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PREFACE: PART OF A SPECIAL ISSUE ON FUNCTIONAL–STRUCTURAL PLANT MODELLING

Functional–structural plant models: a growing paradigm for plant studies

Risto Sievänen[1],*, Christophe Godin[2], Theodore M. DeJong[3] and Eero Nikinmaa[4]

[1]*Finnish Forest Research Institute, Vantaa Research Unit, P.O. Box 18, Vantaa 01301, Finland,* [2]*INRIA, UMR AGAP, C.C. 06002, 95 rue de la Galéra, 34095 Montpellier, Cedex 5, France,* [3]*Plant Sciences, University of California, Davis, One Shields Ave, Davis, CA 95616, USA and* [4]*Department of Forest Sciences, University of Helsinki, P.O.Box 27, Helsinki 00014, Finland*
* For correspondence. E-mail risto.sievanen@metla.fi

A number of research groups in various areas of plant biology as well as computer science and applied mathematics have addressed modelling the spatiotemporal dynamics of growth and development of plants. This has resulted in development of functional–structural plant models (FSPMs). In FSPMs, the plant structure is always explicitly represented in terms of a network of elementary units. In this respect, FSPMs are different from more abstract models in which a simplified representation of the plant structure is frequently used (e.g. spatial density of leaves, total biomass, etc.). This key feature makes it possible to build modular models and creates avenues for efficient exchange of model components and experimental data. They are being used to deal with the complex 3-D structure of plants and to simulate growth and development occurring at spatial scales from cells to forest areas, and temporal scales from seconds to decades and many plant generations. The plant types studied also cover a broad spectrum, from algae to trees. This special issue of *Annals of Botany* features selected papers on FSPM topics such as models of morphological development, models of physical and biological processes, integrated models predicting dynamics of plants and plant communities, modelling platforms, methods for acquiring the 3-D structures of plants using automated measurements, and practical applications for agronomic purposes.

Key words: Functional–structural plant model, plant modelling, modular plant architecture, resource acquisition and partitioning, simulation.

BACKGROUND

As developmental structures, plants have always attracted human interest. Pioneered by the early example of Leonardo da Vinci's studies of trees (cited by Zimmermann, 1983), the quest has been to understand the mechanisms that produce such remarkable biological structures and their magnificent diversity in response to different environments (Prusinkiewicz and Runions, 2012). Evolving plant structures result from a complex interaction of environment, physiology, developmental processes and genes operating at different scales of space and time. Such complexity presents stimulating challenges for experimental and model-based studies, but also offers considerable potential for tackling current challenges faced by society (e.g. anticipating climate change, food and energy production for the planet, sustainability of the environment).

This complexity has been tackled in the various branches of plant science within the contexts of their specific methods. These pursuits have produced a wealth of research about the spatial–temporal dynamics of plants, e.g. in botanical, agricultural and ecological forestry contexts. As a part of, and in addition to, studies in specific disciplines, the consideration of plant development as a result of the interaction of their structural and functional properties, irrespective of the scale considered and object of interest, has become a discipline of study in its own right (Fourcaud *et al.*, 2008; DeJong *et al.*, 2011). One goal has been – at least partly – lead by a fundamental and overarching question: do similar models and rules of development apply across scales and between types of plants? Over the last 20 years, this has raised important methodological questions, such as how to combine credible representations of 3-D plant structures with realistic considerations of metabolic/physiological mechanisms in computational models, how to measure plant architectures and how to assess model results (Le Roux and Sinoquet, 2000; Godin and Sinoquet, 2005, Hanan and Prusinkiewicz, 2008). Several research groups in various areas such as agricultural science, horticulture, forest ecology and remote sensing have addressed these problems. They also have engaged the interest of computer scientists and applied mathematicians, who have had to develop new methods for building these models. This has resulted in the development of functional–structural plant models (FSPMs; Godin and Sinoquet, 2005).

