

Perspectives on Computation in Plants

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Abstract Plants thrive in virtually all natural and human-adapted environments and are becoming popular models for developing robotics systems because of their strategies of morphological and behavioral adaptation. Such adaptation and high plasticity offer new approaches for designing, modeling, and controlling artificial systems acting in unstructured scenarios. At the same time, the development of artifacts based on their working principles reveals how plants promote innovative approaches for preservation and management plans and opens new applications for engineering-driven plant science. Environmentally mediated growth patterns (e.g., tropisms) are clear examples of adaptive behaviors displayed through morphological phenotyping. Plants also create networks with other plants through subterranean roots–fungi symbiosis and use these networks to exchange resources or warning signals. This article discusses the functional behaviors of plants and shows the close similarities with a perceptron-like model that could act as a behavior-based control model in plants. We begin by analyzing communication rules and growth behaviors of plants; we then show how we translated plant behaviors into algorithmic solutions for bioinspired robot controllers; and finally, we discuss how those solutions can be extended to embrace original approaches to networking and robotics control architectures.

Keywords

Behavior, control, bioinspiration, perceptron, network, adaptation

1 Introduction

Plants have inspired researchers in many fields, including robotics, for the development of artificial growing robots (Del Dottore, Sadeghi, et al., 2018) or continuum robots (Walker, 2015) and in informatics to develop novel heuristics for search and optimization problems (Akyol & Alatas, 2017; L. Ma et al., 2015). However, because of their apparent immobility and lack of brain, there are frequently animated debates concerning possible forms of intelligence in plants (Cvrčková et al., 2009; Firn, 2004; Robinson et al., 2020; Trethewas, 2003). Most definitions of intelligence (Legg & Hutter, 2007) refer to the ability of a system to adapt to variable conditions in the surrounding environment. Disagreements about plant intelligence are probably due to the different means of adaptation in nature across the animal (a widely accepted model in computation and robotics) and plant kingdoms. In some animals, but apparently not in plants, adaptation is manifested in learning (forming associations of ideas necessary for survival) (Estes, 2014). Plants adapt to their environments by continuously modifying their physiologies and morphologies, known as plant plasticity or phenotypic plasticity. This is very different from the strengthening of synaptic connections, that is, synaptic plasticity, that takes place during learning processes in cognitive animals (Estes, 2014). In biology, *adaptation* refers to any process by which a system modifies itself to improve

performance in its environment (Holland, 1992). This involves the transmission of information from the environment to the organism through a selection of phenotyping or behavioral alternatives (Estes, 2014). On the basis of this definition, plants are organisms that act intelligently. Through evolution, they continuously improve their adaptive strategies to survive in mutable environments (Gratani, 2014). The environment is central to plant life, development, and evolution. Different ecological niches have generated many species variations with specialized physiological and morphological adaptation mechanisms. Preprogrammed genetics is shaped in real time by environmental stimuli. Plants and other organisms release traces into the environment that impact latent plant plasticity. Intelligence is forged by the interactions between plants and the environment. There is thus a clear analogy between intelligent behavior in plants and the approach to artificial intelligence and robotics proposed by Rodney Brooks (1999). Brooks suggested that intelligent behavior exists only in the observer's eye as a phenomenon resulting from the interactions among multiple perception-action modules that make up the control architecture of an embodied and situated system (Arkin, 1998). He suggested the existence of behaviors, not produced by a high-level cognitive process (implying representation or reasoning), but emerging from the interactions between body and environment. The way the system behaves modifies the environment where it is situated and, consequently, its future perception-actions. His view has led to a modern approach to artificial intelligence called *new AI* (Brooks, 1999), which emphasizes the embodiment of behaviors and the unavoidable interdependence of a physical system with its environment (Floreano & Mattiussi, 2008; Scheier & Pfeifer, 1999). The concepts Brooks proposed then evolved over multiple paths. From a control theory perspective, several schemas have been proposed in behavior-based control architectures. They differ in how behaviors are combined or suppressed to generate purely reflexive systems or hybrid architectures, in which reactive behaviors might be complemented with a deliberative part (Arkin, 1998). From a physical perspective, the shaping of system behavior mediated by environment interactions has converged into embodied intelligence and morphological control concepts (Pfeifer & Gómez, 2009; Pfeifer & Scheier, 2001). According to these theories, a physical system embodies part of its computation by exploiting mechanical properties and material nonlinearities to lighten the complexity of robot control. These theories express body-integrated behavior-based controls, with behaviors combined by design. Purposeful design and choice of components and materials are keys to programming such systems. Nature has designed embodied intelligent systems, reaching maximal performance with plants. Plants have thus been taken as a source of inspiration to mimic nastic movements into functional materials (Sydney Gladman et al., 2016) or, for example, to embody inherent adaptation to heterogenous environments in a growing robot based on additive manufacturing (Sadeghi et al., 2020). Reflexive adaptation in plants, in some cases, precedes a subsequent active information processing with different levels of complexity that can be captured in computational models. Following this idea, computation in plants is the perception processed through multiple interacting behavioral modules or perception-action nodes, with an intelligence emerging from these interactions. This article presents examples of different adaptive behavioral strategies of plants (section 2). We first provide an abstraction of the concept of plant computational architecture by discussing selected plant behaviors, that is, tropisms, and show how we translated them into computational models (section 3). We then discuss how to extend the proposed abstraction to capture computation at different levels of the plant hierarchy, up to a community of plants, briefly discussing the case study of plant-to-plant communication mediated by mycorrhizal networks (section 4). We conclude with some final remarks on achievements, future directions and possible applications of plant-inspired control strategies (section 5). This perspective serves as a guideline for the engineering interpretation of plant intelligent behaviors for bioinspired robotic control and network models.

