LINEAR ANALYSIS OF SOIL DECOMPOSITION: INSIGHTS FROM THE CENTURY MODEL

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Abstract. All terrestrial ecosystem models track the decay of soil organic matter (SOM). Most current models use SOM modules that closely follow the Century model, a powerful but complicated model of decomposition and other terrestrial ecosystem processes that was originally designed for temperate grasslands but has since been extended to many terrestrial ecosystems. Using the linearity property of Century's SOM model, we can simplify it to a set of differential equations with little loss of generality. The simplified model can estimate the equilibrium state of the Century model in closed form, or, using a numerical algorithm, can reproduce its seasonal patterns; it also gives us a framework for making SOM models less complex and producing parsimonious, statistically defensible models of decomposition processes in terrestrial ecosystems.

Key words: carbon dynamics; decomposition; ecosystem; model; process; simplification; terrestrial.

Introduction

One of the largest research areas in applied ecology is the effort to determine the effects of anthropogenic change on terrestrial ecosystems, and in particular to understand and predict the feedbacks between terrestrial ecosystems and global climate, in order to estimate the climatological and biological effects of human activities on a global scale over the next century (Pastor and Post 1988, Ågren et al. 1991, Raich et al. 1991, Rastetter et al. 1991, McGuire et al. 1993, Melillo et al. 1993, Ojima et al. 1993, Potter et al. 1993). Terrestrial ecosystems influence climate in many ways (Sellers et al. 1997): through feedbacks in the hydrological cycle (Schimel et al. 1991, Pollard and Thompson 1995), through changes in albedo (Bonan et al. 1992) and in the atmospheric boundary layer (Sellers et al. 1986), and through control of the carbon cycle (and hence of radiative forcing) by plant production and decomposition. This paper focuses on the carbon cycle; because of the large carbon inventories stored in terrestrial plants and soil, small proportional changes in growth and decomposition processes could have far-reaching effects on atmospheric CO_2 concentrations and climate.

Soil organic matter (SOM) dynamics affect the carbon cycle in two ways. First, SOM contains essential plant nutrients such as nitrogen, so its dynamics regulate the availability of nutrients to plants and hence can limit net primary productivity (NPP). Second, SOM contains large quantities of carbon—globally, $\sim 1.5 \times 10^6$ Mg (1 Mg = 1 metric ton) or twice as

much as is currently contained in the atmosphere (Houghton et al. 1990)—so small changes in the size of the SOM pool can have important climatic effects. Terrestrial ecosystem models include SOM modules for both reasons, although models such as CASA (Potter et al. 1993) that use measured rather than modeled NPP model only the fate of carbon and not the dynamics of nutrient limitation.

This paper focuses on the Century SOM model, which has become a standard for soil carbon–nutrient modules in global ecosystem models (Rastetter et al. 1991, Comins and McMurtrie 1993, Potter et al. 1993, Kirschbaum et al. 1994). Century is an ecosystem model originally designed for temperate grasslands but since extended to many biomes worldwide that has been remarkably successful in simulating the steady-state values and seasonal patterns of plant production and carbon storage around the world (Parton et al. 1987, 1988, 1993). Century tracks both carbon and nutrients, and we will analyze the full model; however, we will focus on the dynamics of the carbon pool rather than the details of nutrient limitation, which have been studied elsewhere (Rastetter et al. 1992, Comins and McMurtrie 1993, Comins 1994, McMurtrie and Comins 1996).

This paper analyzes the mathematical structure of Century's SOM model, drawing new conclusions about the behavior of decomposing organic carbon, and showing that we can simplify Century-like models drastically while preserving their essential dynamics. We also discuss some of the implications of the mathematical structure for parameterizing terrestrial biospheric models and using them to predict future terrestrial carbon storage.

We use a somewhat atypical approach to ecosystem

modeling. Normally, modelers add terms or compart-
ments based on common sense in order to improve
prediction accuracy or account for perceived shortcom-
ings of the models; in this paper we focus on analytical
and statistical tractability, which modellers may not
consider as carefully. Our approach provides a clearer
picture of the really important terms and interactions
in the model. Serendipitously, the CENTURY model has
a very convenient analytical structure, despite having
been built in the normal pragmatic fashion. Almost all
of the biology described by the CENTURY model can
be redescribed in an analytically simple form by treat-
ing some effects (such as water and temperature) as
external forcing terms and by averaging some slowly
varying terms in the model. We hope that some of the
insights achieved this way will be useful to designers
and users of future ecosystem models.

The first section of the paper describes the overall
structure of the CENTURY model, focusing on the flows
of plant and soil carbon and nitrogen that will be the
subject of the rest of the paper, but also describing
linkages between different parts of the model. The sec-
ond section discusses the detailed structure of the sub-
model that regulates the gradual decay of carbon out
of the terrestrial biosphere and back into the atmo-
sphere as respired CO_2, showing that under most con-
ditions it is equivalent to simple fractionation and first-
order decay of plant-produced organic carbon; the next
section analyzes CENTURY's coupled plant–soil dynam-
ics. The final section discusses the simplification and
parameterization of large-scale ecosystem models in
light of our results.

OVERVIEW OF THE CENTURY MODEL

CENTURY tracks the quantities of carbon and nutri-
ents in plant tissues, litter, and soil organic matter
(SOM) pools (Fig. 1a). All material moves among pools
in the model by linear transfers (flows proportional to
the amount of material in the originating pool). Even
though these flows depend on soil temperature, mois-
ture, and texture and other factors in complicated ways,
this underlying linearity makes it possible to analyze
the model mathematically. Although CENTURY's orig-
inal scope was the analysis and prediction of carbon
and nitrogen cycling in temperate grasslands, it now
includes modules for forests, savannahs, and agro-eco-
systems; we only consider the original grassland model
in this paper, although many of our points are generally
applicable to the "global" version of CENTURY, as well
as to the wide variety of ecosystem models that share
its SOM module and general structure. Potential plant
production in CENTURY is the product of humped func-
tions of soil temperature and moisture, which are in
turn determined from air temperature (modified by
plant cover) and precipitation (modified by the dynam-
ics of a hydrological model, including feedbacks from
plant cover and plant uptake). In recent versions of the
model, soil texture also modifies potential plant pro-

duction. The actual rate of plant production per unit
time is the minimum of the potential rate and the actual
rate allowed by available amounts of nutrients (nitro-
gen, phosphorus, sulfur, and potassium); this paper, like
most biogeochemical models for global change, fo-
cuses on nitrogen limitation.

Death and deposition of plant material vary accord-
ing to season and temperature; plant litter is divided
into structural and metabolic pools according to its car-
bon to nutrient ratio (a function of available nutrients)
and lignin content (a function of soil moisture).

Once plant material enters the organic matter pools,
it circulates (by linear transfers, as described above)
among the pools until eventually all of the carbon has
been respired and all of the nutrients have been min-
eralized (transferred back to the available nutrient
pool), except for leached material. The rates of transfer
among pools are modified by soil texture. The basic
rates of decomposition are fixed; however, all transfers
and decomposition speed up and slow down according
to a single decomposition factor computed from soil
moisture and texture. As carbon is respired or trans-
ferred to another compartment, excess nitrogen (that
which exceeds the C:N ratio of the receiving com-
partment) moves into the mineralized pool.

Although this overview is specific to the CENTURY
model, many of the general points (particularly those
about SOM dynamics, as opposed to plant production
and uptake) also apply to other ecosystem models built
on the foundation of the CENTURY SOM model, as well
as to the Rothamsted soil turnover model and its de-
scendants (Jenkinson 1990, Post et al. 1996).

We will start by considering the flow of a single
"cohort" of carbon, for example one month's worth of
litterfall and dead root material, as it gradually passes
from one soil compartment and is eventually (over an
extremely long time scale) entirely metabolized by mi-
crobes and turned into carbon dioxide.

