

CHAPTER 13

CANONICAL MODELLING

An approach for intermediate-level simulation of carbon allocation in functional-structural plant models

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Abstract. Functional-structural models that include detailed mechanistic representation of underlying physiological processes can be difficult and expensive to build, and the resulting models are often very complicated. This is particularly true when representing carbon allocation, as the various processes involved are relatively poorly understood. Purely empirical models, on the other hand, are simpler and easier to construct, but are of limited use in simulating, predicting and explaining the way that plants adapt and respond to varying environmental conditions. In this chapter, we discuss an intermediate approach to modelling plant function that can simulate plant responses, including changes in carbon allocation patterns, without requiring a detailed knowledge of the underlying physiology. In this approach, plant function is modelled using a 'canonical' modelling approach, where processes such as carbon allocation are represented by a number of fluxes between compartments, and these fluxes are in turn represented using flux functions of a standard mathematical form. The values of the parameters of these flux functions are then determined by fitting the global output of the model to global data, rather than attempting to make the functions represent underlying processes in a quantitatively accurate way. Here we demonstrate the canonical modelling using an example involving the cotton plant, where two alternative hypotheses explaining observed compensation after defoliation are represented. We discuss some potential advantages of this canonical approach over both more mechanistic and more empirical approaches to representing carbon allocation, and conclude that canonical modelling offers a useful, flexible and relatively simple way of simulating plant function at an intermediate level of abstraction.

INTRODUCTION

Species-specific variations in the morphogenetic process are key to the diversity of structure seen in plants, both among species and between individuals of the same species in different environments. Various aspects of the physiology or function of

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the plant are behind these variations, and one of the important differences between species is the strategy with which a plant allocates available carbon to its different components.

One way of trying to understand plant morphogenesis is to construct structural plant models based on the classification and quantification of growth patterns using analysis of architectural data (Hallé et al. 1978; Hayes et al. 1990; Godin et al. 1999; Suzuki 2000). Such models, which are designed to describe plant growth without explicitly representing underlying physiological processes, such as carbon allocation, can be called descriptive or empirical models. However, such models cannot capture the interaction between the development of plant structure and physiological processes such as carbon allocation.

The alternative is to build computational models that represent both the function and structure of a plant, often termed functional-structural plant models (FSPMs) (Room et al. 1996; De Reffye et al. 1997; Kurth and Sloboda 1997; Special issue on functional-structural tree models 1997; Fournier and Andrieu 1998; Special issue second international workshop on functional-structural tree models 2000; Godin et al. 2004). Such models can provide a theoretical framework for experimental investigations aimed at deepening our understanding of plant growth. The general approach underlying many FS models is to represent the plant as a large number of interconnected components (such as internodes and leaves). Various physical, chemical and physiological processes (such as light interception, photosynthesis, nutrient transport and carbon allocation) that take place within and between these components are then represented explicitly (Perttunen et al. 1998; Lacoite 2000; Sievänen et al. 2000; Sinoquet and Le Roux 2000; Le Roux et al. 2001) in what are called process-based or mechanistic models.

In many situations, we would like to construct a model that does not require in-depth experimental investigations or a high level of model complexity, yet is capable of capturing the most important, interesting or relevant aspects of the function and structure of the plant. We would need a model that is adaptable and able to represent causal hypotheses (unlike a purely descriptive or empirical model), yet is simpler and easier to construct than the detailed process-based models. A modelling approach that tried to find this balance between the advantages of empirical and mechanistic modelling could be called an 'intermediate-level' approach.

The intermediate-level FS approach discussed here (Renton 2004) is based on integrating canonical models (Savageau 1969; 1976; Voit 2000) of plant function with L-system (Lindenmayer 1968a; 1968b; Prusinkiewicz and Lindenmayer 1990) simulations of plant structural development. Previous presentations of this approach (Renton et al. 2005a) have focussed on how canonical modelling can be used to simulate various aspects of plant function in FS models, and how a structural L-system model can be linked to an existing canonical model (Kaitaniemi 2000) of plant function (Renton et al. 2005b). Here we focus on how canonical modelling can be used to represent carbon allocation in particular.

