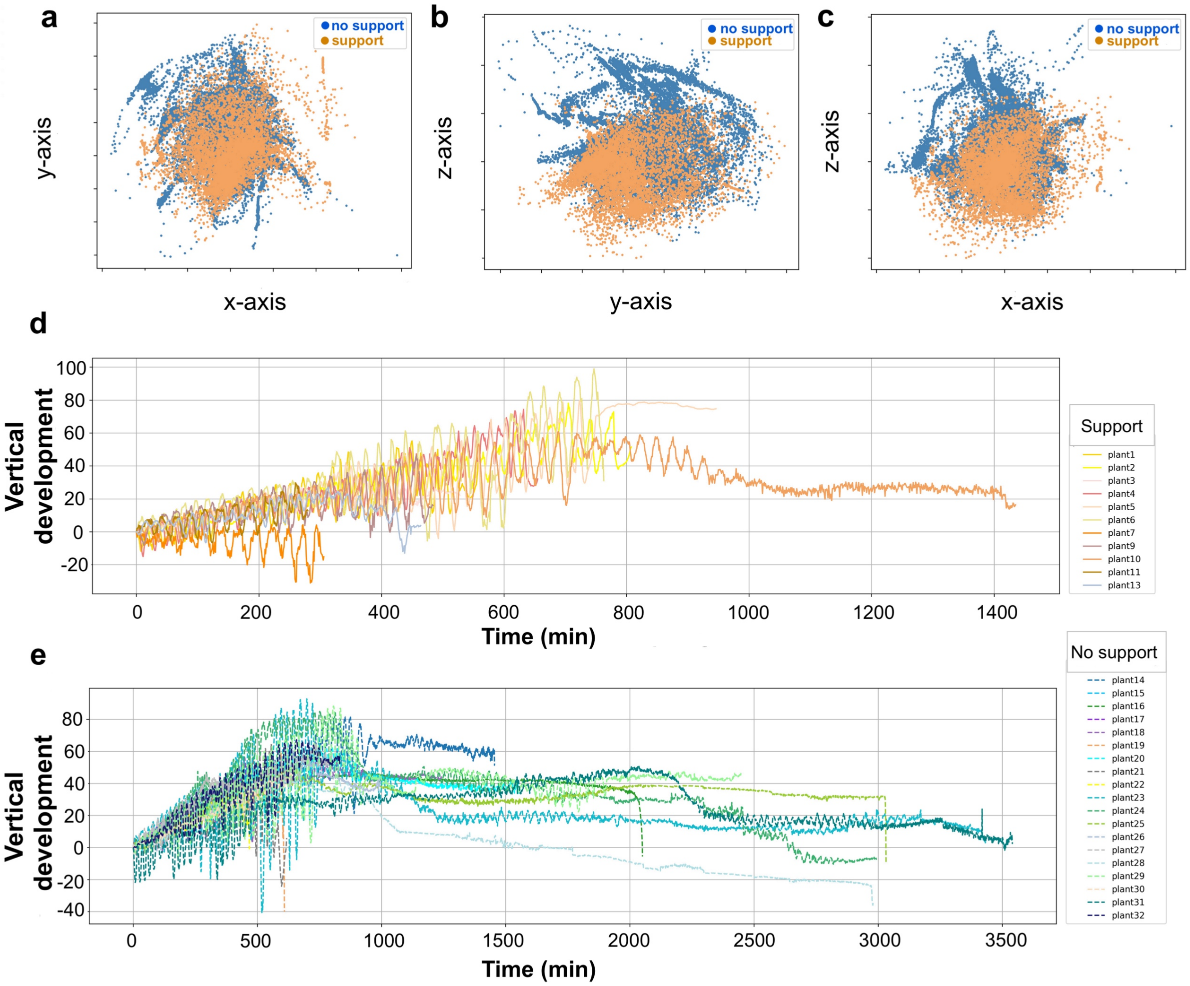

Figure 10.2. Data acquisition. Coordinates of junction trajectory and plant vertical development in time. (a) Junction trajectory for all plants in the x-y dimension for the two experimental conditions. (b) Junction trajectory for all plants in the y-z dimension. (c) Junction trajectory for all plants in the x-z dimension. (d) Junction vertical development in time for the "support" condition. (e) Junction vertical development in time for the "no support" conditions. In panels "d" and "e," different colors represent different plants. Note that for the "no support" condition, the length of the time index, indicated as the number of frames, has a longer range than the "support" conditions.

10.2.4. Data preprocessing

The *z*-score (standard scaling) data normalization method was adopted, by using the formula $z = (x - \mu)/\sigma$, where μ stands for the mean value of the feature and σ for the standard deviation of the features. A value equal to the mean of all the features was normalized to 0 and the standard deviation to 1. To avoid biases toward features of the dataset and, at the same time, to prevent the classifiers from learning information from the test dataset, a transform method was used to keep the same features from the training data to transform the test data. To split the training and test sets, each derived feature was labeled with two different conditions, "support" and "no support," as a binary labeled dataset. The stratified shuffle split cross-validator was applied to the dataset, which is a merge of StratifiedKFold and SuffleSplit to return stratified randomized folds (Pedregosa et al., 2011). The set number of re-shuffling and splitting iterations equals 25, test size as 0.25, default random state.

10.2.5. Model's classifications tasks

The modeling process was carried out with Python (Van Rossum & Drake Jr, 2009). I performed modeling of pea plant behavior based on supervised classification frameworks. The purpose of a Machine Learning Classifier is to produce models that, on the basis of a binary-labeled training set, learn to discriminate between different growth circumstances and to provide exact predictions on the basis of an unlabeled test set. Random decision forests (RF), logistic regression (LR), and support vector classifier (SVC) are the classifiers that were applied and compared through cross-validation (Pedregosa et al., 2011). These approaches are optimized and validated in a variety of research areas (Salvatore et al., 2014;

Wijeyakulasuriya et al., 2020). The percentage of test data that were successfully classified for the two conditions is counted under the accuracy of classification. The classification task employed each of the generated kinematic features separately, and the classification accuracy for each feature was evaluated. I also assessed the accuracy of “all features,” where permutation importance was computed following the fitting of the classifiers (Breiman, 2001); feature importance was analyzed for all the derived features. The “overall movement classification” and the “circumnutation classification” are the two broad categories that constitute the model classification task. Each classification task consists of 25 trials, which include 25 iterations of the training and test. The absolute movement duration was typically longer for the plants growing in the presence of a support (Figure 10.2d) than for the plants growing in the absence of a support. For the “overall movement classification” task, I considered the features extracted from the whole movement for each individual plant (Figure 10.2e). For the “circumnutation classification task” the data were partitioned into circumnutations, smoothing the data set by generating an approximation function that captured the key patterns, namely the waves of the movement in coordinates (i.e., circumnutation). Then, the waves were divided into single circumnutation by splitting between the peaks of waves. The related features that were extracted from each circumnutation, then the classifiers were fitted to predict which condition a single circumnutation corresponded to.

10.3. Results

Classifiers performance: accurate predictions depending on the presence/absence of the support.

The classifiers generated models based on a binary-labeled training set, learned to discriminate between the presence/absence of the support, and formulated precise predictions based on an unlabeled test set. The performance corresponds to the accuracy of classification (i.e., the rate of discriminating plants growing in the presence/absence of the support on the test set correctly). When considering the totality of the circumnutations performed by the plant (i.e., "overall movement classification"), the classifiers were able to distinguish between the "support" and the "no support" conditions with a mean accuracy across all classifiers and all features of 66.80% (SD = 15.39; Table 10.1). When considering circumnutations singularly (i.e., "circumnutation classification"), the mean accuracy was 68.52% (SD = 12.63; Table 10.2). These results demonstrate that the classifiers were capable of differentiating the pattern of circumnutation depending on the presence/absence of the support rather accurately above the chance level (>50.00%).

Table 10.1. Accuracy in the "overall movement classification" task. This table shows the mean and standard deviation of the accuracy for each classifier.

	Accuracy % Mean (standard deviation)			
	Random forest	**Logistic regression**	**Support vector**	**Feature mean accuracy**
Junction trajectory	71.00 (18.30)	80.50 (13.54)	71.50 (9.89)	74.30 (14.80)
Junction velocity	78.50 (12.24)	78.00 (9.04)	75.50 (12.23)	77.30 (11.19)
Junction acceleration	66.50 (11.81)	72.00 (12.12)	71.00 (11.81)	69.80 (11.99)
Tendril trajectory	67.00 (16.49)	56.50 (14.93)	66.00 (11.13)	63.2 (14.95)
Tendril velocity	75.50 (10.51)	68.00 (15.34)	72.50 (10.21)	72.00 (12.47)
Tendril acceleration	51.00 (11.92)	57.00 (10.87)	63.50 (10.16)	57.20 (12.01)
Tendril aperture	62.50 (15.73)	49.50 (12.23)	60.00 (6.25)	57.30 (13.17)
Movement duration	48.50 (17.43)	65.00 (16.54)	56.50 (10.90)	56.70 (16.48)
All features	76.50 (12.14)	71.00 (13.84)	72.00 (10.38)	73.20 (12.27)
Classifier's mean accuracy	66.30 (17.36)	66.40 (16.37)	67.60 (11.94)	66.80 (15.39)

Note. A string of accuracy for each classifier and feature is obtained after repeating the classification task 25 times.

Overall movement classification: specific contribution of the considered features across classifiers.

As shown in Table 10.1, the SVC performs with a slightly higher average accuracy (mean = 67.60%, SD = 11.94) compared to the RF (mean = 66.30%, SD = 17.36) and LR (mean = 66.40%, SD = 16.37) classifiers. Regarding those features that contributed to the successful classification, the "junction velocity" (mean = 77.30%, SD = 11.99), the "junction trajectory" (mean = 74.30%, SD = 14.80), and "all features" (mean = 73.20%, SD = 12.27) show generally better performance compared with the "tendrils aperture" (mean = 57.30%, SD = 13.17), the "tendril acceleration" (mean = 57.2%, SD = 12.01), and "movement duration" (mean = 56.70%, SD = 16.48). With a mean accuracy of 80.50% (SD = 13.54) obtained with the LR classifier, "junction trajectory" seems to be the best indicator for distinguishing between the "support" and "no support" conditions. Overall, this suggests that the plants exhibit differences in behavioral patterns depending on the presence/absence of the support.

Table 10.2. Accuracy for the "circumnutation movement classification" task. This table shows the mean and standard deviation for accuracy for each classifier.

	Accuracy % Mean (standard deviation)			
	Random forest	**Logistic regression**	**Support vector**	**Feature mean accuracy**
Junction trajectory	71.84 (10.71)	74.87 (12.14)	71.54 (14.03)	72.75 (12.29)
Junction velocity	65.09 (11.09)	71.01 (15.23)	70.42 (14.44)	68.84 (13.78)
Junction acceleration	67.12 (9.50)	70.27 (10.44)	69.33 (12.22)	68.91 (10.72)
Tendril trajectory	59.49 (9.10)	68.65 (14.56)	67.38 (12.01)	65.17 (12.61)
Tendril velocity	67.35 (11.39)	70.84 (15.23)	70.37 (14.28)	69.52 (13.63)
Tendril acceleration	62.87 (10.42)	65.62 (12.31)	66.20 (11.23)	64.90 (11.29)
Tendril aperture	64.82 (11.28)	65.60 (11.80)	64.67 (12.79)	65.03 (11.82)
Circumnutation movement duration	63.24 (12.18)	72.98 (12.82)	69.92 (12.58)	68.71 (13.02)
All features	73.74 (12.91)	73.37 (10.35)	72.14 (11.54)	73.08 (11.51)
Classifier's mean accuracy	66.20 (11.60)	70.29 (12.98)	69.07 (12.96)	68.52 (12.63)

Note. A string of accuracy for each classifier and feature is obtained after repeating the classification task 25 times.

