

The response of the carbon cycle in undisturbed forest ecosystems to climate change: a review of plant–soil models

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Abstract. We compared six plant–soil models from the literature which describe the C-dynamics in forests and include climatic forcing explicitly. Our selection included the two physiological models *FOREST-BGC* and *TCX*, the ecosystem/population model *FORCLIM*, two ecosystem/tissue models, *MBL-GEM* and *CENTURY Forest* and the global model *TEM*. The review revealed a multitude of differences with respect to the model structure, the incorporation of particular processes and the coupling with the abiotic environment. We made an assessment of what kind of questions the models can be best applied to and how well they are suited for studying the response of the C cycle under climate change. In this context organic C in litter and humus play a key role. The number of compartments and the pathways of C flows influence both the transient phase and equilibrium of the system, a fact that has been recognized before, but has not been investigated systematically for any of the models. Hence, the multitude of

aggregation levels used to represent detritus and the variety of decomposition formulations used in the models may result in inconsistencies of the simulation results. Similarly, the control of ecoprocesses via abiotic factors differs among the models. They use distinct abiotic quantities and different mathematical parametrizations, thereby affecting the system's response in a changing environment substantially, even if this is not the case for present conditions. Given the differences in experimental frames of published simulations it was not possible to trace back behaviour deviations to particular model formulations. In order to make consistent projections of the C cycle's response in forests in a changing climate there remains an urgent need to analyse the models from a structural point of view based on quantitative model comparisons under well-defined conditions.

Key words. Review, plant–soil models, carbon cycle, soil organic carbon, forests, climate change.

INTRODUCTION

Forests play a major role in the global carbon cycle (C cycle) with respect to both fluxes and pools: according to Waring & Schlesinger (1985) about 70% of the global exchange of CO₂ between the terrestrial biota and the atmosphere passes through forests. Estimates of the C-stocks in forests amount to 62–78% of the global terrestrial total when combining the values for living plant C of Whitaker (1970) and Olson, Watts & Allison (1983) with the values of soil organic carbon (SOC) reported by Schlesinger (1977) and Post *et al.* (1985), respectively. According to the same sources, SOC amounts to 44–66% of the global total of carbon in forests. This clearly underestimates the importance of forest soils: the most recent estimates of Dixon *et al.* (1994) report 1146 Gt C in forests with 69% stored in soils (Fig. 1). Given this high potential for changing C fluxes at the global scale, it has become crucial within the greenhouse debate to answer the question of whether the forests act as sources or sinks of CO₂ under present conditions and to give an assessment of their

development with respect to the C dynamics assuming a changing climate.

Due to the spatial and temporal scales inherent in the response of the C cycle in forests under a changing climate, current experimental techniques are not directly applicable. In contrast, modelling is adequate to investigate both the aspect of the impact of a changing climate on the dynamics of the C cycle in forests, and to determine what potential feedbacks between the ecosystems and the atmosphere might look like.

Numerous models have been developed in the past, each one emphasizing a particular aspect of C dynamics, which makes comparison difficult and the choice of a particular model for one's objective not a straightforward task.

Analogue approaches assume the future steady-state of the system to be analogous to another currently present system, which has experienced a similar climatic (or equivalent environmental) change in the past. However, similar to other equilibrium models in general, this approach is not applicable to assess transient system responses quantitatively. Moreover, regressions between

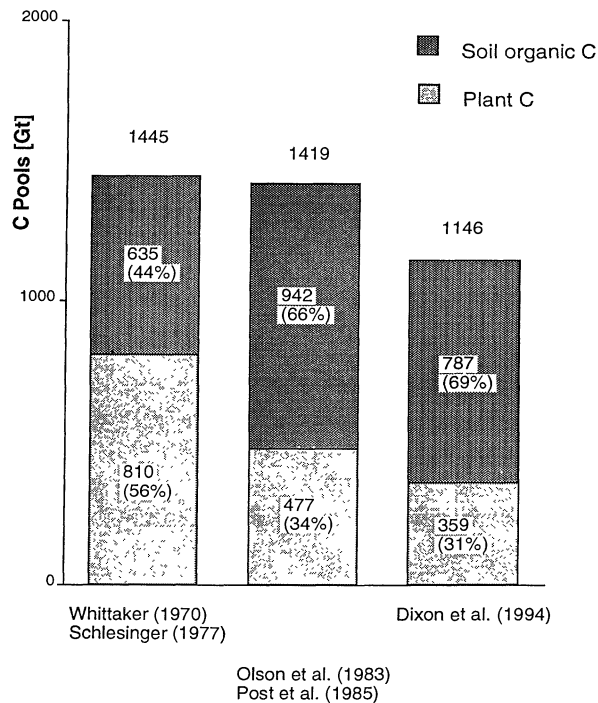


FIG. 1. Global estimates for C pools in forests worldwide. The estimates for plant C in the first and second bar refer to the assessments of Whittaker (1970) and Olson *et al.* (1983); similarly, for SOC the studies of Schlesinger (1977) and Post *et al.* (1985), respectively, were used. Estimates in the third bar are taken from Dixon *et al.* (1994).

ecological and climatic observables used in earlier regional equilibrium models have been shown not to agree with (simulated) transient system responses (Pastor & Post, 1993).

Several models, mainly those used for assessments of forest management practices, often do not include explicit abiotic forcing (Kimmins, 1993; Thornley & Cannell, 1992). On the other hand the influence of climatic parameters on the state of ecosystems and its dynamics is widely recognized and has been studied in many investigations on different spatial scales. At the global scale, for example, Meentemeyer, Gardner & Box (1985) correlated detrital soil C with actual evapotranspiration (*AET*) and soil moisture deficit and Box & Meentemeyer (1991) found similar relations for soil CO₂ emission and litter production. The models that treat climate implicitly, i.e. that assume that its influence is the same over the whole scope of interest, may not be applied to study the impact of climatic change without modifications.

Forests differ with respect to productivity and decomposition of organic matter as a function of climatic and environmental conditions. Production and decomposition may, for example, be decoupled when estimating CO₂ emissions from soil to a global temperature increase (Jenkinson, Adams & Wild, 1991). However, the simulated successional transient response to a step in climate with a concomitant change in biomass and litterfall extends over 400–700 years (Bugmann & Fischlin, 1994). The time

horizon of such a shift overlaps, with time constants of decomposition processes which range from days to centuries. Thus, when assessing the C dynamics in forests, it is not justified to decouple plants and soils according to a 'two-timing'-like approximation (Ludwig, Jones & Holling, 1978).

Coupled plant–soil forest models which are usable to investigate the transient response of the system under a climatic change have hardly been reviewed before in the literature. Ågren *et al.* (1991) have discussed the concepts and gaps of coupled production–decomposition models for grasslands and conifer ecosystems and classified them according to the criterion of process–resolution level. Their work illustrates clearly how much models within one class (six physiologically based models) may vary and comments on the problem of scaling across models with distinct resolution-levels. However, their detailed comparison is restricted to one class only. It has become increasingly necessary to convey rigorous comparisons of model performance in order to achieve a more unified view of ecosystem properties. Numerical comparisons of calibrated plant–soil models are under way but not yet published (Ryan *et al.*, 1994a, b).

