#### CHAPTER EIGHTEEN

# Uncertainty and Sensitivity Issues in Process-based Models of Carbon and Nitrogen Cycles in Terrestrial Ecosystems

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## 18.1. INTRODUCTION

Process-based models designed to simulate the dynamics of carbon (C) and nitrogen (N) cycles in northern forest ecosystems are increasingly being used in concert with other tools to predict the effects of environmental factors on forest productivity (Mickler et al., 2002; Peng et al., 2002; Sands and Landsberg, 2002; Almeida et al., 2004; Shaw et al., 2006) and forest-based C and N pools (Seely et al., 2002; Kurz and Apps, 1999; Karjalainen, 1996). Among the environmental factors, we include everything from intensive management practices to climate change, from local to global and from hours to centuries, respectively. Policy makers, including the general public, expect that reliable, well-calibrated and -documented processbased models will be at the centre of rational and sustainable forest management policies and planning as well as prioritisation of research efforts, especially those addressing issues of global change. In this context, it is important for policy makers to understand the validity of the model results and uncertainty associated with them (Chapters 2, 5 and 6). The term uncertainty refers simply to being unsure of something. In the case of a C and N model users are unsure about the model results. Regardless of a model's pedigree, there will always be some uncertainty associated with its output. The true values in this case can rarely if ever be determined and users need to assume the aberration between the model results and the true values as a result of uncertainties in the input factors as well as the process representation in the model. If it is also assumed that the model results are evaluated against measurements for which the true values are unknown because of measurement uncertainties, it is important to at least know the probability spaces for both measurements and model results in order to interpret the results correctly. All these uncertainties are ultimately related to a lack of knowledge about the system under study and measurement errors of their properties. It is necessary to communicate the process of uncertainty propagation from measurements to final output in order to make model results meaningful for decision support. Pizer (1999) explains that including uncertainty as opposed to ignoring it leads to significantly different conclusions in policy making and encourages more stringent policy, which may result in welfare gains.



# 18.2. UNCERTAINTY

Different sources of uncertainty are generally recognised in models of C and N cycles in forest ecosystems, and in biological and environmental models in general (O'Neill and Rust, 1979; Medlyn et al., 2005; Chapters 4–6):

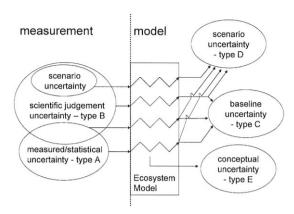


Figure 18.1 Concept of uncertainty: the measurement uncertainty of type A and/or B are propagated through the model and leads to baseline uncertainty (type C) and scenario uncertainty (type D), where the propagation process is determined by the conceptual uncertainty (type E). (Adapted from Wattenbach et al., 2006.)

- data uncertainty associated with measurement errors, spatial or temporal scales or errors in estimates;
- model structure, and lack of understanding of the biological processes;
- the plasticity that is associated with estimating model parameters, due to the general interdependence of model variables and parameters; related to this is the search to determine the least set of independent variables required to span the most important system states and responses from one extreme to another, e.g. from frozen to non-frozen, dry to wet, hot to cold, calm to stormy;
- the range of variation associated with each biological system under study.

## 18.2.1 Uncertainty in measurements

The most comprehensive definition of uncertainty is given by the "Guide to express Uncertainties in Measurements - GUM" (ISO, 1995): "parameter, associated with the result of a measurement, that characterises the dispersion of the values that could reasonably be attributed to the measurand." The term parameter may be, for example, a standard deviation (or a given multiple of it), or the half-width of an interval having a stated level of confidence. In this case, uncertainty may be evaluated using a series of measurements and their associated variance (type A. Figure 18.1) or can be expressed as standard deviation based on expert knowledge or by using all available sources (type B, Figure 18.1). With respect to measurements, the GUM refers to the difference between error and uncertainty. Error refers to the imperfection of a measurement due to systematic or random effects in the process of measurement. The random component is caused by variance and can be reduced by an increased number of measurements. Similarly, the systematic component can also be reduced if it occurs from a recognisable process. The uncertainty in the result of a measurement on the other hand arises from the remaining variance in the random component and the uncertainties connected to the correction for systematic effects (ISO, 1995). If we speak about uncertainty in models it is very important to recognise this concept.

## 18.2.2 Model uncertainty

The definition of uncertainty in model results can be directly associated with the uncertainty of measurements. However, there are modelling-specific components we need to consider. First all models are by definition a simplification of the natural system. Thus uncertainty arises just from the way the model is conceptualised, which is defined as structural uncertainty. C and N models also use parameters in their equations. These internal parameters are associated with model uncertainty and they can have different sources, such as long term experiments (e.g. decomposition constants for soil carbon pools) or laboratory experiments (temperature sensitivity of decomposition), defined as parameter uncertainty. Both uncertainties refer to the design of the model and can be summarised as conceptual uncertainty (type E, Figure 18.1) Models are highly dependent on input variables and parameters. Variables are changing over the runtime of a model whereas parameters are typically constant, describing the initialisation of the system. As both variables and parameters are model inputs, they are often called input factors in order to distinguish them from internal variables and parameters (Wattenbach et al., 2006).

If the data for input factors are determined by replicative measurements, they can be labelled according to the GUM as type A uncertainty. In many cases the set of type A uncertainty can be influenced by expert judgement (type B uncertainty), which results in the intersection of both sets (e.g. the gapfilling process of flux data is as such a type B uncertainty that influences type A uncertainty in measurements). A subset of type B uncertainty are scenarios. Scenarios (see Chapters 4 and 11) are assumptions of future developments based on expert judgement and incorporate the high uncertain element of future developments that cannot be predicted. If we use scenarios in our models, we need to consider them as a separate instance of uncertainty (type D, Figure 18.1) because they incorporate all elements of uncertainty (Wattenbach et al., 2006).

