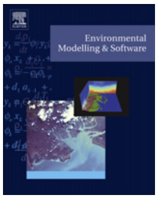
Environmental Modelling & Software 42 (2013) 99–115

Contents lists available at SciVerse ScienceDirect

Environmental Modelling & Software

journal homepage: www.elsevier.com/locate/envsoft



# Using a Bayesian framework and global sensitivity analysis to identify strengths and weaknesses of two process-based models differing in representation of autotrophic respiration

F. Minunno [a,*], M. van Oijen [b], D.R. Cameron [b], S. Cerasoli [a], J.S. Pereira [a], M. Tomé [a]

[a] *Forest Research Center, Faculty of Agricultural Sciences, Technical University of Lisbon, Lisbon, Portugal*
[b] *CEH-Edinburgh, Bush Estate Penicuik, EH26 0QB, UK*

ARTICLE INFO

*Article history:*
Received 30 January 2012
Received in revised form
10 December 2012
Accepted 13 December 2012
Available online 21 January 2013

*Keywords:*
3-PG
Net primary production
Respiration
Bayesian calibration
Bayesian model comparison
Morris screening
Carbon cycle
Uncertainty analysis
Global sensitivity analysis

ABSTRACT

Process-based models are powerful tools for sustainable and adaptive forest management. Bayesian statistics and global sensitivity analysis allow to reduce uncertainties in parameters and outputs, and they provide better insight of model behaviour. In this work two versions of a process-based model that differed in the autotrophic respiration modelling were analysed. The original version (3PGN) was based on a constant ratio between net and gross primary production, while in a new version (3PGN*) the autotrophic respiration was modelled as a function of temperature and biomass. A Bayesian framework, and a global sensitivity analysis (Morris method) were used to reduce parametric uncertainty, to highlight strengths and weaknesses of the models and to evaluate their performances. The Bayesian approach allowed also to identify the weaknesses and strengths of the dataset used for the analyses. The Morris method in combination with the Bayesian framework helped to identify key parameters and gave a deeper understanding of model behaviour. Both model versions reliably predicted average stand diameter at breast height, average stand height, stand volume and stem biomass. On the contrary, the models were not able to accurately predict net ecosystem production. Bayesian model comparison showed that 3PGN*, with the new autotrophic respiration model, has a higher conditional probability of being correct than the original 3PGN model.

## 1. Introduction

During the last decades, forests have been experiencing fast changes in the environmental conditions, to which forest management must adapt. Process-based models (PBMs), based on ecophysiological principles, are invaluable tools for sustainable and adaptive forest management (Fontes et al., 2010). PBMs allow for the estimation of site productivity and can simulate the effects of management and environmental constraints on stand growth and the probable influence of climate change on forest productivity. Furthermore PBMs enable analyses at different spatial and temporal scales (Fontes et al., 2010). However, calibration of PBMs is often difficult because they tend to have many parameters and outputs for which only few data are available. Moreover, because models are simplifications of reality, we need to assess carefully how well their structure allows for simulation of the phenomena of interest. Bayesian statistics, based on probability theory, offers an alternative to the calibration problem and can provide parameter estimates with estimates of their uncertainty (van Oijen et al., 2005). The Bayesian approach also allows for the evaluation of model structure by quantifying the extent to which data support different models (Kass and Raftery, 1995; van Oijen et al., 2011). In addition, the increasing availability of eddy-covariance measurements with high temporal resolution (Pereira et al., 2007) provided by the Fluxnet and other regional networks, allows for calibration as well as for model validation.

In this work a Bayesian framework and a global sensitivity analysis were used in combination to test an improvement of a process-based model (3PGN, Xenakis et al., 2008) and to study model behaviour. Two versions of 3PGN that differ in their representation of autotrophic respiration ($R_{aut}$) were calibrated and evaluated. 3PGN is based on a constant value of carbon-use efficiency (CUE), defined as the ratio between net primary production ($P_N$) and gross primary production ($P_G$) (Gifford, 2003); therefore, $R_{aut}$ is modelled as a fixed proportion of $P_G$. The understanding of the factors regulating $R_{aut}$ is one of the most challenging questions in

---

[*] Corresponding author.
*E-mail addresses:* francescom@isa.utl.pt, checcomi@gmail.com (F. Minunno).

