

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

Using functional–structural plant models to study, understand and integrate plant development and ecophysiology

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Functional–structural plant models (FSPMs) explore and integrate relationships between a plant's structure and processes that underlie its growth and development. In recent years, the range of topics being addressed by scientists interested in functional–structural plant modelling has expanded greatly. FSPM techniques are now being used to dynamically simulate growth and development occurring at the microscopic scale involving cell division in plant meristems to the macroscopic scales of whole plants and plant communities. The plant types studied also cover a broad spectrum from algae to trees. FSPM is highly interdisciplinary and involves scientists with backgrounds in plant physiology, plant anatomy, plant morphology, mathematics, computer science, cellular biology, ecology and agronomy. This special issue of *Annals of Botany* features selected papers that provide examples of comprehensive functional–structural models, models of key processes such as partitioning of resources, software for modelling plants and plant environments, data acquisition and processing techniques and applications of functional–structural plant models for agronomic purposes.

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

INTRODUCTION

Science is about studying, understanding and explaining reality. Inherently, models have always played a central role in structuring scientific thinking and intellectual debates. In biology, the concept of individuals is relatively clear when referring to most animals but has been challenged when referring to plants (Hallé, 1986, 2010). While plants, like animals, are generally thought of as an integrated whole, from a systems analysis perspective they can be studied as a distributed control system composed of numerous semi-autonomous organs. All these organs can function quite independently in terms of development while being dependent on the rest of the plant with regard to access to water, nutrients and carbohydrates as well as the exchange of phyto-hormones. This view of plants makes systems-modelling approaches particularly suitable for analysing them. Considering a plant organ as the functional and structural unit of a plant, the development and functioning of each organ can be studied and modelled somewhat independently, while a complete understanding of whole-plant development and its underpinning functions requires systematic integration of numerous sub-models. For instance, leaf, shoot, fruit and root morphogenesis and function can be studied and modelled in detail quite independent of one another while their complete function can only be fully appreciated in the context of the whole-plant system.

Plant scientists have been engaged in building conceptual models of plant development, growth and function for centuries. Initially these were conceptual models described verbally or in pictures and drawings. By the 19th Century, the quantitative description of plant morphogenesis attracted the attention of botanists and phyllotaxis started to be analysed and described

following geometrical approaches and Fibonacci sequences (e.g. Hofmeister, 1868; Schimper, 1835). At the beginning of the 20th Century, Blackman (1919) pioneered the modelling of plant growth. The advent of computers and the availability of means of rapid computation in the second half of the 20th Century prompted the development of computer-based mathematical modelling of plants and crops. Popularization of personal computers paralleled four decades of plant and crop modelling mainly using compartmental approaches, basically considering plants and crops as consisting of particular amounts of leaves, stems, roots and storage organs (e.g. Loomis *et al.*, 1979; Levy *et al.*, 2000; Le Roux *et al.*, 2001). Most of the plant or crop models developed during this period were limited to modelling the development or function of 'mean' organs or plants without taking into account variation among individuals and the spatial context of each individual organ or plant, and thus could not be used over a wide range of conditions. Increasing computer power attained over the decades and recent developments in computer graphic's capabilities have changed that and the field of functional–structural plant modelling (FSPM) is a natural outgrowth of previous modelling efforts. The FSPM approach focuses on studying and modelling the development, growth and function of individual cells, tissues, organs and plants in their spatial and temporal contexts (Godin and Sinoquet, 2005).

Development, growth and physiological processes at all levels of organization are strongly influenced by spatio-temporal context with regard to exposure to environmental factors, including access to water, nutrients and energy sources, and other biotic and abiotic influences. Ecophysiological studies have shown that the plant morphogenesis responds very plastically to environmental conditions,

so that genetic ‘control’ of morphogenetic traits appears to be operational at upper levels of the regulatory network while environment influences the localized responses. To a certain extent, this plasticity can be explained by putative decentralized self-regulation processes. However, self-regulation hypotheses are difficult to test directly *in vivo* since morphogenesis is the result of integrated system dynamics that cannot be disconnected to identify their respective primary controls (Verdenal *et al.*, 2008).

Development of functional–structural plant models provides a platform to systematically study, understand and communicate how complex, integrated plant systems work, and the resulting knowledge and models have potential value in applied plant sciences where they can assist in the refinement of agricultural, horticultural and forestry practice. This field of science is highly interdisciplinary and many of the recent advances are dependent on new mathematical and computational techniques to analyse, characterize, depict and simulate aspects of plant development and growth at multiple levels of organization, as well as the use of digital technology to study and understand integrated aspects of development. Thus, this special issue of *Annals of Botany* dedicated to FSPM includes papers that are focused on interdisciplinary approaches and techniques used for developing and assessing FSPM; examples of how this approach is used to study, understand and simulate spatio-temporal aspects of plant development, physiology and growth; and how FSPM techniques can be applied to study and provide answers for applied problems in crop production.