Many methodologies have been used to better quantify the uncertainty of model parameters. Traditionally, these methodologies include simple trial-and-error calibrations, fitting model calculations with known field data using linear or non-linear regression techniques and assigning pre-determined parameter values, generated empirically through various means in the laboratory, the greenhouse or the field. For example, Wang et al. (2001) used non-linear inversion techniques to investigate the number of model parameters that can be resolved from measurements. Braswell et al. (2005) and Knorr and Kattge (2005) used a stochastic inversion technique to derive the probability density functions for the parameters of an ecosystem model from eddy covariance measurements of atmospheric C. Williams et al. (2005) used a time series analysis to reduce parameter uncertainty for the derivation of a simple C transformation model from repeated measurements of C pools and fluxes in a young ponderosa pine stand, and Dufrêne et al. (2005) used the Monte Carlo technique to estimate uncertainty in net ecosystem exchange by randomly varying key parameters following a normal distribution.

Erroneous parameter assignments can lead to gross over- or under-predictions of forest-based C and N pools. For example, Laiho and Prescott (2004) pointed out that Zimmerman et al. (1995), using an incorrect C/N ratio (of 30) for coarse woody debris in the CENTURY (http://www.nrel.colostate.edu/projects/century/nrel.htm) model, greatly overestimated the capability of a forest system to retain N. Prescott et al. (2004) also suggested that models that do not parameterise litter chemistry in great detail may represent long-term rates of leaf litter decay better than those models which do.

The success or failure of a model depends to a large extent on determining whether or not expected model outputs depend on particular values used for model compartment initialisation. Models that are structured to be conservative, by strictly following the rules of mass, energy and electrical charge conservation, and by describing transfer processes within the ecosystem by way of simple linear differential or difference equations, lead to an eventual steady-state solution within a constant input-output environment, regardless of the choice of initial conditions. The particular parameter values assigned to such models determine the rate at which the steady state is approached. One important way to test the proper functioning of model parameterisation and initialisation is to start the model calculations at steady state, and then impose a disturbance pulse, or a series of disturbance pulses (harvesting, fire events, spaced regularly or randomly). This is to see whether the ensuing model calculations will correspond to known system recovery responses, and whether these calculations will eventually return to the initial steady state. The empirical process formulation is crucial, in that each calculation step must feasibly remain within the physically defined solution space. For example, in the hydro-thermal context of C and nutrient cycling, this means that special attention needs to be given to how variations of "independent" variables, such as soil organic matter, texture, coarse fragment content, phase change (water to ice), soil density and wettability, combine deterministically and stochastically to affect subsequent variations in heat and soil moisture flow and retention (Balland and Arp, 2005).

## 18.2.2.1 Structural uncertainty

Process-based forest models vary from simple to complex, simulating many different process and feedback mechanisms by integrating ecosystem-based process information on the underlying processes in trees, soil and the atmosphere. Simple models often suffer from being too simplistic, but can nevertheless be illustrative and educational in terms of ecosystem thinking. They generally aim at quickly estimating the order of magnitude of C and N quantities associated with particular ecosystem processes, such as C and N uptake and stand-internal C and N allocations. Complex models can, in principle, reproduce the complex dynamics of forest ecosystems in detail. However, their complexity makes their use and evaluation difficult. There is a need to quantify output uncertainty and identify key parameters and variables. The uncertainties are linked: uncertain parameters imply uncertain predictions and uncertainty about the real world implies uncertainty about model structure and parameterisation. Because of these linkages, model parameterisation, uncertainty analysis, sensitivity analysis, prediction, testing and comparison with other models need to be based on a consistent quantification of uncertainty.

Process-based C and N models are generally referred to as being deterministic or stochastic. These models may be formulated for the steady state (for which inputs equal outputs), or the dynamic situation, where model outcomes depend on time, in relation to time-dependent variations of the model input, and in relation to state-dependent component responses. Models are either based on empirical or theoretical derivations, or a combination of both (semi-empirical considerations). Process-based modelling is cognisant of the importance of model structure: the number and type of model components are carefully chosen to mimic reality and to minimise the introduction of modelling uncertainties.

Many problems are generated by model structure alone. Two issues can be related to model structure: (1) mathematical representation of the processes and (2) description of state variables. For example, several types of models can be used to represent the effect of temperature variation on processes, including the Q<sub>10</sub> model, the Arrhenius function or other exponential relationships. The degree of uncertainty in the predictions of a model can increase significantly if the relationship representing the effect of temperature on processes is not based on accurate theoretical description (see Kätterer et al., 1998; Thornley and Cannell, 2001; Davidson and Janssens, 2006; Hill et al., 2006). Most C and N models contain a relatively simple representation of the processes governing soil C and N dynamics, including simplistic parameterisation of the partitioning of litter decomposition products between soil organic C and the atmosphere. For example, the description of the mineralisation (chemical, physical, and biological turnover) of C and N in forest ecosystems generally addresses three major steps: (1) splitting of the soil organic matter into different fractions, which decompose at different rates, (2) evaluating the robustness of the mineralisation coefficients of the adopted fractions, and (3) initialising the model in relation to the fractions (Wander, 2004).

Table 18.1 gives a cross-section of a number of recent models (or sub-components of models) used to determine litter decomposition rates. The entries in this table illustrate how the complexity of the C and N modelling approach varies, even in describing a basic process such as forest litter decomposition. The number of C and N components in each model ranged from 5 to 10. The number of processes considered varied from 5 to 32 and the number of C and N parameters ranged from 7 to 54. The number of additional parameters used for describing the N mineralisation process, once the organic matter decomposition process is defined, is particularly interesting; it ranged from 1 to 27.

Most soil C models use three state variables to represent different types of soil organic matter (SOM), the active, slow and passive pools. Even though it is assumed that each pool contains C compound types with about the same turnover rate, this approach remains nevertheless conceptual and merely represents an abstraction of reality, which may lead to uncertainty in the predictions (type E, Figure 18.1) (Davidson and Janssens, 2006). Also, these conceptual pools do not directly correspond to measurable pools. In reality, SOM contains many types of complex compounds with very different turnover rates and amplitude of reaction to change in temperature (Davidson and Janssens, 2006). There have been many attempts to find relations between model structure and the real world either by measuring dif-

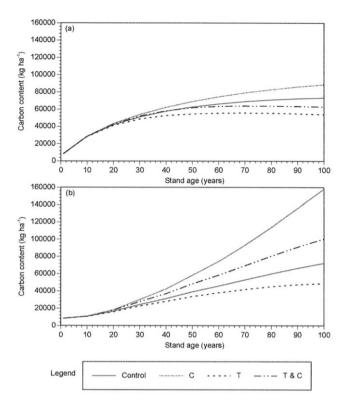
 Table 18.1
 Examples of models used for estimating rate of forest litter decomposition

