



REVIEW

A developmental biologist's journey to rediscover the Zen of plant physiology [version 1; referees: 3 approved]

José R. Dinneny

Department of Plant Biology, Carnegie Institution for Science, 260 Panama Street, Stanford, CA, 94305, USA

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Abstract

Physiology, which is often viewed as a field of study distinct from development, is technically defined as the branch of biology that explores the normal function of living organisms and their parts. Because plants normally develop continuously throughout their life, plant physiology actually encompasses all developmental processes. Viewing plant biology from a physiologist's perspective is an attempt to understand the interconnectedness of development, form, and function in the context of multidimensional complexity in the environment. To meet the needs of an expanding human population and a degrading environment, we must understand the adaptive mechanisms that plants use to acclimate to environmental change, and this will require a more holistic approach than is used by current molecular studies. Grand challenges for studies on plant physiology require a more sophisticated understanding of the environment that plants grow in, which is likely to be at least as complex as the plant itself. Moving the lab to the field and using the field for inspiration in the lab need to be expressly promoted by the community as we work to apply the basic concepts learned through reductionist approaches toward a more integrated and realistic understanding of the plant.

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Corresponding author: José R. Dinneny (jdinneny@carnegiescience.edu)

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From development to physiology and back again

I can remember, as an undergraduate, thinking of plant biology as being divided up into compartments just as the courses I was taking were divided: Physiology, Biochemistry, Genetics, Cell Biology, and Development. Biochemistry dealt with proteins, Genetics genes, Cell Biology cells, and Development the origins of form; but what did Physiology deal with? In our plant physiology course, we learned about hormones, hypocotyls, hydraulics, and the like. The experimental sections of the course were a bit more 'old-fashioned' than others, implementing cores of potato tubers to examine the process of osmosis. Development, on the other hand, was a particularly exciting field at that time. Mutants causing all sorts of surreal changes to the form of the plant were being identified, especially in the flower¹. These pathways fit well into an elementary language of ABCs that is widely conserved across flowering plants². Flower morphology has been used by systematists to classify the diversity of plant families, in part because of the highly stereotypic nature of these structures. Likewise, I think a lot of progress has been made in the molecular understanding of patterning mechanisms controlling flower development, in part because the process is so resilient to environmental cues. Results can easily be reproduced or confidently refuted by other labs, and standard growth conditions, constructed with simple equipment, can be established while accommodating modest budgets.

In graduate school, I followed my dream of studying morphogenesis and my studies identified *JAGGED* and *NUBBIN*, two genes that promoted growth of lateral organs. I hypothesized that these genes regulated organ shape by locally controlling the rate at which tissues differentiate^{3,4}. But what does 'differentiation' actually mean? Developmental biologists often study the outcome of cell-type or organ-type specification pathways by studying the resultant structural features of the cells or tissues. Petals are clearly petals because they develop epidermal cells that are conical and have cuticular ridges, which radiate from the center of the cell¹. But what else, besides structure, might be controlled downstream of these developmental pathways? Could the molecular composition of signaling pathways for environmental stimuli also be differentially regulated in each cell? Surely, a root hair cell would need to express different nutrient transporters than a root endodermal cell. Can development be seen as being integrated into a physiological context? Where did development end and physiology begin?

To address some of these questions, I embarked on a postdoc in the lab of Philip Benfey to determine where physiology and development meet. Recent advances in the use of fluorescence-activated cell sorting enabled cell-type resolution genome-scale transcriptional analyses in plants⁵. The method was being deployed to characterize the steady-state gene expression programs in the root. We had a general belief, not explicitly communicated, that whatever standard environmental conditions we were using to grow our roots, the transcriptional programs we were characterizing represented some sort of ground state. I wondered, however, whether this concept was incorrect and whether environmental conditions had a much deeper influence on cell type-specific transcriptional programs. I addressed this by profiling each tissue layer after the root was exposed to salt stress as a way of perturbing the system

and seeing what changed⁶. With my colleague Terri Long, who generated a similar data set examining the response to iron deprivation, I performed a meta-analysis of the whole data set. Remarkably, the transcriptional programs that defined the functions of specific cell types in the root changed dramatically between conditions even though the expression of cell identity regulators generally did not change. What defined the epidermis was largely dependent on what environment the epidermis was exposed to. Thus, our concept of cell identity, which was based on a ground state, was too simplistic. Cell identity was a context in which environmental change was interpreted, not a fixed state.

