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Modeling plant growth and development

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Computational plant models or 'virtual plants' are increasingly seen as a useful tool for comprehending complex relationships between gene function, plant physiology, plant development, and the resulting plant form. The theory of L-systems, which was introduced by Lindemayer in 1968, has led to a well-established methodology for simulating the branching architecture of plants. Many current architectural models provide insights into the mechanisms of plant development by incorporating physiological processes, such as the transport and allocation of carbon. Other models aim at elucidating the geometry of plant organs, including flower petals and apical meristems, and are beginning to address the relationship between patterns of gene expression and the resulting plant form.

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Introduction

The term 'model' has many meanings in biology. Representative organisms are commonly referred to as model organisms, qualitative hypotheses are referred to as models, and the statistical analysis of experimental data is referred to as modeling. In this review, we consider mathematical models, in which the system under study is described using mathematical formulae. In particular, we look at spatial models of plants, which take plant form into account.

Spatial models may treat plant geometry as a continuum (which is particularly justified in the description of individual organs, such as leaves or petals) or as an arrangement of discrete components (also called modules) in space. In the latter case, the definition of components depends on the level of plant organization at which a study is carried out. Frequently used components include individual cells, architectural modules (e.g. internodes, buds, apices, leaves, and flowers), and whole plants in the case of ecological models. The models may be static, capturing plant form at a particular point in time, or

developmental, describing the form as a result of growth. Developmental models may in turn be descriptive (or reconstructive), integrating the results of measurements of form over time, or mechanistic, attempting to elucidate the development of form in terms of the underlying biological, chemical, and physical processes.

Developmental models are commonly explored using computational or simulation techniques. The simulation software may be general-purpose, intended to capture a variety of developmental processes depending on the input files, or special-purpose, intended to capture a specific phenomenon. Input data range from a few parameters in models capturing a fundamental mechanism to thousands of measurements in calibrated descriptive models of specific plants (species or individuals). Standard numerical outputs (i.e. numbers or plots) may be complemented by computer-generated images and animations.

There is as yet no consensus regarding the value of computational models in developmental biology. Opinions diverge on the most fundamental issues, such as the role of theory in biological understanding, the usefulness of applying chains of mathematical deductions to biological data, and the appropriateness of transplanting research methodologies from physics to biology [1]. Nevertheless, numerous position statements (e.g. [2,3,4]) foresee the use of modeling and simulations as an increasingly important component of plant biology.

Several key benefits have been attributed to the use of computational models. First, they can provide a quantitative understanding of developmental mechanisms when qualitative descriptions are fundamentally inadequate. For example, computational models can assist in the analysis of genetic regulatory mechanisms, characterize phyllotactic patterns, or provide a detailed description of growth dynamics. Second, models might lead to a synthetic (i.e. systemic or integrative) understanding of the interplay between various aspects of development, such as genetic regulation, physiological processes, environmental influences, and the development of the whole plant. And third, the use of computational models can identify areas of ignorance and guide further empirical research.

Adrian Bell, one of the pioneers of plant modeling, summarily characterized these benefits as follows [5]:

“The very process of constructing computer simulations to reproduce a particular branching structure can be a useful experience in its own right, even without proceeding to the use of such a simulation to test an hypothesis. Either the mor-

phology of the organism must be recorded in considerable detail or the underlying features of its developmental architecture fully appreciated. . . Shortcomings of the model will soon become apparent as 'mistakes'."

The models considered in this review have been organized into three classes: models of plant architecture, models of organs and tissues, and models incorporating genetic regulatory networks. The separation between the first two classes reflects the different mathematical structures of the models. This difference is related to the properties of three-dimensional space: the arrangement of components of a branching structure brings about problems that are different to those presented by the arrangement of components that extend over areas or volumes (e.g. cells in a tissue must properly fit without gaps or overlaps). From a practical perspective, architectural models have often been motivated by their prospective applications to forestry, agriculture, or horticulture, whereas models of plant organs have been motivated by more fundamental questions of biological development. The emerging class of models that incorporate genetic regulatory networks is treated separately because of yet another modeling methodology and origin, which are related to the modeling of processes within individual cells.

