CHAPTER 2

MEASUREMENTS FOR FUNCTIONAL-STRUCTURAL CROP MODELS

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Abstract. The aim of this chapter is to give an overview of the measurements needed for development and parameterization of a functional-structural crop model. Special emphasis will be given to measurements for structural/architectural processes. Size (area, length, width, thickness, volume) of the various organs (e.g., leaves, internodes, flowers, fruits and roots), as well as number of organs, 3D position and time of measurement need to be recorded. Existing methods for full 3D data capture and automatic feature extraction still present many problems. Therefore, human-operated sonic or magnetic trackers are at the moment more suitable to extract and store relevant information.

Physiological processes like photosynthesis, transpiration and carbon allocation require measurements of fresh- and dry-matter weight of the various organs throughout the growing season. For vegetables, fruit and ornamental crops, thermal time to harvest needs to be recorded. In many cases a limited chemical analysis (NPK) is also performed. Depending on the crop, we may assume a common assimilate pool. If this is not feasible, we need estimates of flow and sink/source strength of organs in time. However, adequate measurement methods are currently lacking, hampering development of these models.

Environmental measurements are needed to model the interaction of the plant with its environment. In most cases this at least involves measurement of light and temperature near (slightly above) the crop at frequent intervals. Furthermore, a detailed description of the test site, growth system and crop management is needed. Measurements of relative humidity and carbon-dioxide concentration of the air and various attributes of the root system are less frequently used.

INTRODUCTION

Plant models can be grouped in many different ways. One way is to group them along the axis from structural to functional models: at one side of the spectrum, models are mainly architectural or geometrical in nature (structural model, SM) and at the other side of the spectrum, models are predominantly process-based (Bouman et al. 1996), often referred to as functional models (FM).

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Since the mid 1990s emphasis is given on the integration of both types of models in functional-structural plant models (FSPM). In this paper we will try to give an overview of the type of measurements encountered in literature when trying to develop an FSPM of an individual plant. We will not consider models covering the genetics of plants, nor models trying to describe root systems. Furthermore, focus will be on models for annual, vegetable and ornamental crops. Sievänen et al. (2000) focus more specifically on tree models.

Full parameterization and calibration of an FSPM can be tedious and cumbersome. The different levels of detail (temporal, spatial and organizational) of the model are strongly related with the aim of the model. Creating a model consisting of modules at a range of hierarchical scales can lead to emergent properties and interactions of the underlying modules that are difficult to control at the higher level. These models may be hard to calibrate. In many cases, using 2-3 scales of integration in a model is sufficient, a fact well-known in FM, which has gained renewed interest in recent discussions on systems biology (Hammer et al. 2004). In SM, the phytomer (node, internode and its leaves and axillary buds) represents the level of detail that is needed to simulate growth, shape and quality attributes of individual organs. For simulation of the individual phytomers and organs, modelling of processes at lower scales may be required, such as photosynthesis, carbon flow and signalling. Computational problems may arise in FSPM if (Sievänen et al. 2000):

- the implementation of the model requires pair-wise comparison of all the units of the model tree. This situation may arise, e.g., when the radiation extinction is treated as a geometrical problem;
- the material transport is modelled using partial differential equations as, e.g., for the water flow in 3D tree crowns;
- the processes vary in scale (e.g., hourly calculations over years).

De Reffye and Hu (2003) also notice the risk of combining a huge number of spatial entities (e.g., individual leaves of a tree) with a short time step (e.g., hour) over a long period (years), leading to complex, computationally demanding models. This is especially true for trees or forest stands. However, most crops have a rather simple plant structure and a growing period of a few months. In that case a time step of one or several hours for a single plant poses less of a problem.

The time step used at each level of hierarchy should be chosen appropriately (Bouman et al. 1996). Chelle (2005) gives a nice example of the influence of the size of the time step on the result (e.g., daily average response) using different non-linear models. The type and frequency of measurements needed is a direct consequence of the chosen time step. The time step for many SM is often based on the duration of a growth unit (GU), which is a set of phytomers built within the same growth period (De Reffye and Hu 2003). This can range from a few days for shrubs to one year for trees. The time step of FM is generally ranging from less than one hour to a day, to account for various non-linear effects caused by environmental conditions (light, temperature, water).

