

REVIEW PAPER

Functional–structural plant modelling: a new versatile tool in crop science

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Abstract

Plants react to their environment and to management interventions by adjusting physiological functions and structure. Functional–structural plant models (FSPM), combine the representation of three-dimensional (3D) plant structure with selected physiological functions. An FSPM consists of an architectural part (plant structure) and a process part (plant functioning). The first deals with (i) the types of organs that are initiated and the way these are connected (topology), (ii) co-ordination in organ expansion dynamics, and (iii) geometrical variables (e.g. leaf angles, leaf curvature). The process part may include any physiological or physical process that affects plant growth and development (e.g. photosynthesis, carbon allocation). This paper addresses the following questions: (i) how are FSPM constructed, and (ii) for what purposes are they useful? Static, architectural models are distinguished from dynamic models. Static models are useful in order to study the significance of plant structure, such as light distribution in the canopy, gas exchange, remote sensing, pesticide spraying studies, and interactions between plants and biotic agents. Dynamic models serve quantitatively to integrate knowledge on plant functions and morphology as modulated by environment. Applications are in the domain of plant sciences, for example the study of plant plasticity as related to changes in the red:far red ratio of light in the canopy. With increasing availability of genetic information, FSPM will play a role in the assessment of the significance towards plant performance of variation in genetic traits across environments. In many crops, growers actively manipulate plant structure. FSPM is a promising tool to explore divergent management strategies.

Key words: Genetic variation, light distribution, photosynthesis, plant architecture, plant morphology, plant physiology, source–sink relations, transport.

Introduction: process-based versus functional–structural models

In agriculture, and in the plant sciences in general, much work has been devoted to modelling the growth of crops and plants in relation to environmental conditions. The advent of modern computers allowed the development of comprehensive models, which considered many interacting factors and processes. In the agricultural domain ‘process-based models’ (PBM) were the first applications to be developed. PBM simulate physiological processes and give an account of metabolism and crop growth in terms of mass

variables per unit area of land. Growth is derived from light interception; rules are defined to partition incremental growth over components (e.g. leaves, stems, roots), taking into account the factors and processes which affect the growth rate (e.g. temperature, nutrients, water, and ambient CO₂ concentration) (Bouman *et al.*, 1996; Marcelis *et al.*, 1998; van Ittersum *et al.*, 2003). From the 1960s onwards, various authors (Lindenmayer, 1968*a, b*; Honda, 1971; Borchert and Honda, 1984; Kurth, 1994) laid the

foundation for the development of what is now known as ‘functional–structural plant modelling’. Among those, the most influential work was done by Lindenmayer (1968*a, b*) and his successors (Prusinkiewicz *et al.*, 1990). These workers introduced Lindenmayer-Systems, commonly named L-Systems, a formal language developed to describe both static plant structure and its dynamics (driven by functions) in the form of a set of intuitive rules.

Functional–structural plant models (FSPM), or virtual plant models, are models explicitly describing the development over time of the 3D architecture or structure of plants as governed by physiological processes which, in turn, depend on environmental factors (Prusinkiewicz *et al.*, 1990; Sievänen *et al.*, 2000; Godin and Sinoquet, 2005; Vos *et al.*, 2007; Hanan and Prusinkiewicz, 2008). Plants are treated as a set of interconnected elementary units, i.e. phytomers (Fig. 1) or, alternatively named, metamers. The FSPM paradigm considers that plants respond to their environment by not only adapting their functions (e.g. photosynthesis, transpiration, N allocation) but often also their structure (e.g. breaking buds or keeping buds dormant, shape and orientation of organs), which, in turn, modifies the condition (e.g. light) in which functions operate. Thus FSPM explicitly allow the feedbacks between structure and function to be captured. Furthermore, feedbacks can be addressed 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’).

The development of an FSPM poses specific questions, not least with respect to computational matters and software, but also offers opportunities to extend the toolbox of plant scientists in general (Vos *et al.*, 2007).

In the classical PBM, as described in Marcelis *et al.* (1998) and van Ittersum *et al.* (2003), the simulation regards the amount of crop per unit surface area. In FSPM, organs

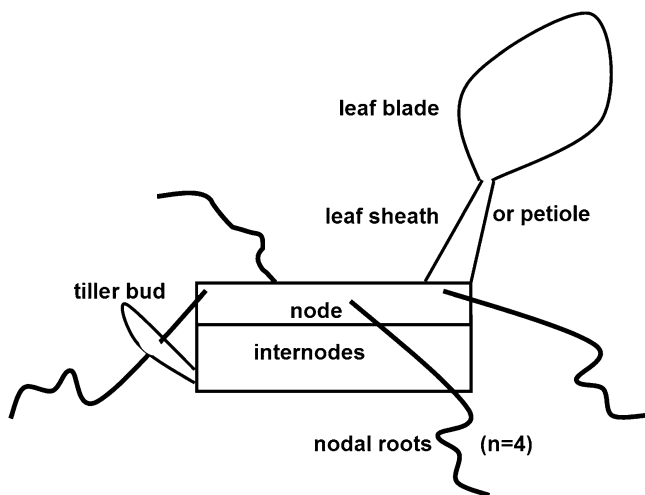


Fig. 1. Schematic representation of a phytomer, the basic unit of simulating plant structure (adapted from Fig. 1 in Vos *et al.*, 2007, and reproduced by kind permission of Springer Science and Business Media) ‘Leaf sheath’ applies to cereals and grasses, ‘petiole’ to broad leaf species. Four nodal root insertions are drawn as in wheat (Klepper *et al.*, 1984).

of individual plants are the primary objects of simulation; yet several different and interacting plants can be included in one simulation. Of course, the specific structure of each model depends on the objective of the study. Dynamic models generate the state of the system at time step $t+\Delta t$ from the state at time t and the rate of change during the time step Δt . There are also ‘static structural models’ that describe a 3D structure at a particular time *in silico*, while the model lacks provisions to calculate the change of the structure over time. The ‘default assumption’ in this paper is dynamic modelling, but several examples of the application of static structural models will be presented as well.

This paper addresses the following questions: (i) how are FSPM constructed, and (ii) for what scientific and applied purposes are they useful?

The construction of (conceptual) dynamic functional–structural plant models

The purpose of the modelling exercise is decisive for the degree of detail that is needed in the simulation of specific structural and functional aspects. Hence, it needs to be borne in mind that it is not possible to provide a manual on FSPM development that applies to all cases. There are, however, a number of generic issues that arise when changing from the crop to the plant perspective.