One unifying feature of FSPMs is the consideration of the plant as consisting of a number of elementary units, for example axes, growth units and metamers (node, internode, leaf and axillary bud; Room and Hanan, 1996; Sievänen *et al.*, 2000). These representations can be used in a straightforward way to model many facets of plants (e.g. growth, architecture, physiological and transport processes) or the distribution of physical quantities of environmental inputs to plants (e.g. canopy light or temperature distribution). In FSPMs, the plant structure is always explicitly represented in terms of a network of elementary units. In this respect, FSPMs are different from more abstract models in which a simplified representation of the plant structure is frequently used (spatial density of leaves, total biomass, etc.). This key feature makes it possible to build modular models and creates avenues for efficient exchange of model components and experimental data.

A representative sample of previous research into FSPMs and related topics can be found in special issues of *Silva Fennica* [**31(3)**, 1997], *Annals of Forest Science* [**57(5/6)**, 2000], *New Phytologist* [**166(3)**, 2005], *Functional Plant Biology* [**35(9/10)**, 2008] and *Annals of Botany* [**101(8)**, 2008; **107(5)**, 2011; and **108(6)**, 2011].

Due to their multidisciplinary character, FSPMs are very diverse. However, based on the main purpose of the models, their topics can be divided into a number of broad categories that highlight different axes of FSPM investigations.

Morphological models. These focus on the structure of the plant (plant architecture). The emphasis may be on plant structures in terms of the organization of their elementary units or their dynamics.

Models of physical and biological processes. Within FSPMs these include radiation distribution within canopies, soil–plant water flow and transport, photosynthetic production, transpiration, respiration, carbon allocation, nutrient distribution, bud outgrowths, plant water status, biomechanics of organ growth, hormone transport, and morphogenesis at the meristem level. Typically, many models combine two or more processes, for example dynamics of water and carbon uptake and distribution in a plant.

Integrated models. These predict the dynamics of a plant or plant community. They may include models of agricultural crops, greenhouse crops, orchard and forest trees or tree stands. The rules of development vary from descriptive, based on stochastic processes, or mixtures of conceptual, process-based or self-organization, based on the concepts of competition and process locality.

Formal languages and modeling platforms. Several formal languages have been developed and implemented to facilitate the development of FSPMs. Most of them are based on L-systems formalisms and their extensions (Prusinkiewicz and Lindenmayer, 1990; Prusinkiewicz, 2004b). The multiscale tree graph (MTG) formalism (Godin and Caraglio, 1998) makes it possible to represent plant architecture in a generic and unified way. Several modelling platforms are available, which facilitate efficient assembling of FSPMs and make it possible to utilize component models from various sources, and to analyse the results of simulations.

Methods and dedicated software components for acquiring the 3-D structures of plants using automated measurements. Previously magnetic and sonic digitizer were used for developing 3-D images of plants: today laser scanners are the prominent tools.

Methods to fit/validate FSPMs. Statistical methods and software to deal with 3-D spatial–temporal data and model responses are being developed and tested.

Practical applications. As FSPM research matures there are an increasing number of models being developed for practical applications.

THIS ISSUE

This Special Issue highlights new advances within the field of the FSPMs and features 22 papers, covering spatial scales from cells to forest areas, and temporal scales from seconds to decades and many plant generations. We discuss them here briefly in terms of the categories of FSPM research listed above.

Morphological models

The early work in this research topic concentrated on modelling and methods to describe branching structures in plants (e.g. Prusinkiewicz, 1998; Godin *et al.*, 1999). Since the early 2000s the emphasis has been increasingly directed towards models and computational techniques for the description of growing spatial structures, especially cellular patterns (Prusinkiewicz and Runions, 2012).

The contributions within this issue in the area of morphological modelling belong to the latter category. Abera *et al.* (2014) formulate a generic model that can account for both symmetrically and asymmetrically dividing cells with isotropic and anisotropic growth. The cells are modelled as closed, thin-walled structures that maintain tension by turgor pressure. The model can produce tissues that have different topological and geometrical properties, and it will be useful for *in silico* investigations of plant cell division. Cartenì *et al.* (2014) study formation of vascular tissues in growing plant stems. They present a spatially explicit reaction–diffusion model defining a set of logical and functional rules to simulate the differentiation of procambium, phloem and xylem and their spatial and temporal patterns from a group of undifferentiated cells. This shows that common genetic–molecular machinery can create different spatial patterns of plant vascular development. The model can be used to test different hypotheses of genetic and molecular interactions involved in the development of vascular tissues. Dale *et al.* (2014) focus on the surface of plant stems: they present a dynamic model of grasstree development that captures both phyllotactic patterns of leaf bases during primary growth and the changes in the trunk's width during secondary growth. A biomechanical model component simulates emergence of fractures during expansion of stem girth. The model produces similar fracture patterns as those seen in real trees, supporting the hypothesis that bark pattern formation is primarily a biomechanical phenomenon.