CANONICAL MODELLING OF PLANT FUNCTION

Canonical non-linear models have been employed to model a variety of complex biological systems (Torres 1996; Voit and Sands 1996a; Martin 1997; Kaitaniemi 2000) in a mathematically standard way (Voit 1991; 2000). The diagrammatic representation of a canonical model consists of ‘compartments’, ‘fluxes’ and ‘influences’. Figure 1 provides a simple example where compartments are drawn as circles, fluxes as solid arrows and influences as dashed arrows. Compartments are associated with a variable that usually represents some real-world quantity. Fluxes represent flows into, out of, and between compartments. An influence drawn between a compartment and a flux indicates that the magnitude of the flux depends on the magnitude of the quantity represented by the compartment variable. It is generally assumed that a flux is influenced by the compartment that it originates from, so these influences are not drawn.

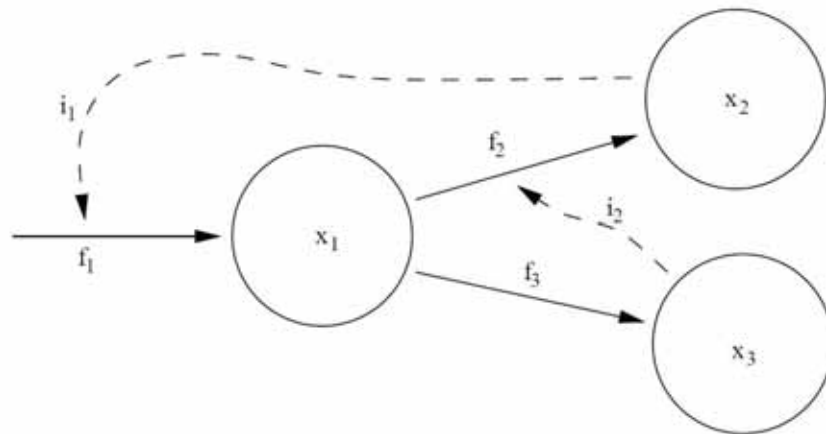


Figure 1. Example graphical representation of a canonical model

As a high-level abstraction representing the physiology of a plant, x_1 would represent unallocated or substrate carbon, x_2 would represent carbon allocated to the shoot and x_3 would represent carbon allocated to the root. The flux f_1 would represent carbon acquisition through photosynthesis, f_2 would represent the allocation of substrate carbon to the shoot and f_3 would represent the allocation of substrate carbon to the root. The arrow i_1 would capture the hypothesis that the rate of carbon acquisition is affected by leaf biomass and the arrow i_2 would represent the hypothesis that the rate of carbon allocation to the shoot is influenced by the amount of root biomass. It is also assumed that the allocation of substrate carbon to both shoot and root will depend on the amount of substrate carbon.

Once this diagrammatic (or compartment) representation of the model has been formulated, fluxes are then represented as ‘canonical’ (or standardized) functions of all compartment variables that influence that flux. The standard canonical power-

law function consists of a ‘rate constant’ multiplied by the product of all associated compartment variables, each raised to a constant ‘kinetic order’ power. In Figure 1, flux f_2 originates from the x_1 compartment and is influenced by the x_3 compartment, so it would be written as

$$f_2(x_1(t), x_3(t)) = \alpha_2 x_1(t)^{k_{21}} x_3(t)^{k_{23}}, \quad (1)$$

where α_2 is the rate-constant parameter and k_{21} and k_{23} are the kinetic-order parameters (with subscript pairs indicating the flux being operated on followed by the compartment-variable identifier).

The way in which these fluxes are aggregated depends on which canonical formalism is being employed. One of the most commonly used formalisms is a Generalized Mass Action (GMA) system, where the rate of change of a compartment variable is written as the sum of all fluxes in, minus all fluxes out. Using a GMA system in this example means the differential equation for x_1 would be

$$\begin{aligned} \frac{dx_1(t)}{dt} &= f_1(x_2(t)) - f_2(x_1(t), x_3(t)) - f_3(x_1(t)) \\ &= \alpha_1 x_2(t)^{k_{12}} - \alpha_2 x_1(t)^{k_{21}} x_3(t)^{k_{23}} - \alpha_3 x_1(t)^{k_{31}} \end{aligned} \quad (2)$$

which is normally written in the abbreviated form

$$\dot{x}_1 = \alpha_1 x_2^{k_{12}} - \alpha_2 x_1^{k_{21}} x_3^{k_{23}} - \alpha_3 x_1^{k_{31}} \quad (3)$$