In this paper we reviewed six plant–soil models designed to simulate C dynamics covering all classes *sensu* Ågren *et al.* (1991). Discussing differences in model structure, process resolution and representation of abiotic forcing on ecoprocesses, we pointed out the models' range of applicability and assessed their suitability for analysing the impacts of a climate change on the C cycle in forests. In many models the importance of soils with respect to the C cycle has been underestimated and SOC has been treated in an oversimplified manner. Thus, we focused on the representation of the soil component's within the selected models and included a detailed discussion of the decomposition models.

METHODS AND MATERIALS

Information on the reviewed forest models stemmed from published model descriptions (e.g. model structure, equations, time step, information on driving data) and results (see 'References' column, Table 1). We used supplementary evidence from field and modelling studies to discuss the models.

For this review we selected plant–soil models using the following criteria:

1. We were interested in dynamic models which allow study of the transient response of the system under a climate change. This ruled out analogue approaches and equilibrium models.
2. The models had to demonstrate the dependence of the processes on abiotic factors explicitly.

This two-step procedure led us to select the following six models (Table 1): the Terrestrial Ecosystem Model *TEM*, the Marine Biological Laboratory's General Ecosystem Model *MBL-GEM*, *CENTURY Forest* emphasizing C dynamics in soils, *FORCLIM* describing *FORests* in a changing *CLIMate*, *FOREST-BGC* for BioGeochemical Cycles

TABLE 1. General description of the reviewed models. For the classification scheme see Ågren *et al.* (1991). The data required to run the model on a specific site do not include climatic variables (see also Table 3)

Name	TEM	MBL-GEM	CENTURY Forest	FORCLIM	FOREST-BGC	TCX
References	Raich <i>et al.</i> (1991) McGuire <i>et al.</i> (1992) McGuire <i>et al.</i> (1993) Melillo <i>et al.</i> (1993)	Rastetter <i>et al.</i> (1991) Rastetter <i>et al.</i> (1992)	Parton <i>et al.</i> (1987) Schimel <i>et al.</i> (1990) Sanford <i>et al.</i> (1991) Metherell <i>et al.</i> (1994)	Bugmann (1994) Fischlin <i>et al.</i> (1994)	Running & Coughlan (1988) Running & Gower (1991) Running & Nemani (1991)	Bonan (1991) Bonan (1993)
Class	Global	Ecosystem/tissue	Ecosystem/tissue	Ecosystem/population	Physiological	Physiological
Focus	C/N dynamics, NPP	C/N dynamics	SOC & soil N, C,N,P,S dynamics	Forest succession, species composition	Dynamic C allocation, hydrological balance	C/N dynamics, dynamics of moisture and energy
Forest type	Tropical, temperate, boreal	Temperate	Tropical	Temperate, boreal	Hypothetical forest	Boreal
Aggregation- level for vegetation	Lumped plant communities	Plant communities	Relative composition of C3:C4 plants	Species	Undefined	Species
Simulation period	Not reported	50 years	100–1000 years	100–1000 years	50 years	10 years
Site-specific inputs	cf. Raich <i>et al.</i> (1991), Appendix 1: Tables 3/5 cf. McGuire <i>et al.</i> (1992), Tables 3/4	C/N stocks in veg. compartments, <i>GPP</i> , <i>N</i> uptake, soil inorg. <i>N</i> , tissue turnover rates, soil org. <i>C/N</i> , litter chemical fractions	Soil texture, lignin & N content of plant residues, plant <i>N</i> , <i>P</i> , <i>S</i> , initial soil <i>C</i> , <i>N</i> , <i>P</i> , <i>S</i>	Field capacity, latitude	Leaf area index, soil water capacity	Height, aspect, slope, elevation, leaf area index, moss & humus thickness, drainage class

TABLE 2. Representation of the C cycle in the reviewed models. The numbers given for plant and detrital C do not refer to individual trees (*FORCLIM*) or litter cohorts (*FORCLIM* and *TCX*), but to compartments with distinct turnover times.

Name	<i>TEM</i>	<i>MBL-GEM</i>	<i>CENTURY Forest</i>	<i>FORCLIM</i>	<i>FOREST-BGC</i>	<i>TCX</i>
No. of plant C compartments	1	7	5	6	3	3
No. of litter: humus C compartments	1	3:1	7:4	6:1	1:1	7:1
Formulation of plant-growth	Gross primary production	Gross photosynthesis	Gross primary production	Diameter at breast height	Gross photosynthesis	Gross photosynthesis
Allocation model	None	Dynamic model	Constant coefficients	Allometry	Dynamic model	Constant coefficients
Formulation of decomposition	Pools	Pools (coupled)	Pools (coupled)	Cohort-pool (coupled)	Pools (uncoupled)	Cohort-pool substrate-quality continuum (uncoupled)

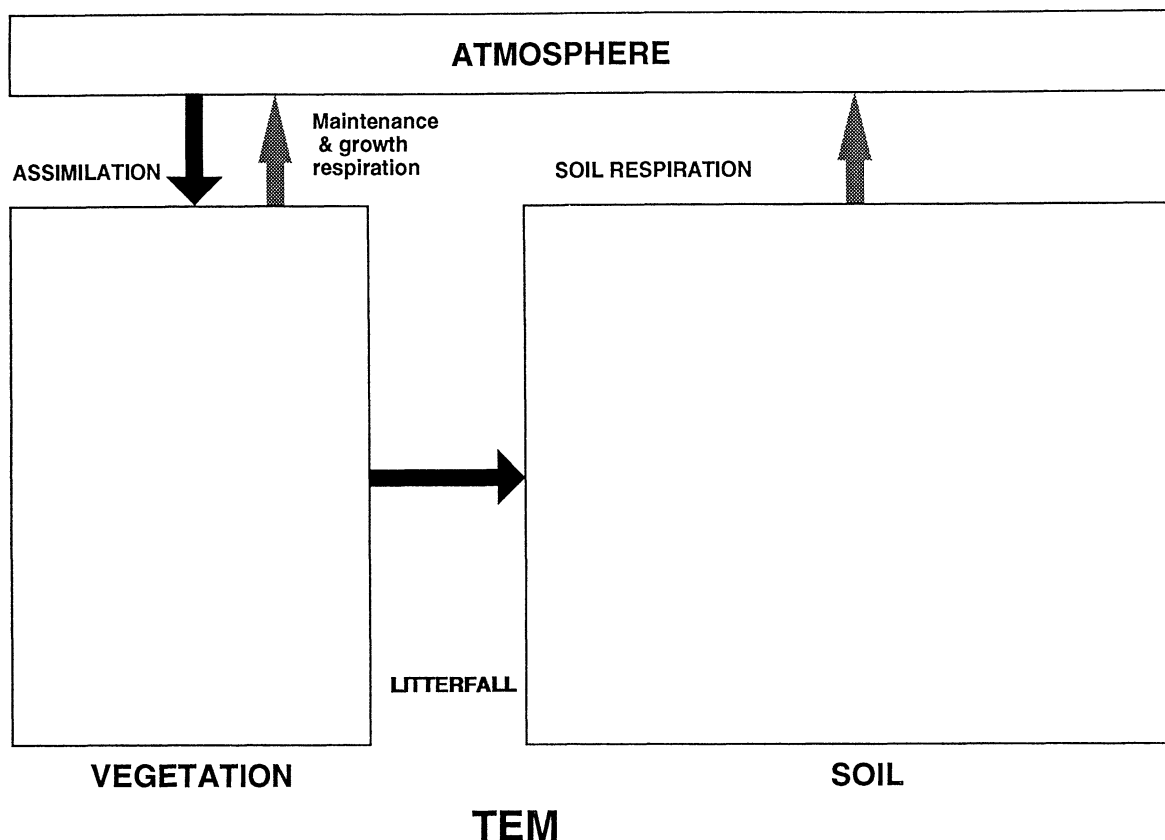


FIG. 2. Carbon pools (boxes) and fluxes (arrows) as modelled in *TEM*. CO₂ effluxes from the system are shown as shaded arrows.

in forests and *TCX* simulating Terrestrial Carbon eXchange (see 'References' column, Table 1).