When starting to make an FSPM of a particular plant species, the first question to address is which characteristic pattern of structural development the species commonly shows. In this context, reference is often made to the work of Hallé *et al.* (1978) who established the basis of architectural analysis and distinguished some 23 ‘architectural tree models’. These models were named after famous botanists, for example, Corner’s model, Leeuwenberg’s model, and Rauh’s model. Among the attempts to make use of these concepts to analyse the architecture of herbal plants is the work of Moulija *et al.* (1999) on maize (*Zea mays*) and pea (*Pisum sativum*). The starting point of the structural model is to make an account of the different types of organs that can be produced and their connections, i.e. the topological body plan of the plant (Fig. 2). In cereals and grasses, for instance, the bud that is present as a lateral component of each phytomer (McMaster, 2005; Forster *et al.*, 2007) can grow out to become a tiller (Fig. 2). Buds on phytomers of first order tillers can produce second order tillers and so on (Moore and Moser, 1995) until tillering is stopped (Tomlinson and O’Connor, 2004; Evers *et al.*, 2006). When the apical meristem becomes generative, primordial buds and young leaf initials are induced to develop into inflorescence structures, while older initials complete their development as leaves; this is a typical example of determinate behaviour. Lower internodes do not expand, only the last ones (about four or five in wheat) form a stem that bears the inflorescence (panicle or ear). Phytomers with unelongated internodes give rise to adventitious roots (‘crown roots’) that increasingly supplement the seminal root axes as the plant develops.

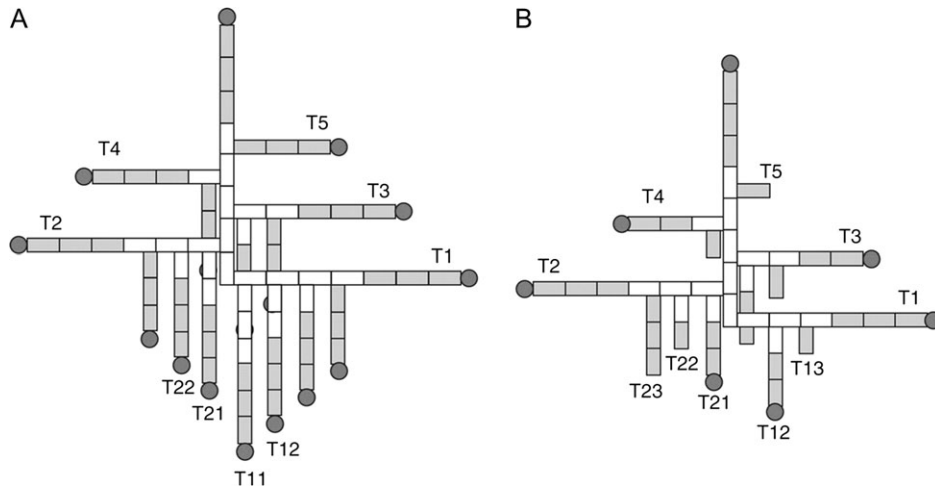


Fig. 2. Illustration of wheat topology, showing the different types of organs and their connections, including main stem (ms), primary tillers (Tx, where x is 1–5), and secondary tillers (Txy, where x, primary tiller number and y, phytomer rank on primary tiller from which the secondary emerges): (A) a potential pattern when all buds grow out and (B) an example as observed in an arbitrarily chosen plant. The white rectangles represent phytomers with short internodes, and the shaded ones represent phytomers with long internodes. A circle represents an ear. Note: the number of phytomers from the base of the plant to any ear (i.e. the ‘summed phytomer rank’) is always 8 (after Kang *et al.*, 2008, and reproduced by kind permission of Oxford University Press).

Potato (*Solanum tuberosum*) is an example of a dicotyledonous crop species with a structural development different from cereals and grasses. Potato is commonly vegetatively multiplied. A variable number of main shoots emerges from the mother tuber. Buds in leaf axils near the soil surface can develop into basal lateral branches. Basal branches and main stem terminate in an inflorescence that develops from the axil of the last leaf, i.e. the ‘*n*th’ leaf (Fig. 3). Pairs of apical branches of several orders can develop from leaf axils of the ‘*n*-1’ and the ‘*n*-2’ leaf positions. Root axes appear in whorls from the subterranean phytomers, even to some extent from stolons.

These two examples represent two divergent forms of ‘basic body plans’ of plants; the exercise to identify the basic pattern needs to be done for each species one wants to model. Hence, *a priori*, the modeller needs to decide on the set of botanical modules that are considered essential in the structural part of the FSPM. The degree of detail depends on the purpose of the study. The inflorescences of cereals and potato, for instance, are composed of a number of different structures, the detailed modelling of which can be important in particular applications.

The next question that arises regards the dynamics of structural development: when does which event happen and can some co-ordination be discerned in appearance of the divergent members of the structure? As an example, Fig. 4 gives a scheme of the rates and durations of leaf production for graminaceous species. To put it more explicitly: information is needed about the rates and durations of both above- and below-ground organogenesis and expansion processes that govern the shaping of constituent members of the structure. Concerning the shoot, these include, for example, the dynamics of leaf expansion and internode extension and whether these are determined by their position in the structure and/or repeated in some fashion across the

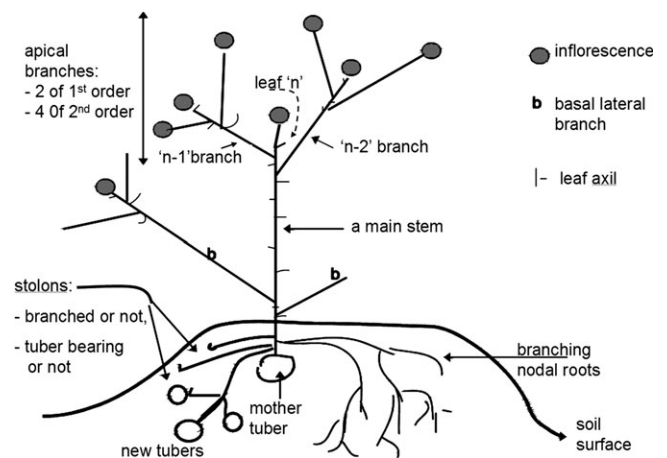


Fig. 3. Schematic representation of a potato plant, showing basal and apical branching and subterranean organ classes (Fig. 1 redrawn from Vos, 1999, by kind permission of Springer Science and Business Media).

different orders of branching or tillering (‘inheritance of properties’). These points are well illustrated in papers on the development of FSPM on maize (ADELmaize: Fournier and Andrieu, 1999), wheat (ADELwheat: Fournier *et al.*, 2003; Evers *et al.*, 2005, 2007b) and barley (Buck-Sorlin *et al.*, 2008), while the example on *Arabidopsis thaliana* is also very illustrative (Mündermann *et al.*, 2005).