The other two differential equations representing the model would thus be

$$\dot{x}_2 = \alpha_2 x_1^{k_{21}} x_3^{k_{23}} \quad (4)$$

$$\dot{x}_3 = \alpha_3 x_1^{k_{31}} \quad (5)$$

The procedure for using the canonical power-law modelling approach to simulate an aspect of plant function can be summarized in five steps, as follows. First, the important or significant quantities must be identified, and associated with a compartment and variable. Second, the fluxes or flows into, out of, and between these compartments must be chosen. Third, the modeller must decide which quantities affect which of these fluxes, and include these influences in the model. At this point, we have formulated a compartment model, such as the one shown in Figure 1, that represents qualitative mechanistic assumptions or hypotheses. In the fourth step, a canonical form, such as the power-law form, is used to represent each flux as a function of the influencing variables. Finally, values for the parameters of

these flux functions are estimated, using one or more of a number of possible approaches, including eliminating unnecessary parameters; recognizing constraints on parameters implied by the modelled system; reformulating equations to give parameters a clearer significance; scaling variables; using *ad hoc* manipulation of parameter values with visual feedback of model output; flux-based estimation and using computational algorithms to fit model output at the global scale (Voit 2000; Renton 2004). The parameterized model can be tested and compared against further data, and modified as necessary.

The first three steps of the canonical modelling process are mechanistic in nature and, in general, the inclusion of more compartments and connections (fluxes and influences) corresponds to a more mechanistic model. The last two steps are empirical in that a general equation form is used to summarize a number of physiological processes, and parameter values are chosen to ensure that model output fits the data rather than using an equation form and parameter values representing a particular mechanism.

LINKING TO A STRUCTURAL REPRESENTATION

A canonical model of plant function can be linked to a representation of plant structure to create a functional-structural plant model (Renton et al. 2003; Renton 2004; Renton et al. 2005b). The basic strategy in linking a canonical model of function to a structural L-system model is to make the L-system rules for expansion (change in size of existing plant components) and/or development (the addition of new plant components) depend on the state variables in the canonical model. If the canonical variables correspond to individual structural component characteristics, such as having a compartment for the size of each leaf, this is a straightforward process. If the canonical variable represents a global characteristic of the plant, such as number of components, or plant height or biomass, increases in the variable can then be 'shared out' to create new components and/or to expand the size of existing components in the L-system model according to hypothesized distribution rules. These distribution rules may be stochastic, simulating structural variability, and may also simulate aspects of plant physiology, by taking into account structural and environmental inputs, such as location within a crown, or availability of light.

CANONICAL MODELLING OF DEFOLIATION IN COTTON

The use of the canonical modelling approach to represent carbon allocation processes can be demonstrated by considering growth of the cotton plant. The model is based on a glasshouse experiment that measured cotton plants at regular intervals as they grew to obtain internode and leaf numbers and lengths, which were processed to give estimates of leaf and stem biomass for an average plant. Further details on experimental procedure; data collection and treatment; the results obtained; and model construction, parameterization and testing are available elsewhere (Thornby et al. 2003; Renton 2004; Thornby 2004; Renton et al. 2005a). A basic canonical model of carbon acquisition and allocation, similar to the example

given in Section "Canonical modelling of plant function", consists of compartments for unallocated or substrate resources (x_u), for resources fixed in leaf biomass (x_l), and in stem biomass (x_s), as shown in Figure 2. The flux f_i represents resource acquisition under the standard conditions in which the plants were grown and f_l and f_s represent allocation of resources to leaf and stem, respectively. The flux f_o represents the allocation of resources to all other parts of the plant, or resources that are used or lost in other ways. The dotted arrow represents the influence of leaf biomass on the rate of resource acquisition. This diagrammatic