RESULTS AND DISCUSSION

The selected models were classified (see 'Class' column, Table 1) similar to the scheme of Ågren *et al.* (1991) by considering the level of resolution at which processes are modelled and the spatial scope.

Although the selected models all deal with the assimilation, redistribution and decomposition of C, they have originally been designed for different purposes (see 'Focus' column, Table 1) and applied to simulate different forest types (see 'Forest type' column, Table 1). Consequently the models differ in their scopes in time and space (see last two columns, Table 1).

Note that all statements made in the following sections apply only to the models in their published form and do not imply principal constraints for improvements nor for intentions of the authors.

Model structures

The representation of living vegetation in terms of tissue classes differs among the models (Table 2). Except *TEM*, all models use the minimal division of vegetation into

foliage, wood and fine roots, but *MBL-GEM*, *CENTURY Forest* and *FORCLIM* refine these classifications. This ranges from discerning fine branches and coarse roots besides stemwood (*CENTURY Forest*, Fig. 4) to using a labile and structural component for any of the above-mentioned three classes (plus heartwood) as in *MBL-GEM* (Fig. 3). From a technical point of view the vegetation classes are implemented as pools (*TEM*, *MBL-GEM*, *CENTURY Forest*, *FOREST-BGC*, *TCX*) and species-specific age-cohorts (*FORCLIM*), respectively. In general, pool models assume a spatially homogeneous canopy, but *TCX* uses a vertical multilayer approach instead.

In the context of the C cycle foliage, wood and fine roots have to be differentiated, since these tissues differ with respect to storage and turnover rates of biomass. Their parameterization, however, is not easy to accomplish. While longevities of foliage are easy to estimate and vary little, the turnover of stemwood may be smaller by an order of magnitude, but is difficult to determine due to the long lifetime of trees and the stochastic nature of mortality agents (fire, wind or insect pests). Production and turnover rate of fine roots are also difficult to assess, albeit their production supposedly represents a major contribution to total annual net primary production. This is due to the fact that for undisturbed soil systems direct methods to estimate the production of fine roots do not yet exist (Hendricks,

TABLE 3. Climatic input requirements of the reviewed models.

Name	Temporal resolution	Meteorological variables															
		T_{mean}	T_{min}	T_{max}	T_{sd}	T_{soil}	R	R_{sd}	$Corr_{TR}$	Rel. humidity	Cloudiness	Irradiance	Evapotran- spiration	Soil moisture	P_{air}	Wind	CO_2
TEM	1 month	•					•						•				•
MBL-GEM	1 month	•												•			•
CENTURY Forest	1 month		•	•			•					•					
FORCLIM	1 month	•			•				•								
FOREST-BGC	1 day		•	•								•					•
TCX	1 day	•					•						•		•		•

Abbreviations: T_{mean} : mean air temperature; T_{min} : minimal air temperature; T_{max} : maximal air temperature; T_{sd} : standard deviation of air temperature; T_{soil} : mean soil temperature; R : precipitation; R_{sd} : standard deviation of precipitation; $Corr_{TR}$: cross correlation coefficient between T_{mean} and R ; P_{air} : air pressure; CO_2 : ambient CO_2 concentration.

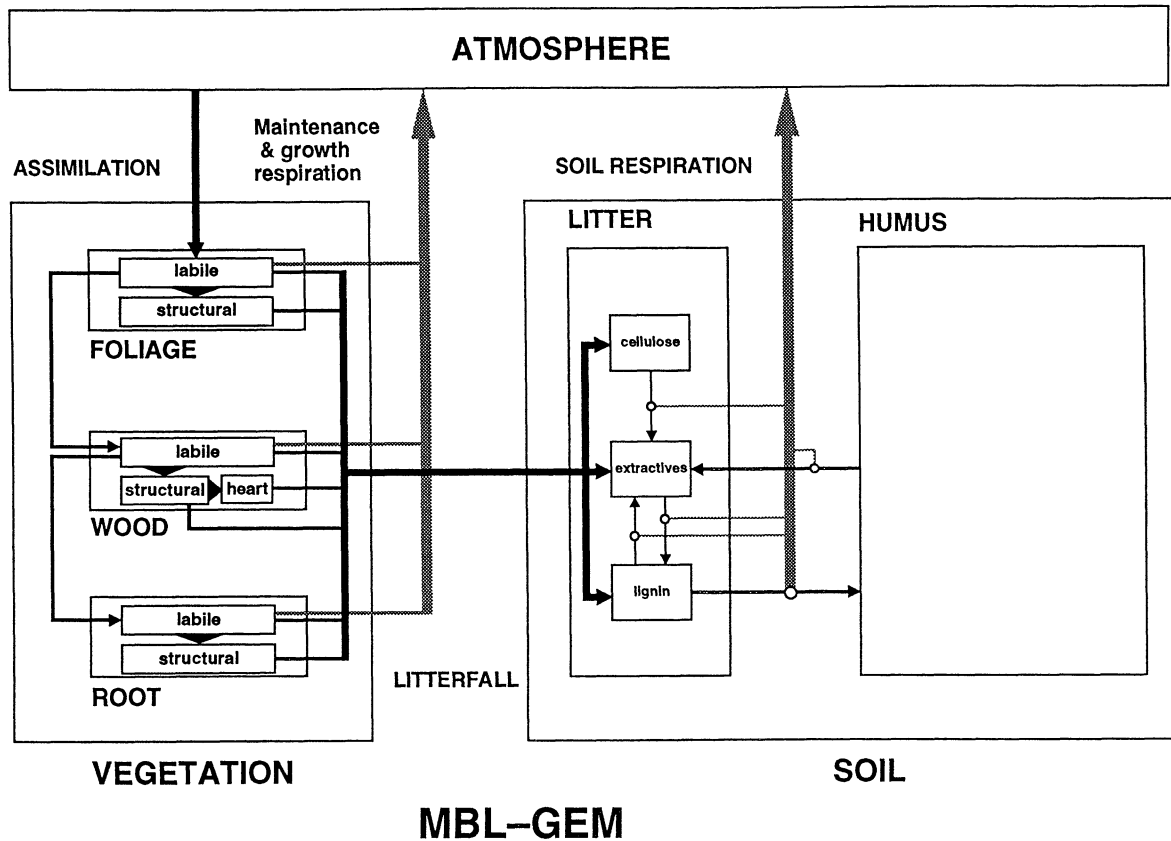


FIG. 3. Carbon pools (boxes) and fluxes (arrows) as modelled in *MBL-GEM*. Note that assimilation is driven by the labile foliage tissue and all litter is lumped and redistributed according to chemical criteria.

