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Plant growth and architectural modelling and its applications

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Over the last decade, a growing number of scientists around the world have invested in research on plant growth and architectural modelling and applications (often abbreviated to plant modelling and applications, PMA). By combining physical and biological processes, spatially explicit models have shown their ability to help in understanding plant–environment interactions. This Special Issue on plant growth modelling presents new information within this topic, which are summarized in this preface. Research results for a variety of plant species growing in the field, in greenhouses and in natural environments are presented. Various models and simulation platforms are developed in this field of research, opening new features to a wider community of researchers and end users. New modelling technologies relating to the structure and function of plant shoots and root systems are explored from the cellular to the whole-plant and plant-community levels.

Key words: Plant morphology, architecture, functional–structural plant model, FSPM, source and sink, root system, photosynthesis, simulation, plasticity, computational plants.

INTRODUCTION

Plant architecture, i.e. the dynamical organization of plant components and their three-dimensional (3-D) distribution, plays a pivotal role in gathering multiple resources from the environment. A plant deploys its photosynthetic apparatus in a 3-D space in order to optimize the interception of incoming radiation; however, the incident angle of direct radiation changes constantly according to the solar trajectory. A plant’s light environment is also modified by diffuse radiation coming from different sections of the sky hemisphere and is perturbed by neighbouring vegetation. Plant roots extend into different soil layers and adjust their direction of growth in order to take up soil water and nutrients (e.g. nitrogen, phosphorus), which have heterogeneous spatial distribution. Simultaneously, the acquired assimilate, water and nutrients are transported and allocated to the whole plant for maintenance, expansion of existing organs and initiation of new organs. The architecture of the plant, in turn, is modified through the allocation of assimilate, which determines the growth rates of different organs. At the same time, the plant is subjected to external mechanical stresses, such as gravity or wind forces, and must adapt its shape and develop support structures. In order to adapt their shape to the constantly changing environment, and in response to competition from nearby plants, individual plants gradually develop their architecture according to source–sink activities and endogenous signals. This adaptation can result in complex structures. In the context of cultivated plants, growers consciously modify plant architecture (e.g. by pruning) in order to optimize biomass production and quality. Plant breeders also select new crop varieties intentionally with desired morphological traits. Plant 3-D structure is then a key factor for integrating and understanding the relationships between functions of different organs at the whole-plant level. This is the reason why describing, analysing, modelling and simulating plant architecture has become an important challenge during the last decade (Fourcaud et al., 2008).

The architectural concepts for analysing the form of tropical trees were established around 40 years ago. These concepts are now being used to describe plants of other types and in other areas (Barthélémy and Caraglio, 2007). The first 3-D computer simulation models of plant architecture were developed in the 1980s by de Reffye and his collaborators (see de Reffye et al., 1988, for example). With the improvement of computer capabilities, more and more accurate models and simulations of spatial structures of herbaceous plants and trees were developed (de Reffye et al., 1988; Prusinkiewicz and Lindenmayer, 1990); however, no plant functional processes were embedded in these pioneer models, which limited their potential applications in agronomy, horticulture and forestry. To overcome this drawback, great efforts have been made from the mid-1990s onwards to develop functional–structural (FS) plant models by combining physical and/or physiological processes (photosynthesis, assimilate partitioning, etc.) with explicit descriptions of plant structure (Pertunen et al., 1996; Room et al., 1996; Le Roux et al., 2001; Godin and Sinoquet, 2005; Fourcaud et al., 2008; Hanan and Prusinkiewicz, 2008; Vos et al., 2010).

