

## Evaluating and Testing Models of Terrestrial Biogeochemistry: The Role of Temperature in Controlling Decomposition

*Ingrid C. Burke, Jason P. Kaye, Suzanne P. Bird,  
Sonia A. Hall, Rebecca L. McCulley, and  
Gericke L. Sommerville*

### Summary

Simulation models have played an important role in the development of terrestrial biogeochemistry. One contemporary application of biogeochemical models is simulating interactions between global climate change and terrestrial carbon balance. The largest global pool of terrestrial carbon is detrital (nonliving) soil organic matter, and one ongoing debate is whether warmer temperatures will increase the amount of soil C released to the atmosphere via microbial decomposition (oxidation to CO<sub>2</sub>). While much of the literature suggests that decomposition rates increase with temperature, several recent papers cast doubt on this general conclusion. Given the difficulty of directly estimating field rates of total organic matter decomposition, models are playing an important role in assessing how ecosystem carbon balance will respond to global change. We evaluated a suite of models to ask three main questions: (1) What are the nature and origin of the equations used to simulate organic matter decomposition? (2) Is there a consensus understanding of the role of temperature in controlling decomposition? and (3) How well do these models serve as resources for the scientific community?

Our review resulted in several important conclusions. First, current models of decomposition are based on very few empirical studies of the process. Instead, soil organic matter decomposition is simulated using data from soil respiration, short-term laboratory studies, or decomposition of recently senesced foliage. Second, while most models represent decomposition as a process that in-

creases with temperature, the shape of the temperature-decomposition curve, and their interactions with soil moisture varied among the models. Ultimately, the development of realistic, mechanistically based models of organic matter decomposition is limited by field data. There is a strong need for long-term experiments with estimates of detrital inputs and detrital pools to test the understanding of decomposition currently incorporated into simulation models. Finally, our evaluation of the models was limited by incomplete documentation of the source of the relationships used in the model and by the evolution of the models through time.

## Introduction

Models provide a forum for synthesis (Parton et al. 1987; Aber et al. 1991) and a tool for extrapolating our understanding to longer time scales and broader spatial extents than we can measure (Running 1986; Burke et al. 1991; Aber et al. 1993). Simulation models also enable us to evaluate complex interactions among element cycles and the processes that drive these cycles. The potential interaction between global climate change and terrestrial carbon (C) balance is one of the most important unknowns of the day (Pastor and Post 1988; Rastetter et al. 1991; Aber et al. 1995; Parton et al. 1995; and many others). Increases in atmospheric CO<sub>2</sub> and potential changes in climate may influence and be influenced by terrestrial C storage. For example, the largest global pool of terrestrial C is detrital soil organic matter (OM), which is decomposed by microorganisms, releasing CO<sub>2</sub> to the atmosphere. If warmer temperatures increase decomposition rates, the resulting increase in atmospheric CO<sub>2</sub> could induce warming that would increase decomposition. The role of temperature in controlling decomposition is an important debate in contemporary global-change science. While much of the literature suggests that decomposition rates increase predictably with temperature (Meentemeyer 1984; Kirschbaum 1995; 2000; Townsend et al. 1997), some recent analyses (Liski et al. 1999; Giardina and Ryan 2000; Epstein et al. 2002) suggest that decomposition may be less responsive to temperature than previously thought.

The process of decomposition is an especially appropriate one to model because it is a conceptual construct, representing an amalgamation of multiple soil processes rather than a real biological process. Ecologists generally conceptualize decomposition as the transformation of organic materials into inorganic materials by heterotrophs, usually focusing on C. Decomposition includes both intracellular and extracellular enzyme-mediated breakdown of multiple classes of molecules and particular chemical bonds, with subsequent intracellular oxidation to CO<sub>2</sub>. Some soil scientists favor a second, counterintuitive definition of decomposition as the transformation of plant litter into soil humic materials

(Paul and Clark 1996). We use the former definition because it is most closely related to the issue of terrestrial C storage.

Initially, biogeochemists abstracted the complex intra- and extracellular processes into a mass-specific litter (recently senesced foliage) decomposition rate, or  $k$ , assuming first- (or larger) order decay kinetics (Olson 1963). However, most detrital soil OM has been microbially, chemically, and physically altered (called humus) and decomposes more slowly than litter. In order to model decomposition of the entire soil OM pool (fresh litter plus humus), some biogeochemical models represented detrital OM as a series of pools with different decomposition rates. Organic matter pools were delineated by the type of material being decomposed; soluble plant and microbial materials were given more rapid decomposition constants than plant structural tissues or stabilized soil humic materials (Jenkinson and Rayner 1977; van Veen and Paul 1981). Many current models use this multiple-pool construct to simulate decomposition (Parton et al. 1994; King et al. 1997) and interactions among decomposition rates, atmospheric CO<sub>2</sub>, and global warming.

Given the widespread use of simulation models to address global-change questions related to decomposition, it is important to evaluate how and how well biogeochemical models simulate the process. Evaluating how models simulate decomposition reveals whether there is consensus among biogeochemists regarding mechanistic controls on CO<sub>2</sub> release from soils. Model comparisons also allow us to evaluate how specific differences in model structure affect predicted decomposition rates. This type of comparison also generates a range of decomposition scenarios that can be used to evaluate our confidence in global-change predictions (VEMAP Members 1995, Chapter 12).

In this chapter, we use the relationship between temperature and OM decomposition as a case study for evaluating terrestrial biogeochemical models. Our approach is to compare extant models to determine if there is consensus about the effects of temperature on decomposition. We first evaluate the source of the empirical data used to develop the temperature-decomposition relationships in several terrestrial biogeochemistry models. Second, we evaluate the different model structures used to represent the process of decomposition and its control by temperature. Third, we compare the net relationship of temperature to decomposition across models; in doing so, we evaluate whether the models have sufficient congruence to conclude that terrestrial biogeochemists understand the role of temperature in controlling decomposition sufficiently well to provide this kind of information to policy makers. Finally, we suggest some alternative modeling approaches and comment on the ability of the extant models to serve as resources for the scientific community.

## Empirical Data Sources

All simulation models require empirical data for development and validation. Several different sources of information have served as the foundation for tem-

perature-decomposition relationships in current biogeochemical models. Throughout the chapter, “litter” always refers to recently senesced plant foliage, and “soil OM” includes all detrital soil OM (litter plus humus).

### *Litter Decomposition*

Numerous experiments have evaluated litter decomposition rates across environmental gradients (Meentemeyer 1978, 1984, Meentemeyer and Berg 1986). These experiments consistently show a strong temperature response of litter decay; from their data Vitousek et al. (1994) and Gholz et al. (2000) calculated  $Q_{10}$ 's from 2 to 11. As with all geographic analyses, these studies are limited by the complex environmental gradients used to mimic climate variability. Factors that co-vary with temperature (precipitation, soil parent material, elevation, etc.) confound simple temperature-decomposition relationships. A second limitation is that these studies are confined to the litter component of decomposition; total soil OM decomposition is not measured.

### *Soil Organic C Pools*

A second potential source of empirical data is geographic analysis of soil organic-C distributions along regional- or continental-scale temperature gradients. Trends in decomposition rates of the total OM pool can be inferred or calculated from knowledge or assumptions of the rates of OM production. These studies have strength in that they evaluate the long-term effect of temperature on total soil OM; however, they require assumptions or measurements of total net primary production. To date, such studies have not consistently shown increases in decomposition rates with increasing temperature. While global analyses (Post et al. 1982; Meentemeyer et al. 1985) and those from grasslands and Hawaii (Burke et al. 1989; Townsend et al. 1995; 1997; Epstein et al. 2002) indicated decreasing soil C with increasing temperature, two forest studies did not. Homann et al. (1995) analyzed soil organic-C patterns in the coniferous region of the Pacific Northwest U.S. and did not find the decreases in soil C that they expected with increases in mean annual temperature. Grigal and Ohmann (1992) found that temperature and AET (Actual Evapotranspiration) played relatively small and inconsistent roles in determining soil C. In addition, Epstein et al. (2002) found that the effect of temperature on decomposition was smaller than anticipated after eliminating the interaction between precipitation and temperature in the Great Plains region.

### *Soil Respiration*

Field experiments have been conducted that analyze patterns in soil respiration across temperature gradients in space or time (Reiners 1968; Kicklighter et al. 1994; and many others reviewed by Singh and Gupta 1977; Schlesinger 1977; Raich and Schlesinger 1992; Lloyd and Taylor 1994) or that analyze the consequences of experimental warming for soil respiration (Billings et al. 1982; Peterjohn et al. 1993; McKane et al. 1997; Hobbie and Chapin 1998; Rustad and

Fernandez 1998; Bridgham et al. 1999; Saleska et al. 1999; and others reviewed in Rustad et al. 2001). Warming studies have strength in that they are controlled experimental manipulations; however, soil or ecosystem warming does not exclusively change temperature. In most systems, warming increases evaporation, decreases soil moisture, and potentially increases aeration, any of which may be proximal controls on decomposition (Shaver et al. 1992; Harte et al. 1995; Bridgham et al. 1999). These results be interpreted as a strength of an integrated field experiment approximating global warming, but it does not provide the kind of simple response to temperature that might be useful in developing or parameterizing simulation models.

