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VIEWPOINT

Plant Growth Modelling and Applications: The Increasing Importance of Plant Architecture in Growth Models

THIERRY FOURCAUD^{1,*}, XIAOPENG ZHANG², ALEXIA STOKES³, HANS LAMBERS⁴ and CHRISTIAN KÖRNER⁵

¹*CIRAD, UMR AMAP, TA-A51/PS2, Boulevard de la Lironde, 34398 Montpellier Cedex 5, France,* ²*LIAMA-NLPR, Institute of Automation, Chinese Academy of Sciences, Beijing 100080, China,* ³*INRA, UMR AMAP, TA-A51/PS2, Boulevard de la Lironde, 34398 Montpellier Cedex 5, France,* ⁴*School of Plant Biology, Faculty of Natural and Agricultural Sciences, The University of Western Australia (CRICOS Provider No. 00126G), Crawley WA 6009, Australia* and ⁵*Institute of Botany, University of Basel, Schoenbeinstr. 6, CH-4056 Basel, Switzerland*

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- **Background** Modelling plant growth allows us to test hypotheses and carry out virtual experiments concerning plant growth processes that could otherwise take years in field conditions. The visualization of growth simulations allows us to see directly and vividly the outcome of a given model and provides us with an instructive tool useful for agronomists and foresters, as well as for teaching. Functional–structural (FS) plant growth models are nowadays particularly important for integrating biological processes with environmental conditions in 3-D virtual plants, and provide the basis for more advanced research in plant sciences.

- **Scope** In this viewpoint paper, we ask the following questions. Are we modelling the correct processes that drive plant growth, and is growth driven mostly by sink or source activity? In current models, is the importance of soil resources (nutrients, water, temperature and their interaction with meristematic activity) considered adequately? Do classic models account for architectural adjustment as well as integrating the fundamental principles of development? Whilst answering these questions with the available data in the literature, we put forward the opinion that plant architecture and sink activity must be pushed to the centre of plant growth models. In natural conditions, sinks will more often drive growth than source activity, because sink activity is often controlled by finite soil resources or developmental constraints.

- **PMA06** This viewpoint paper also serves as an introduction to this Special Issue devoted to plant growth modelling, which includes new research covering areas stretching from cell growth to biomechanics. All papers were presented at the Second International Symposium on Plant Growth Modeling, Simulation, Visualization and Applications (PMA06), held in Beijing, China, from 13–17 November, 2006. Although a large number of papers are devoted to FS models of agricultural and forest crop species, physiological and genetic processes have recently been included and point the way to a new direction in plant modelling research.

Key words: Biomechanics, carbon allocation, functional–structural plant models, meristem, nitrogen, phenotypic plasticity, root architecture, simulation, sink, source, PMA06.

INTRODUCTION

Plant growth modelling has become a key research activity, particularly in the fields of agriculture, forestry and environmental sciences. Due to the growth of computer resources and the sharing of experiences between biologists, mathematicians and computer scientists, the development of plant growth models has progressed enormously during the last two decades. The use of an interdisciplinary approach is necessary to advance research in plant growth modelling and simulation, but is one of the most challenging aspects to be encountered so far. Such a combination of different approaches is at the heart of the Plant-growth Modelling and Applications (PMA) symposium series that was launched in Beijing, China, in 2003 and continued in 2006 (Hu and Jaeger, 2003; Fourcaud and Zhang, 2008), thanks to the initiative of the Chinese Academy of Sciences' Institute of Automation and the Chinese Agriculture University, in connection with the French research institutes CIRAD, INRA and INRIA.

Several types of plant growth models exist, with varying degrees of complexity, depending on their end use and application. Empirical crop and forest growth models, which apply functions fitted to data without considering the physiological processes involved in growth and morphogenesis, continue to be used efficiently for estimating or predicting yield and quality of products. Nevertheless, such models are usually calibrated for a particular species and well-defined site conditions and therefore cannot be valid over a wide range of conditions (Lacointe, 2000). Understanding how plant growth and development interact with environmental factors including light, temperature, soil characteristics and water availability, is extremely important to increase the yield of crop plants, e.g. through breeding programs. To model these interactions we need to take into account the physiological processes involved in growth, e.g. water and nutrient uptake, photosynthesis and carbon partitioning (Gifford and Evans, 1981; see Fig. 1). The term 'process-based model' was introduced to describe those models that considered the interactions between plant functional processes and abiotic factors.