We will begin with a listing of some existing FSPMs that differ considerably in their modelling approach. Focus will be on the type of measurements made to gain

insight in the current diversity of models. Then we will look at the different features and possibilities to measure them with regard to architecture, physiology and environment. We will end with a discussion.

INVENTORY OF MEASUREMENTS FOR FSPM

The original Lignum model (Perttunen et al. 1996) is one of the first FSPMs. It was developed as a model for trees and parameterized for young Scotch pine. The time step is one year. Carbon processes are at the tree-segment level. Measurements are also at the year level and include needle mass/tree-segment area (kg m^{-2}), foliage–root relationship (kg kg^{-1}), maintenance respiration rate of needles, roots and sapwood (kg C kg C^{-1} $year^{-1}$), photosynthetic production in unshaded conditions (kg C $year^{-1}$), tree-segment shortening factor, senescence rate of roots and sapwood ($year^{-1}$), density of wood (kg m^{-2}) and fraction of heartwood in new tree segments. Architectural parameters are limited, inclination angle of branches is set at 45 degrees and azimuth orientation is symmetric. Comparisons can be made with regard to length and diameter of the tree. In a newer version of the model, gradual bending of branches is incorporated. Also effect of light interception, branching and sapwood senescence can be studied. For this, light conditions also need to be measured.

Fournier and Andrieu have developed several FSPMs, like ADEL-maize (Fournier and Andrieu 1999) and ADEL-wheat (Fournier et al. 2003). For wheat, the experiment involved different planting densities, while other crop management conditions were kept constant. Data collected include meteorological data (air temperature at 2 metres, global radiation), soil and organ temperatures (using thermocouples) and biological data, both observational and destructive, every two or three days. The data set includes: (1) developmental state of the shoot apex (number of primordia; time to double ridge stage and of terminal spikelet initiation); (2) kinetics of the lengths of leaf laminae, sheaths and internodes; and (3) final size of all organs. Measurement for main shoot and tillers comprised the insertion height of all leaves, the shape and orientation of the midrib using a 3D digitizer, and the 2D shape of the leaves (leaf width as function of distance to tip). In total, 3D shapes of about 100 leaves were measured.

Pearcy et al. (2005) describe YPLANT, a static geometrical model of a tree, using geometrical measurements of various organs. The model can be used for studying light capture and photosynthesis. The geometry can be measured by observation, angle finder and callipers, or a 3D magnetic digitizer. YPLANT contains detailed physiological models, including a Farquhar leaf photosynthesis model, a stomatal submodel and a leaf energy-balance submodel, to study the reaction on local light, temperature, vapour-pressure deficit and CO_2 pressure. A large number of parameters have to be estimated for the various processes, and parameterization involves gas-exchange measurements using an LI-6400 (LI-COR) photosynthesis system. Stem water fluxes and water potential gradients are simulated according to Tyree (1988). Stem hydraulic conductivity is related to stem size using allometric equations.

De Visser et al. (this volume) describe a virtual plant model of cut chrysanthemum, using L-studio (Prusinkiewicz et al. 2000). It combines an L-system architectural model with a nested-radiosity light-interception model (Chelle and Andrieu 1998) and carbon models, including Farquhar assimilation, growth and maintenance respiration model and a sink/source distribution model, based on relative sink strength. Plants are scanned in 3D using a ScanStation. Measurements include countings and angles of leaves, countings of flowers per shoot, size and weight of leaves, diameter, length and weights of internodes, and size and weight of flowers at biweekly intervals. The time step for the physiological processes is one hour, for the SM one day.

Hanan and Hearn (2003) use the approach of linking an existing physiological model OZCOT with an L-system. OZCOT is a top-down cotton crop simulation model, taking account of resource limitations, like water and nutrients. Care had to be taken to translate the crop characteristics to the 3D plants. The time step is synchronized to one day and temperature (degree days) drives the development in both models. OZCOT is the leading model and no real parameterization of the 3D data is done yet. The combination allowed visualization of the results of OZCOT in 3D, introducing some emergent properties. For example, the position of the first fruiting branch on the main stem varies by several nodes within the simulated population, which is also observed in reality.