Most warming and climate-gradient experiments show that soil respiration increases with temperature, and it is generally assumed that this is at least in part due to increases in decomposition (Schlesinger and Andrews 2000). However, decomposition rates cannot be directly inferred from soil respiration data because the fluxes include both plant-root respiration and heterotrophic respiration. A few studies have separated root respiration from OM decomposition by estimating soil respiration in plots with roots excluded. These studies suggest that  $Q_{10}$ 's for soil OM decomposition fall in the narrow range of 2 to 2.5 (Brumme 1995; Nakane et al. 1996; Boone et al. 1998).

### *Laboratory Incubations*

Many laboratory incubations have been conducted in which temperature is varied and either litter decay or soil  $\text{CO}_2$  evolution is measured in the absence of plants (reviewed by Kirschbaum 1995; Ågren et al. 1996; and Katterer et al. 1998). These experiments generally show increasing laboratory rates of decomposition with increased temperatures;  $Q_{10}$  values range between 2 and 5, with lower  $Q_{10}$  values at higher temperatures. As we will describe later, some of the early incubation experiments (e.g. Drobniak 1962, cited in Hunt 1977; Sorenson 1981) were used to develop the temperature-response curves of current OM simulation models.

While short incubations almost always show increases in decomposition at higher temperatures, longer incubations highlight interactions between substrate availability and temperature in controlling decomposition rates. Holland et al. (2000) incubated a variety of tropical soils and found consistent exponential increases (mean  $Q_{10} = 2.37$ ) in heterotrophic respiration with temperature (up to  $55^\circ\text{C}$ ) only during the first few days of the incubation. After the first week, the optimum temperature for decomposition shifted from  $55^\circ\text{C}$  to  $45^\circ\text{C}$  and then to  $35^\circ\text{C}$  between 10 and 24 weeks of incubation. Changes in the temperature sensitivity of decomposition presumably resulted from declines in labile C availability as the incubation progressed; decomposition of slower turnover C substrates (late in the incubation) may be less sensitive to temperature than more labile substrates. A synthesis of forest-soil incubation studies yielded similar results; decomposition measured in year-long incubations varied only slightly (and negatively) with site mean annual temperature (Giardina and Ryan 2000).

While the relationship between OM decomposition and temperature is clearly isolated in laboratory experiments, soils are typically disturbed such that decomposition is not realistically limited by spatial C substrate heterogeneity or physicochemical protection of OM. In addition, experiments that focus on temperature responses are generally conducted under ideal moisture conditions, so that the many combinations of climatic limitations that might occur in the field are not tested. Finally, even simplified laboratory experiments show complex responses to temperature with time, prompting Daubenmire and Prusso (1963, 591) to state “It appears that outside the natural environment of the forest floor these ratings are of limited scientific value, that the speed of decomposition is to a remarkable degree determined by the temperature levels under which the saprobic communities develop and operate, and that higher temperatures do not always result in greater net decomposition over periods of many weeks.”

### *Isotopic Methods*

Carbon-14 dating and bomb  $^{14}\text{C}$  tracer studies (a pulse of atmospheric  $^{14}\text{C}$  derived from thermonuclear bomb testing in the 1960s) have both been used to justify simulating soil OM decomposition as a series of pools with different turnover times (Jenkinson and Rayner 1977; van Veen and Paul 1981; Trumbore et al. 1997). While recalcitrant soil C decomposition (turnover time = from centuries to millennia by  $^{14}\text{C}$  dating) is apparently insensitive to regional temperature gradients (Paul et al. 1997), decomposition of actively cycling soil C (turnover time = from years to decades by  $^{14}\text{C}$  bomb tracer) showed a  $Q_{10}$  of 3 to 3.8 in one cross-site comparison (Trumbore et al. 1997).

The stable isotope  $^{13}\text{C}$  can also be used to estimate decomposition rates when land-use change is accompanied by a vegetation shift from  $\text{C}_3$  to  $\text{C}_4$  (or vice versa) photosynthetic pathways. Giardina and Ryan (2000) collected data from 44 such land-use change studies and found that decomposition rates were not correlated with mean annual temperature at the sites.

### Brief Introduction to the Models

We selected several terrestrial biogeochemical models that have been validated against field data and are being broadly used to represent ecosystem processes (Table 13.1). For space reasons, we have not included every biogeochemical model for description, but have included what we think are the key varieties of the models (e.g. we did not include MBL-GEM [Rastetter et al. 1991], which is similar in many ways to RothC, CENTURY, and PnET). Three of the models have been compared with one another in a simulation of global responses to climate change (VEMAP Members 1995); several were compared in terms of their representation of litter decomposition (Moorhead et al. 1999) or coniferous forest function (Ryan et al. 1996). Except for the litter decomposition comparison, these analyses revealed large differences in simulated decomposition

rates that in part result from differences in the ways that the temperature-decomposition relationship is treated. Below, we describe each of the selected models, including the empirical data sources, validation against temperature changes, the structure of the decomposition component, and the functional relationship of temperature to decomposition.

Table 13.1. Biogeochemical models evaluated in this chapter.

<i>Model</i>	<i>Decomposition Equation</i>	<i>Terms</i>	<i>C Pool Structure</i>
TEM (Raiche et al. 1991)	$k = k_Q W_s e^{0.0693T}$	$k$ = Decomposition rate (mo-1) $k_Q$ = Site-specific litter quality constant (mo-1) $W_s$ = Soil moisture/texture scalar $T$ = Mean monthly air temperature	Detrital C
Forest-BGC (Running and Gower 1991)	$k_L = k_{\max}[(T_s + W_s)/2]$ $k_s = 0.03k_L$	$k_L$ = Leaf and root decomposition rate (yr <sup>-1</sup> ) $k_{\max}$ = Fixed maximum decomp. rate (0.5 yr <sup>-1</sup> ) $T_s$ = Soil temperature scalar $W_s$ = Soil moisture scalar $k_s$ = Soil C decomposition rate (yr <sup>-1</sup> )	Leaf- and root-litter C Other detrital soil C
Biome-BGC (Hunt et al. 1996)	$k_L = k_Q T_s W_s$ $k_s = k_C T_s W_s$	$k_L$ = leaf and root decomposition rate (d <sup>-1</sup> ) $k_Q$ = site-specific litter quality constant (d <sup>-1</sup> ) $T_s$ = soil temperature scalar $W_s$ = soil moisture scalar	Leaf- and root-litter C Other detrital soil C

Table 13.1. *Continued*

<i>Model</i>	<i>Decomposition Equation</i>	<i>Terms</i>	<i>C Pool Structure</i>
		$k_s$ = soil C decomposition rate ( $d^{-1}$ ) $k_c$ = fixed decomposition rate from CENTURY ( $d^{-1}$ )	
CENTURY (Parton et al. 1994)	$k_1 = k_{\max} T_s W_s C_s$ $k_2 = k_{\max} T_s W_s Q_s$ $k_3 = k_{\max} T_s W_s$	$k_1$ = Soil microbial decomposition rate ( $yr^{-1}$ ) $k_2$ = Structural plant decomposition rate ( $yr^{-1}$ ) $k_3$ = All other pools decomposition rate ( $yr^{-1}$ ) $k_{\max}$ = Fixed maximum decomp. rate ( $yr^{-1}$ ) $T_s$ = Air temperature scalar $W_s$ = Soil moisture scalar $C_s$ = Soil texture scalar $Q_s$ = Litter quality (lignin) scalar	Structural plant C Metabolic plant C Surface microbial C Soil microbial C Slow soil C Passive soil C
FAEWE (Van der Peijl and Verhoeven 1999)	$k = k_{\max}(T_{as}/T_{ms})$	$k$ = decomposition rate ( $wk^{-1}$ ) $k_{\max}$ = maximum decomposition rate ( $wk^{-1}$ ) $T_{as}$ = actual soil temperature scalar $T_{ms}$ = mean annual soil temperature scalar	Detrital soil C
PnET-II (Aber et al. 1997)	$R = 27.46e^{0.0684T}$	$R$ = soil respiration ( $g\ m^{-2}\ mo^{-1}$ ) $T$ = mean monthly temperature	No detrital C pools

Table 13.1. *Continued*

<i>Model</i>	<i>Decomposition Equation</i>	<i>Terms</i>	<i>C Pool Structure</i>
Linkages (Pastor and Post 1986)	$k_L = -\ln\{1 - [0.98 + 0.09AET + (0.5 - 0.002AET)(L:N)]/100\}$ $k_t = 0.2$ $k_{sw} = 0.1$ $k_{tw} = 0.03$ $k_{dw} = 0.05$ $k_s = H\{-0.0004(N:C)/[-0.03 + (N:C)]\}/N$	$k_L$ = Root and leaf decomposition rate ( $yr^{-1}$ ) AET = Actual evapotranspiration L:N = Litter lignin to nitrogen ratio $k_t$ = Twig decomposition ( $yr^{-1}$ ) $k_{sw}$ = Small wood decomposition ( $yr^{-1}$ ) $k_{tw}$ = Large wood decomposition ( $yr^{-1}$ ) $k_{dw}$ = Decayed wood decomposition ( $yr^{-1}$ ) $k_s$ = Soil humus decomposition ( $yr^{-1}$ ) H = Humus mass (Mg/ha) N = Total humus N (Mg/ha) C = Total humus C (Mg/ha)	Leaf + root litter C Soil humus C Twig C Small wood C Large wood C Decayed wood C
RothC (Coleman and Jenkinson 1999, user guide)	$k = 1 - e^{-(T_s W_s S_s k_{max}/12)}$	$k$ = Decomposition rate for each pool ( $mo^{-1}$ ) $k_{max}$ = Maximum decomposition rate ( $yr^{-1}$ ) $T_s$ = Air temperature scalar $W_s$ = Soil moisture scalar $S_s$ = Soil cover scalar (typically 0.6)	Metabolic plant C Structural plant C Microbial biomass C Humic organic matter

*Note:* The left hand portions of decomposition equations are mass specific decomposition rates (heterotrophic respiration/carbon pool size) except PnET. The subscript s denotes a unitless scalar function. Constants in the Linkages model were rounded considerably. Temperature is in Celsius for all models.