In the context of global climate change and rapid population increase, there is an urgent need to solve the serious problems of world food security and environmental deterioration. Breeding high-yielding crops can be achieved by improving both aerial and below-ground morphological traits, for instance to maximize radiation harvesting and nutrient uptake. Another issue is to optimize crops and forest management regimes in order to lessen the pollution problems induced by excessive fertilizer and pesticide applications. Computer models and in silico simulations of plant growth and architecture provide efficient tools to achieve these objectives, in addition to field studies. Computational plants can...
help bridge the knowledge gap in understanding how plant growth responds to a changing environment, and in return how the environment is modified by plant growth. During the last decade, an increasing number of researchers throughout the world have invested in plant growth and architectural modelling and applications (PMA; Hu and Jaeger, 2003; Fourcaud and Zhang, 2008; Li et al., 2010). Diverse approaches and tools are being developed at different temporal–spatial scales. This Special Issue of *Annals of Botany*, which includes 13 papers, highlights new advances in PMA and contains research results for a variety of crop species or trees growing in various conditions, e.g. cultivated fields, greenhouses or natural environments. A wide range of modelling approaches and simulation tools system is presented. New modelling technologies relating to structure and function of plant shoots and root systems are explored from the cellular level up to whole-plant and plant communities.

**PLANT ARCHITECTURAL COMPLEXITY**

The architecture of horticulture and crop plants, as well as trees, is influenced by endogenous factors such as hormone signals and trophic competition between organs, but also by exogenous factors such as light distribution, temperature, soil water and nutrient regimes. Plant morphology can also be artificially modified by humans through agronomic practices, such as pruning and training.

Many efforts have been made in the last decade to model the structural development of plants taking into account their plasticity, i.e. their ability to adapt their shape and to regulate their functions in a changing environment. This is illustrated by the work of Pallas et al. (2011) who investigate the architectural growth of grapevine (*Vitis vinifera*). These authors develop an updated version of the GreenLab model in which axis organogenesis is driven by trophic competition and soil water status. Simulation results show that the model based on the ‘common assimilate pool’ theory reproduces plant organogenesis to a satisfactory degree, although its ability to account for plastic response in grapevine development can be improved (Pallas et al., 2010).

Characterized by vigorous growth and competition for photosynthate between vegetative and fruit growth, the kiwifruit vine (*Actinidia deliciosa*) develops with high architectural plasticity. By incorporating existing biological knowledge, Cieslak et al. (2011) develop a L-system based model of kiwifruit vine that integrates structural development, carbon dynamics, and environmental and management effects on vegetative and generative components. The model is calibrated based on existing experimental datasets, and the simulated architecture plasticity of kiwifruit vine is found to be qualitatively similar to the observations. The influence of topological distance between sink and source and the competition for carbon reserves on shoot growth is investigated, and the work shows that this distance plays an essential role in carbon allocation for plant species such as kiwifruit. In contrast to previous models, the branching pattern of the kiwifruit vine is derived directly from the simulation as an emergent property of the model.

Winter oilseed rape (*Brassica napus*) is a herbaceous crop that has a complex reproductive architecture. The difficulty for quantifying the growth and architectural configuration of winter oilseed rape at the reproductive stage is mainly attributable to the expansion delays of ramifications and inflorescences, the photosynthesis of pods and the energetic cost of their oleaginous seeds. By updating the GreenLab model to account for the expansion delay, pod photosynthesis and oil synthesis, Jullien et al. (2011) evaluate the costs of ramification through quantifying the interaction between architecture and source–sink dynamics in the crop. This work provides promising clues for the construction of FS models for plants with complex architectural plasticity and oleaginous components.

It is of great importance to quantify the growth and development of plants and their interaction with fragile ecosystems. For instance, Mongolian Scots pine (*Pinus sylvestris* var. *mongolica*) is a species growing in the arid and semi-arid regions of East Asia that has been planted for windbreak and sand fixation purposes. The structure of Mongolian Scots pines is usually strongly influenced by the specific environment conditions that prevail (strong winds, extreme temperatures, soil water fluctuation, etc). Using models for simulating deterministic topological development is unrealistic considering the high variability of branching patterns observed in this species, so stochastic FS model is used by Wang et al. (2011) to simulate its architecture. The authors show that the calibration of such a model allows accurate organogenetic and morphogenetic processes to be reproduced. The simulations produce realistic architectures of Mongolian Scots pines that can be used in relation to soil erosion studies and thus provide useful information to assist in combating desertification.

