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Parameter sensitivity and uncertainty of the forest carbon flux model FORUG: a Monte Carlo analysis[†]

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Summary The Monte Carlo technique can be used to propagate input variable uncertainty and parameter uncertainty through a model to determine output uncertainty. However, to carry out Monte Carlo simulations, the uncertainty distributions or the probability density functions (PDFs) of the model parameters and input variables must be known. This remains one of the bottlenecks in current uncertainty research in forest carbon flux modeling. Because forest carbon flux models involve many parameters, we questioned whether it is necessary to take into account all parameters in the uncertainty analysis. A sensitivity analysis can determine the parameters contributing most to the overall model output uncertainty. This paper illustrates the usefulness of the Monte Carlo simulation technique for ranking parameters for sensitivity and uncertainty in process-based forest flux models.

The uncertainty of the output (net ecosystem exchange, NEE) of the FORUG model was estimated for the Hesse beech forest (1997). Based on the arbitrary uncertainty of ten key parameters, a standard deviation of 0.88 Mg C ha^{-1} $year^{-1}$ NEE was found which is equal to 24% of the mean value of NEE. Sensitivity analysis showed that the overall output uncertainty of the FORUG model can largely be determined by accounting for the uncertainty of only a few key parameters. The results led to the identification of the key FORUG parameters and to the recommendation for a process-based description of the soil respiration process in the FORUG model.

Keywords: least square linearization, photosynthesis, probability density function, soil respiration.

Introduction

In the context of a changing climate, the primary objectives of forest modeling studies are to predict how forests will respond to climate change and to enhance our current knowledge of the ecophysiological processes affected by climate change. Process-based models provide an opportunity to achieve both objectives. However, these models usually predict discrete outputs and provide no assessment of the reliability of the output. Gertner (1987) concluded that an assessment of the variance or uncertainty of model outputs is desirable and useful: (1) to gauge the reliability and precision of predictions; (2) to calculate confidence intervals; (3) to statistically test hypotheses when experiments are performed with the model; and (4) to weight outputs used as an auxiliary source of information in combination with field-sample estimates.

The Monte Carlo technique can be used to estimate model output uncertainty. Moreover, the main disadvantage of the Monte Carlo technique, which is the long computational time (Gertner et al. 1996), has diminished in importance as the computational capacity of computers has increased. However, to carry out Monte Carlo simulations, the uncertainty distributions or the probability density functions (PDFs) of the model parameters must be known. The PDFs can be estimated based on experimental data, as has been done for forest growth and allocation models. For example, MacFarlane et al. (2000) estimated the PDFs of 14 physiological or morphological parameters of the Pipestem model based on published data. Mäkelä (1988) described this type of analysis for a forest growth model based on the functional balance and the pipe model theory. For more complex ecophysiological flux models, however, the estimation of PDFs is time consuming and so tends to severely limit the frequency with which uncertainty analyses are conducted (MacFarlane et al. 2000), even though estimation of the PDFs of parameters based on “expert knowledge” rather than experimental data is better than failing to conduct uncertainty analyses.

Parameters can be ranked for uncertainty by the Monte Carlo technique in combination with a multiple linear regression. This sensitivity analysis estimates the uncertainty contribution of all parameters to the overall output uncertainty. This catalogue of error sources is also called the “error budget” (Gertner et al. 1996). Parysow et al. (2000) applied this method to a process growth model based on the pipe model

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theory and the self-thinning rule and concluded that the method provides an efficient strategy for building error budgets of process models with many model inputs.

Most complex forest models have many parameters. The goal of our study was to identify, by sensitivity analysis, the parameters of the FORUG model—a process-based forest flux model—contributing most to overall output (net ecosystem exchange (NEE)) uncertainty, and thereby determine if it is necessary to estimate the uncertainty of all parameters of a model to determine overall output uncertainty. We made no attempt to verify the validity of the FORUG model, although we recognize that the characterization of errors and the contribution of each model parameter to the total error are key aspects of the evaluation of forest growth models (Vanclay and Skovsgaard 1997).

Materials and methods

The FORUG model

The FORUG model is a multi-layer process-based model that simulates CO_2 and H_2O exchange between forest stands and the atmosphere. Main model outputs are NEE, total ecosystem respiration (TER), gross primary production (GPP) and evapotranspiration. We focused on NEE as output because net exchange of carbon between forests and atmosphere determines the role of forests in the global carbon cycle (Law et al. 2001).

One understory and three upperstory canopy layers were considered. A radiation module calculates the available direct and diffuse photosynthetic active radiation (PAR) in each vegetation layer (Spitters 1986, Spitters et al. 1986). In each layer, intercepted PAR is calculated for the sunlit and shaded leaf fraction (Lemeur 1973). This intercepted PAR drives the photosynthesis submodel. Photosynthesis and stomatal conductance are calculated according to Farquhar et al. (1980) and Ball et al. (1987). Photosynthesis and leaf respiration parameters are temperature dependent as described by Medlyn et al. (2002) and de Pury and Farquhar (1997). Soil respiration is calculated based on a simple exponential function of soil temperature as described by Granier et al. (2002). Woody biomass respiration is calculated with a temperature function according to Ceschia et al. (2002). To simulate NEE, the FORUG model uses 54 parameters. All relevant equations are listed in the Appendix and Table A1. For a detailed model description, see Samson (2001) and Boonen et al. (2002).

Data

The data used in this modeling study are the meteorological and flux data of the beech (*Fagus sylvatica* L.) site in Hesse (France, 48°40′ N, 7°05′ E, 300 m above sea level) measured within the framework of the EUROFLUX project (Moncrieff et al. 1997, Valentini 1999, Aubinet et al. 2000). The Hesse forest is 30 to 35 years old and has been described by Granier et al. (2000, 2002).

