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RESEARCH ARTICLE

Plant Individuality: A Physiological Approach

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While plants provide some of the most interesting cases for individuality related problems in philosophy of biology (e.g. Clarke 2012; Gerber 2018), no work has examined plant individuality through specifically focusing on physiological processes, a lacuna this paper aims to fill. We think that different domains of biology suggest different approaches and our specific focus on physiological processes, such as plant hormone systems and source-sink balance regulations, will help to identify coordinated systems at different scales. Identifying physiological individuals is crucial for a wide range of research in plant biology, including research on plant nutrition, transport and accumulation of nutrients in edible parts, and plant responses to various stress conditions such as plant diseases and changing abiotic conditions. Although plants do produce systemic responses to local stimuli (e.g. a sudden wound on one leaf can result in a whole plant response), considering them as individuals is (often) problematic. They are highly modular organisms, and they can grow vegetatively, constituting clones of what seem superficially to be individual organisms. Moreover, as with animals, there are problems raised by their symbiotic relations to micro-organisms, most notably the mycorrhiza, through which they may be connected to other plants. We argue that coordinated plant systems can be distinguished at multiple scales from a physiological perspective. While none of these is a unit that must be necessarily called "the individual," they offer integrated approaches for various research problems in plant science.

Keywords

coordination • plant individuality • physiological individuality • promiscuous individualism

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1. Introduction

Individuality has been a hot topic for philosophers of biology for a considerable time.[1] Various conceptions of biological individuality have been proposed, and several of them have been seriously challenged by the specific characteristics of plants (Dupré 2010; Clarke 2012; Gerber 2018). We think that different domains of biology suggest different approaches to the problem of biological individuality, and highlight different aspects of the problem. In this paper, we consider what plant physiology can offer. We argue that it challenges how one might normally think of boundaries, pointing to them as vague, rather than distinct, while also indicating both vertical and horizontal coordination of physiological processes, which allows us to see coordinated systems at multiple scales. In this paper, we support this proposal with attention to the special attributes of plants.[2]

Philosophers have mostly approached plant individuality via conceptions of evolutionary individuality which focus on the unit of selection.[3] Here we instead consider plants as physiological individuals. Since physiological individuality is about the unit of functioning, we believe it aligns well with the concept of the organism as a cohesive whole with differentiated parts that function in coordination (Mossio and Moreno 2010; Nuño de la Rosa 2010). We examine the extent to which plants can be seen as individual organisms, based on those physiological processes that enable them to coordinate their physical parts. Since we approach plant individuality through a focus on physiology and coordination, we also discuss plant parts and the practices through which these are individuated in plant science. Although we are not investigating plant cognition in this paper, we find it plausible that this coordination provides instances of plant cognition. Whereas in the case of animals much of this regulation and coordination is accomplished by the nervous system, in plants a similar function is served by the flow of hormones and other information-bearing molecules around the system. We think that plant physiological individuality often more or less coincides with plant cognitive individuality, as plants actively interact with their environments, perceive salient features of the environment, and coordinate their actions in ways appropriate to environmental conditions.[4]

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[1] Some of this literature: Hull (1978); Dupré (2010, 2021); Clarke (2012, 2013); Godfrey-Smith (2016); Pradeu (2016a, 2016b); Skillings (2016); Lidgard and Nyhart (2017); Love and Brigandt (2017); DiFrisco (2018); Gerber (2018); Waters (2018); Suárez and Triviño (2019); Baedke (2019b); Kaiser and Trappes (2021).

[2] Plants have not been prominent in the philosophy of biology. Only a few philosophers have written specifically about them. Some notable examples from the literature on philosophy of plant biology are Leonelli's work (2007, 2013, 2016) on data science, model plants, and knowledge in plant science, and Clarke's (2012) and Gerber's (2018) work on plant individuality. Although the reasons for this lack of interest in plant biology are no doubt complicated, we do think that it reflects an objectionable element of zoocentrism (see also Gagliano et al. 2017). When confronted with an example of work in the philosophy of plant biology, philosophers often ask how it is related to ideas grounded in animal research. What are the differences and similarities between plants and animals with respect to the problem under investigation? How are similar problems understood in the philosophy of animal biology? It is of course true that comparative research is very useful and important both in biology and in philosophy of biology, and plants and animals exhibit interesting similarities—for example, homologous molecules that play similar metabolic roles. Still, we do not expect to see a plant comparison in every paper on the philosophy of animal biology, so why treat philosophy of plant biology differently? In this paper, we will be investigating plant individuality and plant physiology in their own right.