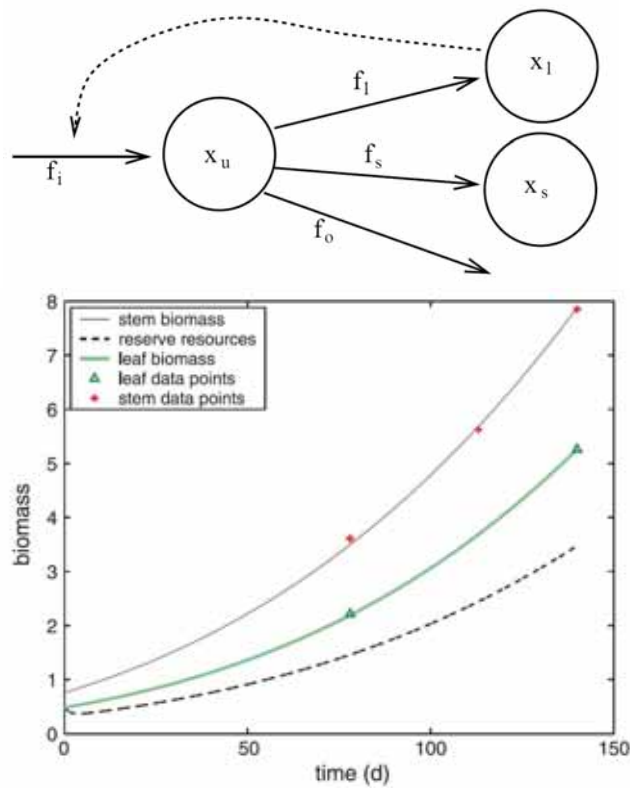


Figure 2. Compartment representation of the basic cotton growth model (top) and the output of this model compared to the data points (bottom). In this model, x_u represents the amount of unallocated resources, and x_l and x_s represent the leaf and stem biomass, respectively. The flux f_i represents resource acquisition and f_l , f_s and f_o represent the allocation of resources to leaf, stem and other destinations, respectively

representation was translated into a system of canonical equations, which was then parameterized to fit the data for the control treatment. This basic cotton growth model was able to simulate the observed data for the control treatment plants, as shown in Figure 2.

To construct the FS model, we began with this basic canonical model and an existing ‘template’ structural L-system model of cotton development (Hanan and Hearn 2003; Thornby et al. 2003; Hanan 2004; Thornby 2004). Since we were interested primarily in defoliation and leaf biomass compensation, the models are linked using the total leaf biomass variable (x_l) of the canonical model. Apart from this link, the two sub-models run in parallel, with development (that is, the rate of appearance of new plant parts and the types of parts being produced) being controlled by the original L-system model independently of the canonical model. The canonical sub-model is integrated with a very small (approximately continuous) time step and the structural sub-model is updated with a daily time step. At the end of each day, the ‘potential growth’ of each immature leaf in the L-system sub-model is calculated using a function that first rises, then falls with the age of the leaf. The ‘total potential growth’ is calculated as the sum of all biomass requirements for the potential growth of all immature leaves in the L-system structure; the ‘total actual growth’ is set to be the amount of new leaf growth indicated by the canonical model for that day (which generally differs from the total potential growth indicated by the structural model); and the ‘growth proportion’ is set equal to the ‘total actual growth’ divided by the ‘total potential growth’. The actual growth of each individual leaf is then calculated as this ‘growth proportion’ multiplied by the original potential growth of that leaf. This ensures that the total leaf area in the structural model is the same as that indicated by the canonical model at the end of the day, and that each leaf grows according to a sigmoid function in ideal conditions. It also causes the rate of individual leaf growth to slow when many leaves are growing at the same time.

This model can then be extended to consider more detailed aspects of physiology. Here, we use the model to investigate different functional hypotheses regarding physiological responses to defoliation, using data from an experiment involving defoliation of cotton seedlings (Thornby 2004). In the canonical sub-model, defoliation is modelled as a reduction in the leaf compartment value at the appropriate time. In order for compensation to occur, as was found in the data, there must be an additional mechanism that increases the leaf production rate following defoliation. We formulated two alternative explanatory hypotheses regarding this mechanism. One hypothesis is that the defoliation causes the production of some signalling compound in the plant, and it is the presence of this compound that causes increased allocation of resources to leaf production. The other hypothesis is that leaves constantly produce some compound such that the concentration of this compound within the plant remains relatively constant unless defoliation occurs, in which case production, and thus concentration, of this compound drops. According to this hypothesis, it is this drop in concentration that, in turn, causes the increased rate of leaf growth. Based on the original cotton growth model (Figure 2), we