Leaf appearance and tillering appear to proceed in a highly co-ordinated manner (where the exact mechanisms giving rise to the co-ordination still remain to be unravelled). The concept of ‘relative phytomer number’ (RPN) helped to simplify modelling. For phytomers of the main axis their RPN is equal to their rank number. RPN of phytomers on tillers is the sum of the rank of that phytomer on the tiller in question plus a ‘shift’ value, which is unique

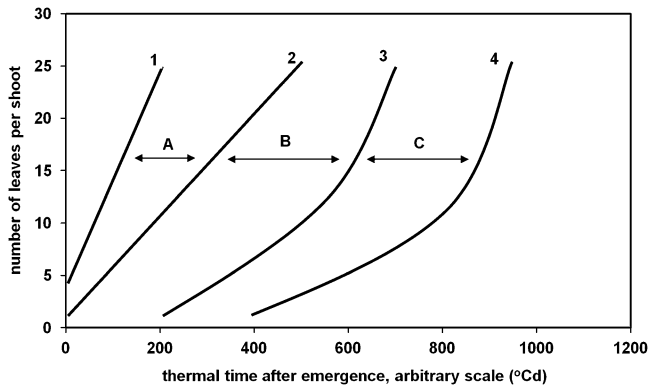


Fig. 4. Schematic representation of the leaf production variables that need to be quantified for the development of a structural model. This scheme is applicable to cereals and grasses (the units on the abscissa and ordinate are arbitrarily chosen). Line 1, number of primordia initiated; line 2, number of leaf tips appeared; line 3, number of leaf ligules appeared; line 4, number of dysfunctional leaves. The slopes of these lines represent the rate of primordial initiation, the leaf tip appearance rate, the rate of appearance of ligules, and the leaf death or leaf senescence rate. The periods A, B, and C represent the period of growth of leaves while covered by the sheaths of preceding leaves, the period of expansion of the visible leaf area, and the active period of mature leaves.

for each tiller type (i.e. $RPN = rank + shift$, 'shift' being zero for the main stem). A cereal or grass plant can develop into quite a complex structure, but the utility of RPN is that phytomers with equal RPN share the same biometric properties, which keeps the description of patterns simple. Furthermore, conservative allometric relations between properties of the components of phytomers are useful in modelling plant structure, for example, the association between maximum leaf blade width and the final length of the internode of wheat phytomers (Evers *et al.*, 2005).

For root development, information is needed regarding the dynamics of root axis extension and the development of lateral axes (root branching), but also on the types of roots that are formed ('heterorhizy'), radial growth, and decay of roots (Pagès *et al.*, 2004).

The treatise in this section can be summarized as follows: information is needed on the type of organs that appear, their time of appearance relative to other organs, and their characteristics relative to preceding organs. This sounds quite descriptive and, in the first instance, it is. Data collection and searching for patterns, co-ordination rules, and conservative properties are indispensable starting points in order to arrive at an understanding of the interaction between structure and function.

Options for adaptation of plant structure to resources

Plants adapt their structural development to the available resources. *A priori* knowledge on options and strategies of structural adaptation of plant species to available resources

helps the efficient development of an FSPM. Plant species differ in the options they possess to adapt to conditions. This paragraph discusses some major possibilities for the adaptation of cereals and grasses versus those of potato.

In cereals and grasses, the process of tillering is, in principle, an exponential process. In practice, the number of tillers on a plant is limited in response to environment (Tomlinson and O'Connor, 2004); in wheat, this results in low frequencies of second and third order tillers in agricultural practice. If buds in a particular position on the cereal or grass plant do grow into another tiller, the parent shoot itself is still developing at the same time. Thus, the properties of the parent and the offspring shoot are more or less determined concurrently, and this is part of the reason why some properties of distant phytomers are equal, for example, the dimensions of leaves of phytomers with the same RPN as mentioned above. Floral development and stem extension approximately coincide with the cessation of tillering in wheat (but not in all cereals, e.g. teff). The next options the plant can use to adapt to environment and resources include the degree of tiller survival (Sparkes *et al.*, 2006), the number of grains per inflorescence, and grain size (Darwinkel, 1978).

In potato, some of the major possibilities for adaptation during plant development are sequential rather than concurrent. The number of basal lateral branches is determined early in plant development; major factors of influence being nitrogen supply and stem density. When the main shoot has been formed, the first order of apical laterals grow out or remain arrested. If the two first order laterals are produced then the four second order apical branches (Fig. 3) could appear, *etc.*, the final level of branching being dependent on genotype and environmental factors.

Plants not only adapt by varying the number of axes (tillers, branches) but also by adapting the properties of individual phytomers. Leaf size (varied by leaf expansion rate) appeared very responsive to nitrogen supply in potato (Vos and van der Putten, 1998) and very conservative in maize (Vos *et al.*, 2005). Lemaire *et al.* (2008) also acknowledged different strategies among plant species to cope with nitrogen deficiency. Andrieu *et al.* (2006) investigated the compensation between rate and duration of lamina extension in maize in response to plant population density. Properties such as specific leaf area and dry matter distribution over internode, petiole, and leaf sheath, leaf insertion angle, and leaf shape can also show adaptation to conditions. The 'shade avoidance syndrome' (Franklin, 2008) is a clear example of plant adaptation triggered by a low ratio of red:far red light received by sensitive organs. Other examples are the adaptation of leaf azimuth distribution in response to planting pattern in maize (Maddonni *et al.*, 2001) and greenhouse-grown cucumber (Kahlen *et al.*, 2008).

Data acquisition

Creating an FSPM requires the gathering of architectural, topological, and geometric data. Plant architecture (or:

structure) is a term applied to the arrangement of plant components in space which can change with time. At a given time, plant architecture can be defined by topological and geometric information. Topology deals with the physical connections between plant components (Fig. 2), while geometry includes the shape, size, orientation, and spatial location of the components (Godin *et al.*, 1999). For topological analysis of the more complex structures like trees, Godin and Caraglio (1998) developed a formalism to describe and analyse plant topological structure, called a multi-scale tree graph (MTG). MTGs are suitable for the concise representation of tree-like topologies with respect to scale and time.