[3] Most debates on animal individuality also focus on evolutionary individuality (e.g., Godfrey-Smith 2016). Pradeu (2016a) notes that the debate on biological individuality mainly concerns evolution-based accounts, but insists that attention to physiology is also crucial for a comprehensive account of biological individuality.

[4] There is a recent debate among plant biologists on whether plants can be considered as intelligent (see Brenner et al. 2006; Alpi et al. 2007; Gagliano et al. 2016, 2017; Taiz et al. 2019; Calvo et al. 2020). Although this debate is recent, its roots go back centuries. Whether concepts like behaviour and agency can be applied to plants or only to animals is an ancient question (Hiernaux 2019).

To study plants as organisms with coordinated parts requires observing how they organise interactions between their parts at a particular developmental stage, as well as how this organisation projects the plant toward the organisation of later stages. The next part of the paper examines this coordination in plants and how it is regulated through source-sink balance in interaction with the environment. Source and sink concepts in plant science were first proposed by Mason and Maskell (1928), in their work on transport of carbohydrates in cotton plants (Chang and Zhu 2017). Source-sink balance, which is maintained via dynamic interactions between source and sink tissues, concerns the distribution of carbohydrates and minerals in a plant's body. We argue that the coordination via source-sink balance (i.e., the physiological processes which enable this balance) can provide the basis for distinguishing the physiological individuality of a plant. We especially stress the importance of hormones in the maintenance of this stability. We will show how, depending on our research questions, we may think of plant physiological individuality as extending to wider limits in, for example, the cases of plant-plant interactions mediated by the microbiota, the growth of new ramets in a genet, and so on.

In the third part of the paper, we discuss the implications of this physiological perspective for the attribution of individuality to plants, arguing that while plants do often have a strong individuality, it is also often possible to divide plant processes into individuals in various non-overlapping ways. Finally, in the fourth part of the paper, we discuss this "promiscuous individualism" with specific reference to the processual nature of plants.

2. Coordination in Plants

Coordination, through the many physiological processes that maintain the source-sink balance, is a necessary capacity of plants. Although plants do not move like animals, they do move in several ways, including through their growth.[5] Examples of growth processes that involve an adaptive response to the environment include the growth of branches towards areas which receive more light, the growth of roots towards a part of the soil with better composition or availability of nutrients, and the searching for support structures by vine tendrils. Other adaptive movements by plants include the timing of the opening and closing of stomata, regulated through a complex web of processes to optimise water content and carbon dioxide intake, and the movements of carnivorous plants to trap and digest their prey. A plant's response to environmental cues, signals, and stressors is the outcome of internal signalling processes that enable plants to coordinate their bodies in ways appropriate to specific environments and maintain optimal source-sink balance regulation.[6]

2.1. Source-Sink Balance

Maintaining source-sink balance, that is, moving nutrients from sites of production to sites of use, is one of the main system-wide goals of physiological processes in plants. The complex web of physiological processes that makes this possible includes reacting to environmental and internal signals by producing relevant responses in the appropriate part of the plant. Source tissues are parts of the plants where there is production and acquisition of nutrients; for example, leaves are the source of photosynthates (products of photosynthesis) and roots are the source of many nutrients (nitrogen, zinc, phosphorus, etc.). Sink tissues are parts where there is a need for nutrients and photosynthates; for example, a newly developing fruit or leaf, or a growing root

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[5] Arber (1950) proposes that morphology in plants corresponds, in some respects, to behaviour in animals.