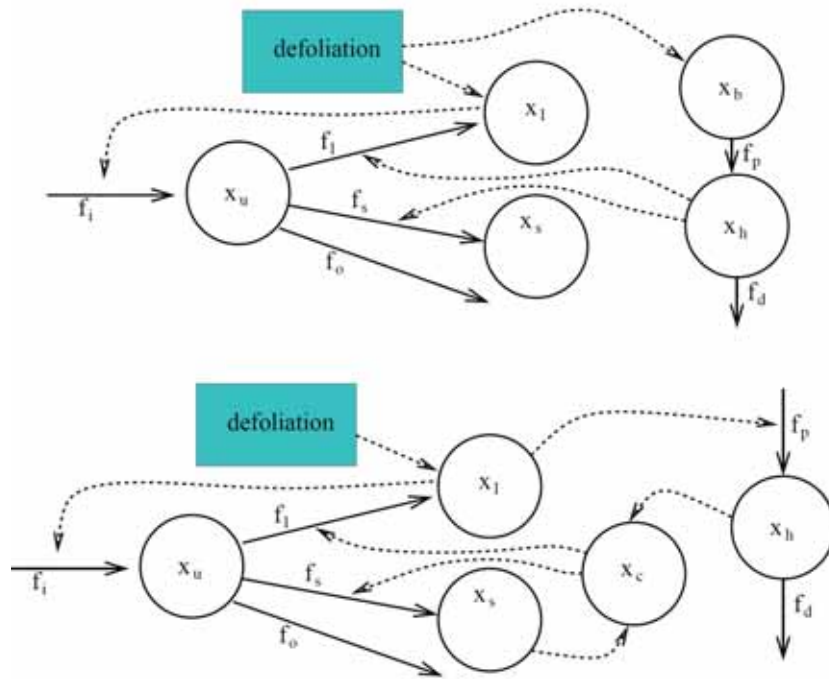


Figure 3. Compartment representations of canonical models of growth and compensation in cotton, based on the hypotheses that compensation following defoliation is caused by the presence (top) or the absence (bottom) of a regulating compound. In these models, x_h represents the amount of the compound in the plant, x_c represents the concentration of the compound, and x_b is a Boolean trigger variable that is 'turned on' following defoliation for an amount of time proportional to the level of defoliation. The flux f_p represents the production of the compound and f_d represents its degradation

developed the two compartment models shown in Figure 3 to represent these two alternative hypotheses. These were translated into canonical equations in the standard way and parameterized to fit the observed data for the two defoliation treatments used in the experiment. These two alternative models of compensation were both able to simulate the observed compensation behaviour (Renton 2004; Figure 4, Renton et al. 2005a).

