

THEMATIC ARTICLES

Computer Modeling of Plant Development

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Plant morphology is visually particularly attractive. Perhaps this is not surprising given the geometrical and often symmetrical shapes and patterns associated with plant structure. Whether it is the polyhedral shape of individual cells, the symmetry of phyllotaxis, or the fractal nature of branching patterns, plant structures seem to hint at underlying biological mechanisms that may be especially amenable to mathematical analysis. Hence plant architecture has long inspired a mathematical approach to understanding its developmental origins. What is particularly exciting at present is that this approach is now being augmented both by a rapidly growing body of molecular biological knowledge as well as by cheap and powerful computational power. This issue of *Journal of Plant Growth Regulation* reflects the current synergism by presenting a collection of five articles that discuss and present new analyses of various aspects of plant development using computer modeling.

The issue starts with a perspective paper by a physicist who has helped pioneer the modeling of gene regulatory circuits, especially in *Drosophila* development. Eric Mjolsness places the problem of

development in the broader context of dynamical systems and suggests ways in which various mathematical tools previously developed for problems in the physical and computer sciences may be newly applied in the biological context. According to Mjolsness, the full complexity of development, from protein–protein interactions, to cell mechanics and divisions, to tissue-level interactions, can be described by a single language or grammar. The development of such a dynamical grammar could then facilitate the integration of modeling at different levels, simplify analysis, and facilitate model exchange between researchers.

Chaos and others focus on how genes control organ type patterning of the flower. Drawing on the wealth of experimental data available enabled these investigators to construct a network consisting of 15 genes. Simplifying gene output to either “on” or “off,” they find that out of a possible 2^{15} network states (each network state being a unique combination of gene outputs), only 10 different states are stable, and these stable states correspond to the combinations of gene activity that are observed in different whorls of the flower and in the inflorescence meristem. In their study, Chaos and others also show how the reduction from a three-state model recently presented to the two-state model introduced here still

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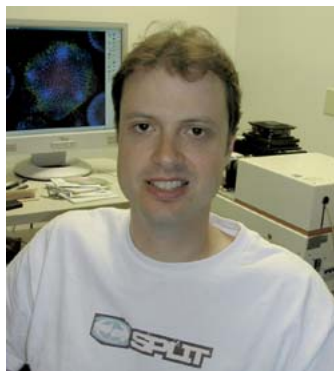


Figure 1. Marcus G. Heisler, guest editor.

results in similar behavior, hinting at the robustness of the outcome for this experimentally derived network architecture. Finally, nice examples of model predictions that have been verified by experiments are discussed.

Two articles in this issue discuss the importance of the hormone auxin in plant development. In the contribution by Eric M. Kramer, its potential role in wood grain pattern formation is reviewed and a model is presented to explain how complex large-scale patterns can be obtained from local interactions. The model is based on the influence of auxin flux on wood fiber orientation and builds on earlier work by the author. In this contribution Kramer shows how the model is capable of simulating the gradual changes in fiber orientation often observed after wounding, including the formation of whirled wood grain patterns in regions where there are sudden changes in grain alignment. Last, a critique of an alternative theory for wood grain patterning based on physical stress patterns is also presented.

In the article by Marcus G. Heisler and Henrik Jönsson the role of auxin influx carriers is discussed in the context of auxin transport in the shoot apical meristem (Figures 1 and 2). In particular, the authors review the development of the chemiosmotic theory, and they focus on possible mechanisms controlling the polarity of auxin transport proteins according to feedback from local auxin concentrations or fluxes. New simulations applied to the shoot apical meristem suggest that auxin influx carriers are important for keeping the auxin in the epidermal layer, as has been previously proposed, as well as for stabilizing large-scale auxin patterns within the epidermis, which is important in the context of auxin-based phyllotaxis models.

Finally, Scott Hotton and others compare the phyllotactic patterns of sunflower and artichoke to those generated by a simple geometric model based



Figure 2. Henrik Jönsson, guest editor.

on available space. A previously developed methodology is used to characterize the meristem surface over time to accurately monitor the development and location of primordia. The extracted primordial positions are then compared to the positions of primordia predicted by the model. An interesting and important aspect of this work is the introduction of the ontogenetic graph as central for describing a pattern. In contrast to commonly used descriptors such as divergence angle or a predefined lattice, the ontogenetic graph enables patterns to be extracted locally and more robustly for more accurate comparisons to model outputs.

It is an interesting time for the field of developmental biology. Experimental tools enable the quantification of morphology and protein expression data at cellular resolution over time. How do we digest all these data? Are we going to be able to intuitively understand the multitude of feedback loops and non-linear behavior of the molecular mechanisms underlying growth and differentiation? Are our commonly used arrow diagrams going to be adequate? As the articles in this issue demonstrate, computer simulations of mathematically defined models help us to tackle these challenges in a number of ways. First, we can state our hypotheses explicitly. Often this leads to a much more careful consideration of the problem at hand. Second, computer simulations enable researchers to play out the consequences of their hypotheses when it may be difficult to do so experimentally. Many times, simulations can lead to unexpected behaviors, forcing a reconsideration of the model's assumptions. This may then lead to the conclusion that small details have important consequences, or conversely, that the model can be simplified to enable the investigator to concentrate on just a few key players. From our experience, this type of analysis helps to obtain a better intuitive understanding of the problem, which then leads to new

hypotheses, and these, in turn, lead to new experiments.

Often, to pursue this approach requires multidisciplinary collaborations, as can be seen in this special issue, where biologists, physicists, computer

scientists, and mathematicians are all contributing authors. We hope the synergism between modelers and experimental plant biologists continues, and that more opportunities arise for those lucky few who can do both!