GreenLab (De Reffye and Hu 2003; Yan et al. 2004) is a general framework for FSPM, integrating realistic structural and functional modelling. Its functional part is inherited from AMAPHydro, developed at the same time as LIGNUM. Architectural parameters like number of organs per metamer and number of metamers in a branch are determined. Physiological parameters relating to sink–source relations are estimated through model inversion: two resistivity parameters for the leaves and two parameters per organ (per physiological age) for the expansion are estimated with a generalized least-squares method (Zhan et al. 2003).

Canonical modelling (Renton et al. 2005) is proposed with the same idea in mind as de Reffye: detailed mechanistic models can be expensive to construct, direct observations are sometimes (nearly) impossible, or knowledge about the underlying processes is incomplete. Examples are sink strength of organs and processes of resource allocation.

ARCHITECTURAL MEASUREMENTS

If we try to model a realistic plant, simple observations and countings are not sufficient, and at least some measurements of size, position and direction of different organs are needed. Compass, angle finder, ruler and callipers can serve as elementary measurement tools, but in most cases more substantiate measurements are required. Preferably one should be able to make 3D point measurements. From these point measurements, several geometrical plant features can be extracted, like size (length, width, thickness) and shape of various organs (internodes, leaves, flowers, fruits and/or roots). Two main approaches exist: contact measurements,

where the 3D coordinate of each point is individually captured, requiring extensive human interaction, and non-contact point-cloud measurements.

Contact measurements

According to Godin et al. (2005), the first 3D digitizer for plants is described by Lang (1973), who used articulated arms where rotation angles were recorded from high-precision potentiometer resistance values. This device directly determines 3D distributions of plant parts, but it has never been commercially available (Takenaka et al. 1998). Therefore, Takenaka developed a so-called pocometer, which does not require electricity and can be carried around in the field. It is a simple device, consisting of a tape measure to measure distance and two protractors to measure zenith angle and azimuth angle. Accuracy depends on distance between base and sample plants: the closer the pocometer is to the sample plant, the wider the angles vary, reducing the relative importance of reading errors. For a 15-cm long object, measured at a distance between 1 and 3 m of the pocometer base, bias is about 1 or 2 mm, and standard deviation is between 6 and 8 mm.

A commonly used contact measurement device within the plant community (e.g. Sinoquet and Rivet 1997; Rakocevic et al. 2000; Evers et al. 2005) is the FASTRAK® magnetic 3D digitizer (Polhemus, Colchester, VT, USA). It includes a magnetic signal receiver and pointer, allowing the user to record the 3D spatial coordinates of the pointer within a hemisphere of 3 m diameter from the receiver. Individual plants are digitally reconstructed by recording a series of point coordinates and the relevant connectivity between the points. Due to its principle of creating a magnetic field, it can be used outdoors at relative ease, but in greenhouse environments the surrounding iron frames can disturb measurements.

Also commonly used (e.g. Sinoquet et al. 1991; Watanabe et al. 2005) is the sonic digitizer GTCO Freepoint 3D. It consists of a hand-held probe with two or more sonic emitters and a triangular detector array with 3 microphones. Calibration is necessary to correct for differences in temperature and humidity of the air. Godin et al. (2005) recommend sonic digitizers to be used only in the laboratory, since they are very sensitive to wind fluctuations in the field.

A large advantage of contact point measurements is that the points to be measured can be annotated directly, especially when recording is done in a structured way using software like Floradig (CSIRO, Australia) or AMAPmod (AMAP, France).

Non-contact point-cloud measurements

Various non-contact optical approaches exist, which provide massive point clouds. Commonly used is laser triangulation, where a laser point or laser line (sheet of light) is projected on the scene. A sensor (camera), which is at fixed angle with respect to the laser, observes the reflection of the laser line, and the position in the image corresponds to the distance between point and camera. By scanning the scene point- or line-wise, a distance profile can be extracted (sometimes together with a

texture scanner). By recording the plant under multiple angles, a 3D reconstruction of the entire plant outline is possible. The method is rather robust, although shininess, absorption by the surface or abundance of ambient light may cause insufficient contrast. Translucency of plant material makes the position estimation less accurate. Occlusions can occur if the object has concavities. Texture mapping can add colour/texture to the object. Major advantages of laser triangulation are its high accuracy, the dense cloud of points that can be measured, and its robustness. It can measure distance from the camera to plant parts, still generating a reasonable 3D outline (profile) of the object in complex situations. Disadvantages are the fixed resolution (depending on the thickness of the laser beam), which may be crucial for scanning small flowers, and scattering as a result of the translucent character of most plant parts. Kaminuma et al. (2004) use a laser range finder (type Voxelan Hew-50HS, Hamano Eng, Japan) to reconstruct *Arabidopsis* plants. Loch (2004) used the Polhemus FastSCAN hand-held laser scanner (triangulation principle) extensively for the generation of leaf-surface models. The hand-held device keeps track of its position by means of a magnetic field, hence being vulnerable for nearby metallic objects or electromagnetic fields.

