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Return of the organism? The concept in plant biology, now and then

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Abstract This essay argues for the importance of an organismic perspective in plant biology and considers some of its implications. These include an increased attention to plant-environment interaction and an emphasis on integrated approaches. Furthermore, this essay contextualizes the increased emphasis on the concept of organism in recent years and places the concept in a longer history. Recent developments in biology and worsening environmental crises have led researchers to study plant responses to changing environments with *whole plant* approaches that situate plants in their environments, emphasizing the intricate and dynamic interaction between them. This renewed attention to the organism recalls the debates of the early twentieth century, when organicism was one of the three main frameworks in biology (along with vitalism and mechanism). Some scholars see this renewed importance today as a "return" of this earlier period. This essay argues that including insights from plant biology will benefit philosophy of biology research that examines the concept of organism and organicism now and in earlier periods. A comprehensive account of the concept of organism should involve a botanical conception of the organism as well as a zoological one (which is more frequently considered). Although this essay does not aim to present a conceptual analysis, it presents examples of how an organismic perspective can be useful for understanding concepts (such as phenotype, stress, etc.) and research processes (such as experiment setups, data processes, etc.) in plant biology. Philosophy of biology investigations that aim at a comprehensive understanding of the concept of organism can benefit greatly from examinations of cases in plant biology, both now and in the past.

Keywords Organism · Organismic perspective · Phenotype · Integrated approach · Plant organism

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1 Introduction

Biology is a discipline that investigates organisms. This alone makes philosophical inquiries on the concept of organism valuable and helps explain its enduring appeal to philosophers and historians of science. This brief essay aims to contribute to this extensive literature via its two arguments: *first*, it will argue for an organismic perspective for plant biology, which has entered the twenty-first century as a broad discipline with many new priorities in addition to its never-ending curiosity about plant life. *Second*, it will argue that philosophy of biology needs to look into the history of plant science for a more comprehensive understanding of organicism and the concept of organism. Both organism and organicism have a history; they change over time through their interactions with other concepts and scientific, political, sociological, and economic processes. Organicism is a philosophy in biology that emphasizes the concept of organism—i.e., an integrated whole—as a fundamental explanatory concept in biology and it defends the distinction of biology from physics and/or chemistry.[1] Biology has its own methodologies and theoretical frameworks that are required to investigate organisms, which are living systems maintaining their stability through their active interaction with the environment (Allen 2005; Nicholson 2014; Nicholson and Gawne 2015; Baedke 2019). Although organisms have connected and coordinated parts (which can also be analysed separately), investigating the organism requires integrated approaches.

In order to discuss the two arguments, I will consider (in section two) how organismic perspectives that do not exclude operative mechanism (or explanatory mechanism) seem to be prevalent in today's plant science. I will argue that such organismic perspectives can be helpful for philosophical work on concepts and research processes in plant biology. Biology, while investigating organisms, looks into *mechanisms*: how a system's parts work together. Biologists investigate complex networks of mechanisms at different levels. They investigate in detail how tiny molecules can be part of mechanisms in the smallest organelles; how these mechanisms connect to mechanisms in other organelles and the cytoplasm of the cell; and how all these connect to mechanisms between cells, in the tissues, and on other levels. Biology aims to produce more and more detailed descriptions and explanations of all the components of the complex processes of organism system. The methodologies and theories of such investigations are mechanistic approaches. Here, however, I would like to point out a crucial distinction, following Allen (2005), between *operative* and *philosophical* mechanism. While the first is a widespread epistemological approach in biology, the second takes the ontological position that organisms are complex machines. Philosophical mechanism, which is closely connected with reductionist approaches, was especially widespread during the second half of the twentieth century. Organisms in philosophical mechanism are thought be no different than complex machines. This thought entails ignoring crucial differences such as organisms being self-organised while machines are not, or the dependence of an organism's parts on the whole while a machine's parts are independent (Nicholson 2013).[2]

Although today's biology uses "mechanisms" widely, I would argue that this approach is mostly *operative/explanatory* mechanism, which uses the concept of organism (rather than "organisms as machines") as its central concept.[3] Section two will show the centrality of the *organism* concept in *plant biology*, and argue that this centrality can be observed via the rising emphases on *organism-environment interaction* as well as *systemic*, *integrated,* and *whole plant* approaches. I will also note how these trends have risen hand-in-hand with advancements in plant science research programs and growing global environmental problems. This essay does not examine the operative/explanatory mechanism in biology, which is clearly present, useful, and widely examined (e.g. Machamer et al. 2000; Allen 2005; Bich and Bechtel 2021). I will only hint at how these organicist approaches are intertwined with operative/explanatory mechanism.

While many contemporary historians and philosophers of biology have worked on *organicism in biology*, there are very few works that focus in this regard on plant biology.[4] Plant biologists are only mentioned once in a while. Yet a focus on plants is necessary in history and philosophy of biology research that examines the concept of organism. Despite important commonalities, plant organisms and animal organisms are different. In fact, I agree with Gerber and Hiernaux (2022) that "even the general idea of an 'organism' is problematic in its application to plants and should

[1] For a detailed discussion of organicism as well as mechanism and vitalism, see Allen (2005), for example.

