CHAPTER 1

FUNCTIONAL-STRUCTURAL PLANT MODELLING IN CROP PRODUCTION

Adding a dimension

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Abstract. The role acquired by modelling in plant sciences includes integration of knowledge, exploration of the behaviour of the plant system beyond the range of conditions covered experimentally and decision support. The purpose of the model determines its structure. Initially process-based models (PBM) were developed separately from structural (or: architectural or morphological) plant models (SPM). Combining PBMs and SPM into functional-structural plant models (FSPM) or virtual plants has become feasible. This adds a dimension to classical crop growth modelling. FSPM are particularly suited to analyse problems in which the spatial structure of the system is an essential factor contributing to the explanation of the behaviour of the system of study. Examples include intra-specific and interspecific competition phenomena, analyses of mechanisms of physiological response to environmental signals that affect allocation of carbon and nitrogen in the plant, and exploration of alternative, manipulated plant architectures on production of fruits or flowers. Good modelling practice involves different steps in model development. These steps are discussed and include the conceptual modelling, data collection, model implementation, model verification and evaluation, sensitivity analysis and scenario studies.

A SHORT HISTORY OF (PLANT) MODELS

Ever since mankind settled and started to manipulate nature to the benefit of people, i.e. started agricultural activities, people have been seeking to improve the ‘performance’ of the systems they managed. People learned by trial and error how best to manipulate the environment. Gradually concepts developed, representing a mental abstraction of reality and its functioning that could be communicated to following generations. It would probably be difficult for us to comprehend the perceptions on the relations between cause and effect that were manifest in eras before the development of chemistry, physics and botany. Especially since the Enlightenment the human activity called science, in which hypotheses on the nature and behaviour of the real world were tested, has expanded enormously. Results from

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experiments were used to guide management of crops and animals. Concepts on how ‘reality works’ were expressed as texts, or at best with mathematical equations. For instance, the ‘laws’ of von Liebig, Liebscher and Mitscherlich, published in 1855, 1895 and 1925, respectively (De Wit 1992), on yield response to input of one or two fertilizers can be regarded as early quantitative models in crop production. Since the advent of computers the effects of larger numbers of factors can be analysed in numerical calculations. Systems analysis began to be applied to agricultural sciences, with computer-based models gaining a place as a tool to aid researchers in expressing their ideas on ‘how reality works’. In this context a system is defined as a limited part of reality, characterized by components, interrelations between the components and an explicit boundary separating the system from the outer world. Ideally the boundaries are chosen such that the outer world does affect the behaviour of the system, but conversely the system does not or negligibly affect the outer world. Driving forces from outside govern the behaviour of the system. The use of a computer to study how such a model behaves is called simulation. Such a model is a simplified representation of a system serving particular purposes. The purposes of modelling include: (i) integration of knowledge (exceeding the capacity of the human brain), (ii) quantitative testing of hypotheses, (iii) extrapolation of effects of factors beyond the range of conditions covered experimentally, (iv) revelation of knowledge gaps and ‘guiding’ research, and (v) to support practical management decisions (input of resources, climate control in greenhouses, planning of processes).

Computer modelling has become a tool of historically unprecedented power to enhance understanding of how physical and biological reality works and to explore the possible behaviour of systems when implementing alternative hypotheses in these models.

PROCESS-BASED MODELS

In agricultural sciences much emphasis has been on modelling the growth of crops in relation to environmental conditions. We’ll refer to this class of models as ‘process-based models’ (PBMs). In PBMs, the components a crop commonly include leaves, stems, roots and reproductive or storage organs (state variables), of which attributes are expressed as quantities (e.g. weight, surface area, N content) per unit area of soil surface (e.g. Van Ittersum et al. 2003). From the total leaf area per unit surface area, i.e. the leaf area index (LAI), light interception and photosynthesis can be computed. Various levels of sophistication are possible in the calculation of the light-driven rate of dry-matter accumulation or photosynthesis and respiration (Van Ittersum et al. 2003). Plant development (phenology) is commonly expressed as a function of thermal time (i.e the accumulation of ‘degree time units’ above a minimum temperature, e.g. degree days). Partitioning of carbohydrates among component organs, i.e. the coordination of growth of components, is often programmed as a more or less fixed function of the phenological stage (Marcelis et al. 1998; Van Ittersum et al. 2003; cf. Marcelis and Heuvelink this volume).