Uncertainty

The overall uncertainty of any model is a combination of three sources of uncertainty (Beck 1987): uncertainty of the input variables (e.g., measurement errors), uncertainty of the model parameters (e.g., lack of information to calibrate all parameters) and uncertainty of the model structure (e.g., underlying equations and assumptions). We focused on the second source of uncertainty.

The Monte Carlo technique is a numerical technique to calculate output uncertainty of a model. The Monte Carlo approach was developed by Stanislaw Ulam and John von Neuman to simulate probabilistic events for military purposes in 1946 (Frey and Li 2001). The method, which has been described extensively (e.g., Hammersley and Morton 1964, Vose 1996, Cullen and Frey 1999), is robust and relatively easy to implement. Whereas error propagation methods can be difficult to implement when the uncertainty distributions or PDFs are not normally distributed, the Monte Carlo technique can handle different distribution types and can always be implemented in a relatively straight-forward manner (Gertner et al. 1996).

To use the Monte Carlo technique, a PDF is needed for each model parameter and input variable that is considered to be uncertain. To start the Monte Carlo analysis, one random sample from the PDF of each parameter and input variable is selected and the set of samples is entered into the deterministic model. The model is then solved as for any deterministic analysis. The model output variables are stored and the process is repeated until a specified number of model simulations is completed. Instead of obtaining a discrete number for the model output as in a deterministic simulation, a set of output samples is obtained (Cullen and Frey 1999). After a sufficiently large number of simulations, the distribution function of the output can be determined.

We made no distinction between the uncertainty and the natural variability of the parameters. Uncertainty of a parameter can usually be reduced by collecting more information about that parameter. Natural variability is a characteristic of a parameter that cannot be reduced by collecting more information. To make this distinction, a second-order Monte Carlo analysis should be applied (Cullen and Frey 1999). Most of the FORUG parameters are only uncertain. Although some of the parameters of the FORUG model are both uncertain and variable, the uncertainty of these parameters is dominant. Therefore the distinction between uncertainty and variability of the FORUG model parameters was considered irrelevant and all FORUG parameters were considered as uncertain. The uncertainty of the measured input variables (e.g., temperature, incoming radiation) was not taken into account because this uncertainty is mainly due to relatively small measurement errors.

In Monte Carlo simulations, the PDF of the parameters and input variables are required. If enough data are available, input PDFs can be determined based on knowledge and measurements. Unfortunately, information about distributions of parameters is often unavailable and as a result, input distributions are often estimated based on an “expert guess.”

Beside the PDFs, the minimum number of simulations has to be determined which depends on the model structure and the statistic of interest. Our statistic of interest was the variance of the FORUG model output. Because forest models can be complex and can require substantial computational resources, it may be important to reduce the overall requirements for calculation.

It is important that each simulation of an analysis is a feasible scenario. To exclude impossible parameter combinations, correlations between the different uncertain parameters should be taken into account. This is possible when the correlation coefficients are known. Burmaster and Anderson (1994) state that the presence of moderate to strong correlations will have little effect on the central portions of the output distributions, but may have larger effects on the tails of the output distributions. Therefore, when there is interest in the tails of the distributions, correlations should be taken into account. Several techniques exist to simulate correlations in Monte Carlo analysis (Iman and Conover 1982, Vose 1996, Cullen and Frey 1999).

Sensitivity analysis to rank for sensitivity and uncertainty

It is difficult to determine the probability density function of all parameters in a process-based forest model. For models with a large number of parameters (the FORUG model has 54 parameters), we can question whether it is necessary to take all parameters into account in the uncertainty analysis. To determine the parameters contributing most to the output uncertainty, a sensitivity analysis can be conducted to rank the parameters.

One drawback of the Monte Carlo technique is that a combined output uncertainty is calculated. This means that it is impossible to determine the contribution of each parameter to the overall output uncertainty. A possible solution is to use the least square linearization (LSL; Lei and Schilling 1996) which splits output uncertainty into its sources and can be conducted on the results of a Monte Carlo analysis. The LSL is a multiple regression between the parameter deviation from the mean and the output. All parameters are varied at the same time, whereas some sensitivity analysis methods perturb only one parameter at a time. By using the LSL, the contribution of each parameter to the overall output uncertainty is estimated. Parameters contributing little to the output uncertainty can be excluded.

The LSL method in combination with Monte Carlo analysis has the advantage of being able to simultaneously: (1) rank parameters according to their importance in influencing output uncertainty; (2) predict output uncertainty as a function of uncertainty in model input variables and parameters; (3) partition the error contribution of the model input variables and parameters in terms of output variance; and (4) provide the foundation for the optimal reduction of output uncertainty or cost associated with additional data collection (Parysow et al. 2000). Moreover, as Saltelli et al. (2000) stated, sensitivity estimators such as standardized regression coefficients are easy to implement, relatively inexpensive and intuitive.