SOIL CARBON DYNAMICS

Basic description

In CENTURY (and the Rothamsted model), carbon in
litter and microbial pools decays immediately (con-
verting into CO_2 and leaving the SOM pool) or trans-
ferring to lower, slower decomposing compartments
(Fig. 1b). Carbon appears to cycle back and forth
among the lower pools (microbes, slow SOM, and pas-
sive SOM). A single cohort of carbon enters the system
as metabolic and structural litter from roots (below
ground) and standing dead plant material (above
ground); it then flows linearly through and around the
SOM system, with rates proportional to the amount in
each of eight compartments, until all carbon in the
cohort has been metabolized into CO_2 by the action of
soil microbes. The compartments in the SOM model
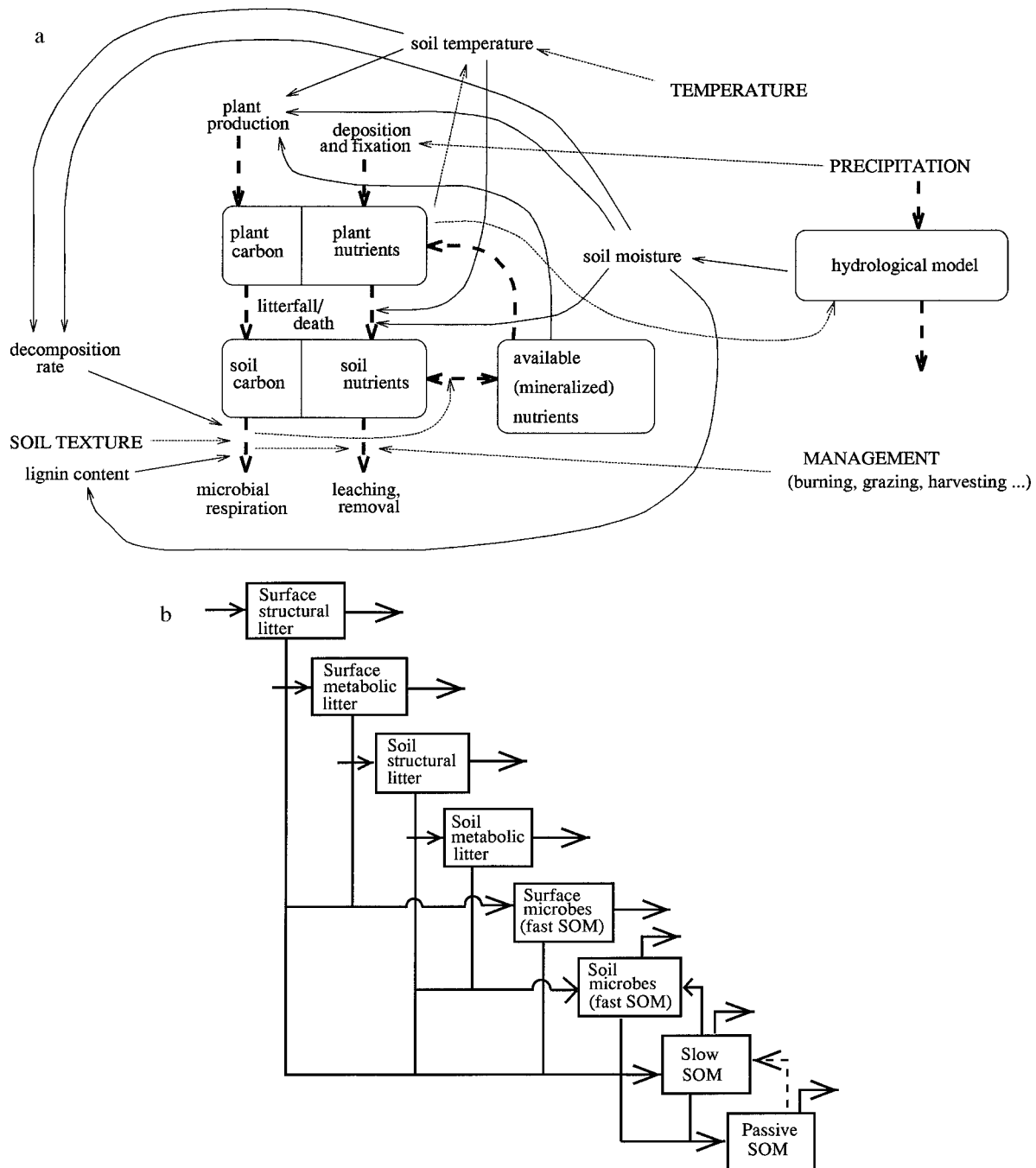represent different fractions of soil carbon that decay

FIG. 1. Schematic views of the CENTURY model. (a) Overview of the CENTURY model. Carbon and nutrient submodels are shown as two halves of divided boxes. Heavy dashed arrows show flows of material (water, carbon, or nutrients) between submodels; solid arrows show other rate-determining connections. (b) CENTURY SOM (soil organic matter) carbon model. The order of compartments emphasizes the main direction of flow from litter pools, to microbial pools, to slowly decomposing pools. The dotted arrow from the passive to the slow pool represents a very small flow.

at different rates (Parton et al. 1987). The flow rates among SOM compartments are determined by soil texture, and those between litter and SOM compartments determined by C:N ratios and structural lignin content (which ultimately depends on annual precipitation).

The overall decay rate is governed by soil moisture and soil temperature, which are combined in a single decomposition factor.

A compact mathematical description of the linear carbon dynamics in CENTURY is given by

TABLE 1. List of symbols. All vectors (e.g., **x**) take subscripts $i = 1 \ldots 8$ for different decomposition compartments; matrices (**X**) take subscripts $i = 1 \ldots 8, j = 1 \ldots 8$.

Symbol	Description (units)
$\mathbf{C}(t) = \{C_i\}$	carbon in CENTURY SOM pools (g C)
$C_{\text{tot}}(t)$	total carbon (g C)
$\delta(t)$	decomposition factor
$\mathbf{M} = \{m_{ij}\}$	proportional carbon flows from SOM pool j to i (yr^{-1})
$\mathbf{c}(t) = \{c_i\}$	carbon in diagonalized SOM pools (g C)
$\varepsilon = \{\varepsilon_i\}$	carbon loadings into diagonalized SOM pools
$\mathbf{\Lambda} = \text{diag}(\lambda_i)$	diagonalized flow matrix (decay eigenvalues) (yr^{-1})
$\tau(t)$	decay time (year)
$\mathbf{E}$	normalized eigenvector matrix
$\gamma = \{\gamma_i\}$	C:N ratio of CENTURY SOM pools
$\mathbf{N}(t)$	nitrogen in CENTURY SOM pools (g N)
$\mathbf{M}' = \{m'_{ij}\}$	proportional nitrogen flows from SOM pool j to i (yr^{-1})
$\mathbf{n}(t) = \{n_i\}$	nitrogen in diagonalized SOM pools (g N)
$\varepsilon' = \{\varepsilon'_i\}$	nitrogen loadings into diagonalized SOM pools
$N_{\text{m}}(t)$	mineralized nitrogen (g N)
v_{g}	volatilization fraction from gross mineralization
$\mathbf{G}(t) = \{G_i\}$	gross mineralization (CENTURY pools) (yr^{-1})
$\mathbf{G}'(t) = \{G'_i\}$	gross mineralization (diagonalized pools) (yr^{-1})
r_i	fraction of carbon lost from box i that is lost by respiration
F_{ij}	fraction of unrespired material flowing from i to j
v_{e}	volatilization rate from mineralized pool (yr^{-1})
$n_f(t)$	nitrogen fixation rate (g N/yr)
$\rho(t)$	water and temperature-limited plant growth rate (g C/yr)
γ_{p}	average C:N ratio of new production
f_{av}	proportional nitrogen uptake rate of plants (yr^{-1})
a	fraction of total plant growth above ground
$\mu_{\text{r}}(t)$	death rate of roots (yr^{-1})
$\mu_{\text{s}}(t)$	death rate of shoots (yr^{-1})
μ_{d}	turnover rate of standing dead material (yr^{-1})
S	carbon in shoots (g C)
D	carbon in dead aboveground plant material (g C)
R	carbon in roots (g C)
$\varepsilon'_{\text{r}}(0) = \{\varepsilon'_{\text{ri}}(0)\}$	root nitrogen loading to diagonalized pools
$\varepsilon'_{\text{s}}(0) = \{\varepsilon'_{\text{si}}(0)\}$	shoot nitrogen loading to diagonalized pools

$$\frac{d\mathbf{C}}{dt} = \delta(t)(\mathbf{MC}) \qquad (1)$$

where **C** is the vector of carbon in each compartment, $\delta(t)$ is the temperature- and moisture-dependent decomposition factor, and each element m_{ij} of the transfer matrix **M** gives the proportional rate at which material from compartment j flows to compartment i (see Table 1 for a complete list of symbols). Linear systems are dynamically and analytically straightforward. The behavior of the SOM model in particular is determined by the eigenvalues λ_i of the transfer matrix (which represent the decay rates in homogeneous pools made up of linear combinations of the original pools) and the loadings ε_i, fractions of deposited plant material that go into each of the homogeneous pools. We obtain the eigenvalues by standard linear algebra; we determine the loadings by converting the fractions of plant material deposited in each litter compartment into fractions in each compartment in the diagonalized model (formally, multiplying the input vector by the transposed eigenvector matrix). Appendix A gives technical details.