Time of flight is used by Sinoquet et al. (1993). They describe a device for automated measurement of laser-beam interception (DALI). It is based on a laser distance meter moving within a horizontal frame of 5 m x 5 m above the canopy. A laser beam is emitted and backscattered radiation hits a photodiode via the receiver optics. The distance to the first beam–vegetation contact is inferred from the time interval between emitted and received beams measured by a quartz-stabilized clock. The distance meter can be moved across the frame by means of two perpendicular stepping motors.

Volumetric intersection is used by De Visser et al. (this volume) for chrysanthemum plants. Here a 3D object is reconstructed by capturing the silhouette of an object against a monochrome background, which can be easily discarded by a process called chroma-keying. By turning the object on a turning table, a silhouette is created from different angles of view. The 3D shape can be reconstructed by volumetric intersection of the silhouettes: starting with a filled 3D cube (voxel space), parts of the cube that do not belong to the silhouette are cut out. The method requires good calibration and the approach can give good results if the objects are reasonably simple, i.e. if there is not too much occlusion/overlap of plant parts. Thin stems can cause a problem: often the reconstructed 3D object has broken parts, due to movement of plant parts or small calibration errors. An alternative approach, which is less prone to this type of error, is reverse volumetric intersection, used to extract stems of roses (Noordam et al. 2005).

Stereo vision has been used by Ivanov et al. (1995), where a canopy of maize plants has been reconstructed. In this set-up, two cameras at a fixed distance apart record the same scene. Extensive calibration of cameras leads to an estimate of the perspective-transform matrix for each of the cameras. From the shift of corresponding points in both views, the 3D position in real-world coordinates can be computed. Sequential manual removal of leaves and image recording was necessary to obtain a full reconstruction of the stand. A standard deviation of about 1 cm in X- and Y-direction and 5 cm in Z-direction could be obtained, whereas bias was rather

low. Stereovision as applied by Ivanov et al. required extensive manual intervention. Nowadays, many different photogrammetry software tools exist, where pictures of a scene are taken under a large number of angles with a calibrated camera. By interactively indicating object features like points, lines or edges, the software will try to reconstruct the points across the photos, resulting in a 3D model. Phattaralerphong and Sinoquet (2005) created artificial 3D scenes of trees, using digitized data at leaf scale. The hence created scene was used to synthesize plant images using POV-Ray®. From these images, canopy volume parameters were estimated, using photogrammetic principles.

Another imaging method is structured light, where a special pattern of light (e.g., a grid) is projected on the object and from the transformation of the grid, depth is estimated. This method works well on reasonably smooth surfaces that do not have too many discontinuities. It is probably not suitable for complex plants. Mangoldt et al. (2004) try to adapt existing methods for 3D recording, using structured light in combination with a phase-shift technique, as an improvement for plant material with regard to the commercially available DigiScan (RSI) 3D scanner.

All these imaging methods only record the outline of the plant. For complex plants the outline does not contain enough information and we need to revert to internal imaging methods, like X-Ray CT-scans or MRI to capture a full 3D structure of a plant. Furthermore, although a 3D volume of the plant might be created automatically with point-cloud techniques, plant features still have to be extracted interactively since current software is not yet capable of fully automatic extraction of plant features in complex images.

MEASUREMENTS FOR PHYSIOLOGICAL PROCESSES

Process-based or functional modelling of annual crops has been studied extensively since the 1970s. One of the pioneers in this area was C.T. de Wit (Bouman et al. 1996). He distinguished between potential, attainable and actual crop production. For potential production, temperature and radiation are the main controlling factors. For attainable production, water and nutrient stress have to be taken into account. For actual production, the plant also has to deal with weeds, diseases and pests. The complexity of the model depends on the processes integrated in the model.

Current FSPM mainly aim at integrating processes for the potential and attainable production level. Processes at the third level are mainly studied in isolation, like plant–insect interaction.