Circumnutation classification: specific contribution of the considered features.

On the basis of the features derived from a single circumnutation, the classifiers can reliably predict whether the plants are moving in the presence/absence of a potential support (Table 10.2). In comparison to the RF (mean = 66.20%, SD = 11.60) and the SVC (mean = 70.29%, SD = 12.98), the LR has a slightly greater average accuracy (mean = 69.07%, SD = 12.96). As for the contribution of the different features, "all features" (mean = 73.08%, SD = 11.51), "junction trajectory" (mean = 72.75%, SD = 12.29), and "tendril velocity" (mean = 69.52%, SD = 13.63) exhibit better performance compared with "tendril trajectory" (mean = 65.17%, SD = 12.61), "tendrils aperture" (mean = 65.03%, SD = 11.82), and "tendril acceleration" (mean = 64.90%, SD = 11.29). With a mean accuracy of 74.87% (SD = 12.14) obtained with the LR classifier, "junction trajectory" seems to be the best indicator for distinguishing between the "support" and the "no support" conditions. This is in accordance with the findings for the "overall movement classification." Again, this demonstrates that the classifiers are able to extract from the kinematics of circumnutation whether the plant is moving in the presence/absence of a potential support.

The accuracy of the classification depends on organs and features.

When looking more deeply into the contributory role played by the features considered for classification, the kinematic features for the tendrils appear to be less relevant with respect to junction-related features for both classification tasks. When considering movement duration, this feature appears to be less informative when the overall movement classification is considered. However, this very same feature appears to be a reliable indicator when single circumnutations are considered (68.71%, SD = 13.02).

A full kinematic profile favors classification.

When all the extracted features were considered, a high level of accuracy was obtained across all classifiers (overall movement classification: mean = 73.20%, SD = 12.27; Table 10.1; circumnutation classification: mean = 73.08%, SD = 11.51; Table 10.2). After the models had been fitted, the importance of kinematic features was determined by applying permutation importance (Figure 10.3a,b). Different feature importance is detected among classifiers when considering the overall movement and single circumnutations separately. For instance, when the overall movement is considered, "junction velocity," "junction trajectory," and "junction acceleration" appear to be the most crucial classification features, whereas "tendril acceleration," "tendril aperture," "tendril trajectory," and "movement duration" appear to be less essential. The negative value (< 0.00) for the less important features mentioned above indicates that predictions based on shuffled data typically turn out to be more accurate than real data. "Junction trajectory" and "junction acceleration" appear to be more important than "tendril acceleration" and "tendril aperture" for classification when single circumnutations are considered. Movement duration is an important feature for distinguishing between the presence/absence of the support when it is referred to single circumnutation, but not when "overall movement duration" is considered.

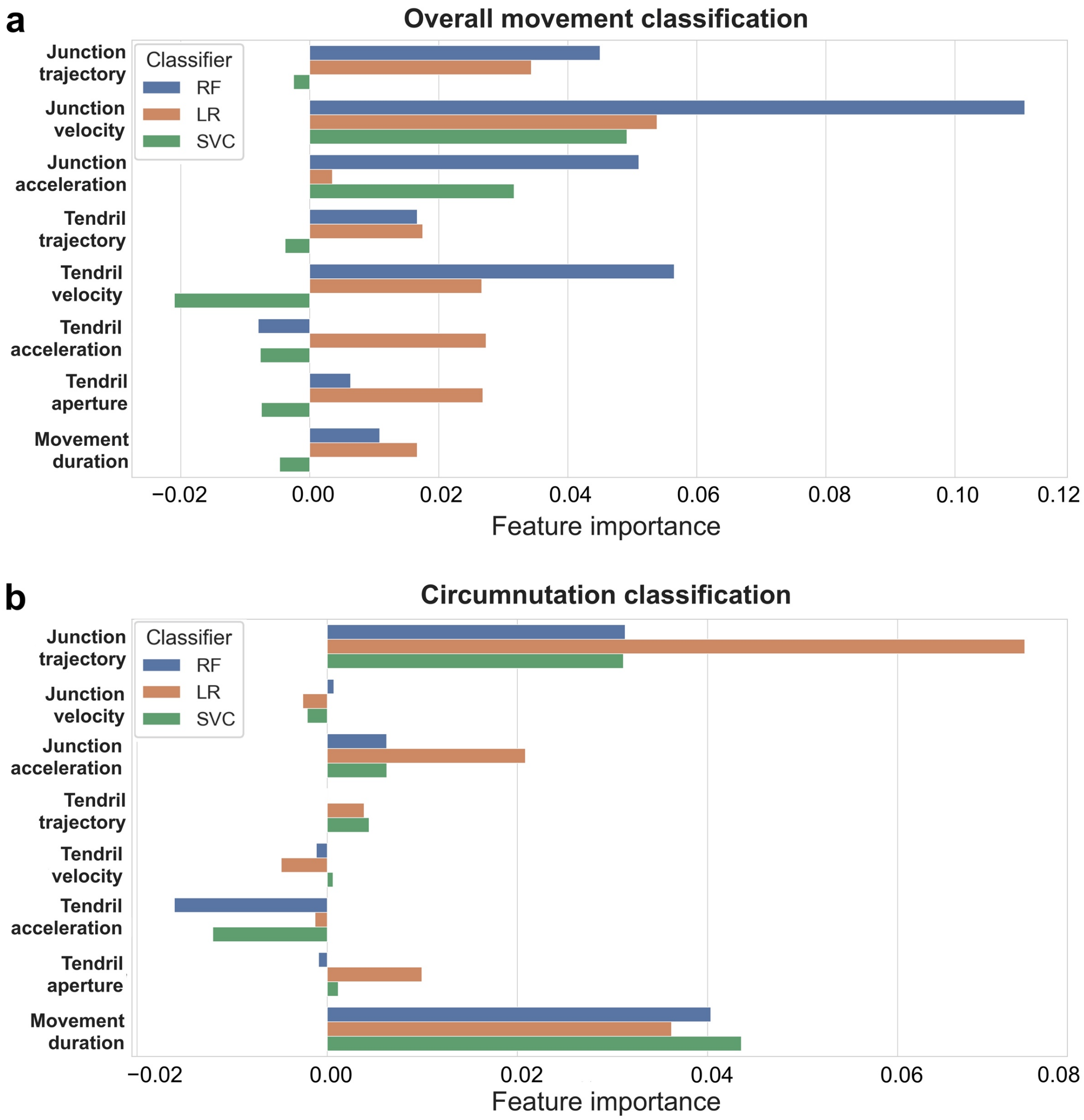

Figure 10.3. Feature importance for "all features." Kinematic feature importance of three classifiers random forest (RF, blue), logistic regression (LR, orange), support vector classifier (SVC, green). (a) Feature importance for the "overall movement classification" task. (b) Feature importance for the "circumnutation classification" task.

10.4. Discussion

Here, a general framework to classify pea plants' circumnutation movement is proposed. This framework has been operationalized via various machine learning models fed with kinematic data. The findings show that machine learning techniques have the ability to unveil how kinematic patterning is modulated in key organs when pea plants “hunt” for a support.

Nutation kinematics of different organs has served to lay a foundation of several mechanisms responsible for the movement in question with tendrils being amongst the most investigated (Isnard & Silk, 2009; Raja et al., 2020; Simonetti et al., 2021). Tendrils serve climbing plants by providing a parasitic alternative to building independently stable structural supports, allowing the plant to wend its way to sunlight and numerous ecological niches (Gerbode et al., 2012). Accordingly, previous evidence provides a degree of support that some climbing plants can modify their circumnutation patterns to a greater or lesser extent depending on the presence/absence of a potential support in the environment (Tronchet, 1946, 1977). Experimental evidence demonstrating that this is the case has been forthcoming from recent studies that used kinematic analysis to characterize the movements of the tendrils of pea plants (Castiello, 2020; Ceccarini et al., 2020a, 2020b; Guerra et al., 2022). Guerra et al. (2019), for example, demonstrated that pea plants (*P. sativum*) are able to perceive a support and modulate the kinematics of the tendrils according to the features of a potential support. Therefore, it seems that the tendrils of climbing plants reaching to grasp a support play a pivotal role as far as support detection is concerned.

The findings of the present study, however, seem to suggest that, rather than the tendrils, the junction underneath them is a superior indicator for discerning the presence/absence of the support. The fact that the kinematics of the junction is a stronger predictor than the kinematics of the tendrils for the presence of the support points to this organ as a navigator guiding the tendrils towards the support. Indeed, if one looks carefully at how circumnutation unfolds once the support has been somewhat detected, it is evident that the junction of the tendrils modifies its velocity and timing to launch the tendrils toward the support. In addition, once informed that the "take-off" is approaching, the tendrils open and assume a choreography so as to accommodate the thickness and the shape of the support (Guerra et al., 2019). All of this corroborates the idea that plant movements are adaptive, flexible, anticipatory, and goal directed. They are somewhat organized and structured, with different organs "cross-talking" to accomplish a crucial endeavor for the plant's survival. This study using machine learning techniques illuminates and quantifies this proposal.

Another novel observation that stems from the present investigation is the classifiers being able to extract a tremendous amount of information from a single circumnutation, which represents the smallest unit of the entire movement. The very fact that the classifiers can make accurate predictions from the emergence of the very first circumnutation reveals that the plants, at the time they initiated to circumnutate, were already well-aware of their surroundings.

Further machine learning research should aim at characterizing how circumnutation changes as far as support characteristics are concerned. Predictions and modeling of the cost-benefit analysis of climbing plant behavior should be helpful to infer the selective pressures that have operated to shape current climber ecological communities. In addition to plant movement, as a direct reflection of plants' internal state, other physiological markers could be added to obtain a more complete, reliable, and consistent picture of how the environment shapes climbers' behavior. Such technologies will enable the investigation of unknown aspects of the helical growth performed by the tendrils and their junction on an evolutionary scale, shedding some light on the mechanisms involved in the acquisition and evolution of the climbing habits of terrestrial plants.

CHAPTER 11

CLASSIFYING SUPPORT-SEARCHING VIA ENSEMBLE LEARNING

11.1. Introduction

Previous chapters have demonstrated the validity of machine learning as a viable approach for understanding plant movements (Wang et al., 2023a). The application of machine learning techniques presents compelling advantageous outcomes through its ability to enhance data processing, recognize hidden patterns, and boost interpretation of plant behavior. For instance, by employing unsupervised anomaly detection techniques as discussed in Chapter 9, machine learning algorithms were able to reveal concealed connections and emergent patterns in the movements of plants. More importantly, machine learning techniques possess a fundamental advantage, that is predictability. This ability allows classifiers to predict plant behavior by leveraging previously learned data, and it has the potential to facilitate the prediction of plants' anticipatory responses to different scenarios or stressors. In the context of supervised machine learning classification, as discussed in Chapter 10, a new finding regarding plant movement control has come to light. I uncovered that the anatomical landmark, defined as the "joint" (i.e., the point where the tendrils tie together), plays a pivotal role in guiding the movement towards a potential support. This was achieved by feeding the machine learning classifier with kinematical features.

