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Belowground processes in forest-ecosystem biogeochemical simulation models

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Abstract

Numerical simulation models of forest ecosystems synthesize a broad array of concepts from tree physiology, community ecology, hydrology, soil physics, soil chemistry and soil microbiology. Most current models are directed toward assessing natural processes or existing conditions, nutrient losses influenced by atmospheric deposition, C and N dynamics related to climate variation, and impacts of management activities. They have been applied mostly at the stand or plot scale, but regional and global applications are expanding. Commonly included belowground processes are nutrient uptake by roots, root respiration, root growth and death, microbial respiration, microbial mineralization and immobilization of nutrients, nitrification, denitrification, water transport, solute transport, cation exchange, anion sorption, mineral weathering and solution equilibration. Models differ considerably with respect to which processes and associated chemical forms are included, and how environmental and other factors influence process rates. Recent models demonstrated substantial discrepancies between model output and observations for both model verification and validation. The normalized mean absolute error between model output and observations of soil solution solute concentrations, solid phase characteristics, and process rates ranged from 0 to >1000%. There were considerable differences among outputs from models applied to the same situation, with process rates differing by as much as a factor of 4, and changes in chemical masses differing in both direction and magnitude. These discrepancies are attributed to differences in model structure, specific equations relating process rates to environmental factors, calibration procedures, and uncertainty of observations. Substantial improvement in the capability of models to reproduce observed trends is required for models to be generally applicable in public-policy decisions. Approaches that may contribute to improvement include modularity to allow easy alteration and comparison of individual equations and process formulations; hierarchical structure to allow selection of level of detail, depending on availability of data for calibration and driving variables; enhanced documentation of all phases of model development, calibration, and evaluation; and continued coordination with experimental studies. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Forest models; Biogeochemical models; Soil models; Soil processes; Nutrient dynamics; Carbon dynamics

1. Introduction

Biogeochemical simulation models consider the transfer of chemical constituents in the environment.

They can include exchange of elements among gas, liquid and solid phases, and changes in chemical form. Common chemical constituents include specific elements or specific forms of elements, such as nutrients, contaminants and organic C. Soil characteristics and belowground processes are incorporated into models of forests to varying degrees. Some models of tree

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dynamics do not include soil properties, while other models consider soil to be constant over time but to vary among locations (Loehle and LeBlanc, 1996; Talkkari and Hypén, 1996). Conversely, models of soil development may not include changes in vegetation over time (Hoosbeek and Bryant, 1994; Santore et al., 1995). The integration of both vegetation and soil processes into forest-ecosystem models permits feedback between the vegetation and soil, yielding dynamic vegetation and soil characteristics (Rastetter et al., 1991) or an evaluation of steady state conditions (King, 1995; Arp et al., 1996).

Models serve a variety of functions. They guide inquiry (Oreskes et al., 1994), provide a process-based context in which to synthesize and analyze experimental data, and yield estimates or “predictions”. Estimates from forest-ecosystem biogeochemical models may be relevant to public-policy decisions, as are those from earth-science simulation models (Oreskes et al., 1994). For example, the evaluation of critical loads of atmospheric deposition in Europe, which might be used in negotiations of emission reduction protocols, has been undertaken with biogeochemical models (De Vries et al., 1995). The potential productivity of timberlands in Montana, which provides a basis of taxation, has been generated with a model (Milner et al., 1996). Assessments of the quality of model output are particularly relevant at these interfaces between public policy and model use (Oreskes et al., 1994).

Recent reviews of forest-ecosystem models have focused on atmospheric deposition (Tiktak and van Grinsven, 1995) and climate change (Ågren et al., 1991; Perruchoud and Fischlin, 1995; Ryan et al., 1996a,b). Tiktak and van Grinsven (1995) summarized forest–soil–atmosphere models that are applicable to the effects of atmospheric deposition on forests and forest soils. Ågren et al. (1991) synthesized information about physiological, population, ecosystem, regional and global models that might be used for climate change analysis. Perruchoud and Fischlin (1995) qualitatively assessed the applicability of forest physiological, population, and ecosystem models for their suitability to address changes in the C cycle in response to climate change. Ryan et al. (1996a,b) compared seven conifer models by calibrating them with common data sets and simulating the effect of climate change scenarios.

Our objectives are to (1) summarize the applications of forest-ecosystem biogeochemical simulation models, which extend beyond the use of the models in atmospheric deposition and climate change research, (2) examine agreement between model output and observations over a broad range of model applications, with emphasis on belowground processes, and (3) illustrate reasons for discrepancies between model output and observations.