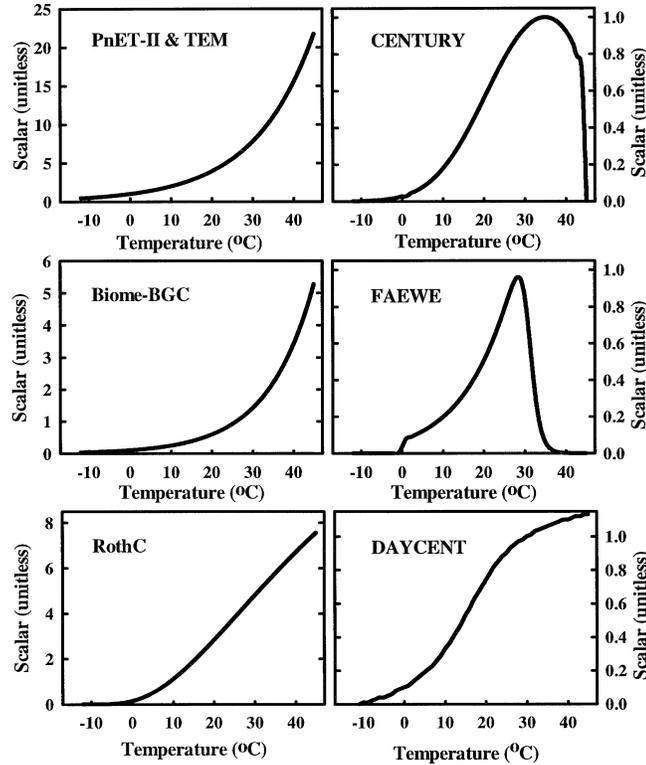


Figure 13.1. The temperature scalars used by models evaluated in this chapter. These scalars are multiplied by fixed decomposition constants to simulate the temperature effect on organic matter decomposition.

### *Rothamsted (RothC)*

The Rothamsted model was the first simulation model published that represented soil OM decomposition as a multipool process (Jenkinson and Rayner 1977; Coleman and Jenkinson 1999). RothC models four detrital OM pools on a monthly time step using the same basic equation (Table 13.1); preset maximum decomposition rates ( $k_{\max}$  in  $\text{yr}^{-1}$ ) are modified by temperature, moisture, and plant cover scalars. Pools include structural plant material ( $k_{\max} = 0.3$ ), metabolic plant material ( $k_{\max} = 10$ ), microbial biomass ( $k_{\max} = 0.66$ ), and humified organic matter ( $k_{\max} = 0.02$ ). The pool structure was based on laboratory incubations of  $^{14}\text{C}$ -labeled materials, radiocarbon dating of soil OM, and long-term measurements of soil OM content. Fixed  $k_{\max}$  values were based on model runs tuned to field data from Rothamsted (Coleman and Jenkinson 1999). The temperature scalar ( $T_s$ ; Figure 13.1a) is:

$$T_s = \frac{47.9}{1 + e^{\left(\frac{106}{T+18.3}\right)}} \quad (13.1)$$

where  $T$  is the average monthly air temperature ( $^{\circ}\text{C}$ ). This relationship was developed from decomposition of  $^{14}\text{C}$ -labeled litter (Jenkinson and Ayanaba 1977; Ayanaba and Jenkinson 1990) but is used for all OM pools. The model was used to simulate changes in decomposition following global climate change (King et al. 1997), and results suggested that decomposition would increase but would be nearly balanced by increases in net primary production producing no net change in terrestrial C storage.

### CENTURY

The CENTURY model was originally developed for grasslands and semi-arid agroecosystems (Parton et al. 1983, 1987, 1994); it has been modified to represent numerous ecosystem types (Schimel et al. 1996). Current versions exist with either monthly (Parton et al. 1994) or daily (Kelly et al. 2000) time steps. Similar to RothC, CENTURY represents OM decomposition as several pools with preset  $k_{\text{max}}$  values ( $\text{mo}^{-1}$ ) modified by site-specific scalars (Table 13.1). The pools include aboveground plant structural material ( $k_{\text{max}} = 3.9$ ), belowground plant structural material ( $k_{\text{max}} = 4.9$ ), aboveground metabolic plant components ( $k_{\text{max}} = 14.8$ ), belowground plant metabolic plant material ( $k_{\text{max}} = 18.5$ ), aboveground microorganisms ( $k_{\text{max}} = 6.0$ ), soil microorganisms (a.k.a. “active” soil OM,  $k_{\text{max}} = 7.3$ ), slow-turnover soil OM ( $k_{\text{max}} = 0.2$ ), leached OM (does not decompose), and passively turning over soil OM ( $k_{\text{max}} = 0.0045$ ). The source of the initial  $k$  values for these pools is not described in the literature. CENTURY modifies  $k_{\text{max}}$  using temperature, moisture, and for some pools, soil-texture and litter-quality scalars (Table 13.1). The temperature scalar ( $T_s$ ) is a generalized Poisson function (Parton et al. 1987; 1994):

$$T_s = (t_{\text{max}} - t)/(t_{\text{max}} - t_{\text{opt}})^{0.2} * \exp[(0.2/2.63)(1 - (t_{\text{max}} - t/t_{\text{max}} - t_{\text{opt}})^{2.63})] \quad (13.2)$$

where  $t_{\text{max}}$  is  $45^{\circ}\text{C}$  and  $t_{\text{opt}}$  is  $35^{\circ}\text{C}$ .

The temperature scalar is multiplied by a logistic moisture scalar to derive an abiotic scalar (DEFAC [Decomposition factor based on temperature and moisture]; Kelly et al. 2000). The original form of  $T_s$  (Parton et al. 1987) was determined by fitting data from an incubation experiment in which cellulose was labeled and decomposed in the laboratory at three different temperatures (Sorenson 1981). Monthly versions of CENTURY use this original  $T_s$ , and the daily version (DAYCENT) uses an arctangent function (R. Kelly, pers. comm.; Figure 13.1). The effect of temperature on maximum decomposition is identical for each pool.

CENTURY has been tested against field data in several ways. Simulated and measured soil OM values were compared across the Great Plains of the United States (Burke et al. 1989); this “validation” did not directly test the relationship of temperature to decomposition but provided support for the integrated-model representation of all processes influencing soil OM. Litter decomposition data were compared directly to the model (Vitousek et al. 1994), resulting in some modification of the litter decomposition model (which did not influence the temperature relationship). More recently, Gholz et al. (2000) found a strong correlation between DEFAC and litter decomposition rates from a continental scale field experiment, LIDET. Short-term estimates of CO<sub>2</sub> flux were compared to DAYCENT simulations of decomposition; this comparison is somewhat limited because soil CO<sub>2</sub> fluxes represent both heterotrophic and autotrophic respiration (Kelly et al. 2000).

When CENTURY was used to predict the responses of ecosystem C to global change, the simulations predicted that simple climatic warming reduced soil C globally, but that combinations of CO<sub>2</sub> increases with global climate change generally resulted in net C storage (Parton et al. 1995, VEMAP Members 1995, Schimel et al. 2000). With this model, simulated land-use change has more impact on stored C than does climate change or CO<sub>2</sub> increases.

### *TEM*

The Terrestrial Ecosystem Model (TEM) model (Raich et al. 1991; Melillo et al. 1993; McGuire et al. 1995; 1997) was developed to simulate continental-to-global scale C and N balance. TEM contains only one detrital soil C pool, and decomposition is the only C loss from this pool (Raich et al. 1991; McGuire et al. 1995). Rather than scaling a fixed  $k_{\max}$ , as in CENTURY and RothC, TEM determines a site-specific decomposition constant (here called  $k_Q$ ) by comparing litter quality at the site to litter quality at one of the TEM calibration sites. This  $k_Q$  is then modified by temperature and moisture scalars on a monthly time step to simulate decomposition rates (Table 13.1). The temperature scalar is a simple exponential such that decomposition has a  $Q_{10}$  of 2.0 over all temperatures (Table 13.1). This fixed  $Q_{10}$  is based on a literature review of soil respiration from temperate forest soils (Kicklighter et al. 1994). The sensitivity of the model results to temperature have been explored extensively and compared with total C values (McGuire et al. 1995). Simulations of global climate change with TEM showed decreases in soil C and ecosystem C as a consequence of the decomposition sensitivity to temperature; however, simultaneous increases in CO<sub>2</sub> offset C losses by increasing NPP (Melillo et al. 1993; McGuire et al. 1995; 1997; VEMAP members 1995).