It must be said that although the classifier's performance exhibited accuracy levels that were above chance, it did not achieve superiority. In relation to this matter, a refined approach, through the use of ensemble learning classifiers, could be adopted to boost the classifier's robustness and precision. Ensemble learning classifiers contribute to the enhancement of machine learning performances through the amalgamation of many computational models (Sagi & Rokach, 2018). This methodology, in contrast to the utilization of other classifiers enables the generation of enhanced predictive performance, reduces the problem of overfitting, and enables the achievement of a balance between bias and variance (Breiman, 2001; Efron, 1992).

In Chapter 10, by analyzing the extracted averaged features, the classifiers successfully predicted the specific conditions in which the plant grew in the presence/absence of the support. During that task, each feature of the plant was represented by a single value within the "overall classification task." The classifier did not take into account the detailed profile of each circumnutation performed by a plant. The rationale behind choosing this approach is that plants show variation in the time lengths of their movements, leading to an unequal dataset that poses a challenge for the application of machine learning classifiers. The issue of unequal time series has been reported in several study domains when employing machine learning techniques (Soto et al., 2019; Widiputra et al., 2011). Here this issue could be resolved by employing a polynomial regression model that considers all circumnutations in a plant. As so, each circumnutation performed by a plant could be regarded as interdependent. And the machine learning classifier could learn to make predictions regarding the growth condition of a plant by analyzing a sequence of circumnutations.

The aim of the present study was to evaluate the efficacy of ensemble learning classifiers based on the data concerned with plant decision-making behavior during support-searching reported in Chapter 8. I expected the new approaches would yield a superior level of accuracy in predicting plant movements. Moreover, by addressing the variation in time lengths among plants, I should be enabled to examine plants at an individual level. The overall purpose was to expand the understanding of plant decision-making behavior through the application of supervised machine learning techniques.

11.2. Materials and Methods

11.2.1. Subjects

In the present study, a total of 37 pea plants (*P. sativum*) were chosen.

11.2.2. Experimental conditions

For details related to the experimental conditions please refer to Chapter 8. Eight plants were grown in the presence of a single thin support (i.e., S-thin condition); 10 plants were grown in the presence of a single thick support (i.e., S-thick condition). 19 plants were grown in the presence of both thin and thick supports (i.e., DM condition). The plants for the DM condition were further divided into two groups: the DM-thin group includes the 13 plants that chose the thin support, and the DM-thick group includes the six plants that chose the thick support. During the experiment, the classifiers were assigned three tasks to learn the behavioral patterns shown by the plants and then utilize this knowledge to make predictions about plant's growth condition:

i. DM vs. Single: to classify the plants grown under the DM and the Single conditions.

ii. S-thin vs. S-thick: to classify the plants grown under the S-thin and the S-thick conditions.

iii. DM-thin vs. DM-thick: to classify the plants preferred thin support or thick support under DM conditions.

11.2.3. Derived features

The anatomical landmarks of interest were the "tendril," the "junction" developing from the considered leaf, as well as the "apex" which denotes the shoot apex where new leaf growth occurs (Figure 11.1). The final frame was defined as the frame at which the tendrils begin to coil. Moreover, in order to mitigate any possible location bias that may impact the learning performance of the classifiers, the first frame was designated as the origin (0, 0, 0) for all plants. The trajectory of the plant movement was described by a sequence of coordinates (x_i, y_i, z_i) that were indexed by time.

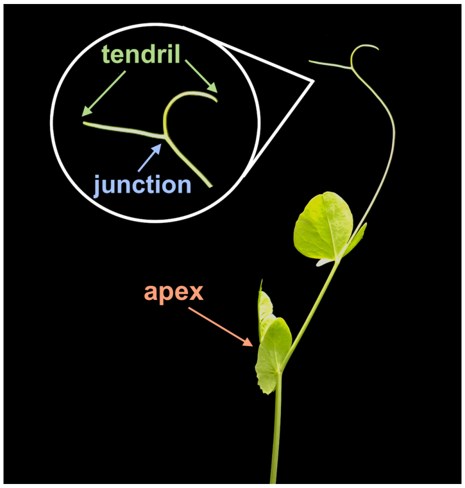

Figure 11.1. The anatomical landmarks of interest were the tendril, junction, and apex. The tendril refers to the tip of the shoot, the junction refers to the point where the tendrils tie together, and the apex refers to the shoot apex where the new part of the plant will develop.

11.2.4. Data preprocessing

In order to classify plants at an individual level, the extraction of plant-related features was conducted based on the analysis of their circumnutations in tendrils, joints, and apexes. The circumnutations were split using a filtering method that employed a mobile average window on the plant's trajectory, followed by the division of each plant's trajectory (Simonetti et al., 2021). Plant's trajectories were therefore divided into circumnutations (Figure 11.2). Subsequently, several features of circumnutations were computed so to describe the movement of a plant.

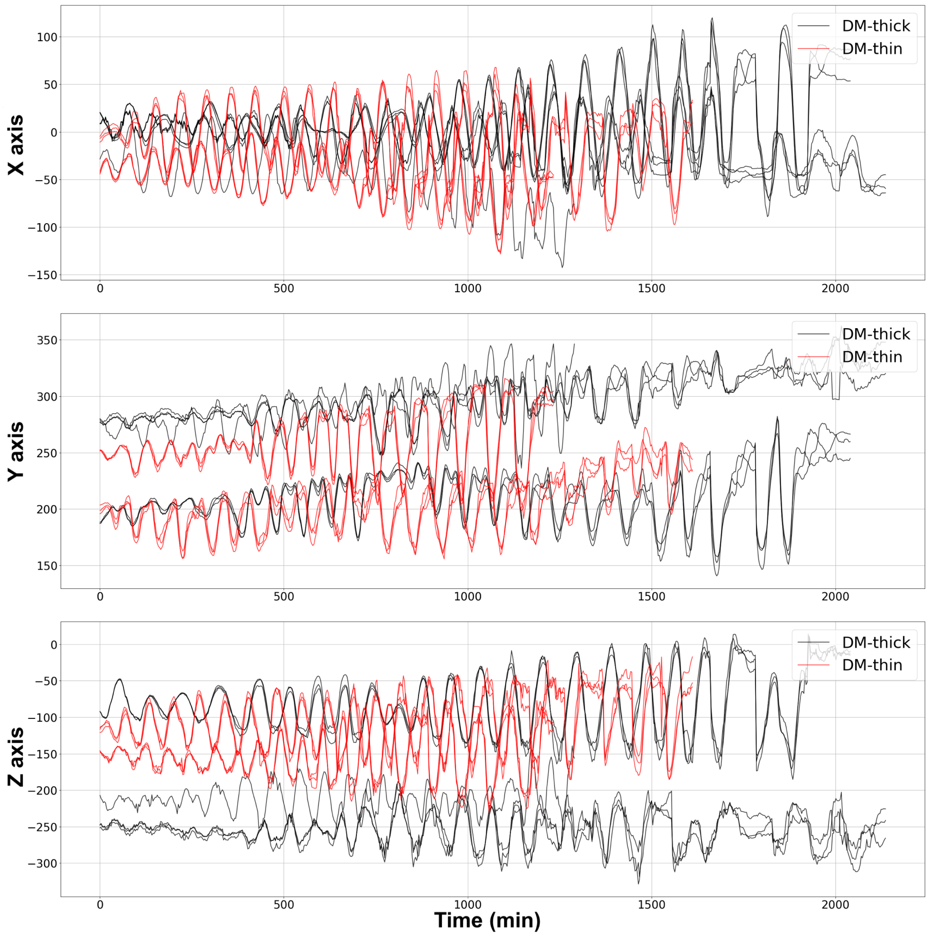

Figure 11.2. Coordinates of tendrils' trajectory for the DM-thin and DM-thick conditions along the x, y, and z axes over time.

The features extracted from the split circumnutation were:

i. Circumnutation duration (min).

ii. The circumnutation center of gravity (Figure 11.3. Segment a).

iii. The velocity of the circumnutation center of gravity (mm/min).

iv. Circumnutation length (mm; Figure 11.3. Segment b).

v. The amplitude of circumnutation average velocity (mm/min).

vi. Distance from the circumnutation center of gravity to the origin of the plant

(Figure 11.3. Segment c).

vii. Distance from the circumnutation center of gravity to the support (Figure 11.3. Segment d).

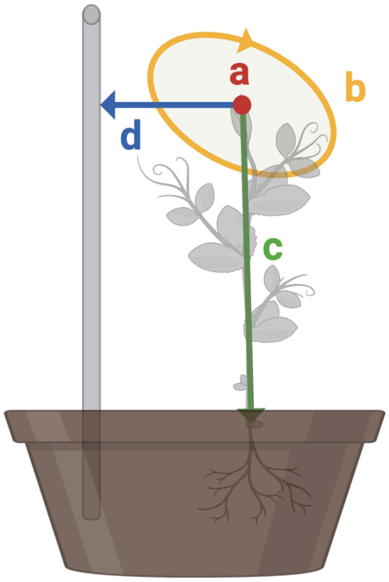

Figure 11.3. Graphical representation for some of the extracted features: (a) the circumnutation center of gravity represented by a red dot; (b) the circumnutation length marked in yellow; (c) the distance from the circumnutation center of gravity to the origin of the plant marked in green; (d) the distance from the circumnutation center of gravity to the support marked in blue.

Due to variations in the duration and quantity of the circumnutations exhibited by individual plants, the result is a matrix containing rows of unequal data lengths. Generating a proper description of the dataset for this scenario was technically unfeasible, therefore, the approximation theory was employed (Powell, 1981). The study of approximation theory focuses on the optimal approximation of functions using simpler and fewer functions. This involves implementing several operations to achieve results that closely resemble the underlying reality. To achieve the standardization/normalization of feature lengths over a predetermined number of features, a polynomial function regressor was utilized (Khuri & Conlon, 1981; Powell, 1981). This can be achieved by approximating the strings of features collected from each plant using a polynomial function $f(n)$, where n is an input parameter representing the degree of the polynomial function approximation. The concept is articulated as:

$$f(n,x) = a_n x^n + a_{n-1} x^{n-1} + \cdots + a_1 x + a_0$$

where the coefficients $\{a_n, a_{n-1}, \cdots, a_1, a_0\}$ are solutions from the minimization problem:

$$\{a_n, a_{n-1}, \cdots, a_1, a_0\} = arg \min_{\{a_n, a_{n-1}, \cdots, a_1, a_0\}} \sum_{i=0}^{k} |f(n, x_i) - y_i|^2$$

Figure 11.4 provides a representation of examples of the polynomial function regressor. The method of approximation yielded a fixed set of numbers representing the degree of the polynomial function approximator. In this way, the challenge of encoding features extracted from circumnutations for each plant was effectively solved by retaining the time evolvement of these features. Here, the degree of the polynomial function is set as six (i.e., hexic). The generated matrix, which has equal lengths in rows, and captures this temporal information, was then used as the input dataset for the classification models.

