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# Networks and ramifications: Relational perspectives in plant cognition

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**Abstract** This paper aims to propose a relational approach to the study of cognition that can offer a perspective on the cognitive behaviours of plants – sessile organisms without a nervous system – when considered in the reciprocal interrogation of philosophy and the cognitive and ecological sciences. When leveraging the inspiring, clarifying, and occasionally heuristic potential of different epistemic tools, plant cognition can be understood as the result of processes constantly shaped by multiple co-constructive relationships between organisms and their ecological niches. Organisms and niches are conceivable as dense multi-functional systems of resources and information interchange. The concepts of network and ramification are fruitful keys to frame forms of dynamic relationships between elements. In their alternatively iconical, metaphorical, and conceptual-modelling potentialities, networks and ramifications have been used to identify different types of relationships and transmitted information. The explanatory and heuristic scope of these two concepts needs to be further investigated when linked to cognitive aspects, especially with regard the concept of ramification. Looking at the plant world, whilst much has been written about networks, relatively little has been said explicitly about ramifications (branching capacity, branching characteristics and habits) and their relationship with aspects related to plant behaviour and cognition.
KEYWORDS: Plant Cognition; Ramifications; Networks; Ecology; Cognitive Science

**Riassunto** *Reti e ramificazioni: prospettive relazionali nello studio della cognizione vegetale* – Questo lavoro intende proporre un approccio relazionale allo studio della cognizione che possa offrire una prospettiva sui comportamenti cognitivi delle piante – organismi sessili privi di sistema nervoso – considerati dalla prospettiva filosofica e delle scienze cognitive ed ecologiche. Dato il potenziale ispiratore, chiarificatore e a volte euristico dei diversi strumenti epistemici, la cognizione delle piante può essere vista come risultato di processi costantemente plasmati da molteplici relazioni co-costruttive tra gli organismi e le loro nicchie ecologiche. Organismi e nicchie sono infatti concepibili come un denso sistema multi-funzionale di scambio di risorse e informazioni. I concetti di rete e ramificazione sono utili chiavi di lettura per inquadrare forme di relazione dinamica tra elementi. Nelle loro potenzialità iconiche, metaforiche e concettuali, le reti e le ramificazioni sono state usate per identificare diversi tipi di relazioni e informazioni trasmesse. Lo scopo esplicativo ed euristico di questi due concetti necessita di essere ulteriormente indagato, quando legato agli aspetti cognitivi, specialmente per quanto riguarda il concetto di ramificazione. Guardando il mondo vegetale, mentre molto è stato scritto sulle reti relativamente poco si è detto esplicitamente sulle ramificazioni (capacità di ramificazione, caratteristiche e abitudini di ramificazione) e sulle loro relazioni con aspetti legati al comportamento e alla cognizione.
PAROLE CHIAVE: Cognizione vegetale; Ramificazioni; Reti; Ecologia; Scienza cognitiva

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## 1 Introduction

THE EMERGING FIELD OF PLANT cognition (within the broader framework of rethinking cognition)[1] suggests that plants can explore and modify their environment, solve survival problems, and interact with each other and with other organisms. Accordingly, plants can discriminate amongst different factors to make decisions by modulating their responses in their ever-changing ecological contexts.

An organism that can detect such information about its environment and use this to promote its condition whilst discriminating signals of various types and modulating its responses according to the type and intensity of the stimulus encountered could be argued to be capable of (minimal) cognition. This way of approaching cognition makes it possible to broaden the framework of consideration to include many other organisms that are part of the evolutionary tree (including plants), understanding how[2] they identify and exploit elements of their ecological niche.

In modern day, there have been attempts to describe plant intelligence, using models of explanation based on functional molecular networks and a systemic view of body organization, for example, by Anthony Trewavas[3], the molecular biologist and plant physiologist. Similarly, the philosopher Paco Calvo[4] has advanced principles of distributed plant intelligence stemming from physiological networks characterized by chemical and electrical signalling.

In summary, the idea emerging from the scientific literature regarding the study of plant-internal networks is that chemical-electrical signalling systems may create functional constraints alternative to those found in the animal nervous system. Essentially, these systems would allow plants to process information, adapt phenotypically, and behave accordingly.[5] The vascular system of the plant plays a key role in this process of signalling and integrating chemical-electrical information, connecting the various plant systems and organs through a network structure.[6]

Whilst research at a microscopic level based on intra- and inter-cellular signalling networks is constantly increasing, research at a macroscopic level that considers branching processes as a potential tool for understanding plant behaviour is scarce. Firstly, I will outline the most promising options for developing a theoretical framework within which to explain plant cognition.[7] Then I shall consider the logic underlying branching dynamics to verify whether it might concretely help to understand the expression of plant behaviour suggestive of cognitive activity.[8] Is this idea potentially helpful to deepen certain aspect(s) of plant cognition? The purpose behind my article is not conclusive; instead, it is an invitation to consider whether certain aspects of the plant's responses can be considered as plant cognition.

One might ask what networks and branching have to do with plant behaviour and cognition. A preliminary (partial) answer is that the concepts of networks and ramifications might help to explain some aspects of plant cognition. These concepts can frame the consideration from both a systems perspective, i.e., as dynamics emerging from the interaction of numerous networks of signals within and outside bodies, and a behavioural perspective, focusing on individual-level activities with members of the same and other species (and even with organisms from different kingdoms). Through this perspective, cognition is a phenomenon emerging from the non-decontextualizable processes of relational elements in various natures within specific contexts of meaning acquisition (operational, non-reflective, or metacognitive) which are essential to perform communicative, reproductive, and general survival activities.