Key processes that need to be modelled at the potential and attainable level include:

- light extinction and photosynthesis;
- thermal-time-based plant development, e.g., leaf area that captures the light;
- interactions between developing sinks and available sources of carbohydrates;
- water and heat balance.

The parameter set that was first developed for wheat in the SUCROS model (see Bouman et al. 1996) served as a good starting point for modelling physiological processes of other C3 plant species. Some of the parameters in this model vary only slightly between crop species (e.g., photochemical efficiency), yet others are crop-

and even cultivar-specific. A standard procedure has been developed at our institute for calibrating the Intkam model, a more advanced, SUCROS-type FM (e.g. Marcelis et al. 2000). The protocol for sweet pepper is listed in Box 1.

Box 1. *Protocol for calibrating the Intkam model for sweet pepper*

Plants are grown under controlled conditions. The main source of assimilation is photosynthesis and for this, light-response curves are determined for sun- and shade-adapted leaves regularly.

In order to model plant development, the organ appearance, growth, flower abortion and fruit ripening of approximately 8 selected plants per treatment are followed. These plants are randomly selected and tagged at the start of the experiment. At weekly intervals the following are registered:

- number of flowers and their location on the stem;
- number of aborted flowers and their location on the stem;
- number of fruits and their location on the stem;
- length and diameter of these fruits until they are harvested;
- dates of these measurements.

For monitoring plant growth, approximately 8 plants per treatment are harvested destructively at regular intervals (ca. 1 month). The first harvest is at planting, another one is on the day the treatments start. The following are determined:

- fresh weight of leaves, stems and fruits separately;
- dry weight of the leaves, stems and fruits separately (dried 48 h at 70 °C followed by 24 h at 105 °C). If dry weight is determined of a sample of the harvest, fresh weight of this sample has to be determined as well;
- leaf area. For example, the length of every third leaf can be measured if a conversion factor is known. This conversion factor can be established by scanning the area of a random set of leaves for calibration;
- nutrient concentrations (N, P, S, K, Ca, Mg) of samples of the dried leaves, stems and fruits separately;
- dates of these harvests;
- location of the harvested plants.

For fruit growth, once or twice a week, fruits from 12 plants per treatment and per replicate are harvested. The following are recorded:

- number of harvested fruits;
- fresh weight of the harvested fruits (average per plant);
- class, disorders, plus their definition; e.g., Blossom End Rot;
- dates of harvests;
- fresh and dry weight of a randomly selected sample of the harvested fruits (dried 24 h at 70 °C followed by 24 h at 105 °C), and derived from this the fruit dry-matter concentration (not every harvest necessary).

The sweet-pepper protocol can serve as an example for calibration of the physiological processes. For development of an FSPM, it is advisable to determine the features of each individual organ and even to determine the stem features at internode basis. Also note that dry matter rather than fresh matter is used for explanatory photosynthesis-driven models.

For sink/source-related processes, two main approaches exist. Either we can regard all assimilates as a common pool or we have to model specifically the local sinks and sources and transport of assimilates throughout the plant. Heuvelink (1996) found no local effects of leaves on fruit production of tomato, and he concluded that a tomato plant can be regarded as one common assimilate pool. This agrees with Bancal and Soltani (2002), who concluded that for wheat grain filling, the use of resistances in modelling is just a mathematical burden, and that potential growth under optimal conditions can be used to estimate sink strength of an organ as a function of its thermal time. Under these assumptions, the method of Box 1 will be sufficient if treatments without source limitation are carried out and individual organs are carefully monitored. However, if local effects do play a role, estimates of carbohydrate and water flows would be needed. These are difficult to obtain from direct measurements, and we would have to revert to approaches like functional NMR. Alternatively, we can assume a certain mechanism, and try to estimate the parameters of this mechanism using inverse modelling techniques.

For studying photosynthesis, reflection/absorption/transmission characteristics of leaves and other organs are needed. A spectrophotometer can be used for this.

ENVIRONMENTAL MEASUREMENTS

Environmental recordings include a detailed description of the test site. E.g., if the test is done in a greenhouse, the arrangement of the greenhouse would need to be recorded like location of treatments, plants for the different harvests, border plants, dimensions and characteristics of greenhouse, as well as planting density and relevant crop management operations, like dates of spraying, pruning or bending.