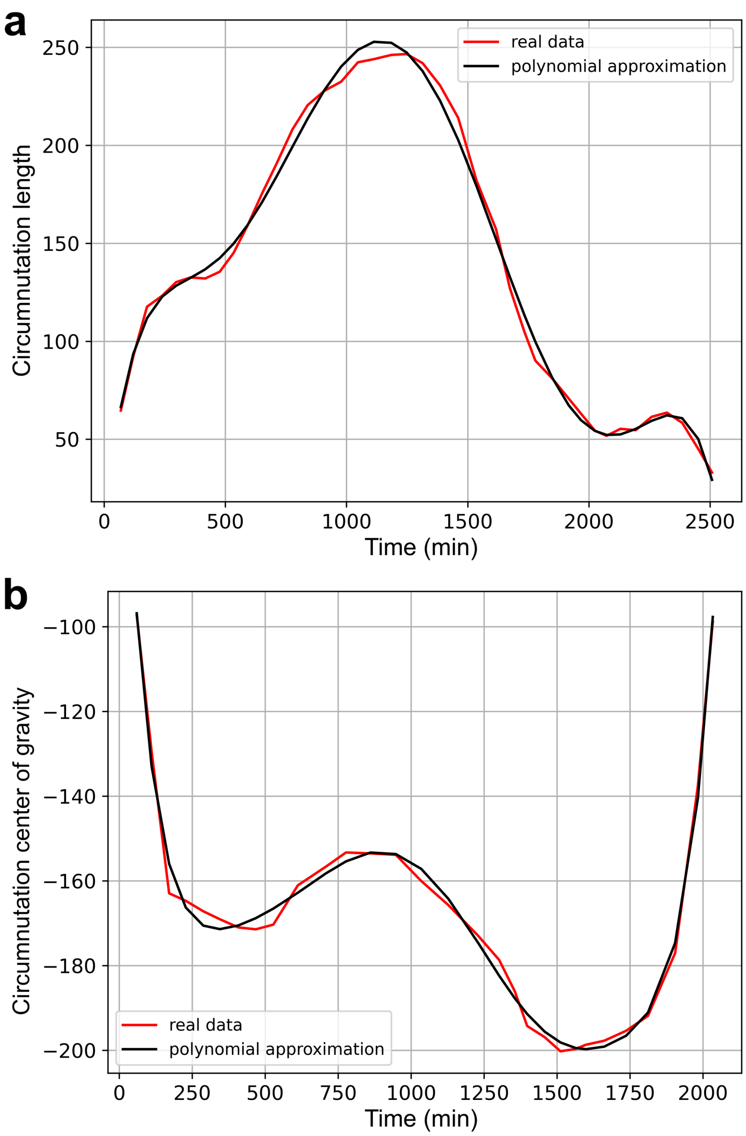

Figure 11.4. Exemplars of the polynomial function regressor over time on the features (a) "circumnutation length" in a joint, and (b) "circumnutation center of gravity" in tendrils are presented. The red line represents the real data over time, whereas the black line represents the polynomial approximation function.

11.2.5. Classifications

Once the input dataset has been prepared for classification, the procedure of training/test sets and classifiers' assignment commenced. To split the training and test sets, each derived feature was labeled with two different conditions as a binary labeled dataset:

i. DM (label: y_i = 1) and Single (label: y_i = 0);
ii. S-thin (label: y_i = 1) and S-thick (label: y_i = 0);
iii. DM-thin (label: y_i = 1) and DM-thick (label: y_i = 0).

The stratified shuffle split cross-validator was applied to the dataset to obtain the stratified randomized folds (Pedregosa et al., 2011). 90% of the dataset was allocated as the training set, while the remaining 10% was designated as the test set for classification. This process was iterated 100 times, whereby the shuffling operation is performed priorly. This ensures that each iteration of the process yields a training/test dataset that comprises different plants. The objective of this operation was to ascertain the statistical significance of accuracy evaluation concerning models, taking into account the ill-posed aspect of the issue caused by the limited number of plants. Given the unique characteristic of the dataset, the selection of ensemble models was deemed appropriate for the machine learning classification task. The chosen ensemble models were Decision Tree Classifier with bagging (Breiman, 1996; Von Winterfeldt & Edwards, 1986), Random Forest Classifier (Breiman, 2001) and the Gradient Boosting Classifier (Breiman, 1996; Mason et al., 1999).

i. The Decision Tree classifier with bagging is a composite model that integrates the principles of decision trees (Von Winterfeldt & Edwards, 1986) with bagging (Breiman, 1996; Efron, 1992). The decision tree is a hierarchical model used for decision analysis, which has a structure similar to that of a tree, depicting decisions and their possible corresponding outcomes. Bagging, also known as bootstrap aggregating, is a meta-algorithm that aims to enhance the stability and accuracy of machine learning classifiers (Breiman, 1996; Efron, 1992). The implementation of bagging in statistical modeling can effectively decrease the variance and reduce the issue of overfitting. The bagging procedure often involves the reconfiguration of a dataset into three distinct types: the original dataset, the bootstrap dataset, and the out-of-bag dataset. The original dataset is inputted into the model, and the process proceeds to randomly choose items from the original dataset while maintaining its original size. The dataset that has not been selected for the bootstrap dataset is referred to as the out-of-bag dataset. The model will use bootstrap and out-of-bad datasets to create decision trees.

ii. The Random Forest Classifier is regarded as a highly effective ensemble learning model for classification, characterized by the construction of a multitude of decision trees (Breiman, 2001). The classification output of the random forest model is determined by selecting the class that is most frequently chosen by the ensemble of decision trees. This approach integrates the decision tree algorithm with the techniques of bagging and random feature selection. This implies that the trees inside a random forest model possess knowledge just regarding the data associated with a variable number of samples, which is either fewer than or equal to the original dataset. Consequently, the trees would acquire a greater breadth of information through random processes. During the classification process, each tree contributes to the decision by voicing its decision, and the final result is determined based on the majority vote.

iii. The Gradient Boosting is a machine learning classifier that generates a prediction model by combining many weak prediction models (Breiman, 1997; Hastie et al., 2009; Mason et al., 1999). The method that emerges when a decision tree is utilized as the weak learner is commonly referred to as a gradient-boosted tree. Empirical evidence suggests that gradient-boosted trees generally exhibit superior performance compared to Random Forest (Breiman, 1997). The construction of a gradient-boosted trees model follows a stage-wise strategy, similar to previous boosting techniques. However, it distinguishes itself by enabling the optimization of any differentiable loss function. Every successive model is trained with the goal of minimizing the loss function, which might be the mean squared error or cross-entropy, of the preceding model by the utilization of gradient descent. During each iteration, the algorithm calculates the gradient of the loss function in relation to the predictions made by the current ensemble. Subsequently, a new weak model is trained to minimize this gradient. The predictions generated by the novel model are then incorporated into the ensemble, and this iterative process is continued until a predetermined stopping threshold is satisfied.

The classifiers ought to perform the three tasks by classifying the test set using the polynomial approximation of the features extracted from each circumnutation performed by tendrils, joints, and apexes. Then it will obtain a classification decision, indicating to which condition the plants belong to for each task. During classification, the parameters of each model were configured at random 100 times in order to identify the optimal combination for the best accuracy performance. The accuracy was computed in terms of average performance accuracy, represented by the mean and standard deviation (SD), as well as the best performance accuracy, represented by the maximum value.

11.3. Results

All classifiers were assigned to three tasks, wherein they were required to learn the movement of each plant under varying conditions. The performance metrics of each classifier for all comparisons are reported in Table 11.1.

In general, the ensemble learning classifiers demonstrated a high level of accuracy in predicting the specific growth condition associated with each plant. This accuracy was achieved by utilizing the features extracted from the relevant circumnutations (i.e., circumnutation duration, the circumnutation center of gravity, velocity of the circumnutation center of gravity, circumnutation length, the amplitude of circumnutation average velocity, distance from the circumnutation center of gravity to the origin of the plant, distance from the circumnutation center of gravity to the support), for the tendrils, the joint, and the apex nested of each plant. Furthermore, it is worth noting that all the classifiers exhibited superior performance compared to the classifies reported in Chapter 10.

Task-specific classification performance

For the task “DM vs. Single,” all the classifiers demonstrated successful learning and prediction regarding the growth condition of the plant, achieving a mean accuracy of 0.796, and a maximum accuracy of 0.859. The circumnutation patterns in a plant differ depending on whether it is grown with a single support or double supports. For the task “S-thin vs. S-thick,” all of the classifiers accomplished the task of distinguishing between plants grown with a thin support and plants grown with a thick support. The classifiers achieved a mean accuracy of 0.715 and a maximum accuracy of 0.799.

The aim of the third task "DM-thin vs. DM-thick" was to make predictions regarding a plant's preference for either a thin or a thick support, referred to as DM-thin and DM-thick, respectively. The classifiers demonstrated a high level of accuracy in predicting the individual behavior of plants inside the same growing condition, with a mean accuracy of 0.796, and a maximum accuracy of 0.857.

Performance of classifiers

The performance for all classifiers demonstrated refinement, with mean accuracy scores of 0.771 for the Decision Tree Classifier with bagging, 0.803 for the Random Forest Classifier, and 0.734 for the Gradient Boosting Classifier. The Random Forest achieved the highest maximum accuracy and average accuracy, with a mean of 0.803 and a maximum of 0.859. The Decision Tree with bagging demonstrated superior stability as a predictor compared to the other models, as seen by its minimal variation reflected by the low standard deviation in classification.

Table 11.1. Classifiers' performance accuracy across comparisons.

	Decision Tree			**Random Forest**			**Gradient Boosting**		
	Mean	**SD**	**Max**	**Mean**	**SD**	**Max**	**Mean**	**SD**	**Max**
DM vs. Single	0.789	0.006	0.807	0.843	0.019	0.859	0.756	0.021	0.836
S-thin vs. S-thick	0.728	0.007	0.743	0.727	0.005	0.749	0.690	0.012	0.799
DM-thin vs. DM-thick	0.795	0.009	0.815	0.838	0.019	0.857	0.756	0.020	0.831

Note. Accuracy is reported in average performance accuracy (i.e., mean and SD), and best performance accuracy (i.e., max).

11.4. Discussion

The present study, I applied predictive classifiers to examine decision-making behavior of plants growing in the presence of a single support differing in size (i.e., S-thin and S-thick) or two differently sized supports (i.e., DM conditions). Further, plants that for the DM conditions grasped either the thin or the thick support were compared (i.e., DM-thin vs. DM-thick). The ensemble approach was employed, which was found to be effective in generating valid predictive models. This approach exhibited a high level of accuracy in performing all the classification tasks. By implementing a polynomial function regressor to address the time lengths issue, the classifiers were able to learn the pattern of circumnutations performed by a plant and predict the corresponding growth condition at an individual level across all comparisons.

Being successful in classification is in resonance with the kinematical findings reported in Chapters 7 and 8. In the current study, the behavior of plants was simulated mathematically using machine learning classifiers by formulating tailored functions. By doing so, the classifier demonstrated the capacity to learn the circumnutation pattern specific to each plant and make predictions on the condition. This suggests that variations in behavior among these plants match up at a group level. Plants exhibit distinct reactions when faced with different conditions, as evidenced by the accurate classification of plants growing in S-thin and S-thick conditions. Furthermore, plants can display divergent behaviors even when subjected to identical condition as shown in a preferential selection of the support for the DM condition. This implies that the decision-making process could be influenced by the plants' perceptions and interpretations of the environmental cues, which leads to a movement shaped by contextual factors such as the number and the size of the support.

The findings of this study not only validate previous kinematical studies (Guerra et al., 2019; Wang et al., 2023b), but also strengthen these results by providing a holistic examination of plant movements. Especially, the classification tasks have considered not only features like velocity, but have also incorporated temporal and relative spatial features throughout time. Together with the tendrils and the joint from the considered leaf, and the apex, all of these features exhibited goal-directed and contextually sensitive movements. This in-depth data exploitation shows that when viewed from an interconnected and dynamic standpoint, it becomes evident that plant's natural hallmark is to be able to exhibit anticipatory movement.