Getting straight to the point: how can we define networks and ramifications?

Typically, "network" (e.g., in computer science) means a set of interconnected nodes (modules) that allow the exchange of signals.[9] Often, networks present a hierarchical structure in which the main nodes (hubs) connect many other secondary nodes that, if damaged, unlike the main nodes, cause minor damages. Network structures have different properties that, taken all together, are antinomian (e.g., robustness/elasticity or plasticity). It is precisely this aspect that allows structures endowed with this functional organization to preserve their basic constitution whilst simultaneously modifying themselves plastically in changing circumstances (e.g., perturbations). Amongst the main properties of networks there is redundancy, which enables same-type elements to perform the same function, and degeneracy, which enables different elements to perform the same function.

Redundancy increases the overall resilience, i.e., robustness, while elasticity and plasticity make networks resilient to perturbations. Therefore, the notion of network is a particularly well-suited concept for describing some of the relational dynamics that are typical of life, involving exchanges of information of various kinds and at different levels: in ecosystems, between organisms, and into bodies. As living networks are dynamic, they can be contingently modified and, as they are functionally structured, they keep their peculiar constitution relatively stable. Excess rigidity would have the disadvantage of providing slow responses, which would hinder the system from adapting to new conditions and environmental challenges in time for survival. On the other hand, an excess of variability due to internal fluctuations would risk breaking the organization of the system's activities. Thus, we can describe a network as a relatively stable but not rigid system, suitable to explain many typical dynamics of life, including cognitive ones.

With regards to the concept of ramification, I intend to suggest that the ability to branch properly to plant organisms represents a process that could be useful for explaining some peculiarities of the intelligent behaviour of plants that are incapable of locomotion. It might subtend the ability to make choices thanks to the acquisition of resources and information through exploratory movements within aerial and subterranean environments. It is important to note that, for water and nutrient uptake, most plant roots cooperate in a symbiotic association (mycorrhyzae) with fungal hyphae, which are thinner to grow in the narrow pores of the soil, branch more densely and frequentely, not having the limitations imposed by the cellulose of plant cells.

The "branching events" – based upon a spatially directed extension – then expand the pre-existing structure of the plant through the formation of new elements that allow approaching targets (light and nutrients) to establish chemical communication contacts (between roots of the same or different species and with other organisms), to avoid obstacles (rocks in the soil) and potential dangers (pathogenic attacks or harmful substances).

Therefore, using the perspective of relational co-determination, we will see that when plants exhibit these basic cognitive abilities, e.g. discriminating between different elements, the ability to orientate growth to obtain light and nutrients, and the avoidance of obstructions and harmful substances, all emerge from a continuous ecological interaction of the organisms with their environments.

## 2 The theoretical framework and the search for epistemic tools

The theoretical framework upon which this proposal stands is the ecological approach to the phenomena of life.[10] Ultimately, "ecological" means "relational". Ecology is the science that studies the interactions between organisms and their environment. As it is relational, the perspective is broadly systemic (multi-factorial, multi-functional, and multi-level).

To compose a comprehensive understanding of the behaviour of plants that would appear to be guided by cognitive abilities (of discrimination and choice, learning and anticipation), limiting oneself to the study of the evolutionary origins and current manifestations of the bodily structures and organizations from which these behavioural possibilities originate, however indispensable, would be insufficient. To have a complete framework, it is necessary to consider the ecological relationships that characterize the living environments of these organisms, which underly the possibility of expression – and even modification during the onto-genetic development – of these behavioural traits in changing contexts of interaction.[11] Thus, an ecological approach to the study of behaviour and cognition can provide a more accurate and realistic explanation of these phenomena.

When theorizing about plant cognition, one of the most challenging tasks is selecting the epistemic tools able to explain a variety of processes in the absence of a well-established theoretical framework within which to describe these phenomena at a different level of explanation (from the physiological to the systemic-behavioural or cognitive ones). In the last few decades, observations related to the cognitive abilities of plants have increased significantly, though the theoretical frameworks for a more accurate understanding and thematization of these issues are still scarce. Nowadays, part of the work is devoted to adapting (extending, integrating, or completely reformulating) categories, terminology expressions,[12] and behavioural tests in the cognitive sciences and in the philosophy of mind for the study of animal cognitive abilities in order to then apply them to the plant world.

I will now discuss some of these epistemic tools (concepts, models, and approaches) that can guide research in plant cognition, including those that are already available but whose potential need further investigation. Images of branching structures, metaphors of networks, and models of explanation, such as the *Network Theory* could, in different ways, be helpful tools for a more detailed understanding of plant cognitive behaviour, as with the basic theoretical approach of disciplines such as systems biology. Moreover, a promising key to understanding plant cognitive phenomena can be found in the various approaches to the study of cognition that emerged from the existing interdisciplinary research program known as *4E-Cognition* (*embodied, embedded, enacted, and extended*). Each of these tools[13] offers potential that, in terms of rigor and explanatory scope, does not deliver the same level of accuracy in the analysis. My aim here is to stimulate research on plant cognition in its various branches. Therefore, I believe that it can be helpful at an introductory level to consider tools that are able to initiate diverse reflections on these aspects based on different but ultimately integrable explanatory possibilities and methods.

In some cases, the value of using some of these conceptual tools will have to be understood as (no more than) a source of inspiration to start/orient the research in a specific direction. In other cases, the worth will be a synthesis and theoretical clarification of extremely complex multifactorial processes. Moreover, the worth may be heuristic/prepredictive, as in the case of the most tested models that have emerged from the most recent approaches to the study of cognition. Future research will reveal which options are worthy of further investigation. Thus, given that this is ongoing research[14] and there is a need to explore new research possibilities, I support adopting a flexible pluralist perspective which can remain open to possible future modifications.