2. Applications of forest-ecosystem biogeochemical models

Recent investigations involving dynamic forest-ecosystem and forest–soil biogeochemical models have covered a range of topics, spatial scales, and chemical constituents. To quantify the topics and scales, we examined abstracts and papers identified by search words “forest, soil, model” in 1996 and 1997 calendar years of Biological Abstracts. Of those papers that dealt with transfer of nutrients and other elements (Table 1), most were at the stand or plot scale, but applications to regions and the globe have evolved with the development of geographic information systems and access to spatial environmental information (Jenkinson et al., 1992; Hunt et al., 1996; Schimel et al., 1996; Thompson et al., 1996; Aber et al., 1997; Post et al., 1997). Many studies have focused on understanding natural processes and current conditions (Table 1), such as C dynamics in boreal forests (Bonan, 1993), cation dynamics in southeastern USA forests (Currie et al., 1996), and the relation between succession and N availability (Pastor and

Table 1
Recent topics and spatial scales addressed in papers incorporating forest-ecosystem biogeochemical models based on 93 publications from mid-1995 through 1997

Topic	Spatial scale (% of papers)		
	Stand	Regional	Global
Natural processes or existing conditions	24	8	4
Climate and/or CO ₂ change	10	9	2
Atmospheric deposition	20	8	0
Fertilization	5	0	0
Harvesting	6	1	0
Radionuclide transport	2	0	0

Post, 1986; Pastor et al., 1987). Understanding natural processes is requisite to the use of models in the evaluation of forest responses to environmental perturbations, such as atmospheric deposition (De Vries et al., 1995; Fenn et al., 1996; Johnson et al., 1996; Aber and Driscoll, 1997; Emmett et al., 1997; Oja and Arp, 1997), climate variation (Jenkinson et al., 1991; McKane et al., 1995, 1997a,b; Oja and Arp, 1996), atmospheric CO₂ changes (Thornley and Cannell, 1996; Comins, 1997), and contaminant transport (Berg and Shuman, 1995a,b). Application of models to forest management have included harvesting influences on tree growth, soil organic matter, nutrients and sustainability (Morris et al., 1997), and effects of amendments including lime and fertilizers (Running and Gower, 1991; Johnson et al., 1995b). The models differ considerably in the range of chemical constituents they represent (Table 2).

Models have evolved to address new questions and accommodate new situations. The original Rothamsted model (Jenkinson and Rayner, 1977) has been calibrated to emulate long-term soil C accumulation following abandonment of agricultural land (Jenkinson, 1990), provide an estimate of global soil

organic matter decomposition in response to climate change (Jenkinson et al., 1991), and estimate net primary production under the assumption of correctly understanding soil C dynamics (Jenkinson et al., 1992). It has been coupled with a photosynthetic model to indicate C balance in tundra, boreal forest and humid tropical forest (Wang and Polglase, 1995), and combined with estimates of net primary production to indicate global C storage (Post et al., 1997). The litter-cohort decomposition submodel of the forest population model Linkages (Pastor and Post, 1986) was incorporated into the forest population model ForClim (Bugmann, 1996) and modified to include cation dynamics in Forswas (Currie et al., 1996).

Forest-BGC has evolved to extend its application to longer temporal and larger spatial scales (Waring and Running, 1998). The original Forest-BGC (Running and Coughlan, 1988) incorporated water dynamics from prior models and C allocation. A later version included soil N dynamics (Running and Gower, 1991). The latter evolved into Biome-BGC for global analysis of photosynthesis, autotrophic respiration, and heterotrophic respiration (Hunt et al., 1996). The aggregated stand-level estimate of C gain and respira-

Table 2
Chemical constituents represented in a selected subset of forest-ecosystem biogeochemical models

Model	Chemical constituents											References
	C	N	S	P	“Base” cations	Al	H ⁺	HCO ₃ ⁻	Si	Dissolved organics		
Rothamsted	x											Jenkinson and Rayner (1977), Jenkinson (1990), Jenkinson et al. (1991, 1992)
PnET-CN	x	x										Aber and Driscoll (1997), Aber et al. (1997)
Forest-BGC	x	x										Running and Coughlan (1988), Running and Gower (1991)
MBL-GEM	x	x										Rastetter et al. (1991, 1992), McKane et al. (1995, 1997a,b)
ITE	x	x										Thornley and Cannell (1992, 1996)
Treodyn3	x	x										Bossel (1996)
Linkages	x	x										Pastor and Post (1986), Pastor et al. (1987), Post and Pastor (1996)
TCX	x	x										Bonan (1993)
Century Forest	x	x	x	x								Parton et al. (1987), Metherell et al. (1993)
Forswas	x	x			x							Currie et al. (1996)
SAFE		x			x	x	x	x		x		Warfvinge et al. (1993), Jönsson et al. (1995)
SASD-CHESS	x		x		x	x	x	x	x	x		Santore et al. (1995)
ForSVA	x	x	x		x	x	x	x				Arp and Oja (1997), Oja and Arp (1997)
NuCM	x	x	x	x	x	x	x	x	x	x		Liu et al. (1991), Johnson (1995), Johnson et al. (1995a,b,1996)

tion of Forest-BGC (Running and Gower, 1991) was distributed to individual trees in Tree-BGC (Korol et al., 1996). Forest-BGC was combined with MT-CLIM, a climate simulator for mountainous terrain, and GIS to estimate potential productivity across the state of Montana, using available water capacity from the state geographic soils database (STATSGO) as an input layer (Milner et al., 1996).