Equations 1 and 2 provide some mathematical background to the LSL method which is in essence a multiple regression between the parameter deviation from the mean and the output. Consider a variable, y, that depends on a number of independent variables, $v_1, v_2, \ldots, v_n$. The variation of y as a function of small variations in independent variables can be expressed as:

$$\Delta y = \frac{\partial y}{\partial v_1}\Delta v_1 + \frac{\partial y}{\partial v_2}\Delta v_2 + \ldots + \frac{\partial y}{\partial v_n}\Delta v_n \tag{1}$$

If y is considered as $\bar{y} + \Delta y$, then:

$$y = \bar{y} + \frac{\partial y}{\partial v_1}\Delta v_1 + \frac{\partial y}{\partial v_2}\Delta v_2 + \ldots + \frac{\partial y}{\partial v_n}\Delta v_n \tag{2}$$

The LSL conducted on the Monte Carlo simulation results can be expressed as follows: Δv_i is defined as the difference between v_i, the random chosen sample of parameter i and m_{Vi}, the mean value of parameter i of all the random samples. The value of Δv_i is assumed to be equal to δ_{Vi}, the “true” uncertainty of parameter i and $V_{i,true}$ is the “true” value of parameter i.

$$\Delta v_i = v_i - m_{v_i} \approx \delta_{v_i} = v_i - V_{i,\mathrm{true}} \tag{3}$$

When m Monte Carlo simulations are carried out, Δv_i for each parameter and the model output y are calculated for each simulation. Next, a multi-linear regression on the obtained dataset is performed. The Δv_i values are considered as independent variables and the output y is the dependent variable. This gives the following regression equation:

$$y \approx w_1\Delta v_1 + w_2\Delta v_2 + \ldots + w_n\Delta v_n + b \tag{4}$$

The regression coefficients (w_i) are estimated by minimizing the sum of squared errors. Comparing this with Equation 2, it can been seen that the coefficients w_1, w_2, …, w_n are estimates of the partial derivatives of y with respect to v_i and b is an estimate of the value of y at default parameter values (i.e., when $\Delta v_i = 0$ for all i).

If the uncertainties of the independent parameters are statistically independent, the overall variance of the model output ($\sigma^2_{\delta_y}$) can be calculated as:

$$\sigma^2_{\delta_y} \approx \sum_{i=1}^{n} w_i^2 \sigma^2_{\delta_{v_i}} \tag{5}$$

where $\sigma^2_{\delta_{v_i}}$ is the variance of the calculated difference δ_{Vi}.

Based on the regression coefficients and the variations of the parameter uncertainties, the sensitivity coefficient of each parameter i (S_{Vi}) can be approximated as:

$$S_{v_i} = \frac{w_i^2 \sigma_{\delta_{v_i}}^2}{\sigma_{\delta_y}^2} \times 100\% \tag{6}$$

Depending on the scale of the parameter variation, different variants of the sensitivity analysis can be conducted (Frey and Patil 2002). We used two variants of the sensitivity analysis. First, sensitivity of the model output to an infinitesimal small variation of all 54 parameters was assessed because no proper PDFs are available for all parameters. An infinitesimal variation is approximated by using uniform distributions with a maximum deviation of 1% for all 54 parameters. This analysis assessed the impact of the parameter values on the output without the effect of their individual distributions. This method is helpful for screening the most important parameters when no information on their uncertainty is available, which was the main goal of this study. This variant of sensitivity analysis is used to rank the parameters of the FORUG model for sensitivity.

Second, simulations were run in which parameters were assigned probability distributions and the effect of variance in the parameters on the output distribution was assessed. These distributions were based on "expert knowledge." This second variant of sensitivity analysis was used to test the effect of arbitrary PDFs on the ranking of the parameters of the FORUG model. This ranking is called ranking for uncertainty.

For both variations of the sensitivity analysis, correlation between parameters was not taken into account. All parameter combinations of the FORUG model were checked systematically based on the available information. This exercise led to the conclusion that some of the parameters were expected to be correlated. For a few parameters, relationships are available in the literature. For example the relationship between maximum electron transport rate (J_{max}) and maximum carboxylation rate (V_{cmax}) has been described in several papers, e.g., Wullschleger (1993), Niinemets et al. (1998) and Medlyn et al. (1999). However, correlation was expected to have no major influence on the first sensitivity analysis because only small deviations with a maximum of 1% were used. Because the second sensitivity analysis was used only to test the effect of arbitrary PDFs and given the current poor knowledge of PDFs, including the PDFs of J_{max} and V_{cmax}, it was considered irrelevant to take correlations into account.

Results

Number of simulations

The variance was selected to represent the output uncertainty. In Figure 1, the variance of the simulated NEE is plotted after every simulation. Figure 1 shows that after 2000 simulations the variance of the model output converged. Thus, 2000 simulations are sufficient to predict the output variance of the FORUG model. This compares well to the 2048 simulations necessary to obtain good approximations of variances found by Gertner et al. (1996). Running only 2000 simulations instead of 10000 (a commonly used number of simulations) results in an 80% reduction in calculation time.

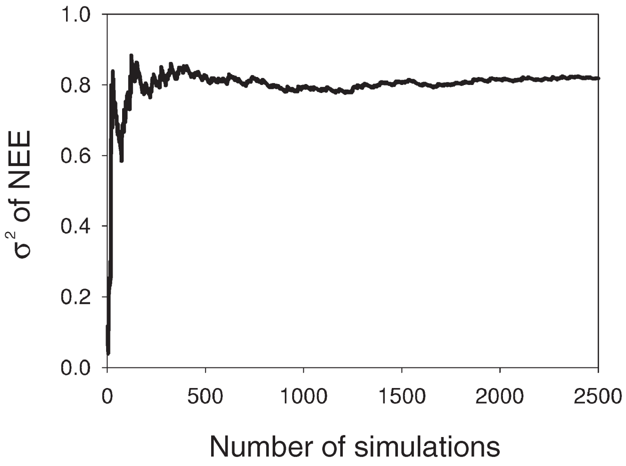

Figure 1. The variance of the FORUG output net ecosystem exchange (NEE; Mg C ha^{-1} year^{-1}) for the Hesse forest in 1997 plotted as a function of the number of Monte Carlo simulations. For these simulations, all 54 uncertain parameters were taken in account.