Models of physical and biological processes

The explicit representation of the plant structure in terms of a network of elementary units makes it possible to model plant-level processes at high levels of structural detail. However, such accurate spatial resolution poses challenges to the mathematical methods that are being used in implementing the models.

Partitioning of resources as a result of long-distance carbon transport of substrates has been a challenging topic for FSPMs (Minchin and Lacointe, 2005). Da Silva *et al.* (2014b) extend the L-PEACH model's sink–source formulation of transport of non-structural carbohydrates with carbohydrate storage, and test it with the aid of field data. They are able to successfully simulate annual dynamics of transport and storage of carbohydrates as a function of the collective capacity of active xylem and phloem tissues of peach trees. This shows that sink–source formalism is a suitable conceptual and functional framework for simulating annual long-term carbohydrate storage and mobilization in FSPMs of trees. The results of Nikinmaa *et al.* (2014) in

part corroborate this claim: they apply a model that combines phloem transport based on the Münch hypothesis with a cohesion–tension approach of xylem transport and gas exchange in a realistic 3-D crown of Scots pine. The simulations produce the observed patterns of pressure gradient and sugar concentration and show how diurnal variations of environmental conditions influence tree-level gradients of turgor pressure and sugar concentration. Vandegehuchte *et al.* (2014) explain totally different patterns in daily stem diameter variations in two co-occurring mangrove species using *in situ* measurements and a mechanistic water flow and storage model based on the cohesion–tension theory. The analysis reveals that carbon-driven osmotic adaptation of storage tissue water potential is an important driver determining different stem diameter variation patterns in mangrove. The models of Vandegehuchte *et al.* (2014) and Nikinmaa *et al.* (2014) show how endogenous factors combined with environmental factors influence the diurnal course of growth processes in trees.

FSPM research has produced methods to measure and generate detailed architectural structures of plants. They can be used as mock-ups in the applications of various models and thus virtually remove the error caused by using a simplified representation of the plant structure (Dauzat *et al.*, 2001). Studies by Chen *et al.* (2014), Stenberg *et al.* (2014) and Yang *et al.* (2014) follow this path. Chen *et al.* (2014) use accurate radiation and photosynthesis models to evaluate the importance of different limiting factors of photosynthesis in virtual 3-D canopies constructed using digitized cucumber plant data. They conclude that biochemical and light limitations are the most prominent ones and that diffusional limitations (stomatal and mesophyll) only contribute less than 15 %. This approach can be expected to provide insights into the influences of horticultural practices on canopy photosynthesis and the design of optimal crop canopies. Stenberg *et al.* (2014) study crown clumping (defined as crown silhouette to total needle area ratio) of Scots pine trees, using virtual trees that closely resemble real ones in forests. Crown clumping is independent of height, needle area and growth conditions. As a result, variation in the whole-stand clumping index can be expected to depend on the spatial pattern of trees rather than on changes in the degree of self-shading within individual crowns. Yang *et al.* (2014) provide the first model of the tree anchorage strength (applied to *Pinus pinaster*) derived from the mechanical strength of individual roots. Simulations of tree-pulling tests compare well with measurements and exhibit realistic successive root breakages during uprooting. Broken roots can be visually located within the 3-D root system in the user interface of the model. This generic model is expected to provide useful information, for example on underground responses in landscape wind-risk models.