The original Century grassland soil organic matter model (Parton et al., 1987) was expanded to include aggregated aboveground forest components (Metherell et al., 1993). The Century soil model, modified with respect to soil moisture effects on decomposition rates, was coupled with a tree population model (Friend et al., 1997). A simplified version of the Century soil model was combined with a trace-gas emission model in which NO, N₂O, and N₂ production and emission depended on gross N mineralization rate and water-filled pore space (Potter et al., 1997). The G'DAY model combined some simplifications and modifications of the Century model with a physiologically based forest vegetation model (McMurtrie et al., 1992). Further simplification of the combined model, by incorporating the assumption of equilibrium of short-term processes, yielded a model more conducive for long-term and comparative assessments (Murty et al., 1996; Comins, 1997). The Century soil model coupled with global soil, vegetation, and climate maps has yielded a global assessment of evapotranspiration, net primary production, and N mineralization (Schimel et al., 1996). Principles of the Century model were used for soil C dynamics in a global biosphere model of net primary production and heterotrophic respiration (Thompson et al., 1996).

3. Comparison of model output and observations

Many biogeochemical models have been developed within the context of land-use and environmental issues (Table 1), with the implicit or explicit potential to interface with policy analysis. There is interest in “predicting” masses or concentrations of chemical constituents or rates of biogeochemical processes over long timescales or broad spatial areas, under different environmental conditions.

To examine the agreement between belowground observations and model output from current biogeo-

chemical models, we synthesized the results of model verification and validation. We use the term verification to mean the process of comparing model output with the data that was used to calibrate the model, and validation to mean comparing model output with data that was not used for calibration. Other definitions and explanations of these terms are common (Oreskes et al., 1994; Brown and Kulasiri, 1996; Rykiel, 1996). Two contrasting approaches of calibration relate to the philosophy under which a model is developed. The Century model (Parton et al., 1987) exemplifies the approach in which many processes in a model are calibrated independently based on small-scale experimental studies, and the integration of the calibrated processes determine system behavior. MBL-GEM (McKane et al., 1997a) illustrates the approach in which the behavior of the system is examined and parameter values are set to reproduce the behavior of the system. Most models combine these approaches.

The variables reported in published studies were classified as soil solution solute concentrations, soil solid phase characteristics, or belowground process rates. For each variable, values could have been aggregated in the original studies in one of the three ways:

1. no aggregation, in which both model value and observation value are for a single point in time;
2. spatial aggregation, in which a single model value was compared with the mean or median of observations from many stands or plots;
3. temporal aggregation, in which the mean or sum of many model values was compared with the mean or sum of many observations from many points in time, such as expressing an annual rate based on summing monthly rates.

The comparison was quantified with percent normalized mean absolute error (NMAE), which is one of the many techniques of model evaluation (Janssen and Heuberger, 1995; Monte et al., 1996). For unaggregated values,

$$\text{NMAE} = 100\% \times \frac{\sum |\text{observation} - \text{model}|/n}{\text{observation mean}}$$

where the summation is over a set of n related observations, such as a time series. For spatially or

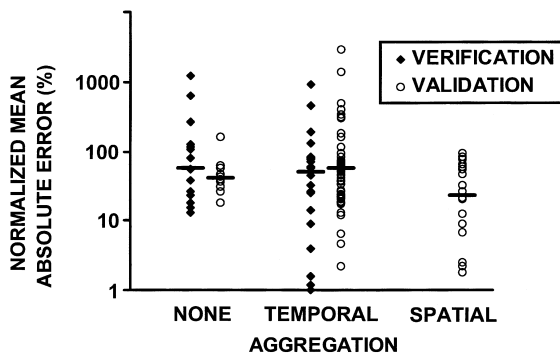


Fig. 1. Normalized mean absolute error between output of forest-ecosystem biogeochemical models and observations of soil-solution solute concentrations for model verification and validation (synthesized from Warfvinge et al. (1993), Jönsson et al. (1995), Morell et al. (1996), Van der Salm et al. (1996), Sogn and Abrahamsen (1997)). Horizontal bars indicate median values.

temporally aggregated values,

$$\text{NMAE} = 100\% \times \frac{|\text{aggregated observation} - \text{aggregated model}|}{\text{aggregated observation}}$$

NMAE varied considerably for solute concentrations ranging from 0 to >1000% (Fig. 1). Median verification NMAE for the different aggregation categories was 24–56%. We expected validation to yield higher NMAE than verification, but there was no strong indication of this. This is encouraging, because it suggests that the “predictive” ability of models might be improved through better calibration. Alternatively, the similar magnitudes of NMAE for verification and validation may be coincidental. Data for soil solid phase characteristics such as base saturation, extractable ions, and soil C mass were more limited (Jenkinson, 1990; Bonan, 1993; Jönsson et al., 1995; McKane et al., 1995; Johnson et al., 1996) and represented only three categories. Median NMAE was 20–24% for the unaggregated verification, unaggregated validation, and spatially aggregated validation categories. These are lower values than for solute concentrations and indicate greater ability of the models to mimic solid phase properties. For fluxes such as net N mineralization, net nitrification, and solute leaching, data were limited to the temporally aggregated validation category (Bonan, 1993; Johnson et al., 1996; Ryan et al., 1996a; Aber et al., 1997; Potter et al., 1997) and yielded a median NMAE of 52%.

