



Time-dependent sensitivity of a process-based ecological model



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ARTICLE INFO

Article history:

Received 31 December 2012

Received in revised form 5 June 2013

Accepted 10 June 2013

Available online 7 July 2013

Keywords:

3-PG

Fourier amplitude sensitivity test

Process-based model

Temporal

Sensitivity analysis

Forest growth model

ABSTRACT

Sensitivity analysis is useful for understanding the behaviour of process-based ecological models. Often, time influences many model processes. Hence, the sensitivity of model outputs to variation in input parameters may also change with simulation period. We assessed the time-dependence of parameter sensitivity in a well-established forest growth model 3-PG (Physiological Principles for Predicting Growth) (Landsberg and Waring, 1997) as a case study. We used a screening method to select influential parameters for two key model outputs, i.e., stand volume and foliage biomass, then applied the Fourier amplitude sensitivity test (FAST) to quantify the sensitivity of the outputs to these selected parameters. Sensitivities were assessed on an annual time-step spanning 5–50 years of forest stand age. The influence of climatic and soil variables on time-dependent sensitivities was also quantified. We found that the sensitivities of most parameters changed substantially with forest stand age. Different climate and soil data also influenced the sensitivities of some parameters. Time-dependent sensitivity analysis provided much greater insight into model structure and behaviour than previous snapshot sensitivity analyses. Failing to account for time-dependence in sensitivity analysis could lead to misguided efforts in model calibration and parameter refinement, and the mis-identification of insensitive parameters for default value allocation. We concluded that sensitivity analysis should be conducted at simulation periods compatible with the process of interest. A more comprehensive sensitivity analysis scheme is required for temporal models to explore parameter sensitivities over the full simulation period and over the full variation in forcing data.

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1. Introduction

Uncertainty analysis is an important part of the successful development, calibration, and application of process-based ecological models (Vrugt and Robinson, 2007). Due to the complex nature of ecological systems and the limited knowledge of the underlying processes, uncertainty is usually unavoidable. However, by identifying those parameters and processes most influential on model outputs through sensitivity analysis (SA), efforts could be guided towards improving the accuracies of the most influential parameters and be used to better understand model structure and behaviour, and reduce model uncertainty (Marino et al., 2008; Makler-Pick et al., 2011; Song et al., 2012). This is especially

important for complex, process-based ecological models which can be richly parameterized (Wang et al., 2009).

Process-based ecological models often include time-dependent, non-linear processes (Landsberg and Waring, 1997; Thornton et al., 2002). This suggests that the contributions of each parameter to the variation in model outputs may also change with time. For forest growth models for example, the coupled non-linear reduction in stomatal conductance and hydraulic conductivity as trees age will inevitably influence all related physiological processes, e.g. photosynthesis and biomass allocation (Landsberg and Waring, 1997; Ryan and Yoder, 1997). Thereby, some parameters influential at young stand ages may decline in influence in older stands, and vice versa (Song et al., 2012). A time-dependent sensitivity analysis, which analyses model behaviour over the full simulation period horizon, is necessary for providing a more comprehensive understanding of the model structure, and to assist model calibration. However, many studies have undertaken

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SA only at a single simulation period (e.g. Lu and Mohanty, 2001; Esprey et al., 2004; Makler-Pick et al., 2011). These types of *snapshot* SA may give a biased or unrepresentative view of parameter sensitivities corresponding to certain model outputs. Song et al. (2012) and Makler-Pick et al. (2011) suggested that time-dependence may change parameter sensitivities and highlighted this area for further research. A few other studies have also recognized this issue but have fallen short of quantifying the implications for temporal process-based ecological models (Cariboni et al., 2007; Marino et al., 2008; Xu et al., 2009). Further, model forcing data (e.g. climate and soil texture) may also influence parameter sensitivities (Fuentes et al., 2006; Almeida et al., 2007a). Ignoring the influence of forcing data may produce misleading results, especially when the environmental factors differ between sites. The influence of climate data is of great interest in this perspective as climate is likely to change over time.

Two types of SA are often used – local and global. Local SAs estimate the sensitivity of one parameter while holding all other parameters at central values. This provides an accurate estimate of parameter sensitivity under a very specific model condition and is only suitable for simple linear or additive models (Saltelli et al., 2008). For complex and parameter-rich models, global SAs are required which explore the full parameter space. Global SAs can be used to quantify the contribution of each parameter to the variation in the corresponding model output, and are useful for characterizing model structure and behaviour (Saltelli, 2000; Helton, 2008). Methods for global SA include the Fourier amplitude sensitivity test (FAST) (Cukier et al., 1973; Xu and Gertner, 2007), variance-based methods such as Sobol' (Sobol', 1990) and Saltelli's (Saltelli et al., 2010), and moment-independent method (Borgonovo, 2007). Variance-based methods can quantify both the main effect – the partial variance contributed by a certain parameter to the total variance of corresponding model output – and the interaction effects between parameters, but they are computationally intensive. Moment-independent method (Borgonovo, 2007) can also capture dependence among model parameters and consider sensitivity across the full distribution of model outputs, and are computationally efficient (Plischke et al., 2013). FAST is also computationally efficient (Saltelli et al., 1999; Xu and Gertner, 2011) and has been widely applied in analysing sensitivities in a wide range of models, including models of ecological (Xu et al., 2009), chemical (Lu and Mohanty, 2001), biological (Thogmartin, 2010), and atmospheric (Kioutsioukis et al., 2004).