It is probably safe to state that PBMs have contributed enormously to our understanding of differences in potential production levels as related to factors such as latitude, planting time (defining the radiation regime), temperature, nutrients and water and crop species. The models also have contributed to insight into the significance of the distribution of photosynthesis-related parameters in the canopy to the productivity of the plant stand (e.g. distributions of light-saturated rates of photosynthesis, stomatal conductance and effects of mechanisms of stomatal control). Such models are also suitable to explore effects of genetic variation in 'global' plant properties; 'global' meaning properties that pertain to the plant as a whole and not to specific, single organs. For instance, the time of flowering of cereals terminates the accumulation of vegetative mass and leaf area, both of which determine the potential grain yield. Too early flowering reduces potential yield and late flowering may also result in low yield when the suitable growing season has ended before the crop matures (e.g. Yin et al. 1997).

Classical PBMs do not address feedbacks between processes at the level of an individual organ (the 'local level') and the functioning of the plant or plant stand as a whole (the 'global level'). Since the 1980s (Field 1983; Hirose and Werger 1987), awareness has grown in general plant ecology and crop ecology that the spatial distribution of nitrogen (N) in the canopy and the associated photosynthetic capacity is significant for the rate of photosynthesis of the stand. Optimization of allocation of N in the plant became a subject of study (e.g. Anten 2005). Also in the domain of physiology and modelling of trees it became apparent that the three-dimensional (3D) structure of a tree strongly affects the processes involved, such as the distribution of carbohydrates between autotrophic and heterotrophic tissues, the interception of light, and the gas-exchange properties of the foliage (Sievänen et al. 2000 and references therein).

ARCHITECTURAL MODELS AND FUNCTIONAL-STRUCTURAL MODELS

In the literature the phrases architectural model, structural model, morphological model and geometric model were used more or less interchangeably (e.g. Sievänen et al. 2000); they refer to representations of the shape and orientation in space of the components comprising a plant. An important line of work started when Lindenmayer (1968a; 1968b) introduced a formalism for simulation of the development of multicellular organisms, later named L-systems. That approach was developed further and applied to plants, resulting in the publication of the book 'The Algorithmic Beauty of Plants' (Prusinkiewicz and Lindenmayer 1990). Computer graphics provided life-like visualizations of plants. However, in these models, plant development is contained exclusively in the formalisms describing the shape, position and properties of the $(n+1)^{st}$ element as functions of those of the n^{th} element. In other words: plants were treated as closed cybernetic systems; development was regarded as autonomous and there was no interaction between plant development and environment. Still, in these models provisions were already included to simulate the transport of signals through the structure, mimicking physiological control (e.g., the *Mycelis* example in Prusinkiewicz and Lindenmayer 1990).

Functional-structural plant models, FSPMs (Sievänen et al. 2000; Godin and Sinoquet 2005); or virtual plant models (Room et al. 1996; Hanan 1997) are the terms used to refer to models explicitly describing the development over time of the 3D architecture or structure of plants as governed by physiological processes which, in turn, are driven by environmental factors.

Of course, there is no *a priori* limit to the physiological functionality that can or should be included in FSPM. Photosynthetic carbon gain is among the prime processes of interest in agricultural and horticultural applications of FSPM. Methods are available to simulate the light distribution over any 3D object (e.g. Chelle this volume). Given the distribution of photosynthetic properties in the canopy, calculation of an instantaneous photosynthetic rate is rather straightforward (Müller et al. this volume). It is more difficult to model how these photosynthetic properties change with the development of the 3D structure and with change in environmental conditions. In plant modelling, the partitioning of available carbohydrates among competing centres of growth (sinks) has for long been an issue (Marcelis and Heuvelink this volume). FSPM offers new ways to advance that issue (e.g. contributions by Minchin, Allen et al., Drouet and Pagès, Kang and de Reffye, Renton et al. to this volume). In principle FSPMs offer the possibility to model the flow of material within the 3D structure and between the 3D structure and the environment.