4. Comparison of outputs among models

Comparisons among models provide an alternate approach to evaluate model performance and gauge the reliability of model estimates. Of the model comparisons that have included belowground processes, several focused on intensive research sites, for which there was considerable, but sometimes incomplete, data for calibration and comparison. Net N mineralization was evaluated by Ryan et al. (1996a) at the 10–20 year old *Pinus radiata* plantation of the Biology of Forest Growth experiment, west of Canberra, Australia. Following calibration based on several years of field data, model output of net N mineralization (kg N ha^{-1} per year) for the 1986 test year was 29 for Century Forest, 35 for Q, 40 for Biome-BGC, 42 for MBL-GEM, and 77 for PnET-CN. These values were substantially greater than the 7 kg N ha^{-1} per year measured by sequential coring and in situ field incubation for 1986, although measured values in other years were as high as 38 kg N ha^{-1} per year.

Fourteen forest–soil–atmosphere models were evaluated by using long-term records of the spruce site at Solling, Germany (van Grinsven et al., 1995). There was large variation among model outputs of soil water content and flux. For example, the coefficient of variation of annual drainage flux among models was 25% (Bouten and Jansson, 1995). General temporal trends of some soil solution solute concentrations could be reproduced by the models, although emulating trends in pH, Al, and nitrate was generally unsuccessful (Kros and Warfvinge, 1995). Mohren and Ilvesniemi (1995) concluded that the models showed no general agreement regarding the influence of soil chemistry on nutrient uptake and tree growth. Van Heerden and Yanai (1995) concluded that there was general agreement among models in indicating drought and nutrient deficiency were more important factors of forest damage than direct air pollution stress, but the magnitude of forest response differed among models. Reasons given for differences in model output included calibration procedures (Bouten and Jansson, 1995), incomplete links between soil chemistry and vegetation (Kros and Warfvinge, 1995; Mohren and Ilvesniemi, 1995), model complexity (Van Heerden and Yanai, 1995), and assumed mechanisms of response to stress (Van Heerden and Yanai, 1995).

Large variation among model outputs also occurs for agricultural settings (Diekkrüger et al., 1995). For cultivated sites near Neuenkirchen, Germany, model estimates of annual net N mineralization differed among nine models by a factor of as much as 4, but there were no measurements with which model outputs could be compared. Interestingly, there was no systematic difference between models from one year to the next, indicating complex feedbacks within the models and difficulty in identifying a singular cause for differences among the model outputs, if in fact, a singular cause exists.

At a much coarser scale, VEMAP Members (1995) evaluated the net primary production and terrestrial vegetation-plus-soil C storage over the continental USA by three models. They also examined responses to scenarios of climate change and doubling of atmospheric CO₂. The models were in agreement with respect to enhanced C storage with increased atmospheric CO₂ alone, but the magnitude of response differed among models. The models indicated very different responses to climate change alone and to climate plus CO₂ change. With climate change, decreased C storage in Biome-BGC was caused by decreased water availability lowering net primary production coupled with higher temperature increasing plant and soil respiration. In contrast, Century and TEM responded to increased N availability that

yielded higher net primary production and ultimately higher vegetation C, but they had different responses because of temperature and moisture effects on net N mineralization rates.

5. Model structure

The general structure of the forest-ecosystem biogeochemical models is a series of compartments representing chemical constituents occurring in different chemical forms or different physical locations. Flows between these compartments represent processes. The rates of flows between compartments are influenced by user-supplied driving variables, such as temperature and moisture.

There is a considerable range of complexity exhibited by the belowground portions of models, evolving from differences in chemical constituents represented, number and type of soil compartments, number and type of belowground processes, user-supplied driving variables that influence rates, and timestep with which processes are calculated. Examples of models exhibiting this diversity are presented in Tables 2–6.

The vegetation in forest biogeochemical models is represented as vegetation components or as individual plants. In the former, at least three components are specified (foliage, wood, and fine roots), except

Table 3
Structure of a selected subset of forest-ecosystem biogeochemical models

Model	Timestep of soil processes	No. of vegetation compartments	No. of forest floor or litter compartments	No. of mineral soil layers	No. of solid phase organic compartments per mineral soil layer	No. of other compartments per mineral soil layer
Rothamsted	Month	0	0	1	5	0
PnET-CN	Month	5	1	1	1	2
Forest-BGC	Year	4	1	1	1	0
MBL-GEM	Month	4	0	1	4	1
ITE	10 min, day	5	4	1	2	0
Treedyn3		5	1	1	1	1
Linkages	Year	Trees	Cohorts	1	1	0
TCX	Day, year	3	4	>1	1	0
Century Forest	Month	5	3	2	3 or 5	5
Forswas	Year	Trees	Cohorts	1	1	0
SAFE	Year	0	1	>1	0	3
SASD-CHESS	Century	0	0	20	2	3
ForSVA	Annual	3	1	1	1	3
NuCM	Day, week, or month	6	4	>1	1	4