Nadehoffer & Aber, 1993; Nadelhoffer & Raich, 1992). It is not clear either whether fine root growth flushes and turnover occur more than once a year.

We analysed the models with respect to the representation of litter and found differences regarding the fractionation scheme and number of litter classes (Table 2). Models such as *FORCLIM* and *TCX* pass on the structure used to fractionate the vegetation compartments to the litter classes (Figs 5 and 7) in order to seize differences in their decomposition rates. (*TCX* introduces four additional compartments for forest floor resulting in seven instead of three litter classes.) *MBL-GEM* and (in part) *CENTURY Forest* redistribute litter into classes according to their chemical composition (Figs 3 and 4).

Different chemical quantities have in fact been shown to correlate with the decay rate of foliar litter and are used as substitutes for litter quality (Meentemeyer, 1978; Melillo *et al.*, 1989; Melillo, Aber & Muratore, 1982). However, there is no universal litter quality index, because litter decomposition depends on qualities which differ among species (Taylor, Parkinson & Parsons, 1989) and plant parts. Edmonds (1987) has reported higher decomposition rates for branches than twigs although their lignin concentration would claim the contrary. For snags and boles we are not aware of any relation between decay rate and litter chemistry. It is therefore questionable to which extent

purely chemical litter classifications can be used to cover the range of decay rates for fine litter (Aber, Melillo & McClugherty, 1990) as well as coarse woody debris (Harmon *et al.*, 1986).

For understanding the transient response of the C cycle in forests SOC is crucial, in particular for soils in the boreal and temperate zones of the northern hemisphere. They contain more SOC in proportion to vegetation than estimated by the global average (Dixon *et al.*, 1994) and are expected to experience the largest shifts in climate change (Houghton, Callander & Varney, 1992). However, many models treat SOC in humified organic matter in an oversimplified way (Table 2). Leaving aside *TCX*, *CENTURY Forest* is the only model distinguishing SOC pools with turnover rates which vary by orders of magnitude. (*MBL-GEM* defines three pools for litter plus young soil organic matter and one for humus; their time scales are, however, not documented.)

Estimating the mean residence time of SOC in the bulk soil with the radiocarbon method suggests a slow turnover of this pool relative to the living vegetation and litter within the C cycle. However, equal ^{14}C mean residence times can originate from one single pool or a combination of more than one pool and result in different fluxes to and from the pool (Trumbore, 1993). This becomes particularly important if the soil experiences a perturbation such as, for

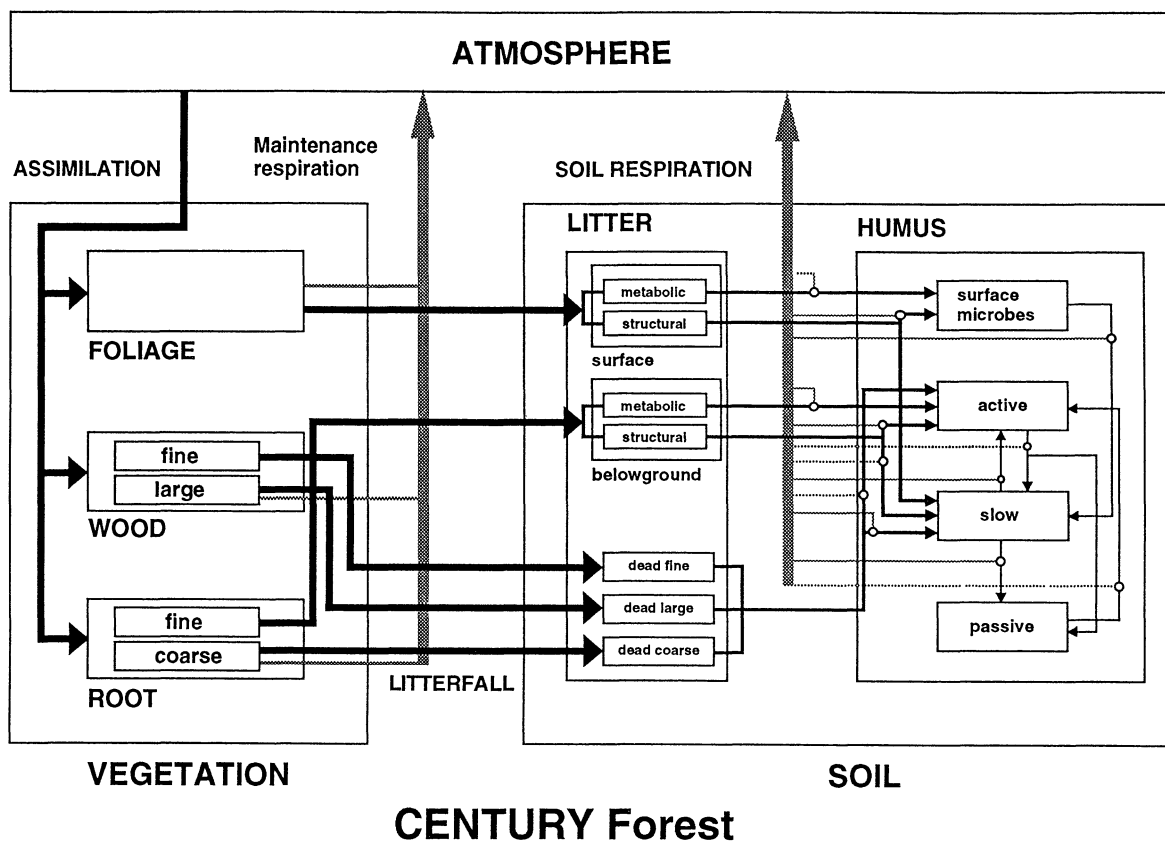


FIG. 4. Carbon pools (boxes) and fluxes (arrows) as modelled in *CENTURY Forest*. Foliage and fine root residues are assigned to chemically defined pools, while woody debris are differentiated based on morphological criteria.

example, a climate change. Isotope studies have in fact suggested the existence of an easily mineralizable C component and a large pool of very stable organic matter in forest and prairie soils (Harkness, Harrison & Bacon, 1986; Balesdent, Wagner & Mariotti, 1988), therefore rejecting the assumption of an uniformly mixed carbon reservoir. The faster pool's turnover rate lies in the range of a few decades to one century depending on the type of soil, whereas the slow part of SOC is slower by one or two orders of magnitude.

It is important to realize that the model structure and the aggregation level used for representation of detritus in particular are likely to affect the system's entire C cycle. In a comparison of C pool models for the terrestrial biosphere, Harvey (1989) has demonstrated that, first, the system's equilibrium is determined by selection of particular pathways (e.g. litter transfer) among the compartments. Secondly, his analysis has revealed that the transient response under climatic perturbations depends on the number of pools. These findings are likely to be transferable to the pool models in the present review. Indeed, to compute steady states we recommend use of a model (e.g. *TEM*) which lumps all green biomass and detritus for reasons of computational expense (A. D. McGuire, pers. comm.), but discourage the use of such models when investigating the transient response of the C cycle in forests. In particular,

the aggregation of all soil organic matter as modelled in *TEM*, *MBL-GEM*, *FORCLIM* and *FOREST-BGC* (Figs 2, 3, 5, 6) results in an overestimate of the turnover of the bulk SOC.