[2] See Nicholson (2013) for a detailed discussion of differences between organisms and machines.

[3] This essay examines the concept of organism since the early twentieth century (for a discussion of the concept and its transformations in earlier periods, see for example, Cheung (2010) which gives a lot of space for plants too).

[4] Examples of works that focus on plants in philosophy of biology include Gerber and Hiernaux's (2022) historical analysis of the "plants as machines" thesis; Clarke's (2012) and Gerber's (2018) examinations of plant individuality, which have connections with the concept of organism. Also, while not specifically focusing on plants, Pradeu (2010) mentions plants' immunological responses with several examples in his work on the concept of organism.

be revised." For example, while most animals have a centrally controlled neural network, plants have no neurons or brains; instead, they have a distributed system including their xylem and phloem to transfer molecules necessary for their whole control. Or, another striking example: while most animals are unitary, plants are modular and clonal.[5] Such differences are the subject of many debates in past decades on topics including plant cognition[6] and plant individuality,[7] which are both connected to the concept of organism.

In the section three, I will place this organismic perspective in an historical context. In the twenty-first century, the importance of the concept of organism has been a central concern in many works in philosophy of biology and in biology.[8] Some of these works (e.g., Nicholson 2014) suggest that the centrality of the concept marks a "return," pointing back to debates in the early twentieth century.[9] Therefore, I will look back to this period as well, considering the three main frameworks of biology in the early twentieth century (i.e., organicism, mechanism, and vitalism).[10] In particular, I will look at organicism and the work of Agnes Arber, whose writings provide an example of organicism in this period. Her example highlights perspectives that have been potentially overlooked in scholarship on history of biology that focuses on organicist movements. By drawing on examples from plant biology like Arber, my account in this section adds nuance to contemporary discussions on the concept of organism.

Overall, this paper will emphasize the importance of the concept of the organism in the twenty-first century and "its return" from the early twentieth century, when the concept was vigorously debated. Between these two periods, the concept was not as prevalent in biology. In the mid-twentieth century, according to Nicholson (2014), "The epistemological focus shifted to sub-organismic entities (like genes) on the one hand, and to supra-organismic entities (like populations) on the other." Moreover, mechanistic approaches (both operative and philosophical) with their focus on the research of genes and molecules became prevalent as they were thought to be the most important means for understanding living entities. It took several decades for the concept of organism

[5] As I discuss in section two, we might also consider that the ways human beings interact with plants are different than human-animal interactions.

[6] For debates on plant cognition, see Taiz et al. (2019), Calvo et al. (2020), and Calvo and Segundo-Ortin (2023).

[7] The "individual organism" is a crucial topic in debates on individuality among philosophers of biology (e.g., Hull 1978; Dupré and O'Malley 2009; Clarke 2012; Godfrey-Smith 2016; Pradeu 2016; Gerber 2018). Although many scholars use the terms "individual" and "organism" interchangeably (e.g. Clarke 2012), other scholars argue that the notion of "biological individual" is different from "organism," as biological individual can refer to entities that are not organisms—a gene, a leaf, etc. (Pradeu 2016). Also, Pradeu (2016) argues that there are different subcategories of biological individuals such as evolutionary, physiological, and ecological. I discuss these scholars' work in another paper which focuses on plant physiological individuality specifically (under-review paper, Yilmaz and Dupré 2024).

[8] E.g., El-Hani and Emmeche (2000), Ruiz-Mirazo et al. (2000), Rehmann-Sutter (2000), Gutmann et al. (2000), Gilbert and Sarkar (2000), Callebaut et al. (2007), Kendig (2008), Huneman and Wolfe (2010), Pradeu (2010), Nicholson (2014), Nicholson and Gawne (2015), Sultan (2015), Soto et al. (2016), Drack and Betz (2017), and Fábregas-Tejeda and Martín-Villuendas (2023). In addition, one of the most significant international philosophy of biology societies (ISHPSSB, *International Society for History Philosophy and Social Studies of Biology*) had an open workshop on "Organism" at its 1999 meeting. The workshop discussed how attention in the field had turned towards more integrated approaches in recent years (Gutmann et al. 2000).

[9] The state of plant biology in the second half of the twentieth century—i.e., before the "return" of the organism—is also an important topic (albeit one that this essay is not examining).

Footnote 9 (continued)

These years were characterized by the rise of molecular biology and the dominance of mechanistic thinking in biology. For this period too, it is crucial to look into plant biology and specifically into different branches of plant biology as there may be important differences. These differences may highlight slightly different conceptual changes than those that occurred in zoology and other branches of biology in terms of organisms and environments. For example, controlling plants' environment has always been a crucial problem in plant research and has a significant place in the history of plant biology. Munns's examination (2015) of plant physiology in the cold war era and how phytotrons were developed illustrates this history. Another example is the whole-plant physiology perspective, which Lüttge (2012b) examines in the 1970s and 1980s.

[10] Though I briefly discuss vitalism in relation to organicism and mechanism in the early twentieth century philosophy of biology, I do not examine it extensively in this paper. In general terms, vitalist framework "claimed that living organisms defy description in purely physico-chemical terms, because organisms possess some non- material, non-measurable forces or directive agents that account for their complexity" Allen (2005). In other words, organisms' vital force cannot be investigated by science.

to regain its centrality as an explanatory concept.[11] I hope that the arguments in the following two sections of this brief essay will be another step toward a comprehensive understanding of the organism that includes plant organisms as well.