[6] Yilmaz (2021) has written about the importance of source-sink balance regulation in plants as a useful example in teaching the concept of organism in philosophy education.

is a sink. Of course, a particular part of the plant will sometimes be a source, sometimes a sink, and usually both. Source-sink transitions, which happen throughout the life cycle of plants, are regulated actively and dynamically in plants. For example, Yu and colleagues (2015) describe how, in cereals, different parts of plants (e.g., shoots, roots, spikes, and seeds) become sources or sinks or both at different stages of development (i.e., germination, seedling development stage, vegetative stage, or reproductive stage; Yu et al. 2015). Many molecules—mainly hormones and sugars—have important roles in source-sink balance regulations. If there is a decrease in sugar transport from the leaf cells (which may be caused by, for example, magnesium or potassium deficiency), accumulated sugar in the cells may send signals for reducing photosynthetic activity.[7] These responses interact. Yilmaz and colleagues (2017), for instance, applied elevated carbon dioxide and magnesium deficiency to young wheat plants. Elevated carbon dioxide enhanced photosynthetic rate in plants with adequate magnesium, but not in plants grown in low magnesium conditions, as these plants most probably had lower photosynthetic activity because of accumulated sugar levels in their cells (Yilmaz et al. 2017).

As mentioned earlier, source-sink balance regulations depend on the specific plant's life-cycle, developmental trajectories, and environmental conditions. Depending on the kind of plant, plants' life cycles involve the growth of diverse kinds of organs, such as shoots, roots, trunks, branches, seeds, spikes, or fruits. A coconut, a cucumber, or a bamboo have very different kinds of shoots, roots and fruits, very different life cycles, and very different source-sink balance regulations throughout their life cycles. Since plants are in constant interaction with their environments, these regulatory systems will be shaped by environmental cues and signals, and they will be actively fine-tuned through dynamic physiological and developmental processes. The allocation of resources to parts will depend on current, but constantly changing, priorities. If there is deficiency of a mineral nutrient in the soil, the roots will become stronger sinks (enabling further growth and searching for the mineral, or releasing specific compounds in the soil in order to change its chemistry, making the mineral available for uptake), and more of the photosynthates will go to roots, instead of contributing to the growth of more branches and leaves. The plant will prioritize certain processes over others. Canarini and colleagues (2019) review the plant biology literature to show how root exudates are controlled by source-sink processes and also affected by plant related microorganisms in the soil. Plants also regulate microbial communities around their roots with their root exudates, selectively promoting beneficial communities (Walker et al. 2003; Jacoby 2017). Although these regulated interactions between plant parts in pursuit of source-sink balance may look competitive, they actually depend on the priorities of the whole plant. How does a plant coordinate the activities of its parts?

2.2. Plant Hormones

There is no centre of coordination in a plant's body.[8] Vascular tissues that carry water, nutrients, sugars, hormones and other molecules, are distributed throughout the plant and the movements of all of these are regulated by complex processes that mediate between plant parts and that interact dynamically with the environment. The first usage of the term hormone in plant physiology was derived directly from the concept of hormone in mammalian physiology, involving a site of synthesis, transport to a target tissue and the control of a physiological response via hormone

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[7] This is part of the sink regulation of photosynthesis, and these regulations do not occur not via simple linear pathways, but through networks with many points of reciprocal control (Paul and Foyer 2001, 1384).

[8] Although it does have a central brain, two thirds of the neurons in an octopus are distributed among its legs, and these can communicate among themselves in ways that do not involve the brain at all. In certain respects, it might seem that the octopus resembles a plant as much as an animal.

concentration, but it soon came to be understood that plant hormones have their own characteristics (Davies 1987). Plant hormones play crucial roles in plant physiology and in regulating many kinds of interactions between the plants and their environment, including development, growth, reproduction, abiotic stress[9] responses, and interactions with pathogenic and symbiotic fungi and other microorganisms.

Both pathogenic and symbiotic fungi can significantly affect plant growth and morphology. Furthermore, many plant hormones are produced by fungi (Chanclud and Morel 2016; Eichmann et al. 2021) and also by some bacteria,[10] so the hormones have various kinds of roles depending on specific conditions and relations. If it is a symbiotic fungus, the hormone that it produces may simply contribute to the regulation of normal processes, whereas in pathogenic interactions it may spread the damage, and in such a case it seems that the fungus is manipulating the plant. In some experiments, it is unclear whether the plant or the fungus is the source of the hormone (Chanclud and Morel 2016), although, either way, the hormone mediates important aspects of the interaction; there is a kind of communication between plant and fungus via hormones and other signalling molecules.

