

Climate and litter quality controls on decomposition: An analysis of modeling approaches

D. L. Moorhead,^{1,2} W. S. Currie,^{3,4} E. B. Rastetter,⁴ W. J. Parton,⁵ and M. E. Harmon⁶

Abstract. Four mathematical models simulated decay of two litter types of contrasting quality over a 2-year period at four sites in North America. The litter types were *Drypetes glauca* and *Triticum aestivum*, representing litter with high and low nitrogen:lignin ratios, respectively. The field sites were an Arctic tussock tundra (Alaska, United States), a warm desert (New Mexico, United States), a temperate deciduous forest (New York, United States) and a tropical rain forest (Puerto Rico). Models captured the overall patterns of site and litter quality controls on decomposition; both simulated and observed mass losses were higher in warm, moist environments (both forests) than in cold (tundra) or dry sites (desert), and simulated and observed decay was more rapid for *Drypetes* than *Triticum*. However, predictions tended to underestimate litter mass loss in the tropical forest and overestimate decay in the desert and tundra, suggesting that site controls in model formulations require refinement for use under such a broad range of conditions. Also, predicted nitrogen content of litter residues was lower than observed in *Drypetes* litter and higher than observed for *Triticum*. Thus mechanisms describing loss of nitrogen from high-quality litter and nitrogen immobilization by low-quality litter were not captured by model structure. Individual model behaviors revealed different sensitivities to controlling factors that were related to differences in model formulation. As these models represent working hypotheses regarding the process of litter decay, results emphasize the need for greater resolution of climate and litter quality controls. Results also demonstrate the need for finer resolution of the relationships between carbon and nitrogen dynamics during decomposition.

1. Introduction

The balance between primary production and decomposition is an important aspect of ecosystem dynamics, with the decomposition of dead organic matter playing a key role in determining nutrient availabilities and soil carbon stores. Among the many controls on decomposition, litter quality and climate are probably the best known and most studied. *Olson* [1963] showed that the overall decay rate of litter diminished as decomposition progressed, *Minderman* [1968] was among the first to note that different chemical constituents of litter decayed at different rates, and *Meentmeyer* [1978] demonstrated that interactions between climatic factors and initial litter quality were primary determinants of litter decay. Others have expanded our knowledge of these phenomena [e.g., *Melillo et*

al., 1982; *McClougherty et al.*, 1985; *Aber et al.*, 1990; *Harmon et al.*, 1990], and a general paradigm has emerged: decay rates tend to increase with moisture, temperature, and initial litter nitrogen concentration, while they decrease for initial lignin content.

Human activities are modifying the global environment through the enhanced deposition of nutrients, elevated atmospheric CO₂ concentrations, higher levels of UVB radiation at the Earth's surface, and shifts in global climate. Decomposition should respond directly to changes in climate, whereas litter quality may change as a consequence of altered tissue chemistry and species composition of plant communities, as plants respond to global changes. Past investigations provide limited insight into the possible impacts of these changes on litter decay because experiments usually examined a narrow range of litter types and site conditions. In contrast, many types of environmental changes are occurring concurrently over broad temporal and spatial scales. Thus most ecosystems are being subjected to many, simultaneous changes [*Vitousek*, 1994].

Recently, studies have begun to address decomposition processes in a broader context of site, climate, and litter quality interactions, including the Long-Term Intersite Decomposition Experiment Team (LIDET) [*LIDET*, 1995] in the United States, Decomposition Study (DECO) [*Berg et al.*, 1993] in Europe, and Canadian Intersite Decomposition Experiment Team (CIDET) [*Trofymow et al.*, 1995] in Canada. In these experiments, litter types spanning a range of initial quality characteristics have been placed in ecosystems that differ in cli-

¹Now at Department of Biological Sciences, University of Toledo, Toledo, Ohio.

²Department of Biological Sciences, Texas Tech University, Lubbock.

³Now at Appalachian Laboratory, University of Maryland Center for Environmental Science, Frostburg.

⁴The Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts.

⁵Natural Resource Ecology Laboratory, Colorado State University, Fort Collins.