2 Behaviors in Plants

Plant behavior is the phenotypic plasticity expressed in response to external events during a plant's lifetime. Plants are multicellular organisms living in communities and have hierarchical structures

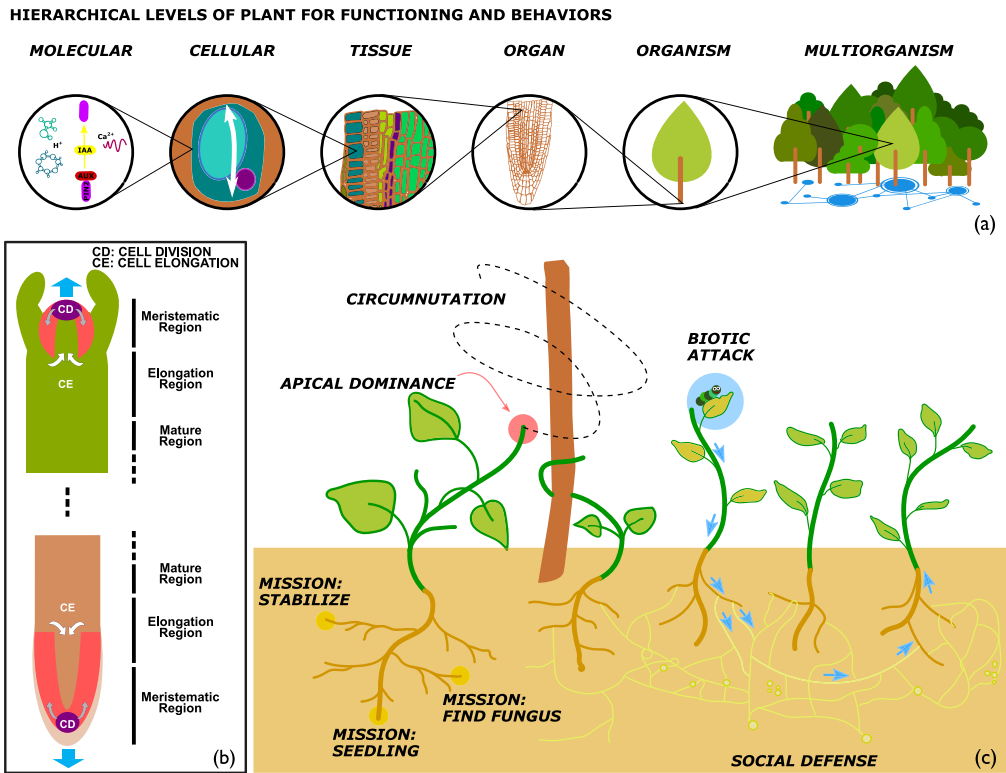


Figure 1. (a) Hierarchical structure of a plant, starting from its internal arrangement and moving to its organization in communities, where underground mycorrhizal networks interconnect with multiple organisms. (b) Apical growth in plants. Roots and shoots have a meristematic region where cells divide. The cells produced start to elongate, pushing the apex forward (light blue arrows). The elongation of cells is pronounced in the elongation region and stops in the maturation region, where cell specialization for secondary growth occurs. (c) Examples of different behaviors observed in plants. In the organs: circumnutations, stabilization, seedling, search for symbiosis. In the organism: apical dominance. In the community: social defense mechanisms.