Since the effects of soil temperature and moisture on the system affect all the flows equally, the solution is a simple exponential, modified by changes in the decomposition rate, $\delta(t)$; warm, moist soil increases δ and speeds up decomposition. The total decomposition potential, $\tau(t)$, is the integral of the decomposition factor over time:

$$\tau(t) = \int_0^t \delta(t)\,dt. \qquad (2)$$

In terms of the diagonalized model, the dynamics of an entire cohort of carbon are a sum of simple exponentials:

$$C_{\text{tot}}(t) \equiv \sum_i C_i(t) = C_{\text{tot}}(0) \sum_i (\varepsilon_i e^{\lambda_i \tau(t)}). \qquad (3)$$

Because the SOM model represents decay (carbon enters the system in the litter pools and decreases continuously), the real parts of all of the eigenvalues must be negative. In addition, since the sum of the loadings adds up to one, because they represent the fractionation of deposited carbon, at least one of them must be positive. Within these constraints, there are three possible qualitative types of behavior that depend on the nature of the eigenvalues and loadings. If the system has complex eigenvalues, material cycles around through the boxes (Fig. 2a); if the system has all real eigenvalues with some negative loadings, then material experiences transfers through successive boxes (Fig. 2b); if the system has real eigenvalues and all positive loadings, then material experiences pure first-order decays at a variety of rates (Fig. 2c).

The dynamics of the CENTURY model (Fig. 1b) appear to involve cycling and serial transfers (Fig. 2a, b). For a wide variety of conditions, however (Parton et al. 1993), it actually has real eigenvalues and positive loadings, corresponding to a set of pure decays (Fig. 2c). Fig. 3 shows that, for a range of data from 34 SCOPE sites around the world (a total of 272 carbon pool decay rates and loadings), there is no cycling and only five pools have negative loadings representing serial transfer. Similarly, SOM in the five-pool Rothamsted model (Jenkinson 1990) apparently cycles between fast and slow pools, but for the parameters given by Parshotam (1996) all the eigenvalues are real and all the loadings are positive.

a) Complex eigenvalues

b) Real eigenvalues,
   positive and negative
   coefficients

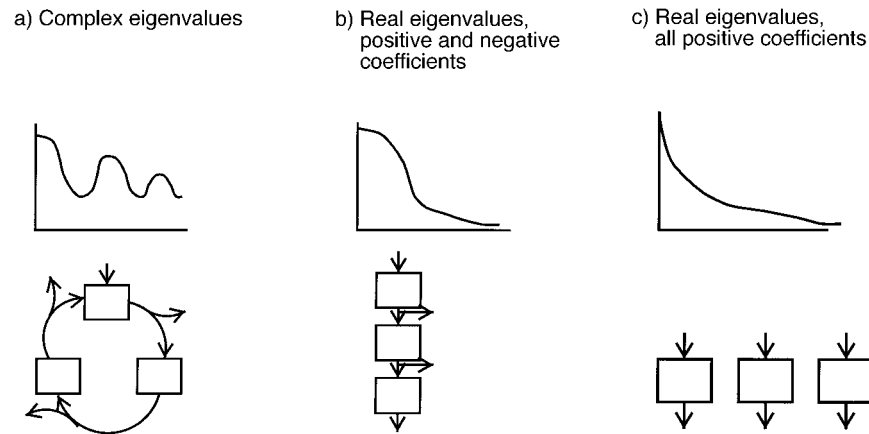c) Real eigenvalues,
   all positive coefficients

FIG. 2. Dynamical possibilities of a linear decay system: (a) damped oscillations; (b) serial transfer; (c) pure decay.

The pure-decay model implies that every particle of carbon in the CENTURY model is processed just once, decomposing completely in the process. The CENTURY SOM model thus represents a special case of the model suggested by Bosatta and Ågren (1991a), where carbon can be either metabolized or excreted and returned to the system in a more recalcitrant (slower decomposing) form. In CENTURY, which has established its ability to predict the behavior of real ecosystems (Parton et al. 1987, 1993), and whose SOM module is the de facto standard for global ecosystem models, the excretion process is missing, suggesting that all the complicated soil processes contributing to humification need not appear in a model of gross carbon cycling. Humification and other soil processes making organic carbon

more recalcitrant are obviously real and important, but for the purposes of modeling carbon accumulation we can partition incoming carbon into different pools instantaneously, probably because the time scales involved in humification and other recycling processes are short relative to the lifetime of slow and passive soil carbon.

The CENTURY SOM model, and the Rothamsted model, are not only representable as a diagonal system (with immediate fractionation and first-order decay), they are nearly diagonal already. Even though the pools of the diagonalized model are in general arbitrary linear combinations of the carbon pools in the CENTURY model, in practice each pool in the diagonalized model is largely derived from a single CENTURY pool, so that

○ structural litter
△ metabolic litter
+ surface microbes
▽ soil microbes
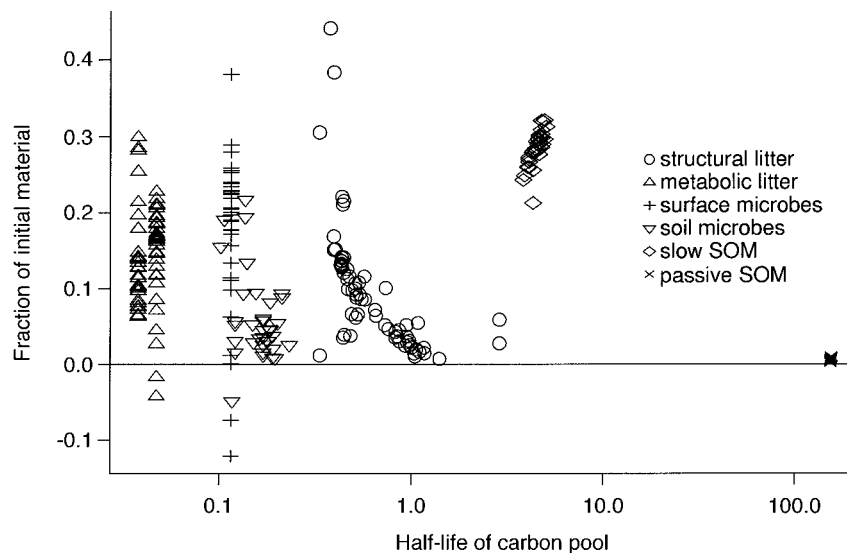◇ slow SOM
× passive SOM

FIG. 3. Decay rates (shown as half-lives) and loadings for 34 SCOPE sites around the world, determined by calculating the eigenvalues and eigenvectors for the soil texture, precipitation, and C:N ratios at each site. The horizontal axis shows the base decomposition half-life [$\log_2(e)/\lambda$; based on a decomposition factor of 1] for each carbon pool; the vertical axis shows the fraction of each incoming cohort of carbon in each pool (negative values represent serial transfers as in Fig. 1b). The passive pool appears as a tight cluster near (100, 0); the quantity and half-life of passive material vary little between sites.

the diagonalized pools are still identifiable with pools in the original model (Fig. 3). Most of the pools in the diagonalized model have decay constants exactly equal to their counterparts in the original CENTURY model. The slow SOM pool's diagonalized equivalent does have a significantly different decay rate from the original slow SOM pool; there is enough flow between the slow and fast pools that the homogeneous pool in the diagonalized model represents a mixture of slowly and quickly decaying material. However, the eigenvalues of both the fast and slow pools are nearly linear functions of soil texture. Therefore, the decay rates for the SOM model can all be computed directly from texture and rainfall (which determines structural lignin content in the model and hence the decay rates of the structural litter pools) and the decomposition factor.

EXTENDING THE CARBON MODEL

Understanding the dynamics of carbon flows in CENTURY is sufficient to simplify a model like CASA (Potter et al. 1993), where plant production and carbon and nutrient deposition are all determined by remote-sensing information that is independent of the model dynamics. More ambitious models such as TEM (Melillo et al. 1993) or CENTURY itself, which attempt to predict plant production based in part on available soil nutrients, also incorporate nutrient dynamics.