Hormones can trigger many processes in plants. For example, the hormone abscisic acid (ABA) has a role in closing stomata in response to a water deficiency in the environment. A plant may need to close its stomata when its environment is water deficient, in order to reduce transpiration, but it may also need to open them to let in carbon dioxide necessary for synthesizing sugar. A plant under water deficient conditions thus needs to find an optimal balance of its stomatal movement for keeping water from going out while still taking in sufficient carbon dioxide. Many hormones and other signalling molecules, whose synthesis, transport, and turnover are distributed throughout the plant, collaborate in regulating these stomatal movements, enabling the optimization of the metabolic upshot for the whole plant. Like stomata opening and closing, all variable processes in plants will involve many plant hormones and metabolites working interactively through the whole plant body. Müller and Munné-Bosch (2021) examined the crucial roles of hormones in the regulation of photosynthetic activity and photoprotection, and how hormonal responses that involve much interaction, complementation, and crosstalk are integrated at the whole plant level; from the tips of the roots to the cuticle on the leaves, the whole plant is coordinated via these interacting processes regulating plant growth, development, and reproduction. Vanstraelen and Benková (2012) emphasize how hormonal pathways are interconnected by a complex network of interactions that involve feedback mechanisms providing plants robustness, stability and flexibility.

We have spoken throughout the foregoing discussion of “the plant” or “the whole plant,” and this may seem question-begging in the context of addressing the question of what, if anything, distinguishes a plant as a distinct individual. We do think, however, that these networks of hormonal interaction can often provide a criterion and a motivation for distinguishing the boundaries of the individual plant. In a patch of annual weeds, such as the massively studied model organism *Arabidposis thaliana*, there is no ambiguity about the number of organisms. The passage from seed to flowering, seed production, and death follows a reliable pattern for each successfully germinated seed. Its ability to follow this path is dependent on the kind of regulatory networks we have been discussing, and these also respond to environmental contingencies in ways that maintain this trajectory. However, there are some major qualifications. First, we should not assume that because we have distinguished distinct countable organisms, we can

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[9] Stress conditions can be caused by high or low temperature, frost, high light, water deficiency, flood, salinity, etc.

[10] Plant growth-promoting bacteria produce phytohormones like auxin, cytokinin, and gibberellin (Compant et al. 2019).

unambiguously discern their precise boundaries. The intimate connections of a plant with symbiotic microbes greatly complicates such identification. And the extended life cycles of some plants do not lend themselves so readily to the kind of distinction that applies to an annual plant. We shall discuss some of these complications in the following sections.

2.3. Plant Microbiota and Implications for Plant Individuality

The plant microbiome is crucial for plant life and problematizes any simple attempt to define the individual plant. There is a lively debate in the philosophy of biology concerning whether or not holobionts, the sum of a multicellular organism and all its associated microbes, are biological individuals.[11] Recently, the volume of research on the importance of the plant microbiome for plant growth, health and stress resilience has been growing.[12] In many cases, when we measure a physiological parameter of a plant, we are measuring its associated organisms' activities too (as noted above, in some experiments it is unclear whether the fungus or the plant is the source of some plant hormones).[13] Molter (2019) argues that mycorrhizal fungi can form a huge physiological individual since they are integrated networks connecting trees and allowing them to share nutrients and signaling molecules (Molter 2019; Gorzelak et al. 2015). Are the trees thus connected then part of a truly massive individual? Dupré and Nicholson (2018) emphasize that organisms live in interconnected communities; they are ecologically interdependent. In these communities, we observe a spectrum of degrees of intertwining of processes, not autonomous individuals with distinct boundaries (Dupré and Nicholson 2018). We argue that plants as organisms can sometimes be treated as physiological individuals with reasonably well-defined boundaries, but also that they live in close—usually very intimate—interaction with their microbiota and thereby, sometimes, with other plants. Often this interaction, or intertwining, is so close that, in the context of some research questions, they may be better understood as parts of the same physiological individual. Their source-sink balance regulations affect and are affected by their microbiota; their physiological processes are intertwined with those of their microbiota.

In the cases where an entire forest is connected by a massive mycorrhizal fungal network, the transport of signalling molecules and nutrients between trees can be seen as providing a much greater extension of their physiological individuality, since this process can contribute to the regulation and coordination of the whole forest. Here, we should also consider other ways of signalling between the plants, for example, the gaseous hormone ethylene or other compounds that plants release and receive, reorganising themselves accordingly, and ask whether these interactions may also contribute to the formation of a physiological individual. Plants produce thousands of different volatile compounds for their interactions with each other, and other organisms, including pollinators, herbivores, and micro-organisms, convey information from one plant to another. Although these semiochemicals usually work locally, they can some-

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[11] Many philosophers have examined this problem (e.g., Dupré and O'Malley 2009; Dupré 2010, 2012; Skillings 2016; Pradeu 2016a; Gilbert and Tauber 2016; Chiu and Eberl 2016; Suárez and Triviño 2019; Molter 2019).