Ranking parameters for sensitivity

For this analysis, a uniform distribution with a maximum deviation of 1% was attributed to all 54 uncertain parameters. Based on 2000 Monte Carlo simulations (Figure 1), the contribution of all 54 parameters to the overall output uncertainty was calculated according to Equations 3–6. Table 1 shows that 96% of the output uncertainty is caused by the uncertainty of the 10 most important parameters, i.e., the other 44 parameters determined only 4% of the output uncertainty.

More than 70% of the overall output uncertainty is determined by the two coefficients (a_{soil} and b_{soil}) of the soil respiration model. Two important parameters determine the photosynthesis process: the initial quantum yield (α_F) and the maximum carboxylation rate (V_{cmax}). Table 1 also shows that the light extinction coefficient for diffuse radiation (k_d) plays an important role. Other sensitive parameters appearing in the list are associated with the photosynthetic process: the activation energy of the temperature dependence of V_{cmax} (E_{av}) and the Michaelis-Menten constant for carboxylation (K_c). The rest of the list contains less sensitive parameters: the Michaelis Menten constant for oxygenation (K_o), the CO_2 compensation point (Γ^*) and the partial pressure of oxygen in the air (O). The other 44 parameters do not appear in the list and have an individual contribution that is less than 0.94%.

Ranking parameters for uncertainty

Because of lack of information of the different parameter values of the FORUG model, the PDFs of the parameters could not be estimated based on experimental data. Therefore, in contrast with the ranking for sensitivity, a wider range and sometimes different type of distribution was attributed to all 54 uncertain parameters for this analysis. The choice of

Table 1. Results of the ranking for sensitivity. The contribution (%) of the uncertain parameters to the overall uncertainty of the FORUG model output net ecosystem exchange (NEE). Results are based on 2000 Monte Carlo simulations for the year 1997 for the Hesse forest in France.

Parameter	Description	Process	Contribution to overall uncertainty (%)
b_{soil}	Coefficient	Soil respiration	54.16
a_{soil}	Coefficient	Soil respiration	16.03
α_{F}	Initial quantum yield	Photosynthesis	6.36
V_{cmax}	Maximum carboxylation rate	Photosynthesis	6.18
k_{d}	Extinction coefficient for diffuse radiation	Light extinction	3.71
E_{av}	Activation energy of temperature dependence of V_{cmax}	Photosynthesis	3.54
K_{c}	Michaelis-Menten constant for the carboxylation	Photosynthesis	3.32
Γ^*	CO_2 compensation point	Photosynthesis	2.70
K_{o}	Michaelis-Menten constant for oxygenation	Photosynthesis	0.98
O	Partial pressure of oxygen in the air	Photosynthesis	0.94

the distributions was based on “expert knowledge.” Although there are enough published data from measurements on seedlings to fit a lognormal distribution for J_{max} and V_{cmax} (Jarvis 1999, Medlyn et al. 1999, Levy and McKay 2003), the PDFs of these parameters were also based on “expert knowledge” because our study was conducted in a more than 30-year-old beech stand.

Normal and lognormal distributions are widely adopted PDFs for modeling uncertain parameters. Because these distributions are unbounded at two sides and one side, respectively, they are inappropriate for bounded parameters (Wu and Tsang 2004). To exclude random values that cannot appear in the environment, truncated distributions were useful. Therefore, a uniform or triangular distribution was used for all parameters (see Appendix, Table A2).

A uniform distribution was attributed to a parameter with a minimum and a maximum boundary, but without information about the uncertainty. Maximum deviations of 5, 10 and 20% were used. A triangular distribution was attributed to parameters that were thought to have a higher probability close to the mean value. It is easier to estimate minimum and maximum boundaries of a parameter (which has to be done for uniform and triangular PDFs) than to estimate the variation of a PDF (which is needed for normal and lognormal PDFs).

A maximum deviation of 10% was chosen for most parameters (see Appendix, Table A2) which is a common deviation that corresponds with other carbon flux studies, e.g., Hirsch et al. (2004). The triangular probability distribution function was also used by Paul et al. (2003) who applied Monte Carlo simulations to the carbon accounting model GRC3. A triangular distribution with a maximum deviation of 10% means that the parameter has a probability of one at the mean value and a probability of zero at ± 10% of the mean value.

The contribution to the overall uncertainty of the ten most important parameters is shown in Table 2. Compared with the ranking for sensitivity (Table 1), the order of importance changed. Parameter H has appeared in the list. This is the deactivation energy of the temperature dependence of J_{max}. On the other hand, parameter O (the partial pressure of oxygen in the air) has disappeared. When the contributions are summed, more then 97% of the overall uncertainty appears to be due to these ten parameters.

Again soil respiration coefficients appear high in the list contributing more than 63% of the output uncertainty. The light extinction coefficient for diffuse radiation (k_{d}) gained in importance. As expected, the remainder of the list comprises parameters describing the photosynthetic process.

Output uncertainty

The distribution of the simulated NEE for the year 1997 for the Hesse forest is shown in Figure 2. This distribution is based on 2000 Monte Carlo simulations. The uncertainty analysis accounted for only the ten parameters appearing in Table 2. The mean simulated output value is -3.63 Mg C ha^{-1} year^{-1} (a negative value of NEE indicates a net carbon uptake by the ecosystem). The standard deviation of the output distribution is 0.88 mg C ha^{-1} year^{-1}. The variance is 0.77. In the Euroflux project, a total NEE value of -2.83 Mg C ha^{-1} year^{-1} was mea-

Table 2. Results of the ranking for uncertainty. The contribution (%) of the uncertain parameters to the overall uncertainty of the FORUG model output net ecosystem exchange (NEE). Results are based on 2000 Monte Carlo simulations for the year 1997 for the Hesse forest in France.