Since my postdoc, my group has been interested in understanding environmental responses by using tools that are often associated with studies in developmental biology. The main hypothesis driving this work is that cell type, organ type, and developmental stage influence how an environmental stimulus is interpreted⁷. Context informs environmental response.

Underestimating the plant

I must admit that I had originally underestimated the complexity of environmental stress responses. The first underestimation was in time. Although our initial tissue-specific map analyzed the salt-stress response at a single time point, we now know that the root transitions through a series of strikingly different growth and transcriptional programs over the course of the stress treatment⁸. The second underestimation was in space. Root systems of adult plants are usually composed primarily of lateral root branches. The primary root, though important, essentially provides the foundation for this subsequent development, which is much more extensive and ultimately determines the efficiency with which water and nutrients are absorbed from the soil. I initially assumed that lateral roots would exhibit similar responses as the primary root to salt; however, we were pleasantly surprised that major specialization between root types was apparent in their growth and hormone signaling pathways⁹. The third and most recent underestimation came with the realization that roots are much more keenly aware of the spatial distribution of environmental cues than expected^{10,11}. In Bao *et al.*¹⁰, we described how roots could sense the distribution of available water around the circumference of a single root tip and use this as a cue to bias the patterning of lateral root branches. Discovery of this phenomenon, termed hydropatterning, indicated that even under presumably homogeneous environmental conditions, such as the agar media in a petri dish, roots sense micro-scale differences in water availability to regulate many aspects of plant development likely to influence water and nutrient uptake.

Considering these experiences, I can see that I am likely to continue to underestimate the complexity of the plant-environment interaction. Part of this experience is inherent in the standard reductionist approach to science that is often needed to understand anything with a high degree of certainty. I also think, however, that some level of complacency can be involved. Working in highly controlled environments can be challenging, but nowhere near as challenging as studying plant physiology in the field. I have seen this first-hand as we collaborate with Andrew Leakey at the University of Illinois at Urbana-Champaign on water-deficit responses in *Setaria viridis*.

Field experiments require specialized training and organizational skills to work with large teams of undergraduates and field workers who may be non-scientists. It also requires a longer-term perspective on experiments than is supported through many grants. Although such ecophysiological studies are needed, they need not be a requirement for all research questions. However, every plant biologist should have the experience of digging in the dirt if only to gain inspiration for how to design experiments in the lab that mimic aspects of the field environment¹².

The new development is the old physiology

Development is the process by which form originates, but it is itself influenced by the *a priori* physical state of the organism. If environmental stimuli and physiological states of cells are constantly influencing development, then we see that development is one way that the plant responds to a change in environment and just one aspect of a larger physiological continuum. Form influences function, function provides a context for environmental response, environmental response regulates form, and so on in a cycle I like to call the ‘Zen of plant physiology’ (Figure 1).

These concepts are actually quite well established in physiology, though perhaps not as well appreciated, given that interest in determining molecular mechanisms has taken over much of modern physiology. Researchers such as Paul Green understood that the physical properties of cells in a multicellular system resulted in complex emergent properties at the systems level that influence future events¹³. Green and colleagues found that the orientation of cellulose microfibrils changed as morphogenesis occurred in the meristem and they postulated that resultant stress patterns might influence future organogenesis. Recently, there has been a renaissance in appreciation for concepts initially established by Green¹⁴. In the pursuit of the origins of phylotaxy, the pattern by which new organ primordia initiate at the shoot apex, a realization that biophysical properties of tissues may play more than a permissive role in the process is becoming apparent¹⁵.