Processes

The models differed with respect to the resolution level with which processes are represented according to the model's particular focus. Plant growth may serve as an example (Table 2). *TCX*, on one hand, discriminates between foliage CO_2 assimilation, growth and maintenance respiration of foliage, wood, and roots (Fig. 7) while *FORCLIM*, on the other hand, determines tissue growth based on incremental growth in stemwood cross-section (diameter at breast height) and allometric relationships (Fig. 5). Since processes are characterized by particular time scales, their incorporation defines the model's temporal resolution, the resolution of driving data (Table 3), its simulation period and last but not least the range of the model's applicability.

Physiological models (*FOREST-BGC* and *TCX*) integrate ecophysiological knowledge at temporal resolutions of hours to days and constitute the basis for deducing more empirical formulations of ecoprocesses. Individual canopy processes (e.g. photosynthesis, transpiration) are modelled

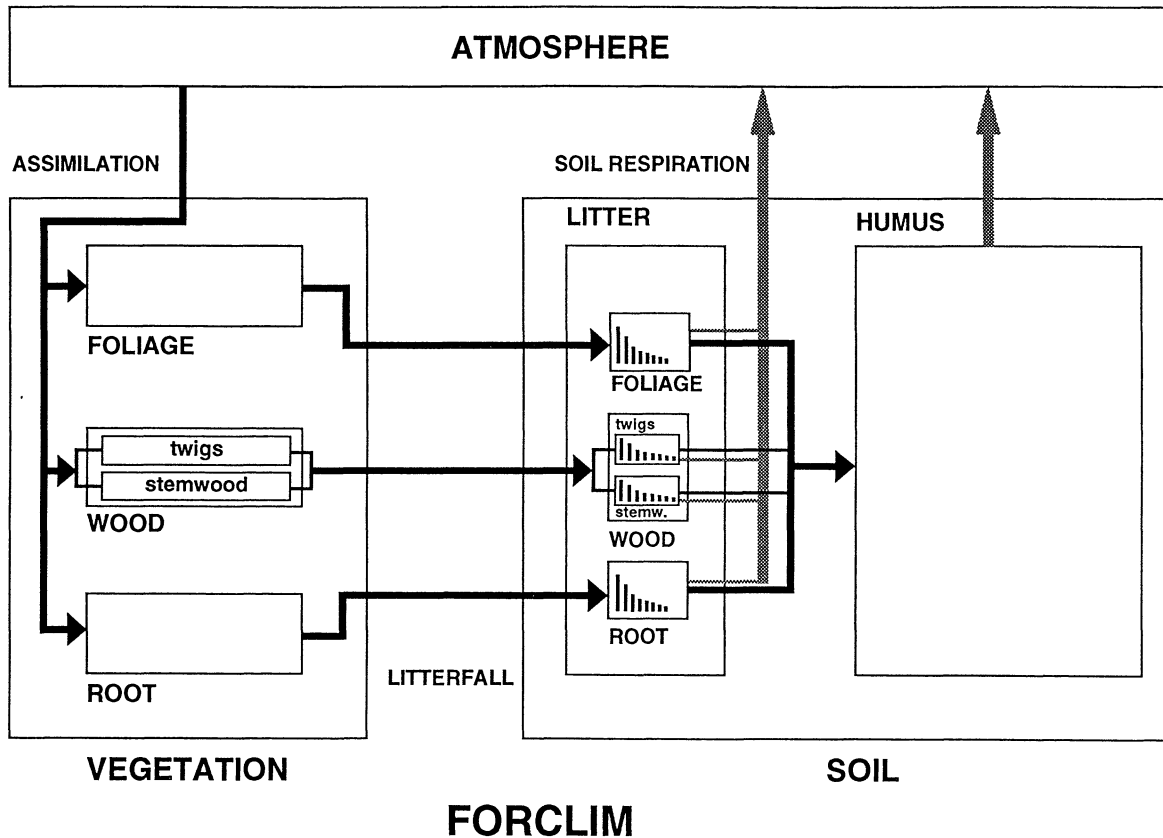


FIG. 5. Carbon pools (boxes) and fluxes (arrows) as modelled in *FORCLIM*. The icon used for litter compartments indicates that decomposition is kept track via litter cohorts. Note that the species-specific character of the plant submodel and the three functional types for foliage litter are not represented in the figure.

explicitly and depend on meteorological variables such as temperature, precipitation, radiation and CO_2 concentration. However, due to the representation of rapidly evolving processes modelled at a high temporal resolution their projections are constrained, in general, to a few decades.

TCX has been designed to study the effects of species-specific differences (e.g. nutrient requirements, growth rate potential, litter quality) on the C balance and has been applied to mature boreal forest ecosystems; *FOREST-BGC*, on the other hand, simulates differences in net primary production and hydrological balance among ecosystems in contrasting climates without species-specific tuning (see 'Site-specific data' column, Table 1). *FOREST-BGC* allows for a spatial extrapolation (with remotely sensed data) through use of leaf area index as a measure of vegetation structure. Its usefulness for analysis of the C cycle is limited, since decomposition of woody debris is neglected and SOC is represented by only one single pool (Fig. 6).

Ecosystem/tissue models (*MBL-GEM* and *CENTURY Forest*) incorporate decomposition in a more detailed way, since the main focus lies on the dynamics of elemental cycles between vegetation and soil. Abstracting from individuals or species, the ecosystem is represented as an association of tissues; ecoprocesses are formulated empirically. Ecosystem/tissue models have to be distinguished on the basis of the time step used (< 1 day v. > 1 month) and

whether feedbacks with nutrient cycling are incorporated (Ågren *et al.*, 1991).

MBL-GEM and *CENTURY Forest* represent explicitly the linkage of the C and N cycles and neglect shifts in species composition. This restricts their application to time spans before the onset of succession or forests where climatic disturbances have not yet led to substantial shifts in community. *MBL-GEM* can be used to explore how CO_2 , temperature and N inputs control ecosystem C storage. It requires a higher amount of site-specific input data (Table 1) to estimate model parameters with a calibration routine than *CENTURY Forest*. The latter simulates the cycling of elements in the soil in all details, thereby also incorporating very slow soil processes (see 'Model Structures'). It distinguishes soil texture and its effect on the cycling of C. Finally, the incorporation of phosphorus (Table 1) enlarges the range of applicability to tropical systems.