## 2.1 Images of branching structures

In the legacy of collective memory, images, networks and ramifications, can indicate the relationship, exchange of signals, and connection (physical or functional) between spatially distant elements. Ramifications also indicate the development of new components and directional changes (deviations) in a path of growth and transformation.

To evidence this dynamic, I will briefly dwell on the visual and explanatory power of two images of branching structures that have been of great value in the history of the biological sciences. The reference is to Darwin's attempts to offer visual models (tree first and coral later) that interpret the relationships amongst living species in the genealogical succession of evolutionary history not as linear but as a multi-branched process unfolding over time.[15]

Darwin used the heuristic power of the coral image to conceptually visualize descent through modifications from common ancestors, highlighting the genealogical and functional relationships (represented graphically) that link living organisms.[16] It is precisely in this potential that the explanatory power of images in research lies. In the Darwinian sketches where the natural evolutionary history began to have its visual form of understanding, a differentiation of lines and dots is evident, indicating, respectively, the living and extinct species. According to Darwin, «the tree of life should perhaps be called the coral of life»[17] since (as he observed while studying the structures of corals) the calcified parts of these organisms reject, through an evocative image, the Lamarckian thesis of a continuous transformation in favour of an evolutionary process that included the aspects of extinction.

This is just one example of how the biological field attempts to find the most appropriate images and graphic models to represent natural relationships and dynamics.[18] Accordingly, the description and understanding of biological aspects may depend, in part, upon the images used. In the images, on the other hand, there remains a margin of openness and autonomy, a characteristic that allows for new possible interpretations. Beyond the historical examples reported and the types of images considered, the aspect that I intend to emphasize upon here relates to the clarifying and sometimes heuristic potential of some graphic models. The case examined allows for the representation of the geometric characteristics of (motivated) construction and the subdivision of branched structures.

In the fourth section of this paper, dedicated to the branching process, I will highlight how the reference to these dynamics of subdivision and geometric growth, typical of branched structures, can be usefully transferred from the two-dimensional images (just described) to the processes of phenotypic adaptability. This feature, together with the capacity of synthesis and chemical recognition, allows for plants to make decisions regarding directional growth that are indicative of basic cognitive activity. From an ecological perspective, this aspect is evident in the dynamics of competition for light (in the case of branches) and nutritional strategies (in the case of roots).

## 2.2 Metaphors of networks

When considering metaphors, specifically their production in science, I begin my reflection by dwelling on the ability of these rhetorical figures to represent real moments of heuristics.[19]

Metaphors are carriers of previously non-existent mental connections that can concretely help new theories (or areas of research) to emerge, migrating from already known areas to those still in formation or completely unexplored. Herein lies the power of the human imagination, which can find practical use even in the most technical areas of application, contributing to the advancement and transformation of scientific research.

To provide an example of influential metaphors, let us recall the computational and modular mind-computer metaphor, which has triggered trends of interdisciplinary research in cognitive sciences that range from computer science to neurophysiology. This example emphasizes that the very idea of network was born as a metaphor when applied to studies on the nervous system. Based on new neuroanatomical knowledge and technologies that are available from time to time, different descriptions of the brain and its functioning were progressively offered.[20] Nowadays, thanks to recent technological advances and specialized knowledge, it is no longer possible to talk about the brain and its cognitive activities without considering the multiplicity of heterogeneous yet interacting factors. It became essential to link the study of nervous systems to the functioning of the entire body of organisms, inserted into dense networks of exchange and interaction within the environment.

In line with this increased focus on bodily specificities, another metaphor worth investigating is: "the plant is a network" or "the plant is a branching network". By testing the implications of this original metaphor, we have begun to study plant cognition and behaviour by giving more explanatory weight to the overall structural and functional peculiarities of bodies rather focusing exclusively on the brain. We will see that although plants do not have brains, their physical bodies can be interpreted as a branching network that enables various types of adaptive behaviour.

## 2.3 The Network Theory

In this area of research, as far as models are concerned, the *Network Theory* could have a prominent heuristic role (because of its ability to analyse a high number of components and interactions). *Network Theory* has been applied to various levels of biological organization, from molecules, cells, and organs to trophic and ecological networks encompassing many species. These systemic studies investigated both the levels of networks within organisms and those of supra-individual and interspecific networks. Applying the model of *Network Theory* to the form and organization of plants could be a valuable tool for studying the intercommunication of plant bodies when divided into multiple modules of development. Modules are a popular notion but in the appropriate meaning here they represent the nodes of a highly interconnected network, specialized (but not rigidly determined) in performing one or more functions during the ontogenetic development of the plant (reproduction, resource gathering, energy storage, etc.). Plants are indeed considered modular organisms, where modules are produced by a set of totipotent cells located in meristems. An essential characteristic of modular organisms is their open developmental program. Although the structure within each module is contextually defined from time to time, the system of modules is flexible and able to vary its components both quantitatively and qualitatively over time when interacting with the environment.

Beata Oborny,[21] a theoretical biologist who studies self-organizing models in ecological systems, proposed that it would be possible to interpret plants as a set of units with a distinct degree of autonomy. Accordingly, we could represent plant bodies as networks of semi-autonomous agents that collect information of various kinds from the environment. Connections between units constitute pathways for the exchange of resources and information. Plant networks transform dynamically over their lifetime due to the birth and death of their units. Nodes may be at different stages of development and in different nutritional conditions, specializing in sexual reproduction or resource-harvesting, depending on their location and environmental conditions. Links can vary in their capacity to transmit resources/information over time and are constantly exposed to the risk of fragmentation (they can be broken). Plant networks are rooted in the soil and simultaneously expanding in it, shifting their initial shape and size.