Model	Reference	Predicted variables	Initialization variables	Predictor variables	Compartment number	Compartment type	Compartment Compartment Flows Parameters Comments number type	Comments
SOMM	SOMM Chertov and Komarov (1997)	C and N remaining	Initial C, N, ash content	Annual, monthly or daily soil moisture and temperature estimates	3x C, 3x N; C & N litter, (x represents fermentation number of and humus cohorts cohorts considered) (leaves, roots, coarse woody debris, etc.)	3x C, 3x N; C & N litter, 7C, (x represents fermentation 7N number of and humus cohorts cohorts considered) (leaves, roots, coarse woody debris, etc.)	7C, 58 C, 3N 7N	Parameters common across locations, initialised by species (cohort); C/N ratios prescribed per compartment
CEN- TURY	Parton et al. (1987)	C and N remaining	Initial C, N, C/N ratios, lignin	Monthly precipitation and air temperature estimates	5 C, 5 N	Structural, metabolic, active, slow and passive C & N compartments	13 C, 20 C, 5 N 13 N	Parameters common across locations; initialised by species
CANDY	CANDY Franko et al. (1995)	C and N remaining	Initial C, N	Monthly or daily soil moisture and temperature estimates	3 C, 3 N	3 C, metabolic and 3 N stable C & N compartments		5 C, 1 N, Parameters + 2 climate common across parameters locations; (differs decomposition from not species original) specific

(continued on next page)

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Model	Reference	Predicted variables	Initialization variables	Predictor variables	Compartment number	Compartment Compartment Flows Parameters Comments number type	Flows Param	eters	Comments
МОБ МОБ	Currie and Aber (1997)	C and N remaining; dissolved organic C and N	Initial C, N, by Annual actual compartment evapotranspiration tion estimates	Annual actual evapotranspira- tion estimates	5 C, 5 N	Lignin- cellulose, unprotected cellulose, extractives, microbial and humus C & N compartments	11 C, 17 C, 4 N 10 N		Parameters common across locations; C/N of humus prescribed
FLDM	Zhang et al. (2007)	Mass, C and N remaining	Initial mass, C, January & July N; initial ash air temperature and acid and annual non-acid precipitation, b hydrolysable year; or fractions, or monthly or lignin fraction daily soil moisture and temperature estimates	s >	3 mass, 2 N	Fast C; slow 3 C, 11C, 1 N and very slow 2 N C & N compartments	3 C, 11C, 1 2 N		Parameters common across locations; CIDET calibrated; C/N ratios process determined
DE- COMP	(2006)	Wallman et al. CO <sub>2</sub> , soluble (2006) compounds, C remaining	Mass, chemical Soil constituents of temperature, the soil organic soil moisture matter (e.g., field capacity lignin, wilting point holocellulose) potential eval transpiration, precipitation	perature, moisture, l capacity, ing point, ential evapo- spiration, ipitation	4 C, 1 soil solution	Cellulose, 9 C, lignin easily 9 decomposable Wa-and resistant ter C, cellulose, soil solution	9 C, 24 C, 8 9 water Wa- ter		Very detailed description of the chemistry. Remains to be tested for different sites



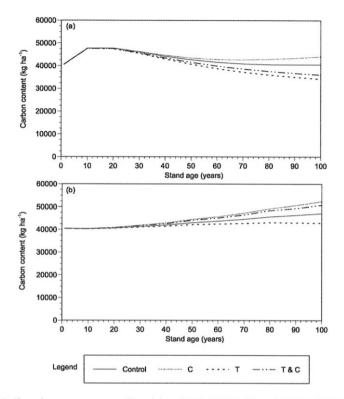
**Figure 18.2** Carbon content in stems, coarse roots and branches (large wood) predicted by CENTURY (a) and FOREST-BGC (b) under different scenarios of climate change based on CO<sub>2</sub> increase from 350 to 700 ppm (C) and a gradual increase in temperature by 6.1 °C (T). The control includes the simulation results when the actual conditions remained unchanged. (Adapted from Luckai and Larocque, 2002, with kind permission of Springer Science and Business Media.)

ferent decomposition rates of different soil fractions (Zimmermann et al., 2007) or by restructuring the model pools (e.g. Fang et al., 2005).

Complex models have, in theory, the challenge of being more precise and/or accurate than simple models. This being so, data requirements for the initialisation and calibration of complex models need to be tightly controlled, and need to stay within the range of current field experimentation and exploration. The degree of model complexity also needs to be controlled, because this affects the overall model transparency and communicability, as well as affordability and practicality. Also, making models more complex can increase their structural uncertainty simply by increasing the number of parameters that are uncertain or affecting the correctness of the description of the processes involved.

This can be illustrated by a study conducted by Luckai and Larocque (2002), who compared two complex process-based models, CENTURY and FOREST-BGC, to predict the effect of climate change on C pools in a black spruce (*Picea mariana* [Mill.] B.S.P.) forest ecosystem in northwestern Ontario (Figures 18.2)

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**Figure 18.3** Soil carbon content predicted by CENTURY (a) and FOREST-BGC (b) under different scenarios of climate change based on a CO<sub>2</sub> increase from 350 to 700 ppm (C) and a gradual increase in temperature by 6.1 °C (T). The control includes the simulation results when the actual conditions remained unchanged. (Adapted from Luckai and Larocque, 2002, with kind permission of Springer Science and Business Media.)

and 18.3). For the prediction of the long-term change in C content in the large wood and soil pools, both models predicted relatively close carbon content under scenarios of actual climatic conditions and a gradual increase in temperature, even though the pattern of change differed slightly. Substantial differences in C content were obtained when two scenarios of CO2 increase were simulated. For the effect of gradual CO<sub>2</sub> increase (actual temperature conditions remained unchanged), both models predicted increases in C content relative to actual temperature conditions. However, the increase in large wood C content predicted by FOREST-BGC was far larger than the increase predicted by CENTURY. The scenario that consisted of a gradual increase in both CO<sub>2</sub> and temperature resulted in widely different patterns. While CENTURY predicted a relatively small decrease in large wood and soil C content, FOREST-BGC predicted an increase. The discrepancies in the results can be explained by differences in the structure of both models. Both models include a description of the above- and below-ground C dynamics. However, CENTURY focuses on the dynamics of litter and soil carbon mineralisation and nutrient cycling and FOREST-BGC is based on relatively detailed descriptions of ecophysiological processes, including photosynthesis and respiration. For instance,

CENTURY considers several soil carbon pools (active, slow and passive) with specific decomposition rates, while FOREST-BGC considers one carbon pool. Both models also differ in input data. For instance, while CENTURY requires monthly climatic data, FOREST-BGC uses daily climatic data.

