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

Computational botany: advancing plant science through functional–structural plant modelling

Jochem B. Evers[1,*], Veronique Letort[2], Michael Renton[3] and Mengzhen Kang[4,5]

[1]Centre for Crop Systems Analysis, Wageningen University, Wageningen, The Netherlands, [2]Mathématiques et Informatique pour la Complexité et les Systèmes, CentraleSupélec, Université Paris-Saclay, Gif-Sur-Yvette, France, [3]Schools of Biological Sciences, Agriculture and Environment, University of Western Australia, Perth, Australia, [4]State Key Laboratory of Management and Control for Complex Systems, Institute of Automation, Chinese Academy of Sciences, Beijing, China and [5]Qingdao Academy of Intelligent Industries, Qingdao, China
**For correspondence. E-mail: jochem.evers@wur.nl*

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The need to integrate the ever-expanding body of knowledge in the plant sciences has led to the development of sophisticated modelling approaches. This special issue focuses on functional–structural plant (FSP) models, which are the result of cross-fertilization between the domains of plant science, computer science and mathematics. FSP models simulate growth and morphology of individual plants that interact with their environment, from which complex plant community properties emerge. FSP models can be used for a broad range of research questions across disciplines related to plant science. This special issue presents the latest developments in FSP modelling, including the novel incorporation of plant ecophysiological concepts and the application of FSP models to address new scientific questions. Additionally, it illustrates the breadth of model evaluation approaches that are performed. FSP modelling is a very active domain of plant research which brings together a wide range of scientific disciplines. It offers the opportunity to address questions in complex plant systems that cannot be addressed by empirical approaches alone, including questions on fundamental concepts related to plant development such as regulation of morphogenesis, as well as on applied concepts such as the relationship between crop performance and plant competition for resources.

INTRODUCTION

Plant growth, development and functioning are the combined result of a wide range of genetically regulated physiological processes, environmental influences and a multitude of complex interactions between them (see Fig. 1). In the quest for full understanding of how plants function, why they grow the way they do and how this is driven by environmental conditions, plant science is diving into ever more mechanistic detail. Breakthroughs in understanding of how detailed processes regulate plant functioning, derived from experimental approaches, are reported on a daily basis. This occurs at all levels of integration (molecular, tissue, organ, plant and community) and across scientific disciplines (plant physiology, ecology, crop science and many others). However, with the rapid advance of botanical knowledge, it is becoming more and more difficult to grasp how all these processes interact to affect plant functioning. As more pieces of the puzzle are being identified, integration and synthesis of all this knowledge are hampered by the sheer complexity of the systems studied. At the same time, there is a growing demand for scientific tools that allow for testing hypotheses with existing empirical methods, for instance when a plant physiological trait or environmental process cannot be manipulated. Also, existing experimental methods do not always allow broad exploration studies, due to limited resources.

The need to integrate new and existing knowledge on how plants develop, grow and function, and the desire to perform complex hypothesis testing and scenario analyses, have both led to the development of a range of plant modelling approaches that aim at tackling research questions at a range of integration levels (Prusinkiewicz and Runions, 2012). These modelling approaches can be used to complement experimental approaches in understanding plant functioning at all levels, and for applications in ecological, horticultural, agronomical and even evolutionary science.

This issue focuses on a growing group of such modelling tools: functional–structural plant (FSP) models (Godin and Sinoquet, 2005; Vos *et al.*, 2010). FSP models are simulation models that simulate plant growth and development in time and three-dimensional (3-D) space (Fig. 1). Two defining properties of all FSP models are that (1) plant architecture, i.e. the topological and/or 3-D geometrical characteristics of a plant, is considered explicitly, as either model input or output; and (2) plants and often separate components of plants are treated as individual entities. These two characteristics set FSP modelling apart from other well-established plant simulation tools such as general crop models (e.g. Brisson *et al.*, 2003; Jones *et al.*, 2003; Keating *et al.*, 2003;