Parameter	Description	Process	Contribution to overall uncertainty (%)
b_{soil}	Coefficient	Soil respiration	49.67
k_{d}	Extinction coefficient for diffuse radiation	Light extinction	14.91
a_{soil}	Coefficient	Soil respiration	13.66
α_{F}	Initial quantum yield	Photosynthesis	5.24
V_{cmax}	Maximum carboxylation rate	Photosynthesis	4.51
K_{c}	Michaelis-Menten constant for the carboxylation	Photosynthesis	3.17
E_{av}	Activation energy of temperature dependence of V_{cmax}	Photosynthesis	2.80
Γ^*	CO_2 compensation point	Photosynthesis	1.84
H	De-activation energy of temperature dependence of J_{max}	Photosynthesis	1.02
K_{o}	Michaelis-Menten constant for oxygenation	Photosynthesis	0.55

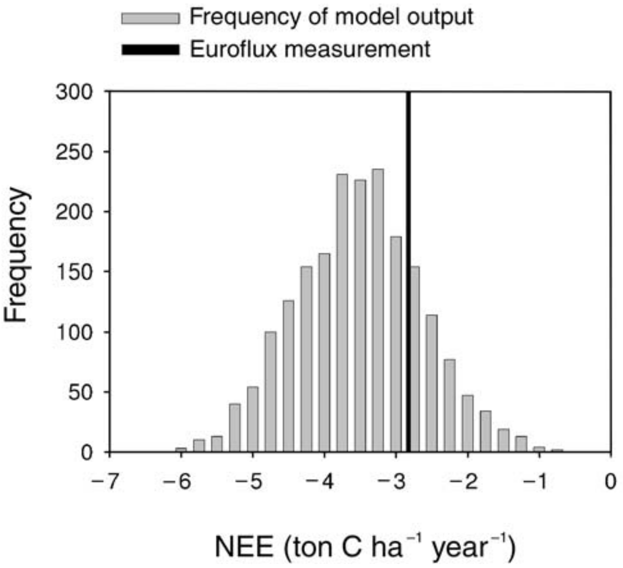

Figure 2. Distribution of the total net ecosystem exchange (NEE; Mg C ha^{-1} year^{-1}) in 1997 for the Hesse forest in France. The calculation of this distribution is based on 2000 Monte Carlo simulations. Only the uncertainty of ten key parameters was taken into account. The black bar above shows the measured (Euroflux) NEE value and does not represent a frequency.

sured for the year 1997. The measured value of the NEE differs from the mean simulated value, but falls within the range of one standard deviation of the output distribution.

Discussion

The ten key parameters found in both rankings correspond to critical parameters found in the literature. Before discussing the ecological meaning of the sensitivity analysis and the output uncertainty, we emphasize two limitations of the analyses.

First, the PDFs used for the ranking for uncertainty are arbitrarily chosen based on “expert knowledge.” This second variant of the sensitivity analysis based on these PDFs was conducted to see if these PDFs would give new information about the key model parameters. The ranking for uncertainty, however, did not give any additional information about the key parameters compared with the ranking for sensitivity. Therefore, because proper PDFs are not known, the discussion focuses only on the key parameters found by ranking for sensitivity. The only conclusion that can be drawn from this ranking for uncertainty is the need for experimental data to quantify these PDFs. However, such experimental data are not easy to obtain.

Second, the mean values for each parameter were assumed for both rankings, representing a particular scenario. The major conclusion that can be drawn is that the ten most important parameters determine more than 90% of the output uncertainty. However, the analysis does not suggest that the mean output value is determined by these ten parameters alone. A sensitivity analysis on the same model using different mean parameters may give different results.

Soil respiration parameters

The high ranking of the soil respiration parameters a_{soil} and b_{soil} is noteworthy. The simple soil respiration model used in the FORUG model is dependent only on soil temperature (see Appendix, model description). The high sensitivity of the model output uncertainty for soil respiration could be expected because flux measurements give a mean annual soil respiration that is 69% of the total ecosystem respiration in European forests (Janssens et al. 2001). The correspondence with findings of eddy covariance measurements (Valentini et al. 2000) can be considered as a verification of the FORUG model. High sensitivity for soil parameters and processes has also been found for other carbon flux models, e.g., EFIMOD (Komarov et al. 2003).

The high sensitivity for the individual parameters of soil respiration points to the importance of the soil respiration process, but it also partly reflects the fact that this soil respiration model uses only two parameters. This is a small number of parameters compared with, for example, the photosynthesis model. Use of a more complex soil respiration model will likely not decrease the contribution of the soil respiration process, but it will decrease the sensitivity to each individual parameter. Epron et al. (1999) have already recommended that soil water content be incorporated in further development of predictive models of NEE because summer drought may occur at irregular intervals in Western Europe. Clearly, a more complex soil respiration model which is process-based and not empirical like the current model is needed to predict the soil respiration process more accurately. The model should differentiate between heterotrophic and autotrophic respiration and should be based on several environmental factors including temperature, soil water content and soil organic matter.

In addition, soil respiration has a year-round influence on NEE in contrast to, e.g., the photosynthetic process. During winter, soil respiration is almost the only factor influencing carbon exchange between the forest stand and the atmosphere which is another reason for the high ranking of the soil respiration parameters.

The impact of the soil parameters also depends on the type of ecosystem. For example, in tropical forest, where relatively small amounts of carbon are passed to the soil pools and turnover times are fast, soil submodel parameters have a smaller effect on the predicted NEE (Hirsch et al. 2004).