Previous findings have already documented the anticipatory nature of the movements for the tendrils and the joint (Guerra et al., 2019; Wang et al., 2023a). Further, the apex of the plant was found in the current study to also exhibit similar goal-directed behavior, which can be classified accurately condition-wise. This implies that decision-making triggered by conditioning does not occur exclusively at the tip of the grasping leaf, but rather in a more integrative manner. The shoot apex, which plays an essential role in morphogenesis, serves as the developing tip of the plant shoot and is responsible for the emergence of new leaves (Steeves & Sussex, 1989). In pea plants, the development of tendrils occurs at the apex and they, subsequently, have to be accountable for future support-searching and -grasping.

Overall, the use of machine learning approaches to plant movement investigation has given encouraging findings, adding to a better understanding of plant behavior and decision-making processes. Researchers could gain useful insights into how plants make decisions, adapt to their surroundings, and demonstrate goal-directed actions by exploiting machine learning's predictive capabilities.

PART V

GENERAL DISCUSSION

CHAPTER 12

INTERPRETING MY RESEARCH

12.1. An Overview

My thesis was developed with the aim of exploring the potential embodiment of motor cognition in plants movements. Six experiments were conducted by employing kinematic and machine learning approaches.

The kinematic experiments revolved around the examination of whether and how the movement patterns of plants could be modulated under different conditions. To achieve this, I used time-lapse photography and 3D motion analysis to track the movements of pea plants. These three experiments exposed plants to different conditions including growing with or without a support, as well as growing with single supports of different sizes and two supports of different sizes. My analyses were based on a wide array of dependent measures that were extracted from the spatial and temporal features of circumnutation patterns.

In the first experiment (Chapter 6), the primary goal was twofold: to substantiate previously observed kinematic differences in movements depending on the presence/absence of a potential support in the environment. These data served for the subsequent implementation of machine learning tasks. The results showed that in the absence of a support, the plants explored their surroundings in a search for potential support, and if any, the plants stopped circumnutating and fell. In contrast, when the plants detected the presence of a support nearby, their circumnutation pattern underwent rapid adjustments, redirecting their movement toward the support, as purposefully approaching and attempting to grasp it. These variations observed in the plants provided empirical confirmation of previously reported findings in the literature (Guerra et al., 2019).

The findings that plants can modulate their movements anticipatorily appear to indicate that plants are capable of making decisions. This aspect compelled me to conduct further experiments to examine the decision-making behavior underlying support-searching.

Therefore, the next steps of my work were designed to investigate the decision-making ability. To accomplish this, I conducted an experiment in which pea plants were subjected to a condition in which they were simultaneously exposed to both thin and thick supports (i.e., DS condition), with the results being compared to plants exclusively exposed to a single support (i.e., SS condition). Interestingly, the outcomes of this experiment revealed that plants in both conditions exhibited a proclivity for approaching and grasping the thin support. The considered dependent measures differed markedly between the DS and SS, suggesting that plants can factor in the presence of both supports while choosing one. This signifies that, despite achieving the same goal (i.e., approaching thin support), for the DS condition, they engaged in a different decision-making process that manifested in the kinematics of circumnutation. Further, the movement of pea plants conformed to the isochrony principle (Viviani & Mccollum, 1983). They tended to maintain their movement duration constant for differently sized supports by scaling velocity.

So, it became increasingly apparent that plants are endowed with the ability to make decisions with respect to the size of a potential support, thus choosing the most suitable option and avoiding the unsuitable one. At this stage, the natural question of "why do plants consistently prefer the thin support over the thick one" arises. A hypothesis posited that the plants' decision might be rooted in metabolic considerations. Approaching and grasping a thick support would require the growth of longer tendrils, a process that exacts a greater metabolic toll in terms of energy consumption. This metabolic-based decision-making process was also reflected at the kinematic level. Therefore, the absence of instances where plants approached and grasped the thick support (with a diameter of 40 mm) strongly suggested that this support size represented a mechanical and metabolic demand that might surpass the plants' capabilities.

In the subsequent experiment (Chapter 8), the investigation continued by introducing a nuanced modification to the size of the thick support. Plants were grown under conditions akin to the previous experiment, with a single thin support, a single thick support, and decision-making where both thin and thick supports were present. This time, plant movements yielded even more complex patterns. Notably, differences emerged at the level of kinematics between the single and the DM conditions, mirroring the findings from Chapter 7. Within the DM conditions, where the size of the thick support was reduced to 30 mm in diameter, certain alterations in the choice of preferred supports became evident. While the majority of plants still exhibited a preference for the thin support, a small portion of plants went for the thick support and succeeded in grasping it. In terms of movement pattern, plants for the DM conditions exhibited a swifter pace, reduced number of circumnutations, and a broader coverage area compared to the single conditions, driven by the number of supports presented. Furthermore, distinct kinematic differences emerged based on the size of the support.

In contrast to the findings presented in Chapter 7, in which plants refrained from grasping the thick support with a diameter of 40 mm possibly due to its heightened energy demands and associated morphological costs. A support of 30 mm in diameter (Chapter 8) emerged as a viable alternative, potentially favoring the future growth and development of plants, as it exhibited a greater capacity to bear additional mass and thereby facilitate their abundance.

The second part of my experiments centered on the use of machine learning techniques for a better understanding of the above behavioral findings. In Chapter 9, I adopted an exploratory unsupervised anomaly detection to investigate the behavior of two plants: one growing in the presence of a support (i.e., Plant S) and the other in the absence of it (i.e., Plant N). The models revealed distinctions in the movement trajectories of these two plants. Plant N exhibited a more pronounced alteration in motion compared to plant S. The anomaly scoring patterns remained largely consistent across different models, implying that plant N displayed a propensity for erratic movements, whereas plant S demonstrated a tendency toward more regular and predictable motion. However, it is crucial to acknowledge that, as a case study, this experiment could not definitively determine whether the observed differences stemmed from individual variances or the influence of the support's presence or absence.

The experiment reported in Chapter 10 considered a widely validated method to investigate plant movement by employing supervised machine learning classifiers to discern plants' growing conditions (i.e., the presence or absence of a support). The outcomes of this experiment underscored the remarkable capacity of machine learning techniques to unveil the modulation of kinematic patterns in critical plant organs, namely the "tendrils" and the "junction", with respect to support-searching." Intriguingly, the results hinted that rather than the "tendrils," the "junction" located beneath them emerged as a superior indicator for discriminating the presence/absence of a support. Another noteworthy revelation stemming from this investigation was the classifiers' ability to extract a wealth of information from a single circumnutation, which is the smallest discernible unit within the overall movement.

The aim of the study reported in Chapter 11 was to improve the machine learning approach by assessing the effectiveness of ensemble learning classifiers based on plant decision-making data (see Chapter 8). The results showed that the ensemble approach exhibited a remarkable level of accuracy across all classification tasks. To address the variability in unequal time length, a polynomial function regressor was integrated into the classifiers. This approach enabled the classifiers to grasp the distinct patterns of all the circumnutations performed by a plant and make predictions of corresponding growth conditions accurately across all comparisons. When viewed holistically within the context of plant behavior, it becomes evident that plants possess a natural propensity for anticipatory movements. Notably, the "apex" of the plant, as revealed in the current study, exhibits goal-directed behaviors that can be accurately classified. This implies that the decision-making processes triggered by environmental conditioning are not exclusive to the tip of the grasping leaf, represented by the "tendrils" and "junction," but rather occur in a more integrated manner. These findings provide valuable insights into how plants navigate their surroundings, make informed choices, and exhibit goal-directed actions, harnessing the predictive capabilities of machine learning.

In conclusion, by merging kinematics and machine learning, I was able to gain several insights into the fascinating interplay between plants and the environment. These findings provide valuable insights into how plants navigate their surroundings, make informed choices, and exhibit goal-directed actions.

At this stage, the question is what are the possible mechanisms behind such behavior? In the next section, I shall provide, though at a very speculative level, some hypotheses regarding the mechanisms subserving the fascinating aspects of plant's goal-directed actions.

12.2. A Possible Mechanistic Hypothesis

12.2.1. The path of choice

The fact that plants adjust their behavior based on the presence or absence of a potential support raises questions regarding their decision-making ability and the mechanisms underlying them. My studies, with kinematics and machine learning classifiers, may ignite further inquiries into the cognitive abilities of plants.

One particularly interesting behavior I have observed is the plant's capacity to adaptively choose between supports of varying diameters. What are the mechanisms that might subserve such behavior? The choices made by the plants appear to be influenced by several factors, including the presence of a support, the number of supports available, and their respective sizes. In Chapter 7, for instance, plants consistently favored the thin support when presented with a choice between two supports. This preference for the thin support suggests a potential trade-off related to metabolic energy expenditure. The act of touching and grasping a thick support may entail the growth of longer tendrils, which could demand more energy resources. This metabolic consideration could, in turn, impact the kinematics of their movements.

Nevertheless, in Chapter 8, when I reduced the size of the thick support, a small group of plants approached the thick support instead of the thin one. One plausible explanation is that, this time, the diameter of the thick support, might not have significantly disrupted the plant's homeostasis, making it a viable option. Interestingly, studies have suggested that certain characteristics of host trees can influence the distribution of climbing plants in forests. While it's known that climbing plants have "failsafe" mechanisms (Isnard & Rowe, 2008; Isnard & Silk, 2009), larger trees were found to have more climbing plants attached to them (Dewalt et al., 2000; Ladwig & Meiners, 2010; Leicht-Young et al., 2010; Pérez-Salicrup & De Meijere, 2005; Putz, 1984). This might be due to larger trees in older forests being better at supporting larger biomass, thus securing more canopy space for light acquisition and increasing the abundance of climbing plants.

The small portion of plants who chose thick supports might be more "ambitious." They seem to seek stable and robust attachments that can potentially support more weight, increasing their chances of thriving in the future. If this hypothesis holds, it implies that plants possess the ability to perceive not only the size of a potential support but also other properties such as its color, density, and mass. Evidence for such perceptual abilities has been found in other studies (Gianoli & Carrasco-Urra, 2014; Price & Wilcut, 2007; Runyon et al., 2006), where climbing plants exhibited preferences based on the material of the support, showing aversion to materials like glass (Darwin, 1875) or favoring natural objects over artificial ones (Runyon et al., 2006).

Moreover, pea plants have demonstrated the ability to modulate their movements when facing one and two supports, suggesting that they may possess a sort of numerical competence. Especially since the differences in kinematics appear to be more fundamental when comparing decision-making with single conditions (Chapter 8). This indicates that plants could discern differences in the number of supports, pointing to a potential numerical competence that enables them to process quantitative magnitudes of the objects present in the surroundings. This is not unusual, as plant species have already demonstrated their numerical proficiency in nature. For example, the carnivorous plant *Dionaea muscipula* can monitor the frequency of stimulation experienced by the trigger hairs situated within the inner region of its snap trap (Böhm et al., 2016; Hedrich et al., 2016; Segundo-Ortin & Calvo, 2022).