* For correspondence. E-mail thierry.fourcaud@cirad.fr

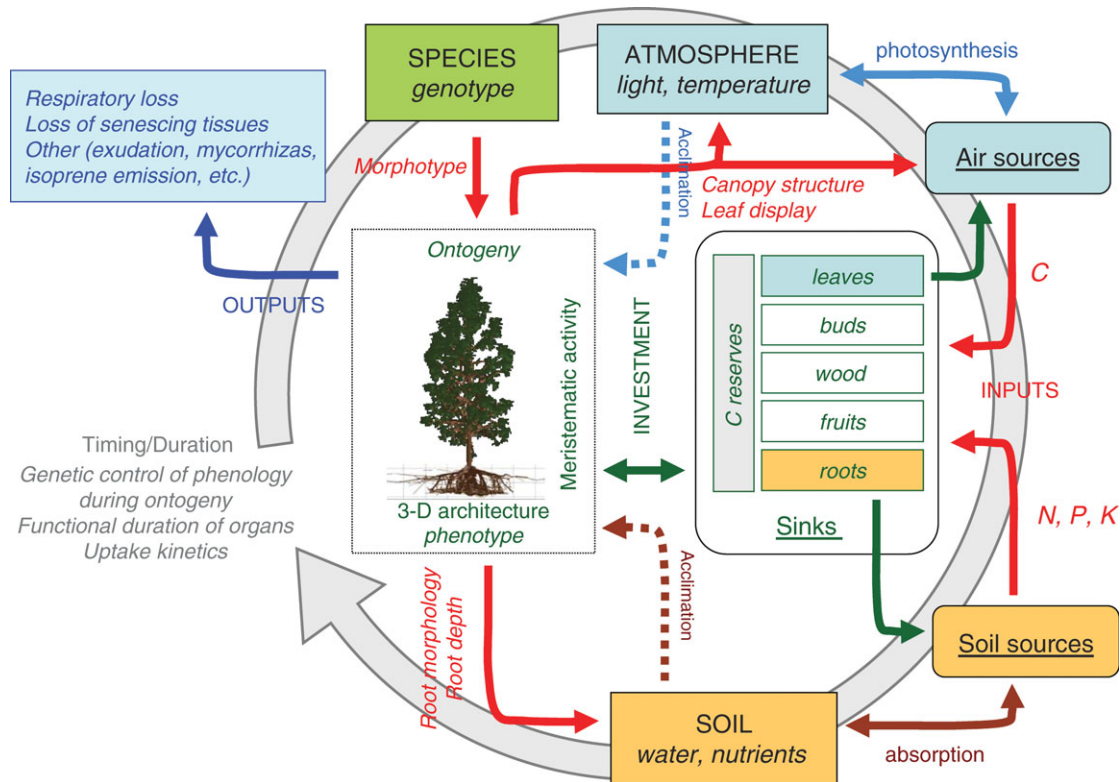


FIG. 1. A schematic representation of interactions between a plant and its environment, based on space/architecture and timing/duration components. FS plant models consider the physiological processes associated with organ function in connection with the 3-D architecture. Most FS growth models are driven by sources that provide the basic input elements to the plant, i.e. C, N, P, K. Plant investment consists of resource allocation and use by demanding organs, i.e. sinks, within the architecture, after considering the output or losses. Input, investment and output variables are spatially and temporally under environmental control, i.e. both climate and soil, and each variable can interact with and influence the others.

Such models usually focus on the description of carbon (C) or nitrogen (N) balance and consider that plant development depends on a change of matter in different compartments, based on uptake (e.g. photosynthesis) and loss (e.g. senescence) either within an individual (Heuvelink, 1996, 1999; Marcelis *et al.*, 1998; Carvalho *et al.*, 2006; Gayler *et al.*, 2008) or a population (Battaglia and Sands, 1998; Gayler *et al.*, 2006; Pretzsch *et al.*, 2008). Usually, no explicit representation of plant morphology (i.e. the geometry and topological connectivity between organs) is considered in such models. Hence models linking growth-driven processes with plant morphogenesis, i.e. the 3-D evolution of plant structure over time, were developed and the interaction of these processes with environmental variations included, for example, temperature, soil characteristics and water availability. This class of models is known as functional-structural (FS) plant models (Godin *et al.*, 2004). Models taking into account the interaction between plant architecture, functions of organs (e.g. root absorption, leaf photosynthesis, sap flow conduction) and growth processes have been developed extensively over the last decade (Perttunen *et al.*, 1998; de Reffye *et al.*, 1999; Godin *et al.*, 2004; Prusinkiewicz, 2004; Vos *et al.*, 2006; Génard *et al.*, 2008). The progress made in improving the 3-D reconstruction of real plant structures (Godin, 2000; Cheng *et al.*, 2007; Xu *et al.*, 2007) has allowed the computing of plant physiological functioning

as an integration of organ-level processes at the whole-plant scale. Technical advances in visual data acquisition also makes the measurement of real plants easier with 3-D reconstruction (Godin, 2000; Cheng *et al.*, 2007). Furthermore, architectural concepts (Barthelemy and Caraglio, 2007) have allowed a temporal evolution of the 3-D development of plant structure to be reconstructed from a small number of morphological variables measured at different growth stages (Bouchon *et al.*, 1997). A typical application of such 3-D virtual plants is for the exploration of light interception and photosynthesis at the plant and stand scale (Sinoquet *et al.*, 2001; Soler *et al.*, 2002; Evers *et al.*, 2007; Dauzat *et al.*, 2008; Louarn *et al.*, 2008; Rey *et al.*, 2008). Digital 3-D tree architecture has also been used when investigating the biomechanical responses of trees to static or dynamic external loads (Fourcaud *et al.*, 2003; Fourcaud and Lac, 2003), including crown oscillations of trees submitted to strong winds (Sellier and Fourcaud, 2005) and root anchorage (Dupuy *et al.*, 2007). However, the feedback between plant morphogenesis and physiology over time (de Reffye *et al.*, 1997; Lambers *et al.*, 2006; Prusinkiewicz and Rolland-Lagan, 2006) is still a key issue that requires further development. The temporal integration of biological processes in models will not only improve our knowledge of plant functioning, but will also advance research in other disciplines where interactions between plants and the physical medium have

to be taken into consideration (Room *et al.*, 1996). Eco-engineering of slope stability (Stokes *et al.*, 2007), which uses data concerning the mechanical interaction between roots and soil, is a good example of such an application of structural plant models (Reubens *et al.*, 2007; Danjon *et al.*, 2008).