To see a plant as a network of semi-autonomous agents could help us to understand how the occurrence of an event in one module affects others, whether directly or indirectly. In addition, this model allows us to compare different elements of the same genet, which are at different stages of development and under different environmental conditions (favourable or stressful).[22]

The mastery of these systemic and integrated analyses underlies the possibility of studying a range of processes co-occurring between spatially distant elements. Since there is currently a strong demand in ecology to classify species according to their functionally relevant traits, *Network Theory* can help to extrapolate the study of larger systems over a longer time.[23]

## 2.4 Inclusive considerations on cognition: A chance for plants

One of the most promising epistemic tools for understanding and thematizing plant cognitive behaviours are the *embodied, embedded, enactive,* and *extended* approaches to cognition.

First, it might be helpful to remember two macro-expansions of classical cognitive science.[24] With the first expansion, we moved from the study of the mind in functional terms to the neuroscientific study of the brain's functioning and then of the whole body. According to the second expansion, to study the mind it is essential to study the organism-environment relationships. This link led towards an enactive view and dynamicist psychology of the interactions between organisms and environments, a condition of possibility and development of cognitive activity. Therefore, the study of the mind (or cognitive abilities) could no longer consist of studying a system isolated from the environmental, social, and sometimes cultural context in which the organisms are embedded.

The "post-classical" phase in which cognition begins to be investigated in its relationships with bodies and environments dates to the last quarter of the twentieth century. In particular, the theoretical background from which embodied cognitive science emerged can be traced back to *The embodied mind* by the biologist, philosopher, and epistemologist Francisco J. Varela, the philosopher Evan Thompson, and the psychologist Eleanor Rosch. Broadly speaking, the primary purpose of the embodied approach is to understand the links that bind the bodies of organisms to the world,[25] and to overcome the legacy of Cartesian-derived thinking, which focuses primarily on the elitist role of the mind/brain for the description of cognitive processes.

This key to interpreting cognitive phenomena has been further developed (and diversified in various theoretical positions) in the multi-disciplinary research program *4E-Cognition* mentioned previously. According to this paradigm, cognitive abilities would be strictly dependent on the sensorimotor capabilities[26] and on the overall sensory organization of organisms. Cognition would, therefore, always be contextually situated and also extended beyond the boundaries of the body.[27]

Cognitive states would no longer coincide with the internal representations of isolated systems exposed to sensory input from outside but would instead be the outcome of a multiform and multilevel relationship of acting organisms with their world-environment. Although all these approaches to the study of cognition can be traced back to the same theoretical matrix, "labelling" with different terms reflects different positions, not overlapping.[28] From these philosophical accounts for the study of cognition, it appears that the cognitive capacities of living systems have emerged and may continue to manifest due to a complex intertwining of factors, most notably the sensorimotor capacities for coordinating behaviour and the role played by the environment.

In this attempt to explain cognitive processes and capacities closer to organisms' biological and ecological reality, a systemic-relational and behavioural approach to the study of plant-specific cognition deserves to be further developed by integrating traditional laboratory studies with the results of a growing multidisciplinary theoretical elaboration.[29] Therefore, even if plants do not possess a sensorimotor organization like that of animals for the coordination of behaviour, they can still alter their metabolism, their morphology, rhythm, and direction of growth (this is particularly evident in roots), to adapt to changing environmental conditions and solve survival problems thanks to their high phenotypic plasticity.[30] Adaptive problem-solving behaviour in plants is a property of the entire organism conceivable as a network resulting from a communication system that includes different signals. The basis for discussing the cognitive abilities of plants would seem to be represented by information systems. These systems composed of networks of cells, together with the ability to expand thanks to a spatially directed growth (branching) and use subtle capacities of tactile perception and chemical recognition, allows the possibility for exchanging signals of various kinds, achieving goals and avoiding harms.

### *2.5 Extended cognition in plants? A case of application*

A recent example[31] of one of these theoretical positions, namely *Extended Cognition*, would seem promising in helping to frame certain plant capabilities. In this example, it appears that plants perceive obstacles in the soil through the accumulation of exudates between the exploring root and the obstruction, resulting in the inhibition of root growth toward the accumulated exudates.[32]

In humans and other animals, e.g., spiders,[33] the extension of cognition beyond body boundaries by active forms of niche manipulation has been investigated.[34] Parise and colleagues[35] used the criterion of mutual manipulability[36] to suggest that plants can extend their cognitive abilities in the environment through transformations of soil chemistry, and by enhancing their performance through association with soil microorganisms (e.g. nitrogen-fixing bacteria) and mycorrhizal fungi.

Plants can considerably expand their range of perception and reception of several signals from the root system by connecting to the dense mycorrhizal network in the soil. Fungal hyphae can extend over long distances to absorb water and nutrients, which they can then transfer to the associated plant in exchange for carbon as needed. Thanks to mycorrhizae, a plant can make better decisions regarding the growth of its roots toward areas where there are more resources or even prevent future causes of stress well before detecting them (because of the proximity to the sources). Therefore, through the release of root exudates, plants can actively alter soil chemistry and modify the activity of the microbiota in the rhizosphere. The plant's fitness is, in turn, conditioned by the composition of the microbial community (a "memory of the soil") that can influence the chemical activity and plant growth within a complex circle of interaction.