Photosynthesis parameters

The high ranking of the parameters that determine the photosynthetic process directly and indirectly reflects the fact that this process drives carbon uptake. Leuning et al. (1998) report a high sensitivity to the quantum yield of photosynthesis. This also corresponds with the results of Mäkelä (1988) where parameters related with shading and potential photosynthesis were found to be critical. In forest ecosystems, most leaves are not light saturated; therefore, a small change in quantum yield has an important impact on overall canopy CO_2 uptake. However, maximum carboxylation rate (V_{cmax}) has almost the same contribution as quantum yield (Table 1), indicating that these two parameters are most important in determining overall canopy photosynthesis. Parameters V_{cmax} and α_F determine A_n(c) and A_n(j), respectively (Equations A10 and A11). In contrast, some photosynthetic parameters have only a small impact on NEE. For example, dark respiration rate (R_d) has a contribution of only 0.35%.

Crown architecture

The importance of light regime as a driving factor for photosynthesis is indicated by the high ranking of k_d. This is because, in contrast to direct radiation, diffuse radiation is intercepted by sunlit, as well as by shaded, leaves. Moreover, diffuse radiation affects the ecosystem every day, even when it is cloudy, whereas the direct radiation component is present only on sunny days.

Although leaf area index (L) has an indirect influence on the output through the extinction coefficient for diffuse radiation (Equations A2–A4), L itself contributes only 0.75%.

Ranking for sensitivity versus ranking for uncertainty

When both rankings are compared, differences are relatively small (Tables 1 and 2) because for most parameters the same triangular PDFs with a maximum deviation of 10% are used to rank for uncertainty. Because the expert knowledge about most parameters is quite limited, only a few parameters were attributed PDFs with a different shape or range. Use of more differentiated PDFs would result in larger differences between the rankings for sensitivity and uncertainty and would make the ranking for uncertainty more valuable.

Output uncertainty

The analysis of output uncertainty resulted in a standard deviation of 0.88 Mg C ha^{-1} $year^{-1}$ which is 24% of the mean value of NEE. Because the uncertainty we calculated is based on arbitrarily chosen PDFs based on expert knowledge, the estimated uncertainty has no absolute value and is largely subjective. It only indicates the effect of the chosen PDFs on the output uncertainty. Uncertainties with the same order of magnitude can be found in the literature. For example, Hirsch et al. (2004) found an uncertainty of 35% of the mean value of the net carbon flux simulated with the CARLUC (3PG) model for the Brazilian Amazon. Our uncertainty analysis took account of only the ten key parameters that explained more than 90% of the output uncertainty (Figure 2). More accurate parameter distributions of these key parameters (Tables 1 and 2) and detailed knowledge of their corresponding processes will lead to a decrease in the overall uncertainty of the FORUG model output.

In conclusion, the standard deviation of the uncertainty of the output (NEE) of the FORUG model for the year 1997 for the Hesse beech forest, based on arbitrary PDFs of ten key parameters, was calculated as 0.88 Mg C ha^{-1} $year^{-1}$, which is 24% of the mean value of NEE. Future research on the FORUG model should focus on a better description of poorly described key processes. In particular, the exponential soil respiration model needs revision. More accurate estimates of the key parameters (Tables 1 and 2) are necessary to make more reliable FORUG predictions. Determination of the parameter PDFs and the correlations between the different uncertain parameters remain bottlenecks in uncertainty analysis for complex forest flux models. Because of lack of information about the key parameters, the final uncertainty analysis of the FORUG model is based on simple PDFs of the key parameters and correlation was not taken into account. Future research should attempt to obtain proper parameter PDFs and to describe correlations where present. We conclude that sensitivity analysis allows efficient error resource allocation which can help focus future research on the key parameters. The Monte Carlo simulation technique is a useful tool for ranking the uncertainty of parameters of process-based forest flux models.

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Appendix: Description of the FORUG model

PAR interception model (Lemeur 1973)

For the direct and diffuse component of the PAR radiation, the penetrated irradiance can be written as:

$$I_\mathrm{b}(L) = (I - \rho_\mathrm{b}) I_\mathrm{o,b} \exp(-k_\mathrm{b} L) \quad \text{(A1)}$$

$$I_\mathrm{d}(L) = (I - \rho_\mathrm{d}) I_\mathrm{o,d} \exp(-k_\mathrm{d} L) \quad \text{(A2)}$$

The shaded fraction of a leaf intercepts only diffuse radiation:

$$I_\mathrm{shade} = k_\mathrm{d} (I - \rho_\mathrm{d}) I_\mathrm{o,d} \exp(-k_\mathrm{d} L) \quad \text{(A3)}$$

Sunlit leaves intercept diffuse and direct radiation:

$$I_\mathrm{sun} = I_\mathrm{shade} + k_\mathrm{b} I_\mathrm{o,d} \quad \text{(A4)}$$

Biochemical photosynthesis model (Farquhar et al. 1980, de Pury and Farquhar 1997)

$$V^*_\mathrm{cmax} = V_\mathrm{cmax} f(D_\mathrm{n}) \quad \text{(A5)}$$

$$\alpha^*_\mathrm{F} = \alpha_\mathrm{F} f(D_\mathrm{n}) \quad \text{(A6)}$$

$$f(D_\mathrm{n}) = \left(\frac{365 - D_\mathrm{n}}{365 - b_1}\right)^{b_2} \exp\left\{\frac{b_2}{b_3}\left[1 - \left(\frac{365 - D_\mathrm{n}}{365 - b_1}\right)^{b_3}\right]\right\}$$