In this Special Issue, Pretzsch *et al.* (2008), give an overview of models used in forest ecosystem management. These authors describe the very first ecosystem ‘models’ to be used, which were maps displaying the location of hunting grounds, forests and pastures, as early as the 16th century. Yield tables for forest stands were introduced in the 19th century, using stem height and width data measured over long periods of time. Eco-physiological models of forest growth were then developed in the 1960s that predicted growth processes under various ecological conditions. Several reviews exist describing these process-based FS models, for example Lacoite (2000) described the four major carbon partitioning models, which are currently used in FS models. These approaches involve (1) empirically determined allocation coefficients; (2) models based on a description of growth patterns or relationships within the plant; (3) transport-resistance models; and (4) models based on source–sink relationships. Le Roux *et al.* (2001) reviewed 27 tree growth models that use the same main physiological processes involved in C metabolism. The concluding remarks of these authors with regard to FS models were that C allocation and the effects of architecture on growth are poorly represented; reserve dynamics are poorly accounted for and an understanding of below-ground processes and nutrient assimilation is lacking in most models. Most FS models in the literature are also concerned with crop species growing in optimal conditions. If such models were tested on plants growing in wild communities, it would be interesting to compare results with those tested on plants growing in isolation under controlled conditions.

WHAT DRIVES PLANT GROWTH AND HOW DO MODELS TAKE INTO ACCOUNT THESE PROCESSES?

Growth is the consequence of the functioning of meristems. Therefore, the location and temporal activity of meristems determines plant morphology and growth rate (Körner, 1991; Sussex and Kerk, 2001; Barthelemy and Caraglio, 2007). In the recently developed model EcoMeristem, where meristem activity in rice (*Oryza sativa*) is driven by gene activation, Luquet *et al.* (2006) concluded that plant growth and development depend on both assimilate supply and organogenesis-based demand. Meristem cells thus maintain a large variety of specific cellular activities, which in turn encode complex developmental processes, but are notoriously difficult to experiment with (Dupuy *et al.*, 2008). Therefore models that focus on the rate at which meristems produce new cells and differentiate, and how this activity is regulated, are essential for a better understanding of plant development. The CellModeller software developed by Dupuy *et al.* (2008) is the first step towards the creation of a model that can simulate cell–

cell interactions within meristems and specific tissues, and shows how biophysical and biomechanical processes determine cell production. These models focus therefore on the activity of sinks, e.g. stems, leaves, roots and inflorescences, within a plant, whereas most crop models usually only consider the environmental effects on source processes, e.g. photosynthesis. The type and size of sinks are traditionally adjusted to the incremental source and determined using empirical, phenology-dependent partitioning functions or tables (Dingkuhn *et al.*, 2006b).

Although most plant growth models use photosynthesis as the driver for growth (see, for example, reviews by Le Roux *et al.*, 2001; Génard *et al.*, 2008), except for horticultural conditions, this source-driven paradigm lacks effects-based justification (Körner, 1991). Plant primary production depends on several resources other than C. Therefore, plant growth rate is not simply determined by the rate of photosynthetic CO₂ uptake per unit leaf area, but also depends on allocation of resources to leaf area (the amount of photosynthetically active tissue constructed) and on leaf longevity (how long the photosynthetic tissues are deployed). Moreover, C is used within the plant for both growth and respiration, and the fraction used for respiration varies greatly among plants, increasing with decreasing plant growth rate (Lambers *et al.*, 2008). Growth is driven by several processes simultaneously and is thus highly complex to understand and to model; photosynthesis being only one out of several drivers. Other important aspects of plant growth that can also be considered as drivers are the way in which dry matter is invested into the different plant organs, the feedbacks involved, and the plant’s capacity for additional resource acquisition, as well as the metabolic costs/expenses (tissue specific rates of respiration; Körner, 2006). Plant investment strategies with regard to the above sink-driving processes are a very important aspect to be considered in analysing and modelling morphological plasticity, in particular in stress conditions and a heterogeneous environment (Lambers and Poorter, 1992). Added to this complexity is the further problem of situating a given species within an ecosystem and understanding the interactions taking place, especially concerning below-ground processes. In response to this need, and using a holistic optimization approach, Marks and Lechowicz (2006) developed an original model of plant function, Tree-seedling Adaptive Designs (TAD). TAD is one of the first models that incorporates key shoot and root traits associated with water, light, C and N, and also considers the multi-task nature of plant organs. The effects of interactions and trade-offs among 34 traits on whole-plant fitness were examined by Marks and Lechowicz (2006), rather than studying the individual traits in isolation. As plant traits modify the environment and thereby also the selection on these traits, these feedbacks on the environment were thus modelled in a spatially explicit manner. The development of such models will therefore allow the investigation of major ecophysiological issues such as how individual plant traits affect plant performance, phenotypic plasticity and competition with neighbours, and can determine the potential for alternative designs of similar performance (Marks and Lechowicz, 2006).