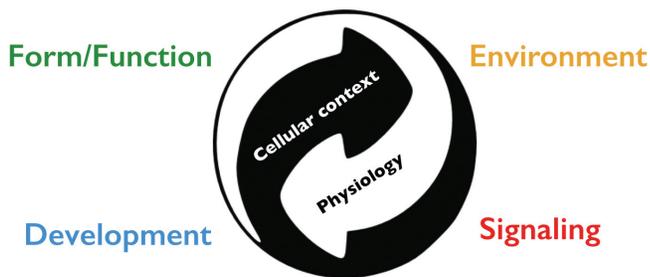


Figure 1. The Zen of plant physiology. The environment is sensed by the plant and leads to changes in the activity of signaling pathways that influence developmental decisions. Development determines the form of the organism and the function of cells that are specified and organized in tissues and organs. Shape, biophysical properties, and sensory pathways are controlled downstream of development and influence how future environmental change is experienced and responded to by the plant. Continuous development throughout the lifecycle of the plant results in a dynamic physiological state that influences, and is influenced by, development and the environment.

Meeting future challenges through an integrative understanding of the plant

The classic physiological concept, of the organism as an integrated system, needs to be resurrected as a guide to modern molecular studies of mechanism. The need for such a perspective becomes obvious when considering how water-deficit responses are often studied. Agar-based media are poorly suited to mimic water deficit in a realistic way. Shoots are typically enclosed in a high-humidity environment that does not allow adaptive responses involving changes in stomatal aperture to conserve water. As soil dries, many physical changes occur that increase osmolarity, air space, and impedance to root growth¹⁶. Only osmolarity can be easily modified in gel-based media. Furthermore, heat often co-occurs with water deficit during droughts, and recent work suggests that plants may use temperature as a proxy for monitoring drought¹⁷. Currently, we are developing an integrated growth-and-imaging system that allows root structure and gene expression to be simultaneously imaged in soil-grown roots¹⁸. Our efforts are aimed at developing a system that preserves many aspects of plant growth in the field while being amenable to studying the mechanisms controlling changes in root growth.

Our imaging system currently uses standard potting mix as the ‘soil-like’ media, and this is certainly another oversimplification of the diverse array of soil types that exist in nature and we will have to address this in the future as well. It is important to realize that the environmental conditions that plants experience have multidimensional complexity that matches or exceeds the complexity of the plant itself. The interface between plant and environment is multifaceted and we need to think of novel ways to characterize this interface. Microbiome studies of root- and shoot-associated microbial populations are an important start^{19–21}. It may be possible to enlist the help of microbes and plant cells themselves in the effort to characterize the environmental inputs that plants experience. Development of chemical and physical biosensors will help in this regard as will determining the exact molecular mechanisms that plants use to sense the various environmental cues that are critical for their survival^{22,23}.

The next decade in plant physiology looks extremely exciting and challenging. As classic non-model species become easier to explore at the molecular level, the design of growth and phenotyping platforms for these species will become ever more important to place these fine-scale measurements in context. *Arabidopsis* is small and easy to grow, whereas crops usually require special growth facilities with adequate lighting and nutrients. Larger organs that lack optical transparency prevent many of the standard microscopy methods used in model species.

Two paradigms are currently being established regarding plant phenotyping and they diverge in their approach to solving the cost-versus-throughput challenge. LemnaTec and others are developing plant growth and imaging platforms that move plants on conveyor systems to deliver hundreds of individuals to stations where watering, treatments, and imaging are performed automatically^{24,25}. Alternative approaches using low-cost equipment such as flat-bed scanners or modified cell-phone cameras deployed *en mass* allow phenotype-genotype relationships to be explored at a small fraction of the cost^{26,27}. Cost and physiological relevance need to be balanced, however, if the data obtained are aimed at identifying allelic

variants that affect adaptive responses. Simulating environmental conditions is an art that needs further attention. How precise must lighting, temperature, and soil conditions be to fool the plant into responding to environmental stimuli as they occur in nature? If we are not mindful of the plant environment we study, we may find that, in the end, we have only been fooling ourselves.

Competing interests

The author declares that he has no competing interests.

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Jan Traas

Laboratory of Plant Reproduction and Development, École Normale Supérieure de Lyon, 46 Allée d'Italie, Lyon, 69364 Cedex 07, France

I have read this submission. I believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard.

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David Salt

Institute of Biological and Environmental Sciences, University of Aberdeen, Cruickshank Building St Machar Drive, Aberdeen, AB24 3UU, UK

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Christophe Maurel

Biochemistry and Plant Molecular Physiology Division, Campus INRA, CNRS, Montpellier, cedex 2, 34060, France

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