FSPMs are particularly suited to analyse problems in which the spatial structure of the system is an essential factor contributing to the explanation of the behaviour of the system of study. Examples include:

(i) Competition phenomena within species. Plants have divergent options to adapt their architecture to the available space. Options include branching (dicots) or tillering (Gramineae), and changes in leaf width, leaf length, leaf mass per unit area, leaf angle, leaf longevity, and leaf:stem weight ratio. Some of these options can be used simultaneously, whereas others come into play sequentially. In particular, the spatial distribution of plant material in the canopy space is decisive whether outgrowth or dormancy of tiller or branch buds occurs. For instance, the number of tillers per plant declines for higher plant population density in wheat (Evers et al. 2006). In turn, the growth or dormancy of a particular bud of a branch or tiller affects the distribution of plant material in the canopy space. FSPMs offer capacity to analyse such feedback between processes at the local (i.e. organ) and the global level (i.e. the whole plant or canopy).

(ii) Competition phenomena between species. Plants of different species possess different morphological options for occupying available space. Just as explained under (i), FSPM can help to understand the competitive advantage of such adaptive options in mixed plant communities (e.g. inter-crops, multiple crops, crop–weed associations, grassland and natural vegetations) (Karley and Marshall this volume).

(iii) Exploration of alternative physiological hypotheses, explaining properties of the structure. For instance, light has been postulated to govern the allocation of N in plants (Drouet and Bonhomme 1999). Alternative hypotheses involve the distribution of transpiration of water over the 3D structure and the associated distribution of cytokinins (Pons et al. 2001). When coupled with microclimate modules, FSPM can help to quantitatively explore, compare and expand such hypotheses and derived postulates. The role of local assimilate production or red:far-red ratio in the determination of the fate of tiller buds of wheat is another example in this category (Evers et al. 2005; 2006).

(iv) Analyses of alternative canopy structures in production systems. In perennial fruit trees and vines, and in ornamental crops (e.g. glasshouse roses) pruning is applied to optimize the production of fruits or flowers over a number of years. Such strategies are commonly empirically developed and FSPM offers opportunities to strengthen their theoretical basis.

Models in applications (i) - (iv) are most useful if they are dynamic in nature, i.e. simulate the changes in the system over time. However, there are also applications in which the dynamic or functional aspect is less important than the adequate structural representation of the system. Canopy structure helps to improve the interpretation of remote-sensing data (Lewis this volume). Physiological functionality is not required in such models. Also in analyses of interactions between insects, micro-organisms, plants and environment, plant structure is important (e.g. Skirvin this volume). When only snapshots of the structure at some points in time are needed for a particular study, the digitization of real systems and their reconstruction in the computer is the most efficient way to proceed (e.g. Sonohat et al. 2002; Drouet 2003; Kahlen this volume).

PLATFORMS AND MODELLING TOOLS

Basically there are two ways to arrive at FSPMs (Sievänen et al. 2000): architectural models could be expanded to accommodate ‘function’ and allow influence of environmental factors, or PBMs should be expanded to accommodate the third dimension. A step towards realization of the first option was the extension of the L-system alphabet with communication symbols, which can exchange parameter values with other models (Měch and Prusinkiewicz 1996). Later improvements, i.e. the L+C modelling language (Karwowski and Prusinkiewicz 2003), facilitated the development of FSPM such as, for instance, L-Peach (Allen et al. this volume). L-systems and associated programming environment (as presented in this volume by Prusinkiewicz et al.) do not constitute the exclusive toolkit to make FSPMs. Alternatives described in this volume include models programmed in C++ (Drouet and Pagès this volume), models using the modelling language XL on the GroIMP platform (Kniemeyer et al. this volume), programming in Matlab (Wernecke et al. this volume) and the Greenlab methodology, which is implemented in several programming languages (Kang et al. this volume). Hanan and Hearn (2003) showed an application linking L-Cotton, an architectural model of cotton using L-systems, with a process-based crop model called OZCOT. The latter is well calibrated, simulating growth and yield to several environmental factors (e.g. water, nitrogen, temperature). It can be efficient and in the interest of managing the models to keep such a growth model intact and have a separate structural model that calculates the development of the architecture, based on the daily growth rate provided by the crop growth model.