Also regular logging (at least hourly) of temperature and light is required. It is recommended to measure outside global radiation (J m^{-2} s^{-1}), e.g., using a LI-COR quantum sensor, outside air temperature (°C), inside air temperature (°C), inside relative air humidity or vapour-pressure deficit (kPa), and inside CO_2 concentration (ppm). If artificial lighting is used, also on/off times of the lights, the total radiation at crop level and the spectral specifications of the light source are to be recorded.

For exact studies of light interception, one could measure the incident light spectrally just above the crop using a spectrophotometer from multiple directions (Power Distribution Function). Temperature needs to be measured close to the canopy and can be measured with a range of devices. Small-scale temperature effects can be measured, modelled or simply ignored. For outside plants humidity and rainfall measurements are important.

If the model includes nutrient or water stress, soil characteristics need to be measured: nutrients requiring sensors for EC conductivity, pH meters or ion-specific sensors, permeability of the soil, free-water content.

When we want to use an FSPM for very detailed processes, Chelle (2005) proposes a set of physical variables for phylloclimate modelling, i.e. the physical environment perceived by each aerial organ of a plant population (Table 1).

Table 1. *Physical variables for phylloclimate modelling (from: Chelle 2005, reproduced with permission from the New Phytologist Trust)*

	Variable	Plant function affected
Radiation	Spectral irradiance	Photosynthesis
	Ultraviolet	Photomorphogenesis
	PAR (red, blue)	Stomatal opening
	Near infrared	Energy budget
	Thermal infrared	
Surrounding air	Wind speed	Photosynthesis
	Temperature	Thigmomorphogenesis
	Humidity	Stomatal opening
	CO_2 content	Energy budget
	Pollutants content	
Organ temperature	Surface temperature	Growth and development
	Internal temperature	Photosynthesis
		Pathogens development
On-leaf water	Quantity	Pathogens development
	Wetness duration	Pollutant deposition
		Energy budget

DISCUSSION

Non-contact vision-based data capture can be used for relatively simple plants or for individual organs. The measurements can directly reconstruct the 3D plant on screen, showing many full details. Automatic feature extraction is still in its infancy and it requires human interaction to extract the relevant features of the plant structure and dimensions. However, by storing the raw data in a database, 3D plants can eventually be used for automatic feature extraction.

Clearly, for complex plants, non-contact data capture is not adequate, since the inner part of the plant can not be measured. It would require advanced and expensive techniques like CT-scanning to have information also of the interior of plants.

Touch sensors are often laborious to use, and are not able to reconstruct the plant fully. They have the important advantage of direct human interpretation. Therefore, all relevant details, as defined beforehand, can be extracted, reducing the amount of information stored to a minimum. Especially when using computer programs like those developed by the AMAP group or Floradig, the storage can efficiently be used in reconstructing the architectural model. Two types of touch sensors are often used where sonic sensors can be used when no wind is available. Magnetic trackers are to be preferred, but care should be taken with disturbing nearby metal objects.

Measurements for physiological processes often require dry and fresh biomass, sometimes extended by nutrient or sugar measurements. If light interception is studied, absorption and reflection of leaves and stems should be measured.

Which environmental measurements are needed strongly depends on the aim of the model, but a detailed description of the experimental conditions should always be included. In most cases regular logging of temperature and light is needed.

De Reffye and Hu (2003) and Renton et al. (2005) try to limit the amount of detail in the model and the number of measurements needed by making assumptions on the mechanisms and using inverse modelling to estimate certain process parameters. Whether their assumptions are generally applicable strongly depends on the aim of the model and the specifics of the crop. If the modeller wants to use the framework to study processes (like phylloclimate) not implemented in the original framework, this concept might not be applicable. In general, the level of detail in the model (and therefore the measurements needed) should always be driven by the aim of the model.

A plant is the result of organogenesis and physiological processes. The architectural and biophysical measurements of individual organs reflect the results of these processes. By recording them under different conditions, insight can be obtained in the control of these processes by external factors.

A detailed FSPM incorporates our knowledge on plant processes and can serve as a tool to study their relationship. Often the aim of an FSPM is to help explain the results in terms of the underlying processes or predict the result under different conditions. For example, it is interesting to know whether the influence of planting density on biomass production can be fully explained by detailed modelling of light interception. A way to better understand and explain interactions within plants and between plants and environment is to study the processes at smaller scales, taking into account spatial variability of microclimate and intra-plant variability (Chelle 2005). However, this requires many more measurements and coupling of different spatial and temporal scales, and will be a great challenge for future FSPM.