These cases are relevant for two main reasons: firstly, because they involve organisms coming not only from different species but from different kingdoms, and secondly, because they are processes in which non-negligible information circulates: self-recognition, discrimination of non-self, cooperation/competition, reward / deprivation / sanction.[37] Although one must avoid anthropomorphizing these plant relational behaviours, it is hard to speak of mere mechanical and stereotyped reactions as not influenced by specific needs and changing contexts of interaction.

## 3 Signalling networks in (and between) plants

In the scientific field, the idea of "network" has allowed reflection on the exchange of different signals and the presence of functional relationships, not only material connections. Biological signalling networks rely on systems to exchange information inside and outside bodies over short and long distances.

When applying this idea specifically to plant organization and forms of communication,[38] we can begin by stating that a series of structural, physical, and biological constraints have shaped plant signalling systems. Internal signalling, for example, occurs from cell to cell through plasmodesmata which connect the cytoplasm of adjacent cells. Communication of electrical, molecular, and hydraulic signals through the vascular system is possible within the same plant (or clonal colonies) that share conducting tissues. In contrast, aerial communication, through volatile organic compounds, does not require structural connections but works only over relatively short distances.[39] Finally, mutualistic fungal networks associated with plant roots enable communication over long distances. The wide mycorrhizal network, also known as the *Wood Wide Web*, plays a fundamental role in redistributing water and nutrients within plant communities and making plants more resistant to disease.[40] It also allows young plants that grow in adverse situations of high competition or lack of light to receive the resources that they need.[41]

From a functional point of view, the explanatory potential of the network concept has recently been expressed through the concepts of connectome and interactome, which find application in contemporary research as related to the dynamics of interaction between cells.[42] A connectome is the resulting overall map of connections between neurons in a nervous system, whereas an interactome is the set of molecular interactions (especially proteins) in a cell. In a broader context, the term denotes the set of all macromolecular interactions between cells that regulate the metabolism of organisms.

The network maps of the connectome and the interactome share the capacity for relative self-organization resulting from various constraints, the capacity for learning, and morpho-functional modification following perturbations.

Trewavas[43] used the concept of the interactome to explain the ability of plants to adapt to changing environments by learning and memorizing changes encountered during their development at a cellular level. For instance, by forming new networks, channels of information flows and developing new tissues, rather than by reinforcing synaptic connections as in the connectomes of animal nervous systems.

## 4 The branching process

In this section, as anticipated, my purpose is to reflect on the branching process as a possible tool for understanding some of the behavioural abilities of plants emerging from frameworks of ecological interaction. Branching dynamics, although genetically constrained, are neither rigidly determined nor entirely random. These processes depend on both endogenous factors and local environmental and climatic conditions. They result from interactions involving signal detection and retention that underly subsequent phenotypic adaptations.

The concept of ramification – as seen in the case of the two-dimensional images used to explain the historical development of the relationships between different elements[44] – recalls a geometry of accretion based on multiple changes of direction obtained with the development of new components that become part of the previously constituted structure. Thus, branching refers to the idea (both metaphorical and physical) of multi-directional composite growth.

Referring now to the branching capacity of branches and roots, we can reflect on the characteristics of a sessile "lifestyle" like that of plant organisms (incapable of locomotion, but not of growth and movement) whereby the most efficient (and perhaps the only possible) strategy to achieve goals or avoid obstacles and dangers, is a multi-directional growth of aerial and root systems. In other words: if an organism cannot move from the place where it is rooted, an effective solution to solve survival problems is to branch;[45] that is, to develop organs (sometimes more components at the same time) toward stimuli, according to a growth process that consumes many resources and energy. Not all branching is goal-directed: plants extend into the aerial and underground portions as a preventive measure to occupy available space. Plants branch their branches to get light with the largest surface to photosynthesize and direct their roots to get water and minerals. Branching structures are also essential for reasons of stability and soil anchorage. In addition, the roots' branching ability, combined with tactile and chemical perception, allows for cooperative or competitive interaction with members of the same or other species.

All these processes seem to involve goal-directed behaviours based on the selective abilities to recognize beneficial or harmful elements to plant development. The ability to see a difference, discriminating between different elements, is a basic cognitive capacity, not necessarily related to the presence of metacognitive or reflective skills: therefore, a kind of "knowing how to do" rather than a "knowing about knowing".[46]

By mentioning the scientific literature related to the description of plant architecture and plant branching patterns, it is possible to briefly recall the biological mechanisms (factors and processes) and contextual conditions involved in branching processes. The branching architecture of a plant is the result of combining multiple components of endogenous (genome, meristems activity, concentration of plant hormones) and exogenous nature,[47] such as local climate (light, humidity, and temperature), and the characteristics of the specific growth site (water and nutrient availability, competition or cooperation for resources, presence of competitors, herbivores, or pathogens).

In the broader field of modern plant biology, the multilevel study of the dynamics from which the typical architecture of various species emerges, though primarily a genetically constrained character, is a promising key to understanding the flexible behaviour of plants.[48]

Branching patterns, which express the spatial arrangement of modules (metameres) or plant growth units, are, therefore, the manifestation of an evolving balance between endogenous growth processes controlled by meristems and a series of exogenous stimulations exerted by the climate and the biotic and abiotic environment. The kind of branching a plant achieves influences its ability to adapt to its environment and, ultimately, its ability to survive.[49] This multifaceted process of exchanging various signals determines, for example, which buds will develop on the branches at new growth sites, and which will remain dormant.[50]

Several modelling efforts have been made to understand the branching process and fully visualize (and even anticipate) the development of plant systems in a specific area or direction. These modelling efforts have relied on both direct descriptions and figurative representations of branching systems, such as statistical and revealing analyses of meristem physiological states and 3D reconstructions of plant structures.[51] The elaboration of models in the study of branching structures promotes the understanding of the branching habits of various plant species to understand how much, in the relationship of a plant with its environment, an external alteration affects its structural development, genetically constrained, but not determined.[52]

Each plant can explore its environment by expanding through the directional growth of its branches and roots in a constant but changing chemical-tactile interaction with the matter surrounding it.