Modellers must carefully consider the tradeoff between the potential uncertainty that may result from adding additional variables and parameters and the gain in accuracy or precision by doing so. It may be argued as well that existing models of the C cycle are still in their infancy. It is not evident that modellers involved in the development of process-based models have considered all the tools, including mathematical development, systems analysis and programming, to deal with this complexity.

# 18.2.2.2 Input data uncertainties and natural variation

Data uncertainties are linked to:

- The high spatial and temporal variations associated with forest soil organic matter and the corresponding dynamics of above- and below-ground C and N pools. For example, Johnson et al. (2002) noted that soil C measurements from a controlled multi-site harvesting study were highly variable within sites following harvest, but that there was little lasting effect of this variability after 15–16 years.
- Determining the parameters needed to define pools and fluxes (e.g. forest and vegetation type, climate, soil, productivity, and allocation transfers), and knowing whether these parameters are truly time and/or state-independent. Calibration parameters are, as a rule, fixed within models. They are usually obtained from other models, derived from theoretical considerations or estimated from the product of combinatorial exercises.
- Data definitions, sampling procedures, especially those that are vague and open to interpretation, and measurement errors. For example, Gijsman et al. (2002) discussed an existing metadata confusion about determining soil moisture retention in relation to soil bulk density.
- Inadequate sampling strategies, in the context of capturing existing micro- and macro-scale C and N pool variations within forest stands, and across the land-scape, at different times of the year. On a regional scale, failure to account for the spatial variation across the landscape, and the vertical variation with horizon depth (due to microrelief, animal activity, windthrow, litter and coarse woody debris input, human activity and the effect of individual plants on soil microclimate and precipitation chemistry), may lead to uncertainty.
- Knowing how errors propagate through the model calculations. For example, soil C and N estimates of individual pedons are generally determined by the combination of measurements of C and N concentrations, soil bulk density, soil depth, and rock content (Homann et al., 1995); errors in any one of these add to the overall estimation uncertainties.

By definition, process-based models should be capable of reflecting the range of variation that exists in ecosystems of interest. This is an important issue in forest management. In boreal forest ecosystems, quantifying the range of variation has become a practical goal because forest managers must provide evidence that

justifies their proposed use of silviculture (e.g. harvesting, planting, tending) as a stand replacing agent. The range of variation has been defined by Landres et al. (1999) as "the ecological conditions, and the spatial and temporal variation in these conditions, that are relatively unaffected by people within a period of time and geographical area to an expressed goal." Assuming that reasonable boundaries of time period, geography and anthropogenic influence can be identified, the manager or scientist must then decide which metrics will be used to quantify the range of variation. Common metrics include mean, median, standard deviation, skewness, frequency, spatial arrangement and size and shape distributions (Landres et al., 1999). The adoption of the range of variation as a guiding principal of forest resource management is well-suited to boreal systems because (1) large, stand replacement natural disturbances continue to dominate in much of the boreal forest and (2) such disturbances may be reasonably emulated by forest harvesting (Haeussler and Kneeshaw, 2003).

The boreal forest is a region where climate change is predicted to significantly affect the survival and growth of native species. Consequently, policies and social pressures (e.g. Kyoto Protocol, Certification) may intensify efforts to improve forest C sequestration by reducing "low-value" wood harvesting. However, high prices for crude oil and loss of traditional pulp and paper wood markets may do the opposite by identifying "low-value" forest biomass as a readily available and profitable energy source. Quantifying the range of variation therefore becomes practical as companies and communities responsible for forest management have the obligation to provide evidence to justify proposed choices and use of harvesting/silviculture as stand-replacing procedures. However, including variables that account for the range of variation increases the number and costs of required model calibrations, even for simple C and N models.

Structurally, process-based models often include a choice for the user — "stochastic or mean values." Stochastic runs usually require an estimate of the variation in some aspect of the system of interest. For example, CENTURY has a series of parameters that describe the standard deviation and skewness values for monthly precipitation as main drivers of ecosystem process calculations. This allows the model to vary precipitation, but not air temperature. Another option in CENTURY allows the user to write weather files that provide monthly values for temperature and precipitation. However, neither of these options allows for stochasticity in stand replacing events that subsequently affect drivers, such as moisture or temperature, and processes, such as decomposition or photosynthesis.

From a philosophical point of view, it makes sense to build the range of variation into model function. Boreal systems are highly stochastic, the evidence of which can be found in the high level of beta and gamma diversity often reported. From a logistic point of view, however, including variables that account for the range of variation increases the number of required calibration values and subsequently the cost of calibrating even a simple model. Data describing the range of variation is itself hard to come by. An operational definition of the range of variation is therefore needed, but has not been widely adopted (Ride, 2004).

## 18.2.3 Scenario uncertainty and scaling

Models are used at very different temporal and spatial scales, e.g. from daily to monthly to annual, and from stand- to catchment- to landscape-levels (Wu et al., 2005). The change in scales in model and input data introduces different levels of uncertainty. Natural variation is scale-dependent. For example, at the landscape level, it may be possible to: (1) estimate the range of stand compositions and ages, and therefore of structures; (2) determine a reasonable range of climatic conditions (mainly minimum and maximum temperatures and precipitation) for timeframes as long as a few rotations (i.e. several hundred years); and (3) identify the successional pathways that reflect the interaction of (1) and (2). This information could then be used to provide a framework of stand and weather descriptions within which functional characteristics, such as SOM turnover, growth, and nutrient cycling, could be modelled. Assuming that we have reasonable mathematical descriptions of key biological, chemical, and physical processes - such as photosynthesis and decomposition, weathering and complexation, soil moisture, and compaction - we could then "nest" our models one inside of another. This approach assumes that the range of variation in the pools and fluxes normally included in process-based models is externally driven (i.e. by weather or disturbance) rather than by internal dynamics.