Factors that co-determine growth vary throughout the life of a plant and hence may undergo ontogenetic drifts. These drifts in turn will therefore determine whether growth continues or ceases, both spatially and temporally (Körner, 1991). Körner (1991) drew up a list of plant factors, which combined with environmental factors co-determine the C balance during vegetative growth. Ranging from metabolic factors (i.e. leaf photosynthesis and dark respiration) to temporal factors (e.g. leaf duration), Körner (1991) emphasized the importance of morphogenetic features that govern plant spatial design and architecture. Not only do these inherent genetic factors influence growth, but the ‘starting design’ or dimensions of a plant at the beginning of a particular growth period will have a long-lasting influence on growth rate and final biomass production (Gayler *et al.*, 2006). Similarly, the response type and time of individual plant organs to a new environment or external factors can differ hugely, thus altering overall plant growth. However, two of the principal determinants of plant growth are C partitioning and respiration rates between different plant organs. There is strong evidence that nutrient factors not only influence respiration and growth but also, directly or indirectly, regulate gene expression and trigger many metabolic and developmental responses (Bijlsma and Lambers, 2000; Yang and Midmore, 2005; Gayler *et al.*, 2008). Therefore, the growth decision of each organ will depend on the most-limiting nutrient factors. The effects of nutrient status on growth and development are in turn mediated by plant growth regulators, which can also be modelled using FS models (Buck-Sorlin *et al.*, 2008). Nevertheless, before modelling growth for any plant, it is necessary to consider the life history strategy of that species. The inherent relative growth rate of a species depends largely on its ecological niche: in optimum conditions, plants from fertile habitats grow faster than plants from nutrient-poor or stressful habitats. Although resource supply in stressful environments is often limited, the investment in specific features of plants found in these habitats (e.g. leaf longevity) will reduce the plant’s growth potential, but will increase success. Therefore, it is likely that there are trade-offs between growth potential and performance under adverse conditions (Lambers and Poorter, 1992).

In a review on the potential for a C-driven stimulation of tree growth, Körner (2003a) proposed the hypothesis that growth is not limited by C supply in many cases. Contrary to the hypotheses used for the development of many FS models (Lacointe, 2000; Le Roux *et al.*, 2001), where growth is driven by source activity, Körner (2003a) provides evidence that growth in trees, regardless of climatic zone, is driven by sink activity. Exploring non-structural carbohydrate (NSC) concentrations in tree tissues and the hypothesis that low NSC pools indicates low source and high sink activity and high NSC concentrations show that photosynthesis meets or exceeds that needed for growth, Körner (2003a) demonstrated that NSC pools in trees are generally high during periods unfavourable for tissue formation (low turgor, low temperature). Thus, source activity exceeds demand. NSC pools are significantly, but only temporarily, affected by severe

defoliation (Li *et al.*, 2002; Hoch *et al.*, 2003), with most of the variation being in starch rather than in sugar concentration. Although the influence of sugars on gene expression associated with photosynthesis, respiration and development is of utmost importance (Smeekens, 2000; Rolland *et al.*, 2006), in natural conditions, sink activity will more often drive growth than source activity, because sink activity is often controlled by finite soil resources or developmental constraints. In particular, cell division in the meristem region is affected by temperature and, as discussed at the beginning of this section, growth is the consequence of the functioning of meristems. Therefore, FS models of meristem activity with respect to environmental parameters and how this relates to source activity should be focussed on more in the future (Dingkuhn *et al.*, 2006a; Luquet *et al.*, 2006). Molecular studies can also elucidate the relationship between sink and source activity and have indicated that sugar signalling of plant assimilate resources to meristems occurs via cell-wall invertases and their coding genes (see Dingkuhn *et al.*, 2006b). If cell-wall invertase regulation is largely responsible for the phenotypic plasticity of plant traits, the implications for plant growth modelling are major. However, whether or not meristem activity is considered as driving the plant growth process, the resulting architecture, which is due to primary meristem development, is a key component of many plant growth models.

PLANT ARCHITECTURE AS A KEY COMPONENT OF PLANT GROWTH MODELS

Plant architecture is an important concept that describes the topological and geometrical development over time at the whole-plant level, i.e. ontogeny (Barthelemy and Caraglio, 2007). Architecture is concerned with the time-evolution of plant shape that can be directly measured in the field, but has only recently been considered to include the amount of resources invested into different functional units (dry matter partitioning), which is another component of plant morphogenesis. The development of plant structure in a 3-D space results from a multi-objectives survival strategy, including light interception and mechanical stability, which is specific to sessile organisms (Niklas, 1992; Rowe and Speck, 2005; Mouliia *et al.*, 2006; Sterck and Schieving, 2007). Plant form diversity is thus closely related to evolutionary perspectives in different ecological niches (Farnsworth and Niklas, 1995; Körner, 2003b; Fournier *et al.*, 2006).