Models of plant architecture

Models of plant architecture are based on the ecological concept of a plant as a population of semi-autonomous modules, and describe a growing plant as an integration of the activities of these modules [6,7]. The mathematical basis for architectural plant modeling is most explicitly articulated in the theory of L-systems [8–10]. L-systems harness the complexity of a multicellular organism by dividing modules into types. All modules of the same type share the same description (i.e. behave according to the same algorithm), irrespective of the number of occurrences of a given module type within the whole structure. This makes it possible to keep model specifications concise, even if the simulations eventually yield extensive structures that are made of a large number of modules. Modules of the same type may have diverse behaviors due to different states (i.e. values of variables that are associated with the modules) and to signaling between the modules. The convenience of expressing signaling in dynamically changing branching structures (using so-called context-sensitive productions) is an essential feature of L-systems. An example is the use of context sensitivity in the simulation of the branching pattern and flowering sequence of *Mycelis muralis* [9]. The model incorporates an acropetal flower-inducing signal and a basipetal signal that lifts apical dominance. Extensions of L-systems also make it possible to capture interactions between modules that are mediated by the environment, such as the competition of tree branches for light or root subsystems for water in the soil [11,12].

A distinctive feature of L-systems is that they give rise to a class of programming languages for specifying the models. This makes it possible to construct generic simulation software that is capable of modeling a large variety of plants, plant parts, and processes in plants at the architectural level, given their specifications in an L-system-based language [9,13,14]. Entire model specifications, as well as model parameters, can easily be manipulated in simulated experiments, providing answers to a variety of 'what if'-type questions.

Although other architectural models are not explicitly expressed using L-systems, they share the underlying philosophy of describing a growing branching structure in terms of the activities of individual plant modules. The available software includes both packages intended for modeling a wide range of plants, structures and phenomena, such as AMAP [15] and LIGNUM [16], and specialized programs. The convergence of approaches is reflected in successful conversions of models between different modeling packages (e.g. [11,12]).

Architectural models range from the description of entire plants, in isolation or within an ecological context, to models of plant parts, such as the individual branches of a shoot or root system, inflorescences, or compound leaves. Descriptive models can have inspiring applications (e.g. reenacting the development of extinct plants [17] or recreating the form of plant mutants [18]), but mechanistic models provide more insight into the way that plants function. These latter models are referred to as virtual plants [2] or functional–structural models [19].

The concept of functional–structural modeling is well illustrated by the model of root growth coupled with the transport and partitioning of carbon proposed by Bidel *et al.* [20]. This model consists of a source of assimilates, summarily representing the shoot, connected to a growing branching structure that represents the root. The root axes are divided into segments that have defined transport and sink properties. Each axis is terminated by an apical meristem. The meristems produce segments of variable length depending on the amount of available assimilates. A review of other root models is presented in [21^{*}], and of carbon-based tree models in [22].

Many other physiological or physical processes can also be treated as the transport of some entities throughout plant structure. For example, Früh and Kurth [23] created a model of water transport in trees that was intended for the use in functional–structural tree models. Alméras *et al.* [24] and Fourcaud and colleagues [25^{*},26] captured the mechanical influence of branch weight and tropisms on the shape of developing tree branches. Soler *et al.* [27^{*}] developed an efficient model of radiant energy transfer in tree canopies. These developments make the incorporation of individual physiological or biomechanical

processes into functional–structural models relatively routine, yet the construction of comprehensive models, which combine several of these processes, remains a challenge. A technique for reducing the complexity of functional–structural models was explored by Hanan and Hearn [28], who coupled an essentially descriptive model of cotton architecture with a physiologically based non-spatial (crop-level) model.

Models of organs and tissues

Although plant architecture is commonly treated in a modular fashion, the choice between discrete and continuous descriptions of tissues (which form surfaces or volumes) is less obvious. Both approaches, as well as their combinations, are used. These approaches echo two competing views of the relation of cells to an organism: ‘cells make an organism’ and ‘an organism makes cells’. The emphasis on cells as the building block calls for a discrete model. Emphasis on an organism, on the other hand, makes it possible to treat tissues in a continuous fashion, either abstracting from their cellular composition or treating cellular patterns as an effect of higher-level processes. The concurrent use of both approaches also reflects the fact that models of growing surfaces and volumes are mathematically more complicated than models of linear and branching structures, and definitive modeling methods are yet to emerge.