**DYNAMICS OF SOURCE–SINK ACTIVITIES**

Indeterminate plants initiate new leaves gradually, which first act as sinks competing for photosynthate and then operate as individual photosynthetic factories (Barthélémy and Caraglio, 2007). The growth of fruit affects the expansion of new leaves and results in wide fluctuations in the pattern of fruit-set, as a fruit is a substantial sink competing for assimilates. In commercial horticultural production, growers try to reduce such large fluctuations in fruit-set and hence yield, and plant modelling can be used for optimizing management strategies through the manipulation of the dynamics of source–sink activities. Ma et al. (2011) conduct a greenhouse experiment where the growth of six *Capsicum* cultivars is determined; these plants are characterized by large differences in fruit size and fruit-set. The observation data are used to calibrate the GreenLab model and to analyse the dynamics of carbon partitioning within the whole plants. The resulting simulations show that the fruit size has a substantial impact on the variation in fruit-set and yield. It is shown that a reduction in fruit-set heterogeneity and an increase in yield could be achieved by following different management strategies that consist of adjusting source and sink activities within the plants (e.g. by thinning). Kang et al. (2011) analyse the dynamics of source–sink activities in tomato (*Solanum lycopersicum*) plants using a similar approach. They also conduct greenhouse experiments, with contrasting planting densities in which fruit-set probability is estimated by regular observations. Parameter values of source and sink forces are estimated by fitting the GreenLab model with measured data at the organ and plant level. They find that the relationship between dynamic fruit-set and source–sink ratio of tomato plants can be described with a single regression
line. This modelling approach is promising and could be used to suggest new agronomic practices in order to optimize highinput commercial production systems and thus to minimize their impact on the environment.

Rice (Oryza sativa) is one of the dominant cereal crops in many Asian countries. The morphology of rice has been substantially modified by breeding in recent decades in order to enhance its yield potential. In this context, genetic analyses of morphological traits have been investigated in detail (Yang and Hwa, 2008; Qian et al., 2011). A FS model of rice is developed by Xu et al. (2011), which allows computation of various phenotypes as a result of basic ecophysiological processes (e.g. light interception, photosynthesis and growth, and source–sink activities) controlled by QTL information. This model is developed under the GroIMP platform that implements the Relational Growth Grammar formalism. Here, the emphasis is put on linking the rice model to a quantitative genetic model, which is a promising approach and paves the way for rice ideotype breeding using FS modelling.

FROM ROOT SEGMENT TO THE WHOLE PLANT
Most FS plant models have mainly concentrated on the aerial parts, whereas the root system has been neglected or simplified as a sink compartment. However this ‘hidden half’ of the plant plays a key role in soil water and nutrient uptake, as well as plant anchorage. The spatial distribution of root segments, which affects the volume of soil that can be exploited, is an essential factor for plants in a suboptimal soil environment. 3-D root models can be powerful tools for analysing and optimizing root architecture of plants subject to low soil fertility (Lynch, 2007). Root cortical aerenchyma (RCA) formed by programmed cell death is generally an adaptation to hypoxia. However, considering that RCA can also be induced by suboptimal soil conditions, Postma and Lynch (2011) hypothesize that the plant could benefit from its formation to reduce the carbon and phosphorus cost of roots for soil exploration. They couple a shoot model with SimRoot, a dynamic 3-D model of root growth and architecture, to analyse the functional benefit of RCA on the growth of maize (Zea mays) and common bean (Phaseolus vulgaris) in contrasting degrees of soil phosphorus availability. To assess the effects of global climate change, the growth of plants with RCA in a high CO2 environment is also simulated. RCA formation is shown to be a positive trait for phosphorus acquisition and evidence is given that the carbon costs of soil exploration can indeed be reduced. Given the substantial depletion of soil nutrient reserves in many arable lands, breeding new crop cultivars with the RCA trait for low phosphorus area is a promising direction for research.

The trade-offs related to RCA formation must be quantified. The capacity of a root segment to absorb and transport water and nutrients depends on the anatomical structure of its epidermis, cortex and endodermis layers, and RCA may reduce radial water or nutrient transport. As RCA formation changes longitudinally within a root segment, information about the 3-D spatial relationships of root cells is thus valuable. Wu et al. (2011) present a computer-aided 3-D reconstruction and visualization technique for exploring spatial distribution of vessels, passage cells and lateral roots along a root segment of winter wheat (Triticum aestivum). This method has the significant advantage of being based on a classical, serial-section method, which does not involve expansive and sophisticated equipment.