One example of such a model dealing with the range of variation in scaling issues is the General Ensemble Biogeochemical Modelling System (GEMS), which is used to upscale C and N dynamics from sites to large areas, with associated uncertainty measures (Reiners et al., 2002; Liu et al., 2004a, 2004b; Tan et al., 2005; Liu et al., 2006). GEMS consists of three major components: one or multiple encapsulated ecosystem biogeochemical models, an automated model parameterisation system, and an input/output processor. Plot-scale models such as CENTURY (Parton et al., 1987) and EDCM (Liu et al., 2003) can be encapsulated in GEMS. GEMS uses an ensemble stochastic modelling approach to incorporate the uncertainty and variation in the input databases. Input values for each model run are sampled from their corresponding range of variation spaces, usually described by their statistical information (e.g. moments, distribution). This ensemble approach enables GEMS to quantify the propagation and transformation of uncertainties from inputs to outputs. The expectation and standard error of the model output are given as:

$$E[p(X_i)] = \frac{1}{W} \sum_{i=1}^{w} p(X_{ij}), \tag{18.1}$$

$$S_E = \sqrt{\frac{V[p(X_i)]}{W}} = \sqrt{\frac{\frac{1}{W-1} \sum_{j=1}^{w} (p(X_{ij}) - E[p(X_i)])^2}{W}},$$
 (18.2)

where W is the number of ensemble model runs, and  $X_{ij}$  is the vector of EDCM model input values for the jth simulation of the spatial stratum i in the study area, p is a model operator (e.g. CENTURY or EDCM), and E, V, and  $S_E$  are the expectation, variance, and standard error of model ensemble simulations for stratum i, respectively.



## 18.3. MODEL VALIDATION

Model validation is an additional source of uncertainty as, among other mechanisms, it compares model results with measurements, which are again associated with uncertainties. Thus the choice of the validation data base determines the accuracy of the model in further ad hoc applications. However, model validation remains a subject of debate and is often used interchangeably with verification (Rykiel, 1996). Rykiel (1996) differentiated both terms by defining verification as the process of demonstrating the consistency of the logical structure of a model and validation as the process of examining the degree to which a model is accurate relative to the goals desired with respect to its usefulness. Validation therefore does not necessarily consist of demonstrating the logical consistency of causal relationships underlying a model (Oreskes et al., 1994). Other authors have argued that validation can never be fully achieved. This is because models, like scientific hypotheses, can only be falsified, not proven, and so the more neutral term "evaluation" has been promoted for the process of testing the accuracy of a model's predictions (Smith et al., 1997; Chapter 2). Although model validation can take many forms or include many steps (e.g. Rykiel, 1996; Jakeman et al., 2006), the method that is most commonly used involves comparing predictions with statistically independent observations. Using both types of data. statistical tests can be performed or indices can be computed. Smith et al. (1997) and Van Gadow and Hui (1999) provide a summary of the indices most commonly used:

mean residual = 
$$\left(\sum (y_i - \hat{y}_i)/n\right)$$
, (18.3)

root mean square error = 
$$\left(\sqrt{\sum (y_i - \hat{y}_i)^2/n - 1 - p}\right)$$
, (18.4)

model efficiency = 
$$\left(\sum (y_i - \hat{y}_i)^2 / \sum (y_i - \bar{y}_i)^2\right)$$
, (18.5)

variance ratio = 
$$\sum (\hat{y}_i - \overline{\hat{y}}_i)^2 / \sum (y_i - \overline{y}_i)^2.$$
 (18.6)

Several examples of the comparison of predictions with observations or field determinations exist in the literature (Smith et al., 1997; Morales et al., 2005). However, these mostly involve traditional empirical growth models in forestry as part of the procedures used to determine the annual allowable cut within specific forest management units (e.g. Canavan and Ramm, 2000; Smith-Mateja and Ramm, 2002; Lacerte et al., 2004). In contrast, reports on a systematic validation of C and N cycle models are rare (e.g. De Vries et al., 1995; Smith et al., 1997) and needed. The validation of C and N cycle models based on the comparison of predictions and observations has been more problematic than the validation of traditional empirical growth and yield models. Long-term growth and yield data are available for the latter because forest inventories, including permanent sample plots with repeated measurements, have been conducted by government forest agencies or private industry for many decades. Therefore, process-based model testing has been largely

based on growth variables, such as annual volume increment (Medlyn et al., 2005). Although volumetric data can be converted to biomass and C, direct measurements of C and N pools and flows in forest ecosystems have been collected mainly for research purposes and historical datasets are relatively rare. Therefore, it is often difficult to conduct a validation exercise of C and N models based on the comparison of predictions with statistically independent observations.

So, what options exist for the validation of forest-based C and N cycle models? The most logical avenue is the establishment and maintenance of long-term ecological research programs and site installations to generate the data needed for both model formulation and validation. However, these remain extremely costly and do not receive much political favour in this day and age. One alternative consists in using short-term physiological process measurements (e.g. Davi et al., 2005; Medlyn et al., 2005; Yuste et al., 2005), although careful scrutiny should be given to the long-term behaviour of the models in predicting C stocks in vegetation and soils (e.g. Braswell et al., 2005). Recent technological advances in micrometeorological and physiological instrumentation have been significant, such that it is now possible to collect and analyse hourly, daily, weekly or seasonal data under a variety of forest cover types, experimental scenarios and environmental conditions at relatively low cost. The data from flux tower studies are just now becoming extensive enough to capture the broad spectrum of climatic and biophysical factors that control the C, water and energy cycles of forest ecosystems. The fundamental value of these measurements derives from their ability to provide multi-annual time series at 30-minute intervals of: the net exchanges of CO2, water, and energy between a given ecosystem and the atmosphere at a spatial scale that typically ranges between 0.5 and 1 km<sup>2</sup>. The two major component processes of the net flux (i.e. ecosystem photosynthesis and respiration) are being collected. Since different ecosystem components can respond differently to climate, multi-annual time series combined with ecosystem component measurements are carried out to separate the responses to inter-annual climate variability. These data are essential for development and validation of process-based models that could be a key part of an integrated C monitoring and prediction system. For example, Medlyn et al. (2005) validated a model of CO<sub>2</sub> exchange using eddy covariance data. Davi et al. (2005) also used data from eddy covariance measurements for the validation of their C and water model, and closely monitored branch and leaf photosynthesis, soil respiration, and sap flow measurement throughout the growing season for additional validation purposes. The age factor, the effect of which takes so long to study, can be integrated by using a chrono-sequence approach (using stands of different ages on similar sites as a surrogate for time), which deals with validating C and N models by comparing model output with C and N levels and processes in differently aged forest stands of the same general site conditions. There is also the need to develop new methodologies that are able to integrate the above approaches to allow for model validation at fine and coarse time resolution

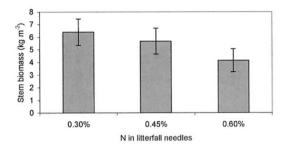


Figure 18.4 Sensitivity of simulated stem biomass to N content in needles after abscission.