Here is the relevance of the topic: the branching process is as a process of phenotypic adaptability that – based on genetic constraints, epigenetic changes,[53] hormonal signalling, and environmental influences – is shaped, not randomly, at the level of variable ecological interactions in which the organism plays an active role (due to its ability to detect and flexibly respond to different signals).

Taking these aspects into account could facilitate a greater understanding of some plant cognitive behaviours, such as competition for light and foraging strategies involving morphological adaptations of aerial branches and root systems. Interesting cases related to this sort of reasoning are the behaviours of root cooperation/competition between, respectively, genetically related plants (kin) and non-genetically related plants, resulting in less or more distribution and production of root mass for the uptake of resources.[54]

### *4.1 The behaviour of a branching network: The case of foraging*

An example of plant behaviour (of branching network structures) is foraging behaviour via root hairs. Oborny[55] points out that while in (non-modular) animals, capable of locomotion, the nutritional strategy occurs through movement within their habitat, for plants, it occurs through the uptake of resources from modules at a local site and (often simultaneously), through the growth of links for the development of new nutrient uptake units.

Plant foraging is particularly interesting because, unlike animals that generally move, plants can move (by exploratory growth and the placement of new modules for resource-harvesting) and, simultaneously, remain (necessarily) anchored to the place in which they are rooted. Because of these responses, which involve both «*stasis and movement*», not only the current behaviour but also a portion of a plant's past behaviour can be reconstructed. The structure of a tree reflects its branching history, in which many branches continued to grow, and originate new components, while others, which have been "unsuccessful" due to unfavourable circumstances or simply due to senescence, have died.

The complexity of plant behaviour lies in the fact that many events can occur simultaneously. In branching processes, epigenetic inheritance allows the accumulation of information about past states and its transmission to newly developing parts. Thus, we can argue that the form of a plant (its overall branching structure) is not a "mirror image" of the outside world. Instead, each plant actively interacts with its environment for several reasons, using many parts of its bodily structure.

## 5 Conclusions

Plant cognition could be thus understood as a behavioural trait (the result of different factors and processes). This kind of behaviour emerges from the relationship of an organism with its environment, the ecological theatre of every interaction, exchange, and acquisition of contextually meaningful information (at least from an operational point of view).[56]

We can refer to (plant) cognition as the capacity for non-random self-regulated adaptation (involving aspects of prediction and anticipation) to changing environments. Plants can choose among different options for solving survival problems through forms of morpho-functional learning and modification. Plants possess, at least, forms of procedural memory and anoetic "awareness" of their environment[57] that allow them to manage elementary distinctions, identifying identities and differences. The ability to enhance the response to a given stimulus over time, when repeated during an individual's lifetime, has allowed us to speak of forms of intelligent behaviour.

A processual conception of cognition, more adherent to the structure and organization of organisms, inserted in dense relational networks of exchange with the surrounding environment, allows us to widen the field of consideration and to include plant organisms in the analysis of different forms of cognition.

The capacity for selected "knowing" of one's environment is a trait common to every living being. Living systems are conceivable as cognitive systems that act to preserve (and improve) their organization.[58] Even organisms without nervous systems, such as plants, can perceive, respond to, and therefore "know" their environment according to their needs and possibilities.

In the activities of biological organisms (including cognitive ones), the characteristics of the biological *medium* (its structure and functional organization) and the behavioural variability in the contexts of action are inseparable.[59] Therefore, the cognitive systems of organisms adapt along trajectories that can be defined only in a tendential way, always remaining open to alternative outcomes. On the one hand, cognitive systems adapt to contextual circumstances and, on the other, they directly or indirectly affect the environment, making modifications and leaving conditioned traces.[60]

Solving problems has made it possible to put the question in cognitive terms. Not all responses are the result of, or require, cognition, but all biological systems need to be adequately robust to maintain their organization (to survive) and, at the same time, flexible enough to cope with environmental uncertainty. It is probably from this flexibility that cognitive behaviour originates. A cognitive system always must deal with the unpredictability of the world, related to a changing environment and the presence of other agents, both collaborative and competitive.

A set of modules capable of controlling their behaviour constitutes the whole plant at a macroscopic level, conceivable therefore as a self-organized network (even if always located and dependent for sustenance on numerous external factors). As a result of a large and complex network, plants, even in the absence of a nervous system, can actively procure nourishment, synthesize the organic compounds they need, and cope with environmental perturbations.

The so-called "plant intelligence" would seem to be the result, at the cellular level, of the interaction of several biological networks of signalling and, at the individual level, of adaptive morpho-functional behaviours that vary in the organism's lifetime. The study of branching dynamics may help understand some macroscopically observable manifestations of these behaviours.

We have reflected on how networks and ramifications as images, metaphors, and models of explanation are fruitful keys for explaining information exchanges and relational dynamics. Specifically, we have considered how these tools can be used to understand plants' structure, organization, and some forms of behaviour. In this framework of ecological-relational analysis, networks and ramifications appear as two effective tools to talk about certain phenotypic (also behavioural) adaptive capacities of plants, which enable the interaction, at various levels, of these organisms with their environment. A network organization (such as the functional one between cells) and a branching capacity (such as that of branches and roots) in interaction with the environment would therefore seem to provide the conditions for the expression of some cognitive behaviours in sessile organisms such as plants.