Excessive soil nitrogen often results in severe problems of environmental pollution. Nitrogen fixation in root nodules of legume plants can provide a huge amount of nitrogen that is environmentally friendly. As nodulation is a costly process, legume plants have developed a signal system for autoregulation of nodulation in order to achieve a balance between nodulation and plant growth. In order to understand the complex temporal–spatial features of signalling-development processes in a legume root and shoot system, Han et al. (2011) create a model of soybean (Glycine max) by utilizing a context-sensitive L-system for simulation of root structure and nodule distribution, as well as multi-rate signal co-ordination in the whole plant. Their work opens the possibility for implementation of virtual experiments to analyse mechanisms of nodulation autoregulation in legume plants, and it is a promising step for linking plant architectural modelling with plant systems biology.

INTERFACE FOR PLANT–ENVIRONMENT INTERACTION
The surfaces of plant organs are the main interfaces of plant–environment interactions, and leaf shape thus constitutes a critical feature of a plant. It can be modified by growth conditions and according to ontogenetic stages. Leaf shape has been widely investigated in cereals and different mathematical functions have been proposed for their description. Dornbusch et al. (2011) take measurements on leaf shape of different cultivars of winter wheat (Triticum aestivum), barley (Hordeum vulgare) and maize (Zea mays) with contrasting planting densities and cultivated under various conditions, e.g. in the field or in a growth cabinet environment. They fit the measured leaf shapes with an empirical model and find for wheat and barley it is rather stable for a comparable ontogenetic stage, but differs between juvenile and adult phases. This is a valuable finding for the improvement of FS models of cereal crops.

3-D static structural models, i.e. representations of the real or simulated shape of a plant at a given stage of its development, are a useful alternative to dynamic models of plant growth for describing leaf distribution in space and for studying plant–environment interactions. Sarlikioti et al. (2011) build 3-D structural models of tomato grown in a greenhouse and use a nested radiosity model to compute the spatial distribution of direct and diffuse radiation in the canopies, and a Farquhar, von Caemmerer and Berry model (FCB, Farquhar et al., 1980) to estimate photosynthesis. They show that simulations based on these 3-D structural models are in good agreement with the measured light distribution, and that an explicit description of morphological traits (e.g. leaf angle) is essential for computing accurate light distribution and photosynthesis within heterogeneous canopies.

FS models can also provide interfaces for modelling pathogen or pest dispersal dynamics in plant structures and crop canopies, which is useful for optimizing pesticide applications and thus minimizing impacts on the environment and public health. Burie et al. (2011) utilize a model combining the
3-D structural dynamics of individual grapevine plants with the dispersal and disease dynamics of the powdery mildew pathogen, *Erysiphe necator*. They show that this model can be used to optimize management strategies in order to control the disease at a low level under different climatic scenarios. Although such a mechanistic model is suitable for understanding complex interactions at the individual plant scale, it is difficult to extend to the vineyard scale partly because of computational limitations; a compartment model is thus recommended for application at a larger scale. Moreover, such a large-scale model can be preliminarily calibrated at the plant level using FS models.

**PERSPECTIVES**

Functional–structural plant models become more and more popular as they allow interactions between plant growth and environment to be considered with a high level of accuracy. This modelling approach opens exciting perspectives, in particular for optimizing crop production whilst minimizing the environmental impact of agricultural practices.

The ideotype approach is a good example of the potential use of FS models, and has been utilized to improve crop yield potential. The concept of ‘new plant type’ (NPT), for instance, was adopted at the International Rice Research Institute (IRRI) for breeding high-yielding rice cultivars by modifying the source and sink sizes of individual rice plants (Peng et al., 2008). Inspired by the NPT program, breeders in China initiated a super-rice breeding program using a combination of an inter-subspecific heterosis and ideotype approach, in which accurate definitions of morphological traits were made for leaf geometrical shape, leaf angle, plant topology (panicle and tillers), etc. Some super-rice cultivars with high-yield potential have recently been released (Peng et al., 2008). The use of FS models is a promising and quick way to assess and select yield-related morphological traits. This approach, however, necessitates describing organ geometrical shapes with good accuracy. For this reason, technologies such as 3-D laser scanning have been used to collect data on super-rice.