PLANT ARCHITECTURE

Based on the work of Hallé and Oldeman (e.g. Hallé et al. 1978) the term ‘architectural model’ has acquired a special meaning in the botanical literature. These authors drew attention to the various typifying patterns of branching and flowering of plants, called architectural models, named after botanists. Examples of such models include: Corner’s model, Leeuwenberg’s model and Rauh’s model. In the context of FSPM, the terms architecture and architectural model have a slightly different meaning. Godin (2000) defined plant architecture “… as any individual description[1] based on decomposition of the plant into components, specifying their biological type and/or their shape, and/or their location/orientation in space and/or the way these components are physically related one with another”. Important implications of the definition are that a representation of plant architecture needs to provide information in at least three areas:

- plant composition, providing a description of the different types of components the plant consists of;
- geometrical properties, describing the shapes and relative spatial positions of each of the components; and
- plant topology, specifying which components are connected to each other, implicitly containing information on the hierarchy among components of a branching system.

STEPS IN MODEL DEVELOPMENT

To be effective and communicable through publications, the modelling process has to proceed in an orderly fashion. Descriptions of Good Modelling Practice (GMP) have been articulated in water management (e.g. Scholten et al. 2001; Refsgaard and Henriksen 2004). Scholten (pers. comm. 2006) provided the definition: “GMP are practices to use models, shared and accepted by a substantial part of the professional modelling community and consisting of explicit guidelines for quality assurance of the modelling process”. It is wise to apply GMP in PBM (Van Oijen 2002) and FSPM. Without pinning GMP down to strict rules the sections below deal with features of GMP. In practice the development of a model often proceeds in a cyclic series of activities, including development of concepts (mental work), modelling (computer work) and experimentation. The steps in model development outlined below are more or less in a logical and chronological order, but there are numerous reasons to deviate from the sequence that is presented.

The conceptual model

Any modelling exercise starts off with the specification of the model’s purpose. In research environments, modelling commonly serves purposes such as integrating knowledge or the quantitative testing of hypotheses. Next, the system of interest needs to be described. In horticultural and agricultural sciences the system of interest is commonly a plant and very often a collection of interacting plants, i.e. a row of plants or a homogeneous crop canopy. At this stage important decisions have to be made on which aspects of function and structure the model needs to explain. For those aspects the modeller should provide an explanation of the desired functions as emergent from the behaviour of the relevant components. In other words, these aspects need to be included in a 'mechanistic way'. To keep the complexity of the model within limits, it is wise to model those aspects of structure and function in a descriptive manner that are of secondary importance in the context of the purpose of modelling exercise. For instance, for the study of insect behaviour in the 3D plant canopy space (Skirvin this volume) it is an adequate choice to model the plants in a descriptive fashion.

In FSPM the conceptual model includes:

- Recognition of the important components of which a plant consists. Monocotyledonous and dicotyledonous plants, for instance, differ widely in architecture. When emerging from seeds, cereals and grasses show a seminal root system, composed of a defined number of main axes, and a crown root system with four possible positions of roots on each main stem node (Klepper et al. 1984). The main shoot develops a particular number of main stem leaves defined by environmental cues inducing the terminal meristem to switch to the initiation of floral structures. Buds in axils can grow out to form 'side shoots' i.e. tillers, which in turn also produce a terminal inflorescence. Main stem and tillers develop simultaneously.

  A potato plant, growing from a seed tuber, produces a variable number of main shoots. Below ground, root axes emerge from the nodes. At some stage belowground nodes also give rise to stolons, i.e. 'lateral stems' that stop elongating in response to internal signals and start to swell to form a tuber. Buds in the axils of the lowest main shoot leaves can grow out to produce a variable number of basal lateral branches (Vos and Biemond 1992). Apical meristematic activity is terminated with the formation of an inflorescence that forms flowers and berries. Shoot growth can continue from buds in axils in the 2nd and 3rd leaf below the inflorescence to give rise to apical laterals; several orders of apical lateral branches can be produced sequentially till shoot production ceases.