2 Organismic perspective in plant biology

Before discussing the concept of *plant organism*, we should look at plant science in the twenty-first century and the world in which present-day plant scientists find themselves. This context highlights the conditions that have led scientists to give extra attention to dynamic organism-environment interactions.

Today, we face major effects of environmental changes on crop plants and plants in natural environments. We are losing many of the world's forests and climate change is becoming drastic. These issues create a challenge for plant science: the need to better understand plant life, in order to better predict plant responses to future *environments*. Here, 'environments' is emphasized because climate change does not just create separate factors (temperature change, floods, droughts, etc.) for plants (or for any other organisms) to respond to; rather, it affects the multiple, intricate processes that collectively constitute different *environments* in different locations of the world. For example, imagine we are considering a specific degree of rise in temperature and how this may affect plants. This change in temperature can affect different regions differently depending on many other interacting factors, all of which, collectively, can cause changes in the plants' environments. A comprehensive project that is researching plants' acclimation and adaptation processes to high temperature will most probably contain investigations related to plants' drought response, high light response, high concentration of carbon dioxide response, various nutrient deficiencies, interaction with the soil and microbiota (which are, simultaneously, facing the changes under investigation), and the interactive effects of *all* these factors on the plants. And, moreover, since plants will interact with environments that have different combinations of degrees of these factors, the observed or measured phenotypic traits will be not only specific for the particular plant that is under investigation (its genome, epigenome, development, and physiology) but also specific for the particular experimental conditions (i.e., its particular environment—or particular "field" (Leonelli and Williamson 2022), or "location" (Taylor 2012)).[12]

This dynamic interaction is always found between an organism—for the purposes of this paper, a plant—and its environment. Organisms organise themselves through this interaction. They continuously sense their environment and organize themselves according to signal transduction pathways initiated by environmental cues. By responding to environmental signals, plants constantly regulate their metabolic and developmental processes and thereby maintain their stability. For example, they may begin to produce more or less of certain hormones, or they may increase or decrease their photosynthetic activity, or they may open or close their stomata, etc. This constant and dynamic interaction is necessary for the continued existence (i.e., life) of the organism. Every phenotypic trait that is measured or observed occurs through this interaction. The phenotypic traits, or "phenomes" (which is the more precise term if we are talking about a particular individual organism), belong to certain temporal points or periods of the organism's life-time.[13]

[11] See Nicholson (2014) for a more extensive explanation for the "return of the organism."

[12] I discuss the connection between phenome occurrences and particular conditions in an earlier work focused on causation and explanation in plant research (Yilmaz 2017).

[13] Plant phenomes can be any features or traits of plants (other than their genomes), which attract the attention of investigating humans. These investigations can focus on any level of the organisation, from the electron microscopy images of the membranes of the tiniest organelles to satellite images showing plant communities. The definitions of *phenotype*, *phenome*, and *phenomics* are important to consider, and many research and review papers in plant science include definitions of these concepts to clarify how they are used in their work. For example, *phenotype*, according to the Stanford Encyclopedia of Philosophy, "is the descriptor of the phenome, the manifest physical properties of the organism, its physiology, morphology and behavior" (Taylor and Lewontin 2017). Nicotra et al. (2010) define it as, "The appearance or characteristics of an organism resulting from both genetic and environmental influences." *Phenome*, according to Furbank and Tester (2011) is, "The expression of the genome as traits in a given environment," and *plant phenomics* is "the quantitative measurement of these traits in high throughput and high resolution" (Furbank et al. 2019). In addition to these examples, Arnold et al.'s paper on phenotypic plasticity contains a helpful glossary box

A phenotypic trait of a plant that we observe at a point of time is actually a continuous process, continuously being built up on previous processes. Plant scientists always pay attention to many details related to controlling the conditions in the experiment settings because they know that the phenotypic trait in which they are interested is happening through a complex plant-environment interaction (PxE), not simply a genome-environment interaction. While a plant's genome has a crucial role in its phenome occurrence, it is far from being the determinant of phenome. As Lewontin and Levins (1997) write, an organism's development "is not an unfolding of an internal autonomous program, but the consequence of an interaction between the organism's internal patterns of response and its external milieu." Nonetheless, in many experiment settings, where a particular environmental parameter's effect is being tested on a particular phenotypic trait of a particular plant (with a known genome) at a particular developmental stage, it is *convenient* to think of phenome as "genome-environment interaction" (GxE). This is how that data is analysed (i.e., by showing genome-environment interaction). However, it is important to appreciate that the results are reported with a detailed, material-methods section of experiment settings, which gives attention to PxE. This material-method section is important because the results are tied to it. In short, plant phenome is considered as embedded in many intricate processes in plant (*plant organism*)-environment interaction.