## 18.4. SENSITIVITY ANALYSIS

Sensitivity analysis consists in analysing differences in model response to changes in input factors or parameter values (see Chapter 5). This exercise is relatively easy when the model contains a few parameters, but can become cumbersome for complex, process-based models. It is beyond the scope of this paper to review all the different methods that have been used, but one of the best examples of sensitivity analysis for process-based models may be found in Komarov et al. (2003), who carried out the sensitivity analyses for EFIMOD 2. These authors showed that the tree sub-model is highly sensitive to changes in the reallocation of the biomass increment and tree mortality functions while the soil sub-model is sensitive to the proportion and mineralisation rate of stable humus in the mineral soil. The model is very sensitive to all N compartments, including the N required for tree growth, N withdrawal from senescent needles, and soil N and N deposition from the atmosphere. For example, the prediction of stem biomass is sensitive to the N concentration in needles after abscission (Figure 18.4), reflecting the degree to which the plant (tree) controls growth by retention and internal N reallocation (Nambiar and Fife, 1991). However, although uncertainty surrounds initial stand density (often unknown), modelled soil C and N and tree stem C (major source of carbon input to the soil sub-model) are not very sensitive to initial stand density (Figure 18.5).

This type of uncertainty associated with sensitivity analysis could be addressed more thoroughly in the future by including Monte Carlo simulations and their variants. Very few examples of this type of integration for carbon cycle models exist (e.g. Roxburgh and Davies, 2006). One of the likely reasons is the computer time required. However, the evolution in computer technology is such that this might not be a major issue in a few years.



# 18.5. CONCLUSIONS

Many approaches have been developed and used to calibrate and validate process-based models. Models of the C and N cycles are generally based on sound

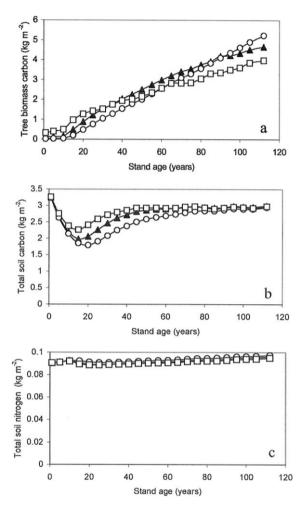


Figure 18.5 Sensitivity of simulated (a) tree biomass carbon, (b) total soil carbon and (c) total soil nitrogen by EFIMOD 2 to initial stand density.

mathematical representations of the processes involved. However, as previously mentioned, the majority of these models are deterministic. As a consequence, they do not represent adequately the error that may arise from different sources of variation. This is important, as both the C and N cycles (and models thereof) contain many sources of variation. Much can be gained by improving and standardising the use of calibration and validation methodologies both for scientists involved in the modelling of these cycles and forest managers who utilise the results.

Upscaling C dynamics from sites to regions is complex and challenging. It requires the characterisation of the heterogeneities of critical variables in space and time at scales that are appropriate to the ecosystem models, and the incorporation of these heterogeneities into field measurements or ecosystem models to estimate

the spatial and temporal change of C stocks and fluxes. The success of upscaling depends on a wide range of factors, including the robustness of the ecosystem models across the heterogeneities, necessary supporting spatial databases or relationships that define the frequency and joint frequency distributions of critical variables, and the right techniques that incorporate these heterogeneities into upscaling processes. Natural and human disturbances of landscape processes (e.g. fires, diseases, droughts and deforestation), climate change, as well as management practices, will play an increasing role in defining carbon dynamics at local to global scales. Therefore, methods must be developed to characterise how these processes change in time and space.

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### REFERENCES

- Almeida, A.C., Landsberg, J.J., Sands, P.J., Ambrogi, M.S., Fonseca, S., Barddal, S.M., Bertolucci, F.L., 2004. Needs and opportunities for using a process-based productivity model as a practical tool in Eucalyptus plantations. Forest Ecology and Management 193, 167–177.
- Balland, V., Arp, P.A., 2005. Modeling soil thermal conductivities over a wide range of conditions. Journal of Environmental Engineering Science 4, 549–558.
- Braswell, B.H., Sacks, W.J., Linder, E., Schimel, D.S., 2005. Estimating diurnal to annual ecosystem parameters by synthesis of a carbon flux model with eddy covariance net ecosystem exchange observations. Global Change Biology 11, 335–355.
- Canavan, S.J., Ramm, C.W., 2000. Accuracy and precision of 10-year predictions for Forest Vegetation Simulator—Lake States. Northern Journal of Applied Forestry 17, 62–70.
- Chertov, O.G., Komarov, A.S., 1997. SOMM: A model of soil organic matter dynamics. Ecological Modelling 94, 177–189.
- Currie, W.S., Aber, J.D., 1997. Modeling leaching as a decomposition process in humid Montane forests. Ecology 78, 1844–1860.
- Davi, H., Dufrêne, E., Granier, A., LeDantec, V., Barbaroux, C., Francois, C., Bréda, N., 2005. Modelling carbon and water cycles in a beech forest: Part II. Validation of the main processes from organ to stand scale. Ecological Modelling 185, 387–405.
- Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feed-backs to climate change. Nature 440, 165–173.
- De Vries, W., Posch, M., Oja, T., van Oene, H., Kros, H., Warfvinge, P., Arp, A.P., 1995. Modelling critical loads for the Solling spruce site. Ecological Modelling 83, 283–293.
- Dufrêne, E., Davi, H., François, C., Le Maire, G., Le Dantec, V., Granier, A., 2005. Modelling carbon and water cycles in a beech forest: Part I. Model description and uncertainty analysis on modelled NEE. Ecological Modelling 185, 407–436.
- Fang, C., Smith, P., Smith, J.U., 2005. A simple equation for simulating C decomposition in a multi-component pool of soil organic matter. European Journal of Soil Science 56, 815–820.
- Franko, U., Oelschlagel, B., Schenk, S., 1995. Simulation of temperature-, water- and nitrogen dynamics using the model CANDY. Ecological Modelling 81, 213–222.