  These descriptions of cereals and potato include information on their composition and topology and qualitative information on their changes over time. For each plant species of interest such concepts are on the basis of architectural modelling. This volume present examples of Gramineae (Fournier et al.), chrysanthemum (de Visser et al.), faba bean (Ruiz-Ramos and Mínguez), peach (Allen et al.) and cucumber (Kahlen).
- A choice of the basal unit of plant modelling. Apical meristems produce cells, cells differentiate into tissues and organs, organs form modules, e.g. phytomers (or: metamers), phytomers form components such as a tiller or a branch, components make plants and plants form a canopy. The phytomer or metamer has been advanced as a convenient unit to describe vegetative composition. The phytomer (Figure 1) consists of an internode with a bud at its bottom, and a node at the top to which a leaf is attached. The leaf is composed of a sheath (monocotyledonous plants) or petiole (broadleaf species) and a leaf blade. The

botanical idea that a plant is a collection of basically similar units matches with object-oriented modelling approaches. A conceptual FSP model should include ‘ideas’ on the timing of initiation of phytomers, the appearance and expansion of its components (e.g. phyllochron, duration of leaf expansion), and the coordination of initiation and expansion among components.

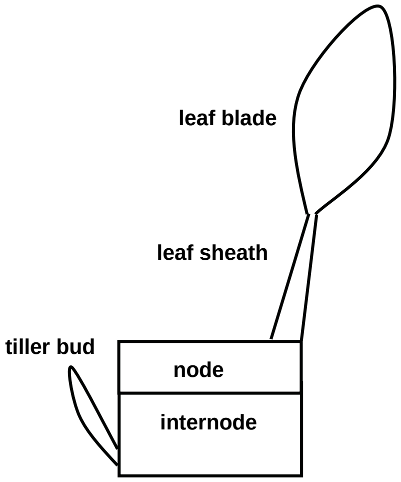

Figure 1. *An example of a typical Gramineae phytomer, and its components internode, node, tiller bud, leaf sheath and leaf blade*

- The physiological ‘functions’ to be included in the model, for instance: photosynthesis, respiration, carbon allocation and sink–source interactions, transport of water, nutrients and signals in the plant structure (cf. Section "*Process-based models*").
- The assumed relationship between environmental variables (particularly temperature) and rate variables determining plant development (progression in phenological stages) or growth processes.
- The time step of relevance to the purpose of the model.
- The construction of a diagram, e.g. Forrester diagram (Leffelaar 1999), showing all the important components of the modelled system, their interrelations, the flows of material and the flows of information, the external driving forces and the processes they affect, using standardized symbols (Figure 2).
- Decisions on the modelling platform and software to program the model. Also it needs to be tested whether intended communications between different models are technically feasible. It is subject to debate whether actual programming activities still belong to the conceptual phase.

The deliverables of the conceptual modelling phase include at least a list of parameters that are needed to construct a functional-structural model. Also it needs to be specified how parameter estimates can be obtained, either from literature, existing data or from dedicated experiments. Protocols need to be made specifying how unknown parameters will be measured in experiments.

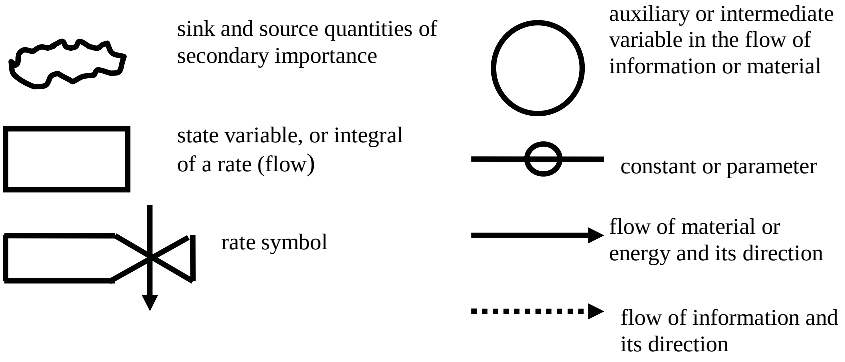

Figure 2. *Symbols – as defined by Forrester (Forrester 1961; Leffelaar 1999) – used in the construction of relational diagrams*

Experimentation, collection and analysis of data

A thorough account of experimentation, collection and analysis of data is provided in the contribution of van der Heijden et al. to this volume. Therefore the issue is not treated here. Very specific to FSPM is the collection of geometric attributes of components and plant topology (see section "*Plant architecture*").