Table 4

Belowground plant and microbial processes represented in a selected subset of forest-ecosystem biogeochemical models

Model	Plant processes			Microbial processes					
	Root death and detrital production	Root respiration	Nutrient uptake from soil	Microbial decomposition, respiration	Microbial mineralization, immobilization	Nitrification	Denitrification	Nitrogen fixation	Soluble organic production
Rothamsted				x					
PnET-CN	x		x	x	x	x			
Forest-BGC	x	x	x	x	x				
MBL-GEM	x	x	x	x	x				
ITE	x	x	x	x	x	x	x		
Treedyn3	x	x	x	x	x			x	
Linkages	x			x	x				
TCX	x	x	x	x	x			x	
Century Forest	x		x	x	x			x	x
Forswas			x	x	x				
SAFE									
SASD-CHESS				x	x				x
ForSVA	x		x		x	x			
NuCM		x	x	x	x	x		x	x

for TEM which represents vegetation as a single compartment. Additional components include buds (PnET-CN), fruit (Treedyn3), mobile assimilates (MBL-GEM, PnET-CN, Treedyn3), wood subdivided into branch, stem, and coarse roots (Century Forest, ITE), and understory (NuCM). Plant growth responds to nutrient and water availability in all of the models. The response of plant growth to atmospheric CO₂,

relative humidity, wind speed, and solar radiation is also represented in physiologically based models (e.g., MBL-GEM, ITE, TCX). Plant production is simulated in some models (e.g., Century) as a maximum or representative rate of net primary production that is modified by environmental factors, whereas the physiologically based models disaggregate the processes of photosynthesis and respiration. Because

Table 5

Belowground chemical and physical processes represented in a selected subset of forest-ecosystem biogeochemical models

Model	Chemical processes					Physical processes	
	Cation exchange	Anion sorption	Weathering	Solution equilibration	Ammonia volatilization	Water flows	Solute leaching
Rothamsted							
PnET-CN						x	x
Forest-BGC						x	x
MBL-GEM							x
ITE					x	x	x
Treedyn3							x
Linkages							
TCX						x	
Century Forest		x			x	x	x
Forswas			x				
SAFE	x		x	x			x
SASD-CHESS	x		x	x		x	x
ForSVA	x	x	x				x
NuCM	x	x	x	x		x	x

Table 6

Driving variables that directly or indirectly influence belowground process rates in a selected subset of forest-ecosystem biogeochemical models

Model	Driving variables influencing belowground processes						
	Precipitation	Soil moisture	Air temperature	Soil temperature	Evapotranspiration	Soil atmospheric CO ₂	Ecosystem outputs of chemical constituents
Rothamsted	x		x				
PnET-CN	x		x				
Forest-BGC	x			x			
MBL-GEM		x	x				
ITE	x			x			
Treedyn3							
Linkages	x		x				
TCX	x		x		x		
Century Forest	x		x				
Forswas	x						x
SAFE	x	x				x	
SASD-CHESS	x				x		
ForSVA							
NuCM	x		x	x			

photosynthesis and respiration respond differently to temperature, the latter approach may more closely simulate vegetation response to climate change and consequent changes in organic matter inputs to soils.

Individual trees of different species represent vegetation in “gap” or population models, so-called because they attempt to simulate the dynamics of the populations of trees that occur in forest gaps. The vegetation responds to temperature and precipitation. In many population models, soil influences tree growth by a constant soil fertility parameter. Talkkari and Hypén (1996) used total N content of the O layer to indicate site fertility and soil texture to determine water holding capacity. Only a few forest population models include soil processes (e.g., Forswas, Linkages), although the importance of including soil and nutrient dynamics in population models has been recognized (Vanclay, 1995; Loehle and LeBlanc, 1996).

A combination of these two approaches is found in Tree-BGC in which total stand growth is determined first, then the growth is distributed among individual trees (Korol et al., 1996). In addition, some models lack vegetation components (Rothamsted, SAFE, SASD) and require specifying vegetation-related processes such as solid detrital inputs, dissolved organic inputs, and nutrient uptake.

The models are arrayed along a continuum from purely soil organic matter to purely soil chemistry. The organic matter models deal with organic C and N (Rothamsted, PnET-CN, Forest-BGC, MBL-GEM, ITE, Treedyn3, Linkages, TCX). An extension to include organic S and P occurs in Century Forest, which also considers sorbed inorganic forms of these elements. Forswas is organic-based, but also considers Ca, Mg, and K associated with organic matter. Models that mimic soil chemistry (SASD-CHESS, ForSVA, NuCM) in addition to organic matter also consider, to various extents, dissolved and sorbed sulfate, dissolved and exchangeable “base cations” (Ca, Mg, K, Na) and Al, dissolved carbonate and dissolved organics. Inorganic N is represented in various forms, including “available N” or “mineral N” (Linkages, Forest-BGC, Treedyn3, TCX, Forswas, Century Forest, GEM), dissolved nitrate (SAFE), dissolved ammonium and nitrate (PnET-CN, ITE), and dissolved nitrate plus dissolved and exchangeable ammonium (ForSVA, NuCM).