There is a wealth of papers describing the use of different types of equipment (e.g. rulers, protractors, sonic or magnetic digitizers) to collect data on the spatial orientation and shape of organs and to process such data to arrive at mathematical descriptions of shapes and angles and, finally, at the reconstruction of the real-life plant structure *in silico* (Sinoquet *et al.*, 1997; Drouet, 2003; Evers *et al.*, 2005; Dornbusch *et al.*, 2007b; Dauzat *et al.*, 2008; Zheng *et al.*, 2008).

Digitizers record the position of a point in 3D space. Such a position can refer to the point of emergence of the main stem from the soil, the positions of nodes along the main stem, i.e. insertion points of leaves, a number of points along the midrib of leaves, and points that identify characteristic positions along the edges of (compound) leaves. The points are chosen such that the geometry of the elements of the real life structure can be reconstructed *in silico*, using, for example, logistic or bell-shaped functions that are fitted to the recorded data points. The reconstruction of the shape of a cereal leaf from points along the midrib is an early example developed by Prévot *et al.* (1991).

Root structure is more difficult to assess. Rhizotron systems allow monitoring of the time-course of root system development and extension (Devienne-Barret *et al.*, 2006). However, these authors used rhizotrons of limited thickness and, hence, the data concern 2D rather than 3D information. To capture true 3D information on root architecture, computed tomography (CT) and nuclear magnetic resonance (NMR) methods have been proposed (Lontoc-Roy *et al.*, 2005).

Modelling the light environment perceived by plant organs

As outlined in the preceding sections, the 3D structure of plants can be represented *in silico*, although at different degrees of detail among modelling approaches. In a detailed approach, the plant (or a number of plants) is represented by a collection of geometric primitives (polygons) of which the spatial co-ordinates are known. In another approach, the canopy space is divided into volume elements or voxels in each of which the amount of leaf present is characterized by mean properties such as the distribution of leaf density and orientation (Sinoquet and Bonhomme, 1992; Godin,

2000). 3D representation of structure opened up new possibilities to calculate light absorption, compared to how this is done in PBM.

A light ray incident on a leaf surface is subject to three fates: reflection, absorption, and transmission. Each of these fates occurs with a particular probability. The optical properties of the (plant) material involved express these probabilities as a function of wave length. Light absorption can be calculated using various methods, many of which were developed in the domain of computer graphics (Chelle and Andrieu, 1999). In all cases, one needs to start with the definition of the light sources, for example, the radiation incident from the sun as a source in a clear sky, where the solar position depends upon the position on earth (latitude), the day of the year, and the time of the day (Goudriaan and van Laar, 1994). Applications in greenhouses or growth rooms require the description of the spatial arrangement of multiple sources. For instance, the spatial distribution of assimilation lamps and their 3D light emission patterns need to be known (Buck-Sorlin *et al.*, 2009a), as well as other greenhouse settings such as those for opening and closure of shade gauze that is used to reduce incident solar radiation and temperature.

Monte Carlo ray tracing is a stochastic method consisting of casting light rays from a given light source (for example point and directional light sources or a spotlight) in different directions and following their paths through the canopy. At each encounter with an object (e.g. green tissue) the subsequent path of a ray depends on the optical properties of the plant material. The ray tracing method involves only a few assumptions and allows multiple scattering in different wavelengths to be calculated. Monte Carlo ray tracing can be used for remote sensing applications (España *et al.*, 1999; Wernecke *et al.*, 2000; Lopez-Lozano *et al.*, 2007) and ecophysiology (Chelle, 2006; Wernecke *et al.*, 2007; Kniemeyer, 2008) and is considered as a reference for other methods, such as the radiosity method described below. Efficient sampling of positions and directions is a key issue when casting rays. Multiple variants have been implemented, to seek for higher efficiency, such as Quasi-Monte Carlo ray tracing (Cieslak *et al.*, 2008).

The radiosity method was developed to calculate the energy exchange between all the surface elements within a scene, first in heat transfer (Sparrow, 1963) and then in computer graphics (Goral *et al.*, 1984). It was adapted for crop canopies (Soler *et al.*, 2003). Moreover, Chelle *et al.* (1998; Chelle and Andrieu, 1998) developed the nested radiosity model (NR), that couples the radiosity method to calculate the energy exchanges between close surfaces with a statistical approach for exchanges between far surfaces. NR has been coupled with L-systems implemented in *cpfg* (see the 'Platforms and software' section below), using the dedicated interface Caribu (Chelle *et al.*, 2004). NR is available on the OpenAlea platform (Pradal *et al.*, 2008). Radiosity methods allow multiple scattering to be quantified with computational costs generally less than ray tracing. In a recent application, NR was used in combination with ADEL-wheat to simulate the distribution of the

red:far red ratio of light in a virtual wheat canopy (Chelle *et al.*, 2007). Further examples of the application of NR include Evers *et al.* (2007a) for wheat (Fig. 5) and de Visser *et al.* (2007) for chrysanthemum.

For static models ('mock-ups') VegeSTAR (Sinoquet *et al.*, 1998; Sonohat *et al.*, 2002) is, next to NR, an example of software allowing the visualization of 3D digitized plants and the computation of light interception from virtual plant pictures. The software computes the values of the 'silhouette to total area ratio' (STAR values) by counting the coloured pixels corresponding to an organ class on the picture. The computation thus disregards multiple scattering and assumes leaves are black. False colours are attributed to plant organs in order to distinguish them on the virtual plant pictures.

Dauzat *et al.* (2001, 2008) developed the simulation platform ARCHIMED in order to connect different biophysical modules for calculating, in 3D structures, (i) the radiative balance of plant organs, (ii) their energy balance (and ultimately their temperature and transpiration) and (iii) their carbon assimilation. In the context of the analysis of plant–environment interaction light is an important variable, but also important are temperature, wetness, and turbulent flow. These aspects were reviewed by Chelle (2005); he introduced the term 'phylloclimate', which basically means (the simulation of) the climate as perceived by individual plant organs. 'Phylloclimate' is distinct from 'microclimate' which is a set of variables characterizing the properties of ambient air.

Plant functions in FSPM

Once light absorption has been simulated satisfactorily, all the approaches developed for modelling leaf photosynthesis in process-based crop modelling can be implemented (Vos and Heuvelink, 2008). These include photosynthesis–light response curves, determined by parameters such as the dark respiration rate, the asymptote for light-saturated rate of net photosynthesis, and the initial efficiency (Marcelis *et al.*, 1998), or the biochemical model of Farquhar *et al.* (1980) and related approaches (Nikolov *et al.*, 1995; Yin *et al.*, 2004). Concepts of growth and maintenance respiration can

be applied as in process-based modelling. Growth respiration represents the carbon loss associated with the production of additional plant material. Extensive analysis of biochemical pathways yielded a set of universally applicable factors quantifying the conversion of assimilate into plant components such as carbohydrates, proteins, lignins, oils and fats, and minerals (Penning de Vries, 1974; Cannell and Thornley, 2000). Maintenance respiration regards the energy that needs to be spent to maintain the steady-state of existing plant material (Penning de Vries, 1975) and its quantification is less accurate than growth respiration (Cannell and Thornley, 2000).