In pioneer studies carried out on tropical trees, Hallé and collaborators (Hallé and Oldeman, 1970; Hallé *et al.*, 1978) provided a classification of tree architectures based on earlier studies on plant morphology complemented by field observations. This classification was the starting point of tree architecture modelling studies carried out by de Reffye and collaborators since the 1980s (de Reffye *et al.*, 1988, 1999; Bouchon *et al.*, 1997). The first architectural models were purely structural, based on stochastic processes used to simulate branching sequences and internode distribution due to meristem activity, observed at different levels within the tree structure (Guédon *et al.*, 2001). Simultaneously, the fundamentally important concept of

the reference axes, which allowed the botanical theory of physiological age to be implemented (Barthelemy and Caraglio, 2007), was introduced. This major concept allows us to consider longer time scales, and also to include the appearance of reiterated complexes, structural metamorphosis and ageing that are often neglected in FS plant models. Both stochastic processes and reference-axis definition were derived from multi-scale analyses of real plants (Godin and Caraglio, 1998) and were implemented initially in the AMAPsim simulation software (Barczy *et al.*, 2008). In the same period, Prusinkiewicz and Lindenmayer (1990) adapted the well-known Lindenmayer system (L-system) formal grammar to generate virtual tree architectures (Prusinkiewicz *et al.*, 2000).

More recent modelling studies have aimed at introducing retroactions between physiological processes and morphogenesis in FS models (de Reffye *et al.*, 1997; Perttunen *et al.*, 1998; Prusinkiewicz and Rolland-Lagan, 2006). Plant growth is now often simulated considering biomass acquisition and partitioning within the plant (Drouet and Pages, 2003; Yan *et al.*, 2004; Drouet and Pages, 2007). L-systems are also widely used to implement FS models (see Allen *et al.*, 2005, as an example). Relational growth grammar (RGG), extending the L-system to dynamic structures and processes, has recently been developed by Kurth *et al.* (2005). RGG is a promising improvement of the L-system and facilitates the simulation of plant morphogenesis in a heterogeneous and changing environment (Buck-Sorlin *et al.*, 2008). Significant modelling studies linking complex tree architectures to physiology were also carried out by Perttunen *et al.* (1998) and a simulation platform based on the AMAP methodology was specifically developed for linking models of plant architecture to external physiological functions (Barczy *et al.*, 2008). The approaches mentioned above were usually based on an accurate description of architectural units considered as independent elements connected through topological rules. As a consequence, a complete description of the plant structure has to be computed at every growth stage, often making the calculation time-consuming and limiting the use to individual plants.

The FS model GREENLAB was recently developed to allow fast calculations of plant growth (Yan *et al.*, 2004). This new conceptual model based on studies by de Reffye *et al.* (1997) can be reduced to a mathematical equation where plant architecture is aggregated under the form of a combinatorial formula, giving the evolution of organ numbers with regard to a source–sink ratio of assimilates. The aggregate version of the model is suitable for simulating a large number of plants. A growth model was developed on this basis at the stand scale, which takes into consideration light competition between individual trees (Cournède *et al.*, 2008). It is, however, possible to consider plants at different levels of structural detail, i.e. splitting the plant into substructures through a structural factorization of the GREENLAB equation (Cournède *et al.*, 2006), or to consider each organ separately at a more detailed level. The latter type of structure decomposition corresponds to the more classical FS models described above. GREENLAB is therefore comparable to a physical model (usually formulated in the form of a partial differential

equation) that can integrate both temporal and spatial evolution of the system in connection with the associated functions of organs. This conceptual model is built on the generic basis of plant morphogenesis given by Barthelemy and Caraglio (2007), and has been calibrated and tested on several crop species (Guo *et al.*, 2006; Kang *et al.*, 2008; Ma *et al.*, 2008). Calibration tools were developed and used to estimate hidden parameters of the model from morphological data measured on the plant and, in particular, the source and sink strength of carbohydrates associated to a family of organs. Such fitting has allowed different C partitioning in plants submitted to different environmental conditions to be quantified, and has also included data on architectural variability (Dong *et al.*, 2008; Ma *et al.*, 2008). In GREENLAB, organogenesis is resource-dependant (Dong *et al.*, 2008; Mathieu *et al.*, 2008), i.e. mainly driven by sources. Demand and supply are perfectly matched at all times and it is assumed that final organ biomass is responsive to supply until the organ stops growing. Dingkuhn *et al.* (2006b) argue that final organ size is determined at an early stage of organ development (not only for fruits but also for leaves). Therefore, if organ size is determined early on, potential sink size must be regulated before the sink becomes effective. In the model EcoMeristem developed by Dingkuhn *et al.* (2006a, b) and Luquet *et al.* (2006), organ size, leaf appearance rate and assimilate-partitioning patterns are affected by internal competition for resources and thus lead to different plant architectures. This phenotypic plasticity adjusts organ number and size on the plant, through modified rates of organogenesis and longevity, to variable C resources.