- Gijsman, A.J., Jagtap, S.S., Jones, J.W., 2002. Wading through a swamp of complete confusion: How to choose a method for estimating soil water retention parameters for crop models. European Journal of Agronomy 18, 77–105.
- Hill, M.J., Roxburgh, S.H., McKeon, G.M., Carter, J.O., Barrett, D.J., 2006. Analysis of soil carbon outcomes from interaction between climate and grazing pressure in Australian rangelands using Range-ASSESS. Environmental Modelling and Software 21, 779–801.
- Haeussler, S., Kneeshaw, D., 2003. Comparing forest management to natural processes. In: Burton, P.J., Messier, C., Smith, D.W., Adamowicz, W.L. (Eds.), Towards Sustainable Management of the Boreal Forest. NRC Research Press, Ottawa, pp. 307–368.
- Homann, P.S., Sollins, P., Chappell, H.N., Stangenberger, A.G., 1995. Soil organic carbon in a mountainous forested region: Relation to site characteristics. Soil Science Society of America Journal 59, 1468–1475.
- ISO, 1995. Guide to the Expression of Uncertainty in Measurements. International Organization for Standardization, Geneva.
- Jakeman, A.J., Letcher, R.A., Norton, J.P., 2006. Ten iterative steps in development and evaluation of environmental models. Environmental Modelling and Software 21, 602–614.
- Johnson, D.W., Knoepp, J.D., Swank, W.T., Shan, J., Morris, L.A., Van Lear, D.H., Kapeluck, P.R., 2002. Effects of forest management on soil carbon: Results of some long-term resampling studies. Environmental Pollution 116, S201–S208.
- Karjalainen, T., 1996. Dynamics and potentials of carbon sequestration in managed stands and wood products in Finland under changing climatic conditions. Forest Ecology and Management 80, 113–132.
- Kätterer, T., Reichstein, M., Andrén, O., Lomander, A., 1998. Temperature dependence of organic matter decomposition: A critical review using literature data analyzed with different models. Biology and Fertility of Soils 27, 258–262.
- Knorr, W., Kattge, J., 2005. Inversion of terrestrial ecosystem model parameter values against eddy covariance measurements by Monte Carlo sampling. Global Change Biology 11, 1333–1351.
- Komarov, A., Chertov, O., Zudin, S., Nadporozhskaya, M., Mikhailov, A., Bykhovets, S., Zudina, E., Zoubkova, E., 2003. EFIMOD 2—A model of growth and cycling of elements in boreal forest ecosystems. Ecological Modelling 170, 373–392.
- Kurz, W.A., Apps, M.J., 1999. A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. Ecological Applications 9, 526–547.
- Lacerte, V., Larocque, G.R., Woods, M., Parton, W.J., Penner, M., 2004. Testing the Lake States variant of FVS (Forest Vegetation Simulator) for the main forest types of northern Ontario. Forestry Chronicle 80, 495–506.
- Laiho, R., Prescott, C.E., 2004. Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: A synthesis. Canadian Journal of Forest Research 34, 763–777.
- Landres, P.B., Morgan, P., Swanson, F.J., 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications 9, 1179–1188.
- Liu, J., Liu, S., Loveland, T., 2006. Temporal evolution of carbon budgets of the Appalachian forests in the U.S. from 1972 to 2000. Forest Ecology and Management 222, 191–201.
- Liu, S., Bliss, N., Sundquist, E., Huntington, T.G., 2003. Modeling carbon dynamics in vegetation and soil under the impact of soil erosion and deposition. Global Biogeochemical Cycles 17, 1074– 1097.
- Liu, S., Kairé, M., Wood, E., Diallo, O., Tieszen, L., 2004a. Impacts of land use and climate change on carbon dynamics in south-central Senegal. Journal of Arid Environments 59, 583–604.
- Liu, S., Loveland, T.R., Kurtz, R.M., 2004b. Contemporary carbon dynamics in terrestrial ecosystems in the Southeastern Plains of the United States. Environmental Management 33, S442–S456.
- Luckai, N., Larocque, G.R., 2002. Challenges in the application of existing process-based models to predict the effect of climate change on C pools in forest ecosystems. Climatic Change 55, 39–60.