(Ferlian et al., 2018; Jha et al., 2021) with regular patterns, modularity, and spatial organization (Dupuy et al., 2008; Sachs, 1991). Multiple organs (e.g., roots and leaves) constitute a single plant. Organs are organized into tissues, formed by cells, where molecules undergo physiological processes instantiating internal rhythms, propagating from within the cells and crossing the higher layers of the hierarchy (Figure 1a). Mutual interactions of the multiple layers define regulatory mechanisms of plant functioning and behavior.

Plants have evolved several adaptive behaviors to counteract their sessile lifestyle at all levels of their hierarchy. Because of their sessility, their strategies are very different from those used by animals, the main one being apical growth (Figure 1b). Although plants do not locomote, they move by growing, with cell division and elongation occurring at their apices of roots and aerial branches for their entire lives. Based on growth, plants implement various movements to explore, navigate, and colonize their environment. Two key examples of growth-driven movements are *tropisms*, which are irreversible directed growth responses to external stimuli (Hart, 1990; Muthert et al., 2020), and *circumnutations*, which are reversible oscillatory growth-driven movements adopted, for example, in the shoots of climbers to explore their surroundings and find mechanical support (Stolarz, 2009) (Figure 1c). Growth-driven movements affect organs and portions of organs (e.g., apical parts where cell division and elongation occur, named *meristematic regions*) (Perilli et al., 2012). Essentially, directed growth is a form of foraging—hydrotropism (foraging for water), chemotropism (foraging for nutrients), phototropism (foraging for light) (Ballaré et al., 1997;

Cahill & McNickle, 2011)—and oscillatory growth is a form of exploratory behavior (e.g., circumnutations in shoots of twiners) (Stolarz, 2009). Aerial branches differ from roots. For example, phototropism is positive in the shoot and negative in roots, and within the same apparatus, there are priorities dictated genetically with a preprogrammed architecture that are adjusted dynamically with the expressed phenotype (Cahill et al., 2010; Hodge, 2004) (Figure 1c). Dominance hierarchy behavior appears among organs of the same individual, leading to a single apical dominance to reach faster growth and higher resource allocation (Aloni et al., 2006) (Figure 1c). In this case, the observed behavior is at the level of the plant, which invests energy in the most promising searching organ. The symbiotic relationship between plant roots and fungal mycorrhizae (Ferlian et al., 2018) is another key adaptation strategy. The plant exploits this symbiosis to procure phosphorous, among other mineral nutrients, and water, and the fungus uses the plant to gain carbon.