REFERENCES

Bancal, P. and Soltani, F., 2002. Source-sink partitioning: do we need Munch? *Journal of Experimental Botany*, 53 (376), 1919-1928.

Bouman, B.A.M., Van Keulen, H., Van Laar, H.H., et al., 1996. The 'School of de Wit' crop growth simulation models: a pedigree and historical overview. *Agricultural Systems*, 52 (2/3), 171-198.

Chelle, M., 2005. Phylloclimate or the climate perceived by individual plant organs: what is it? how to model it? what for? *New Phytologist*, 166 (3), 781-790.

Chelle, M. and Andrieu, B., 1998. The nested radiosity model for the distribution of light within plant canopies. *Ecological Modelling*, 111 (1), 75-91.

De Reffye, P. and Hu, B.G., 2003. Relevant qualitative and quantitative choices for building an efficient dynamic plant growth model: GreenLab Case. *In:* Hu, B.G. and Jaeger, M. eds. *Plant growth modeling and applications: proceedings-PMA03: 2003 international symposium on plant growth modeling, simulation, visualization and their applications, Beijing, China, October 13-16 2003.* Tsinghua University Press, Beijing, 87-107.

Evers, J.B., Vos, J., Fournier, C., et al., 2005. Towards a generic architectural model of tillering in Gramineae, as exemplified by spring wheat (*Triticum aestivum*). *New Phytologist*, 166 (3), 801-812.

Fournier, C, Andrieu, B., S., Ljutovac, et al., 2003. ADEL-Wheat: a 3D architectural model of wheat development plant growth modeling and applications. *In:* Hu, B.G. and Jaeger, M. eds. *Plant growth modeling and applications: proceedings-PMA03: 2003 international symposium on plant growth modeling, simulation, visualization and their applications, Beijing, China, October 13-16 2003.* Tsinghua University Press, Beijing, 54-66.

Fournier, C. and Andrieu, B., 1999. ADEL-maize: an L-system based model for the integration of growth processes from the organ to the canopy: application to regulation of morphogenesis by light availability. *Agronomie,* 19 (3/4), 313-327.

Godin, C., Costes, E. and Sinoquet, H., 2005. Plant architecture modelling: virtual plants and complex systems. *In:* Turnbull, C.G.N. ed. *Plant architecture and its manipulation*. Blackwell, Oxford, 238-287. Annual Plant Reviews no. 17.

Hammer, G.L., Sinclair, T.R., Chapman, S.C., et al., 2004. On systems thinking, systems biology, and the in silico plant. *Plant Physiology,* 134 (3), 909-911.

Hanan, J.S. and Hearn, A.B., 2003. Linking physiological and architectural models of cotton. *Agricultural Systems,* 75 (1), 47-77.

Heuvelink, E., 1996. *Tomato growth and yield: quantitative analysis and synthesis.* Wageningen University, Wageningen. PhD thesis Wageningen

Ivanov, N., Boissard, P., Chapron, M., et al., 1995. Computer stereo plotting for 3-D reconstruction of a maize canopy. *Agricultural and Forest Meteorology,* 75 (1/3), 85-102.

Kaminuma, E., Heida, N., Tsumoto, Y., et al., 2004. Automatic quantification of morphological traits via three-dimensional measurement of *Arabidopsis*. *Plant Journal,* 38 (2), 358-365.

Lang, A.R.G., 1973. Leaf orientation of a cotton plant. *Agricultural Meteorology,* 11 (1), 37-51.

Loch, B.I., 2004. *Surface fitting for the modelling of plant leaves.* University of Queensland, Brisbane. PhD Thesis University of Queensland

Mangoldt, T., Kurth, W., Bucksch, A., et al., 2004. A system for recording 3D information with applications in the measurement of plant structure. *In:* Godin, C., Hanan, J., Kurth, W., et al. eds. *Proceedings of the 4th international workshop on functional-structural plant models: abstracts of papers and posters, 07-11 June 2004, Montpellier, France*. UMR/AMAP, Montpellier, 28. [http://amap.cirad.fr/workshop/FSPM04/proceedings/4thFSPM04Proceddings.pdf]

Marcelis, L.F.M., Van den Boogaard, R. and Meinen, E., 2000. Control of crop growth and nutrient supply by the combined use of crop models and plant sensors. *In: Agricontrol 2000: international conference om modelling and control in agriculture, horticulture and post-harvested processing, July 10-12, 2000, Wageningen, the Netherlands: proceedings*. IFAC, [S.l.], 351-356.