Since the plant phenome—i.e., the features of a particular plant (other than its genome) that are observed and measured—occurs dynamically through complex *plant-environment interaction*, investigation of the phenome requires meticulous research on many processes of plant development and plant-environment interaction. As plant science is growing at a great pace in an ever-changing world, there is always need for analysis of its main concepts. These include trait, phenotype, phenome, phenotypic plasticity, stress, etc.[14] Rethinking plant phenomes as belonging to *organisms* necessitates more emphasis on plant-environment interactions and the processual nature of plants.[15] Furthermore, an analysis of the concept of phenome needs to consider not only interactions with abiotic and biotic parameters in plants' environment but also interactions with human beings. These can include interactions such as research processes, agricultural activities, and the management of various kinds of lands and aquatic environments. The increasing awareness of the complexity and dynamicity of these intricate processes that collectively cause plant phenome is one of the triggers of the rise of Plant Phenomics research in recent decades.

Another important trigger, of course, is climate change. Although plants are given only limited space in the IPCC reports (e.g. "Land-Climate Interactions" (2019) and "Ocean and Cryosphere" (2019)),[16] one of the main driving forces of current plant research is the aim to understand plant responses to climate change for the purposes of maintaining or increasing crop yields and protecting natural environments. Not surprisingly, many research and review papers and commentaries in plant science journals start their introductions by citing IPCC reports and noting the possible future climate scenarios that they consider in their experiment designs.[17] Given the growing recognition of the complexity and plasticity of plant organisms, as well as of the increasing importance of understanding plant phenomes in light of changing weather systems, a multi-disciplinary research program has arisen to explore plants using a variety of techniques across a variety of experimental contexts.

Footnote 13 (continued)

that notes, "The terms used to describe phenotypic plasticity are numerous and frequently confused or confusing" (2019).

[14] In fact, *regular* reconsiderations of the concepts and research processes in plant science are needed due to the dynamic interactions within the plant science community, its interactions with the public, and the advancements of research methodologies and technologies.

[15] I follow Dupré's processual account of philosophy (Dupré 2012; Dupré and Nicholson 2018), where the "processual nature of plants" means that organisms and their environments are constituted by intertwined processes. Even seemingly "unchanging" biological entities that we measure or observe—such as structures, organelles, and genes—are held stable through intertwined processes. Furthermore, research programs and concepts are processes too since "everything flows."

[16] The authors of these reports: Jia et al. (2019) and Pörtner et al. (2019).

[17] E.g., Rustad (2006), Ainsworth et al. (2008), Nicotra et al. (2010), Yilmaz et al. (2017), Hamann et al. (2021), Yamori and Ghannoum (2022), and Simkin et al. (2023).

Plant phenomics is a broad research area that involves many kinds of conventional and state-of-the-art technologies and tools, and includes research in growth chambers, greenhouses, open fields, and natural environments. Today, in addition to the great number of plant research groups that conduct experiments in laboratories, greenhouses, and fields in many regions around the world, there are also plant phenomics facilities that have large-scale infrastructure for phenome research.[18] Plant science consists of researchers with various backgrounds including (but not limited to) plant physiology, plant molecular biology, forestry, plant ecology, plant genetics, chemistry, physics, data science, and marine biology. This variety constitutes a rich research structure that is dynamically growing and producing new interactions. More than ever before, it is welcoming researchers from social sciences and humanities including philosophers, sociologists, and historians of plant science. It is in this recent context that many plant scientists have emphasized the importance of cross-disciplinary dialogues in research on plant phenomes, plant responses to changing climate, and plant phenotypic plasticity under climate change (e.g. Nicotra et al. 2010; Parmesan and Hanley 2015). This communication within plant science can benefit from conceiving of plant life as situated in the world—that is understanding plants as *organisms actively and dynamically interacting with the environment (which includes humans)*. Such an understanding can also benefit other disciplines that have tight connections with plant science such as geography, anthropology, and climate science.

Many of these advancements in plant science have been accompanied by "Big Data." They call for a meticulous reconsideration of many processes in plant research activities—"data journeys," as Leonelli (2016) describes them—including experiment set-ups, sample productions, measurements, observation activities, and the analysis, interpretation, storage, share, and re-use of data. Examination of these activities can benefit from an organismic perspective. As the number of plant databases rises, there are ongoing efforts to constitute plant ontologies,[19] which organise plant information in accordance with FAIR principles (i.e., findable, accessible, interoperable, and reusable (Wilkinson et al. 2016; Arnaud et. al. 2020)) and in a way that conveys relationships between ontology terms, which are investigated under different knowledge domains. These open sources are continuously developed through the interactive efforts of many collaborators. An example project is Planteome[20] by Plant Ontology Consortium (POC)[21] in which plant ontologies can be browsed under reference ontologies such as "Plant Trait Ontology," "Plant Experimental Conditions Ontology," and "Plant Stress Ontology" (POC; Bruskiewich et al. 2002; Ilic et al. 2007; Arnaud et al. 2020). The relationships between the terms are "structured," i.e. biologically accurate (Bruskiewich et al. 2002). Each ontology term (also referred to as "bioentity" and "data object") is kept and categorized in its specific relation to other terms. These relationships reflect the biological organisation—which is to say, plant organism—and also the source of the data (i.e., specific project references, plant taxons, etc.). The organisation of biological knowledge in such forms embodies *an organismic perspective,* which distinguishes each mechanism (or term) and places it in biological organisation. As this and the examples discussed so far suggest, today's plant science gives significant attention to biological organisation and the dynamicity and complexity of plant-environment interaction. All these can be connected to perspectives that have "organism" as a central explanatory concept.