A problem specific to FSPM is defining the distribution of the parameter values of the photosynthesis submodel over the structure. There are associations between the amount of nitrogen per unit leaf area and values of key parameters of photosynthesis models (Gonzalez-Real and Baille, 2000; Müller *et al.*, 2008; Braune *et al.*, 2009; Yin *et al.*, 2009). This shifts the problem to modelling nitrogen distribution over the structure. The distribution of nitrogen (N) in a plant canopy has been the subject of many studies, focusing on the optimization of vertical N distribution so as to optimize canopy carbon gain (Hirose and Werger, 1987) and mechanisms that explain the apparent correspondence between the distributions of light and nitrogen or photosynthetic capacity in a canopy (Boonman *et al.*, 2007). Such concepts are useful, but the application in spatially explicit FSPM is not straightforward. Bertheloot *et al.* (2008) developed a mechanistic model for N dynamics of wheat after flowering, based on turnover characteristics of nitrogenous compounds; the model allowed the optimization of N distribution to be simulated as an emerging property of light driving the synthesis of photosynthetic proteins; extension of this approach might prove useful to simulate the N economy in an FSPM.

The amount of light, carbon dioxide concentration, and temperature determine the amount of assimilates per plant produced over a certain time interval. These environmental factors vary and hence assimilate production, or source strength, varies and, at times, assimilate availability may limit the growth of competing organs. Several modelling concepts deal with sink–source relations (Borchert and

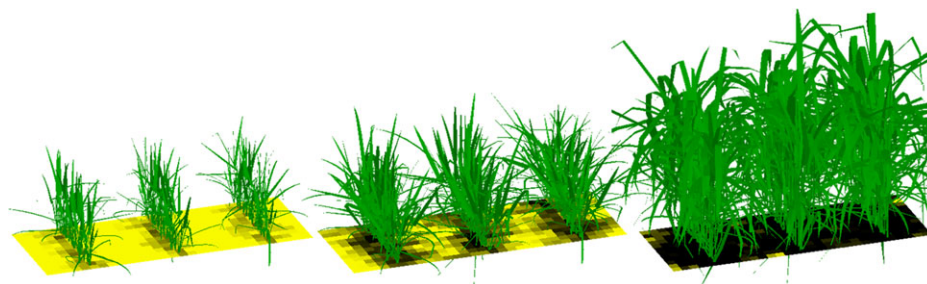


Fig. 5. Visualization of three stages in vegetative wheat development, using ADEL-wheat and Nested Radiosity (see text). The colour of the soil elements represents the percentage of photosynthetically active radiation (PAR, originating from a single light source located in zenith) that penetrated the canopy onto the soil element [ranging from black (0%) to bright yellow (100%)]. [Reproduced from: Evers JB, Huth NI, Renton M, 2009. Light extinction in spring wheat canopies in relation to crop configuration and solar angle. In: *Plant Growth modelling and applications*, PMA09 (©2009 IEEE)]

Honda, 1984; Lacoïnte, 2000; Bancal and Soltani, 2002; Marcelis and Heuvelink, 2007; Génard *et al.*, 2008; Lacoïnte and Minchin, 2008). The simplest concept that can be applied in FSPM is that of ‘sink regulation’. Here, the ‘source capacity’, i.e. the amount of substrates available from concurrent production and reserves at each point in time, is computed and a ‘sink strength’ assigned to growing organs, i.e. a potential growth rate that is realized under conditions of non-limiting assimilate supply (Heuvelink and Buiscool, 1995). At each time step, a particular organ i attracts a fraction f_i of the available substrates equal to its share S_i in the total plant sink strength SS . These models are based on a number of assumptions: (i) all sinks draw on one common source (reserve pool), (ii) there is negligible resistance to transport of assimilates across the plant components, (iii) there is no preferential feeding of a sink by its nearest source, and (iv) the potential growth rate and ultimate size of each organ can be determined. The mathematical, functional–structural GreenLab model (Guo *et al.*, 2006) implicitly uses these assumptions but does not need assumption (iv) as this is one of the outputs of the model (Kang *et al.*, 2008).

In larger plant structures, such as trees, the assumption may not be valid that substrates for growth are equally available to all competing sinks in the plant because distances and associated transport times become significantly long. However, because of the modular representation of a plant, FSPM offer, in principle, the opportunity to simulate the allocation of assimilates over the whole plant. Modelling the movement of substrates through the structure is based on concentration gradients and transport resistances, using Ohm’s law as an analogy. Concentration gradients between modules (phytomers) are altered by the local production or consumption of substrates and by the import of assimilates from, or export to, adjacent modules. This approach is referred to by ‘transport-resistance modelling’ (Minchin *et al.*, 1993; Minchin and Lacoïnte, 2005). Such concepts were implemented in L-PEACH (Allen *et al.*, 2005), while the methodology of solving the transport equations (gradients in driving force and pathway resistances in branched structures) was outlined by Prusinkiewicz *et al.* (2007a); within XL/GroIMP (see next section) differential (transport) equations can also be solved, using a range of ODE (ordinary differential equation) solvers (R Hemmerling, personal communication). In other words: technical provisions have become available to model the transport of substances in branching structures.

Most FSPM focus on development and functioning of shoots. However, growth and functioning of roots and shoots are interdependent (Willaume and Pagès, 2006) and some of these interactions have been expressed in models such as GRAAL-CN (Drouet and Pagès, 2007). In that model, organ initiation is specified for root and shoot members and ‘local rules’ (i.e. at organ level) are defined describing the relative sink strength of competing organs. The behaviour of the plant as a whole arises from interactions between those organs and the integration of the processes over the whole plant.

Certainly more effort is required to integrate in models root growth and architecture with root functioning; models capturing these interactions open up possibilities for modelling spatial aspects of growth and functioning of roots in a heterogeneous soil environment (Pierret *et al.*, 2007). This would also be helpful to face new questions in water and nutrition management in the context of the development of sustainable agriculture and global climate change.

