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Unravelling the output uncertainty of a tree water flow and storage model using several global sensitivity analysis methods

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The output uncertainty of two variables (stem sap flow rate and stem diameter variations) of a tree water flow and storage model is broken down into its different constituents using two global sensitivity analysis methods: extended Morris screening and an extended Fourier amplitude sensitivity test. Using these methods, quantitative and qualitative information about the parameters contributing most to the model output uncertainty was obtained. It was shown that only three parameters (out of the 11 considered) were responsible for the uncertainty on the stem sap flow rate and that three other parameters were accountable for most of the uncertainty in stem diameter variations. Furthermore, the parameters influencing the stem diameter variations were involved in significant interactions. An investigation into the effect of the magnitude of the parameter uncertainty on the results of the sensitivity analysis showed that the contribution of the parameter interactions increased with increasing parameter uncertainty. By combining several global sensitivity analysis methods the results were not only verified but more confidence was gained in the accuracy of the methods used and complementary information was obtained. This allowed a more detailed picture to be constructed of how the individual parameters interact and contribute to the output uncertainty of the model.

1. Introduction

Most stages of the development process of a mechanistic model, in which parameters have a physical meaning, are associated with some degree of uncertainty (Beck, 1987; Chatfield, 1995). It is well-known that models are only simplified representations of reality caused by abstract choices that are made during the development process. These choices involve (1) selecting which processes to model, and which to neglect; and (2) selecting the equations used to represent and link the processes. At this stage, choices related to spatial and temporal aggregation are also made. Many authors acknowledge that the uncertainty associated with these choices is very difficult to quantify, if at all possible (Chatfield, 1995; Jansen,

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1998; Refsgaard *et al.*, 2006). Therefore, one could argue that the errors introduced in this way should not be regarded as uncertainties in the strictest sense of the word.

Once a certain model structure has been chosen, two important sources of uncertainty contribute to the model output uncertainty: input and parameter uncertainty (Beck, 1987; Refsgaard *et al.*, 2006). A first source is related to the uncertainty associated with the (time-varying) driving forces of the model, the inputs. This uncertainty is not only caused by imprecise measurements, but also by the inherent variability of the inputs themselves (e.g., climatic data). A second source of model output uncertainty is associated with the model parameters. In this case, uncertainty arises when imprecise measurements are used to assign parameter values directly or through model calibration.

Quantifying model output uncertainty can be very useful. Especially when judging the quality of the fit of a model to experimental data or, more importantly, when using the model for prediction and decision making. However, knowing the cause of the uncertainty can also be equally important. This knowledge allows the modeller to highlight important sources of uncertainty and, therefore, pinpoint parts of the model that require additional attention or improvement in order to reduce the overall model output uncertainty. Unravelling the model output uncertainty into its different contributions is a task that can be performed through a sensitivity analysis (Saltelli *et al.*, 2000).

In sensitivity analysis, a distinction should be made between local and global methods. A local sensitivity analysis is used to study the importance of model parameters at one point in the parameter domain. At this point, parameters are changed one at a time by a certain fraction of their value and their effect is quantified (Law *et al.*, 2000; Dufrêne *et al.*, 2005; Pathak *et al.*, 2007). The validity of the information obtained through such an analysis is, however, restricted to the selected point in the parameter domain. In order to deal with this issue, a global sensitivity analysis can be performed, which allows the entire parameter domain (or a portion of it) to be analysed. Techniques belonging to this category are regression-based methods (Levy and McKay, 2003; Verbeeck *et al.*, 2006), screening methods and factorial design (Morris, 1991; Campolongo and Braddock, 1999; Pathak *et al.*, 2007) and variance-based methods (Cukier *et al.*, 1973; Saltelli *et al.*, 1999; White *et al.*, 2000; Smith and Heath, 2001; Gottschalk *et al.*, 2007).

From the available global sensitivity analysis methods, the (extended) Morris screening method (Morris, 1991; Campolongo and Braddock, 1999) and the (extended) FAST (Cukier *et al.*, 1973; Saltelli *et al.*, 1999) stand out because of their frequent application in many scientific fields. Besides being useful for quantifying the importance of the model parameters, they also provide valuable information regarding first order, non-linear and interaction effects. It is the aim of this paper to introduce these two techniques to the field of plant science and to apply them to the RCGro tree water flow and storage model that is designed to study and simulate the water transport dynamics and related stem diameter variations in trees (Steppe *et al.*, 2006).

The contents of this paper are outlined as follows. In Section 2, we briefly describe the mathematical model. Section 3 is devoted to the methods used in this contribution, namely uncertainty analysis and the extended Morris screening and the extended FAST, both global sensitivity analysis methods. In Section 4, the results of the analysis are presented and discussed. Finally, Section 5 concludes the contribution.

2. Model description

As with many biological systems, the tree water flow and storage model considered in this study is described by a set of algebraic and ordinary differential equations of the general form:

$$\frac{dx}{dt} = f(x, \theta, u, t), \quad x(t_0) = x_0, \qquad y = g(x, \theta, u, t), \tag{1}$$

where x is a vector of state variables, θ a vector of parameters of size p, y a vector of outputs of size n, u a vector of inputs and t the independent variable.

The model enables simulation of the dynamic water transport in a tree and includes reversible (i.e., daily stem diameter fluctuations) and irreversible (i.e., radial stem growth) changes in stem diameter (D) for a given daily course of leaf transpiration (E) and soil water potential (Ψ_{soil}) as input variables. All model equations were solved using a fourth order Runge Kutta variable step size integrator with accuracy set to 1E−08.

As illustrated in Fig. 1, the model consists of two storage compartments (i.e., a stem and a crown storage pool representing living extensible tissues) and two vertical xylem flow paths (i.e., F(stem) and F(crown), the mass flow rate of water at the stem base and the upper stem section, respectively). The storage compartments are defined by their hydraulic capacitance (i.e., C(stem) and C(crown)). A water potential gradient along the non-living xylem vessels forces water to move upwards. While ascending, water encounters a resistance R^x. Besides vertical water transport, internally stored water can contribute to the transpiration stream because of the hydraulic connection between the xylem and storage pools (Simonneau *et al.*, 1993; Génard *et al.*, 2001; Zweifel *et al.*, 2001; Steppe and Lemeur, 2004).

Furthermore, radial water flow between the xylem and the stem storage compartment is directly linked to the stem diameter variations (see Steppe *et al.* (2006) for more details). In short, the stem is modelled as an outer ring composed of various extensible tissues (single cell stem storage pool) separated from the rigid xylem by a virtual membrane (Génard *et al.*, 2001; Steppe *et al.*, 2006). Stem diameter variations are assumed to result from: (1) shrinkage and swelling due to changes in internally stored water (i.e., reversible D fluctuations); and (2) (irreversible) radial stem growth. Radial water flow into and out of the stem storage pool causes changes in stem water content and, therefore, causes elastic changes in D. However, besides these reversible diameter fluctuations, the tree stem also grows. The mechanistic description of radial stem growth relies on Lockhart's equation (Lockhart, 1965), which states that cell expansion is largely driven by turgor pressure (i.e., positive Ψ_p). Turgor pressure in the model is dependent on radial water flow between the xylem and the stem storage pool and irreversibly