FSPM IS INTERDISCIPLINARY

FSPMs use concepts, tools and frameworks that originate from a wide range of disciplines. Starting with acquisition of data that usually serve as input for the models, we are currently witnessing a massive generation of data at every scale, from remote sensing to DNA chip technology. This amount of data needs to be gathered, organized and analysed to be useful, thus creating new challenges for modellers. This is illustrated by the paper in the current issue entitled ‘Reconstruction and analysis of a deciduous sapling using digital photographs or terrestrial-LiDAR technology’ (Delagrange and Rochon, 2011). New or established concepts are often revisited and adapted to solve problems or provide new approaches to study or illustrate biological problems. For instance, the level set method, a numerical technique for tracking interfaces and shapes, originated from mathematics and has been extensively used in other disciplines such as image processing, computational geometry, optimization, and computational fluid dynamics. Now it has also been adapted to model cambial surface development in the paper titled ‘A mathematical framework for modelling cambial surface evolution using a level set method’ (Sellier *et al.*, 2011). Similarly, new techniques for characterizing light distribution in plant canopies continue to be developed and evaluated, as in ‘How good is the turbid medium-based approach for accounting for light partitioning in contrasted grass-legume intercropping systems?’ (Barillot *et al.*, 2011). The collaboration between biologists and computer scientists spawned the now widely used framework of the L-systems (Prusinkiewicz and Lindenmayer, 1990) to model plants’ morphogenesis.

This framework continues to grow by the addition of new concepts and tools, as illustrated in ‘Towards aspect-oriented functional–structural plant modelling’ (Cieslak *et al.*, 2011). The mixing of disciplines, techniques and concepts during the development of complex models generates its own complexity in terms of model assessment and validation that in turn require new approaches. A rigorous means for such assessment is presented in ‘Assessment of uncertainty in functional–structural plant models’ (Ford and Kennedy, 2011).

FSPM IS MULTI-SCALAR

FSPM concepts, tools and frameworks are used to build comprehensive models that illustrate how several processes behave together. They span from modelling classical process interactions such as light/architecture/growth, as in ‘Simplification of a light-based model for estimating final internode length in greenhouse cucumber canopies’ (Kahlen and Stützel, 2011) and ‘How plant architecture affects light absorption and photosynthesis in tomato: towards an ideotype for plant architecture using a functional–structural plant model’ (Sarlikioti *et al.*, 2011), to modelling dry matter partitioning in ‘Dry matter partitioning models for the simulation of individual fruit growth in greenhouse cucumber canopies’ (Wiechers *et al.*, 2011) and nitrogen economy within plants in ‘NEMA, a functional–structural model of nitrogen economy within wheat culms after flowering’ (I and II; Bertheloot *et al.*, 2011).

FSPM techniques can also be used to model interactions within cells or single organs like fruit, as in ‘Modelling fruit-temperature dynamics within apple tree crowns using virtual plants’ (Saudreau *et al.*, 2011) or an entire crop, as in ‘Towards a functional–structural plant model of cut-rose: simulation of light environment, light absorption, photosynthesis and interference with the plant structure’ (Buck-Sorlin *et al.*, 2011). Some models are also attempting to simultaneously model dynamic interactions among multiple environmental factors and internal processes such as the distribution of water and carbon in whole plants, and their influences on organ and plant growth, as in ‘Linking water stress effects on carbon partitioning by introducing a xylem circuit into L-PEACH’ (Da Silva *et al.*, 2011).

FSPM IS BEING APPLIED

As FSPM becomes more developed and robust an increasing number of researchers are using this approach in a wide range of application-oriented research. The usefulness of FSPM for tackling practical agricultural issues in multiple areas is illustrated by several papers in this special issue. Tree girdling is a horticultural practice that is used to advance fruit maturity and fruit size in specific tree crops but its influences on carbon and water transport in a tree are not well understood. In ‘Tree girdling responses simulated by a water and carbon transport model’ (De Schepper and Steppe, 2011), FSPM is used to provide greater mechanistic understanding of this practice. FSPM methods are used to study and illustrate how wood quality in a timber species is linked to growth processes during stand development in ‘A functional–structural model for radiata pine (*Pinus radiata*) focusing on tree architecture and wood quality’ (Fernández *et al.*, 2011).

The spatial-temporal aspects of FSPM also lend themselves to studying practical issues related to the spread of diseases within plants. This is illustrated in ‘Modelling the effect of wheat canopy architecture as affected by sowing density on *Septoria tritici* epidemics using a coupled epidemic–virtual plant model’ (Baccar *et al.*, 2011) and ‘Characterization of three-dimensional spatial aggregation and association patterns of brown rot symptoms within intensively mapped sour cherry trees’ (Everhart *et al.*, 2011).

The range of practical issues that FSPM techniques can be used to address extends beyond traditional greenhouse, orchard, field crop and forest settings. They have been applied to studying livestock interactions with vegetation in grasslands, as in ‘Simulating the grazing of a white clover 3-D virtual sward canopy and the balance between bite mass and light capture by the residual sward’ (Combes *et al.*, 2011) and to restore threatened marine habitats, as in ‘Modelling seagrass growth and development to evaluate transplanting strategies for restoration’ (Renton *et al.*, 2011).

This collection of papers provides examples of the depth and breadth of research topics, plant species, physiological processes, environmental factors and practical applications that can be addressed through FSPM. FSPM tools are useful extensions of methodologies available to the more fundamental plant sciences. Modelling approaches rarely span more than a few levels of biological organization. FSPM tools fill the niche typically starting at the level of the cell or organ up to the plant or plant community. On the one hand FSPM tools are relevant to the domain of systems biology, particularly for scaling up the effects of events at the cellular level to the behaviour of the whole plant (e.g. signal production and its subsequent distribution in the plant). On the other hand FSPM tools can describe the behaviour of plant communities as emergent from plastic responses to the environment of individual competing plants. The current selection of papers in this issue of *Annals of Botany* also illustrates the power of the application of digital technology in helping plant biologists, ecologists and agronomists to better understand and illustrate the multi-faceted, dynamic interactions between genotypes and their environment that prompt phenotypic responses. This ability to link genotype with phenotypic expression will undoubtedly grow in importance as high-throughput genotyping and phenotyping becomes commonplace.

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