In general, when considering pea plant movements in the context of support-searching, their goal-directedness aligns well with the Judgment and Decision-Making (JDM) model proposed by Karban and Orrock (2018). This model involves (i) a cue or stimulus that provides information, (ii) a judgment whereby the plant perceives and processes this informative cue, (iii) a decision whereby the plant chooses among several options based on their relative costs and benefits, and (iv) action. Originally conceived to elucidate plant-herbivore interactions, this model appears to have broader applicability to various decision-making processes. In the context of support-searching, the properties of support, such as support size and number, act as informative cues. Subsequent judgments about these stimuli lead to decisions manifested as actions, such as grasping a specific support. Even when considering differing outcomes, such as the choice between thin and thick supports, it could be explained. Karban and Orrock (2018) contend that, with accurate judgments, plants may still exhibit variations in the decision-making process due to the influence of cost-benefit considerations that stem from their native range. This variation, shaped by selection pressures, could potentially lead to the development of highly successful adaptations.

12.2.2. The sensory mechanisms

The exact mechanisms by which plants perceive their surroundings and program specific actions remain uncertain. With over 20 senses, plants offer a plethora of sensory avenues that may shed light on their decision-making processes during support-searching. Within this realm of sensory capabilities, several mechanisms could potentially offer valuable insights into the processes underlying decision-making in plants during their search for suitable support structures. In the following discussion, I will focus on three mechanisms that hold the most promise for explaining how plants manifest decision-making behaviors in the context of support-searching. This exploration will be supplemented with evidence drawn from observations in various plant species.

Mechanosensory perception

Pea plants might be capable of detecting mechanical forces exerted on them as they meet a support. These forces could signal the support's size, flexibility, and stability, and eventually affect plant growth and development (Coutand, 2010). The translation of these mechanical cues into growth responses may involve mechanosensitive channels or cells.

One notable tropic movement in plants is thigmotropism, which requires the perception of a stimulus, signal transduction cascades that amplify the signal, and the capacity to respond to tactile stimulation through differential growth (Braam, 2005). Climbing plants, for instance, utilize touch sensitivity to optimize their vertical growth, avoiding the need to invest energy in developing a supporting trunk (Braam, 2005). The distal sections of tendrils exhibit high touch sensitivity, with even a slight 0.25 mg thread causing a rapid coiling response, typically within seconds, enabling secure attachment to an object (Simons, 1992). Remarkably, climbing plants can distinguish between touch stimuli and non-tactile factors, as evidenced by the absence of coiling response to water droplets, preventing nonproductive coiling during rainstorms (Jaffe & Galston, 1968).

In my research, this mechanosensory pathway emerges as a plausible explanation for the precise plant responses associated with decision-making. The above-ground portion of the plant exhibited anticipatory responses in the tendrils, suggesting pre-planned actions before physical contact. However, considering that the support structure may also extend below ground, the roots could potentially access and come into contact with the support, thereby gathering information about it. Roots are capable of sensing the presence and properties of a support structure, and through root-to-shoot signaling, tendril growth can be directed to achieve specific goals.

Darwin and Darwin (1880) contemplated the fate of roots encountering obstacles, such as stones, during their growth through the soil. They observed that when roots encountered obstructions that hindered their downward growth, the root tips would flatten, assume an oblique shape, and pivot nearly 90° to establish a new growth direction along the surface of the obstacle. Darwin later postulated that the root apex possesses touch sensitivity, and upon contact, a signal is transmitted to induce growth changes in more proximal root regions.

Roots serve as a focal point for integrating touch responses, with proper root development necessitating the coordination of gravitropic and thigmotropic reactions. Darwin conducted experiments involving the mechanical stimulation of young root apices by placing small, flat materials like sandpaper against the sides of the root tips. These experiments revealed a loss of gravitropic behavior as thigmotropic growth led to a movement away from the point of contact. Similarly, when *Arabidopsis* roots encounter glass barriers, gravitropism appears to be overridden by thigmotropism (Massa & Gilroy, 2003).

Touch response is controlled by a group of genes known as the TOUCH (TCH) family identified in *Arabidopsis* (Esmon et al., 2004). TCH1 encodes calmodulin (CaM), while TCH2 and TCH3 encode calmodulin-like genes (Sistrunk et al., 1994). Calmodulin is a highly conserved protein that modulates specific target enzymes in response to calcium ions (Allan & Hepler, 1989). Consequently, it is reasonable to propose that calcium ions, acting as second messengers, may play a crucial role in touch-induced responses, much like other tropic reactions (Legué et al., 1997). Recent evidence from *Arabidopsis thaliana* and *Nicotiana tabacum* supports the important role that calcium ions play. Individual leaf epidermal cells have been found to synthesize genetically encoded calcium indicators (R-GERCO and GCaMP3), leading to the induction of local calcium peaks preceding delayed, slowly moving calcium waves in response to compressive forces (Howell et al., 2023).

Different types of waves, such as those triggered by force release, evoke faster calcium waves, suggesting that plants possess the ability to distinguish between touch and release.

Pea plants may use touch-response mechanisms as a fundamental component of their sensory inputs to make informed decisions during support searching. When the plant's roots come into contact with or sense the support, a series of touch-sensitive processes might be awakened. At the cellular level, finely tailored to detect mechanical stimuli, mechanoreceptors initiate cascades of intracellular events. When plants are equipped with this tactile information, they undergo physiological changes by adjusting growth rate/direction and movement patterns so to direct their tendrils towards the support.

Hypothesis of ocelli

Besides the touch response, the hypothesis of *ocelli* draws inspiration from the behavior of young seedlings of the tropical vine *Monstera gigantea*, which have been reported to exhibit skototropism—a directional movement of plant organs toward darkness, enabling them to localize and securely support host trees (Strong Jr & Ray Jr, 1975). The concept of ocelli finds historical roots in Francis's description (1967) of an eyespot in *Nematodinium armatum*, characterized by a pigment cup. This intriguing structure is believed to harbor light-sensitive retinoids and possibly lenses capable of focusing and concentrating light rays, thereby contributing to image formation. Baluška and Mancuso (2016) revived this theory, positing that plants might perceive their environment through ocelli located in both shoot and root areas. Some evidence in roots suggests the plants' ability to discern illuminated and darkened areas during development. This observation has led to the hypothesis that a form of root apex vision may underlie the root apex's skototropic response, possibly mediated by the blue-light phot 1 photoreceptor (Mo et al., 2015).

Plants can mimic the host tree (Gianoli & Carrasco-Urra, 2014), and this phenomenon has been used to support the existence of ocelli in plants. A recent finding on *Boquila trifoliolata* mimics leaves of an artificial plastic host plant provides some evidence that plants can "see" (White & Yamashita, 2021). The plant can change its original three-lobed leaf shape into longitudinal leaves or any other shape depending on the non-living host plant next to its leaves.

However, this assertion has generated controversy, with the discoverer of leaf mimicry highlighting the logical inadequacy of attributing plant mimicry behavior to ocelli, stating: "*Just as animals do not need to photosynthesize, plants do not need to see*" (Gianoli, 2017). The complexity involved in leaf mimicry, including alterations in size, shape, color, orientation, petiole length, vein conspicuousness, and the development of spiny tips, must be orchestrated in a coherent and integrated phenotype. Such morphological intricacies are unlikely to be driven solely by simple changes in light intensity, orientation, or quality that photoreceptors (or hypothetical plant ocelli) may detect.

Based on the hypothesis of ocelli, my observations on plant decision-making could imply that plants can perceive their surroundings through ocelli located in both shoot and root regions, enabling them to make choices. Nevertheless, the clear evidence supporting the existence and physiological structure of ocelli remains elusive.

Integrated view: systemic signaling

As mentioned above, in all the studies, the tendrils did not approach or make contact with the support before initiating coiling, indicating that the above-ground parts of the plants exhibited anticipatory movement. This observation led me to consider the possibility that roots might have access to the support and would send information to the upper parts of the plant. Recent research has demonstrated that root-to-shoot signaling plays a pivotal role in the ability of climbing plants to sense the presence and thickness of support, ultimately influencing the planning and execution of their reach-to-grasp movements (Guerra et al., 2021). Especially, when there was a discrepancy in the information about the support's size between the shoot and root regions, it appeared to confuse the plants. The coding of support thickness seems to be achieved through a delicate equilibrium maintained by crosstalk between the rooted and aerial components of the plant (Guerra et al., 2022).

Furthermore, plants can exhibit diverse behaviors guided by different types of sensory input, such as light and touch. For instance, *Monstera* vines exhibit a unique behavior of traveling along the ground, following the darkness of a tree's shadow (Strong Jr & Ray Jr, 1975). However, this traveling behavior comes to a halt when the vine's apex detects a host tree through touch. In response to this touch, the vine undergoes an immediate change in growth direction, coiling upward along the host tree. Additionally, there are concurrent changes in leaf and stem development, which anticipate increased light exposure and enhanced photosynthesis (Braam, 2005; Strong Jr & Ray Jr, 1975).

How do plants integrate different types of information and respond in ways that are beneficial for their survival? A well-established and plausible theory suggests that plants possess a complex information network, with a focus on the symplastic and apoplastic infrastructure that supports long-distance signaling, in addition to downstream gene networks responsible for information synthesis (Brenner et al., 2006).

In this network, long-distance signaling emerges as fundamental pathways for integrated communication in plants. Numerous studies have demonstrated that plants can activate hydraulic, chemical, or electrical long-distance signals in response to various environmental cues, including exposure to biotic and abiotic stressors (Huber & Bauerle, 2016). The necessity of long-distance signaling between separate plant organs has been documented, encompassing bidirectional communication between roots and shoots, as well as shoot-to-shoot and root-to-root interactions (Giehl et al., 2009; Liu et al., 2009; Soler et al., 2013). It is plausible that the pea plants considered in my studies integrate information from multiple sensory inputs to make informed decisions about their choice of support. These sensory inputs may include tactile, chemical, photoreceptive, and growth-related cues, collectively aiding the plant in determining the suitability of a support for climbing.

Plants may transport and exchange sensory inputs through electrical signals. The discovery of electrical signals in plants traces back to the first recorded instance in *Dionaea muscipula* (Haberlandt, 1890). Generally, there are four types of electrical signals documented in plants, which include action potentials (APs), variation potentials (VPs), also known as slow wave potentials (SWPs), local electric potentials (LEPs), and system potentials (SPs). These signals typically involve the initiation of changes in membrane potential, followed by the activation of secondary messengers that lead to alterations in physiological regulation. This process can span anywhere from seconds to days. These electrical signals can induce the production of phytohormones, which play a crucial role in various aspects of plant growth and development, including the regulation of organ size and reproductive development. Furthermore, electrical signals can instigate metabolic changes in plants. Therefore, the electrical signaling network serves as a primary mechanism for plant responses to stimuli, such as physical damage or wounds.

However, the electrical signaling alone may not provide a comprehensive explanation for the intricate systemic responses observed in plants. Hydraulic signaling, primarily regulated by turgor pressure in plant cells (Taiz, 1984), originates in the xylem vessel conduits and is interpreted by adjacent parenchyma cells. Due to low axial resistance, these signals can propagate rapidly into surrounding cells (Bramley et al., 2007) and potentially transmit throughout the entire plant. In this way, long-distance signaling could be facilitated via the plant's vascular tissues (Notaguchi & Okamoto, 2015). The plant's vascular system consists of xylem vessels, characterized by thickened cell walls that persist after programmed cell death, and phloem tissues, characterized by a complex of living cells, that span the entire plant body. Recent discoveries suggest that these vascular tissues serve as long-distance signaling pathways, coordinating behaviors within the plant as a unified organism (Lucas et al., 2013; Notaguchi & Okamoto, 2015). Phloem sieve element cells, for instance, form a transport network responsible for the long-distance allocation of photosynthates and signaling molecules (Lucas et al., 2013). This includes the directed flow of phloem sap from mature source leaves to various sink organs, as well as the flow of xylem sap from roots to shoots, driven by water loss during transpiration and photosynthesis (Notaguchi & Okamoto, 2015).