ROOT ARCHITECTURE: STILL THE MISSING COMPONENT

Although vitally important for describing C and N fluxes in plants, the consideration of root growth in both isolated individuals and at the population level is notoriously lacking in most FS models. If indeed present, simplistic descriptors of root systems are used, e.g. total root volume or root length density (length of roots per unit area of soil). The true architecture of a root system, and in particular rooting depth, is often neglected, even though the absorptive capacity, order and spatial position of a root within a system, as well as prospected soil volume and layer, determine the ability of the root system to take up water and nutrients (Jourdan and Rey, 1997; Drouet and Pages, 2003; Pages *et al.*, 2004; Lambers *et al.*, 2006; Wu *et al.*, 2007). In turn, soil is highly heterogeneous with local depletion and charging of nutrients, making the modelling of C and N fluxes a highly dynamic process, which fluctuates in time and space. Therefore, it is necessary to consider root and aerial architecture of individual plants in their entirety (Atger and Edelin, 1994) if FS models are to be improved, especially within heterogeneous populations in natural conditions. In a recent FS model, GRAAL-CN, Drouet and Pages (2007) used an approach that integrates processes from the organ level to the whole-plant level through aggregated

levels of organization. The specificity of GRAAL-CN is that it takes into account interactions between C and N and considers shoot and root organs equally. Both shoot and root organs are initiated as a function of temperature, but aerial organ growth is calculated from its fixed individual potential, i.e. maximal growth rate and assimilate availability within the plant. As in the GREENLAB model, GRAAL is still a model driven by source activity, even if growth is regulated by other external factors such as temperature. Similarly, the model SPACSYS (Wu *et al.*, 2007) integrates interactions among above- and below-ground growth with developmental stages, N and C cycling, water and heat movement in the plant-atmosphere continuum. Root architecture is described as 3-D but C, N and water cycling in the soil profile are implemented as 1- or 2-D models, as computational capacity would not be sufficient to model all processes as 3-D. Nevertheless, a 3-D modelling approach for all components is theoretically possible.

At a more detailed level, root architectural strategies can be examined and modelled with regard to, for example, nutrient availability (Ho *et al.*, 2004), water uptake (Clausnitzer and Hopmans, 1994; Tsutsumi *et al.*, 2005) and anchorage strength (Danjon *et al.*, 2005; Dupuy *et al.*, 2007; Fourcaud *et al.*, 2008). Using mechanistic optimization approaches (Parker and Smith, 1990) and sensitivity analyses, it is possible to determine the optimal topology and geometry of a root system in a specific situation. The optimization approach is powerful in that basic plant growth principles are investigated directly and so can be used to make predictions about plant responses to new environmental conditions (Marks and Lechowicz, 2006). Such an approach will be highly useful for quantifying costs and benefits of particular root architectural patterns when comparing the efficiency of any plant trait among phenotypes, and should be focussed on more in future research.

MODELLING PHENOTYPIC PLASTICITY

The ability of a genotype to change its phenotype was originally thought to be an unstable process. However, it is now recognized that this ability to change, termed phenotypic plasticity, is central to plant ecological development (Bradshaw, 2006). Under genetic control, plasticity enables sessile plants to adjust to spatial and temporal heterogeneity, thus minimizing stress (Buck-Sorlin and Bachmann, 2000; Letort *et al.*, 2008). Both morphological and physiological plasticity are important (Vincent and Harja, 2008), but have been interpreted as either signs of weakness or fitness in plants (Bradshaw, 2006). In this Special Issue, the ecological importance of tree-crown plasticity on tree growth was explored in a 3-D model by Vincent and Harja (2008). Results showed that crown plasticity, expressed as a photomorphogenetic response, conferred competitive superiority to rubber trees (*Hevea brasiliensis*) through enhanced light-capture efficiency (LCE), but that interactions with other processes, including stand density, growth rate and below-ground competition, can downplay or enhance this competitive advantage. Such combined effects are considered in most FS plant

models at the whole-plant level where organs compete with each other for resources, and plant development is controlled by available C and N, as well as temperature or light [see, for example, GRAAL-CN (Drouet and Pages, 2007), LIGNUM (Lo *et al.*, 2001) or L-PEACH (Allen *et al.*, 2005)]. Similarly, Buck-Sorlin *et al.* (2008) developed a phytochrome-based shade-avoidance model for barley (*Hordeum vulgare*) that simulates plant interaction with the environment via hormonal control. This model is an application of RGG dynamical grammar (Buck-Sorlin *et al.*, 2005). Although simulations of shade- and object-avoidance were successful, as seen in the reduction of tillering at low phytochrome values, Buck-Sorlin *et al.* (2008) highlight the need for careful calibration and validation of such increasingly complex FS models.