1364-8152/$ – see front matter © 2012 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.envsoft.2012.12.010

ecological forest research. Many studies argue that $P_N$:$P_G$ is constant (Dewar et al., 1998; Gifford, 1994, 2003). Waring et al. (1998) proposed a universal value of 0.47 for most forests. More recently, van Oijen et al. (2010), using a mathematical approach based on the law of conservation of mass, showed that $P_N$:$P_G$ is narrowly constrained. However, owing to the difficulty in measuring carbon-use efficiency and in particular the $P_G$ component, methodological problems can mask variation in $P_N$:$P_G$ (Medlyn and Dewar, 1999), casting doubts about the existence of fixed values of the ratio between net and gross primary production. DeLucia et al. (2007), conducting a literature review, found that CUE varied between 0.23 and 0.83 across 60 different forests, with an average of 0.53.

A different approach is to model $R_{aut}$ as the sum of two components: maintenance ($R_{maint}$) and growth ($R_{growth}$) respiration, the first being proportional to the live biomass and its temperature, the second being proportional to $P_N$. This theory was developed in the 1970s by McCree (1974), and many authors followed this approach (e.g., Penning de Vries, 1974, 1975; Ryan and Waring, 1992). A detailed review of the progress achieved in respiration modelling over the last decades can be found in Amthor (2000). Warmer climates should have higher respiration costs, because the maintenance respiration increases exponentially with temperature (Ryan, 1991). This kind of $R_{aut}$ modelling ($R_{maint} + R_{growth}$) has been used in many process-based models (e.g. CABALA (Battaglia, 2004); PIXGRO (Adiku et al., 2006); MAESTRO (Wang and Jarvis, 1990)).

In the present work the original version of 3PGN, based on a constant $P_N$:$P_G$ ratio, and a new version (3PGN$^*$), in which $R_{aut}$ is modelled as the sum of maintenance and growth plant respiration, were calibrated and evaluated under a Bayesian framework. As proposed by van Oijen et al. (2011), the Bayesian framework consisted of model calibration, model comparison and analysis of model-data mismatch. Sensitivity analyses of the two model versions were also carried out to have a better insight of model behaviour (Campolongo et al., 2007). A Bayesian framework and a global sensitivity analysis, Morris method (Morris, 1991), were used in combination to highlight the strengths and weaknesses of the two model versions and to evaluate their performances.

## 2. Materials and methods

### 2.1. Overview of the methodology

Our study used eddy-covariance data and forest measurements collected at two different sites: a CarboEurope-IP site (Espirra forest) and a field experiment (Furadouro experiment). At a first stage both models were calibrated using the full dataset (i.e., Espirra forest and Furadouro experiment). The Bayesian framework proposed by van Oijen et al. (2011) and the Morris method were used in combination to better understand the behaviour of the models.

Subsequently, two Bayesian model comparisons (BMCs) were performed to evaluate the models. The first BMC was carried out in light of the prior knowledge of the two models (*prior BMC*). Meanwhile, for the second BMC part of the dataset was used for model calibration and the rest of the data were used for model evaluation (*post BMC*). For the *prior BMC* 1000 parameter vectors were sampled from the prior distributions of the two model versions. The models were run with the sampled parameter sets and the distributions of model outputs were used in a Bayesian model comparison. For the *prior BMC* the models were compared in light of the full dataset (i.e., Espirra forest and Furadouro experiment). For the second Bayesian model comparison, the models were calibrated with the Furadouro experiment data and then compared using the Espirra forest dataset.

### 2.2. 3PGN structure

3PGN was developed by Xenakis et al. (2008) coupling two models, 3-PG (Physiological Principles in Predicting Growth) (Landsberg and Waring, 1997) and ICBM (Introductory Carbon Balance Model) (Andrén and Kätterer, 1997). The resulting model structure was comprehensively described by Xenakis et al. (2008) – only a brief outline is given here.

A detailed description of 3-PG was provided by Landsberg and Waring (1997) and by Sands and Landsberg (2002). 3-PG is composed of five sub-models. One is used to calculate the productivity of the stand and another is used for partitioning biomass between different organs (foliage, roots and stem). The other three sub-models are used to determine the changes in stem number, soil water balance and variables of interest to forest managers, such as stand timber volume ($V$, m$^3$ ha$^{-1}$), mean diameter at breast height ($D$, cm) and stand basal area.