### *PnET-II*

The PnET model (Aber et al. 1995) was designed to simulate C and water balance in northeastern U.S. temperate forests. PnET-II does not contain a com-

plete C budget, in that it does not represent biomass production–decomposition feedbacks, track total soil C content, or allocate soil C into various turnover pools. Rather, it combines heterotrophic and live-root respiration into a simple logarithmic equation for soil respiration with mean monthly temperature as the only parameter (Table 13.1). Like TEM, the soil respiration-temperature relationship ( $Q_{10} = 2$  for all temperatures) was developed for temperate zone forests by Kicklighter et al. (1994). PnET has been validated against field data on total net ecosystem  $\text{CO}_2$  exchange and biomass production data. It is not used for climate change assessments since it lacks a soil C pool and feedbacks between temperature-induced decomposition increases and net primary production. An alternate version of the model (PnET-CN) contains one soil C pool similar in turnover to the active pool in CENTURY (Aber et al. 1997).

### *Linkages*

Pastor and Post (1986) generated an individual-based model of tree growth with a link between productivity and decomposition through N availability. The purpose of the model was to simulate the interactions between plant community structure and ecosystem processes. The model differs from others that we evaluated in that cohorts of litter are modeled separately; each year's litter is tracked as a separate pool in the model. The simulations are for plots of 1/12 ha, considered the average gap size created by a dominant tree (Pastor and Post 1986). Linkages contains six detrital OM pools: leaf plus root litter; twigs; wood less than 10 cm DBH (diameter at breast height); wood greater than 10 cm DBH; well decayed wood; and humus. Leaf and root decomposition are modeled using field litterbag results from Meentemeyer (1978) and Melillo et al. (1982), which suggest that litter decomposition depends on AET, litter lignin concentration, and litter nitrogen concentration (Table 13.1).

Every time step, L:N is modified for a given cohort of litter (L:N ranges from 5 to 70) following relationships found by Aber and Melillo (1980) and Berg et al. (1985) between the fraction of OM remaining and N and lignin concentrations. Once the litter reaches a species-specific critical N concentration, it starts to mineralize N and is transferred to the soil humus pool. The humus pool is then decomposed according to the following equation derived from field net N mineralization ( $N_m$ ) data in Wisconsin:

$$N_m = H\{-0.000379(N:C)/[-0.02984 + (N:C)]\} \quad (13.3)$$

where H is humus mass and N:C is the elemental ratio of litter forming the humus. Decomposition rates are determined by assuming that C is released from the humus pool in the same proportion as  $N_m$  is released from the humus pool (Table 13.1). Twig, small wood, large wood, and well-decayed wood pools have fixed decomposition constants (Table 13.1; Pastor and Post 1986), thus, only leaf and root litter decomposition are affected by temperature.

The model has been validated against primary production, biomass, nitrogen cycling, and plant species composition data for sites in Wisconsin, Michigan,

New Hampshire, and Minnesota (Pastor and Post 1986), but apparently not for soil OM content. Two climate-change sensitivity analyses (Pastor and Post 1988, Post and Pastor 1996) demonstrated significant simulated interactions among temperature, N mineralization, species composition, and net primary productivity.

### *Forest-BGC and Biome-BGC*

Forest-BGC was developed to simulate C, water, and N cycles in forested ecosystems (Running and Coughlan 1988). The litterfall and decomposition elements of the model have an annual time step, while water balance and canopy gas exchange are modeled on a daily basis. The model includes two detrital soil OM pools: leaf plus root litter, and all other soil OM. Inputs into both pools come from leaves and roots, and the fraction of litterfall allocated to soil OM is determined by lignin content. Decomposition of large, woody components is not defined.

Forest-BGC initially used Meentemeyer's (1978) multiple regression to incorporate environmental and litter quality controls on decomposition of leaves and roots (Running and Coughlan 1988). A more recent version (Running and Gower 1991) calculates root and leaf decomposition based on climatic variables alone (Table 13.1); the source of these relationships is not clear from descriptive literature. Maximum litter decomposition is assumed to be  $0.5 \text{ (yr}^{-1}\text{)}$  and, like RothC and CENTURY, this maximum rate is then modified by temperature and moisture scalars. The temperature scalar ( $T_s$ ) is:

$$T_s = [\Sigma(T_d/365)]/T_{\text{opt}} \quad (13.4)$$

where  $T_d$  is daily soil temperature and  $T_{\text{opt}}$  is optimum soil temperature set at  $50^\circ\text{C}$  (Running 1994). The rate of soil OM decomposition is a fixed proportion of litter decomposition rates. Running and Gower (1991) and Running (1994) use a fractional constant of 0.03 (i.e., the decomposition rate of the soil OM pool is 3% of the litter pool decomposition rate).

Biome-BGC (Hunt et al. 1996), a recent version of Forest-BGC uses an entirely different decomposition equation but still contains one litter and one soil OM pool (Table 13.1). In Biome-BGC, litter decomposition is determined similarly to TEM: as a site-specific decomposition rate based on litter quality, modified by soil moisture and temperature scalars. Soil OM decomposition is modeled by modifying a fixed  $k$  value ( $0.00035 \text{ d}^{-1}$ ; actually a combination of slow and active  $k$ 's from CENTURY) by the same moisture and temperature scalars used for litter. The temperature scalar ( $T_s$ ) yields a  $Q_{10}$  of 2.4 (Figure 13.1) and is based on soil respiration data (Raich and Schlesinger 1992):

$$T_s = e^{[0.08755(T-26)]} \quad (13.5)$$

where  $T$  is soil temperature.

Forest-BGC has been tested for a range of sites across a climatic gradient in Oregon (Running 1994), focusing on aboveground net primary production, stem biomass, and leaf nitrogen concentration. Biome-BGC showed more sensitivity to combined climate and CO<sub>2</sub> change scenarios than CENTURY or TEM in a recent model comparison (VEMAP Members 1995); warming caused losses in soil organic C that led to total ecosystem C losses. An entirely new decomposition subroutine exists in the current, unpublished, Biome-BGC code (© 2000. Peter Thornton. Biome-BGC Version 4.1.1. Numerical Terradynamics Simulation Group, School of Forestry, University of Montana, Missoula, MT). This new version models decomposition almost identically to CENTURY, with seven soil OM pools decomposed by modifying fixed  $k_{\max}$  values with (again, new) moisture and temperature scalars.

### *FAEWE*

We selected one wetland simulation model (Van der Peijl and Verhoeven 1999) as an example of decomposition modeled for systems with rare moisture limitation. The model was developed as part of the Functional Analysis of European Wetland Ecosystems (FAEWE) project and simulates C, N, and P dynamics in freshwater wetlands on a weekly time-step. The C submodel simulates three detrital OM pools: above- and belowground plant litter, and all other soil OM. Only the soil OM pool produces CO<sub>2</sub>; the plant litter pools are inputs into the soil organic pool, but they do not respire. The model has been calibrated and run for only one site, a riverine grassland in southwestern England.

Like CENTURY, Forest-BGC, and RothC, FAEWE models decomposition by modifying a maximum decomposition rate ( $k_{\max}$ ) by temperature and moisture. However, in the wetland model,  $k_{\max}$  is not fixed; rather it is a function of the redox potential of the soil, the level of the groundwater, and the oxygen content of the soil atmosphere ( $k_{\max} = 7.7 \times 10^{-4}$  in anaerobic conditions and  $7.7 \times 10^{-5}$  in aerobic conditions). Temperature modifies  $k_{\max}$  through a ratio of temperature scalars (Table 13.1):

$$\text{Temperature effect} = T_{\text{as}}/T_{\text{ms}} \quad (13.6)$$

where  $T_{\text{as}}$  is based on actual soil temperature and  $T_{\text{ms}}$  is based on mean annual soil temperature via the following equation:

$$T_{\text{as}} \text{ or } T_{\text{ms}} = [0.003T * 10^{(10.93686-3259.18/T)}] / [1 + 10^{(-632.649+172713.1/T)} + 10^{(113.5406-34516.4/T)}] \quad (13.7)$$

where  $T$  is either actual or mean annual temperature in degrees Kelvin. These 0–1 scalar functions are described by an optimum temperature curve (Figure 13.1) that is based on absolute reaction-rate theory (Schoolfield et al. 1981). The maximum process rate is reached at approximately 30°C, and the left hand side of the curve is comparable to an exponential function with a  $Q_{10}$  near 2. This model has not been used to predict changes in soil C loss following global

climate change. A sensitivity analysis showed that the model is most responsive to changes in the growth rates of plants (Van der Peijl and Verhoeven 1999).

### Model Comparison I: Which Data Were Used?

One of the key questions we asked in evaluating models with respect to the temperature control over decomposition was: How similar were the data used to develop the models? RothC, CENTURY, and FAEWE base the temperature response on laboratory incubations across a range of temperatures under “optimum” moisture conditions. The incubations were conducted on litter, soils, and cellulose, and the models were originally developed for nonwoody ecosystems (grasslands, agroecosystems, and wetlands). These temperature relationships, generated from one substrate, are used to simulate all pools of OM. In addition, Roth-C and CENTURY are currently applied to all types of ecosystems, including forests (VEMAP Members 1995, King et al. 1997). Early Forest-BGC and Linkages both represent temperature-decomposition relationships using the forest-litter decomposition experiments from Meentemeyer (1978, 1984), Meentemeyer and Berg (1986) and Melillo et al. (1982). In more recent versions of Forest-BGC, the litter decay characteristics do not depend on litter quality, and soil OM decomposition is a constant percentage (3%) of litter decomposition. Finally, the temperature-decomposition relationships in TEM, Biome-BGC, and PnET-II were developed primarily from field data on soil respiration (warming experiments and interannual variability in undisturbed systems). The data represent both autotrophic and heterotrophic respiration but are being applied to heterotrophic respiration. Few data points exist above 22°C, and none below 0°C, though TEM and Biome-BGC are applied globally (Hunt et al. 1996; McGuire et al. 1997). As Daubenmire and Prusso (1963) and Niklińska et al. (1999) suggest, it is very likely that optimum temperatures for decomposition vary with the climate and evolutionary history of individual locations.