The study of Defraeye *et al.* (2014) shows how increasing spatial detail can on the one hand reveal deficiencies in spatially averaging models, and on the other hand increase the requirements of computational methods. They analyse boundary-layer conductance of a leaf with a 3-D model of computational fluid dynamics for convective mass transport using fine spatial resolution that allows the modelling individual stomata explicitly. Boundary-layer conductance is strongly dependent on stomatal surface coverage and air speed. Simulations show that existing measures of conductances (e.g. from artificial leaves) can be significantly erroneous because they do not account for microscopic stomata. The output of this model can be used to correct or upgrade existing higher-scale models of boundary-layer conductance.

Integrated models

Since integrated models (FSPMs) capture the spatial arrangement of plant components and their development over time, they are inherently complex. Both morphological development and material balance (metabolism), and their interaction (over time), need to be specified. These complex models make it possible to study complex issues *in silico*, such as whether plant ideotypes or optimal life history strategies exist for specific sets of conditions (Barillot *et al.*, 2014; Da Silva *et al.* 2014*a*; Guillemot *et al.*, 2014; Renton and Poot; 2014, Zhu *et al.*, 2014).

Barillot *et al.* (2014) modify a FSPM for wheat for use with pea by restructuring modules for morphogenesis, vegetative development and organ extension. They study partitioning of light in crop mixtures of wheat and pea in the different phases of growth. Light capture is mainly related to the architectural traits involved with LAI during the early growth stages of development, and in plant height in later stages. This shows that plant architecture is an important criterion for the identification/breeding of plant ideotypes, particularly with respect to light partitioning. Da Silva *et al.* (2014*a*) study the effect of combinations of growth traits (organ geometry and branching habit) on light interception of growing apple trees. The simulations establish connections between growth traits and development of leaf area and light interception efficiency, and the results demonstrate that FSPMs could contribute to screening architectural traits and their relative impact on fruit tree performance. The approach opens up new perspectives for breeding and genetic selection to be assisted by *in silico* ideotype definition. Zhu *et al.* (2014) construct a FSPM of maize development that employs three co-ordination rules between leaf emergence events and the dynamics of organ extension. It gives a good account of the timing and duration of organ extension against experimental data. This shows that a set of simple rules for co-ordinated growth of organs is sufficient to simulate the development of the maize plant structure without taking into account any regulation by assimilates.

Renton and Poot (2014) use a FSPM for dynamics of water uptake and structural growth in evolutionary optimization in order to evaluate structural development strategies of perennial species on shallow soils in seasonally dry environments. They apply two contrasting fitness criteria: the ability to find wet cracks in underlying rock, and the maximizing above-ground biomass. Simulated evolution selects for root system morphologies that are specialized to the habitat, matching those of real species from corresponding habitats.

Guillemot *et al.* (2014) demonstrate the benefits of improving the architectural description of a process-based forest growth model by combining a stand structure module to the growth model. The resulting new model helps to identify the areas where management efforts should be concentrated in order to mitigate near-future drought impact on national forest productivity.

Formal languages and modelling platforms

The specialized software packages available for building FSPMs ease model construction (e.g. Virtual Laboratory and

L-studio, Prusinkiewicz, 2004*a*; GroIMP, Hemmerling *et al.*, 2008; OpenAlea, Pradal *et al.*, 2008; L-Py, Boudon *et al.*, 2012; AMAPstudio, Griffon and Coligny, 2014). They offer powerful tools to specify (for example) morphological development and make it possible to easily reuse model components designed by others. Garin *et al.* (2014) present a modelling framework to simulate foliar fungal epidemics that is hosted on the OpenAlea platform (Pradal *et al.*, 2008). This offers methods to facilitate modelling of the complex dynamics of crop–pathogen systems for a better understanding of major inter-actions, which will eventually lead to improved protection strat-egies. Two contrasting pathosystems are implemented for illustration, and the impact of canopy architectural traits on fungal dispersal is simulated. Based on the programming lan-guage XL and on the GroIMP platform, Ong *et al.* (2014) inves-tigate the potential use of multiscale FSPMs, i.e. models of plant growth that make explicitly use of more than one structural scale in the plant description. Three contrasting models are demonstrated that show how information from different scales can be combined in the models in different ways: bottom up, top-down, and across an extensive range of scales, from cell metabolism to stands.