This symbiosis manifests intelligence in the form of social behaviors (Figure 1c), such as collaborative sharing of resources (Whiteside et al., 2019), warning of biotic attacks (Cabral et al., 2019), competitive behaviors for the acquisition of resources (Selosse et al., 2006), and conquering an area (Stinson et al., 2006). Plant roots release and perceive exudates in their rhizosphere (Bais et al., 2006), similarly to volatile compounds released from the aerial part (Holopainen & Gershenzon, 2010). These molecules act as traces to communicate indirectly with other plant species, bacteria, fungal hyphae, animals, or insects, to warn about biotic attacks or compensate for abiotic stresses within a community of related plants. These examples of intelligent behaviors suggest cognitive processes in plants and have sparked considerable interest in the scientific community. For example, plant neurobiology (Brenner et al., 2006; Segundo-Ortin & Calvo, 2022) is a new discipline to understand how plants process information. Forms of cognitive processes, learning, and memory in plants have been identified, highlighting the information-processing network implemented over distributed computing cells (Calvo Garzon, 2007; Mediano et al., 2021; Parise et al., 2020) and displayed in anticipatory behaviors (Goodspeed et al., 2013; Latzel & Münzbergová, 2018). Well-accepted anticipatory behaviors of plants are those connected to the circadian clock, such as the opening and closing of some flowers and their leaves, anticipating sunshine to regulate their exposure to light (Schwartz & Koller, 1986). Another strategy is being able to anticipate herbivore attacks. Plants can differentiate between the sounds of chewing, wind, and insects and prime their defense responses to vibrations induced by herbivore chewing in their proximity (Appel & Coccoft, 2014). Plants can store and process data from the environment, integrating information over time (Meroz, 2021) to optimize acclimation and immune defense responses (Hilker & Schmülling, 2019). Ultimately, all behaviors have a physiological basis at molecular and cellular levels (Aloni et al., 2006; Ferlian et al., 2018; Salvi et al., 2020; Scheres & Van Der Putten, 2017). Behaviors are mediated by the perception of the environment, with perception-action nodes distributed in plants at different levels of tissues and cells. Perception-action nodes share similarities with sensory neurons (Scott, 1992). These are cells connecting perception to motor cells (or motor neurons) through neural pathways composed of other motor or internodes (Arber, 2012). It is justified to introduce sensory and motor neurons while talking about plants if we recall that all biological cells can generate action potentials used for signal transmission. These action potentials are generated by the migration of ions (e.g., calcium) across cell membranes when the concentration goes above an activation threshold (Aidley, 1998; Volkov, 2012). Although plants do not have a nervous system, their cells trigger chemical reactions similar to animals' spiking neurons (K. Takahashi et al., 2021). It is not yet clear whether those spikes also encode information used by plants, for instance, at distal parts. Nevertheless, some of the biosynthetic pathways underlying plant behaviors have been discovered. Tissue-dependent calcium signatures (Krogman et al., 2020) may, for instance, downstream gravity-dependent growth regulation (Huang et al., 2013) or govern nutrient homeostasis (Vigani & Costa, 2019).

3 Tropisms

Plants respond to a wide range of external stimuli, and tropisms are perhaps the most evident behavior in plants at the level of the organs. Tropisms are directed growth responses toward attractive

stimuli (e.g., physical and chemical) from the environment or away from repulsive signals. For each stimulus, there is a corresponding tropism, for example, gravitropism (response to gravity), hydrotropism (water), chemotropism (nutrients and salts), thigmotropism (mechanostimulation), and magnetotropism (response to magnetic fields). The same type of signal can even produce different reactions in different organs of the same plant. For example, roots grow toward gravity (positive gravitropism), while shoots display negative gravitropism by growing upward. Because this results in an organ following an attractor, tropisms are essentially foraging behaviors in plants.

Tropic responses are essentially individual behaviors acting in parallel on the plant and connecting sense to actuation, that is, the directed growth of cells. In a previous study (Sadeghi et al., 2016), our research group exploited this behavioral concept with a motor scheme as a behavior-based architecture (Arkin, 1998) in plant-inspired robotic roots to enable biomimetic autonomous navigation for environment exploration. Motor schemes are suitable for treating continuous responses (Arkin, 1989, 1998). A robot can have an infinite space of potential reactions to its world, unlike with subsumption architectures, where discrete behaviors (possible actions, discrete directions to take) must be defined and treated as discrete states of a finite state machine. Potential field methods can be used to implement a continuous response. Typically, potential field methods are adopted to define the world as a vector field space of repulsive signals to avoid obstacles (Arkin, 1998; Laue & Röfer, 2004). In behavior-based systems, the vector field is evaluated only at the time of perception and for the close surroundings of the robot. This solution limits the computational power required to evaluate the vector field and allows for a fast sense–actuation coupled response. Plants do not necessarily need to anticipate and avoid obstacles. However, a similar concept to repulsive vectors can be postulated to define a field of attractive signals, whose preferential attractive direction can be formulated as