Parameterization, model verification, calibration and sensitivity analysis

Once data requirements are satisfied, the modeller can proceed to finish programming the model. Once technically running, the next step is to verify whether the model assembly really represents the functioning of the system. That process is called model or model code verification, i.e. the question at stake is “is the model built right?” Verification is achieved by analysing the structure and results of the model for their consistency. Mass balances and dimensions, for instance, need to be checked.

In the technical sciences, the term ‘model calibration’ is used to refer to the procedure of adjustment of parameter values of a model to reproduce the response of reality within the desired range of accuracy. When using models as a research tool, calibration should be applied judiciously, for instance to improve the performance of the functions of the model that are necessary but of secondary relevance in the context of the objectives of the study.

The objective of sensitivity analysis is to explore whether the model results are critically dependent on the values of particular parameters. This is commonly done by analysing the relations between variation in input parameters and output variables. Plots can be made of relative change in output versus relative change in input (e.g. stepwise increment from -20 to 20% of the initial value). The slope represents the elasticity; the smaller its value, preferably <1, the less sensitive the model reacts to the value of the input parameter (Figure 3). When varying values of input parameters, only those within the biologically relevant range should be used, nor should associations be violated between variables that are dictated by the biological reality. The deliverables of this stage include a technically sound model with insight into sensitivity to variation of input-parameter values. Results of the sensitivity analysis may inspire new experimentation or adjustment of the model structure.

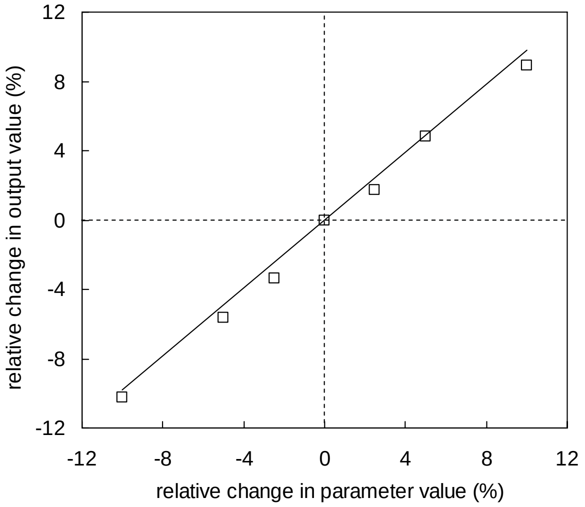

***Figure 3**. A typical figure associated with a sensitivity analysis; the x-axis represents the relative change in the input parameter, and the y-axis represents the relative change in output. The slope of the regression line is the elasticity*

Model validation, scenario studies and uncertainty analysis

Model validation seeks to answer the question “was the right model built?” The answer to that question is commonly obtained by comparing model results with data from the real system. These data should not have been used during model development. Such tests of the performance of the model gain in value if independent data include data from conditions that differ from the ones for which the model was derived, for example from a different agro-ecological zone. Validation of a model under a wide range of conditions using independent data sets is perhaps not practised as widely as desirable, while it is of utmost importance if we want to have reliable models.

If the model passed the testing phase successfully one can proceed to conduct scenario studies, basically to answer ‘what if?’ questions. For instance: what if conditions change? what if plant properties change? Such studies yield insight into the quantitative significance of various processes and parameters and can help to explore divergent management options. This process of ‘deriving insight into reality through analyses of model output for different conditions’ is also simply called ‘simulation’ (Refsgaard and Henriksen 2004).

CONCLUSIONS

Functional-structural plant models (FSPM) seek to integrate plant structure with plant functioning, i.e. the flow of material and energy through the system as dependent on the genotype and as driven by the environment. FSPMs are particularly suited to analyse problems in which the spatial structure of the system is an essential factor contributing to the explanation of the behaviour of the system of study. In that sense, FSPM adds a dimension to conventional crop growth models.

NOTES

[1] Alternative: ‘description of individuals’, stressing that the individual plant is the unit of measurement

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