The objectives of this study were to quantify the time-dependent parameter sensitivities for selected model outputs, and to demonstrate the significance of time-dependence in understanding model behaviour. A well known forest growth model, Physiological Principles for Predicting Growth (3-PG) (Landsberg and Waring, 1997) was used for this purpose. We first applied the computationally efficient Morris method to screen out the least influential parameters for each model output. We then applied the FAST method to analyse the sensitivities of the remaining parameters. Sensitivities were calculated at annual step from 5 to 50 years. The agreement among parameter sensitivities for each model output over time was quantified by computing the correlation coefficients on the ranking using Savage scores (Iman and Conover, 1987), and graphically visualized. We also analysed the influence of forcing data (e.g. climate and soil texture) on the time-dependence of parameter sensitivities. We discuss the impact of time-dependence on the effectiveness of sensitivity analysis in enabling the understanding of model structure and behaviour, and in informing model calibration. We also discuss the interrelationships among parameter distributions, sensitivities, and model output uncertainties.

2. Methods and data

2.1. Model description

Applications of process-based forest productivity models have increased recently due to their ability to simulate underlying physiological processes and to address questions in a range of fields such as forestry production (Almeida et al., 2010), carbon sequestration (Bryan and Crossman, 2013), biodiversity conservation (Crossman et al., 2011), bioenergy (Bryan et al., 2010), and food security (Paterson and Bryan, 2012). The 3-PG model is a simple process-based and stand-level deterministic forest growth model which captures the basic physiological principles of forest growth (Coops et al., 1998; Landsberg et al., 2001). 3-PG simulates growth in even-aged, homogeneous forests or plantations, and has been applied to a range of species including *Eucalyptus* species (Sands and Landsberg, 2002; Paul et al., 2007; Almeida et al., 2010), loblolly pine (Landsberg et al., 2001), and Douglas-Fir (Coops et al., 2010).

The 3-PG model has been continuously improved since its first publication in 1997. A detailed description of 3-PG can be found in Landsberg and Waring (1997), Sands and Landsberg (2002), and Paul et al. (2007). Important versions include 3-PGpjs (Sands and Landsberg, 2002; Sands, 2004), 3PG-Spatial (Tickle et al., 2001; Coops et al., 2010), and 3-PG2 (Almeida et al., 2007a). The latter includes a more detailed water balance calculations in forested landscapes. In this study, we used 3-PG2 and ported this Visual Basic for Applications (VBA) model into the Python programming language (<http://python.org>) to enable SA.

The 3-PG2 model can be used to predict a range of outputs, which include forest gross primary production (GPP), net primary production (NPP), foliage and stem biomass, water balance in forest soils and evapotranspiration. The model runs on a monthly time step. The input data required includes monthly average climate data (short wave solar radiation, mean maximum and minimum air temperature, vapour pressure deficit (VPD), frost days, rainfall and number of rainfall days), and site-specific parameters including latitude, soil texture, fertility rating (*FR*) (hereafter model parameters are represented as italic letters and model outputs in regular font), and initial number of stems per hectare. *FR* describes soil nutrient status as a score between 0 (for low fertility) and 1 (for high fertility) (Almeida et al., 2007b). Soil texture is classified into 12 classes. There are seven common soil attributes under each class to describe soil water related properties (Almeida et al., 2007a). Whilst 3-PG2 has more than sixty parameters, we selected 38 species-specific parameters for sensitivity analysis, excluding those parameters which have constant values (e.g. ratio of NPP and GPP, and molecular weight of dry matter) (Esprey et al., 2004; Almeida et al., 2007a; Song et al., 2012).

2.2. Data sources

We used one plot named Greenvale of *Corymbia maculata* and *Eucalyptus cladocalyx* located in Queensland, Australia, to demonstrate the time-dependent sensitivity properties of parameters in 3-PG2. This plot has a long climate record from 1930 to 2006, a *FR* of 0.2, and a clay soil texture. Two important biomass-related output variables, namely StandVol (stand volume excluding bark and branch ($\text{m}^3 \text{ha}^{-1}$)) and WF (foliage biomass (t ha^{-1})), were used in the following analysis.

Due to a lack of information about the prior probability distributions for each parameter, we assumed an independent uniform distribution for each parameter with bounds set at 30% either side of its reference value (Esprey et al., 2004; van Oijen et al., 2005; Song et al., 2012). Without loss of generality, the

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