$$y = \sum_{i=1}^m w_i x_i - b, \quad (1)$$

where x_i is the directed growth response for each of the external aggregated signals associated with a specific behavior, $i =$ gravitropism, hydrotropism, thigmotropism, chemotropism, and so on; w_i is the specific weight for the aggregated signal; and b is the specific activation threshold. A summation coordinates the incoming behaviors. Given this description, y represents the global directed growth response entering into motor nodes to command cell elongation. This equation also refers to a single-layer perceptron model (Arkin, 1998; Reed & Marks, 1999), which, in this case, is used for direct association of perception with motor control. With this control, the robot activates independent behaviors in parallel as soon as the corresponding incoming stimulus goes above the activation threshold. Individual responses are summed together to obtain the attractive vector direction. The response, thus the direction the robot takes, depends only on the current perception, with no world map reconstruction. In Sadeghi et al. (2016), we connected incoming environmental signals to motor control to achieve a directed differential elongation of robotic roots, seen as independent agents of the plant. The robotic roots were equipped with humidity, temperature, and tactile sensors, distributed around a conical tip and with an accelerometer. The roots were able to bend thanks to three soft spring-based actuators (Figure 2a). An embedded board with a microcontroller was used to read the sensors and connect perception to motor control (Figure 2b). In this example, all the agents are identical, with w_i fixed by the user and b set to zero. Different weights were assigned to the behaviors to analyze conditions to achieve different robot reactions to various settings and stimuli from the surrounding world (Figure 2c). The robotic roots were developed to demonstrate plant roots' exploratory and monitoring capabilities and to implement plantlike behaviors for application in soil or air exploration. Such systems can be applied to reach a rapid localization of attractor sources, for example, for underground water source detection or localization of harmful signals according to embedded receptors. We extended the same control to include tropisms shown in shoots of climbing plants and used it to analyze the emergence of shadow avoidance, tolerance, or attraction

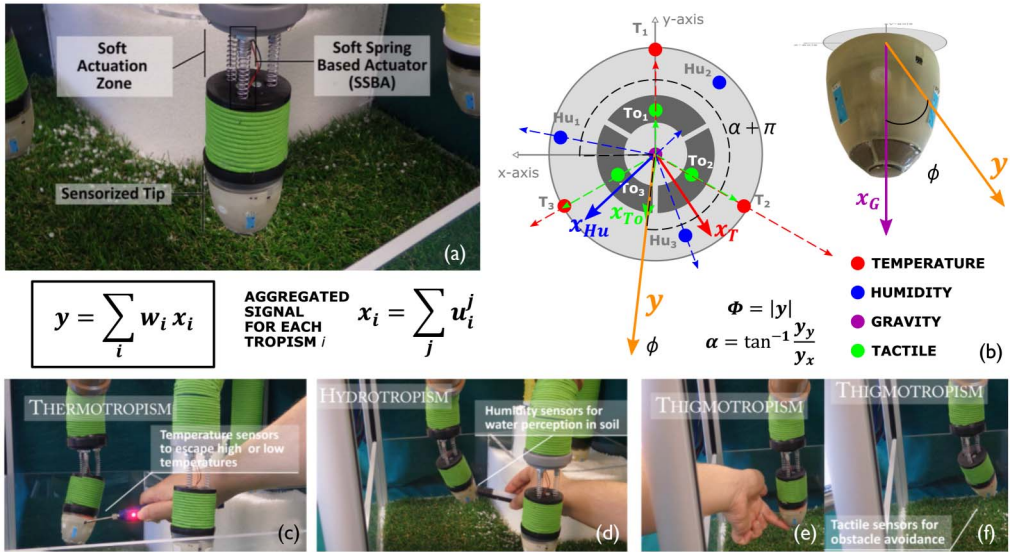


Figure 2. (a) Example of a plant-inspired robot to imitate plant organ behaviors (Sadeghi et al., 2016). The robotic agent in the figure has three soft springs arranged in a shaft to induce linear actuation. By differentially commanding the motors of the springs, the robotic agent bends. (b) Robot sensor scheme and vector field generation. The tip embeds humidity, temperature, tactile sensors, and an accelerometer. A specific tropism (x_i) results from a summation of the vector field generated from each stimulus (u_i^j , with j going over the sensors associated with tropism i). The preferential direction to take is obtained by aggregating all the tropisms. (c) Example of the robotic agent response when stimulated with a high-temperature source (a soldering iron). (d) Example of the robotic agent response when stimulated with a source of humidity (wetted soil). (e–f) A sequence of the robotic agent’s response to tactile stimulation. After contact with the finger, the robot moves away. If no other signals are present, gravitropism prevails, guiding the robotic agent to orient itself toward the vertical.

behaviors (Del Dottore et al., 2021). Organs in plants have different specializations and thus can offer alternative and complementary sets of behavioral responses to aid exploration strategies in different scenarios. In addition, different incoming signals undergo different internal processes in plants (Ponce et al., 2017; Shkolnik & Fromm, 2016). This suggests that for a better understanding and definition of plant control architecture, we might need to lower the level of abstraction and provide signal-specific elaboration processes for each possible behavior. Gravity is perceived by plant roots through statolitic cells located in the root cap (Figure 3). These cells have components,