Platforms and software

Ideally, the toolbox for the construction of FSPM includes provisions (i) to model the structural development of plants, including suitable templates to represent plant organs, (ii) to simulate the illumination and light absorption for each element of the structure, for different wavelengths and with a realistic description of light sources (sun and lamps), (iii) to allow photosynthesis to be calculated for each green element, (iv) to keep track of ‘integrated variables’ (e.g. the sum of daily photosynthesis in all green objects of the plant; the sum of all reserve carbohydrates present in each of the objects in the structure; the summed leaf area of all green objects, etc), (v) to simulate source–sink relations, (vi) to allow transport of substances and signals to be simulated through the structure, using different transport mechanisms: active transport, diffusion, convection, or instantaneous redistribution (i.e. pseudo-transport), (vii) to allow metabolic and genetic networks to be simulated, opening up links to systems biology and genetics, and (viii) to generate advanced visual output and animations.

Various methods to model FSPM have been developed. The most widely used modelling platform is L-Studio, which is based on the L-system formalism (Lindenmayer, 1968a, b; Prusinkiewicz *et al.*, 1990). Within L-Studio, FSPM are created using the modelling language L+C (Prusinkiewicz *et al.*, 2007b), which succeeded *cpfg* (Prusinkiewicz *et al.*, 2000). The other increasingly used platform is GroIMP (Growth Grammar-related Interactive Modelling Platform), which is based on Relational Growth Grammars (RGG), a graph-based extension of the L-system formalism, and which uses XL, a modelling language specifically tailored for the purposes of FSPM (Kniemeyer, 2008).

L-systems provide a basically modular approach to modelling. This enables plants and canopies to be described as a collection of interconnected modules, for example, phytomers. Complex structures can be described with a limited set of simple ‘productions’ or rewriting rules, which are applied in parallel to a linear, one-dimensional data structure, a *string*, consisting of simple symbols, some of which can be graphically interpreted. This approach recognizes the repetitive nature of plant structure, as a plant consists of phytomers which are repeated a number of times. For example, a phytomer could consist of an internode I, a leaf [L], an axillary meristem [A], growing into a branch and an apical meristem A at the top. (Note: the square brackets [...] around a module indicate that the module is a structure that forks off from the main shoot,

such as a branch or a leaf). A rewriting rule for the construction of a vegetative shoot could be:

$$A \rightarrow [A]I[L]A$$

meaning A is replaced by the right hand symbols. When the starting point (axiom) of the simulation is A, after two time steps in which the rule is applied, the string looks like:

$$\text{Step 1: } [A]I[L]A$$

$$\text{Step 2: } [[A]I[L]A]I[L][A]I[L]A$$

Hence, when applying the rewriting rule several times, the string changes (i.e. usually it becomes longer, but rules may also specify the elimination of symbols), and the description of the virtual plant is expanded in each time step. Few simulation steps result in an extensive string, which can be interpreted as a branched 3D structure, composed of several branches with the same repeated basic unit.

Whether a rewriting rule is applied in a specific time step can be made dependent on, for example, temperature sum or the developmental state of the virtual plant, using a conditional statement in a rewriting rule, for example:

$$A : T_{\text{sum}} > 700 \rightarrow G$$

Here, the vegetative apex A is replaced with a generative apex G when the temperature sum has exceeded 700 °C d. Obviously, a separate rule is needed to increase the value of the variable Tsum at each time step, based on temperature input. The symbols can be extended by assigning one or more parameters to them: such parameterized symbols are called modules (note: not to be confused with botanical modules defined above) and the resulting set of rules is called parametric L-systems (Prusinkiewicz and Hanan, 1990). Such parameters usually represent organ properties such as, for example, the length of an internode or the angle of divergence of a leaf from the stem axis:

$$L(n, l, a) \rightarrow L(n, l+g, a+c)$$

In this example leaf module L has three parameters (n =leaf number, l =leaf length, a =basal angle), two of which are updated (g =length increment, c =angle change). The values of g and c can be fixed, or be made functions of other parameters, such as the time step, temperature sum, developmental stage, etc.

FSPM are also implemented in other computer languages. The mathematical FSPM GreenLab (Yan *et al.*, 2004) can be implemented in Matlab (Kang *et al.*, 2008) or its open source equivalent Scilab. GreenLab applications are also implemented with the software Digiplante, which is based on C++ (Christophe *et al.*, 2008, for *Arabidopsis thaliana*; Mathieu *et al.*, 2009, for sink–source interactions in different species). Another example of a structural cereal model in Matlab is the one of Dornbusch *et al.* (2007a).

In principle, modelling research can be advanced more rapidly if researchers have access to and can use each other's models, even if implemented in different softwares or environments. The French OpenALEA initiative (Pradal

et al., 2008) is dedicated to provide a homogeneous software platform which could integrate various tools and models already available within the FSPM community.

Applications of 3D plant models

Static 3D representations

'Static' structural models represent the structure of a 3D plant or plant canopy and can be made in a process of digitizing an existing structure, analysing the collected data and the faithful reconstruction of the real life structure *in silico* (Sinoquet *et al.*, 1997, 1998, 2007; Sonohat *et al.*, 2002; Drouet, 2003; Dauzat *et al.*, 2008). 'Mock-up' is one term to refer to such models.

The focus of static structural modelling is on the assessment of the consequences of crop structure for interactions with the (a)biotic environment. In such applications one could use a fully fledged dynamic FSPM if available, but in its absence a series of mock-ups, representing different stages of the crop *in silico* can serve as an efficient alternative.

There is a series of examples of applications in horticulture and field crop production. Several studies addressed the effect of architectural and morphological plant properties or plant arrangement on light interception (Sinoquet *et al.*, 1998, 2005, 2007; Drouet *et al.*, 1999; Maddonni *et al.*, 2001; Sonohat *et al.*, 2002; Kahlen, 2007) and gas exchange as driven by light energy distribution (Dauzat *et al.*, 2008). One of the authors' recent projects aims at exploring the light interception of different greenhouse crops (rose and tomato) in relation to the position, colour, and power of assimilation lamps with the backdrop of a virtual greenhouse (the latter being necessary to account for the effects of multiple scattering of daylight and assimilation light by the greenhouse roof, walls, and floor). The 3D models, which have been implemented in GroIMP, compute the distribution of local light absorbed by the different components of the canopy as well as local leaf photosynthesis (Buck-Sorlin *et al.*, 2009a), and in the near future will also account for the spectral composition of light. We think that such simulations represent a time-saving and cost-efficient partial alternative to expensive and tedious experiments. In a further step, net primary production will be estimated for different growth stages and at different light strategies. This will enable us to evaluate the illumination strategies for their impact on growth and associated light and energy use efficiency, while taking the adaptation of leaf functioning to the radiance regime into account.