In a study by Mathieu *et al.* (2008) where the FS model, GREENLAB, was developed with full interactions between organogenesis and photosynthesis, cyclic patterns (i.e. rhythms and alternating patterns) in branch formation or fruiting were generated by changing only the source-sink ratio within the plant. The latter key variable defines the competition level between all plant organs in GREENLAB. Therefore, plant organogenesis is dynamically controlled by the available biomass, and consequently driven by sources. If this is the case, morphogenetic adjustment in different environments could be modelled relatively easily. Nevertheless, the study by Mathieu *et al.* (2008) remains purely theoretical and needs validating with experimental data. In contrast to this model of shoot morphological adjustment, where the number and size of new shoots produced on individual shoot parts is modulated by carbohydrate supply that depends on the photosynthetic production of the whole plant, Yang and Midmore (2005) developed a dynamic model where an individual plant is treated as a population of relatively independent subunits depending on the local endogenous nutrient supply status. As recent studies have shown that the growth of an individual shoot or root part depends on the local light or nutrient conditions as well as on the environmental conditions, the model developed by Yang and Midmore (2005) allows the allocation of nutrients to different parts of the shoots and roots depending on the structure of the vascular network. Simulations have shown that plants were thus able to integrate activities at the whole-plant level and allocated proportionally more growth to their organs situated at the most favourable positions. Similarly, in a model of daily canopy photosynthesis taking into account light and N distribution and applied to *Solidago altissima*, Hirose and Werger (1987) showed that both irradiance and leaf N concentration per unit area decreased exponentially with increasing cumulative leaf area from the top of the canopy. To determine the optimal pattern of N distribution that maximizes photosynthesis in open and dense canopies, daily canopy photosynthesis was calculated for various N allocation patterns in different canopy architectures. It was found that leaf N redistribution in whole-canopy photosynthesis becomes smaller in a stand with an open canopy than in a stand with a dense canopy, therefore this redeployment of leaf N to the top of the canopy with ageing should be more effective in increasing total canopy photosynthesis

in a dense stand. Such mechanisms for investing or redistributing resources in different organs and functions in an optimal way with regard to a specific strategy can be modelled using a teleonomic approach (Lacointe, 2000; van Wijk *et al.*, 2003), although such models cannot always explain behaviour observed in the field. For example, van Wijk *et al.* (2003) studied biomass allocation and root morphology of non-acidic tussock tundra after 4 years of N and P fertilization. In these sub-arctic conditions, where plants are adapted to low N availability, N uptake far exceeded that required for growth in slow-growing species in fertilized plots, and the relative investment in root growth was significantly enhanced compared with control plots. This strategy of ‘luxury consumption’ allows some species to outcompete faster-growing species, by limiting their access to those nutrients. The teleonomic C-allocation model used for simulating growth in these plants was unable to provide realistic results, thus highlighting the necessity for considering growth within the context of each species’ ecological niche (van Wijk *et al.*, 2003). Such an experiment therefore highlights the need that in order to better understand plant responses to any environmental parameter, it is always necessary to consider the ecological niche of that plant and its coexistence with other species.

PERSPECTIVES FOR FUTURE RESEARCH

To our knowledge, only a limited number of plant growth models, described below, centre on sink-driven processes. To develop a model aiming at simulating the genetic and physiological control of plant morphogenesis and architecture but assuming that plant growth is mostly driven by sink regulation (which depends on the plant’s resource and stress status), it can be considered that the ultimate drivers of growth will be the available soil resources. These resources depend on water, litter recycling and cation exchange capacity and should thus be considered as starting points for the model. In such a model, Bijlsma and Lambers (2000) integrated the specificity of regulatory signals controlling metabolism with the partitioning of photosynthate between organs. Such a model is also one of few (Buck-Sorlin *et al.*, 2005; Gayler *et al.*, 2008) allowing a comparison of growth performance and ecology of wild species in variable environments with respect to the availability of nitrate and ammonium, their flux being modelled with regard to the high-affinity transport system. Plant responses to nutrient and light limitation are described using a C-allocation rule driven by concentration differences of the cytosolic NSC pools between sinks. Differences in specific growth rate result from differences in uptake and assimilation capacities for CO₂ and inorganic N, maintenance requirement and morphology. At high N status, the sink size of the shoot increases, cytosolic NSC decreases and NSC import increases. Photosynthate is unloaded into C buffers, which degrade at a constant specific rate. The sugar fluxes arising from these buffers then drive the growth rate of the stem and root. Although their model is sink driven, Bijlsma and Lambers (2000) and Bijlsma *et al.* (2000) nevertheless conclude that

growth rate depends on internal substrate concentrations, not directly and unequivocally on external edaphic factors.

Again, using the notion that plant growth is driven by sink regulation, Dingkuhn *et al.* (2006b) developed a conceptual framework for the analysis and simulation of crop growth. Such a framework needs to take into consideration the feedback effects of the plant’s resource status on meristem behaviour as well as mechanisms to cope with temporary source–sink imbalances (due to the time elapsing between organ initiation and expansion). These mechanisms include the management of transitory reserves, organ senescence and end-product inhibition of photosynthesis and are generally related to sugar metabolism. These phenomena were incorporated into the model EcoMeristem, which has successfully demonstrated that crop parameter values change when a physiological stress is applied, e.g. P deficiency, drought or light stress (Dingkuhn *et al.*, 2006a, b; Luquet *et al.*, 2006). If sugar sensing by meristem cells is the key process determining architectural plasticity, Dingkuhn *et al.* (2006b) argue that the ratio of daily demand (aggregate sinks) and supply (aggregate sources) can be used as the indicator variable and that empirical sensitivity coefficients can then be defined relating meristem response to this variable. Although complex, such whole-plant models may not necessarily be useful to end-users concerned principally with crop yield, but models such as EcoMeristem can be used to analyse quantitatively the traits governing phenotypic plasticity and meristem behaviour.