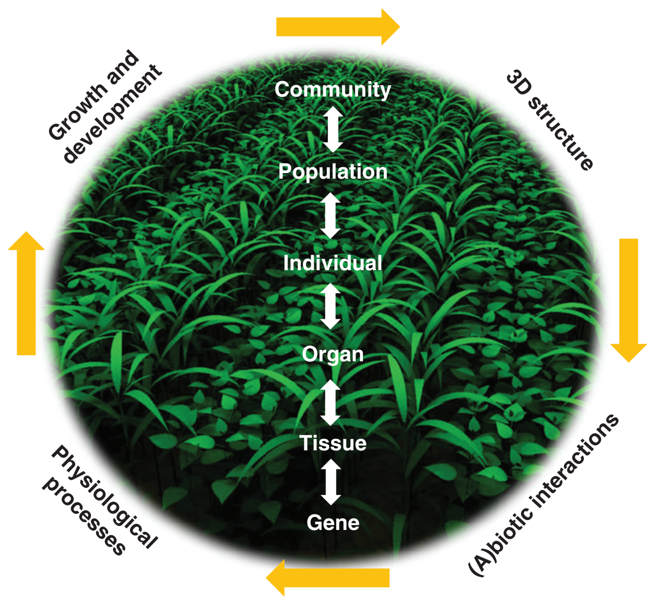

FIG. 1. Conceptual diagram of functional–structural plant (FSP) modelling, which can be used to scale from gene to community integration levels (centre of the figure). FSP models typically simulate the 3-D structure of plants as the result of individual plant growth and development, which is driven by plant physiological processes which, in turn, are under the influence of (a)biotic canopy factors (light, temperature, fungi, insects, etc.). In turn, the distribution of those factors in the canopy is determined by the 3-D structure of the plants, closing the loop (edges of the figure). Background: simulated vegetative canopy with two plant species competing for light.

Van Ittersum *et al.*, 2003). FSP models can range from purely descriptive static representations of plants or plant canopies to highly mechanistic dynamic simulations in which plant form and functioning depend on underlying physiological and/or environmental abiotic or biotic factors and their interactions. The level of realism, detail and the included processes are normally tailored towards the research question being addressed with the model.

Interestingly, the development of these FSP models has in turn given rise to many questions on how to best represent the functioning of plants in computer models, both internally and in relation to their immediate environment. Additionally, very fundamental questions on how growth and development can be captured in relatively simple rules needed to be addressed. The modelling itself generated biological questions and hypotheses. These developments led to strong collaborations between computer scientists, mathematicians and plant scientists, addressing questions on modelling concepts as well as efficient technical implementations. The concepts that define FSP models today have been built on the foundations laid by pioneering work on plant architecture (Prusinkiewicz and Lindenmayer, 1990) initiated around 50 years ago for cellular structures (Lindenmayer, 1968) and trees (Honda, 1971).

This special issue of the *Annals of Botany* represents the state of the art in FSP modelling and its applications that are the result of highly collaborative and interdisciplinary work, connecting the broad fields of plant science, computer science and mathematics.

EXTENDING MODELS OF PLANT ARCHITECTURE

The influential work of Lindenmayer mentioned above as well as of other independent schools (e.g. de Reffye, 1979; de Reffye *et al.*, 1988) essentially defined how plant architectural development, i.e. the production of plant organs over time, can be described mathematically. Soon after the conception and establishment of such mathematical models of plant architecture, the opportunities for using them to inform both fundamental and applied plant research were recognized (Kurth, 1994; Room *et al.*, 1996). Combining these simulations of architectural growth and development of individual plants with models of underlying physiological processes and interactions with the immediate environment paved the way for the model-aided plant research that we now capture under the FSP modelling moniker.