[12] For example, Vandenkoornhuyse et al. (2015), Müller et al. (2016), Compant et al. (2019), Trivedi et al. (2020), Babalola et al. (2020).

[13] Albornoz and colleagues (2021), while fully acknowledging numerous non-nutritional benefits of mycorrhiza (for example in soils with high concentration of toxic metals), investigate some untested, even dogmatic assumptions about them. They observe that although it is generally accepted that 80–90% of vascular plant species form some mycorrhizal associations, actually only less than 1% of plant species have been tested in this regard. Although they accept that those estimates are correct as far as we know, still they emphasize the need for caution. Another assumption they highlight is that, in recent reviews, mycorrhiza are assumed invariably to promote plant growth, especially through phosphorus acquisition, but in fact this assumption needs to be examined across different groups in the plant kingdom.

times work over considerable distances; some insects can perceive plant volatiles from several hundred meters away (Bouwmeester et. al. 2019). We do not mean to suggest that the insect is thereby part of the tree. But where a large number of plants are connected by a continuous mycelial net, the existence of parallel systems of communication reinforces the argument that it may be legitimate to see the whole plant community as an individual. Identification of the molecular communication networks that mark the boundaries of the single plant provides us with a way of addressing the question of the individuality of such a larger putative individual. Are the interactions mediated by the mycorrhizal networks or by dispersed molecules comparable in their ability to coordinate the distribution of resources around the system and thereby optimize the condition of the whole? If so, then we have a strong claim to have identified an individual with a status similar to the individual plant. If we can clearly identify such optimizing processes across the system, but much less strongly so than for the individual plant, then the claim to individuality will be proportionately weaker, but perhaps still defensible for certain theoretical purposes.

We do not propose to offer a decisive answer to these questions about the extent of plant individuality here. Rather, in accordance with the position of promiscuous individualism (Dupré 2012, 241), we propose that there are many ways of distinguishing individual plants for different purposes. Importantly, this is not the view that there are no real boundaries and individuals are carved randomly from an amorphous mass of living material. The problem, rather, is that there are multiple discontinuities in the living material, many of which may sometimes be appropriately treated as the boundaries of an individual. In the case of plants these boundaries may be quite fuzzy, and in the case of highly rhizomal plants, as we shall discuss further below, it may even be possible to carve out individuals with a sharp spade. Nonetheless, the closure or partial closure of physiological networks may often provide firm ground for distinguishing an individual.

3. Plants as Physiological Individuals

Plants are living systems, and as such, they are continuously self-organising through their interaction with the environment. This interaction constitutes a complex net of intertwined processes that extends into other plants and the environment. Although these extensions blur plants' boundaries (for example through the arbuscular mycorrhiza-plant interaction), we can still frequently distinguish an individual plant as an individual organism, a dynamic entity actively changing its body and its environment through the behaviour that it produces in response to environmental cues. The organism as *a whole*, acts as *one individual* (a physiological individual).

Baedke (2019a) claims that both early twentieth century organism-centered biology and the recent revival of the centrality of the organism (Nicholson 2014) are challenged by perspectives that point to the lack of clear boundaries demarcating the organism. The entanglement of the organism with its environment does indeed challenge the attempt to delineate sharp boundaries for the former. Interactions between organism and environment, the latter including many other putative organisms, may directly or indirectly effect the metabolic pathways in various candidate organisms, or may even become parts of those pathways. This challenge is even more pressing for plants than animals, since in addition to having intimate interactions with microbiota, as do animals, they are also modular organisms[14] that have semi-autonomous parts, can grow or

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[14] Of course, this challenge in terms of modularity for the concept of organism can be similar for animals which are modular, such as bryozoans. Godfrey-Smith (2016) compares such modular animals, where each module has its own nervous system and between-module and within-module connections are different, with plants, where this difference is much less marked, due to the "fluid transport in a pipe-like system" through which compounds,

reproduce in many different kinds of ways, and can become clones.