Ecosystem/population models operate on similar scales as ecosystem/tissue models, but are species- or individual-oriented. Some of these models have been designed for forest management purposes which are of limited use for addressing the question of C cycling under a changing climate since abiotic forcing is contained implicitly. However, gap-models such as *FORCLIM* simulate forest succession and contain deterministic and stochastic elements

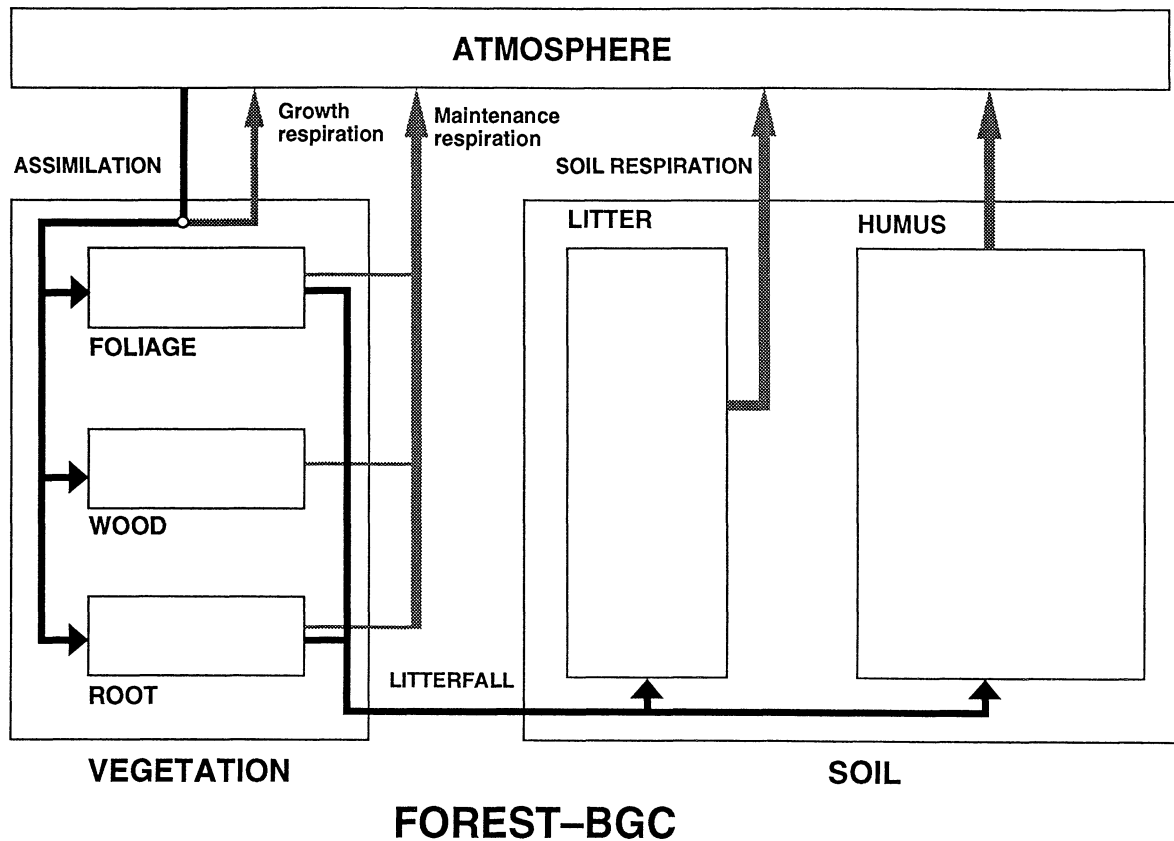


FIG. 6. Carbon pools (boxes) and fluxes (arrows) as modelled in *FOREST-BGC*. The inputs to the decoupled litter and soil pools stem from annual leaf fall and root mortality (Running & Gower, 1991).

which allow expression of their dependence on abiotic factors explicitly.

FORCLIM simulates the inter-species competition for natural resources. It explicitly models abiotic forcing, and feedbacks of soil moisture and *N* availability on plant growth. Among the reviewed models it is the only non-deterministic one, since it contains two stochastic processes, i.e. establishment and mortality of trees. Consequently, 200 runs are needed to estimate reliably model behaviour (Bugmann & Fischlin, 1992).

Global models extrapolate information simulated on a geographical grid to obtain estimates of primary production, litterfall, carbon storage, vegetation distribution and CO_2 soil efflux at the global scale. This approach requires locally referenced information at every grid cell point and climatic data to drive the model in particular. Some of the models are purely statistical (and as equilibrium models are a priori not suited for studying transient responses) while others are mechanistically based.

The global model *TEM* has been designed to estimate the C and *N* fluxes and pools for different biome types. The effects of CO_2 and *N* availability on plant growth have been modelled explicitly and analysed spatially on a grid of 0.5° longitude \times 0.5° latitude. Although formulated as a process-orientated model, *TEM* is limited to predict only the equilibrium states of the system due to its high aggregation (see 'Model structures' and Fig. 2).

Despite the importance of SOC for the C budget and the C cycle decomposition is poorly understood, which is reflected in the wide variety of formulations used in the models (Table 2). Decomposition is generally assumed to be a continuous time, biologically mediated process. In forests it is typically studied via litterbag experiments (Melillo *et al.*, 1989; Aber *et al.*, 1990; Berg *et al.*, 1993) or in agricultural systems with ^{14}C -labelled plant residues incubated under field conditions (Ayanaba & Jenkinson, 1990; Ladd, Oades & Amato, 1981; Sørensen, 1987). Assuming the decrease in organic matter to be proportional to its present amount, a first order kinetic reaction is widely used for its phenomenological description.

Given the continuous time nature of decomposition and the wide spectrum in chemical substrates an arbitrary discretization of the decay continuum is a common modelling approach. An implementation often used to describe decomposition involves several interconnected C pools each characterized by a single decay rate. This model type was first proposed by Jenkinson & Rayner (1977) and a realization of this idea is found in *MBL-GEM* and *CENTURY Forest* (Table 2 and Figs 3 and 4). In contrast to this connected pool model approach, *FOREST-BGC* (Running & Gower, 1991) uses a litter and soil pool which are not coupled to each other (Fig. 6). In *FORCLIM* litter decay of fine litter is kept track of by litter-cohorts (Fig. 5) where each cohort represents the content of a litterbag. When a