In remote sensing the signal that is received by a sensor depends on the plant structure, and optical properties of the soil and the phyto-elements. While an approximation of the canopy structure as a turbid medium is still widely used, it presents significant flaws, for example, in predicting hot spot patterns, that mainly depend on canopy height and leaf size (Hapke *et al.*, 1996). (A hotspot is a canopy reflectance peak that is observed if the direction of view is (almost) the

same as the direction of solar illumination; the peak is caused by the absence of mutual shading of leaves in that particular viewing direction. The intensity and the breadth of the peak depends on the canopy architecture, mainly the leaf size and the canopy height.) Moreover, plant tropisms and shade avoidance behaviour result in non random positioning of phyto-elements, necessitating the incorporation of largely empirical parameters, such as a ‘clumping parameter’ in the turbid medium models. Virtual plant modelling in combination with the realistic simulation of light distribution and reflection is applied to sort out such uncertainties (España *et al.*, 1999; Lewis, 1999, 2007; Luquet *et al.*, 2004). It also opens the possibility to use the same representation of the structure to predict a range of signals, from optical to SAR (synthetic aperture radar) regions of the electromagnetic spectrum (Lewis *et al.*, 2003). FSPM also allow the high resolution images that can be obtained by close range imagers to be simulated, thus opening a rationale for the applications of imagery in high rate plant phenotyping. Finally, the use of FSPM in remote sensing is not restricted to static 3D representations. Similar to crop models, progress is being made in coupling and inversion of dynamic FSPM and reflectance simulation models (Koetz *et al.*, 2005).

Skirvin (2004) examined the impact of plant architecture and canopy connectedness on the movement of predators within a complex canopy, using virtual plants. Dorr *et al.* (2008) combined droplet movement (spray) models and plant architecture using virtual plant scenes to develop a probabilistic model of turbulence-related spray transport around various plant architectures. The behaviour of rain on plant surfaces determines the transport of spores or chemicals present on a leaf surface. The physics behind these processes can hardly be simulated without a realistic description of plant structure; therefore, the availability of plant mock-ups is promoting the development of plant–rain interaction models (Bussi ere *et al.*, 2002; Saint-Jean *et al.*, 2004; Bassette and Bussi ere, 2008).

Dynamic models

In dedicated dynamic FSPM, a collection of mutually interacting plants can be simulated. Each simulated plant can be unique due to variation in initial properties among plants, spatial heterogeneity in the environment, or due to stochastic elements. A pioneer example of a dynamic FSPM expressing interactions between individual plants is that of Fournier and Andrieu (1999). Simulation showed that increasing population density resulted in increasing plant to plant variability, even when all plants had identical parameter values. Crop characteristics such as the development of leaf area and the number of shoots per unit of ground area emerge from properties and processes at the level of plant and plant organ. A recent example of a dynamic FSPM can be found in Evers *et al.* (2007a), in which small canopies of wheat plants were simulated at several population densities. In wheat, the outgrowth of tiller buds is influenced by the ratio of red to far-red light

irradiance (R:FR), among other factors. At each location in a canopy the R:FR of the light is affected by light scattering (reflection, transmission) from surrounding plant tissues. The R:FR dependence of bud outgrowth was implemented in the wheat model, using hypothetical responses of bud extension to R:FR. Bud break was implemented to occur when a threshold bud length was reached. In this study, it was shown that, in accordance with experimental observations, fewer tillers per plant were simulated for higher plant population densities, caused by the feedback mechanism between the simulated plant development and local light environment. Such models allow the testing of divergent views on the mechanism of response to R:FR. A similar approach was implemented in an FSPM of barley (Buck-Sorlin *et al.*, 2008). The local R:FR values perceived by virtual sensors attached to tiller meristems were transformed into phytochrome ratios (P_{FR}/P) applying a model by Burema (2007). These phytochrome ratios were then used to predict tillering at different stand densities, exploring different thresholds for P_{FR}/P . In a variant of the same model, the ‘*BarleyBreeder*’ (Buck-Sorlin *et al.*, 2005, 2008), information on the morphology and biometry (visible phenotype) of the genotypes of a mapping population and of certain monogenic mutants is used to predict the phenotype of any (including new) combination of considered genes and quantitative trait loci (QTL). Employing a relational graph data structure within XL (Kniemeyer, 2008), two network models were included: one for the biosynthesis of the plant hormone gibberellic acid (GA1) and another one to simulate the transduction of the GA1 signal to induce the elongation of internodes locally, in concert with genes known to encode enzymes involved in GA biosynthesis. The initial parameters for the two networks were extracted from the published literature and enzyme databases, and then fitted to a very detailed dataset describing phytomer extension as a function of thermal time. Kahlen *et al.* (2008) used a parametric L-system to simulate leaf phototropism in response to gradients in red:far red ratios across leaf blades of cucumbers in greenhouses.

The technical provisions to simulate the movement of substances and signals in a 3D plant structure open up new possibilities to link up with systems biology. The latter discipline is primarily occupied with processes at the cell level. FSPM could help in scaling-up understanding at the cell level to the behaviour of the whole plant. For instance, analysis of the networks and pathways that result in the local production of the signal, inducing transition of the apex from the vegetative to the generative phase, is the domain of systems biology. FSPM could come in to help with analysing the whole plant response to signal production in different sites of the plant, as dependent on plant environment; simulation of signal transport in the structure would be a key issue.

Several authors have argued that modelling helps to evaluate the effect of genetic differences across divergent environments, i.e. to quantify genotype×environment interaction (Hoogenboom *et al.*, 2004; Hammer *et al.*, 2005;

Tardieu *et al.*, 2005; Yin *et al.*, 2005; Chapman, 2008; White *et al.*, 2008). The study by Yin *et al.* (2005) on a segregating population (e.g. recombinant inbred lines) is an example showing the different analytical steps that need to be taken: (i) laboratory analysis to obtain molecular markers (genotyping) and marker linkage analysis to construct a marker map, (ii) experiments to measure the trait in question of the phenotypes (i.e. phenotyping), (iii) analysis of the association between marker genotype and trait phenotype to identify QTL, and (iv) the derivation of values of model parameters as a function of QTL allelic information. The last step is essential: modelling can help to improve the understanding of the significance of genetic variation in specific traits across environments or management practices if, and only if, the genetic information can be expressed in or related to model parameters. Another proviso is that the ‘quantitative genetic information’ (e.g. QTL) is not subject to environmental variation. The latter point is outlined in Hammer *et al.* (2006), summarizing the work of Tardieu and co-workers (Reymond *et al.*, 2003; Tardieu *et al.*, 2005) on the genetic variability of sensitivity to drought stress of leaf extension in maize. Leaf elongation rate could be quantified in relation to three environmental variables: meristem temperature, evaporative demand, and soil water potential; QTLs for these sensitivities were established, allowing prediction of responses for ‘virtual genotypes’ in different climatic scenarios.