[18] For example, the Australian Plant Phenomics Facility (APPF), which was established in 2007, provides many greenhouses, chambers, and "smart houses," which can be controlled in many ways, providing constant monitoring of plant growth and function. These facilities offer the possibility for various kinds of experiment designs, which otherwise would be very hard to conduct. Additionally, the APPF has many sophisticated tools and instruments that allow phenotyping in the field (e.g., drones; aircrafts that can perform hyperspectral and thermal imaging; field-explorer vehicles that have many sensors conducting non-destructive phenotyping; sensor networks, which are small stations in the field doing real-time phenotyping; portable photosynthesis systems providing measurements of photosynthetic activity related phenotypic traits). APPF. Last accessed May 25, 2023. Available at: https://www.plantphenomics.org.au/.

[19] Here, "ontology" is understood as, "a classification methodology for formalizing a subject's knowledge in a structured way (typically for consumption by an electronic database)" (Bruskiewich et al. 2002).

[20] https://planteome.org/about.

[21] Plant Ontology Consortium (POC): http://www.plantontology.org.
https://wiki.plantontology.org/index.php/Main_Page.

The benefits of approaches that involve an organismic perspective (such as *integrated* and *whole plant* approaches) become evident as we look further into the plant organism and its organisation (i.e. plant coordination through plant-environment interaction). This interaction enables organisms to actively maintain their internal processes, which allow them to use nutrients for their survival, growth, and reproduction. These internal processes are *coordinated* at the organismal level. Through evolution, organisms have acquired various ways of coordinating their bodies. In the plant kingdom too, there are different ways of coordination, each uniquely complex. Plants coordinate their bodies via physiological processes that enable them to maintain the stability of their internal processes, produce systemic responses, and organize their interactions with their environments.[22] This coordination—which is to say *systemic physiological processes*—represent the *whole plant* (i.e., organism). Through their physiological processes, plants perceive environmental signals, transmit them in their bodies, re-regulate certain processes according to these transmissions, and produce responses (i.e., their phenomes).

An example of this coordination can be seen in the way that plants acquire minerals and water. If a plant needs more of some minerals or water, the sink strength of its roots rises, which means more photosynthates start to move towards the roots instead of other parts of the plant (i.e., shoots, newly growing leaves, branches, etc.). Thanks to these sources, roots can grow more and forage further in the soil for water and mineral nutrients.[23] They can also produce and release specific molecules (i.e., various kinds of root exudates[24]), thereby making mineral nutrients more available for uptake. In many cases, they can also change microbial communities around them via their exudates, thereby improving their access to mineral nutrients and other needs they have for their development and protection. How much of these sources can be directed towards roots depends not only on roots' sink strength but also on all the other parts' sink and source strengths (i.e., the rates of production and the changing needs), which are interacting through a complex web of many processes. This means that while it has parts such as shoots and roots, a plant is a coordinated *whole*. The whole plant actively maintains a stable source-sink balance through its physiological processes, which are tightly connected to its environment.

Plant modularity does not conflict with this whole plant coordination. Plants are modular organisms, meaning that they have modules with meristem tissues. (Here, however, I do not use the term module in a general meaning, rather I use "module" as meaning "a self-reproducing and semi-autonomous unit that is iterated to make up a larger unit or colony" (Clarke 2012)).[25] Because of their meristem tissue, each module has the capacity to produce any part of the plant or even a whole new plant if it gets separated. In some cases, they can produce a new plant even without getting separated—i.e., a new ramet. As long as modules are connected, however, they collectively act as a whole, e.g., maintaining a source-sink balance or producing systemic stress responses as described in this section. This collective action at the whole organism level is more than a "collection of modules," because the whole is more than its parts, since at each level of organization, there is *emergence*. "Emergence is the inevitable unfolding of new functions and structures of a system on a higher scalar integrative level" (Lüttge (2012a). Because of emergence, properties on a level of organization cannot be reduced to properties of lower levels. As Souza et al. (2016a) emphasize in their paper on irreducibility in biological systems in the case of plant ecophysiology, "the key aspect in emerging phenomena lies in the interactions between the components of the system."

[22] I have previously discussed plant coordination through source-sink balance regulations in connection to its importance in terms of both plant physiological individuality (under-review paper with John Dupré) and stigmergic coordination and plant minimal cognition (Sims and Yilmaz 2023).

[23] See Lynch (2022) for a recent discussion on root architecture and allocation of carbon to root system.

[24] See Badri and Vivanco (2009) for a discussion of regulation and function of root exudates.

[25] Many scholars argue that autonomy is an important aspect of being an organism since organisms are self-organised through their active interaction with environments (e.g., Baedke 2019). Modules, however, should not be understood as autonomous, but rather as semi-autonomous. Oborny (2019), for example, illustrates "semi-autonomy" by describing how "the ramet receives and/or sends some material from/to other ramets, but can also take up some of the resources independently of the others."