This review suggests that the temperature-decomposition relationships in modern biogeochemical models (assuming the models we reviewed are representative of the discipline) are based on just a few, imperfect data sources: environmental gradients in litter decomposition or soil respiration, or laboratory decomposition experiments. On one hand, these shortcomings are not surprising; there have been few, if any experiments that are completely appropriate for the development of relationships between OM decomposition and temperature (see Empirical Data Sources section), and model builders worked with the best data available. On the other hand, it is clear that these very restricted datasets (representing specific OM substrates, ecosystems, and climatic condition) have been used to generate models that are broadly applied outside the range of those datasets. We feel that there is a very strong need for long-term experimental data on the relationship of temperature to decomposition. Many such experi-

ments have been initiated (Rustad et al. 2001); the challenge now is to estimate decomposition rates (as opposed to CO<sub>2</sub> flux) from those experiments.

## Model Comparison II: Consensus Understanding of Temperature Controls on Decomposition?

The models evaluated in this chapter contain fundamentally different structures based on a few imperfect data sources. To test how variation in model structure affects simulated decomposition rates, we conducted a sensitivity analysis of decomposition to changing air (and soil) temperature. All models were parameterized for a single site, the Konza Prairie Long-Term Ecological Research Site in Kansas (Appendix A includes details regarding parameterization data [<http://www.ecostudies.org/cary9/appendicies.html>]). In most cases, only the decomposition equations (Table 13.1) were parameterized, but for models with complex C-pool structure (CENTURY and RothC), models were run to steady state to obtain pool sizes for the model-specific C fractions. We could not parameterize Linkages for this grassland site because species- and site-specific relationships determining critical N concentrations and net N mineralization rates were not available. We did not simulate interactions between temperature and C inputs; rather, we focused solely on decomposition.

There was great variability in the sensitivity of simulated decomposition rates to large changes in air temperature (Figure 13.2). At the mean annual air temperature for Konza (~ 13°C), decomposition rates varied by an order of magnitude (from 0.02 for TEM to 0.18 for CENTURY) among the models. For reference, field data for total net primary production (225 g C m<sup>-2</sup>yr<sup>-1</sup> both above and below ground; John Blair, Kansas State University, pers. comm.) and total soil C (5000 g C m<sup>-2</sup> in top 15 to 20 cm) suggest that actual decomposition rates at Konza are about 0.09 yr<sup>-1</sup>. However, soil depth varies greatly (from 10 to 200 cm) at Konza, so soil C values could be higher, and thus *k* values lower, in deeper soil profiles. Similarly, C inputs vary greatly as a result of wildfire, and lower inputs could decrease our calculated reference *k* value.

The shape of the response of *k* to changing temperature ranged from linear to exponential to unimodal. In general, the shape of the temperature scalar (Figure 13.1) could be used to predict the shape of the *k* response. Biome-BGC and PnET-II had exponential temperature scalars, and both showed exponential responses to changing temperature, although *k* values differed greatly between these two models. RothC had a linear temperature scalar over most of the range we analyzed, and *k* responded linearly to changes in temperature. Models with optimal temperature scalars (CENTURY and FAEWE, Figure 13.1) showed optimal responses to changing temperature. However, the peaks in *k* (between 18 and 20°C) did not coincide with maxima in the temperature scalars for these models (30 or 35°C). Two factors likely caused this shift in maximum decomposition. In both models, decomposition during some months (CENTURY) or

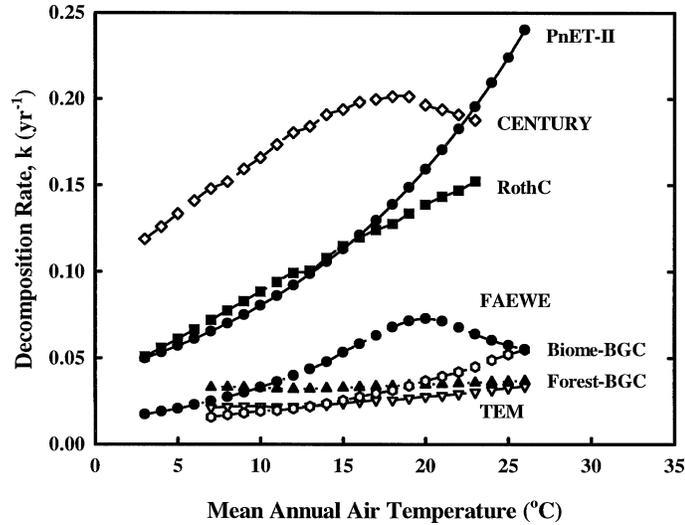


Figure 13.2. The relationship between temperature and mass specific decomposition at the Konza Prairie Long-Term Ecological Research site as simulated by seven biogeochemical models.

weeks (FAEWE) exceeded the optimum temperature, causing a decrease in annual  $k$  values at higher temperatures, and in CENTURY, the soil moisture scalar decreased  $k$  at higher temperatures.

In one model, the temperature scalar and  $k$  response curves did not have similar shapes. TEM has an exponential temperature scalar, but  $k$  changed only slightly with temperature and in our sensitivity analysis. The lack of temperature response in TEM resulted from a strong moisture limitation to decomposition. When we fixed  $W_s$  in TEM to reflect optimal soil moisture,  $k$  increased exponentially (from 0.02 to 0.09  $\text{yr}^{-1}$ ) with temperature.

Finally, in Forest-BGC the temperature scalar and  $k$  had similar shapes (linear), but both were insensitive to temperature changes. This model contains a site-specific temperature scalar that increased linearly from 0.31 to 0.44 at Konza. Similarly,  $k$  increased linearly from 0.033  $\text{yr}^{-1}$  near mean annual temperature to 0.038  $\text{yr}^{-1}$  at 15°C above mean temperature. When we optimized  $W_s$  (fixed soil moisture at field capacity) in Forest-BGC, the  $k$ -temperature relationship still varied only slightly with temperature, increasing from 0.034 to 0.049  $\text{yr}^{-1}$  over the entire range.

Many of the other models included moisture scalars in the decomposition equation. In these cases, moisture limitations dampened linear or exponential increases in  $k$  with temperature (Biome-BGC, RothC) or shifted the temperature at which  $k$  was greatest (CENTURY and FAEWE; see above). In PnET, soil

moisture has no direct effect on mass-specific soil respiration (here decomposition), so increases in temperature result in a simple  $Q_{10}$  response. Soil moisture would also affect actual (as opposed to mass-specific) decomposition in most of the models by affecting C inputs and thus pool sizes. In this temperature sensitivity analysis we avoided moisture effects on substrate availability; however, in a complete climate-change simulation, variation in moisture or any other factor that alters primary production might alter  $k$  if simulated C inputs change at a different rate than the C losses we are focusing on here.

Most of the models simulate decomposition by modifying a base or maximum  $k$  (e.g.,  $k_{\max}$  and  $k_Q$  in Table 13.1) by temperature and moisture scalars. Variations in these base or maximum  $k$  values lead to variation in the magnitude of  $k$  without affecting the shape of the  $k$ -temperature relationship. Direct connections between field data and these fixed  $k_{\max}$  or  $k_Q$  values were rarely available in model documentation. In some models, baseline  $k$ 's are calculated using litter quality (TEM and Biome-BGC). Thus, we assume that litterbag studies were important sources. In other cases, very recalcitrant OM pools are included, so we assume that  $^{14}\text{C}$  dating (RothC and CENTURY) was an important source.

In a final analysis of model consensus regarding temperature controls on decomposition, we calculated changes in the  $Q_{10}$  of the temperature scalars for each model over a range of temperatures (Fig. 13.3). The  $Q_{10}$  for a given temperature was calculated by dividing the scalar value at 5 degrees above the temperature of interest by the scalar value at 5 degrees below the temperature of interest [(scalar at  $T + 5^\circ\text{C}$ )/(scalar at  $T - 5^\circ\text{C}$ )]. This analysis assumes that temperature is the only factor affecting decomposition rates and that the  $Q_{10}$  of the scalar is equal to the  $Q_{10}$  of decomposition (which is true for the multiplicative scalars).

All of the models suggest that OM decomposition should have a  $Q_{10}$  between 1 and 3 over the temperature range of 17 to 22°C (Fig. 13.3). PnET, TEM, and Biome-BGC had constant  $Q_{10}$  values over the entire temperature range. All of the other models predict that decomposition is highly sensitive to temperature at low temperatures and less sensitive to temperature at higher temperatures. CENTURY and RothC show  $Q_{10}$  values greater than 4 for temperatures less than 10°C. Similarly, DAYCENT and FAEWE show large increases in  $Q_{10}$ 's for temperatures less than 5°C. At temperatures greater than 25°C, CENTURY, RothC, and DAYCENT suggest a  $Q_{10}$  near 1, and with FAEWE, it drops to zero.