DiFrisco proposes that "physiological individuality is characterized by stable interaction gradients that are present when physiological interactions between parts are stronger or more frequent with each other than they are with parts of the environment" (DiFrisco 2018, 20). On the basis of source-sink balance regulations, we can often distinguish individual plants as physiological individuals on such a criterion. The coordination of plant parts (e.g., regulating source-sink balance) through interactions of many molecules and hormonal networks is stronger and more frequent than interactions with the environment. However, as discussed in the previous section in relation to plant-microbiota interactions involving chemical communication, we sometimes observe physiological individuality conceived in such a way as extending beyond the intuitively apparent physiological boundaries.

Another much-discussed case is the genet,[15] which may consist of many individual-like ramets. A genet is a collection of modules or ramets developed from a single zygote (Clarke 2012) and can be as big as a forest. A famous example is Pando, a quaking aspen clone in the United States (Mitton and Grant 1996). The individual trees are ramets, and the whole clone is the genet. The genet is often considered to be the fundamental biological individual because it is taken to be the unit of evolution, the entity that confronts natural selection. Pando might also be considered as one physiological individual if we are concerned with the interactions between ramets and how they share nutrients and other molecules and how they send and receive signalling molecules between each other and affect each other's physiological processes. Tracing the system through rhizomal connections, or in the absence of these, through the mycelial web and even thereby into other plants, it appears that DiFrisco's criterion provides a boundary that will vary from case to case. Hence it is legitimate, and often appropriate, to consider the genet as one physiological individual for particular research purposes. On the other hand, once again depending on the processes that are under investigation, there may be cases in which it would be better to consider each ramet as one physiological individual.

Suppose we are investigating a volatile signalling molecule in a big genet such as Pando. After the molecule is released, the branches of other trees will receive the signal and plants will respond accordingly. It is likely that this sender-receiver interaction between two ramets which are very close to each other (let's say ramet A and ramet B) is stronger than the interaction with ramet C on the further end of the genet since distance and the environmental parameters such as wind will reduce the density of the signal. So, in an experiment like this, if ramet C appears to be less clearly a part of the system of which ramets A and B are parts than are A and B, it might be better to say that all the ramets are discrete individuals with varying strengths of pairwise interactions.

It is easy to find usages in which both individual ramets and the complete genet are referred to as individuals. For example, the creosote bush (*Larrea tridentata*) grows as a ring of clones moving slowly outwards from an initiating plant. It is sometimes claimed that individuals, the entire circular genet, are the longest living organisms on the planet, with continuous growth processes that stretch back over ten thousand years. On the other hand, individual bushes (ramets) are said to live between 100 and 200 years (Vasek 1980). Here we might draw parallels with classically processual phenomena such as rivers. Sometimes we refer to an entire river system as a single entity, sometimes we distinguish (individuate) various tributaries and a central flow. There is no right answer to a question such as "how many rivers are there in the Amazon

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including hormones, flow.

[15] Oborny calls ramets physiological individuals and genets "individual[s] in the genetic sense" (2019, 3). But better to refer to genets as "the product of a single zygote" since ramets in a genet (even modules in a ramet) may not be genetically identical.

system?" But note that this doesn't mean that divisions are arbitrary and unconstrained. We might, for instance have taken the Missouri to be a river continuous with the lower Mississippi, and the upper Mississippi to be a tributary, but we cannot sensibly take the last 100 miles of the lower Mississippi (going upstream) and the first 100 miles of the Missouri as a candidate for a named river. Similarly, we suggest, for ramets and genets.

4. Plant Individuality and Process

Plant physiology provides us with a useful and naturalistic approach for individuating plants, even though it yields multiple physiological individuals that are distinct but also overlapping. The resolution of any apparent tension between the distinctness and plurality of individual boundaries, we propose, is to take seriously the observation that a growing plant is a process, not a thing, and is necessarily, rather than contingently, dynamic. The dynamic interactions between its parts and with its environment are what sustain the plant, maintaining a complex and coordinated structure capable of continued growth.

Waddington (1957) has provided us with an important distinction between homeostatic processes and homeorhetic processes, the former maintaining a specific structure, the latter maintaining a specific trajectory towards a more or less well-defined final state. In the case of animals, we can generally identify homeostasis with short term survival, dependent on metabolism, broadly construed, and behaviour. Homeorhesis, then, is the maintenance of the organism on an approximately determinate developmental pathway. Although we recognise the importance of developmental plasticity, perhaps its decisive importance from an evolutionary perspective, on the individual time scale, it is reasonable to distinguish a developmental norm and the limits of functional developmental variation. The individual, despite important disagreements about its limits, is what persists through the developmental pathway.