Increasing photosynthetic capacity is another major approach for enhancement of crop yield potential (Murchie et al., 2009). Different functions are used in plant models for computing plant photosynthesis. The biochemical FCB model is the most popular one because of its elegance, simplicity and robustness (Yin and Struik, 2009); this model has been recently introduced into FS models (Sarlikti et al., 2011; Xu et al., 2011). However, an integrative modelling framework based on a combination of biochemical photosynthesis models and 3-D radiation models, accounting for temperature heterogeneity and leaf N content in a canopy, would be necessary to quantify the photosynthetic activity of a plant with regard to its microclimate. Implementing these models within FS models that consider the source–sink interaction at the whole-plant scale is also a major objective in order to quantify the interactions between the key growth processes (e.g. assimilation, carbon transport and allocation) and plant development. Such integrative models already exist (Jullien et al., 2011; Kang et al., 2011; Ma et al., 2011), but up to now they have not been applied at the stand scale in order to optimize high-yielding food and biofuel crop production.

The geometry of incident radiation can be modified (e.g. by an increase of aerosols in the atmosphere) and corresponding terrestrial primary production can be substantially affected (Farquhar and Roderick, 2003). The impact of geometrical characteristics of radiation (e.g. the variation of diffuse radiation intensity over the sky hemisphere) may be more important than previously thought and should be reconsidered in FS models (Zheng et al., 2011). It is also interesting to consider the geometrical features of incident radiation for specific environments such as greenhouses (Buck-Sorlin et al., 2010).

Beyond the use of plant models in optimal cultural conditions, e.g. in high-yielding crops, substantial scientific investment will be necessary to improve the yield in poorest areas where water and fertilizers are limited. Here again a FS modelling approach would be helpful in order to optimize yield production at low fertility with little fertilizer input (Lynch, 2007). Minimizing the application of inorganic fertilizer and pesticide is a big challenge for sustainable agriculture and environmental protection in high-input agroecosystems, and FS modelling could be an alternative approach to provide solutions.

A plant can develop into a complex topological and geometrical structure in response to environmental factors that have strong temporal–spatial variation. Although most of the existing FS models are able to describe plant structure and plant–environment interactions with rather high spatial resolution, their computational costs can be an obstacle to application where a population of plants is required. In this case it is necessary to simplify both the description of plant geometrical structure and the underlying ecophysiological processes involved in plant growth. The influence of such simplifications must be evaluated in relation to the variety of scientific objectives and potential applications that are sought. If understanding plant functioning at the individual scale – and in particular its response to changing environmental factors – often necessitates encapsulating accurate physiological and biophysical sub-models within a global plant model, then this approach is no longer adapted for making simulations at larger scales, for instance to predict CO₂ acquisition or biomass production at a regional level. However, facilitating communication (or feedbacks) between models with different levels of detail is a way to select the more relevant parameters and improve predictive models for specific goals. Another way to adapt simulation models to specific applications is also to link relevant sub-models with different accuracies, as proposed by Renton (2011). However, simulation of plant–environment interactions is complex and time-consuming and requires high computational capacity. This is particularly true when the heterogeneity of environmental factors (e.g. incident radiation, soil water and nutrients), as well as plant morphology, must be described with high spatial resolution. A specific effort is thus required to adopt efficient computational methods and facilities. Promising high-performance computation methods have been developed recently to overcome these constraints (Host et al., 2008; Postma and Lynch, 2011; Zheng et al., 2011); however, these methods require a high level of technology. The multi-disciplinary framework of the PMA network,
involving plant biologists, agronomists, foresters, computer scientists and mathematicians, should facilitate the development and the use of such advanced technologies.

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LITERATURE CITED