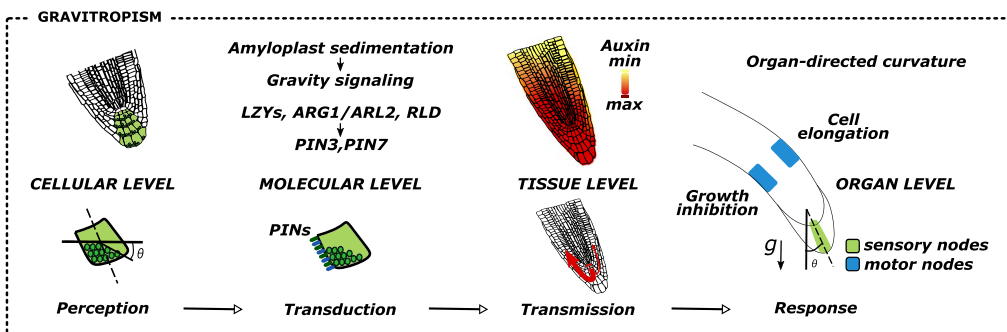


Figure 3. An example of information processing in plants. Root apical regions perceive gravity by amyloplast sedimentation in statolitic cells. The information transduces at the molecular level, affecting protein (PIN3, PIN7) distribution and alignment. Auxin is transported differentially on tissues through PIN distribution. Tissue-specific responses to auxin level elongate the motor cells with an overall curvature toward gravity in plant roots.

called amyloplasts, that move following the gravity vector. When their inclination with respect to gravity goes over a minimum threshold (Abas et al., 2006; Swarup et al., 2005), it triggers the re-orientation of auxin transporters at the flanks of the roots so that auxin is differentially distributed (Furutani et al., 2020). Different auxin concentrations activate tissue-specific responses (Di Mambro et al., 2017) to reach a macroscopic behavior called *gravitropism* (Ge & Chen, 2019). Differential distribution of auxin has also been observed in thigmotropic curvature responses (touch responses). In fact, mechanostimulation induces a polar orientation of cell auxin transporters, accelerating the active bending response of a root encountering an obstacle (Lee et al., 2020). Mechanosensing may also be implicated in amyloplast sedimentation perception, triggering calcium-mediated gravity response pathways (Perbal & Driss-Ecole, 2003; K. Takahashi et al., 2021). In contrast, no auxin gradient distribution has been observed in hydrotropism (Shkolnik et al., 2016). This, however, does not rule out the involvement of auxin in water signal transduction and transmission. In fact, genes in *Arabidopsis* plants involved in auxin signal transduction are affected during hydrotropic responses (Miao et al., 2018). Amyloplast degradation is also observed in roots under water stress (N. Takahashi et al., 2003; Ponce et al., 2008), suggesting the need to suppress gravity signals by hydrotropism. Amyloplast degradation is also induced in high soil salinity conditions (Sun et al., 2008), reducing gravity perception and prioritizing escaping from dangerous conditions. Chemotropism (Ferrieri et al., 2017), on the other hand, remains largely under investigated. Each nutrient, metal, or salt stimulates different responses (Galvan-Ampudia & Testerink, 2011; Hodge, 2004; J. F. Ma, 2005; Sun et al., 2008), suggesting that chemotropism is made up of multiple subbehaviors. Of these subbehaviors, foraging strategies are particularly interesting (Cahill & McNickle, 2011). The Michaelis–Menten kinetics is known to drive nutrient uptake, which adapts to the plant nutrient content (Epstein, 1972; Marschner, 2011). From this principle, in a previous article we proposed a feedback control to adjust nutrient-specific weights and, consequently, the contribution of chemotropic behaviors in the overall collaborative behavior observed in a swarm of rootlike robotic agents addressing the survival of the plant individual (Del Dottore, Mondini, et al., 2018). Each agent acted independently from the other agents, with no overall world knowledge or consciousness of other agents' actions but relying only on local perception, shared resources on the basis of each agent's needs, and local nutrient memory. The swarm reached a balance of nutrients at the level of the plant maximizing its wellness, without needing a central coordinator to set a global goal or function or to act as a task allocator. Crosstalk exists between tropisms (Massa & Gilroy, 2003; H. Takahashi & Scott, 1991; N. Takahashi et al., 2002), implying the co-contribution of different signals (x_i with $i = 1 \dots m$ sensory nodes) in the achievement of a unified growth response (Φ_i) and justifying the use of a behavior coordination module (e.g., cooperative summation), which might be guided by the same messenger (e.g., the growth hormone auxin; Retzer et al., 2014) or by alternative biosynthetic pathways converging into analogous responses (Muthert et al., 2020). The single perceptron model (Equation 1) needs to mutate into a multilayer perceptron (Reed & Marks, 1999; Scheres & Van Der Putten, 2017) (Figure 4), in which the first layer of hidden nodes represents all the possible behaviors obtained with some activation function (Φ_j , e.g., sine law in gravitropism; Mullen et al., 2000) for the aggregated value of weighted (w_{ji}) input signals (x_i) that go above the activation threshold (b_j). To consider the possible mutual suppression of behaviors, as in the case of hydrotropism over gravitropism, a fully connected network with all the external signals entering the behaviors in the motor scheme architecture can be built. The w_{ji} can then be set to activate or deactivate specific connections and define the signal summation or inhibition (negative weight). At the same time, the mutualistic effect of behaviors in plants that express phenotyping during their lifetimes suggests using an adaptive module for short- and long-term memory, by which weights of individual behaviors are adjusted to reflect adaptation over time (Figure 4). The interrelation among tropisms likely significantly influences circumnutation movements in plant roots (Mullen et al., 1998; Stolarz, 2009). In agreement with the multilayer perceptron-like model proposed in Figure 4, we previously adopted continuous-time recurrent neural networks (a class of multilayer perceptron) to describe tissue-dependent responses to auxin fluxes and investigate the role of circumnutations and their emergence in roots (Loshchilov et al., 2021). This study highlighted the