Another crucial aspect of whole plant coordination—i.e., organism—is a plant's microbiota. Investigations of the roles that plant microbiota play in plants' physiological, evolutionary, developmental, and ecological processes are a crucial part of integrated approaches in plant science. The interactions between plants and their microbiota have great effects on many processes in plants and soil ecosystems. Through their active interactions, plants and microorganisms organise their internal processes and affect their environments and each other by competing, collaborating, etc. Many researchers who investigate these interactions also emphasize the importance of "holistic" perspectives for understanding plant life, as plants cannot be considered as single entities since they always live with their microbiota with which they constitute the holobiont (Vandenkoornhuyse et al. 2015). Holobiont constitutes an important topic in biological individuality debates. These include discussions by Skillings (2016) on whether holobionts are multi-species communities or integrated individuals, Gilbert and Tauber's (2016) on the ecological approach in immunology and the holobiont as being continuously constructed through interactions, and Suárez and Triviño (2019) on holobionts as emergent individuals. While discussing holobiont further would exceed the limits of this paper, I would like to point out that integrated approaches investigating plant life involve considering plant microbiota as a crucial part of the plant organism. In fact, following Dupré and O'Malley's (2009) discussion of "associations of a variety of …lineage-forming entities" or "interactors," we can think of holobionts as "complex systems involving the collaboration of many highly diverse lineage-forming entities …the most fundamental unit of selection" (Dupré and O'Malley 2009).

Stress is a process where whole-plant-coordination can be clearly observed. Moreover, stress is a plant-life phenomenon that requires *an organism-centred stance* to grasp. When plants face stress, there is a stressor stimulus (or stimuli) in their particular environment. These stimuli—which can be biotic (e.g., some species of bacteria, fungi, etc.) and/or abiotic (e.g., drought, high or low temperature, high light, etc.)—are not like daily or seasonal changes and they cause much more "altered" phenomes. These alterations may even be described as "injuries," meaning deteriorations in some parts of the plant's body. There is a degree of injury (or even death) in stressed organisms depending on the resistance ability of the individual organism to the stressor and the wider context in which the organism encounters the stressor. Investigating stress conditions like these requires integrated approaches that consider different levels of organisation. In comparing searches for a single indicator with a cross-scale multivariate analysis, for example, Bertolli et al. (2014) examine the importance of emergent properties in water stress and conclude that the multivariate analysis is "an appropriate method for establishing models that will allow for a systemic understanding of the complex interactions between plants and their changing environment."

Through stress-related physiological processes, we can observe plants responding at the whole-plant level even to local stimuli. Intervention by wounding, for example, can result in rapid systemic responses in plants. In their investigation of wounding responses, Fichman and Mittler (2021) show that the wounding of a single leaf in *Arabidopsis thaliana* plants results in a rapid, systemic wave of reactive oxygen species[26] production in the whole plant along with a change in redox concentrations. These responses can be the cause of altered concentrations of metabolites in tissues resulting in "an enhanced state of SAA and SWR" (systemic acquired acclimation and systemic wound response)[27] (Fichman and Mittler 2021). Phenotypic traits such as these, which are related to stress responses, are processes that are nested in many other processes in a plant. Therefore, it is crucial to consider all the other processes carefully as they may have both indirect and direct effects on the stress responses. With this concern in mind, Forsman (2015), for example, emphasizes a "whole organism" rather than a "single trait" approach for "an increased understanding of the roles of plasticity in the ecological success of populations and species."

These "whole organism" approaches in stress physiology research clearly consider and examine the organism in its relation to its environment and

[26] ROS (reactive oxygen species) are signaling molecules in organisms and they have important roles in many biological processes such as growth and response to environmental stimuli.

[27] Systemic acquired acclimation (SAA) and systemic wound response (SWR) are both systemic states of plants responding to environmental stimuli (Baxter et al. 2014; Fichman and Mittler 2021).

development. In doing so, some see them as returning to conceptions of the organism from the early twentieth-century. Sultan, for example, argues that "eco-devo actually represents a return to the more holistic approach to individual development embraced by early twentieth-century researchers in embryology and genetics" and, she continues, "in evolutionary biology too" (Sultan 2015).[28] This assessment is coherent with what contemporary philosophers such as Nicholson (2014) have described in biology as "the return of the organism."

3 Organicism: now and then

In the previous section, I briefly described some aspects of contemporary plant biology, pointing to several reasons why organismic perspectives are becoming widespread (and needed) in plant research. These reasons were: (1) the challenge of understanding plant responses to changing environments (i.e., global environmental problems); (2) the greater attention to organism-environment interaction and the increased tendency to use whole organism and integrated approaches; and (3) developments in plant science research programs, whose highly-developed, fast-growing research infrastructures emphasize multidisciplinary approaches and entail "big data" production. My aim was to direct the attention of philosophers and historians of biology to aspects of plant science that belong uniquely to *plant biology* and *plant organisms*. I argue that, because of these unique aspects, a comprehensive account of the concept of organism and/or organicism should specifically include an examination of plant biology in addition to other branches of biology such as zoology (the branch of biology to which philosophers most frequently look). As this section suggests, our understanding of organicism can also be aided by a consideration of the rich history of plant biology, particularly its theoretical debates in the early twentieth century.