A number of broad categories of FSP models can be distinguished. A substantial number of current FSP models essentially reconstruct plant and canopy architecture over time, without taking into account the underlying drivers. Such an approach has proven to be instrumental in, for example, the analysis of the effects of single and combined plant traits on light capture (Barillot *et al.*, 2014; Zhu *et al.*, 2015). A second important category are the models that are used to study the mechanisms underlying morphogenesis – essentially capturing the physiological basis of the mathematical rules that described development in the first models of plant architecture. This group includes models used to study, for example, leaf initiation (Smith *et al.*, 2006), branch formation (Prusinkiewicz *et al.*, 2009) and leaf shape determination (Runions *et al.*, 2017). A third major category contains models that simulate plant growth and development as emerging from underlying ecophysiological processes such as photosynthesis, allocation of assimilates, uptake of nutrients and water, or responses to environmental signals (Mathieu *et al.*, 2009; Pantazopoulou *et al.*, 2017; Postma *et al.*, 2017). There are also a number of smaller categories such as FSP models of plant biomechanics (Dupuy *et al.*, 2007) and plant evolution (Renton and Poot, 2014). The diversity of these categories means that FSP modelling now provides a broad array of modelling tools operating across a wide range of different areas of plant science research.

This special issue reveals a number of interesting trends in the development and extension of FSP models today. A great deal of attention in the work presented here is devoted to transport and allocation processes within plants. Regulation of flows in the xylem and the phloem, the role of water and carbon sources, sink control of allocation, and how all of this can be conceptualized and captured in simulation, is an active area of research that has clearly benefited from applying an FSP modelling approach. At different levels of detail, transport of water and allocation of carbon are studied on a theoretical level (Coussement *et al.*, 2018; Seleznyova and Hanan, 2018) as well as in specific case studies on grape (Zhu *et al.*, 2018), cotton (Gu *et al.*, 2018) and maize (Ma *et al.*, 2018). In a comprehensive review, the sieve network conducting the water transport in plants is put into the context of the pipe model theory widely used in plant models (Lehnebach *et al.*, 2018). This attention to transport and allocation processes illustrates how FSP modelling can serve as a tool to integrate existing knowledge, test hypotheses on driving mechanisms and also predict the consequences for plant performance.

A second important trend is the increasing focus on belowground plant growth and interaction with the soil. Even though root systems have been represented in FSP models for a long time (e.g. Diggle, 1988; Pagès *et al.*, 1989; reviewed in Dunbabin *et al.*, 2013), root models have been under-represented in the FSP domain, despite the obvious relevance to plant growth and development. With the increasing attention on roots, soils and rhizosphere processes in plant ecophysiological research, and increasing recognition of the complexity of below-ground interactions (e.g. Mommer *et al.*, 2016), FSP modelling of roots and soils has been gaining momentum. In this issue, new root modelling frameworks are presented that allow for easy simulation of root growth and development over time for a range of root architectures (Barczi *et al.*, 2018; Schnepf *et al.*, 2018). Particular attention is given in these studies to the ability to couple simulation of root growth to simulations of other relevant components, allowing for, for example, analysis of the effects of below-ground interactions on whole-plant performance. In an integrated model specific for legumes, this root–shoot link has allowed the most important drivers of whole-plant growth in competitive plant stands to be elegantly captured (Louarn and Faverjon, 2018). In a novel application of a root FSP model, strategies for optimal soil coring are explored (Wu *et al.*, 2018), showing how reconstructions of root architecture can help optimize experimental protocols.

NOVEL APPLICATIONS OF FSP MODELS

As FSP models are extended to address new plant or environmental concepts, their capacity to address questions in several botanical domains increases. In this special issue, a number of studies address the effects of environmental and management factors on a range of crop species, showing the relevance of applying FSP models to questions related to crop–environment–management interactions, a domain previously addressed only by more traditional (1-D) crop models. For specific questions, the need to treat plants in a crop stand as individual entities interacting with their surroundings, as well as the need to take plant architecture into the equation, has widened the scope for application of FSP models in the domain of crops. Examples in this special issue assess the effects of salinity combined with high light intensities (Chen *et al.*, 2018) and elevated CO_2 levels (Rakocevic *et al.*, 2018) on crop photosynthesis in cucumber and coffee, respectively. Photosynthesis is also the focal process in a study on the consequences of the management practice of branch girdling in apple (Poirier-Pocovi and Buck-Sorlin, 2018). An additional promising application of FSP models in crops is the possibility to find plant traits and whole phenotypes that optimize crop resource capture, as is shown for light absorption and photosynthesis in oil palm (Perez *et al.*, 2018).