Plant–N model

Since the dynamics of nutrient mineralization are entirely determined by the dynamics of its associated carbon in the CENTURY model, we can derive a nitrogen model that ignores the explicit dynamics of carbon and retains only the flows between nitrogen in plants, soil nitrogen bound to carbon, and soil nitrogen in an available (mineralized) form. In CENTURY, the C:N ratios of different pools are allowed to fluctuate within bounds according to the amount of nitrogen flowing into the pool; we will fix the C:N ratios at an average value (C:N ratios were static in the original version of the CENTURY model [Parton et al. 1987]). With this assumption, the equations for carbon flow can be converted directly (with a few terms for the details of nitrogen "overflow" from source pools to receiving pools, volatilization of free nitrogen, and possible immobilization of mineralized nitrogen by microbes; see Appendix B) to equations in terms of nitrogen flow.

The equations of nitrogen transfer from the soil pools to the mineralized pool closely parallel the carbon decay equation, and depend similarly on the decomposition factor. The nitrogen model, however, is a closed system (excepting atmospheric deposition and volatilization) that includes the nitrogen contained in plants. Flows in the nitrogen model depend on the mineralization rate (determined by the decomposition rate, which is in turn a function of soil moisture and temperature), potential plant production (determined by different functions of moisture and temperature), and

plant death and deposition (determined by temperature, moisture, and season). Plant production is the minimum of the water- and temperature-limited production and the nutrient-limited production; thus, the full nitrogen model is only piecewise linear. Starting at the beginning of the growing season (when, for the Great Plains sites originally modeled by CENTURY, growth is usually water and temperature limited), the system is linear with an input rate depending on soil moisture and temperature as long as there is enough mineralized nitrogen available. As soon as the mineralized nitrogen pool falls below the level required to sustain plant growth at the maximum water- and temperature-limited rate, the system changes over to nitrogen-limited growth; in this regime, the nitrogen system's dynamics are self-determined because growth is regulated by nitrogen levels. Nitrogen-limited growth continues until the end of the growing season or until the temperature and moisture drop enough to return the system to water- and temperature-limited growth.

Equilibrium solutions

Because of the external forcings of temperature, precipitation, and seasonal plant growth, there is no analytical equilibrium solution for the nitrogen model. If we simplify the external forcings by taking the average annual values of all the time-varying parameters (decomposition and production rates, root and shoot turnover, and nitrogen deposition), we can calculate an equilibrium solution (Appendix C). We calculate the water-limited and nutrient-limited equilibria for plant production and determine which one actually holds given the equilibrium amounts of available nitrogen in the system.

Fig. 4 compares the long-term annual dynamics of the nitrogen pools in the CENTURY model using the Central Prairie Ecological Research (CPER) site parameters with the equilibrium dynamics of the plant–N model using the same parameters. The overall fit is quite good; however, the quality of the match between CENTURY and its equilibrium solution is only meaningful when put in the context of some prediction problem. How well does the full time-varying model match the data? Are the annual variations, or the long-term average behavior, of interest in the particular modeling context?

The equilibrium solution has several potential advantages over the full CENTURY model. First, one can easily look at the effects of different parameters on the equilibrium values, over the entire feasible parameter space, without exhaustive runs of the model.

Second, global ecosystem models typically "spin up" each of many grid cells to a long-term equilibrium state at current climate parameters before testing the effects of, e.g., anthropogenic climate changes. Spin-up can require several thousand years of model solution (because the longest half-lives are more than a century) and a nontrivial amount of computer time. The equi-
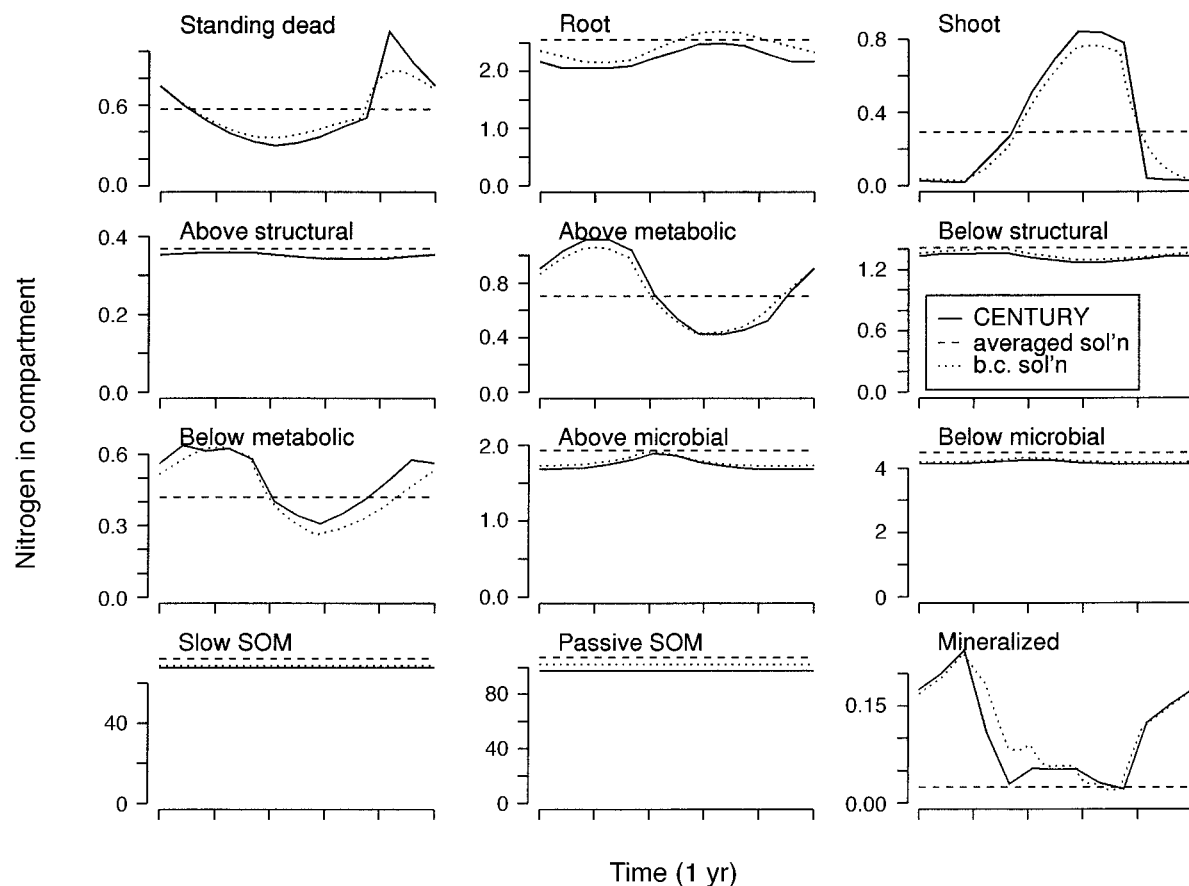
FIG. 4. Output of the CENTURY equilibrium equations (Appendix C) and boundary-condition solver compared with long-term stable seasonal variation in the real model (CENTURY model run for 5000 yr). Each subfigure shows the nitrogen content of each nitrogen pool in the model over the course of 1 yr. Abbreviations: sol'n = solution; b.c. = boundary condition.

librium solution can immediately take the model to a state very close to the true long-term annual cycle, with a trivial amount of computation.

Boundary-condition solutions

To get even closer to the long-term annual cycle (at the expense of analytical tractability), without running the model for thousands of years, one can take the simplified model and use standard boundary-condition methods (Press et al. 1994) to find the long-term annual pattern of all nitrogen pools: at a particular site, what values of all of the state variables at the beginning of the year will lead to a stable annual cycle (such that they all return to the same values at the beginning of the next year)? Starting at the (analytically determined) long-term equilibrium solution, the simplified model typically took fewer than ten iterations to converge—a total of 130 model years' worth of numerical integration (there are 12 state variables, requiring 13 separate 1-yr integrations for each iteration), seven times faster than a brute-force 1000-yr spin-up run.

The boundary-condition solution matches the full CENTURY model quite well. The solution shown in Fig. 4 still uses fixed C:N ratios as determined from the

CENTURY model itself; however, moving to variable C:N ratios does not change the results significantly.

MODEL SIMPLIFICATION

Overview

The plant–N model discussed above starts to tackle the problem of plant–SOM interaction, but ignores other potential complexities of plant–nutrient dynamics under anthropogenic change such as multiple nutrient limitation, plant allocation strategies, and changing C:N ratios. Many researchers are studying both the physiological and ecological details of these processes and how to model them (McMurtrie and Comins 1996). In this paper, having established some practical techniques for speeding up computation in complex models of plant–SOM interactions, we return to the simpler question of carbon storage and decomposition, and how we can simplify CENTURY SOM model without compromising its predictive ability.