In the discrete approach, the simulation software must manage structural changes that occur in a system described as a growing assembly of modules. For example, when a cell divides, the state variables that characterize the parent cell are no longer part of the description of the whole system and must be removed; the state variables that characterize the daughter cells must be inserted; and the set of equations that relate all of these variables must be updated, taking into account the position of the new cells with respect to their neighbors in the structure. Parametric L-systems [9] offer a solution to these problems for filamentous and branching structures, but extensions of L-systems to surfaces [29] and volumes are still inconclusive. However, fundamental research on the modeling of developing systems that are not restricted to branching configurations is underway [30].

In the continuous approach, the tissue is treated as a whole without division into components (at least conceptually; division may be imposed by numerical methods used to implement the models). The problem of dealing with the dynamically changing arrangement of modules is thus avoided. The fundamental notion for describing growth in continuous terms is the strain tensor, a notion defined in the mechanics of continuous media to characterize local expansion or contraction of a material in various directions. Local growth directly affects the local (Gaussian) curvature of surfaces, and causes global changes to the shape of surfaces and volumes. Accordingly,

physical experiments, mathematical analyses and computer simulations have demonstrated that the wrinkled shapes of leaves and petals can be produced as emergent phenomena due to differential growth, without direct genetic control [31]. In a more specific biological setting, experiments and a combined continuous-discrete reconstructive model have been used to show how local growth rates determine the global shape of developing *Antirrhinum* petals [32]. Simulations made it possible to discern the key developmental parameters that determine this shape. A reconstructive model has also been employed to evaluate the surface growth (strain) rates and curvatures of a growing *Anagallis arvensis* vegetative shoot apex [33]. A combination of a continuous growth model with a discrete model of cell division has led to a simulation of cell division patterns in a generic shoot apex [34].

Models incorporating genetic regulatory networks

Within the bounds of geometric and mechanical constraints, developmental patterns and forms are, in the final account, determined by genes. Pursuing this relationship, Mendoza and Alvarez-Buylla [35] integrated numerous experimental data into a regulatory network of 11 genes that control the shoot branching pattern and switch to flowering in *Arabidopsis*. The network was described as a logic circuit, analogous to those found in computers. Simulations showed that it had several stable states, which could be associated with different cellular fates in flower morphogenesis. Subsequently, the same authors applied a similar formalism to capture the regulatory pathways underlying the differentiation of *Arabidopsis* root hairs [36]. Neither model, however, was incorporated into a developing spatial structure.

As the methodologies for modeling individual cells [37,38] are being extended to the modeling of multicellular structures [39,40], the first applications of these extended methodologies to plants are beginning to appear. In a study of the *Arabidopsis* shoot apical meristem [41], the objective was to explain the mechanism by which the expression zones of three key genes, *CLAVATA1*, *CLAVATA3* and *WUSCHEL*, are maintained in the apex. The three-dimensional model captures the self-organization of the *CLAVATA1* and *CLAVATA3* expression zones, assuming that *WUSCHEL* is expressed in its known region. This model treats the apex as a static structure. A related model [42] is the first step towards capturing the dynamic structure of the apex. It takes into consideration both cell divisions and displacement within the apex. In this case, however, only the two-dimensional, longitudinal section of the apex was modeled, and the results do not yet exhibit the stability of the apical structure characteristic of real meristems. In both the three-dimensional and the two-dimensional models, the regulatory network was captured using differential equations that combine the effects of gene regulation and

cell–cell signaling. The simulations were implemented using the Cellerator software [39].

Conclusions

The methodology for modeling plant development at the architectural level, taking into account diverse physiological processes and ecological interactions between plants, is already well established. Several modeling packages exist, and advanced architectural models are routinely presented in the literature. These models are often created with practical applications to forestry, agriculture and horticulture in mind.

The introduction of mathematical modeling and computer simulations as a research methodology in fundamental plant biology is a new phenomenon. A combination of established models that operate at the architectural level with emerging models that operate at the tissue and molecular levels may produce rapid advancements in modeling methodology. The increased availability of detailed data resulting from genomic studies, complemented by the construction of models that incorporate these data, may lead to an in-depth understanding of the mechanisms of plant development from genes to phenotypes. In the meantime, computational modeling of plants is becoming a fascinating area of interdisciplinary research.

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