The models differ considerably in the number of compartments that represent the belowground environment (Table 3). The compartments are distinguished physically by soil layer or conceptually by maximum decomposition rates. Litter or detritus is often maintained in separate compartments by origin, such as woody litter or foliar litter. Some models

(Linkages, Forswas) track decomposing litter in annual cohorts until it reaches an advanced stage of decomposition and becomes “humus”. In some models the humus is represented by several theoretical compartments having different decomposition rates (Jenkinson, 1990). The compartments have been labeled with various names that indicate their relative decomposition rates, such as microbial, fast, slow, passive, and inert. The different rates have been attributed to chemical recalcitrance and physical protection, but hypothesized causes differ among studies. For example, Chertov and Komarov (1997) suggest a slow-rate compartment in forest floor F and H layers caused by impregnation of undecomposed plant debris with humic acids.

PnET-CN has the simplest soil structure, with a single dead wood compartment and a single soil layer containing a single organic matter compartment that turns over at a moderate rate. Aber et al. (1997) chose this structure because analysis of more complex designs indicated the limited influence of faster turnover litter pools on N dynamics. The model does not include organic matter that turns over at a very slow rate (Aber and Driscoll, 1997). Forest-BGC has a similar simple structure. Other models include additional litter compartments, theoretical organic matter compartments, and/or additional soil layers (Table 3). Within a single soil layer, none of the current models contains more compartments than the five-compartment Rothamsted model, about which Jenkinson and Rayner (1977) stated “it seems pointless to postulate a more complex model until we have data that are irreconcilable”. An alternative to multiple compartments with different decomposition rates is an individual compartment with a continuously changing decomposition rate (Bosatta and Ågren, 1991), a concept implemented in TCX.

Other compartments represent dissolved, sorbed, exchangeable, and solid phase mineral forms of one or more chemical constituents. Transfers of material among these compartments represent processes of cation exchange, anion sorption, equilibration between solution and solid phase, and mineral weathering. These processes are represented by a variety of mathematical formulations. For example, removal of anions from soil solution varies with type of anion. Sulfate is assumed to be in equilibrium between dissolved and sorbed phases, and pH influences the

equilibrium. This is formulated in different ways. In SASD,

$$(\text{sorbed SO}_4) = \text{constant} \times (\text{SO}_4) \times (\text{H}^+) \times \text{free anion exchange sites}$$

where free anion exchange sites are those sites not occupied by organic anions or SO_4 . Therefore, SO_4 sorption is inherently competitive with organic anions, which are represented by a triprotic organic acid. In ForSVA, a non-competitive pH-dependent Langmuir formulation is used:

$$(\text{sorbed SO}_4) = \frac{\text{maximum SO}_4 \text{ sorption} \times (\text{SO}_4)}{A \times 10^{(\text{pH}-B)} \times (\text{H}^+)^{-2} + (\text{SO}_4)}$$

where A and B are constants. In NuCM, a similar formulation is followed:

$$(\text{sorbed SO}_4) = \frac{\text{maximum SO}_4 \text{ sorption} \times (\text{SO}_4)}{A \times (\text{H}^+)^{-2} + (\text{SO}_4)}$$

NuCM also considers non-competitive sorption of a triprotic organic acid and of phosphate, whose sorbed amounts are proportional to solution concentrations. Other models (Lükewille et al., 1995) also incorporate precipitation of minerals in the control of dissolved SO_4 . Details on representation of other processes and their rates are given in references listed in Table 2, and are summarized by Tiktak and van Grinsven (1995) and Jandl (1998).

6. Discrepancies and model structure

The discrepancies between model output and observations and among models may be caused by model structure, specific equations used to alter process rates, calibration procedures, and data quality. Quantitative examination of the influence of model structure on model behavior is problematic, because it requires a common framework that can accommodate the differences among models, including definitions of compartments and driving variables. Jans-Hammermeister and McGill (1997) examined three residue-decomposition models by connecting them to a common soil model, but focused on comparison of calibrated models to observations, rather than on influence of model structure on model behavior.

Perruchoud and Fischlin (1995) indicated that the variety of formulations to aggregate organic matter may result in inconsistencies in simulation results among models. We examined this concept by recoding the soil C models from the Century, GEM, Rothamsted, and Linkages models and running them under identical conditions. This approach allowed the concepts in the soil models to be separated from the vegetation models. The structural elements that were retained in the recoded models were number of soil C compartments, pathways of transfer between the compartments, and relative rates of transfers between pools. Implementation approaches were standardized: timestep was set at 1 month and fluxes were represented by difference equations. Total soil organic C was compared, because definitions of individual soil C compartments differed among models.

The response of steady-state soil organic C to detrital input was similar for all models (Fig. 2). In contrast, the transient response to change in detrital input yielded different behaviors (Fig. 2). There is no single cause for the different behaviors; rather, this is the combined result of the different number of soil C compartments, the flow paths connecting them, and the relative transfer rates. Linkages responded most quickly; it is dominated by a humus compartment that

receives material from litter cohorts but releases its C only to CO₂. In contrast, MBL-GEM responded the slowest; it has four compartments that circulate organic C among themselves, as well as releasing some to CO₂.