Do these long-distance signaling channels operate independently from each other? The answer is no, though the potential crosstalk among hydraulic, chemical, and electrical long-distance signaling pathways within plants represents an area that warrants further exploration (Huber & Bauerle, 2016). Some intriguing evidence has been observed in pea plants, suggesting an interaction between slow wave potentials (SWPs) and hydraulic signals. SWPs are not self-sustaining; instead, they are consistently preceded by a positive change in hydraulic pressure, making their depolarization hydraulically induced (Stahlberg & Cosgrove, 1996, 1997). For instance, positive pressure changes are succeeded by SWPs in pea epicotyls (*P. sativum*). Depending on the applied pressure, SWPs can also be delayed. However, when the hydraulic signal, in the form of positive pressure, reaches or exceeds 80 kPa, both electrical and hydraulic signals occur simultaneously. The range of SWP intensities provides plants with a wealth of information about the injury's intensity, allowing them to discern the distance from the source of damage based on subtle variations in signal pressure, shape, and intensity (Stahlberg et al., 2006).

The discovery of systemic crosstalk which characterizes plant behavior suggests a coordinated process involving integrated signaling, communication, and response systems across the entire organism (Brenner et al., 2006). Examining plant behavior reveals a web of interconnected pathways and responses that allow plants to perceive, adapt to, and thrive in their environments. The evidence presented here highlights the role of electrical signals, hydraulic pathways, and chemical communication in orchestrating plant behaviors.

The long-distance signals may serve as a means of communication within the plant, allowing information about the environment, especially the support, to be transmitted from the point of sensory input to other parts of the plant. These signals could convey information regarding the size, material or general suitability of the support. These signals transfer from on point to another, and some local changes may occur. Or it may disperse throughout the entire plant, and the goal-directed behavior may be carried out locally as a result of integrative cooperation; especially when it comes to the very first exploration of support in peas life in my scenarios.

12.3. Integrating Data into Theories

Examining covert intentions through overt actions provides novel insights into the possible cognitive architecture of plants. Overall, my findings strongly suggest that plants demonstrate a remarkable level of adaptability and resource allocation, influenced by environmental conditions. By adopting a perspective that scrutinizes plant movements from the standpoint of motor intention, one can effectively study cognitive abilities in these organisms. In essence, plant movements can be construed as manifestations of intentionality, characterized by purposeful, goal-directed, and unreflective bodily actions. Their motor control is underpinned by a decision-making process, as evidenced by the programmed movements exhibited in the context of support-searching studies. It can be regarded as an integral facet of cognition, as it bears the functional responsibility of planning, coordinating, and executing movements — a repertoire vital for comprehending and interacting with the surrounding environment.

Undoubtedly, there exists a discernible convergence between plant movements and cognitive behaviors, irrespective of the degree of this overlap. So rather than striving to establish this overlap, the focus should lie in understanding it. The challenge in interpreting plant behavior is the prevalent influence of anthropomorphism within the scientific community — a tendency to employ human experiences as the primary reference point, often focusing on uniquely human cognitive activities (Bechtel & Bich, 2021). This approach consigns organisms without a brain to a secondary status, as it assumes that only species equipped with brains are capable of hosting mental representations, which, in turn, are the door to cognition. Consequently, researchers sometimes overlook the potential universality of cognitive phenomena across diverse forms of life. In this context, I shall try to discuss my data under the umbrella of a-representational cognitive theories.

Does mental representation hold such significance that cognition cannot exist without it? As introduced in Chapter 1, the paradigms of post-cognitivism challenge this classic view by providing space for alternative forms of cognitive existence. Many theories within this framework do not require cognition to be grounded in mental representations such as ecological psychology (Gibson, 1979), enactivism (Varela et al., 1991), and extended cognition (Clark & Chalmers, 1998). Hutto and Myin (2017) contend that intentionality should not be perceived solely in the sense of mental states that translate into representations. Instead, they propose conceiving intentionality as an attitude directed toward an object. In this view, intentionality becomes an expression of the entire organism's attitude, evident in its behavior (Hutto, 2012). This is not to suggest that 4E cognition disregards the importance of the nervous system for certain species; rather, it acknowledges that more advanced cognitive phenomena may indeed involve representational content (Schlicht & Starzak, 2021). Intentionality therefore can be seen as a continuum across life forms, bridging the biogenic and anthropogenic perspectives (Sims, 2021a). Especially that, even in humans, intentionality does not manifest as a predisposed toolkit; rather, it evolves over time. Intentionality can still exist in humans, even when the central nervous system is not fully developed. Sensorimotor behaviors exhibited before birth can incorporate anticipatory structures directed toward future consequences, even though such actions in early development may not necessarily be conceptually or cognitively complex (Hofsten, 2009; Lee, 2009; Legrand, 2006; Trevarthen, 1984). Derived from the efficient prospective motor control observed in humans from birth, an adaptive form of intentionality, primarily pre-reflective and pre-conceptual, is termed "sensorimotor intentionality" (Delafield-Butt & Gangopadhyay, 2013). This highlights that even seemingly simple and discrete movements can be attributed to the purposeful actions of an intentional agent. All of this underscores that the concept of mental representation in the human context may not be as rigid as traditionally conceived. Consequently, the proposition of an embodied agent action at the core of cognition is put forth, suggesting that this concept resonates with human behavior as well.

To explain cognitive behavior observed in plants, one should consider the body–environment coupling as a fundamental principle. In the context of plant movements, a plant response to its environment can be viewed as a manifestation of embodied cognition. The plant perceives the support from its surroundings and enacts movements as a way to interact with and adapt to that support. Cognition is not just a function of the brain but is inherently linked to an organism's interaction with its environment. When a plant encounters a potential support, it perceives the affordances of that support for climbing.

Remember that affordances are the potential interaction that an object or environment offers or enables. This perception-action coupling, where the plant movement is a direct response to perceived affordances, aligns with enactivist principles. In this scenario, their behaviors are not pre-programmed but are shaped by the meaningful properties of their environment. The concept of affordances emphasizes that organisms perceive opportunities for action in their environment. Following my results, peas connection with potential supports could be established by the environment offering physical objects (support), and peas in turn would imbue with meaning — affordances. This is evident in their circumnutating pattern, which is goal-directed and responsive to perceived affordances in its environment.

Further, plants making different decisions can be seen as attributing varying affordances to the decision-making condition. Some plants make metabolic decisions to approach the thin support, thereby avoiding the potential risk of expending excess energy and compromising their physical balance due to overreaching and asymmetrical morphological development in the tendrils. Alternatively, they may choose the thick support and take the risk in pursuit of greater abundance. The plant's ability to make rational decisions based on the risk sensitivity theory (RST) has already been documented (Dener et al., 2016). RST might provide an explanation for why most plants tend to favor thin supports, as this choice could be seen as a rational decision driven by a preference for less risk (exhibiting risk-averse behavior). I contemplate that during support-searching, plants view any option that could disturb their homeostasis as potentially risky. The greater the potential disruption and energy-demanding, the higher the perceived risk.

Within the framework of the extended cognition theory, the relationship between plants and supports can be interpreted as the composition of a cognitive space encompassing both the pea plants and the supports themselves. Plants integrate information from their external structures, such as tendrils, with their internal processes to make decisions about support selection. These tendrils can be viewed as extensions of their cognitive processes, serving as tools for interacting with the environment and accessing new opportunities (affordances) for support.

Taking the post-cognitivist approach, plants emerge as cognitive agents through their movements and interactions with their environment. Cognitive processes may not be exclusively tied to mental representation. Instead, they can be seen as embodied in action, an interconnectedness between organisms and their environment.

The ability of biological systems to thrive in intricate, ever-changing, and fiercely competitive environments necessitates of some forms of cognitive abilities (Conrad, 1996; Holcombe & Paton, 2012). Debono and Souza (2019) suggest that plants may serve as plastic interfaces (PIs) mediated by the "electrome," a term which involves constant spontaneous emission of low voltage potentials. It is considered that the electrome is an early marker and a unifying factor of whole plant reactivity in a constantly changing environment and is therefore the key to understanding the cognitive nature of plants. Plants could use perceptual binding as an operative mode through plasticity complexes (PCs) to detect their immediate environment without a nervous system, without the need to integrate or represent it but with the ability to locally bind or synchronize, deploying behaviors that are adapted to their survival or well-being. And the electrome could play a significant role in processes such as perception, learning, memory, and cognition in general. Because it ensures a continuous spectrum of actions and a range of behaviors in response to environmental cues across all levels of plant organization. Local associations formed within the plant can prompt direct actions within the environment. These local associations, in conjunction with the plastic and protoneural organization of plants, might have contributed to the activation of the perception-action loop and the development of complex intellectual behaviors (Debono, 2013; Debono & Souza, 2019).

In the light of the above, I feel that the integration of cognitive theories and empirical evidence I presented in my thesis not only challenges our preconceived notions of cognition but also highlights the diverse ways in which living organisms engage with and adapt to their environments.

12.4. Conclusive Remarks

Throughout the course of my thesis, I learned so many fascinating facts about plants that never ceased to amaze me. I attempted to utilize kinematic analyses and machine learning techniques to gain insights into the decision-making processes that govern the interactions of plants with their environment. Espousing the concept of motor intention, I have observed how pea plants respond to the presence, absence, and properties of supports through a series of experiments. The results show that plants can distinguish between supports of varying sizes, and make economic decisions, extending beyond mere simple reflexive responses. These findings challenged the traditional view of plants as passive organisms by demonstrating that they engage in purposeful, goal-directed actions that are guided by motor control and decision-making processes.

I have explored, speculatively, potential sensory mechanisms that could underpin these behaviors, including mechanosensory pathways, the hypothesis of ocelli, and other long-distance signaling pathways. While the precise mechanisms remain a subject of ongoing investigation, it is clear that plants integrate information from multiple sensory inputs to make informed decisions about support selection. And most importantly, I explored the possibility of interpreting plant movements under the framework of motor cognition and provided new resources for the debate on the nature of cognition. Through plant behavior, the concept of intentionality was highlighted in the way that it is a manifestation of an attitude toward an object. This broader perspective will enable us to recognize intentionality as a continuum. Taking the lens of post-cognitivism, plants were shown to make decisions based on the perceived affordances, demonstrating their ability to adapt to ever-changing environments. And that cognition could manifest itself through the body–environment coupling.

My work opens to more questions. For instance, what kind of decisions plants would make when facing a size-suitable support and a material-suitable support? To what extent can plants intentionally plan their movements? Can plants change their intentions and redirect their movements accordingly? Can plants interpret the motor intentions of other organisms?

In closing, I would like to conclude my thesis by stressing that plant behavior can serve as a reminder that intelligence can exist in the most seemingly humble organisms. Future research should continue to uncover new aspects of plant cognition and revolutionize our understanding.

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APPENDIX I

DESCRIPTIVE STATISTICS

This appendix consists of the full statistic profile reported in Chapter 8 *Decision-making underlying support-searching in pea plants: study 2*. The descriptive statistics, including the median, interquartile range (IQR), range, and quartiles (Q_1, Q_3) are provided for each dependent measure across all groups (i.e., S-thin, S-thick, DM-thin, DM-thick).