Our review suggests three points of consensus in the way simulation models treat the temperature-decomposition relationship. First, there appears to be a consensus that a practical mathematical representation of decomposition is a fixed maximum or baseline rate modified over time by a series of temperature, moisture, and litter-quality scalars. Second, all models agree that the temperature scalar should increase with increasing temperature (at least up to 30°C) and that a  $Q_{10}$  of 1 to 3 is likely for temperatures between 17 and 22°C. Finally, the

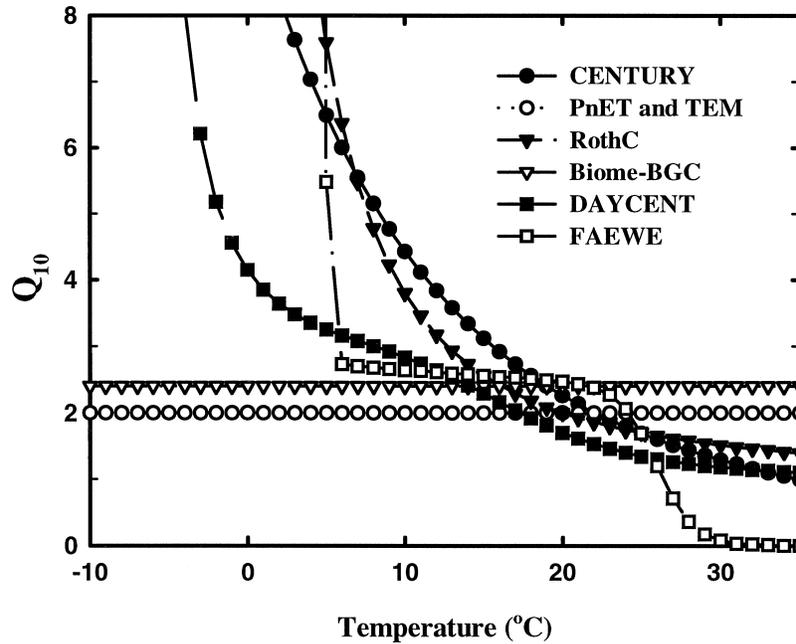


Figure 13.3. The relationship between temperature and the  $Q_{10}$  of temperature scalars used to calculate decomposition in the models evaluated in this chapter.

models agree that mass-specific decomposition is not negatively affected by increasing temperatures.

Beyond these (perhaps trivial) points of agreement, the models varied greatly. Carbon-pool structure ranged from a single detrital C pool to seven pools (Table 13.1). Temperature scalars were linear, exponential, optimal, or mixed (Figure 13.1). In some models moisture had no effect on  $k$ , but in others the moisture scalars caused  $k$  to remain constant with increasing temperature (Figure 13.2). Differences in these three factors (C-pool structure, temperature scalars, and moisture interactions) caused simulated  $k$  values to differ by an order of magnitude among the models. We conclude that there is little consensus among models in the response of  $k$  to temperature change and that this lack of consensus constrains our ability to predict ecosystem responses to global change. For example, in the VEMAP (1995) comparison, predicted terrestrial C storage ranged from -39 to +32% of current C storage depending on which biogeochemical model was used. The best way to reduce variability in simulated decomposition is not to make all models arbitrarily similar, but rather, to increase the amount of real OM decomposition data available to build and validate the models.

## Some Alternative Modeling Approaches

Our sense is that modeling is such an important activity for our discipline (Lauenroth et al. 1998 and this volume) that it is very important that a diversity of models be developed and tested. A diverse array of models provides alternate hypotheses that may stimulate further empirical investigations and augment our understanding of ecosystem behavior (Chapter 12). We suggest that two underused modeling approaches could yield insight into decomposition dynamics under climate-change scenarios. First, all of the models we evaluated represent decomposition as a series of discrete pools with different decomposition rates. However, another interpretation of decomposition is that OM decays through a continuum of stages starting with fresh litter and continuing through recalcitrant humus (Bossatta and Ågren 1991). A continuous, rather than discrete, interpretation of OM decomposition can be modeled by following individual cohorts of litter and calculating OM quality as a function of time, mass loss, or N concentration (Pastor and Post 1988; Bossatta and Ågren 1991). An important advantage of these models is that they could simultaneously predict changes in plant species composition and biogeochemistry under altered climates (Pastor and Post 1988). Currently, species changes are predicted from biogeography models, and biogeochemical changes are predicted in separate biogeochemical models such as those evaluated here (VEMAP Members 1995).

A second underused approach is to model discrete soil C pools with differential responses to changing temperature. The models we evaluated apply one temperature scalar to all detrital C pools. For example, in CENTURY passive OM decomposition uses the same temperature scalar as active OM decomposition. The assumption that all pools of OM respond similarly to temperature is contradicted by both theory and data (Trumbore et al. 1997; Ågren 2000; Giardina and Ryan 2000; Holland et al. 2000). In at least one case, simulating recalcitrant OM turnover with a weaker response to temperature improved the model agreement with a regional OM gradient (Liski et al. 1999), although this result may reflect the structure of the model more than a mechanistic explanation of the climate gradient (Ågren 2000). The models we evaluated also assumed that the temperature-decomposition relationship was constant across ecosystem types and climatic locations. A recent laboratory incubation suggests that this assumption is not always valid: decomposition of OM beneath Scots pine in northern Europe was more sensitive to changes in temperature than OM beneath Scots pine in southern Europe (Niklińska et al. 1999).

## Models as a Community Resource

Model builders have the unique responsibility of synthesizing theory and data from the greater scientific community into a cohesive representation of the state of knowledge in biogeochemistry. Model users (we acknowledge a false di-

chotomy here because many are both builders and users of models), in turn, have the responsibility of applying these models to test and develop biogeochemical theory and discover their implications for global change. Thus, we view models as resources, by which our collective knowledge is synthesized into working theories that are tested and retested through various applications. One goal of this model comparison was to evaluate certain models as tools for the scientific community.

It seems clear that model builders agree that models are a community resource; most models used for this review were readily available at websites with detailed documentation and instructions for use. It was relatively simple to run the models and dissect model structure to isolate the decomposition equations and parameters that controlled decomposition. It was much more difficult to determine the source of the empirical data used to develop the relationship that defined how temperature controls decomposition. In some cases we noticed significant changes in this functional relationship among papers that represented different versions of the models, but contained no descriptions of the data used to adjust those relationships. In other papers, we found detailed descriptions of the models and the functional influence of temperature on decomposition without citations of how the relationship was developed. Details were also lacking on the origin of  $k_{\max}$  and  $k_Q$  values. This lack of documentation placed constraints on our ability to evaluate the models and to test them on independent datasets (since we do not know what is independent).

## Synthesis

Perhaps the most important conclusion in our evaluation of decomposition-temperature relationships in current biogeochemical models is that they are based on a few, imperfect data sources. Litter decomposition, soil respiration, and laboratory incubations were the main sources of data used to develop temperature-decomposition relationships in the models we evaluated. Well-controlled field measurements of OM decomposition rates are exceedingly rare but are required to build more realistic decomposition algorithms.

The lack of field data was not the only cause of variability among models; similarities and differences in model structures were also important. Most models fix a maximum or baseline decomposition rate that is modified by temperature and moisture scalars. The temperature scalars all suggest that decomposition should increase with temperature; however, there is little agreement among models regarding the shape of the temperature-decomposition relationship. Scalar shape was a particularly important difference among the models because it usually predicted the shape of the  $k$ -temperature relationship. Finally, the origins of the temperature scalars and of maximum and baseline  $k$  values are poorly documented, making model comparison and validation difficult.

While there was some agreement among the models, our analysis suggests that there are sufficient differences to cast doubt on the solidity of our understanding of temperature-decomposition relationships. Clearly, temperature increases the decomposition rates of some soil OM, but we lack knowledge about the range of the response for parts of the globe that are very cool or very warm, and for recalcitrant pools of OM, which comprise most of the terrestrial C storage. Thus, modeled estimates of global changes in C due to warming will have a very high degree of variability and depend strongly upon the model used. Consequently, we suggest prudence in providing detailed simulation results on global warming to policy makers (Chapter 7). We also suggest that there is an exciting area of new research into the mechanistic control of decomposition by temperature.