Biological thought has been profoundly influenced by the three frameworks of organicism, mechanism, and vitalism. Considering the rich history of biology and natural philosophy, stretching back centuries, it is no surprise that these frameworks themselves are historical processes that interact with cultural, political, and economic processes. As a consequence, each contains a diversity of thought, and, from time to time, can partially overlap. In the last century too, as different branches of biology were taking shape, these frameworks also interacted with each other. Many contemporary philosophers of biology, who emphasize the importance of organicism, point to the early twentieth century as a crucial time when there was intense discussion and debate about these frameworks (e.g., Allen 2005; Nicholson 2014; Nicholson and Gawne 2015; Baedke 2019). And yet, when we look at these excellent works, we find little or no mention of plant biology. For example, in Nicholson and Gawne's (2015) meticulous investigation of scholarly interactions among organicists in the early twentieth century, none of the scholars mentioned is a plant biologist. Similarly, Baedke (2019) presents a useful table listing the "Central Works on the Concept of the Organism or Biological Individual, 1908–1945," but includes only two works on plants among the thirty-five citations. As there were certainly plant biologists engaging with these frameworks at the time, these absences should prompt us to identify these individuals and look closely into their work. Considering their use of these frameworks and their contributions to the theoretical discussions of their era can contribute to our understanding of organicism. Pursuing such investigations requires us to look into the history of plant biology.

The early twentieth century was characterized by hectic political, cultural, and technological changes including rapid industrialization, the mechanization of daily life, World War I, and the turmoil of the interwar period. Likewise, during this time, biology went through significant changes. Sub-branches emerged and set their own methodological and theoretical frameworks. Unsurprisingly, amid this ferment, significant dichotomies emerged in plant biology including physiology vs morphology, experimentalists vs naturalists/taxonomists, physico-chemical processes vs phylogeny and natural history. There were many discussions around these branches of plant biology and debates over concepts and methodologies. Plant biologists read, followed, and discussed each

[28] Other examples of contemporary plant biologists calling for systems approaches, integrated approaches, and/or organismic approaches in biology are Somerville et al. (2004), Lüttge (2012a, b), Bertolli et al. (2014), Souza et al. (2016a, b).

other's work.[29] Even between sub-branches that were understood to be on opposite sides of these dichotomies—or seen as inhabiting "incompatible 'conceptual worlds'"[30]—there were collaborations leading to important turns in plant biology. Hagen, for example, considers several instances of these collaborations and argues that, "without denying either the existence or the significance of controversies among twentieth-century biologists …the naturalist-versus-experimentalist dichotomy is an oversimplification" (Hagen 1984).

In the midst of this tumultuous time, plant biologists discussed methodologies, theories, concepts, and the philosophical foundations of their research. A striking example can be found in the writings of Agnes Arber (1879–1960). Arber is known for her meticulous collection of plant morphological data and elaborated interpretation of this data in the light of both biology and philosophy literature.[31] Her interpretation of plant morphology involves "the description and interpretation of the entire external and internal organization of the plant, from the beginning to the end of its life-history" (Arber 1950). Her understanding of plant form expands from the Aristotelian concept of form as "the whole of the intrinsic nature of which any given individual was a manifestation," and as a "student of nature" herself, she considers the "four causes as falling into two classes—the mechanical and physico-chemical causes (material + efficient causes), and the teleological causes (final + formal causes)" (Arber 1950). This teleology that she emphasizes is connected to "the urge to self-maintenance." In plant form, particularly, this self-maintenance can be observed as repetitive branching since each part of the plant at growing points has the urge to be *a whole plant*.[32] Intrinsic purposiveness and organismic teleology, which are significant themes in Arber's work, are the sort of "recurring themes" that Nicholson and Gawne (2015) argue "enable us to legitimately speak of an 'organicist school' or an 'organicist movement.'" In general, they highlight early twentieth century biologists' search for a "third way," avoiding mechanism and vitalism. More specifically, they emphasize a shared focus on "the centrality of the organism concept in biological explanation; …the importance of organization as a theoretical principle; and …the defence of the autonomy of biology" (Nicholson and Gawne 2015).

Arber's position in relation to the mechanism-vitalism-organicism debates of her time can be clearly seen in much of her work. For example, in her 1933 paper "Floral anatomy and its morphological interpretation," she examines the work on vascular anatomy by many scholars (including both her mentor/colleague, Ethel Sargant, and herself). Her unflinching critical stance throughout the paper is apparent from the start, as she makes it clear that she will question even widely accepted facts. While she touches on multiple points in this article (not all of which are relevant for the purpose of *this* essay), mentioning a few can give a sense of her position in the philosophy of biology debates of the early twentieth century. She criticizes, for instance, the mystical approach of Wilhelm Troll (1897–1978) for treating morphology as unanalysable and unexplainable. She argues that, "He puts aside 'explanation,' in the sense in which that word is used in the exact sciences, and treats it as having no place in morphology" (Arber 1933). Arber thinks that "whole" or "unity" or "organism" is open to scientific investigation, it is not "unanalysable," as vitalists argue.