One key to understanding plant individuality is to recognise that plants vary considerably in the extent to which they exhibit a normal developmental pathway. While all plants exhibit homeostasis, homeorhesis is much less clear-cut. Here we must distinguish some rather different life history strategies deployed by plants. For many plants, individuality is not significantly more problematic than it is for animals. Almost all plants probably exhibit greater developmental plasticity than almost all animals, but, nonetheless, there is a reasonably clear developmental norm. The clearest cases are perhaps typical annuals, where a single seed goes through a brief life cycle, producing a number of leaves and flowers. The size, shape and form of the whole may vary dramatically in response to soil, light, and other environmental variables, but many factors, especially at the molecular level, will be fairly reliably produced. Many trees, shrubs and perennial herbs may also fit this general picture on longer time scales.

A second case is exemplified by Pando, and applies to many plants for which much or all reproduction is vegetative, or clonal. The homeostatically stable process is clear enough, but homeorhesis is more obscure. For plants like these, it seems that there is no obvious terminus of the life cycle beyond a kind of growth, but a growth that consists in the multiplication of the entities (trees) that we naturally think of as individuals. The natural way of describing the situation in process-ontological terms is as a homeostatic process (genet) with homeorhetic ramets (trees). Living systems with homeostasis but no homeorhesis are best seen as more or less pure process; it is homeorhesis that is the core characteristic of distinct individuals. The ahomeorhetic process may be considered an individual in the way an epidemic or a biological lineage might.[16] It is a process with a particular origin, and all the parts are connected by

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[16] Dupré (2017) provides a processual interpretation of the Hull-Ghiselin thesis that species (qua lineages) are

a similar kind of causal process. The causal process is sustained by the kind of physiological activities we have described. But familiar individuals, with distinctive life histories, are only to be found as the ramets that emerge from this underlying process.

The degree to which such a plant process generates homeorhetically stabilised ramets, finally, is variable. If we think, for example of the ground elder (*Aegopodium podagraria*), much despised by gardeners, homeorhesis is much less apparent. There are multiple stems emerging from the rhizomal root system, some of which produce flowers. Perhaps the flowering stems look like individuals, but probably no more than individual flowering stems on an individual perennial herb. As we noted at the beginning of this paper, there are plenty of botanical individuals—leaves, flowers, and so on—that are certainly not organism-level individuals, and the flowering stems of *Aegopodium* surely belong among these. The "organism" is closer to pure distributed process, in which the only individual is the whole process. If we think of the whole lineage as a process, then parts of it are not very interesting individuals, as is readily demonstrated by the fact that they can be created simply by careful deployment of a spade, separating a distinct part of the rhizome mass from the whole. Finally, perhaps further down the route to pure process, we can locate many non-vascular plants such as mosses. These, we suggest, are as much individuals as the individual aspens thrown out by Pando, if a lot shorter lived.

5. Conclusion

The individual plant subjects that are coordinated and sustained by physiological activities are highly diverse. In all cases, there is some diffusion of the individual into the environment constituted by its intimate symbiotic connections with the surrounding microbiota. But the extent to which there are well coordinated individuals beyond the whole growing system is highly variable.

The regulation of source-sink balance in interaction with the environment throughout the life cycle is a distinct aspect of self-organisation in plants. This balance is actively achieved and continuously regulated at every stage of development. Plant parts become sources or sinks or both in different stages of their development, and these transitions are strongly dependent on environmental factors. Given their roles in perceiving the environment, coordinating the body through the life cycle, and responding to the environment, it seems reasonable to say that plant hormones, sugar molecules and other signalling molecules (ion channels, second messengers, receptors) constitute a coordinated system. This system helps us to see plants as individual organisms. These organisms have somewhat vague boundaries and they may be parts of clones, and they may be profoundly intertwined with other symbiotic or conspecific individuals. Plant physiology offers us ways to indicate coordinated plant systems (with vague boundaries) at multiple scales. Depending on the context, their physiological individuality can be as a big as a forest or as small as a little module on a branch.

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individuals.

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