### References

- Aber, J.D., C. Driscoll, C.A. Federer, R. Lathrop, G. Lovett, J.M. Melillo, P. Steudler, and J. Vogelmann. 1993. A strategy for the regional analysis of the effects of physical and chemical climate change on biogeochemical cycles in northeastern (U.S.) forests. *Ecological Modelling* 67: 37–47.
- Aber, J.D., and J. M. Melillo. 1980. Litter decomposition: Measuring relative contributions of organic matter and nitrogen to forest soils. *Canadian Journal of Botany* 58: 416–421.
- Aber, J.D., J.M. Melillo, K.J. Nadelhoffer, J. Pastor, and R.D. Boone. 1991. Factors controlling nitrogen cycling and nitrogen saturation in northern temperate forest ecosystems. *Ecological Applications* 1: 303–315.
- Aber, J.D., S.W. Ollinger, and C.T. Driscoll. 1997. Modeling nitrogen saturation in forest ecosystems in response to land use and atmospheric deposition. *Ecological Modelling* 101: 61–78.
- Aber, J.D., S.V. Ollinger, C.A. Federer, P.B. Reich, M.L. Goulden, D.W. Kicklighter, J.M. Melillo, and R.G. Lathrop. 1995. Predicting the effects of climate change on water yield and forest production in the northeastern United States. *Climate Research* 5: 207–222.
- Ågren, G. 2000. Temperature dependence of old soil organic matter. *Ambio* 29: 55.
- Ågren, G.I., M.U.F. Kirschbaum, D.W. Johnson, and E. Bossatta. 1996. Ecosystem physiology: Soil organic matter. Pp. 207–228 in A.I. Breymeyer, D.O. Hall, J.M. Melillo, and G.I. Ågren, editors. *Global Change: Effects on Coniferous Forests and Grasslands*. New York: John Wiley and Sons.
- Ayanaba, A., and D.S. Jenkinson. 1990. Decomposition of C-14-labeled ryegrass and maize under tropical conditions. *Soil Science Society of America Journal* 54: 112–115.
- Berg, B., G. Ekbohm, and C.A. McLaugherty. 1985. Lignin and hemicellulose relations during long-term decomposition of some forest litters. *Canadian Journal of Botany* 62: 2540–2550.
- Billings, W.D., J.O. Luken, D.A. Mortensen, and K.M. Peterson. 1982. Arctic

- tundra: A source or sink for atmospheric carbon dioxide in a changing environment? *Oecologia* 53: 7–11.
- Boone, R.D., K.J. Nadelhoffer, J.D. Canary, and J.P. Kaye. 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. *Nature* 396: 570–572.
- Bossatta, E., and G.I. Ågren. 1991. Dynamics of carbon and nitrogen in the organic matter of the soil: A generic theory. *American Naturalist* 138: 227–245.
- Bridgman, S.D., J. Pastor, K. Updegraff, T.J. Malterer, K. Johnson, C. Harth, and J. Chen. 1999. Ecosystem control over temperature and energy flux in northern peatlands. *Ecological Applications* 9: 1345–1358.
- Brumme, R. 1995. Mechanisms of carbon and nutrient release and retention in beech forest gaps. III. Environmental regulation of soil respiration and nitrous oxide emissions along a microclimatic gradient. *Plant and Soil* 168/169: 593–600.
- Burke, I.C., T.G.F. Kittel, W.K. Lauenroth, P. Snook, C.M. Yonker, W.J. Parton. 1991. Regional analysis of the central great plains, sensitivity to climate variability. *BioScience* 41: 685–692.
- Burke, I.C., C.M. Yonker, W.J. Parton, C.V. Cole, K. Flach, and D.S. Schimel. 1989. Texture, climate, and cultivation effects on soil organic matter content in U.S. grassland soils. *Soil Science Society of America Journal* 53: 800–805.
- Coleman, K., and D.S. Jenkinson. 1999. *RothC-26.3: A model for the turnover of carbon in soil*. Model description and Windows users guide. November 1999. Harpenden, UK: Lawes Agricultural Trust.
- Daubenmire, R., and D.C. Prusso. 1963. Studies of decomposition rates of tree litter. *Ecology* 44: 589–592.
- Drobnik, J. 1962. The effect of temperature on soil respiration. *Folia Microbiology* 7: 132–140.
- Epstein, H.E., I.C. Burke, and W.K. Lauenroth. 2002. Regional patterns of decomposition and primary production rates in the U.S. Great Plains. *Ecology* 83: 320327.
- Gholz, H.L., D.A. Wedin, S.M. Smitherman, M.E. Harmon, and W.J. Parton. 2000. Long-term dynamics of pine and hardwood litter in contrasting environments: Toward a global model of decomposition. *Global Change Biology* 6: 751765.
- Giardina, C.P., and M.G. Ryan. 2000. Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature* 404: 858–861.
- Grigal, D.F., and L.F. Ohmann. 1992. Carbon storage in upland forests of the Lake States. *Soil Science Society of America Journal* 56: 935–943.
- Harte, J., M.S. Torn, F.-R. Change, B. Feifarek, A.P. Kinzig, R. Shaw, and K. Shen. 1995. Global warming and soil microclimate: results from a meadow-warming experiment. *Ecological Applications* 5: 132–150.
- Hobbie, S.E., and F.S. Chapin. 1998. Response of tundra plant biomass, above-

- ground production, nitrogen, and CO<sub>2</sub> flux to experimental warming. *Ecology* 79: 1526–1544.
- Holland, E.A., J.C. Neff, A.R. Townsend, and B. McKeown. 2000. Uncertainties in the temperature sensitivity of decomposition in tropical and subtropical ecosystems: Implications for models. *Global Biogeochemical Cycles* 14: 1137–1151.
- Homann, P.S., P. Sollins, H.N. Chappell, and A.G. Stangenberger. 1995. Soil organic carbon in a mountainous, forested region: Relation to site characteristics. *Soil Science Society of America Journal* 59: 1468–1475.
- Hunt, H.W. 1977. A simulation model for decomposition in grasslands. *Ecology* 58: 469–484.
- Hunt, E.R. Jr., S.C. Piper, R. Nemani, C.D. Keeling, R.D. Otto, and S.W. Running. 1996. Global net carbon exchange and intra-annual atmospheric CO<sub>2</sub> concentrations predicted by an ecosystem process model and three-dimensional atmospheric transport model. *Global Biogeochemical Cycles* 10: 431–456.
- Jenkinson, D.S., and A. Ayanaba. 1977. Decomposition of carbon-14-labeled plant material under tropical conditions. *Soil Science Society of America Journal* 41: 12–915.
- Jenkinson, D.S., and J.H. Rayner. 1977. The turnover of soil organic matter in some of the Rothamsted classical experiments. *Soil Science* 123: 298–305.
- Katterer, T., M. Reichstein, O. Andren, and A. Lomander. 1998. Temperature dependence of organic matter decomposition: A critical review using literature data analyzed with different models. *Biology and Fertility of Soils* 27: 258–262.
- Kelly, R.H., W.J. Parton, M.D. Hartman, L.K. Stretch, D.S. Ojima, and D.S. Schimel. 2000. Intra-annual and interannual variability of ecosystem processes in shortgrass steppe. *Journal of Geophysical Research* 105 (D15): 20093–20100.
- Kicklighter, D.W., J.M. Melillo, W.T. Peterjohn, E.B. Rastetter, and A.D. McGuire. 1994. Aspects of spatial and temporal aggregation in estimating regional carbon dioxide fluxes from temperate forest soils. *Journal of Geophysical Research* 99: 1303–1315.
- King, A.W., W.M. Post, S.D. Wullschlegel. 1997. The potential response of terrestrial carbon storage to changes in climate and atmospheric CO<sub>2</sub>. *Climatic Change* 35: 199–227.
- Kirschbaum, M.U.F. 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. *Soil Biology and Biochemistry* 27: 753–760.
- . 2000. Will changes in soil organic carbon act as a positive or negative feedback on global warming? *Biogeochemistry* 48: 21–51.
- Lauenroth, W.K., C.D. Canham, A.P. Kinzig, K.A. Poiani, W.M. Kemp, and S.W. Running. 1998. Simulation modeling in ecosystem science. Pp. 404–415 in M.L. Pace and P.M. Groffman, editors. *Successes, Limitations, and Frontiers in Ecosystem Science*. New York: Springer-Verlag.

- Liski, J., H. Ilvesniemi, A. Makela, and C.J. Westman. 1999. CO<sub>2</sub> emissions from soil in response to climatic warming are overestimated: The decomposition of old soil organic matter is tolerant of temperature. *Ambio* 28: 171–174.
- Lloyd, J., and J. Taylor. 1994. On the temperature dependence of soil respiration. *Functional Ecology* 8: 315–323.
- McGuire, A.D., J.M. Melillo, D.W. Kicklighter, and L.A. Joyce. 1995. Equilibrium responses of soil carbon to climate change: Empirical and process-based estimates. *Journal of Biogeography* 22: 785–796.
- McGuire, A.D., J.M. Melillo, Y. Pan, X. Xiao, J. Jelfrich, B.I. Moore, C.J. Vörösmarty, and A.L. Schloss. 1997. Equilibrium responses of global net primary production and carbon storage to doubled atmospheric carbon dioxide: Sensitivity to changes in vegetation nitrogen concentration. *Global Biogeochemical Cycles* 11: 173–189.
- McKane, R.B., E.B. Rastetter, G.R. Shaver, K.J. Nadelhoffer, A.E. Giblin, J.A. Laundre, and F.S. Chapin. 1997. Climatic effects on tundra carbon storage inferred from experimental data and a model. *Ecology* 78: 1170–1187.
- Meentemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. *Ecology* 59: 465–472.
- . 1984. The geography of organic decomposition rates. *Annals of the Association of American Geographers* 74: 551–560.
- Meentemeyer, V., and B. Berg. 1986. Regional variation in rate of mass loss of *Pinus sylvestris* needle litter in Swedish pine forests as influenced by climate and litter quality. *Scandinavian Journal of Forest Research* 1: 167–180.
- Meentemeyer, V., J. Gardner, and E.O. Box. 1985. World patterns and amounts of detrital soil carbon. *Earth Surface Processes and Landforms* 10: 557–567.
- Melillo, J.M., J.D. Aber, and J.F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63: 621–626.
- Melillo, J.M., A.D. McGuire, D.W. Kicklighter, B. Moore III, C.J. Vörösmarty, and A.L. Schloss. 1993. Global climate change and terrestrial net primary production. *Nature* 363: 234–240.
- Moorhead, D.L., W.S. Currie, E.B. Rastetter, W.J. Parton, and M.E. Harmon. 1999. Climate and litter quality controls on decomposition: An analysis of modeling approaches. *Global Biogeochemical Cycles* 13: 575–589.
- Nakane, K., T. Kohno, and T. Horikoshi. 1996. Root respiration rate before and just after clear-felling in a mature, deciduous, broad-leaved forest. *Ecological Research* 11: 111–119.
- Niklińska, M., M. Maryański, and R. Laskowski. 1999. Effect of temperature on humus respiration rate and nitrogen mineralization: Implications for global climate change. *Biogeochemistry* 44: 239–257.
- Olson, J.S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44: 322–331.
- Parton, W.J., D.S. Ojima, C.V. Cole, and D.S. Schimel. 1994. A general model for soil organic matter dynamics: Sensitivity to litter chemistry, texture, and

