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Foreword: Studying plants with functional–structural models

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Abstract. Functional–structural plant models (FSPM) explore the manifold relations between a plant's structure and the processes that underlie its growth and development. Here we introduce selected papers presented at the 5th International Workshop on Functional–Structural Plant Models, held in Napier, New Zealand, 2007. The papers range from the microscopic scale of meristems to the macroscopic scales of whole plants and plant communities, and cover a wide range of plants, from algae to trees. The topics include examples of comprehensive functional–structural models, models of key processes such as partitioning of resources, software for modelling plants and plant environment, data acquisition techniques and applications of functional–structural plant models.

Additional keywords: light, modular plant architecture, plant modelling, resource acquisition and partitioning, simulation.

A plant is a decentralised system, every leaf operating as a photosynthetic factory, each apical meristem and root tip a potential site of new construction, connected by transport systems for distribution of water, carbon and nutrients to the locations where they are most needed. The broad range of physiological processes essential for the plant's survival is coordinated by signals acting over short and long distances, under genetic control. These processes, and the resulting spatio-temporal structure of plants, are further affected by plant environment: light powering the system, the availability of water and minerals, interaction with neighbouring plants and other organisms, and other abiotic and biotic influences. The same factors are also a source of evolutionary pressures on the plant. Computational modelling, driven and validated by field or laboratory experiments, plays an increasingly important role in the analysis and understanding of individual processes and structures, and their integration into a comprehensive view of entire plants. 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.

The state of the art in plant modelling was showcased at FSPM07, the 5th International Workshop on Functional–Structural Plant Models, held on 4–9 November 2007, in Napier, New Zealand (Prusinkiewicz *et al*. 2007). The series began in 1996, with the first workshop held in Helsinki, Finland (special issue of *Silva Fennica* Volume 31, Issue 3), followed by the workshops in Clermont-Ferrand, France in 1998 (special issue of *Annals of Forest Science* Volume 57, Issue 5/6), Montreal, Canada in 2001 and Montpellier, France in 2004 (Godin *et al*. 2004; special issue of *New Phytologist* Volume 166, Issue 3). The series explores relations between plant structure and the processes that underlie its growth and form. In a feedback loop, the structure provides material support for the various functions, but also results from them. The initial focus of the series, functional–structural modelling of trees at the architectural level, was subsequently extended to herbaceous plants and to both the microscopic scale of molecular-level processes and the macroscopic scale of plant communities. The whole gamut of scales and a wide range of plants, from algae to trees, was represented in the 59 oral presentations and 50 posters featured at FSPM07.

This special issue of *Functional Plant Biology* contains 29 papers selected from those presented at FSPM07. As computational modelling inherently depends on appropriate software, the opening papers by Hemmerling *et al*. (2008) and Pradal *et al*. (2008) present examples of versatile software platforms for functional–structural modelling. In the next group of papers, an example of a comprehensive functional–structural model (Lopez *et al*. 2008) is followed by models of specific processes: carbon partitioning (Lacointe and Minchin 2008), nitrogen allocation (Bertheloot *et al*. 2008), photosynthesis (Müller *et al*. 2008) and organ growth under resource limitation (Seleznyova 2008).

Functional–structural plant models are not limited, however, to processes taking place within the plants themselves; an important component is the interaction of plants with their environment. Simulation of plant environment, in particular light distribution in plant canopy, is a particularly challenging task. Many algorithms require substantial computational resources (computation time and memory usage) (Soler *et al*. 2003; Chelle and Andrieu 2007), and thus a trade-off between computational complexity and accuracy of results must be sought. In this issue, different methods for simulating light environment for plants are discussed by Combes *et al*. (2008), Cieslak *et al*. (2008), Chenu *et al*. (2008) and Wang *et al*. (2008).

Applications of such light models are exemplified by studies of phototropism of cucumber leaves (Kahlen *et al*. 2008), the effects

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of cold stress on light utilisation in maize (Louarn *et al*. 2008) and the impact of architecture on light capture in different rice cultivars (Zheng *et al*. 2008). Light interception is also considered as a component of self-regulation of ryegrass form (Verdenal *et al*. 2008).

While modelling at the scale of individual plants is not appropriate for decision support in crops, insights obtained at the architectural level have the potential to improve traditional crop models. With this in mind, Song *et al*. (2008) investigate the effects of water stress on the architectural development of maize.

Trees present further challenges to the modeller due to the large variation between individual structures, reflecting their plasticity. These variations are often captured with statistical methods that characterise the distribution of branches, flowers and fruits along tree axes. Improving on previous approaches, Costes *et al*. (2008) incorporate biomechanics into a statistical model of apple trees to improve the representation of model geometry, while Letort *et al*. (2008) describe a global parameter estimation technique aimed at representing the physiology driving branching patterns in more detail. Moving on from individual trees to tree stands, Sievänen *et al*. (2008) extend their shoot-based model LIGNUM to the forest stand level, while Host *et al*. (2008) investigate high-performance computing requirements involved in the modelling of tree stands.

Functional–structural models can be used as 'dynamic platforms' for simulation studies of interactions between plants and a wide range of biotic and abiotic factors. Examples presented in this issue include pesticide spray interception (Dorr *et al*. 2008) and interaction with pathogens (Robert *et al*. 2008).

From the macroscopic we return to a smaller scale. Billoud *et al*. (2008) present a developmental model of a brown alga, and test the results by comparing simulated growth patterns with those observed in experiments. Likewise, Zagórska-Marek and Szpak (2008) use simulation models and visualisations in their study of phyllotaxis.

Construction of well-calibrated functional–structural models with potential predictive value relies on experimental and field data. Techniques for collecting these data are thus an integral part of functional–structural modelling, prominently featured in the entire series of FSPM workshops. The final five papers in this issue present techniques for data acquisition across scales of plant organisation, from meristems (Routier-Kierzkowska and Kwiatkowska 2008) through root systems (Zenone *et al*. 2008) and individual trees (Chambelland *et al*. 2008) to tree stands (Fuentes *et al*. 2008; Teobaldelli *et al*. 2008).

As we were preparing this editorial note, we learnt that Dr Hervé Sinoquet passed away on 14 September 2008, at the age of 47, after a long disease. Dr Sinoquet was one of the co-founders of the FSPM community and a leading scientist in the domain of FSPM. In 1998, he hosted and chaired the 2nd FSPM workshop in Clermont-Ferrand (France), which contributed decisively to the international success of this series. Dr Sinoquet was an exceptional scientist. At the forefront of his many contributions, he devised one of the first integrated models of plant function, coupling radiation, absorption, transpiration and photosynthesis (Sinoquet *et al*. 2001), which was subsequently used by many other research groups. In parallel, to address the difficult questions raised by the quantitative assessment of FSPM models, Dr Sinoquet designed original methods for digitising tree architecture (Sinoquet and Rivet 1997) and for automatically estimating leaf areas in trees from photographs (Phattaralerphong and Sinoquet 2005). Anticipating the needs of the FSPM community to share models and methods, Dr Sinoquet also developed public-domain software and protocols (http://www2.clermont.inra.fr/piaf/eng/methodologies/digit.htm), and co-organised a series of training schools for researchers worldwide. These methods and tools are now widely used in agronomical research.

Dr Hervé Sinoquet (1961–2008)

The FSPM community has lost a leader in the field, and an irreplaceable, open-minded, generous colleague and a friend. We dedicate this special issue to his memory.

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