EPILOGUE

FUNCTIONAL-STRUCTURAL PLANT MODELS IN CROP PRODUCTION

Where are we and where to go?

This volume brings together many contributions and aspects of functional-structural plant modelling. These last pages draw attention to three significant questions that may emerge while reading this book: (i) to what extent do these models address plant functions? (ii) what is the (future) role of these models in plant sciences? and (iii) how can the use of these models be enhanced? These questions will be discussed in this epilogue.

Are current functional-structural plant models really functional?

Both structural and functional plant or crop models can generally be divided into two categories: empirical models and mechanistic models. Often it is hard to distinguish between them, because 'empirical' and 'mechanistic' are relative terms. Empirical models are simple and descriptive in nature, often resulting from curve fitting of data from particular experiments, with little attempt to understand biological mechanisms behind the data. They have little heuristic value, but they can produce good predictions, especially when the environments for which the models are applied are within the range of variation upon which the model is parameterized. When empirical models are used outside such a range, they may fail or may show that substantial re-calibration is required.

Entirely empirical models are hardly used nowadays. However, empirical elements in models are still common and trivialities are prevailing in many models that are mechanistic in their general structure. It is difficult to model all plant processes and the environmental responses of the plants with regard to these processes while maintaining a consistent level of mechanistic detail.

The current state of the art of functional-structural plant modelling (FSPM) in crop production is reflected in this book. It appears that:

- there is much similarity in the methods used in various research groups to collect and process data on geometric properties
- methods and software to program structural models are well established

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• models calculating light distribution on 3D structures have become available and are being used; a similar remark applies to local rates of leaf photosynthesis.

In the most comprehensive functional-structural plant models (FSPMs) of crop production the functionality is limited to photosynthesis and new ways to model sink–source relations. Transport of material and signals in the 3D structure is an area where some progress is being made; in general this can be regarded as an area where FSPM can offer unique contributions to advancing plant sciences. Bud fate, i.e. the question whether or not a bud remains dormant, is aborted or grows out to become a new member of the structure, is an issue of central importance to FSPM and seems to need more fundamental treatment than it has received so far. There are attempts to model root structure (not addressed in this book); root functioning is a challenging area awaiting further exploration.

FSPM may be criticized, especially by outsiders, because modellers use empirical curve-fitted relationships (especially structural relationships) as underlying equations of the model. This can be perfectly justifiable if such an approach suits the objectives of the model. Very intriguing questions may emerge from such descriptions, e.g., the mechanisms that give rise to the concept of 'phytomer shift', identifying phytomer numbers with similar properties in Gramineae (Chapter 15 in this volume). There are clear ontogenetic changes in properties of successive phytomers that belong to the different orders of shoots and the mechanisms behind these patterns need to be elucidated.

The provisional conclusion that can be drawn from this book is: yes, we have made a good start in combining function and structure, but much more can and must be done to increase the versatility of these models.

Current and future role of functional-structural plant models in plant sciences

Modelling serves several purposes in plant sciences (Chapter 1); prominent among those is the quantitative integration of knowledge. Modellers should not create a virtual reality separated from the real world. They need to look continuously for (new) physiological or morphological concepts that can be implemented and tested. If FSPMs are to fulfil their promise, modellers need to collaborate closely with physiologists and morphologists so that they can base their modelling concepts on realistic physiological theories of plant functioning. Only then can FSPMs contribute to integrate knowledge and yield quantitative insight of a kind that cannot be obtained when physiological processes are studied in isolation. Conversely, FSPMs can provide intriguing research questions to experimenters. Experimental scientists often focus on the illustration and analysis of a biological function. Modellers are also concerned about the absolute and relative relevance of a biological function. Both parties can gain if they collaborate.

The development of FSPM holds promise as a tool to analyse effects of variation in genetic properties on structure or function. Such analyses become possible if values of model parameters can be based on genetic information. Then, options are opened up to analyse and explore genotype \times environment interactions. Steps to include genetic information have been made by Buck-Sorlin et al. (Chapter 21).

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Structural models of the most important model-plant species *Arabidopsis thaliana* (De Visser et al. 2003; Mündermann et al. 2005) and *Antirrhinum* (Enrico Coen, personal information) will be instrumental, and the development of that work for model plants should reinforce work on crop plants. FSPM offers new options, too, to study biotic (insect and disease) interactions with plants (e.g., Skirvin, Chapter 22).

Scaling up from individual plants to a canopy probably requires more thorough thought in FSPM. Indeed, some FSPMs describe the growth and development of single plants well. The usual way to construct a canopy is to duplicate a plant or sometimes a group of slightly differing plants, but the question is whether the canopies that are constructed in these ways behave like real canopies. This question is important for endeavours to estimate distribution within a canopy, e.g., of water, wind, pathogen spores and pollen.

Enhancing the use of functional-structural plant models in plant sciences

More research is needed to enhance the links between morphological, genetic and functional models, thus enlarging the pool of quantitative tools that explicitly take into account architecture. Ideally, such tools should provide the user with a clear and concise parameterization protocol, a set of tools for parameter fitting, the ability to modify the model easily, and precise delineation of the domain of validity of the model. Architectural modelling is relatively advanced in Gramineae, and there are many models that simulate morphogenesis. However, only few of them are userfriendly and accessible for simulation purposes. Models built on formal languages, such as L-systems or graph grammars, allow the (re)phrasing of morphogenetic rules, and provide a library of commands to specify and modify geometric objects easily. However, there is still considerable room for improvement, especially in coupling architectural models to physiological models. Moreover, current FSPMs generally lack tools to facilitate parameter control and post-processing of simulation results. Facilities to communicate with external programs that simulate the environment, like the implementation of open L-systems in L-Studio, generally fit the need of a developer but lack friendliness for the end-user. The OpenAlea initiative (see http://openalea.gforge.inria.fr), which proposes a framework to develop such 'integrated, yet modular tools', may overcome these drawbacks in the near future.

In conclusion: functional-structural plant modelling is an exciting area of research. Its potential is clearly shown by this book. Functional-structural modelling raises new questions that call for collaboration with experimental plant scientists; it provides an incentive to computer scientists to develop dedicated software. We hope this book will be instrumental for developing FSPM further and raise interest in the application of FSPM approach.

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