- management. *Quantitative Modeling of Soil Forming Processes*, SSSA Special Publication 39: 147–167.
- Parton, W.J., D.W. Anderson, C.V. Cole, and J.W.B. Stewart. 1983. Simulation of soil organic matter formations and mineralization in semiarid agroecosystems. Pp. 533–550 in R.R. Lowrance, R.L. Todd, L.E. Asmussen, and R.A. Leonard, editors. *Nutrient Cycling in Agricultural Ecosystems*. Special Publication No. 23. Univ. of Georgia. College of Agricultural Experiment Stations. Athens, GA.
- Parton, W.J., D.S. Schimel, C.V. Cole, and D.S. Ojima. 1987. Analysis of factors controlling soil organic matter levels in great plains grasslands. *Soil Science Society of America Journal* 51: 1173–1179.
- Parton, W.J., J.M.O. Scurlock, D.S. Ojima, D.S. Schimel, D.O. Hall, and SCOPEGRAM members. 1995. Impact of climate change on grassland production and soil carbon worldwide. *Global Change Biology* 1: 13–22.
- Pastor, J., and W.M. Post. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. *Biogeochemistry* 2: 3–27.
- . 1988. Response of northern forests to CO<sub>2</sub>-induced climate change. *Nature* 334: 55–58.
- Paul, E.A., and F. Clark. 1996. *Soil Microbiology and Biochemistry*. New York: Academic Press.
- Paul, E.A., R.F. Follett, S.W. Leavitt, A. Halvorson, G.A. Peterson, and D.J. Lyon. 1997. Radiocarbon dating for determination of soil organic matter pool sizes and dynamics. *Soil Science Society of America Journal* 61: 1058–1067.
- Peterjohn, W.T., J.M. Melillo, F.P. Bowles, and P.A. Steudler. 1993. Soil warming and trace gas fluxes: Experimental design and preliminary flux results. *Oecologia* 93: 18–24.
- Post, W.M., W.R. Emanuel, P.J. Zinke, and A.G. Stangenberger. 1982. Soil carbon pools and world life zones. *Nature* 298: 156–159.
- Post, W.M., and J. Pastor. 1996. Linkages: An individual-based forest ecosystems model. *Climatic Change* 34: 253–261.
- Raich, J.W., E.B. Rastetter, J.M. Melillo, D.W. Kicklighter, P.A. Steudler, B.J. Peterson, A.L. Grace, B.I. Moore, and C.J. Vörösmarty. 1991. Potential net primary productivity in South America: Application of a global model. *Ecological Applications* 1: 399–429.
- Raich, J.W., and W.S. Schlesinger. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus* 44B: 81–99.
- Rastetter, E.B., M.G. Ryan, G.R. Shaver, J.M. Melillo, K.J. Nadelhoffer, J.E. Hobbie, and J.D. Aber. 1991. A general biogeochemical model describing the responses of the C and N cycles in terrestrial ecosystems to changes in CO<sub>2</sub>, climate, and N deposition. *Tree Physiology* 9: 101–126.
- Reiners, W.A. 1968. Carbon dioxide evolution from the floor of three Minnesota forests. *Ecology* 49: 471–483.

- Running, S.W. 1986. Global primary production from terrestrial vegetation: Estimates integrating satellite remote sensing and computer simulation technology. *Science of the Total Environment* 56: 233–242.
- . 1994. Testing Forest-BGC ecosystem process simulations across a climatic gradient in Oregon. *Ecological Applications* 4: 238–247.
- Running, S.W., and J.C. Coughlan. 1988. A general model of forest ecosystem process for regional applications. I. Hydrologic balance, canopy gas exchange and primary production processes. *Ecological Applications* 42: 125–54.
- Running, S.W., and S.T. Gower. 1991. Forest-BGC, a general model of forest ecosystem processes for regional applications. II. Dynamic carbon allocation and nitrogen budgets. *Tree Physiology* 9: 147–160.
- Rustad, L.E., J.L. Campbell, G.M. Marion, R.J. Norby, M.J. Mitchell, A.E. Hartley, J.H.C. Cornelissen, and J. Gurevitch. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126: 543–562.
- Rustad, L.E., and I.J. Fernandez. 1998. Experimental soil warming effects on CO<sub>2</sub> and CH<sub>4</sub> flux from a low elevation spruce-fir forest soil in Maine, USA. *Global Change Biology* 4: 597–605.
- Ryan, M.G., E.R. Hunt Jr., R.E. McMurtrie, G.I. Ågren, J.D. Aber, A.D. Friend, E.B. Rastetter, W.M. Pulliam, R.J. Raison, and S. Linder. Comparing models of ecosystem function for temperate conifer forests. I. Model description and validation. Pp. 313–362 in A.I. Breymeyer, D.O. Hall, J.M. Melillo, and G.I. Ågren, editors. *Global Change: Effects on Coniferous Forests and Grasslands*. New York: John Wiley and Sons.
- Saleska, S.R., J. Harte, and M.S. Torn. 1999. The effect of experimental ecosystem warming on CO<sub>2</sub> fluxes in a montane meadow. *Global Change Biology* 52: 125–141.
- Schimel, D.S., J. Melillo, H.Q. Tian, A.D. McGuire, D. Kicklighter, T. Kittel, N. Rosenbloom, S. Running, P. Thornton, D. Ojima, W. Parton, R. Kelly, M. Sykes, R. Neilson, and B. Rizzo. 2000. Contribution of increasing CO<sub>2</sub> and climate to carbon storage by ecosystems in the United States. *Science* 287: 2004–2006.
- Schlesinger, W.H. 1977. Carbon balance in terrestrial detritus. *Annual Review of Ecology and Systematics* 8: 51–81.
- Schlesinger, W.H., and J.A. Andrews. 2000. Soil respiration and the global carbon cycle. *Biogeochemistry* 48: 7–20.
- Schoolfield, R.M., P.J.H. Sharpe, and C.E. Magnuson. 1981. Non-linear regression of biological temperature-dependent rate models based on absolute reaction-rate theory. *Journal of Theoretical Biology* 88: 719–731.
- Shaver, G.R., W.D. Billings, F.S. Chaplin III, A.E. Giblin, K.J. Nadelhoffer, W.C. Oechel, and E.B. Rastetter. 1992. Global change and the carbon balance of arctic ecosystems. *BioScience* 42(6): 433–441.
- Singh, J.S., and S.R. Gupta. 1977. Plant decomposition and soil respiration in terrestrial ecosystems. *Botanical Review* 43: 449–528.

- Sorenson, C.H. 1981. Carbon-nitrogen relationships during the humification of cellulose in soils containing different amounts of clay. *Soil Biology and Biochemistry* 13: 313–321.
- Thornthwaite, C.W., and J.R. Mather. 1955. The water balance. *Publications in Climatology* 8: 1–104.
- Townsend, A.R., P.M. Vitousek, D.J. Desmarais, and A. Tharpe. 1997. Soil carbon pool structure and temperature sensitivity inferred using CO<sub>2</sub> and <sup>13</sup>CO<sub>2</sub> incubation fluxes from five Hawaiian soils. *Biogeochemistry* 38: 1–17.
- Townsend, A.R., P.M. Vitousek, and S.E. Trumbore. 1995. Soil organic matter dynamics along gradients in temperature and land use on the island of Hawaii. *Ecology* 76(3): 721–733.
- Trumbore, S.E., O.A. Chadwick, and R. Amundsen. 1997. Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. *Science* 272: 393–396.
- Van der Peijl, M.J., and J.T.A. Verhoeven. 1999. A model of carbon, nitrogen and phosphorus dynamics and their interactions in river marginal wetlands. *Ecological Modelling* 118: 95–130.
- Van Veen J.A., and E.A. Paul. 1981. Organic carbon dynamics in grasslands soils. 1. Background information and computer simulation. *Canadian Journal of Soil Science* 61: 185–201.
- VEMAP Members. 1995. Vegetation/ecosystem modeling and analysis project: Comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO<sub>2</sub> doubling. *Global Biogeochemical Cycles* 9: 407–437.
- Vitousek P.M., D.R. Turner, W.J. Parton, and R.L. Sanford. 1994. Litter decomposition on the Mauna Loa environmental matrix, Hawaii patterns, mechanisms, and models. *Ecology* 75: 418–429.