It is hard to determine how much importance to attribute to the simple linear form of the CENTURY model; should one use the original CENTURY model, or its diagonalized form, which is mathematically equivalent
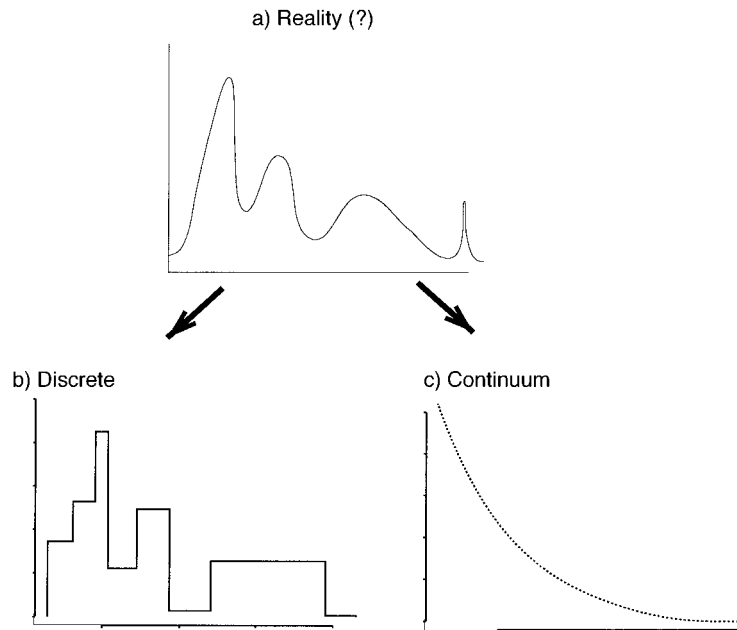
a) Reality (?)

b) Discrete

c) Continuum

FIG. 5. Different approximations of distributions of decay times. The real (unknown) distribution of eventual decay times for the carbon compounds in a given sample of litter may look something like (a), with particular classes of compounds giving rise to particular peaks of different heights (total quantity) and widths (variability in chemical and physical properties). A model could represent this unknown distribution as (b) a series of discrete boxes, as in CENTURY, or as (c) a continuous distribution of decay times (see Fig. 7).

but simpler? On the one hand, the original form of the CENTURY model represents arguably real carbon pools, which are intuitively clear and can be, at least in theory, quantified operationally as the products of well-defined chemical and physical separation processes; giving up this quantifiability for mathematical simplicity could be a mistake. On the other hand, researchers generally only measure these separable fractions during the initial calibration of the model, not during later tests of the model, when total soil carbon and NPP are usually the only available data. For the slow and passive pools in particular, which have enormous significance for carbon sequestration in soils, it is nearly impossible to observe the decay curve on laboratory or experimental time scales, so modelers estimate parameters from long-term dynamics of total soil carbon or, even more coarsely, from the equilibrium levels of soil carbon. If the particular flow patterns found in CENTURY and in the Rothamsted model are just our best guess at what happens below ground, and validation can only be done at the coarse level of total soil carbon and nitrogen, we might as well use the simplest possible modeling framework.

Once we give up the (supposed) direct correspondence of model compartments to particular separable fractions of soil carbon, we can simplify the SOM model by replacing CENTURY's discrete, eight-compartment distribution of decay times with some other distribution that provides either more analytical insight, or easier computation, or both. (The decay process itself, pure exponential decay, could hardly be made simpler.) The

real distribution of decay times in soil organic carbon may be fit by either a discrete or a continuous distribution (Fig. 5). Given the decision to move away from the observable or chemically separable pools used in CENTURY to whatever distribution of decay times will make the model work best with the fewest parameters, the decision between continuous and discrete distributions is purely pragmatic.

All of the simplified SOM models described in the following section were fitted to the decay curve for a single cohort of litter calculated by CENTURY for the Great Plains CPER site parameters. Various simulated annealing algorithms (Szymura and Barton 1986, Press et al. 1994) were used to fit the parameters of the simplified models by least squares.

The fits of different simplified models depend on which time points are used in the fit: including more points at long times emphasizes the fit to the slowly decaying tail of the distribution, while including more points at short times emphasizes the short-lived, transient material. We compromised by using 1000 time points logarithmically spaced from 0.001 to 100 yr after the deposition of a cohort of litter.

The decision whether to fit the model to short-term or long-term data, and how to weight the data, cannot be made in a vacuum; it really depends on the purpose of the model and the data available for calibration. For a short-term model of interannual variability, for example, only the dynamics of the fast pools would be of interest; all slow pools could be fitted as static sinks. Conversely, for a long-term model the fast pools might
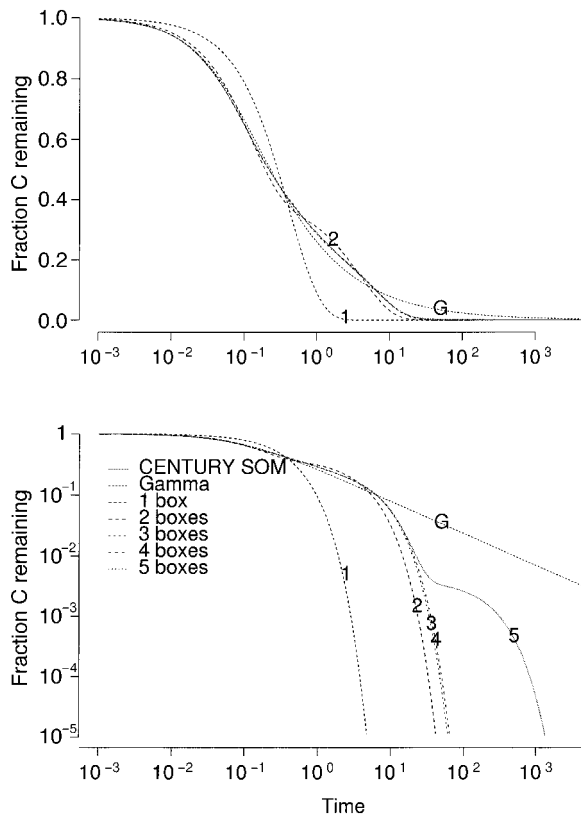
FIG. 6. Decay of one litter cohort over time for typical (CPER) parameters, as approximated by continuous (gamma distribution) and discrete models. The horizontal (time) axis is logarithmic. (a) Linear vertical scale: 3-, 4-, and 5-box models are indistinguishable from the full 8-box dynamics. (b) Logarithmic vertical scale: 5-box model is indistinguishable from the full 8-box dynamics.

be ignorable, or one could separate time scales, calculating plant dynamics on a fast time scale and then incorporating the answer into the long-term model (Comins and McMurtrie 1993, Comins 1994). The examples of fitted parameters below illustrate the shape

and properties of some different approximation schemes.

Discrete models

While many ecosystem models use variants of CENTURY to describe SOM carbon dynamics, few use as many as eight different compartments; many opt for only two or three (Rastetter et al. 1991, Melillo et al. 1993). How many compartments are really needed to describe the dynamics of soil carbon adequately? (Schimel et al. [1994] addressed this question computationally, showing that more than one box is required; we agree—see the "1 box" line in Fig. 6.)

The answer depends on the desired accuracy, but five boxes is certainly an upper bound: a sum of five exponential decays can fit 1000 yr of decay with an upper bound of 10^{-4} on the absolute error (that is, as a fraction of the initial carbon input). The equilibrium amount of carbon from a constant input (proportional to the sum of the loadings divided by the decay rates for all boxes) is within 1% of the CENTURY answer (Fig. 6).

Fitting a discrete model using simulated annealing chooses a sensible distribution of material among different decay pools for each different number of boxes (Fig. 7). With one box, it chooses an intermediate decay coefficient; with two boxes, it splits material between a fast and slow box. As more boxes are included, it spreads material more and more evenly among the pools used by CENTURY. The final model in this series, with five boxes, lumps together material in the above- and belowground metabolic, above- and belowground structural, and above- and belowground microbial pools, and fits the slow and passive boxes almost exactly. This allocation shows that the above- and belowground boxes must be distinguished because of between-site differences in above- and belowground deposition, stemming from different root : shoot ratios and plant chemistry, not because they decay differently.

