EDITORIAL

Why work and discuss the basic principles of plant modelling 50 years after the first plant models?

Plant modelling has not yet become a standard method in Plant Biology for integrating complex mechanisms, nor in Genetics for designing new plants. This contrasts with the situation in industry in which, for example, modelling has in good part replaced costly experiments in wind tunnels for the design of cars or planes.

Pioneering papers on plant modelling were published as early as the 1950s, in particular by CT de Wit (De Wit, 1959). There has been constant progress since then with, for instance, the first models of water transfer in the soil–plant–atmosphere continuum in the 1960s and 1970s (Gardner, 1960; Sinclair et al., 1976; Molz, 1981) and the development of crop models in the 1980s and 1990s (Sinclair, 1986; Hammer et al., 1987; Williams et al., 1989). Plant and crop models are now regularly used to calculate transpiration at the canopy level, to predict the consequences of climate changes on crop production, or to design new cropping systems. Conversely, their use in Plant Biology has progressed more slowly, and the design of plant ideotypes with models is still in its infancy. The links between Mathematics and Plant Sciences have mainly involved the structure of genomes and gene networks rather than the simulation of phenotypes in a changing and fluctuating environment.

Why is this progress so slow compared with that in other areas? Our colleagues in the ‘hard sciences’ are often puzzled that we are still debating the theoretical basis of plant models 50 years after the first models were published. This issue of the Journal of Experimental Botany aims to collect new approaches that will hopefully unlock some of the key questions associated with modelling. Three questions have been addressed.

(1) Which algorithms should represent plant functions?

Contrasting views on the representation of complexity coexist in the Plant Science community. For instance, if one looks at plants from a distance, the simple balance of carbon, water, and nitrogen is sufficient to model their behaviour with rules such as ‘growth stops, with some anticipation, if the plant runs out of an element’. Plants have evolved to improve their fitness via elaborate strategies which mimic this rule, thereby avoiding cellular stresses. This algorithm may therefore be sufficient, after some calibration, to predict plant performance of an ‘average genotype’ in a set of well-known environmental scenarios.

This is not the case if the model aims to simulate the differences in behaviour of several genotypes subjected to new or unusual environmental scenarios, because in this case the model has to be accurate in representing the responses to environmental conditions. This results in more complex models which may or may not be appropriate for routinely simulating yields (Tardieu, 2003; Yin et al., 2004).

If the model aims to predict the phenotypic consequences of the allelic diversity of key QTLs on plant performance, an even more detailed simulation of physiological processes is essential to provide an acceptable prediction (Hammer et al., 2006; Tardieu and Tuberosa, 2010). The equations and algorithms involved in these representations are subject to debate because they are not based on uncontroversial physical laws. This special issue presents papers which propose new equations or algorithms for old subjects.

Two papers compile literature data, databases, and unpublished experiments for a multi-species approach of the responses of developmental processes to environmental conditions, light (Poorter et al., 2010) and temperature (Parent et al., 2010). They propose modelling principles and algorithms that may have significant consequences for future models because of their generality.

The combination of thermodynamic laws with biological controls is also a key subject. De Schepper and Steppe (2010) explore and test with measurements an approach to a coupled model of water and sugar in the xylem and phloem. The paper of Ho et al. (2010) develops equations for gas transport inside fruit, and its consequences for fruit physiology.

(2) How to predict plant architecture and its consequences for the capture of light, water, and nutrients?

Plants are a very special case in which the number of organs and their volume, shape, and spatial distribution have a huge genetic variability and can also vary greatly with environmental conditions. Unlike most modelled objects whose structure is essentially known, the objects we want to model define their own structure during their development, in addition to being...
defined by genetic information. Depending on the genotype and on the environmental scenario sensed by plants, the term ‘maize plant’ can represent a small plant with one stem and a few leaves or a bush of several 3-m high stems with 30 leaves each. The architecture of root systems is also hugely variable depending on the soil characteristics and on the genotype. This variability cannot be predicted with straightforward equations because plant development and architecture are controlled by multiple interacting mechanisms, as discussed in the former paragraph. Its consequence for resource capture raises multiple questions in terms of the most appropriate degree of simplification and of the appropriate algorithms.

The paper by Vos et al. (2010) presents advances in the modelling of structures and functions of individual plants, a domain which has emerged relatively recently and represents one of the key challenges for plant modelling.

Two papers address the question of the best representation of how plants colonize space. Dupuy et al. (2010) review the models of root system development and compare the merits of architectural and continuous models. Prusinkiewicz and Barbier de Reuille (2010) review the representations of shoots in space and the generation of form and ramification.

Two papers model the cross-talk between root system architecture and the uptake of water (Draye et al., 2010) or nitrogen (Brun et al., 2010), thereby combining representations of N/water transfers in the soil, of N/water availability to plants, and of the adaptive response of architecture to this availability.

(3) Which representations are adequate for modelling a plant canopy affected by environmental conditions?

It may seem that we are so far from an adequate prediction of plant functions and architecture that any attempt to represent a plant community in complex environments will be at best empiric and, at worst, a moderately honest exercise (Passioura, 1996). However, simplifications which are unacceptable at a detailed level of representation can become acceptable at a more integrated level. The best example is photosynthesis, which can often be modelled with simple thermodynamic equations per unit canopy area (thereby ignoring the difficulties linked to plant architecture), while it is extremely complex at the leaf level (depending on leaf orientation, position, and neighbouring leaves). Emerging properties can be modelled in an efficient way, so the key question is to identify the level of simplification that is appropriate for a given question. Another challenge is how to link crop models that can simulate yield and transpiration in the field in a parsimonious way, with detailed functional models that can capture the effects of genetic variability at a finer scale (Chenu et al., 2008, 2009).

Two papers (Yin and Stuik 2010; Hammer et al., 2010) address the question of the appropriate way to adapt crop models for their use in Physiology and Genetics. It is interesting to note that they present notably different views. As suggested in the title of this paper, there is still room for debate in plant modelling.

Evers et al. (2010) link crop models to functional-structural models in the case of wheat, thereby opening the way to a dialogue between the two types of model.

Soussana et al. (2010) discuss the adequacy of several principles of modelling for use in simulating the consequences of climate change and identify the key points which may hamper progress in this area.

The above paragraphs suggest that the term ‘mechanistic model’ is unfortunate in the case of plant modelling. We are dealing with objects which are, by nature, not amenable to simple modelling based on straightforward principles. However, plant models have already proved their utility for Biology, Genetics, and Agronomy. Progress in plant modelling is a key challenge for the future of these disciplines so that the increasing amount of knowledge and data can be integrated and used. This issue of the Journal of Experimental Botany will hopefully contribute to this progress by exploring new approaches nearly 50 years after the first plant models were published. We can be reasonably sure that the debate on the principles of plant modelling will be open for many years to come.

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References