7. Discrepancies and other factors

Factors other than model structure that cause discrepancies between model output and observations or among models are specific equations that alter process rates, calibration procedures, and data quality. The potential influence of specific equations is exemplified by the representation of temperature and moisture on rates of microbial processes, such as microbial respiration, N mineralization, and nitrification. In general, these process rates are represented as

microbial process rate

$$\begin{aligned}
 & [\text{mass of C or N transferred/area/time}] \\
 & = \text{size of donor compartment [mass/area]} \\
 & \quad \times \text{maximum turnover rate constant [1/time]} \\
 & \quad \times f(\text{temperature}) [\text{unitless fraction}] \\
 & \quad \times g(\text{moisture}) [\text{unitless fraction}]
 \end{aligned}$$

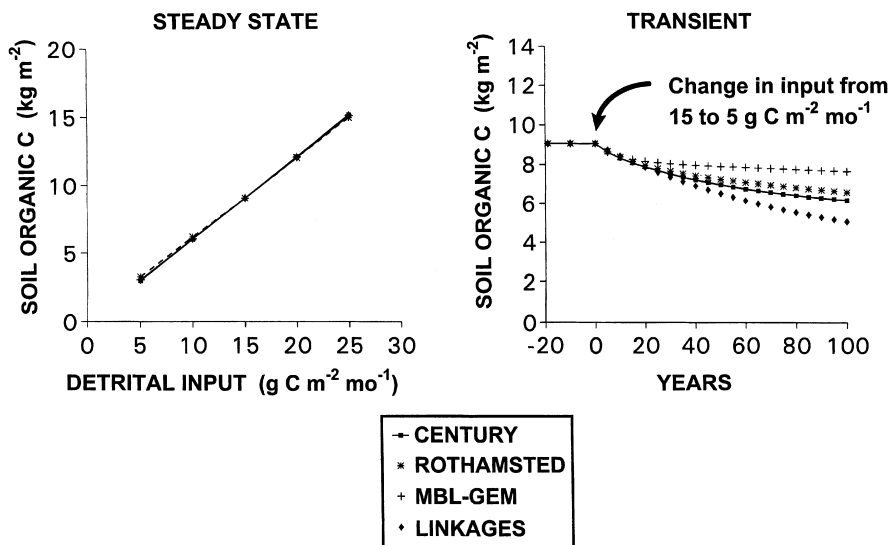


Fig. 2. Estimates from four recoded models indicating effect of detrital input on steady-state and transient soil organic C. Parameters of each model were set to yield the same steady-state soil organic C mass when temperature is 8°C and detrital input is 15 g C m⁻² mol⁻¹.

In a detailed study comparing the f (temperature) and g (moisture) functions of nine models, Rodrigo et al. (1997) found differences in function values to vary with the range of temperature and moisture considered. For example, under high moisture conditions in the absence of vegetation, the average value of g (moisture) was similar among models (CV=6%), while at lower moisture conditions that would be caused by vegetative transpiration, the average value varied much more among models (CV=33%). The combined temperature and moisture functions yielded values that differed by as much as a fivefold among models. Such differences resulting from specific equations contribute to differences in output from complex models.

Different calibration strategies or procedures can lead to discrepancies. In an evaluation of water balance at the spruce site at Solling, Germany, Bouten and Jansson (1995) concluded that different calibration procedures were more important in yielding different results among models than were different model structures. In some cases, optimization procedures have been used to determine “best-fit” parameter values (McKane et al., 1995, 1997a), but systematic, iterative manipulation of parameters to achieve results close to observed values appears common in complex models (Oja and Arp, 1997). Procedures for different types of parameters may differ even with the same model (McKane et al., 1995, 1997a). The quality and uniqueness of a parameter set can be determined by sensitivity analysis, as demonstrated by McKane et al. (1997a).

A key difficulty with both verification and validation of complex biogeochemical models is the limited observations available for a variety of ecosystems (Bonan, 1993; Janssen and Heuberger, 1995; Arp and Oja, 1997; Sogn and Abrahamsen, 1997). Obviously, a model can be well optimized for a particular data set (e.g., biomass and NPP data for a particular site and year) and still be poorly constrained for many of the response functions and feedbacks represented in the model. Ideally, models should be optimized for data representing soil and vegetation responses to a wide range of environmental conditions, e.g., transects or networks of sites across a biome’s climatic and edaphic range (e.g., Parton et al., 1987), or site-specific experimental manipulations of multiple variables including nutrients,

temperature, moisture, light, and atmospheric CO₂ concentration (e.g., McKane et al., 1997a). The problem is to have sufficient data not only to describe the response of individual processes to key driving variables (e.g., photosynthetic rates vs. temperature), but also the consequent interactions among processes represented in the model’s structure. For example, ecosystem response to increased temperature may initially be dominated by the temperature response of individual processes, but subsequent feedbacks among soil and plant processes may dominate system response at longer timescales. Although few ecosystems or biomes have been described in the detail needed to adequately constrain complex models, field research efforts are increasingly being designed and implemented to address this issue (e.g., Koch et al., 1995).