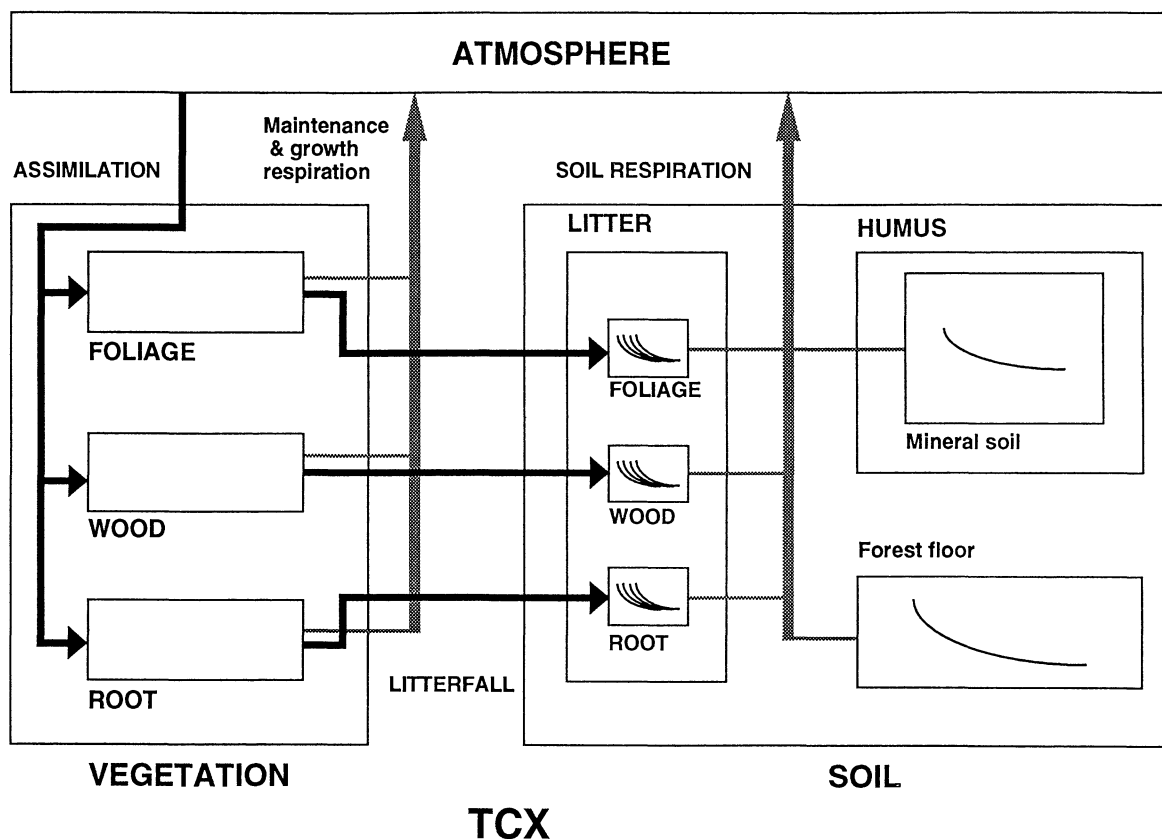


FIG. 7. Carbon pools (boxes) and fluxes (arrows) as modelled in *TCX*. The icon used for decomposition of organic matter refers to the continuum substrate-quality approach. Since *TCX* does not model SOC accumulation in the mineral soil, the uncoupled forest floor and mineral soil pools get no input from decaying litter. Note that the partitioning into four different pools used for the forest floor is not shown.

transition criterion (i.e. a critical C:N ratio) is met, the cohort is transferred to a humified C pool.

More sophisticated is the 'continuum substrate-quality' method introduced by Bosatta & Ågren (1985), which defines litter quality 'as a measure of substrate accessibility expressed through the growth performance of the decomposer community' (Bosatta & Ågren, 1991). Here, decomposition translates to dispersion in litter quality: depending on quality and carbon density distribution, litter is ingested by the microorganisms and later partially returned to the C pool due to microbial mortality; hereby litter quality changes and affects the decomposition rate along the decay continuum. *TCX* uses this formulation for litter-cohorts and the pools of forest floor and mineral SOC, respectively (Fig. 6).

Pool and cohort-pool models are highly application-orientated, whereas the theoretical concept developed by Bosatta & Ågren (1985) tries to explain decomposition by microbial properties. Its limited applicability is mainly due to difficulties in parameter estimation for initial litter quality via an operationally defined quantity and its formulation of a climate dependent microbial growth rate, a difficulty which had to be solved in *TCX*. Note that this model has the ability for humus accumulation since not all litter cohorts

need to decompose completely (Bosatta & Ågren, 1985), but cannot simulate the formation of SOC in the mineral soil.

In contrast, pool and cohort-pool models make direct use of statistical relations between observed meteorological quantities such as air temperature, precipitation, soil moisture and *AET*. The cohort-pool model *FORCLIM* differs from the pool models in its ability to represent shifts in chemistry of decaying litter and their feedback on decomposition rate or the incomplete decomposition of foliage litter reported in long-term litterbag studies (Aber *et al.*, 1990).

To select a particular decomposition model the ease with which its parameterization can be achieved is also to be considered. First, the cohort-concept used for degradation of fine litter in *FORCLIM* and *LINKAGES* (Pastor & Post, 1986) allows for a direct incorporation of measurements as obtained via litterbag studies in forests. To describe the decay of foliar and fine root litter such a model could therefore be favoured over a pool model. Secondly, in forest soils the parameterization of microbial biomass may be difficult despite the conceptual attractiveness of such an approach. This is due to the multitude of methods and their varying suitability under different edaphic conditions (Vance, Brookes & Jenkinson, 1987; Alef, 1993). Among the reviewed models *CENTURY Forest* is the only one

TABLE 4. Technical documentation of the reviewed models.

Name	<i>TEM</i>	<i>MBL-GEM</i>	<i>CENTURY Forest</i>	<i>FORCLIM</i>	<i>FOREST-BGC</i>	<i>TCX</i>
Complete set of model equations	•	•	○	•	○	○
Complete set of initial conditions	•	○	○	•	○	•
Complete set of parameters	•	○	○	•	○	•
Driving data	•	○	•	•	○	•
Computational expense of the model	○	○	○	•	•	○

○ = unpublished feature; • = published feature. A feature is considered as 'published' if all properties and numerical quantities are reported in the reference to reproduce the results produced therein.

which represents surface as well as soil microbes ('surface microbes' and 'active' pool in Fig. 4) explicitly.

Abiotic forcings

The representation of climatic conditions on processes affecting C cycling is of major importance when applying plant-soil models to study climate change. The quantities influencing the ecological processes differ from the standard meteorological observables which are available and are usually used as driving climatic variables. Thus, models generally include abiotic submodels to determine the ecological relevant meteorological quantities (Fischlin, Bugmann & Gyalistras, 1994).

The abiotic models differ with respect to the set of required input data and their temporal resolution (Table 3). All models except the physiological models use climatic input with a monthly resolution. The models with daily resolution also have a finer process resolution and demand more climatic input.

While some of the meteorological requirements, e.g. monthly temperature and precipitation, can be satisfied by standard data sets, other necessary information such as soil temperature and windspeed may not be available routinely on the prescribed spatial and temporal resolution. This restricts the portability of the respective models in space. In view of investigations about the impact of climatic change on ecosystem properties climate scenarios have to be used. To define the abiotic environment characterizing a site, additional information about auto- and cross-correlations of the required variables is needed. Consequently, the expense for creating appropriate scenarios is very high for physiological models such as *FOREST-BGC* and *TCX*.

Although models require a multitude of meteorological variables, temperature and precipitation are thought to act as the key factors regulating both plant-growth and decomposition (Table 3). There are, however, differences among the specific implementations of these quantities as demonstrated below.

First, different operational quantities are used to represent the effect of separate meteorological variables. All models need surface air temperature or some derived quantity (Table 3): considering plant-growth, for example, *CENTURY Forest* uses the simulated monthly soil tempera-

ture to modify the maximum plant growth rate, whereas in *FORCLIM* degree days calculated from air temperature limit the maximum tree growth. Secondly, the models use distinct functional forms to input meteorological variables: surface air temperature enters the calculation of maintenance respiration or *N* uptake in *TEM* and *MBL-GEM*, but the actual shapes of response curves differ.

Finally, the combined effect of warmth and humidity has been implemented differently from model to model. This is seen clearly for the decomposition rates: *TEM*, *MBL-GEM* and *TCX* modify the decay by multiplying it with factors for air temperature and soil moisture. *FOREST-BGC* calculates functions for integrated daily average water fraction and daily temperature degree day summation. They affect decomposition additively, whereas *FORCLIM* expresses the simultaneous effect of warmth and soil moisture on decay by actual evapotranspiration.

Such differences in mathematical parameterizations of climate can have a major consequence on both the system's equilibrium as well as on its transient behaviour (Fischlin, Bugmann & Gyalistras, 1994). This study also showed that differences in model behaviour may be hidden when only applied to a present climate, but may emerge under a changing climate. Similar quantitative comparisons are to be carried out for C cycle models to improve our understanding of the climatic forcing on the functioning of the ecosystem.