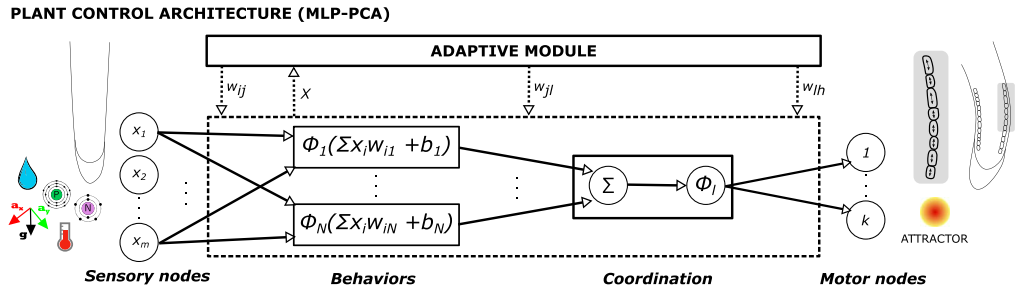


Figure 4. A multilayer perceptron as a model for representing plant control. The coordination among multiple stimuli-associated behaviors produces the final growth response toward an attractor in space.

mutual role of gravitropism and thigmotropism in the occurrence of oscillatory movement patterns and the possible role of these oscillations in exploring resources (chemotropism). However, how precisely behaviors are set, which functions model adaptation best, and what the signaling pathways are for each tropism and, consequently, the signal processing to apply are just some of the open issues requiring a better understanding of molecular changes during plant cell development (Muthert et al., 2020). The multilayer perceptron architecture is a general model that can be detailed for each behavior node and on the adaptive module, on the basis of new knowledge about plant functions or according to the needs of a specific application.