3-PG is based on the principle that the net primary production of a stand is primarily determined by radiation interception. $P_G$ is calculated by multiplying the fraction of the photosynthetically active radiation absorbed by the stand ($\Phi_{aPAR}$) with canopy quantum efficiency ($\alpha_c$). $\Phi_{aPAR}$ is calculated using Beer's law. The canopy quantum efficiency is calculated by multiplying a theoretical maximum canopy quantum efficiency (*alpha*) with an array of site and physiological modifiers that vary between 0 and 1 (functions of atmospheric vapour pressure deficit, air temperature, frost, water balance, age and fertility rating (*FR*)). $P_N$ is calculated as a constant fraction ($Y$) of $P_G$ (Law et al., 2000; Waring et al., 1998). The carbon allocation routine sub model is based on allometric equations, on a single-tree basis. A fraction of $P_N$ is allocated below-ground by a root allocation coefficient that is affected by soil fertility. The remaining biomass is partitioned between the aboveground organs as a function of diameter at breast height and foliage: stem ratio.

The 3-PG model has been applied to many different species and sites and it is widely used in research as well as by companies to assess forest growth and site productivity (Landsberg, 2003). Fontes et al. (2006) parameterized 3-PG for Portuguese plantations of *Eucalyptus globulus*, Labill., demonstrating that carbon allocation of *E. globulus* in Portugal differs strongly from allocation patterns in Australian plantations.

A complete description of ICBM is provided by Andrén and Kätterer (1997) and Kätterer and Andrén (1999, 2001). ICBM/2N considers three pools of C and three pools of N in the soil, consisting of different forms of organic matter: the "young labile" pool, that includes small tree detritus (such as litterfall and root turnover), a "young refractory" pool, that includes coarse woody detritus (coarse root, branches and stems) and an "old" pool, that includes the recalcitrant organic matter. Each pool has a different decomposition rate that varies along the year with environmental conditions (i.e., temperature and soil water content), but does not change during stand development (Mäkelä and Vanninen, 2000; Titus and Malcolm, 1999). Carbon decomposed from the young pools enters the old pool at a constant relative rate of humification. The fraction from each young pool that is decomposed but not humified is considered as respiratory loss. Similarly, decomposition losses take place from the "old" pool. The sum of all the out-fluxes from the three pools gives the heterotrophic respiration. The nitrogen balance is based on fixed C:N ratios and the size of the C fluxes and pools.

In 3PGN, the biomass losses of the stand (litterfall, root turnover, death of trees, but excluding tree harvesting), calculated by 3-PG, are the inputs for ICBM/2N. The latter model is used to calculate the heterotrophic respiration, but not the site fertility parameter (*FR*) of 3-PG. As in the original version of 3-PG (Landsberg and Waring, 1997), the *FR* parameter was site specific. In this work, five different FRs were parameterised for each site by means of Bayesian calibration.

### 2.3. The two versions of 3PGN

In the two 3PGN versions used in this work, tree diameter $D$ was calculated as a function of total aboveground dry biomass (*i.e.*, leaves included).

$$D = StCn^* W_{abv}^{StPw} \tag{1}$$

where $W_{abv}$ is the aboveground biomass (kg per tree) and *StCn* and *StPw* are regression coefficients.

Because average stand height ($H$) is an important stand variable, a new equation for the calculation of $H$ was introduced.

$$H = aH^* W_{abv}^{bW} \tag{2}$$

where *aH* and *bW* are regression coefficients.

The two model versions used in this work calculate autotrophic respiration ($R_{aut}$) in different ways. In the old version (3PGN), $R_{aut}$ is proportional to photosynthesis. In the new version (3PGN$^*$), $R_{aut}$ is the sum of respiration for maintenance ($R_{maint}$) and for growth ($R_{growth}$):

$$R_{aut} = R_{growth} + R_{maint} \tag{3}$$

Maintenance respiration is assumed to be a function of biomass and average temperature ($T_{av}$) and it follows different specific rates for the woody ($r_w$) and foliage ($r_f$) tissues. In the woody pool the branches, stem and the root biomass were included.

$$R_{maint} = \sum W_i r_i Q_{10}^{(T_{av}-20)/10} \tag{4}$$

where $W_i$ and $r_i$ are dry weight and specific respiration rate, respectively, of the $i$th plant pool (woody or foliage); $Q_{10}$ determines the temperature responsiveness of respiration.

Growth respiration is calculated as:

$$R_{growth} = r_g^*(P_G - R_{maint}) \tag{5}$$