Finally, the model system's responsiveness to climatic change may lie within the range of variability inherent to climate scenarios making the interpretation of simulation results questionable. Quantitative model comparisons using standardized climate scenarios are urgently needed to gain insight in these questions, but depend on the free availability of the models.

Documentation

The quality of model documentation differs widely and the authors have not considered a common standard when describing their models (Table 4). Descriptions sometimes even lack a complete set of model equations: the part for *CENTURY Forest* which simulates primary production is not yet published (Sanford *et al.*, 1991); the allocation model of *FOREST-BGC* is not fully documented; or *TCX*

does not describe explicitly how the dynamics of the forest floor is modelled. Note that, even if documented as differential equations, time-discrete difference equations may actually have been used for implementational purposes or even two-time scales are used simultaneously (*FOREST-BGC* and *TCX*). Initial conditions for the model's state variables are sometimes missing partially (Running & Gower, 1991) or completely (Sanford *et al.*, 1991; Rastetter *et al.*, 1991).

Half of the model descriptions, i.e. *TEM* (Raich *et al.*, 1991), *TCX* (Bonan, 1993) and *FORCLIM* (Bugmann, 1994) contain all parameter values, whereas publications of *MBL-GEM* lack any information on parameter values. *CENTURY Forest* lacks information for allocation coefficients, the lignin content of plant residues, the death rates of branches or the decay rates of branches and coarse roots (Sanford *et al.*, 1991). When applying *FOREST-BGC* to contrasting environments across geographical space Running & Coughlan (1988) and Running & Gower (1991) have reported the parameters for some but not all sites.

Plant–soil models have reached a level of complexity which makes concise and complete model descriptions imperative. For instance, the transfer of corresponding parameters from one model to the other is often impossible or can lead to considerable deviation in model behaviour, even among similar models. The reproduction of simulation results or new applications are totally prevented if not all model equations, initial conditions, parameter sets and driving data are fully and precisely published (a plea which we wish to be also heard by journal editors).

CONCLUSIONS

The present review revealed that time frame, forest type and climate scenarios vary widely from model to model. In addition, model comparisons were particularly hampered due to differences with which the models plus their behaviour have been published. Since climate change affects ecosystem properties on different scales both in time and space, a specific model's applicability differs greatly depending on the user's main interest in the types of processes, system components and system responses.

Model applicability. The following assessments of the models' suitability for climate change application were derived from general properties as well as from the more ephemeral characteristics of the model versions as described in the literature.

Physiological models are useful tools to explain the functioning of plant communities from ecophysiological mechanisms (e.g. direct effects of CO₂ on plant production) and important to deduce empirical representations of eco-processes. However, their high requirement on climatic input data conflicts with the high costs and uncertainties in generating climate scenarios and makes them of limited use for analyses of the response of the C cycle in forests in a changing climate.

- *TCX* is suited to analyse the species-specific control mechanisms of the C balance and the dynamics of

detrital organic C over years to decades *but* because of its high resolution and input-free forest floor and humus pools, of little use over larger time spans.

- *FOREST-BGC* is suited to simulate the hydrological cycle and primary production in contrasting climates without species-specific tuning over large areas and time spans of a few decades *but* is of limited use to estimate the transient response of the C cycle, due to the coarse compartmentation of the SOC dynamics.

Ecosystem/tissue models are particularly suited to study elemental fluxes between plants and soils abstracting from individuals or species and use empirical formulations of eco-processes. They are apt for climate change applications in particular if they operate with a monthly to annual timestep and if feedbacks between plant growth and nutrient availability are incorporated.

- *MBL-GEM* is suited to analyse the response of C storage to changes in CO₂ concentration, temperature *but* not precipitation over several decades; due to incomplete documentation its ability to simulate the transient response of the C cycle could not be assessed properly.
- *CENTURY Forest* is suited to make projections of the transient response of the forest's C cycle under changing temperature and precipitation over several centuries *but* in its present form does not simulate direct effects of CO₂ on plant production.

Ecosystem/population models operate on similar process and time scales as ecosystem/tissue models but simulate the competition of species or individuals for natural resources. Only a few models of this class such as *FORCLIM* are really suited for applications to climate change since many of the others have been designed primarily for forest management purposes or to study succession in a constant climate only.

- *FORCLIM* is suited to simulate the species composition and succession in forests along climatic gradients in space and time over centuries *but* does not allow direct assessment of effects of CO₂ on plant production and the transient response of the C cycle; the latter is due to the coarse compartmentation of SOC dynamics.

Global models offer the advantage to predict the global vegetation patterns and C balance by extrapolating grid-cell specific information such as soil types, topography and climate conditions. However, they accomplish this only at the expense of vegetation-specific information; moreover, even if a process-based approach is used, these models can produce only the system's steady state.

- *TEM* is suited to assess the equilibrium fluxes and pools of the interrelated cycles of C and N globally on a resolution of 0.5° longitude × 0.5° latitude *but* of limited use to study quantitatively the transient response of the global C cycle.

SOC and the C cycle. SOC is crucial in understanding the transient response of the C cycle in forests. Its dynamics involve processes whose time scales differ by

one or two orders of magnitude. Discarding the slowly evolving SOC processes does not only restrict the model's applicability to a shorter time span but does indeed change the transient behaviour of the entire system from the start. The pool models which lump all SOC (*FORCLIM*, *FOREST-BGC*, *TEM*) are therefore of limited use to assess the transient response of the local C balance in forests.

The different approaches in modelling decomposition of litter and humification of soil organic matter compare as follows:

- Pool models represent the most direct approach to discretize the decay continuum using morphological, chemical and functional criteria to define the pools disregarding changes occurring during the discrete stages. Pool models have been successfully used for predicting SOC levels at regional scales.
- Cohort-pool models allow for direct parameterization of fine litter decomposition from litterbag studies and keep track of individual changes and their potential feedbacks on the decay rate. They have proved to be useful in simulating litter decay at regional scales.
- Continuum models incorporate the idea of the continuous time decomposition process and keep track of changes in litter quality for every litter entity. They have not yet been applied to study decomposition at a regional scale.

Recommendations. *MBL-GEM*, *CENTURY Forest*, and *FORCLIM* appear to be best suited to study the transient response of the C cycle in forests at the ecosystem level. However, for such an application, we propose, first, to carry out the following minor improvements to the listed models:

- Add a second humus pool to the soil submodel of *FORCLIM* to adequately represent the non-living organic C.
- Drive *MBL-GEM* by climate parameters so that soil moisture can be determined from standard meteorological data sets.

Recommendations for *CENTURY Forest* are currently not possible, since they depend on the availability of a complete documentation of its plant production part as well as on the model's application within climate change simulation experiments.

Since system-theoretical analyses of most of the reviewed models are currently not available, scientific interpretations of simulation results have to be considered with care. This is true, in particular, for model applications under climate change since the sensitivity of single ecoprocesses or of the whole system may differ widely depending on the chosen parameterization of the climate (Fischlin, Bugmann & Gyalistras, 1994).

We therefore recommend sensitivity analyses of the transient response with respect to initial conditions, the system structure and climate parameterization scheme as well as investigation of the steady states and their stability. Furthermore, inter-model comparisons using present condi-

tions and standardized climate scenarios should be set up providing a check for consistency of process formulations across the models.

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