As well as crop science, FSP models are widely used to address questions in plant ecology and ecophysiology. Competition for resources between plants of the same or of different species has been an especially rewarding subject for the application of FSP models in the recent past (Postma and Lynch, 2012; Barillot *et al.*, 2014; Evers and Bastiaans, 2016). Studies in this special issue take simulation of competition a step further by taking into account the effects of shade avoidance mechanisms (Bongers *et al.*, 2018), the interaction with herbivory by insects (De Vries *et al.*, 2018) and competition for multiple resources at the same time (Louarn and Faverjon, 2018) on performance of plants in competition. Furthermore, a novel theoretical study on optimization of carbon allocation investigates the way that competition for resources affects plant fitness over generations, applying FSP modelling in the domain of evolutionary game theory (Yoshinaka *et al.*, 2018). Other new relevant ecological applications of FSP modelling include simulation of plant growth in marine environments (Whitehead *et al.*, 2018), and the simulation of disease development in plant canopies in relation to canopy architecture and developmental stage (Garin *et al.*, 2018; Robert *et al.*, 2018). These studies show that FSP models have reached the stage where it is becoming feasible to apply them to ecological questions that require taking several interacting environmental factors (light, temperature, disease pressure and herbivory) into account simultaneously.

EVALUATION OF FSP MODELS

Whatever the objective of an FSP model, if it cannot represent the system it is supposed to simulate well, its output cannot be used to draw conclusions reliably. For this reason, FSP models need to be parameterized properly, and their output needs to be evaluated. This can be done in a number of ways. Methods are being developed for assessing the accuracy of the 3-D mock-ups built from digitized plants or canopies. Hui *et al.* (2018) propose to compare image-based reconstructions obtained through multi-view stereo approaches with laser scanning in two and three dimensions. The architectural mock-ups can then be used as support for diverse purposes such as optimal experimental design for soil coring (Wu *et al.*, 2018) and estimation of light distribution (Chen *et al.*, 2018; Rakocevic *et al.*, 2018).

Another novel approach for model evaluation is pattern-oriented modelling (POM) (Wang *et al.*, 2018), originally developed in the field of ecology for agent-based models. POM has been defined as the multicriteria design, selection and calibration of models of complex systems, where the criteria comprise patterns observed at different scales and levels of organization. This can be applied to quantitative experimental data or qualitative emergent properties that a model generates. POM can be seen as an attempt to embed what is already done in most studies in a more rigorous formalism. It has the advantage of encompassing the two main categories of criteria used in model validation: thorough validation of independent data sets (Bongers *et al.*, 2018; Gu *et al.*, 2018; Ma *et al.*, 2018; Poirier-Pocovi and Buck-Sorlin, 2018; Zhu *et al.*, 2018) or evaluation of emergent model properties, either qualitative, or a limited set of quantitative outputs (Chen *et al.*, 2018; Coussement *et al.*, 2018; Louarn and Faverjon, 2018; Robert *et al.*, 2018).

However, different combinations of parameter values may lead to similar outputs, which can complicate model calibration. This identifiability problem is also encountered in the POM approach. To avoid this problem, many studies use a mixture of different methods to parameterize FSP models. In this special issue, most studies take values measured experimentally or derived from the literature (Garin *et al.*, 2018; Perez *et al.*, 2018; Robert *et al.*, 2018), in addition to separate parameter estimation by sub-models (Barczi *et al.*, 2018; Chen *et al.*, 2018; De Vries *et al.*, 2018; Garin *et al.*, 2018; Gu *et al.*, 2018; Louarn and Faverjon, 2018; Perez *et al.*, 2018; Poirier-Pocovi and Buck-Sorlin, 2018; Robert *et al.*, 2018; Whitehead *et al.*, 2018; Zhu *et al.*, 2018), and calibration that includes variables that are outputs of the whole model (Bongers *et al.*, 2018; Ma *et al.*, 2018; Robert *et al.*, 2018). This use of mixed methods for model parameterization raises questions regarding how to decide whether to obtain parameter values from the literature or to make estimates using new experimental data, possibly from new techniques. This is related to the sensitivity of model output to parameter values, and the associated accuracy at which these values need to be estimated. In this context, a sensitivity analysis can provide a good indication, especially through global methods such as the Morris method (Perez *et al.*, 2018; Robert *et al.*, 2018) but also, although potentially less informative, through OAT (one-at-a-time) approaches (e.g. Gu *et al.*, 2018).