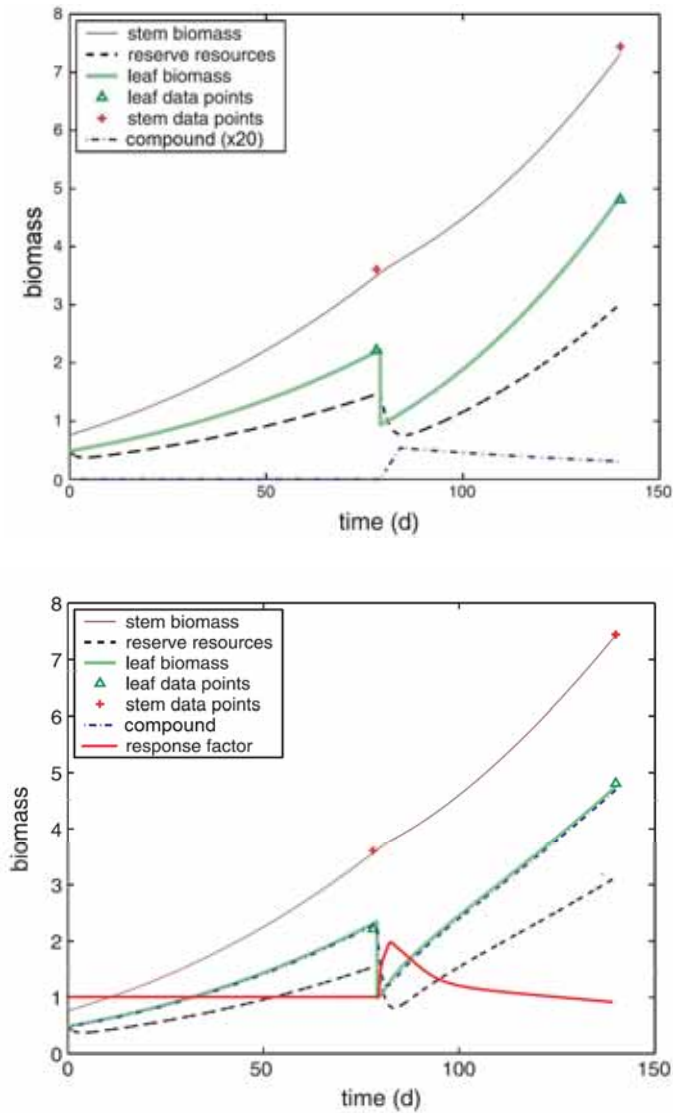


Figure 4. Simulating the effect of 58% defoliation on day 79 using the 'presence' model (top) and the 'absence' model (bottom)

The user of the FS model is able to specify if and when a particular leaf is removed from the structural L-system model; at the same time, the equivalent amount of defoliation is calculated and simulated in the canonical model. The response to this defoliation (simulated by the canonical model according to the presence or absence hypothesis) will involve a boost to leaf biomass allocation in the canonical model, leading to an increase in the rate at which new leaves will grow in the L-system

model. The FS model can thus be used to predict individual leaf biomass (and hence area), and the change in individual leaf biomass as a result of defoliation. Output from the FS model is shown in Figure 5.

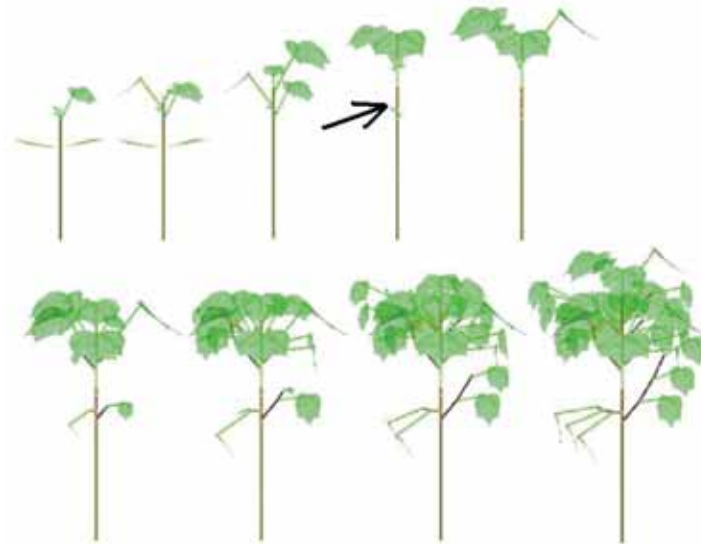


Figure 5. Example output of the FS model of the cotton plant's growth and response to defoliation. The arrow shows where three leaves have been removed in the fourth image. Structural output, such as leaf sizes over time, can now be checked against data

DISCUSSION

Canonical plant models include a representation of underlying processes, mechanisms and interactions, and therefore share some of the advantages that detailed process-based mechanistic models have over empirical models. First, the process of constructing the model requires the modeller to develop a set of causal hypotheses regarding the observed behaviour and represent these hypotheses in a 'formalized' and precise way. Second, the finished model can have explanatory value; the model is capable of explaining observed behaviour in terms of underlying mechanisms. Third, the model can be used to predict behaviour in a wider range of conditions and situations beyond those in which the original data used to construct them was collected (Kaitaniemi 2000).

Because of these three attributes, the canonical approach can be used for exploratory modelling strategies where the model acts as a theoretical framework for experimental investigations. Because the model is a synthesis of a number of mechanistic hypotheses regarding the plant's behaviour, these underlying biological hypotheses can be falsified or refined by comparing the model output to patterns observed in experimental data. Versions of the model representing a number of alternative hypotheses can be constructed, as shown with the 'absence' and 'presence' versions of the cotton model. The approach allows processes and new

variables to be added to the model without changing its overall structure (Voit and Sands 1996a), which facilitates building these alternative versions. These model versions can be used to design experiments or suggest field observations that will distinguish between these different versions, and thus help determine the validity of the alternative hypotheses. In this way, an ongoing process of model refinement and data collection will lead to an increased understanding of biological mechanisms.