Most existing FS plant models are based on processes that are mainly driven by sources, even if plant development is also based on architectural and allocation rules controlled or regulated by environmental variables, e.g. light and temperature. These models are suitable in most situations, but can only partially take into account phenological plasticity in limiting environments. In a ‘sink-driver’ view, the potential growth rate, which can be associated to the organogenesis phenomenon as preformed elements (as referred to by Barthelemy and Caraglio, 2007), becomes a key variable, i.e. not a threshold value, and is possibly affected by local environmental factors through an investment policy or strategic component (Lambers and Poorter, 1992). Phenotypic plasticity is therefore not only seen as an optimal allocation or optimal allometric trajectory in a variable environment, but a plasticity in growth rate (Weiner, 2004).

Only when the relationship between source–sink activity, architectural plasticity and environment is understood can we simulate correctly plant growth at the population level, a major goal for agronomists and foresters. In a study of 54 classical models based on a C mass-balance approach and run for populations of *Ranunculus pelatus*, Garbey *et al.* (2006) found that the way plant architecture was approximated contributed significantly to the modelled biomass results. When plant plasticity was taken into account, biomass production was also greatly modified, especially when adapting to nutrient stress or to seasonal temperature variation. Therefore, more research is required at the individual scale and should take into account the link between morphological and physiological plasticity in

response to environmental conditions, before attempting simulations of plasticity at the population level (Garbey *et al.*, 2006).

The long-term survival of trees also merits more attention in FS models. Architectural sequences resulting from axes differentiation during ontogeny and until senescence can be simulated using the reference axis (Barczy *et al.*, 2008), which is a representation of the different morphogenetic gradients and their associated botanical and functional traits (Barthelemy and Caraglio, 2007). However, to our knowledge, existing FS models do not properly simulate growth decline or the increasing risk of mortality with size/age in a mechanistic way. Developing such models would be noteworthy in a context of global warming where stand decline and conservation of old growth forests constitute a main issue for future research.

Once any plant growth model has been developed and calibrated, then the visualization of growth simulations can allow us to see directly and vividly the outcome of the model, and provides us with an instructive tool useful for practitioners, managers and foresters, as well as for teaching. Geometric modelling of plant architecture has been an aspect of research in the field of computer graphics (Bloomenthal, 1985), with the purpose of constructing shape models of virtual plants using botanical knowledge (de Reffye *et al.*, 1988; Mech and Prusinkiewicz, 1996; Deussen *et al.*, 2002) or human-computer interactions (Lintermann and Deussen, 1999). Fast visualization of plant communities is a challenge in the field of computer graphics due to the complexity of plant architecture (Meyer *et al.*, 2001; Behrendt *et al.*, 2005) and the necessity of including models in a variety of applications (Deussen *et al.*, 2002). Therefore, more research in this area is a priority, given that end-users are highly susceptible to visual data.

In conclusion, developing simulation models that could reproduce plant functional and structural plasticity is still a major challenge. For this purpose, different approaches and tools are currently being developed that are based on different points of views, i.e. centred on different key physiological processes and investigated at different temporal and spatial scales, from the cellular level to whole-plant populations. These choices are obviously driven by scientific as well as practical objectives and are in that sense all legitimate. The feedback between theoretical, even speculative, models and experimental studies will bring new comprehensive knowledge on plant functioning, and this diversity in modelling approaches will help in finding the key processes driving plant growth and plastic responses.

The PMA06 conference in Beijing (see Fourcaud and Zhang, 2008) was organized in eight sessions covering new advances in plant growth modelling, analysing and modelling plant structure, modelling plant interactions with the environment, application of plant growth models in agronomy, model validation and systems in agriculture, application of plant growth models in forestry, plant geometric models, and plant and landscape visualization techniques. This Special Issue consists of a selection of original and technical papers that consider the link between plant growth and environmental factors, e.g. light and temperature, from the cell to the population level. Most of these

plant models are FS models considering architectural plasticity as an important output. Not all the papers in this Special Issue are concerned with the modelling of plant growth and simulation as discussed in this preface. Pretzsch *et al.* (2008) provide an exhaustive review of models used in European forestry, whereas Danjon *et al.* (2008) and Fourcaud *et al.* (2008) highlight the importance of root-system architecture in models of slope stability and biomechanics, respectively. At this current stage, such root architectural models can be used to determine how different rooting patterns alter plant anchorage mechanics. In the future, this type of model could be linked to the shoot or even integrated into FS models and used to explore different strategies, e.g. how plasticity in plant architecture influences whole-plant biomechanics. We hope, therefore, that the diversity of papers published in this Special Issue will fuel a growing literature on plant growth modelling, bringing forth new conceptual materials and tools, as well as stimulating exchanges between different scientific communities.

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