## Notes

[1] Concerning "basal cognition" cf. P. LYON, F. KEIJZER, D. ARENDT, M. LEVIN, *Reframing cognition: Getting down to biological basics*.
[2] By which means and species-specific strategies.
[3] Cf. A. TREWAVAS, *Plant behaviour and intelligence*, pp. 232-241.
[4] Cf. P. CALVO, *What is it like to be a plant?*.
[5] Cf. A. LINSON, P. CALVO, *Zoocentrism in the weeds? Cultivating plant models for cognitive yield*; F. BALUŠKA, M. LEVIN, *On having no head: Cognition throughout biological systems*.
[6] Cf. G.M. SOUZA, A.S. FERREIRA, G.F.R. SARAIVA, G.R.A. TOLEDO, *Plant "electrome" can be pushed toward a self-organized critical state by external cues: Evidences from a study with soybean seedlings subject to different environmental conditions*; M. SEGUNDO-ORTIN, P. CALVO, *Are plants cognitive? A reply to Adams*.
[7] For the sake of brevity, I will not consider all available options. For example, I will not refer to the Ecological Psychology approach, or other possible theoretical frameworks. Which one to choose depends on the kind of problems to be answered.
[8] For an introduction to the concepts of network and ramification cf. M. BIANCHI, *La vita ramificata. Cognizione e comportamento nelle piante fra scienza e filosofia*, pp. 17-18 and 135-140.
[9] Cf. A. CIVELLO, *Rete*.
[10] Cf. M. GAGLIANO, *In a green frame of mind: Perspectives on the behavioural ecology and cognitive nature of plants*; M. GAGLIANO, *The mind of plants: Thinking the unthinkable*.
[11] On evolutionary ecology and developmental biology cf. S.E. SULTAN, *Plant developmental responses to the environment: Eco-devo insights*.
[12] Behaviour, intelligence, consciousness, cognition, mind, mental capacities, etc.
[13] The images, metaphors, models of explanation, and theoretical approaches that we will examine in the following pages.
[14] About state of the art, even if we have been talking about plant cognition for several years, I would like to mention that the first university course specifically on Plant Cognition, at least in Italy, was held in 2021 by Prof. Umberto Castiello at the Department of General Psychology of the University of Padua.
[15] H. BREDEKAMP, *I coralli di Darwin. I primi modelli evolutivi e la tradizione della storia naturale*, p. 31; cf. also F. GIACULLI, *Interpretare e raffigurare la natura. Charles Darwin e la vita delle piante*.
[16] H. BREDEKAMP, *I coralli di Darwin*, p. 114.
[17] Cf. C.R. DARWIN, *The works of Charles Darwin*, B 25, p. 177.
[18] Cf. G. BARSANTI, *La scala, la mappa, l'albero. Immagini e classificazioni della natura fra Sei e Ottocento*; E.

Gagliasso, G. Frezza (eds.), *Metafore del vivente. Linguaggi e ricerca scientifica tra filosofia, bios e psiche*.

[19] Cf. G. Frezza, E. Gagliasso, *Fare metafore e fare scienza*, p. 25.

[20] *Ibid.*, p. 29.

[21] B. Oborny, *The plant body as a network of semi-autonomous agents: A review*.

[22] *Ibidem*.

[23] This aspect also characterizes the study of resource and information exchange between mycorrhizae.

[24] Cf. M. Marraffa, A. Paternoster, *Funzioni, livelli e meccanismi: la spiegazione in scienza cognitiva e i suoi problemi*, pp. 28-29.

[25] Cf. M. Palmiero, M.C. Borsellino, *Embodied cognition. Comprendere la mente incarnata*, pp. 82-83.

[26] On the so-called "motor paradigm" cf. C. Morabito, *Il motore della mente. Il movimento nella storia delle scienze cognitive*.

[27] Cf. A. Clark, D. Chalmers, *The extended mind*.

[28] Cf. F. Caruana, A.M. Borghi, *Embodied cognition: una Nuova Psicologia*, pp. 23-48; K. Cheng, *Cognition beyond representation: Varieties of situated cognition in animals*.

[29] Cf. P. Calvo, F. Keijzer, *Plants: Adaptive behavior, root brains and minimal cognition*.

[30] *Ibidem*.

[31] Cf. A.G. Parise, M. Gagliano, G.M. Souza, *Extended cognition in plants: Is it possible?*.

[32] Cf. O. Falik, P. Reides, M. Gersani, A. Novoplansky, *Root navigation by self inhibition*.

[33] Cf. H.F. Japyassú, K.L. Laland, *Extended spider cognition*.

[34] Based on an interactional and extended interpretation of cognition, chemical (and even visual) signals exchanged within the plant world can retroact and influence animal cognition and behaviour.

[35] Cf. A.G. Parise, M. Gagliano, G.M. Souza, *Extended cognition in plants: Is it possible?*.

[36] Cf. DM. Kaplan, *How to demarcate the boundaries of cognition*.

[37] Cf. U. Castiello, *(Re) claiming plants in comparative psychology*.

[38] On plant communication, cf. R. Karban, *Plant sensation and communication*, University of Chicago Press, Chicago.

[39] C.M. Orians, C.G. Jones, *Plants as resource mosaics: A functional model for predicting patterns of within-plant resource heterogeneity to consumers based on vascular architecture and local environmental variability*. Cf. also M. Gagliano, J.C. Ryan, P. Vieira (eds.), *The language of plants. Science, philosophy, literature*, p. 17.