However, unlike the detailed process-based approach, the canonical modelling approach can be used when detailed hypotheses or data regarding underlying physiological or chemical processes is not available, such as with carbon allocation. This is because the compartment model can be formulated at a relatively abstract level, the flux functions are of a standard power-law form, and the parameters of these functions can be found empirically by fitting model output to relatively easily observed global variables, rather than by direct measurement of physiological processes (Voit and Sands 1996a; 1996b; Kaitaniemi 2000). For example, the cotton model is based on hypotheses regarding causal mechanisms and physiological interactions, but these were formulated and represented at a general and non-quantitative level. In a situation such as this, where there seems to be little conclusive evidence for what physiological processes are involved in changes to carbon allocation patterns after defoliation (Thornby 2004), a more abstract style of modelling, such as the canonical modelling approach, may be the only option.

Even if the eventual aim is to construct a more detailed and process-based model, a canonical model can act as a 'placeholder' for modelling parts of the system that are not yet well understood. More realistic modelling can be used to represent those parts for which a more detailed understanding already exists. For example, a detailed process-based model of photosynthesis could replace the 'resource acquisition' flux f_i in the canonical cotton model, while carbon allocation would remain represented by canonical flux functions. In this way, the model can contain both abstract and more explicit representations of plant function.

Due to the flexibility of the canonical form of their flux functions, canonical models will tend to fit data more accurately than most empirical models. When parameterized to fit global data, they will also be more accurate than process-based models with parameters fitted at the level of the underlying processes (Renton 2004; Renton et al. 2005a). Canonical models can be used directly, or adapted, to simulate a range of aspects of plant function, such as resource acquisition and growth, limits on growth, storage, allocation and suppression, as well as non-continuous changes in behaviour, such as the triggering of fruiting (Renton 2004; Renton et al. 2005a). They can also be used to model environmental influence on plant growth (Voit 1993; Renton 2004); prioritized allocation of resources (Renton 2004); conversion between continuous biomass quantities and discrete numbers of shoots at the end of a season (Kaitaniemi 2000); and thinning dynamics (Voit 1988) and biomass budgets and growth (Voit and Sands 1996a; 1996b) in tree stands. These processes can be represented canonically at whatever scale is most relevant: whole fields, individual plants, or plant components.

The usefulness of a canonical model of plant function depends on the level of abstraction of the model. Very descriptive canonical models (Renton et al. 2005a) can be used for visualizing, describing or communicating experimental results. A

more mechanistic canonical model, such as the cotton example, can be used as a theoretical framework in an ongoing process of experimental investigation, as discussed above. While detailed process-based models tend to aim for a high degree of realism, and thus risk becoming very complex, the canonical approach helps build a functional model that is 'just complex enough', by including only the relevant processes at the necessary level of detail for a particular problem. If the goal is to produce a very realistic and detailed model for research purposes, then the canonical approach may not be appropriate. Nevertheless, if the testing and refining of a canonical model were continued against a broad range of experimental results, the model may eventually have the potential to be used for management applications, such as decision-making, prediction or control.

Canonical modelling of plant function can certainly be employed without a structural representation, but adding structure increases the usefulness of the model in different ways, depending on the model's level of abstraction. Adding a corresponding representation of plant structure enhances the ways that a descriptive model can be used for visualizing, describing or communicating information. With the addition of structure, a descriptive canonical model could also act as a sub-model within broader theoretical investigations, such as looking at how light interception patterns change with the growth of the plant, or understanding patterns of insect movement or spore dispersal through the structure of the plant. Adding structure to a more mechanistic canonical model, like the cotton model, creates many extra aspects of model output, such as branching patterns, size of individual components, and even the visual appearance of the plant, that can be checked against experimental data. Furthermore, adding a model of structure that interacts with the canonical model of physiology in some way – through simulations of endogenous signalling or light capture by individual leaves (Renton et al. 2005b), for example – can enhance the level of mechanism of the model.

The canonical modelling approach provides a means of modelling plant processes, such as carbon allocation, at an 'intermediate' level of abstraction, between that of detailed process-based mechanistic models aiming for a high degree of realism, and empirical models aiming simply to describe observed patterns. The resulting functional model can then be linked to structural plant models to produce FS plant models. Future research could further develop the approach's usefulness for plant modelling by investigating how the approach can be applied to a wider range of experimental and modelling situations; comparing the benefits of different canonical function forms; simplifying and possibly automating the process of parameter estimation; and exploring in greater depth and eventually formalizing the process of linking the canonical model to the structural model.

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