4 Extended Perceptron

Plants create networks with other plants and organisms. They establish underground networks made up of roots and fungi in the soil, called *mycorrhizal networks* (Simard et al., 2012). This intense interconnection facilitates the survival of many species by improving the colonization of large areas, foraging, and activating defense mechanisms (Beiler et al., 2010; Selosse et al., 2006). They likely function as an infrastructure for exchanging nutrients to recover from abiotic stress (Van't Padje, Bonfante, et al., 2021; Van't Padje, Werner, et al., 2021) and propagate warning signals to prevent biotic attacks at far distances (Alaux et al., 2020; Babikova et al., 2013). Mycorrhizae can mediate competing behaviors among enemy plants and promote cooperative behaviors among relatives (Gorzela et al., 2015; Kiers & Heijden, 2006). This underground social network is known as the Wood Wide Web (Beiler et al., 2010). Some attempts to improve its understanding have been made through mechanistic, statistical network models and market or complex adaptive system theories (Simard et al., 2012; Van't Padje, Werner, et al., 2021). The Wood Wide Web is, in fact, a fascinating example of a fault-tolerant, complex adaptive system in nature (Messier et al., 2013; Simard, 2009; Van Dorp et al., 2020). From a phytocentric point of view, plants are nodes and fungi are links in this network. The number of nodes (the plants) in the network is dynamic. Each node is a dynamic multilayer perceptron-like model expressing the phenotype of an individual plant. Each node has a dynamic number of sensory inputs, varying with symbiotic connections that work as a highway to transfer traces sent by distant nodes. Through the network, the perception of a single plant is augmented, with the information processing, enhanced at the community level, having dynamic connectivity patterns. The environment remains central in the dynamics of this complex system. Computation is achieved by opening and closing symbiotic connections, source-sink transfer mechanisms, and possibly other active transport and regulatory mechanisms that define the information flow and its distribution path over the network (Ezawa & Saito, 2018; Jin et al., 2012). The exact rules of message exchange, transport mechanisms, signal molecules, and regulatory pathways of communication, especially concerning biotic alarm signals (Johnson & Gilbert, 2015), are still not clear. Nevertheless, interest in understanding the plant–fungus relationship is rapidly growing due to its crucial importance in regulating the carbon cycle and limiting the effects of climate change. An

engineering-driven approach can provide alternative perspectives and tools to benefit investigations. Our computational model can be extended to describe mycorrhizal dynamics, building up processing on its nodes and connections upon new knowledge about how the information is computed and combined over the network. The extended perceptron would reflect an evolutionary state of the forest over time, displaying intelligent behavior in the form of phenotypic adaptation to perturbations in the environment. This tool would help predict alterations in an ecosystem and could be used to define forest management strategies.

5 Conclusions

We have provided a perspective on plant behaviors and how they can become the basis of computational models. These models can be exploited to develop plant-inspired control strategies and algorithms while favoring biological investigations for a better understanding of plant behaviors. Research on plant-inspired engineering is still underexplored and suffers from a noncomprehensive view of plant functioning. Owing to complex interconnections among biosynthetic pathways, there is still no complete understanding of plant activation functions in response to environmental signals. Nevertheless, in this article we have reported some mechanisms of environmentally mediated responses in plants, allowing us to define an abstraction for a generalizable plant like multilayer perceptron that also complies with the motor scheme of behavior-based architectures. We adopted this approach to imitate plants' behavioral strategies for monitoring (Sadeghi et al., 2016) or foraging (Del Dottore, Mondini, et al., 2018; Del Dottore et al., 2021) with adaptive adjustment of network weights (Del Dottore, Mondini, et al., 2018). This control strategy could be exploited in explorative autonomous robots, for example, to locate resources that dissolve in gradients into the environment, such as water, salts, or some metals in soil. In addition, we have adopted continuous-time recurrent neural networks to investigate the role of circumnutations and the reasons for their emergence in plant roots (Loshchilov et al., 2021). Plants have already been investigated by analogy with multilayer perceptrons (Scheres & Van Der Putten, 2017), focusing on how such information-processing structure can be replicated at the molecular level. Here we corroborate this idea and suggest that this computational structure can help in the study of adaptive behavior dynamics across multiple implementation scales. Multilayer perceptron models convey computations carried out at different levels in the hierarchical structure of plants and could be extended to dynamic computational architectures to capture communication rules behind cooperative and competitive behaviors implemented in communities of plants with mycorrhizal networks. Despite vast and growing research communities on plant biology, ecology, and mycorrhiza, to date, such a specific biological model has rarely been explored. Further investigations into plant and fungi physiology and molecular biology could unravel essential functional rules that would consolidate and refine our proposed plant control architecture by answering some key questions: How are the weights of single behaviors adjusted? Which behaviors involve crosstalk? and What are the specific signal transduction and transmission functions? These questions are nested into a hierarchical organization of plants displaying behaviors at the level of organs, organisms, and communities (Ferlian et al., 2018), appealing to the engineering world. We believe that this approach could facilitate new solutions for autonomous environment exploration, showing better adaptation and compliance in mutable conditions. Our approach could also promote engineering-driven knowledge by raising more awareness for more sustainable management of resources for agricultural applications, forest management, and ecosystem restoration. With this contribution, we hope to stimulate a cross-disciplinary discussion, which is fundamental to boosting the development of novel technologies and stimulating overall scientific progress.

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