[40] Cf. M. Giovannetti, *Flussi di nutrienti e informazione negli ecosistemi*. Cf. also U. Castiello, *La mente delle piante. Introduzione alla psicologia vegetale*, p. 112.

[41] On the ability of mycorrhizal networks to facilitate communication, learning, and memory in plants, cf. S.W. Simard, *Mycorrhizal networks facilitate tree communication, learning, and memory*.

[42] Cf. S. Li, C.M. Armstrong, N. Bertin, H. Ge, S. Milstein, M. Boxem, P.-O. Vidalain, J.-D.J. Han, A. Chesneau, T. Hao, D.S. Goldberg, N. Li, M. Martinez, J.-F. Rual, P. Lamesch, L. Xu, M. Tewari, S.L. Wong, L.V. Zhang, G.F. Berriz, L. Jacotot, P. Vaglio, J. Reboul, T. Hirozane-Kishikawa, Q. Li, H.W. Gabel, A. Elewa, B. Baumgartner, D.J. Rose, H. Yu, S. Bosak, R. Sequerra, A. Fraser, S.E. Mango, W.M. Saxton, S. Strome, S. Van Den Heuvel, F. Piano, J. Vandenhaute, C. Sardet, M. Gerstein, L. Doucette-Stamm, K.C. Gunsalus, J.W. Harper, M.E. Cusick, F.P. Roth, D.E. Hill, M. Vidal, *A map of the interactome network of the metazoan C. elegans*. Cf. also O. Sporns, G. Tononi, R. Kötter, *The human connectome: A structural description of the human brain*.

[43] Cf. A. Trewavas, *Intelligence, cognition, and language of green plants*; A. Trewavas, *The foundations of plant intelligence*.

[44] Cf. the previously cited examples of graphical representations of species evolution in the "Images of branching structures" section (2.1) of this article.

[45] Although it is a very different organism, *Physarum policephalum* also solves survival problems with its ability to branch and leave chemtrails. Specifically, it expands by producing a network of veins formed by numerous subdivisions of cell nuclei. This single-celled organism is much studied today for its remarkable learning abilities despite the absence of a nervous system.

[46] Cf. M. Marraffa, *L'Introspezione*, pp. 200-202.

[47] Cf. D. Barthélémy, Y. Caraglio, *Plant architecture: A dynamic, multilevel and comprehensive approach to plant form, structure and ontogeny*.

[48] Concerning the root system, underlying the branching process is the controlling role of the apical meristem, which inhibits the formation of lateral root buds in the sub-apical region of the root, and which determines the distance separating two successive branching points and the shape, growth orientation, and function of lateral buds. The theoretical branching plan is more regular the fewer the number of potential tissue initiation sites and the fewer the environmental constraints. However, this regularity is only rarely visible, given the constraints exerted by the underground environment that cause many of the young root buds to abort.

[49] Cf. N. Leduc, H. Roman, F. Barbier, T. Péron, L. Huché-Thélier, J. Lothier, S. Demotes-Mainard, S. Sakr, *Light signaling in bud outgrowth and branching in plants.*

[50] Cf. A. Trewavas, *Plant behaviour and intelligence*, p. 186.

[51] Cf. H. Qu, Q. Zhu, *Automatic approaches to plant meristem states revelation and branching pattern extraction: A review*; N. Bessonov, N. Morozova, V. Volpert, *Modeling of branching patterns in plants*.

[52] A. Durrant, *The environmental induction of heritable change in Linum*; cf. also C.A. Cullis, *Mechanisms and control of rapid genomic changes in flax*; A. Trewavas, *Plant behaviour and intelligence*, p. 213.

[53] V. Latzel A.P. Rendina Gonzalez, J. Rosenthal, *Epigenetic memory as a basis for intelligent behavior in clonal plants*.

[54] Cf. S. Dudley, A.L. File, *Kin recognition in an annual plant*; M.L. Biedrzycki, T.A. Jilany, S.A. dudley, H.P. Bais, *Root exudates mediate kin recognition in plants*; M. Semchenko, S. Saar, A. Lepik, *Plant root exudates mediate neighbour recognition and trigger complex behavioural changes*.

[55] Cf. B. Oborny, *The plant body as a network of semi-autonomous agents: A review*, cit.

[56] Some enactivists argue that sense-making (i.e., the ability of an organism to create meaning by discriminating what in the environment is relevant to its potential actions and survival) distinguishes cognitive from

non-cognitive systems. This aspect is also the key to understanding some expressions of biological agency. Cf. M. SEGUNDO-ORTIN, *Agency from a radical embodied standpoint: An ecological-enactive proposal.* Cf. E. THOMPSON, *Mind in life: Biology, phenomenology, and the sciences of mind*; C. MAHER, *Plant minds.*

[57] Cf. D. CHAMOVITZ, *Quel che una pianta sa. Guida ai sensi nel mondo vegetale*, p. 123; F. CVRCKOVÁ, H. LIPAVSKÁ, V. ZÁRSKY, *Plant intelligence, why, why not or where?*.

[58] Cf. H.R. MATURANA, F.J. VARELA, *Autopoiesi e cognizione. La realizzazione del vivente*, pp. 55-58.

[59] Cf. M. PALMIERO, M.C. BORSELLINO, *Embodied cognition*, p. 80.

[60] Based on recursive feedback internal to the process of niche construction, each organism is shaped by its environment, just as each environment results from living activity. Cf. F.J. ODLING-SMEE, K.N. LALAND, M.W. FELDMAN, *Niche construction*.

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