How do these choices of numbers of compartments and parameters affect the dynamics of carbon storage

FIG. 7. Distribution of decay rates and loadings for different fitted models. The horizontal axis shows half-life of carbon decay on a logarithmic scale, as in Fig. 3. The vertical axis shows the coefficients, normalized by the distance between boxes, so that the figure shows a rough frequency distribution of material with different half-lives. (The choice of normalization depends on the minimum and maximum possible decay rates and on the the horizontal axis scaling.) The solid line shows the distribution for the CENTURY model with CPER parameters; different numbers show *n*-box fit parameters; the dashed line shows the fit for the gamma distribution. Some loadings for the 5-box model are offset slightly for legibility.
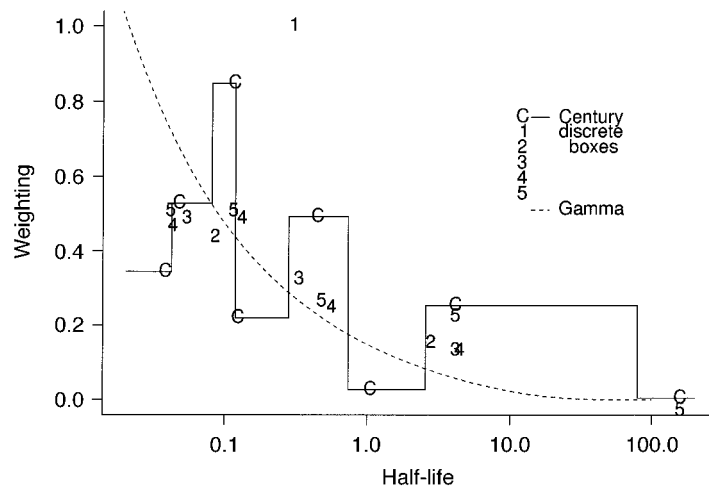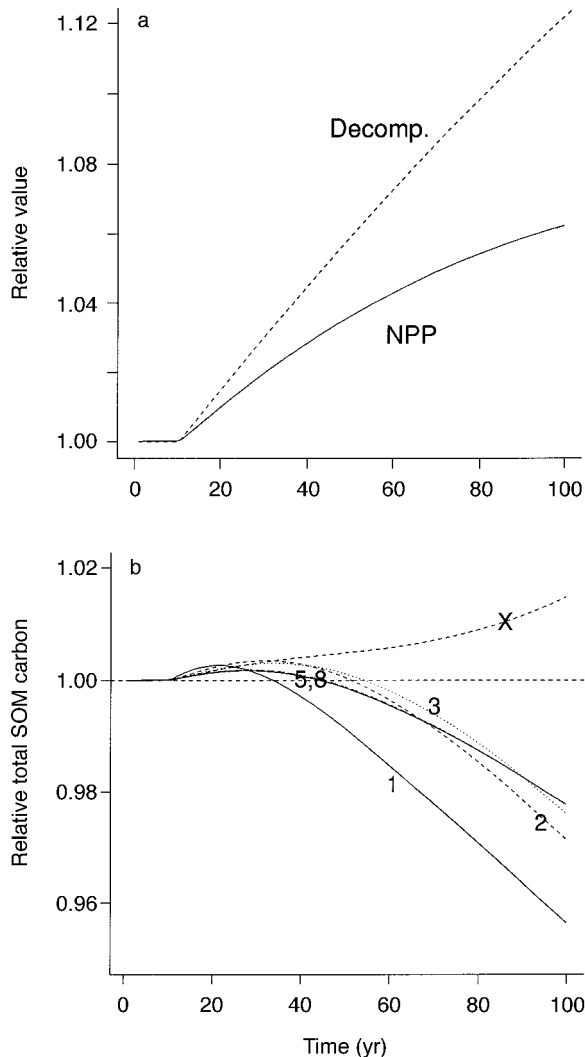
FIG. 8. Effects of SOM model simplification on a global-change scenario. (a) Relative changes in NPP (net primary productivity) and decomposition factor [δ(t)] over time. Decomp. = decomposition. (b) Relative changes in total SOM carbon over time, for different numbers of compartments. Numbers label results from *n*-compartment models; × labels results of increasing passive carbon. (The vertical axis is strongly expanded to show differences among models.)

in a global change scenario? Take an illustrative example: CO_2 and temperature increase linearly over the course of a century, temperature by 4°C and CO_2 doubling (causing a 20% increase in plant production under light-limited conditions). After 100 yr, temperature and CO_2 level off at the new, higher level.

Using the CENTURY model with CPER parameters, the temperature change causes a linear response in the decomposition factor with a total change of ~12% (Fig. 8a). For the CPER parameters, plants are nitrogen limited during most of the growing season, so the primary effect of changed temperature and CO_2 is to increase nitrogen availability from shrinking SOM pools; increased CO_2 adds a small amount of production during

early-season light-limited growth. (Here we consider the slightly simplified version of CENTURY discussed above in *Extending the carbon model: Plant–N model,* which is close to the model presented by Parton et al. [1987].)

In order to look at the effects of SOM simplification on carbon storage without the complications of nutrient limitation, we follow a procedure similar to the CASA model and use the NPP signal calculated from the full CENTURY model in simplified (reduced compartment) versions of the SOM model. To calculate SOM carbon we actually need to know deposition rather than NPP—there may be a lag between increased productivity and increased deposition. However, since this analysis uses annual averages and since plant carbon turns over rapidly in grasslands, NPP is close enough to deposition for our purposes. Because the SOM carbon dynamics are a first-order linear decay, we can evaluate total carbon storage for an *n*-box model analytically, using the equation

$$C_{tot}(t) = C_{tot}(0) + \sum_{i=1}^{n} \varepsilon_i \int_0^t \Delta(s)e^{\lambda_i \int_r^t \delta(r)\,dr}\,ds \quad (4)$$

where $\Delta(s)$ is the total NPP at time *s* (approximately equal to deposition in this fast-turnover grassland) derived from the full CENTURY model.

The result of increased temperature and CO_2 in all cases is a slight (1–2%) initial increase in SOM carbon storage from 10 to 20 yr after the onset of climate change, followed by a larger (2–4%) decrease in SOM carbon storage. Initially, faster decomposition frees nitrogen, increasing NPP and increasing soil carbon, but in the long run the direct effect of faster decomposition on soil carbon overwhelms the increase in NPP. The one-box model responds fastest, while all of the more complex models (2–8 boxes) respond about the same; as in Fig. 6b, the five- and eight-box models are indistinguishable. The line marked × is the result of increasing passive carbon slightly; we will discuss this experiment below in the section *Why simplify?*

Continuous models

Another possibility for simplifying the model is to assume a continuous density of possible decomposition rates, as caricatured in Fig. 5c (see Bosatta and Ågren [1991*a, b*, 1995], Ågren and Bosatta [1987, 1996] for a complete theoretical development of continuously distributed decomposition models; also cf. Tarutis [1992, 1993, 1994]). One possibility is a gamma distribution (fitted results are shown in Figs. 6a, b, and 7). Other possibilities would include beta or Weibull distributions. Finally, hybrid models combining a continuous distribution with a "spike" of carbon at a particular decay rate would be appropriate if, for example, passive carbon constituted a distinct chemical species rather than the tail of a distribution of recalcitrance. As with discrete models, the details of choosing a dis-

tribution and estimating its parameters depend on available data and the purpose of the model.

Why simplify?

Simplifying the SOM model makes ecosystem models easier to understand. The basic dynamics of soil carbon, either the observed pattern of carbon accumulation and loss as observed in a single site or the variation of decay among different regions with different characteristics, are easier to interpret with a simpler model because the function and sensitivity of parameters are clearer.

In addition, reducing the number of parameters of the SOM model will strengthen estimation of soil carbon dynamics. Parameters for soil models are usually estimated from a combination of experimental and observational data; data for estimating short-term (0–10 yr) decay rates are readily available, but data for estimating long-term (50–500 yr) decay rates are rare indeed. There are a few estimates in the literature from long-term soil development studies (Jenkinson 1990), studies of bomb-test fallout ^{14}C data (Harrison and Broecker 1993, Trumbore 1993), and C_3/C_4 replacement series (Parton et al. 1994), but in general separating estimates of ''slow'' (5–20 yr half-life) loadings and decay rates from ''passive'' (50–100 yr half-life) loading and decay rates is extremely difficult. In practice, researchers estimate slow-pool parameters from existing long-term studies, and fit the loadings and decay rates of passive carbon to current total carbon pools which are assumed to be in equilibrium. Current versions of the Rothamsted model go even farther and assume that passive carbon is really ''inert''—it is a completely isolated, nondecaying fraction of soil carbon.