Table 1. Descriptive statistics for kinematics in all groups.

	Group	Median	IQR	Range	Q_1	Q_3
Total movement duration (min)	DM-thick	2091.000	296.250	1332.000	1872.000	2168.250
	DM-thin	1764.000	552.000	1479.000	1551.000	2103.000
	S-thick	2592.000	790.500	4005.000	2191.500	2982.000
	S-thin	1828.500	693.750	1920.000	1638.000	2331.750
Circumnutation duration (min)	DM-thick	69.000	20.250	90.000	60.000	80.250
	DM-thin	72.000	26.250	102.000	60.750	87.000
	S-thick	93.000	42.000	186.000	72.000	114.000
	S-thin	69.000	15.000	114.000	60.000	75.000
Number of circumnutations	DM-thick	26.000	6.250	20.000	22.750	29.000
	DM-thin	25.000	7.000	11.000	20.000	27.000
	S-thick	23.000	10.000	26.000	20.000	30.000
	S-thin	28.000	9.000	21.000	22.000	31.000
Circumnutation major axis (mm)	DM-thick	79.420	59.586	174.967	48.565	108.151
	DM-thin	85.445	62.411	187.541	52.736	115.148
	S-thick	59.085	48.122	173.508	37.754	85.875
	S-thin	65.036	69.147	187.973	36.176	105.323
Circumnutation length (mm)	DM-thick	181.838	154.001	520.083	106.952	260.954
	DM-thin	230.532	181.438	548.856	134.550	315.988
	S-thick	151.862	147.475	465.898	85.154	232.629
	S-thin	166.488	196.104	503.609	85.797	281.900
Circumnutation area (mm^2)	DM-thick	1226.906	3775.906	18244.750	362.047	4137.953
	DM-thin	2828.375	5518.469	19844.688	819.672	6338.141
	S-thick	966.813	3256.500	17338.500	280.688	3537.188
	S-thin	1943.688	5298.375	14870.563	199.438	5497.813
Amplitude of average velocity (mm^2/min)	DM-thick	2.914	2.477	5.873	1.551	4.028
	DM-thin	3.164	2.269	6.023	2.016	4.284
	S-thick	1.789	1.403	4.543	1.159	2.562
	S-thin	2.738	2.647	6.271	1.430	4.077
Amplitude of the maximum peak velocity (mm^2/min)	DM-thick	4.653	4.374	18.271	2.906	7.280
	DM-thin	5.324	4.212	16.558	3.437	7.649
	S-thick	2.817	2.031	11.041	1.813	3.844
	S-thin	4.038	3.813	14.054	2.499	6.313
Maximum aperture (mm)	DM-thick	65.213	30.179	54.930	46.174	76.353
	DM-thin	43.465	20.443	82.395	37.345	57.788
	S-thick	53.400	29.349	208.128	36.932	66.281
	S-thin	40.202	9.058	34.360	38.419	47.477
Direction switching	DM-thick	2.5000	1.000	6.000	2.000	3.000
	DM-thin	1.000	1.000	3.000	1.000	2.000
	S-thick	0.500	2.000	4.000	0.000	2.000
	S-thin	1.500	1.250	6.000	1.000	2.250

Note. IQR = interquartile range; Range = the difference between the maximum and minimum values; Q_1 = first quartile (25%); Q_3 = third quartile (75%).

APPENDIX II

ANOMALY REPORT

This appendix consists of the complete report on anomaly points described in Chapter 9 *Anomaly detection: a machine learning method to investigate plant behavior.* Tables 1 to 3 present the performance results of Isolation Forest, *k*-Nearest Neighbor, one-class Support Vector Machine, respectively.

Table 1. Anomaly report on Isolation Forest.

No-support				Support			
Frame number	*IF anomaly score*	*Progress rate*	*Progress rate interval*	*Frame number*	*IF anomaly score*	*Progress rate*	*Progress rate interval*
557	0.027	89.694%	–				
558	0.055	89.855%	0.161%				
559	0.071	90.016%	0.161%				
560	0.080	90.177%	0.161%				
561	0.088	90.338%	0.161%	381	0.008	68.036%	–
562	0.084	90.499%	0.161%	382	0.018	68.214%	0.179%
563	0.066	90.660%	0.161%	450	0.009	80.357%	12.143%
564	0.039	90.821%	0.161%	451	0.014	80.536%	0.179%
565	0.045	90.982%	0.161%	452	0.020	80.714%	0.179%
566	0.053	91.143%	0.161%	453	0.006	80.893%	0.179%
567	0.059	91.304%	0.161%	459	0.034	81.964%	1.071%
568	0.083	91.465%	0.161%	483	0.010	86.250%	4.286%
569	0.096	91.626%	0.161%	485	0.033	86.607%	0.357%
570	0.047	91.787%	0.161%	486	0.027	86.786%	0.179%
571	0.049	91.948%	0.161%	487	0.012	86.964%	0.179%
572	0.025	92.110%	0.161%	495	0.011	88.393%	1.429%
573	0.021	92.271%	0.161%	496	0.014	88.571%	0.179%
574	0.009	92.432%	0.161%	509	0.016	90.893%	2.321%
575	0.007	92.593%	0.161%	510	0.028	91.071%	0.179%
576	0.013	92.754%	0.161%	511	0.038	91.250%	0.179%
577	0.016	92.915%	0.161%	512	0.036	91.429%	0.179%
578	0.012	93.076%	0.161%	513	0.050	91.607%	0.179%
579	0.022	93.237%	0.161%	514	0.047	91.786%	0.179%
580	0.009	93.398%	0.161%	515	0.036	91.964%	0.179%
581	0.000	93.559%	0.161%	516	0.032	92.143%	0.179%
583	0.009	93.881%	0.322%	520	0.000	92.857%	0.714%
584	0.000	94.042%	0.161%	522	0.002	93.214%	0.357%
599	0.020	96.457%	2.415%	523	0.012	93.393%	0.179%
600	0.011	96.618%	0.161%	524	0.013	93.571%	0.179%
601	0.016	96.779%	0.161%	525	0.042	93.750%	0.179%
602	0.001	96.940%	0.161%	526	0.023	93.929%	0.179%
603	0.003	97.101%	0.161%	560	0.014	100.000%	6.071%

Table 2. Anomaly report on *k*-Nearest Neighbor

No-support				Support			
Frame number	*KNN anomaly score*	*Progress rate*	*Progress rate interval*	*Frame number*	*KNN anomaly score*	*Progress rate*	*Progress rate interval*
373	0.583	60.064%	–				
395	0.554	63.607%	3.543%				
497	0.572	80.032%	16.425%				
530	0.549	85.346%	5.314%				
534	0.648	85.990%	0.644%	310	0.809	55.357%	–
553	0.617	89.050%	3.060%	334	0.682	59.643%	4.286%
554	0.711	89.211%	0.161%	335	0.788	59.821%	0.179%
555	0.575	89.372%	0.161%	336	0.861	60.000%	0.179%
556	1.232	89.533%	0.161%	337	0.834	60.179%	0.179%
557	1.585	89.694%	0.161%	360	0.762	64.286%	4.107%
558	1.799	89.855%	0.161%	361	0.713	64.464%	0.179%
559	2.550	90.016%	0.161%	368	0.737	65.714%	1.250%
560	2.351	90.177%	0.161%	369	0.692	65.893%	0.179%
561	1.762	90.338%	0.161%	370	0.736	66.071%	0.179%
562	1.331	90.499%	0.161%	371	0.754	66.250%	0.179%
563	0.927	90.660%	0.161%	372	0.766	66.429%	0.179%
564	0.652	90.821%	0.161%	373	0.736	66.607%	0.179%
569	0.620	91.626%	0.805%	390	0.742	69.643%	3.036%
571	0.634	91.948%	0.322%	391	0.774	69.821%	0.179%
579	0.606	93.237%	1.288%	418	0.830	74.643%	4.821%
580	0.575	93.398%	0.161%	419	0.771	74.821%	0.179%
581	0.710	93.559%	0.161%	426	0.747	76.071%	1.250%
582	0.820	93.720%	0.161%	443	0.778	79.107%	3.036%
583	1.098	93.881%	0.161%	448	0.687	80.000%	0.893%
584	1.111	94.042%	0.161%	449	0.779	80.179%	0.179%
585	1.284	94.203%	0.161%	450	0.841	80.357%	0.179%
586	0.787	94.364%	0.161%	495	0.915	88.393%	8.036%
587	0.708	94.525%	0.161%	509	0.747	90.893%	2.500%
588	0.568	94.686%	0.161%	510	0.683	91.071%	0.179%
590	0.558	95.008%	0.322%	511	0.689	91.250%	0.179%
620	0.708	99.839%	4.831%	525	1.092	93.750%	2.500%
621	1.169	100.000%	0.161%	560	0.871	100.000%	6.250%

Table 3. Anomaly report on one-class Support Vector Machine

No-support				**Support**			
Frame number	***OCSVM Anomaly score***	***Progress rate***	***Progress rate interval***	***Frame number***	***OCSVM Anomaly score***	***Progress rate***	***Progress rate interval***
567	88.531	89.694%	–				
558	91.372	89.855%	0.161%				
559	102.186	90.016%	0.161%				
560	104.441	90.177%	0.161%				
561	100.985	90.338%	0.161%	418	20.916	74.643%	–
562	97.107	90.499%	0.161%	419	21.120	74.821%	0.179%
563	93.448	90.660%	0.161%	441	23.336	78.750%	3.929%
564	91.759	90.821%	0.161%	443	23.307	79.107%	0.357%
565	92.197	90.982%	0.161%	450	24.267	80.357%	1.250%
566	92.572	91.143%	0.161%	451	24.754	80.536%	0.179%
567	93.411	91.304%	0.161%	452	25.885	80.714%	0.179%
568	94.369	91.465%	0.161%	453	22.699	80.893%	0.179%
569	95.388	91.626%	0.161%	466	24.784	83.214%	2.321%
570	92.900	91.787%	0.161%	467	23.354	83.393%	0.179%
571	93.197	91.948%	0.161%	485	21.938	86.607%	3.214%
572	91.563	92.110%	0.161%	486	21.988	86.786%	0.179%
573	91.151	92.271%	0.161%	493	23.024	88.036%	1.250%
574	90.718	92.432%	0.161%	494	28.352	88.214%	0.179%
575	90.809	92.593%	0.161%	495	27.712	88.393%	0.179%
576	90.635	92.754%	0.161%	496	21.668	88.571%	0.179%
577	90.935	92.915%	0.161%	505	25.005	90.179%	1.607%
578	90.967	93.076%	0.161%	511	20.740	91.250%	1.071%
579	91.950	93.237%	0.161%	512	20.553	91.429%	0.179%
580	92.547	93.398%	0.161%	513	25.843	91.607%	0.179%
581	92.728	93.559%	0.161%	514	25.474	91.786%	0.179%
582	93.324	93.720%	0.161%	515	22.754	91.964%	0.179%
583	94.361	93.881%	0.161%	522	22.751	93.214%	1.250%
584	93.465	94.042%	0.161%	523	26.132	93.393%	0.179%
585	86.017	94.203%	0.161%	524	33.797	93.571%	0.179%
599	84.894	96.457%	2.254%	525	37.213	93.750%	0.179%
600	84.065	96.618%	0.161%	526	23.448	93.929%	0.179%
621	84.930	100.000%	3.382%	560	25.282	100.000%	6.071%