- Medlyn, B.E., Robinson, A.P., Clement, R., McMurtrie, R.E., 2005. On the validation of models of forest CO<sub>2</sub> exchange using eddy covariance data: Some perils and pitfalls. Tree Physiology 25, 839–857.
- Mickler, R.A., Earnhardt, T.S., Moore, J.A., 2002. Regional estimation of current and future forest biomass. Environmental Pollution 116, S7–S16.
- Morales, P., Sykes, M.T., Prentice, I.C., Smith, P., Smith, B., Bugmann, H., Zierl, B., Friedlingstein, P., Viovy, N., Sabaté, S., Sánchez, A., Pla, E., Gracia, C.A., Sitch, S., Arneth, A., Ogee, J., 2005. Comparing and evaluating process-based ecosystem model predictions of carbon and water fluxes in major European forest biomes. Global Change Biology 11, 2211–2233.
- Nambiar, E.K.S., Fife, D.N., 1991. Nutrient retranslocation in temperate conifers. Tree Phisiol. 9, 185–207.
- O'Neill, R.V., Rust, B., 1979. Aggregation error in ecological models. Ecological Modelling 7, 91–105.
- Oreskes, N., Shrader-Frechette, K., Belitz, K., 1994. Verification, validation, and confirmation of numerical models in the earth sciences. Science 263, 641–646.
- Parton, W.J., Schimel, D.S., Cole, C.V., Ojima, D.S., 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Science Society of America Journal 51, 1173–1179.
- Peng, C.H., Liu, J.X., Dang, Q.L., Apps, M.J., Jiang, H., 2002. TRIPLEX: A generic hybrid model for predicting forest growth and carbon and nitrogen dynamics. Ecological Modelling 153, 109– 130.
- Pizer, W.A., 1999. The optimal choice of climate change policy in the presence of uncertainty. Resource and Energy Economics 21, 255–287.
- Prescott, C.E., Vesterdal, L., Preston, C.M., Simard, S.W., 2004. Influence of initial chemistry on decomposition of foliar litter in contrasting forest types in British Columbia. Canadian Journal of Forest Research 34, 1714–1729.
- Reiners, W.A., Liu, S., Gerow, K.G., Keller, M., Schimel, D.S., 2002. Historical and future land use effects on N<sub>2</sub>O and NO emissions using an ensemble modeling approach: Costa Rica's Caribbean lowlands as an example. Global Biogeochemical Cycles 16, 223–240.
- Ride, K.R., 2004. Estimates of ecoregional forest composition derived using modeled bounds of natural variation in northwestern Ontario. Ontario Ministry of Natural Resources, Northwest Sci. and Info., Thunder Bay, NWSI Tech. Rep. TR-136.
- Roxburgh, S.H., Davies, I.D., 2006. COINS: An integrative modelling shell for carbon accounting and general ecological analysis. Environmental Modelling and Software 21, 359–374.
- Rykiel, E.J. Jr., 1996. Testing ecological models: The meaning of validation. Ecological Modelling 90, 229–244.
- Sands, P.J., Landsberg, J.J., 2002. Parameterisation of 3-PG for plantation grown *Eucalyptus globulus*. Forest Ecology and Management 163, 273–292.
- Seely, B., Welham, C., Kimmins, H., 2002. Carbon sequestration in a boreal forest ecosystem: Results from the ecosystem simulation model, FORECAST. Forest Ecology and Management 169, 123– 135.
- Shaw, C., Chertov, O., Komarov, A., Bhatti, J., Nadporozskaya, M., Apps, M., Bykhovets, S., Mikhailov, A., 2006. Application of the forest ecosystem model EFIMOD 2 to jack pine along the Boreal Forest Transect Case Study. Canadian Journal of Soil Science 86, 171–185.
- Smith, P., Smith, J.U., Powlson, D.S., McGill, W.B., Arah, J.R.M., Chertov, O.G., Coleman, K., Franko, U., Frolking, S., Jenkinson, D.S., Jensen, L.S., Kelly, R.H., Klein-Gunnewiek, H., Komarov, A.S., Li, C., Molina, J.A.E., Mueller, T., Parton, W.J., Thornley, J.H.M., Whitmore, A.P., 1997. A comparison of the performance of nine soil organic matter models using datasets from seven long-term experiments. Geoderma 81, 153–225.
- Smith-Mateja, E.E., Ramm, C.W., 2002. Validation of the Forest Vegetation Simulator growth and mortality predictions on red pine in Michigan. In: Crokkston, N.L., Havis, R.N. (Eds.), Second

- Forest Vegetation Simulator Conference, Proceedings RMRS-P-25. Fort Collins, USA, February 2002. USDA Forest Service, Rocky Mountain Research Station, pp. 38–44.
- Tan, Z., Liu, S., Johnston, C.A., Loveland, T.R., Tieszen, L.L., Liu, J., Kurtz, R., 2005. Soil organic carbon dynamics as related to land use history in the northwestern Great Plains. Global Biogeochemical Cycles 19. GB3011.
- Thornley, J.H.M., Cannell, M.G.R., 2001. Soil carbon storage response to temperature: An hypothesis. Annals of Botany 87, 591–598.
- Van Gadow, K., Hui, G., 1999. Modelling Forest Development. Kluwer Academic Publishers, Boston. Wallman, P., Belyazid, S., Svensson, M.G.E., Sverdrup, H., 2006. DECOMP—A semi-mechanistic model of litter decomposition. Environmental Modelling and Software 21, 33–44.
- Wander, M., 2004. Soil organic matter fractions and their relevance to soil function. In: Magdoff, F., Weil, R. (Eds.), Advances in Agroecology. CRC Press, pp. 67–102.
- Wang, Y.-P., Leuning, R., Cleugh, H.A., Coppin, P.A., 2001. Parameter estimation in surface exchange models using nonlinear inversion: How many parameters can we estimate and which measurements are most useful? Global Change Biology 7, 495–510.
- Wattenbach, M., Gottschalk, P., Hattermann, F., Rachimow, C., Flechsig, M., Smith, P., 2006. A framework for assessing uncertainty in ecosystem models. In: Voinov, A., Jakeman, A., Rizzoli, A. (Eds.), Proceedings of the iEMSs Third Biennial Meeting: "Summit on Environmental Modelling and Software". International Environmental Modelling and Software Society. Burlington, USA, July 2006. ISBN 1-4243-0852. CD ROM Internet: http://www.iemss.org/iemss2006/sessions/all.html.
- Williams, M., Schwarz, P.A., Law, B.E., Irvine, J., Kurpius, M.R., 2005. An improved analysis of forest carbon dynamics using data assimilation. Global Change Biology 11, 89–105.
- Wu, J., Jones, B., Li, H., Loucks, O.L., 2005. Scaling and Uncertainty Analysis in Ecology. Methods and Applications. Columbia University Press, New York.
- Yuste, J.Ca., Janssens, A., Ceulemans, R., 2005. Calibration and validation of an empirical approach to model soil CO<sub>2</sub> efflux in a deciduous forest. Biochemistry 73, 209–230.
- Zhang, C.F., Meng, F.-R., Trofymow, J.A., Arp, P.A., 2007. Modeling mass and nitrogen remaining in litterbags for Canadian forest and climate conditions. Can. J. Soil Sci. 87, 413–432.
- Zimmerman, J.K., Pulliam, W.M., Lodge, D.J., Quinones-Orfila, V., Fetcher, N., Guzman-Grajales, S., Parrotta, J.A., Asbury, C.E., Walker, L.R., Waide, R.B., 1995. Nitrogen immobilization by decomposing woody debris and the recovery of tropical wet forest from hurricane damage. Oikos 72, 314–322.
- Zimmermann, M., Leifeld, J., Schmidt, M.W.I., Smith, P., Fuhrer, J., 2007. Measured soil organic matter fractions can be related to pools in the RothC model. European Journal of Soil Science 58, 658–667.