Acquiring the 3-D structures

The rapid development of equipment for retrieving 3-D struc-tures, such as terrestrial laser scanning, is being intensively uti-lized for FSPMs. Such apparatus makes it possible to measure plant structures for FSPMs in large quantities and in great detail. However, the raw data needs to be processed to be useful for the models. The algorithms for plant/plant part recon-struction from raw data are developing quickly. Brunel *et al.* (2014) present a method to identify cells from microscope images of anatomical sections of wood, based on successive aggregations of cells taken from progressively enlarged neigh-bouring regions. On the basis of validation tests the method pro-vides a fast, economical and reliable solution for the identification of cell files.

Possibilities for automatic measurement of root system archi-tecture are much more limited in comparison to aerial parts due to the adverse properties of soil as a medium for propagation of electromagnetic radiation (Butnor *et al.*, 2001; Zenone *et al.* 2008). Thus sample-based measurements remain relevant. Wu and Guo (2014) present a system for quantifying root architecture of field-grown maize that includes a custom-made root-core sam-pling system in combination with proprietary software and a novel program for collecting architectural information on indi-vidual roots. A test shows that field-grown maize root systems can be quantified and reconstructed successfully using this system.

Automatic reconstruction systems of 3-D structures require special methods to assess the accuracy of their measurements. Boudon *et al.* (2014) therefore present an evaluation framework to assess the accuracy of tree reconstructions from 3-D laser scanner data. They develop two indices of geometrical and structural similarities that can be used to compare automatic reconstructions with the reference structures. The evaluation framework is successful at capturing the variation in similarities between two structures. It is used to compare three different re-construction methods, and allows a determination of the sensi-tive parameters of each one.

Practical applications

The two papers in this Special Issue that fall into this category are good examples of phenomena in which the (desired) effects appear during development or are conveyed through the 3-D plant structure. Gigot *et al.* (2014) use a virtual 3-D plant model of wheat combined with a module for predicting splash droplet dispersal of a fungal pathogen and host resistance. They study a number of spatial patterns of wheat cultivars and find that the protective effect against the disease varies by almost two-fold among the various patterns. This shows that in order to maximize the potential mixture efficiency against a splash-dispersed pathogen, optimal susceptible/resistant culti-var proportions have to be established based on host resistance levels.

The growth regulator mepiquat chloride is used worldwide to restrict vegetative growth and promote boll formation and yield in cultivation of cotton. Gu *et al.* (2014) construct a FSPM for cotton in which crop development is driven by thermal time, population density, effects of mepiquat chloride application, and topping of the main stem and branches. Simulations show that application of mepiquat chloride decreases leaf area and internode length, making the canopy more compact, but it does not substantially affect boll density. The model satisfactorily represents the effects of agronomic measures on cotton plant structure and can be used to identify optimal agronomic manage-ment of cotton under varying environmental conditions.

CONCLUSIONS

Recent improvements in data collection technology, such as (ter-restrial) laser scanning, X-rays, NMR and confocal laser imaging, have made automatic acquisition of 3-D structures in-creasingly feasible at various spatial scales for developing FSPMs. This fast-track data source is in the process of making construction and testing of FSPMs more efficient than ever before. Developing algorithms for automatic identification of the elementary units (nodes, internodes, foliage, buds, cells) makes it possible to parameterize FSPMs and to assess them with reference to accurate, real data (e.g. Boudon *et al.*, 2014). The possibility of analysing spectral characteristics of the LiDAR 3-D point clouds (Hakala *et al.*, 2012) opens further pro-spects for identification of plant parts, and even recording their physiological condition.

Modelling of development of groups of cells (meristems) is also progressing rapidly (Abera *et al.*, 2014; Cartenì *et al.*, 2014). Such models will eventually make it possible to link morphological development of plant organs to the action of genes at an unprecedented level of understanding. This will probably lead to hierarchical models that combine structure and functioning at different levels of organization, with con-current development of mechanistic descriptions of plant-level transport and source–sink processes in greater detail than current models.

The developing modelling platforms for FSPMs (Ong *et al.*, 2014; Garin *et al.*, 2014) make sharing of model components in-creasingly feasible. These types of developments will speed up model construction and the creation of application-oriented models and facilitate linkage of different types of models, as illu-strated by Guillemot *et al.* (2014).

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