Conceptually different approaches for model parameter estimation and evaluation have also been considered: (1) conceptual or theoretical modelling where the effect of varying model parameters is analysed qualitatively and estimation of particular values is not important (Coussement *et al.*, 2018; Lehnebach *et al.*, 2018; Seleznyova and Hanan, 2018); (2) parameter estimation through a teleonomic approach, i.e. by selecting parameter values to optimize a given trait such as light interception (Perez *et al.*, 2018; Yoshinaka *et al.*, 2018); and (3) model evaluation using output from other models, as in the metamodelling approach (Garin *et al.*, 2018; Perez *et al.*, 2018) or as a way to validate a novel resolution method of transport equations (Seleznyova and Hanan, 2018).

BOX 1. In memoriam Eero Nikinmaa

During the creation of this special issue, Eero Nikinmaa passed away on 18 March 2017 due to the consequences of a genetic amyotrophic lateral sclerosis (ALS). He was Professor of forest and atmosphere interactions at the University of Helsinki (Fig. 2). The focus of Eero Nikinmaa's research interests was understanding tree life from the interplay of structure and function. This was already shown in his doctoral thesis 'Analysis of growth of scots pine: matching structure with function' in 1992. It is thus no wonder that Eero Nikinmaa was deeply involved with the FSP modelling community from the beginning. He contributed decisively to modelling of 3-D tree growth, especially with studies on shoot growth patterns (Nikinmaa *et al.*, 2003). Eero Nikinmaa's research topics covered a broad range, from city trees to active participation in starting the SMEAR II measuring station of ecosystem–atmosphere relationships (https://www.atm.helsinki.fi/SMEAR/index.php/smear-ii). In the latter context he studied dynamics of xylem and phloem transport in structurally realistic trees. Within these studies, he was able to show that stomatal regulation can be understood on the basis of interaction of assimilate transport in phloem and transpiration flow in xylem (Nikinmaa *et al.*, 2013). Those of us who had the fortune to have known Eero Nikinmaa will miss a creative researcher and a warm person.

Risto Sievänen, Natural Resources Institute, Helsinki, Finland

Fig. 2. Eero Nikinmaa. Image provided by Risto Sievänen, Natural Resources Institute, Helsinki, Finland.

OUTLOOK

The studies in this special issue show that FSP modelling is now an established approach that has matured over the years to become an indispensable tool in the analysis of plant growth and development, as driven by internal processes in interaction with external factors (environment, management and other organisms, including neighbouring plants). FSP modelling is continuing to expand into new arenas of plant science. New questions require new modelling concepts and new implementation techniques, which means FSP model development will always be ongoing. In the coming years, FSP models will be further refined, new modelling concepts and methods will be introduced and more efficient simulation techniques will be developed. As foreseen by studies in this issue, this will allow the study of the effect of combined stresses on plant performance (Chen *et al.*, 2018), determination of factors controlling fruit quality (Zhu *et al.*, 2018), predicting crop infection probability (Robert *et al.*, 2018) and forecasting potential impacts of environmental changes on plant growth (Whitehead *et al.*, 2018). When embedded in a cycle of research in which experiments provide input for model design, and model output aids in the design of new experiments, FSP modelling will be maintained as a powerful and important tool for addressing questions in plant science, and the results will keep finding their way into the annals of botanical research.

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