While acknowledging the value of analysis, she emphasizes the importance of reintegration after each analysis, which reflects her critique of reductionist approaches. She warns against "the habit of isolating structural details and dealing with them, as it were, *in vacuo*," since all these are part of the *plant organism*. Towards the end of the paper, her call for an organismal standpoint becomes especially clear. In discussing work on development and heredity by marine

[29] Tansley's (1924) presidential address to the Botany Section of the British Association for the Advancement of Science's is an excellent example of the discussions among different sub-branches of plant biology and how plant biologists were acknowledging the significance of each other's work.

[30] "Conceptual worlds" comes from Ernst Mayr's "Prologue: Some Thoughts on the History of the Evolutionary Synthesis" (1980), as quoted in Hagen (1984).

[31] For discussions of Arber's life and the significance of her work in both plant biology and the history of plant biology, see Schmid and Stevenson (1976), Schmid (2001), Flannery (2003), and Feola (2019).

[32] She describes this as "partial-shoot theory of the leaf" (Arber 1950).

biologist Edward Stuart Russell,[33] one of the scholars in “organicist movement” of the early twentieth century, she argues that his position:

> …appears to be a much more reasonable one. Though his sympathies are all with the “organismal” standpoint, which is essentially synthetic, he is careful not to rule out analysis, provided it is invariably followed by reintegration. His attitude offers—in theory, if not entirely in practice—a sane compromise between the exclusively analytical and the exclusively synthetic positions. It is greatly to be wished that someone would produce a treatment on broad lines of the *botanical* conception of the organism, to balance and supplement Russell’s brilliant exposition, which is basically zoological. (Arber 1933).

It should be recognized that Arber is emphasizing the need for conceptions of the organism that are *botanical* even as she was producing such a conception herself.

Considering Arber’s critique towards both mechanism and vitalism, her emphasis on a need for an organismic understanding (i.e., a “the third way”), and—as noted earlier—other recurring themes in her work in general (i.e., intrinsic purposiveness, organismic teleology, whole plant), she can clearly be understood as a participant in the organicist movement of her time. Her insights should be considered as we seek to develop a better understanding of that movement’s history.

4 Conclusion

The concept of organism is crucial for *plant biology*. It is also crucial for *philosophy of biology*, whose frameworks of organicism, mechanism, and vitalism can be better understood through more extensive engagement with the *history of plant biology*. An organismic framework can be helpful not only for conceptual analysis in plant biology, but also for understanding various processes in plant research, including organism selection, experiment set-ups, and data processes. Today, plant scientists still use mechanisms extensively. At the same time, they treat these mechanisms as processes happening in plant organisms that are interacting with their environments dynamically and intricately. As I have shown in this essay, there is much to be learned from *the botanical conception of the organism* and the interactions of different plant science branches, both today and in the past century. This paper, however brief, is a step in that direction.

Plant science is a broad discipline with different branches. Each has its own research questions and methodologies, which may entail slightly different conceptualizations of various aspects of plant life. Even though many research questions require an integrated view of plants—which means comprehensive studies that simultaneously look into multiple aspects of plant life (including physiology, evolution, development, ecology, genetics, etc.)—each branch still keeps its own research agendas. Moreover, these branches involve not only specialized plant scientists but also researchers with other backgrounds. While this paper has not aimed to unify plant science, I would nonetheless like to remind and emphasize that, overall, we need a unified concept of plants. I argue that the concept of *plant organism* can help us connect and integrate different branches when needed. The plant organism concept always requires us to consider plant life in its context—that is, plant organisms in their environments and the dynamic and intricate interactions between them.

I would like to finish this essay by quoting two plant biologists, one from today and one from the early twentieth century, both of whom emphasize the importance of an integrated approach in plant biology. While Arthur Tansley, the early twentieth century scholar, emphasizes the importance of coordination between branches and, overall, a “unified notion of the subject,” especially in botany education, he still acknowledges the separated research agendas and practices of branches in his time; more recently, however, Sonia Sultan has argued for the importance of integration in the research programs. Maybe we can read this difference as a development in science. While a century ago, integration was more a theoretical understanding than a practical one, today it can be both equally. Maybe today’s plant science technology and knowledge can enable an integrated approach more easily than those of a century ago could for examining the plant organism—that is, the complex

[33] Here, Arber is discussing Russell’s book *The Interpretation of Development and Heredity* (1930).

plant environment interaction and its implications for plants, environments, and their evolution.

Sultan (2015) argues that, “An organism–environment research program will, of necessity, integrate studies of gene expression and developmental pathways, ecological conditions, and evolutionary trajectories, in ways that promise to illuminate and enrich these formerly separate disciplines.” This call for an integration of disciplines can be especially important in education. Moreover, it resonates with Arthur Tansley’s emphasis on the “unified notion of the subject” (botany), a hundred years ago. In his presidential address to the Botany Section of the British Association for the Advancement of Science, Tansley cautioned that:

> …if botany, as the science of plants, is to retain any meaning as a whole, somebody must retain the power of looking at it as a whole. And if, as teachers, we fail to keep touch with the newer developments, and are consequently no longer able to focus the whole subject from a viewpoint determined by current knowledge, this power will come to be possessed by fewer and fewer botanists, and the subject will definitely and finally break up into a number of specialised and uncoordinated pursuits. (Tansley 1924).

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