Noordam, J.C., Hemming, J., Van Heerde, C., et al., 2005. Automated rose cutting in greenhouses with 3D vision and robotics: analysis of 3D vision techniques for stem detection. *Acta Horticulturae,* 691 (Vol 2), 885-892.

Pearcy, R.W., Muraoka, H. and Valladares, F., 2005. Crown architecture in sun and shade environments: assessing function and trade-offs with a three-dimensional simulation model. *New Phytologist,* 166 (3), 791-800.

Perttunen, J., Sievänen, R., Nikinmaa, E., et al., 1996. LIGNUM: a tree model based on simple structural units. *Annals of Botany,* 77 (1), 87-98.

Phattaralerphong, J. and Sinoquet, H., 2005. A method for 3D reconstruction of tree crown volume from photographs: assessment with 3D-digitized plants. *Tree Physiology,* 25 (10), 1229-1242.

Prusinkiewicz, P., Karwowski, R., Měch, R., et al., 2000. L-studio/cpfg: a software system for modeling plants. *In:* Nagl, M., Schürr, A. and Münch, M. eds. *Applications of graph transformations with industrial relevance: international workshop, AGTIVE'99 Kerkrade, The Netherlands, September 1-3, 1999: proceedings*. Springer, Berlin, 457-464. Lecture Notes in Computer Science no. 1779.

Rakocevic, M., Sinoquet, H., Christophe, A., et al., 2000. Assessing the geometric structure of a white clover (*Trifolium repens* L.) canopy using 3-D digitising. *Annals of Botany,* 86 (3), 519-526.

Renton, M., Hanan, J. and Burrage, K., 2005. Using the canonical modelling approach to simplify the simulation of function in functional-structural plant models. *New Phytologist,* 166 (3), 845-857.

Sievänen, R., Nikinmaa, E., Nygren, P., et al., 2000. Components of functional-structural tree models. *Annals of Forest Science,* 57, 399-412.

Sinoquet, H., Moulia, B. and Bonhomme, R., 1991. Estimating the three dimensional geometry of a maize crop as an input of radiation models: comparison between three-dimensional digitizing and plant profiles. *Agricultural and Forest Meteorology,* 55 (3/4), 233-249.

Sinoquet, H. and Rivet, P., 1997. Measurement and visualization of the architecture of an adult tree based on a three-dimensional digitising device. *Trees: Structure and Function,* 11 (5), 265-270.

Sinoquet, H., Valmorin, M., Cabo, X., et al., 1993. DALI: an automated laser distance system for measuring profiles of vegetation. *Agricultural and Forest Meteorology,* 67 (1/2), 43-64.

Takenaka, A., Inui, Y. and Osawa, A., 1998. Measurement of three-dimensional structure of plants with a simple device and estimation of light capture of individual leaves. *Functional Ecology*, 12 (1), 159-165.

Tyree, M.T., 1988. A dynamic model for water flow in a single tree: evidence that models must account for hydraulic architecture. *Tree Physiology*, 4 (3), 195-217.

Watanabe, T., Hanan, J.S., Room, P.M., et al., 2005. Rice morphogenesis and plant architecture: measurement, specification and the reconstruction of structural development by 3D architectural modelling. *Annals of Botany*, 95 (7), 1131-1143.

Yan, H., Kang, M., De Reffye, P., et al., 2004. A dynamic, architectural plant model simulating resource-dependent growth. *Annals of Botany*, 93 (5), 591-602.

Zhan, A.G., De Reffye, P., Houllier, F., et al., 2003. Fitting a functional-structural growth model with plant architectural data. *In:* Hu, B.G. and Jaeger, M. eds. *Plant growth modeling and applications: proceedings-PMA03: 2003 international symposium on plant growth modeling, simulation, visualization and their applications, Beijing, China, October 13-16 2003*. Tsinghua University Press, Beijing, 236-249.