(Wang 1996) (A7)

$$J_\mathrm{sun}(L) = \frac{\alpha^*_\mathrm{F,L} I_\mathrm{sun}(L)}{\left\{1 + \frac{\alpha^{*2}_\mathrm{F,L}}{J^2_\mathrm{max,L}}\left[I_\mathrm{sun}(L)\right]^2\right\}^{0.5}} \quad \text{(A8)}$$

$$J_\mathrm{shade}(L) = \frac{\alpha^*_\mathrm{F,L} I_\mathrm{shade}(L)}{\left\{1 + \frac{\alpha^{*2}_\mathrm{F,L}}{J^2_\mathrm{max,L}}\left[I_\mathrm{shade}(L)\right]^2\right\}^{0.5}} \quad \text{(A9)}$$

$$A_\mathrm{n}(\mathrm{c}) = \frac{V^*_\mathrm{cmax}(C_\mathrm{i} - \Gamma^*)}{C_\mathrm{i} + K'} - R_\mathrm{d} \quad \text{(A10)}$$

$$A_\mathrm{n}(\mathrm{j}) = \frac{J(C_\mathrm{i} - \Gamma^*)}{4(C_\mathrm{i} + 2\Gamma^*)} - R_\mathrm{d} \quad \text{(A11)}$$

$$K' = K_\mathrm{c}\left(1 + \frac{O}{K_\mathrm{o}}\right) \quad \text{(A12)}$$

$$A_\mathrm{n} = \min\{A_\mathrm{n}(\mathrm{c}), A_\mathrm{n}(\mathrm{j})\} \quad \text{(A13)}$$

$$C_\mathrm{i} = C_\mathrm{s} - \frac{A_\mathrm{n}}{g_\mathrm{b}} \quad \text{(A14)}$$

$$C_\mathrm{s} = C_\mathrm{a} - \frac{A_\mathrm{n}}{g_\mathrm{b}} \quad \text{(A15)}$$

$$g_\mathrm{s} = g_0 + g_1 A_\mathrm{n} \frac{\mathrm{RH}}{C_\mathrm{s}} \quad \text{(Ball et al. 1987)} \quad \text{(A16)}$$

The above equations are analytically solved as described by Baldocchi (1994).

Temperature dependencies

$$K_\mathrm{c} = K_\mathrm{c}(25) \cdot 10^1 \exp\frac{59.4(T - 25)}{298R(T + 273)} \quad \text{(A17)}$$

(de Pury and Farquhar 1997)

$$K_\mathrm{o} = K_\mathrm{o}(25) \cdot 10^1 \exp\frac{36(T - 25)}{298R(T + 273)} \quad \text{(A18)}$$

(de Pury and Farquhar 1997)

$$\Gamma^* = \Gamma^*(25) + 0.188(T - 25) + 0.0036(T - 25)^2 \quad \text{(A19)}$$

(de Pury and Farquhar 1997)

$$V_\mathrm{cmax} = V_\mathrm{cmax}(25) \exp\left[\frac{E_\mathrm{av}(T - 25)}{298R(T + 273)}\right] \quad \text{(A20)}$$

(Medlyn et al. 2002)

$$J_\mathrm{max} = J_\mathrm{max}(25) \exp\left(\frac{E_\mathrm{aj}(T - 25)}{298R(T + 273)}\right) \left[\frac{1 + \exp\left(\frac{298S - H}{298R}\right)}{1 + \exp\left(\frac{S(T + 273) - H}{R(T + 273)}\right)}\right] \quad \text{(A21)}$$

(Medlyn et al. 2002)

Dark respiration

$$R_\mathrm{d} = R_\mathrm{d}(25) \exp\left[\frac{\Delta H_\mathrm{aR}(T - 25)}{298R(T + 273)}\right] \quad \text{(A22)}$$

(de Pury and Farquhar 1997)

Soil respiration

$$R_\mathrm{soil} = a_\mathrm{soil} \exp(b_\mathrm{soil} T_\mathrm{soil}) \quad \text{(Granier et al. 2002) (A23)}$$

Woody biomass respiration

$$R_\mathrm{stem} = R_\mathrm{stem,15} Q_{10}^{((\mathrm{T}-15)/10)} \quad \text{(Ceschia et al. 2002) (A24)}$$

Table A1: Parameters and variables used in the Equations A1–A29.