All the genetic studies just cited concerned what we called ‘process-based models’ (PBM). These models generally lack explicit spatial or morphological representation of the plant. The faithful modelling of morphological phenotypes of different QTL genotypes of a mapping population (Buck-Sorlin, 2002) is an early example using an FSPM. Letort *et al.* (2008) conducted a theoretical study in which they linked parameter values of the GreenLab model (Yan *et al.*, 2004; Guo *et al.*, 2006) to hypothetical genes and simulated the virtual phenotypes resulting from hybridization of homozygous parents. They showed that virtual phenotyping of the resulting cross population could be used for QTL identification. This work represents a quite convincing prototype of what may be possible in the future, even if, as discussed by the authors, real cases are far more complex (see also Luquet *et al.*, 2007).

FSPM offer more detailed architectural representation of the real plant and its properties than PBM. Hence, in principle, there are more options to accommodate quantitative genetic variation in plant properties in the model, particularly traits that constitute plant plasticity. Because of the simulation of the plant structure, FSPM inherently contain more parameters than PBM. This implies that more effort needs to be made to parameterize an FSPM. The error in simulation results not necessarily increases with the number of parameters in a model. As argued by Reynolds and Acock (1985) and Passioura (1996), the inherently better representation of reality by a more complex model may result in smaller errors in simulation results compared to simple models, up to the point where the abundance of parameters (each with their uncertainty) is likely to

aggravate simulation errors. In each concrete case, the type of model (PBM or FSPM) of choice and its degree of complexity depend on the purpose of the study; model verification and sensitivity analysis being instruments helping to decide which way to go.

In genetic research, breeding, and crop improvement via genetic modification, there is always the need to deal with numerous genotypes. Phenotyping procedures have to be quick and cheap. If FSPM are to play a role in this domain, more work is needed to measure attributes that can be converted into model parameters (e.g. via advanced image analysis).

In several (perennial) plant production systems growers interfere with the structural development of the plant so as to maximize over a prolonged period of time the yield and quality of the produce (flowers, fruits). Dedicated FSPM can help to aggregate, test, extrapolate, and apply knowledge to support grower’s decisions on plant manipulation. Examples include peach (Allen *et al.*, 2005), kiwi (Cieslak *et al.*, 2008) and macadamia (D Rodriguez, personal communication), and current work on cut roses grown in greenhouses (Fig. 6) (Buck-Sorlin *et al.*, 2009b).

A central issue in modelling the structural development of plants is understanding why specific buds in specific positions in the structure ‘break’ to produce a new branch (or tiller in cereals and grasses) or remain dormant. Particularly for the simulation of the effects of human intervention with plant structure (e.g. pruning) such insight is indispensable. In such modelling one can search for ‘heuristic rules’ that appear to capture the plant’s behaviour; an example was given by Hanan and Hearn (2003) who specified such model rules to determine the positions in

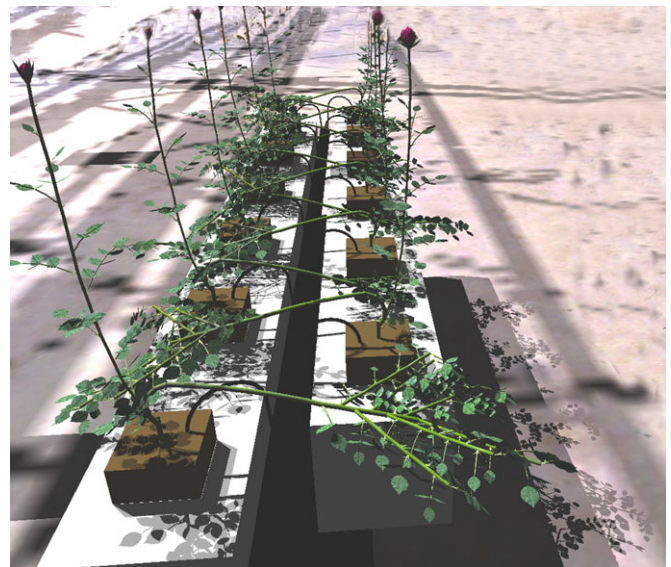


Fig. 6. Visualization of the simulated structure of rose; several plants growing on slabs are shown, each one having one developing upright flower shoot plus a bent shoot. The bent shoots are laid out in opposite directions (bent shoots do not produce flower canes and serve as a permanent source of substrate for the growth of flower canes). (STW project 07435).

the plant structure from which fruits and cotton bolls would develop. Scientifically, it is challenging to try to quantify and implement in a model the knowledge that is becoming available on the molecular mechanisms that determine branching (Leyser, 2009; Prusinkiewicz *et al.*, 2009).

Canopy architecture influences epidemics of foliar diseases: different architectural traits influence the amount and the physiological status of tissue available for lesion development, the spacing between healthy and infected tissues, the microclimate and interception of rain and spores. This system was studied in grapevine (Calonnec *et al.*, 2008) and wheat (Robert *et al.*, 2008) by combining dynamic 3D plant models with dynamic models of fungal development. Both studies highlighted the role of the dynamics of plant structure and the importance of a detailed description of its modular and geometrical aspects in order to understand the outcome of the interactions between the plant and the pathogens. In the second example quoted, this made it possible to investigate how architectural traits, such as the phyllochron and the rate of stem extension, could modulate the dispersion of spores of *Septoria tritici* by rain splash and thus the severity of an epidemic.

Conclusion and outlook

Functional–structural plant modelling is still young and tools and concepts are under continuous development. Many applications can be developed. The modular and realistic representation of plants at different hierarchical scales is a strong feature of FSPM. Features at the canopy level emerge from properties and processes at the plant and organ level. Substantial impact may be expected from FSPM in the analysis of genotype by environment by management interaction and analysis of interactions between function and structure. Efficient and realistic simulation of internal transport opens up possibilities to link up with systems biology. For instance, the role of systems biology would be to explain the generation of a signal at some specific location in the plant (arising from gene expression and metabolic pathways) while FSPM would come in to simulate the transport of signals through the structure and feedback effects elsewhere in the plant. The possibility of generating convincing animations is another strong feature that can be used in extension and teaching.

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