Another data-related difficulty in calibrating and evaluating models is understanding the quality and limitations of the observations (Bredemeier et al., 1995; Kolka et al., 1996). Inherent measurement variability can result in relatively high differences between actual and measured values. For example, soil C masses may be very well related to actual evapotranspiration, but measured values would show a more ambiguous trend because of measurement errors (Fig. 3). Measurement errors occur from random variability in analyses of C concentration, bulk density, and rock volume, and from random variability between potential sampling locations within a plot (Homann et al., 1995). If only several measurements of soil organic C mass and evapotranspiration with

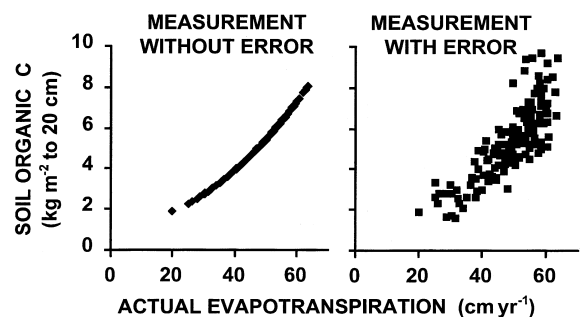


Fig. 3. Influence of measurement error on relation of soil organic C mass to actual evapotranspiration based on a synthetic data set (expanded from Homann et al. (1995)).

their inherent errors were available for model calibration, it is unlikely that the calibrated model would reproduce the true relation between these variables. Further, it is unlikely that the calibrated model would reproduce other measurements, because of the inherent error associated with them.

Additional uncertainty in measurements occurs from measurement deficiencies and data presentation. For example, incorrect soil solution solute concentrations arising from improper lysimeter installation led to a time series whose use in calibration or comparison would be erroneous (Bredemeier et al., 1995). The use of a limited set of highly uncertain observations may result in a successfully calibrated model that incorrectly reflects the real relations among variables. Conversely, failure to calibrate a model to mimic highly uncertain observations may be perceived as a deficiency of the model rather than of the observations.

8. Trends and challenges

Current forest biogeochemical simulation models demonstrate a broad range of complexity arising from differences in the elements and chemical forms represented, vertical heterogeneity of soil layers taken into account, and variety of processes and driving variables considered. Processes are portrayed in different mathematical forms, which represent theoretical concepts in some cases and empirical information in others.

These cumulative differences among models yield considerable discrepancies among model estimates and between model output and observations. Specific causes of discrepancies among models are difficult to isolate because of the cumulative differences in model structure, function selection, and calibration. To facilitate easier comparison, the recommendation has been made for models to be modular to allow easy replacement of individual equations, sets of equations, or entire approaches (Tiktak and van Grinsven, 1995; VEMAP Members, 1995; Ryan et al., 1996a; Reynolds and Acock, 1997; Timlin and Pachepsky, 1997).

Tiktak and van Grinsven (1995) called for models to be better balanced with respect to level of detail of hydrologic, plant, and soil processes. Alternatively,

Luan et al. (1996) developed a hierarchical model of plant–soil interactions that allows selection of level of process detail, depending on availability of data for calibration and driving variables. Such a model structure may be useful for comparing model formulations designed to operate at different time-scales. Combining the concepts of hierarchy and modularity may allow comparison of current representations with those that account for finer-scale temporal or spatial variability, such as the influence of fine-scale soil heterogeneity on solute transport (Mitchell and Mayer, 1998).

The application of biogeochemical models to spatial assessments at local (Gao, 1996), regional- and global-scales (Jenkinson et al., 1991; VEMAP Members, 1995; Aber et al., 1997) is likely to expand. For very heterogeneous landscapes having upland, wetland, and shallow-water habitats, Fitz et al. (1996) emphasized the use of a modular general ecosystem model in a grid-based analysis. This builds on the generality concept of MBL-GEM (general ecosystem model) for upland ecosystems (Rastetter et al., 1991), and simplicity concept of Forest-BGC, which represents “a conscious compromise between mechanistic detail and simplifying generality that will allow it to be implemented for regional-scale ecological research” (Running and Coughlan, 1988). Alternatively, Tiktak and van Grinsven (1995) indicated that modularity would allow adaptation of a model to specific cases, because a single model formulation cannot represent all spatial and temporal scales.

Continued coordination of modeling and experimental studies (van Grinsven et al., 1995; VEMAP Members, 1995) is needed to enhance the potential to obtain observations necessary for calibration and model evaluation. The development of approaches to measure of soil organic matter fractions that correspond to model compartments, or conversely implementation of model compartments that represent measurable soil organic matter fractions, is a pressing need. Enhanced documentation of all phases of model development, calibration, and evaluation is required (Aber, 1997). In combination with the augmented approaches indicated above, these will enhance the potential for forest-ecosystem biogeochemical models to contribute to understanding environmental concerns, resolving natural resource issues, and improving public-policy decisions.

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