Symbol	Parameter or variable	Units
a_{soil}	Regression parameter	µmol CO$_2$ m^{-2} soil s^{-1}
A_{n}	Net photosynthetic rate	µmol CO$_2$ m^{-2} s^{-1}
$A_{\mathrm{n}}(\mathrm{c})$	Carboxylation-limited rate of A_{n}	µmol CO$_2$ m^{-2} s^{-1}
$A_{\mathrm{n}}(\mathrm{j})$	Electron transport-limited rate of $\mathrm{A_n}$	µmol CO$_2$ m^{-2} s^{-1}
b_1	Parameter (150.0)	no unit
b_2	Parameter (10.0)	no unit
b_3	Parameter (0.2)	no unit
b_{soil}	Regression parameter	no unit
C_{a}	CO$_2$ concentration of the atmosphere	µmol CO$_2$ mol^{-1} air
C_{i}	Intercellular CO$_2$ concentration	µmol CO$_2$ mol^{-1} air
C_{s}	CO$_2$ concentration at the leaf surface	µmol CO$_2$ mol^{-1} air
D_{n}	Day of the year	no unit
E_{aj}	Activation energy for J_{max}	kJ mol^{-1}
E_{av}	Activation energy for V_{cmax}	kJ mol^{-1}
g_{b}	Leaf laminar boundary layer conductance for CO$_2$	m s^{-1}
g_1	Conductance slope	no unit
g_{o}	Conductance intercept	m s^{-1}
g_{s}	Stomatal conductance for CO$_2$	m s^{-1}
H	Deactivation energy for J_{max}	kJ mol^{-1}
$I(L)$	PAR intensity at downward cumulative LAI L	µmol photons m^{-2} s^{-1}
I_{o}	PAR intensity above the canopy	µmol photons m^{-2} s^{-1}
J	Electron transport rate	µmol electrons m^{-2} s^{-1}
J_{max}	Maximum electron transport rate	µmol electrons m^{-2} s^{-1}
$J_{\mathrm{max}}(25)$	J_{max} at 25 °C	µmol electrons m^{-2} s^{-1}
k_{d}	Extinction coefficient for diffuse radiation	no unit
K'	Effective Michaelis-Menten constant of Rubisco	Pa
K_{c}	Michaelis-Menten constant of carboxylation	Pa
$K_{\mathrm{c}}(25)$	K_{c} at 25 °C	Pa
K_{o}	Michaelis-Menten constant of oxygenation	Pa
$K_{\mathrm{o}}(25)$	K_{o} at 25 °C	Pa
L	Leaf area index	m^2 leaf area m^{-2} soil area
O	Partial pressure of oxygen in the air	kPa
Q_{10}	Temperature response factor	no unit
R	Gas constant (8.314)	J mol^{-1} K^{-1}
R_{d}	Dark respiration rate	µmol CO$_2$ m^{-2} s^{-1}
$R_{\mathrm{d}}(25)$	R_{d} at 25 °C	µmol CO$_2$ m^{-2} s^{-1}
R_{soil}	Soil respiration rate	µmol CO$_2$ m^{-2} soil s^{-1}
R_{stem}	Total stem and branch respiration rate	µmol CO$_2$ m^{-2} wood s^{-1}
$R_{\mathrm{stem,15}}$	R_{stem} at 15 °C	µmol CO$_2$ m^{-2} wood s^{-1}
S	Electron-transport temperature response parameter	J K^{-1} mol^{-1}
T	Temperature	°C
T_{soil}	Soil temperature	°C
T_{stem}	Stem temperature	°C
V^*_{cmax}	Maximal carbon assimilation rate	µmol CO$_2$ m^{-2} s^{-1}
$V_{\mathrm{cmax}}(25)$	V^*_{cmax} at 25 °C	µmol CO$_2$ m^{-2} s^{-1}
V_{cmax}	Peak value of V^*_{cmax} during the growing season	µmol CO$_2$ m^{-2} s^{-1}
α^*_{F}	Quantum yield	µmol CO$_2$ µmol^{-1} photons
α_{F}	Peak value of α^*_{F} during the growing season	µmol CO$_2$ µmol^{-1} photons
ΔH_{aR}	Activation energy for R_{d}	kJ mol^{-1}
Γ^*	CO$_2$-compensation point	Pa
$\Gamma^*(25)$	Γ^* at 25 °C	Pa
ρ_{b}	Reflection coefficient for direct PAR	no unit
ρ_{d}	Reflection coefficient for diffuse PAR	no unit
Subscripts		
b	Beam (direct) radiation	
d	Diffuse radiation	
shade	Shaded leaf fraction	
sun	Sunlit leaf fraction	
Abbreviation		
RH	Relative humidity	no unit

Table A2: Mean values and probability density functions (PDFs) of the parameters used in Equations A1–A24.

Parameter	Value	PDF (% deviation)
a_{soil}	0.436 μmol CO_2 m^{-2} soil s^{-1} (Granier et al. 2002)	Triangular (10)
b_{soil}	0.156 (–) (Granier et al. 2002)	Triangular (10)
E_{aj}	37.0 (kJ mol^{-1}) (de Pury and Farquhar 1997)	Triangular (10)
E_{av}	64.8 (kJ mol^{-1}) (de Pury and Farquhar 1997)	Triangular (10)
g_1	9.50 (–) (Harley and Baldocchi 1995)	Uniform (10)
g_{o}	17.5 (–) (Harley and Baldocchi 1995)	Uniform (10)
H	220 (de Pury and Farquhar 1997)	Triangular (10)
$J_{\mathrm{max}}(25)$	121.6; 79.6; 64.4* (Jarvis 1999)	Triangular (10)
k_{d}	0.7 (Samson 2001)	Triangular (20)
$K_{\mathrm{c}}(25)$	40.4 (de Pury and Farquhar 1997)	Triangular (10)
$K\mathrm{o}(25)$	24.8×10^3 (de Pury and Farquhar 1997)	Triangular (10)
L_{max}	5.6 (Granier et al. 2000)	Triangular (10)
O	21 (de Pury and Farquhar 1997)	Triangular (5)
Q_{10}	1.33 (Ceschia et al. 2002)	Triangular (10)
$R_{\mathrm{d}}(25)$	0.42 (Harley and Baldocchi 1995)	Triangular (10)
$R_{\mathrm{stem,15}}$	0.239 (Ceschia et al. 2002)	Triangular (10)
S	710 (de Pury and Farquhar 1997)	Triangular (10)
$V_{\mathrm{cmax}}(25)$	49.4; 32.34; 26.16* (Jarvis 1999)	Triangular (10)
α_{F}^{*}	0.24 (Harley and Baldocchi 1995)	Triangular (10)
ΔH_{aR}	66.4 (de Pury and Farquhar 1997)	Triangular (10)
$\Gamma^{*}(25)$	3.69 (de Pury and Farquhar 1997)	Triangular (10)
ρ_{d}	0.092 (de Pury and Farquhar 1997)	Triangular (5)

* Top, middle and lower canopy layer, respectively.