This approach is perfectly justifiable; carbon with a 100-yr half-life is effectively inert on any time scales for which we can make sensible predictions. A slightly more flexible model would let the passive pool be a carbon sink, with a single loading parameter giving the fraction of incoming carbon entering the passive pool. What is worrying, however, is that passive carbon makes up a significant fraction of the total carbon in the soil—33% at equilibrium for the CPER parameters used above, and 4–19% in the Rothamsted examples given by Jenkinson (1990)—and that its equilibrium level is highly sensitive to its loading and decay rate. (The current inert pool in the Rothamsted model was created because the original, more CENTURY-like passive pool with a small loading and slow decay was difficult to fit to data.) For example, suppose that over the course of the 100-yr climate-change scenario shown in Fig. 8 the loading of the slow SOM pool declined by 2%, and that all of this material went to the passive pool instead—possibly as a consequence of increasing C:N ratios, which may slow down SOM decomposition (Coûteaux et al. 1995). This change, small in terms of the slow pool, nearly doubles the loading to the passive

pool and leads to a 1.5% increase, instead of a 2–4% decrease, in total SOM carbon (Fig. 8b, ''×'' line).

Expressing SOM models as sums of first-order decays and reducing the number of compartments will not solve the problem of sensitivity to passive carbon, nor enlighten us about the physical and chemical processes that control it, but it puts the problem in relief. More constructively, it allows us to quantify the sensitivity of the models and to make the best use of available long-term data (Jenkinson 1990, Harrison and Broecker 1993, Trumbore 1993, Parton et al. 1994). Using standard likelihood methods (Edwards 1972), we will be able to choose the best model, find error bounds for the parameters, and see how the errors propagate through the models. Because all models built on the foundations of the CENTURY or Rothamsted models share the same basic structure, the conclusions will be widely applicable.

CONCLUSIONS

Redescribing the CENTURY model in an analytically useful form is surprisingly easy. The coupled plant–SOM model (see *Extending the carbon model*: *Plant–N model*) contains most of the effects incorporated in CENTURY. A complete list of omissions includes: leaching, soil layers, time-varying lignin fractions, effects of management (burning and grazing), changes of nutrient availability with root biomass, and interactions between plant biomass and hydrology. Several of these terms would be straightforward to include (leaching and management) and have been omitted for simplicity.

Analytic understanding of realistic ecosystem models has benefits on many levels. Most immediately (see *Extending the carbon model*: *Equilibrium solutions* and *Boundary-condition solutions*), approximate equilibrium solutions of the model can be useful in speeding up global-scale trials, where the model has to be run for thousands of sites in parallel. It is a straightforward task, taking a week or less of programmer time, to reduce CENTURY or another complex ecosystem model to a constant-forcing submodel that can rapidly calculate approximate equilibria for starting conditions.

More fundamentally, analysis of a successful model like CENTURY, and of its widely imitated SOM model in particular, can point out sensitive areas in the model such as passive carbon loadings (nitrogen volatilization terms are another such area) and inform the design and calibration of future ecosystem models. What is the minimally complex model that will successfully predict long- and short-term changes in terrestrial ecosystems? Our analysis shows that even a realistic submodel such as CENTURY's SOM model can be reduced (with some care) to an analytically tractable linear model using a small number of parameters to characterize a few discrete types or a continuum of soil carbon decay rates.

Building a model where the many interactions among physical forcings and different parts of the ecosystem

are easy to understand, and where the minimal number of parameters need to be fitted from scarce time-series data, should be a major priority if modelers want to improve confidence in their predictions. Parsimony is not a high priority in the current generation of predictive ecosystem models, but as these models are refined and researchers start to focus on statistical support for their predictions, it will become more important to have the simplest possible models.

Finally, analytically clear models give us a way to understand the effects of ecosystem parameters on ecosystem processes. CENTURY's underlying simplicity, surprising from a model that was not built with mathematical analysis in mind, will allow a real look at the effects of physical constraints and biotic interactions on ecosystems, not just in simplified toy models, but in a realistic predictive model. Constructing models by starting with a simple, even oversimplified framework, and then rigorously testing components as they are added, will greatly simplify the task of understanding the dynamics of submodels and interactions between submodels; eventually, this process can help us understand the predicted effects of anthropogenic changes on terrestrial ecosystems.

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APPENDIX A

SOM Carbon Equations

We diagonalize the carbon system (1) by finding the eigenvalues λ_i of the system ($\mathbf{\Lambda}$ is the matrix with diagonal elements λ_i and zeros off the diagonal). If $\mathbf{c}$ represents the new vector of carbon in each diagonalized decay pool,

$$\frac{d\mathbf{c}}{dt} = \delta(t)\mathbf{\Lambda}\mathbf{c}. \qquad (A.1)$$

The eigenvalues λ_i represent the decay rates of each pool in the diagonalized system. The diagonalized system separates into eight first-order equations:

$$\frac{dc_i(t)}{dt} = \lambda_i \delta(t) c_i(t), \qquad i = 1, \ldots, 8 \qquad (A.2)$$

with solution

$$c_i(t) = c_i(0) e^{\lambda_i \tau(t)} \qquad (A.3)$$

where $\tau(t)$ is the decomposition potential (2).

The total amount of carbon in the system is the same whether we look at the original system or the diagonalized system. If a total amount of carbon $C_{tot}(0)$ is deposited at time zero, and the loadings ε_i determine the split of an initial cohort of carbon into diagonalized pools ($\Sigma \; \varepsilon_i = 1$), then $c_i(0) = C_{tot}(0)\varepsilon_i$

and we can write down an expression for the carbon in the system at time t:

$$C_{tot}(t) \equiv \sum_i C_i(t) = C_{tot}(0) \sum_i (\varepsilon_i e^{\lambda_i \tau(t)}). \qquad (A.4)$$

In order to calculate the vector of loadings (ε), we first need to calculate the amount of carbon entering each of the original CENTURY pools in a given cohort of litter. In CENTURY, deposited plant material all goes into the litter pools, in a split between above- and belowground and structural and metabolic pools. The above : belowground or root : shoot ratio varies over time, but is approximately determined by the root : shoot production ratio, which is a function of precipitation. The structural-metabolic split is determined by litter lignin : nitrogen ratios, which are functions of precipitation and C:N ratios. Given the splits between structural and metabolic material above and below ground [represented in the CENTURY pools as $\mathbf{C}(0)/C_{tot}(0)$], we transform to the diagonalized model by multiplying by the eigenvector matrix $\mathbf{E}$ (each column of $\mathbf{E}$ is an eigenvector, normalized so that it its elements sum to unity):

$$\varepsilon = \mathbf{E}^{-1}\mathbf{C}(0)/C_{tot}(0). \qquad (A.5)$$

The decay rates λ_i, loadings ε, and decomposition factor $\tau(t)$ completely determine the dynamics of a cohort of carbon.

APPENDIX B

SOM AND PLANT NITROGEN EQUATIONS

Given fixed C:N ratios, we can convert the transfer matrix **M** of carbon transfer coefficients directly to a matrix **M′** of nitrogen transfer coefficients (let γ_i be the carbon : nitrogen ratio, and the γ_i^{-1} the nitrogen : carbon ratio, of pool i):

$$\frac{dN_i}{dt} = \gamma_i^{-1}\frac{dC_i}{dt}$$

$$= \gamma_i^{-1}\sum_j m_{ij}C_j$$

$$= \gamma_i^{-1}\sum_j m_{ij}(\gamma_j N_j)$$

$$= \sum_j (\gamma_i^{-1}m_{ij}\gamma_j)N_j$$

$$= \sum_j m_{ij}'N_j \qquad (B.1)$$

where $\mathbf{M}' = \{m'_{ij}\}$ is the new linear system for nitrogen. (This transformation preserves the diagonal elements, and the eigenvalues λ_i.) This linear system can be simplified (and initial loadings determined) in exactly the same way as the carbon model, with the minor difference that all of the deposited plant material (expressed in amounts of carbon) is divided by its C:N ratio to get amounts of nitrogen deposited by plants in each litter pool. The eigenvalues are exactly the same as the carbon model eigenvalues λ_i; we denote the diagonalized nitrogen pools, and initial nitrogen loadings into the diagonalized pools, as **n** and ε'.

When nitrogen leaves the soil pools, most of it goes into the mineralized pool N_m (unlike carbon, which returns to the atmosphere as CO_2). The flow from soil nitrogen compartments into the mineralized pool is actually bidirectional, because microbes can immobilize mineralized nitrogen under nitrogen-poor conditions. The net mineralization rate is $\Sigma_j\lambda_j n_j$, since the diagonalized nitrogen model is just a pure decay model; material is deposited in the boxes and flows straight out into the mineralized pool.

However, a constant fraction v_g of the gross mineralization flow is lost by volatilization. To calculate this loss, we return to the original nitrogen model and calculate the gross mineralization vector **G**, which gives the positive flow rates (as a proportion of nitrogen present) from each soil pool into the mineralized nitrogen pool:

$$G_j = -m_{jj}'r_j + \sum_i \min[0, (-m_{jj}'F_{ij}(1 - r_j) - m_{ij}')]. \qquad (B.2)$$

We multiply G_j by the amount of nitrogen in pool j and by $\delta(t)$, which modifies all rates in the system, to get gross mineralization rates. In Eq. B.2 r_j is the fraction of carbon in box j lost via respiration (thereby producing mineralized nitrogen), m'_{ij} are the nitrogen transfer coefficients, and F_{ij} is the fraction of (unrespired) material entering box i from box j; note that m'_{jj}, the proportional flow of nitrogen from box j, is negative.

In words, the gross mineralization coefficient is the sum of nitrogen mineralized because its associated carbon is respired ($-m'_{jj}r_j$) and nitrogen mineralized by overflow, where more nitrogen is transferred into the box $[-m'_{jj}F_{ij}(1 - r_j)]$ than needs to be received by it (m'_{ij}).

We convert the gross mineralization vector, which is written in terms of the original model, to the diagonalized model by multiplying by the eigenvector matrix:

$$\mathbf{G}' = \mathbf{EG}. \qquad (B.3)$$

Volatilization also removes nitrogen directly from the mineralized pool at a rate $v_e N_m$, and atmospheric deposition and nitrogen fixation deposit nitrogen directly into the nitrogen pool at a (monthly) precipitation-dependent rate $n_f(t)$.

Plant growth occurs at the minimum of the water and temperature-limited rate and the nutrient-limited rate. The water- and temperature-limited growth rate is $\rho(t)$ and the C:N ratio of new production is γ_p, so the water and temperature-limited nitrogen uptake rate is $\rho(t)/\gamma_p$. The nitrogen-limited uptake rate is $f_{av}N_m$, where f_{av} represents the availability of nitrogen to plants [in CENTURY, plant uptake per month is $f'_{av}N_m$; to get equivalent dynamics in continuous time (with time still measured in months), we have to choose a new value of f_{av} $\approx -\ln(1 - f_{av})$]. The availability of nitrogen also depends to a small extent on the root biomass as well, but this is a small term.

The net nitrogen mineralization rate is the total rate at which nitrogen leaves all SOM pools, which is simply $\Sigma \lambda_j n_j(t)$: thus the equation for the dynamics of the mineralized pool is

$$\frac{dN_m}{dt} = \delta(t)\left(\sum_j \lambda_j n_j(t) - v_g\sum_j G_j'n_j(t)\right) - v_e N_m + n_f(t)$$

$$- \min\left(\frac{\rho(t)}{\gamma_p}, f_{av}N_m\right). \qquad (B.4)$$

Finally, the equations for plant biomass (divided into root, R; shoot, S; and aboveground "standing dead" material, D) depend on the shoot : total production ratio (a, a function of precipitation), on the production term [$\rho(t)$] and C:N ratio of production (γ_p), and on plant (root and shoot) death. Plant material has a baseline turnover rate, which is also affected (for roots) by moisture and temperature and (for shoots) by moisture and a seasonal cycle; all of these are external forcings, which will just be incorporated as $\mu_r(t)$ and $\mu_s(t)$, the time-dependent death rates of roots and shoots. (When shoots die, they go first to the standing dead pool, which then flows into the litter pool at a constant rate μ_d.) The plant equations are as follows:

$$\text{growth} = \min[\rho(t), f_{av}N_m\gamma_p] \qquad (B.5)$$

$$\frac{dR}{dt} = \text{growth} \times (1 - a) - \mu_r(t)R \qquad (B.6)$$

$$\frac{dS}{dt} = \text{growth} \times a - \mu_s(t)S \qquad (B.7)$$

$$\frac{dD}{dt} = \mu_s(t)S - \mu_d D. \qquad (B.8)$$

APPENDIX C

EQUILIBRIUM CALCULATION

The system described in Appendix B is a linear system with two complications: many of the rates are functions of monthly temperature, precipitation, etc., which makes them time dependent; and the system switches its behavior according to the nitrogen or water and temperature limitation of plant production. If we smear out all of the time-dependent functions to get annual average values, we can actually solve for the equilibrium of the linear system in either of the limitation scenarios. At equilibrium the system will either be N limited or water and temperature limited. We calculate the equilibrium N_m for the N-limited case, and then check whether the system is really limited or not.

The steps to calculate the equilibrium state of the system, assuming annually (arithmetically) averaged values (denoted by an overbar: $\bar{\delta}$, $\bar{\rho}$, $\bar{\mu_r}$, etc.), follow.

1) Calculate N^*_m for the N-limited case. First, calculate the equilibrium plant biomass and the average fraction of live plant material above ground. At N-limited equilibrium, the total rate of plant production is $f_{av} N^*_m \gamma_p$: this leads to equilibrium plant biomasses

$$R^* = \frac{f_{av} N_m^*(1 - a)\gamma_p}{\bar{\mu_r}} \tag{C.1}$$

$$S^* = \frac{f_{av} N_m^* a \gamma_p}{\bar{\mu_s}} \tag{C.2}$$

$$D^* = \frac{f_{av} N_m^* a \gamma_p}{\mu_d}. \tag{C.3}$$

Therefore carbon deposition above and below ground occurs in the proportions a and $(1 - a)$, proportional to $\mu_d D^*$ and $\mu_r R^*$. Now we calculate the loadings—deposition into each diagonalized pool—by calculating the fraction of root and shoot material that flows to each diagonalized pool, and multiplying by $(1 - a)$ and a (we divide the loadings into an aboveground and belowground fraction to make them easier to recompute for different sites):

$$\bar{\varepsilon}'_i(0) = \varepsilon'_{ri}(0)(1 - a) + \varepsilon'_{si}(0)a. \tag{C.4}$$

2) Calculate equilibrium values of n_j. At equilibrium, plants deposit nitrogen at a rate $(\mu_d D^* + \bar{\mu_r} R^*)/\gamma_p = f_{av} N^*_m$, so

$$n_j^* = \frac{f_{av} N_m^* \varepsilon_j'}{\lambda_j \bar{\delta}}. \tag{C.5}$$

3) Substitute the values for n^*_j into (B.4), setting the left-hand side to zero and substituting annual averages for all of the time-dependent forcing functions, and solve for N^*_m. It is convenient to calculate an intermediate value, T, which is proportional to the net rate at which nitrogen flows into the mineralized pool, taking gross mineralization into account:

$$T = \sum_i n_i(0)(1 - v_g G_i/\lambda_i). \tag{C.6}$$

The nitrogen-limited size of the mineralized pool is

$$N_m^*(\text{N limited}) = \frac{\overline{n_f}}{f_{av}(1 - T) + v_e} \tag{C.7}$$

(this expression and all the other equilibria are clearly ratios of inflows over outflows, which is sensible for a linear system).

If the amount of mineralized nitrogen present in the N-limited case is less than the maximum that the plants could take up,

$$N_m^*(\text{N limited}) < \frac{\bar{\rho}}{f_{av}\gamma_p} \tag{C.8}$$

then we are really in the N-limited case, and the equilibrium quantities of nitrogen are given by Eqs. C.1–C.3, C.5, and C.7.

Otherwise, in the non-N-limited case, we repeat all of the above calculations starting with total plant growth rates of $\bar{\rho}$:

$$R^* = \frac{\bar{\rho}(1 - a)}{\bar{\mu_r}} \tag{C.9}$$

$$S^* = \frac{\bar{\rho}a}{\bar{\mu_s}} \tag{C.10}$$

$$D^* = \frac{\bar{\rho}a}{\mu_d} \tag{C.11}$$

$$n_j^* = \frac{\bar{\rho}\varepsilon_j'}{\gamma_p \lambda_j \bar{\delta}} \tag{C.12}$$

$$N_m^*(\text{H}_2\text{O and temperature limited}) = \frac{(\bar{\rho}/\gamma_p)(T - 1) + \overline{n_f}}{v_e}. \tag{C.13}$$