⁶Department of Forest Science, Oregon State University, Corvallis.

matic and edaphic features. A central goal of these investigations is to elucidate patterns of site and litter quality controls on decay by monitoring decomposition over many years (usually ≥ 10 years). Because several litter types have been exchanged between a number of sites, results of these studies may be used to evaluate possible changes in litter decay and nutrient dynamics at particular sites in the face of changing climate and litter quality.

Mathematical models are being used to predict decay patterns as an integral part of the LIDET study. The central objective of the modeling component of this study is to evaluate the generality of mathematical approaches commonly used to describe litter decay. As such models were developed to portray decomposition processes, they represent working hypotheses, expressed in formal mathematical terms, that can be refuted or corroborated by experimental data. Herein, we report the results of a suite of "blind" tests of four models of litter decay. Each model was used to simulate decay of two litter types of contrasting quality over the first 2 years of incubation at four sites of wide geographic distribution and different climate regimes. Only after simulations were completed were the experimental data made available for comparisons. Our primary goals in this exercise were (1) to evaluate model applications to the novel conditions represented by the LIDET field study and (2) to elucidate the effects of model structure on the manner in which interactions between site and litter quality are expressed. To our knowledge, this represents the most critical evaluation of decomposition models ever conducted.

2. Methods and Model Descriptions

2.1. Experimental Study

The Long-Term Intersite Decomposition Experiment Team is monitoring the decay of several different litter types on sites throughout North America [LIDET, 1995]. In brief, litter was collected, dried, weighed, placed in nylon mesh litter bags, and then placed at all sites. Litter bags are collected every year and returned to the Forest Science Laboratory at Oregon State University, United States, for carbon fraction analysis (extractives, holocellulose, and lignin contents), total N, and ash weight. A subset of litter types was deployed at all sites to facilitate comparisons of site and litter quality controls on subsequent decay.

For the purposes of the present study, the decay of two litter types on four sites was examined with four simulation models. Foliage from the tropical broadleaf tree (*Drypetes glauca*) and temperate cereal grain (*Triticum aestivum*) were chosen to represent litter types with contrasting C:N and N:lignin ratios (commonly used as indices of litter quality). The selected sites include a broad range of climatic conditions: (1) an Arctic tussock tundra in northern Alaska, United States (Arctic Tundra), (2) a temperate deciduous forest in New York, United States (Harvard Forest), (3) a warm desert in southern New Mexico, United States (Jornada), and (4) a subtropical rain forest in Puerto Rico (Luquillo). This combination encompasses the range of litter types and site conditions addressed by the full LIDET experiment.

2.2. Modeling Approaches

Four models were used to simulate litter decay in this experiment (Figure 1): CENTURY [Parton *et al.*, 1987], Marine

Biology Laboratory General Ecosystem Model (MBL-GEM) [Rastetter *et al.*, 1991], General Decomposition Model (GENDEC) [Moorhead and Reynolds, 1991], and Dissolved Organic Carbon Model (DOCMOD) [Currie and Aber, 1997]. In each of these models, litter decomposes at rates determined by litter quality (carbon fractions) and climatic conditions. In all but DOCMOD, nitrogen availability also affects litter decay. Flows of carbon and nitrogen are linked to simulate net immobilization or mineralization of nitrogen. While many other models exist, including those with more and less mechanistic detail, this suite of models was chosen for study because they contain enough mechanisms to address some of the specific processes underlying decomposition and yet do not demand parameters that could not be obtained from the LIDET experiment. Moreover, these models already have been applied to novel situations or conditions beyond those for which they were developed [e.g., Burke *et al.*, 1989; Rastetter *et al.*, 1992; Shaver *et al.*, 1992; Moorhead and Reynolds, 1993a; Ojima *et al.*, 1993], so we were confident that they were flexible enough to use in the present study.

These models initially were developed to simulate decomposition of different litter types under different climate regimes at different sites: (1) CENTURY originally was developed for prairie regions of the United States [Parton *et al.*, 1987], (2) MBL-GEM was designed for tundra and temperate forests [Rastetter *et al.*, 1991], (3) GENDEC was developed for warm deserts [Moorhead and Reynolds, 1991], and (4) DOCMOD was designed for temperate forests [Currie and Aber, 1997]. Although these models share some general features, they depict the controls exerted by litter quality, climate, and nutrient availabilities on decomposition processes in different ways. Thus a comparison between model behaviors, given the same litter and site characteristics, will serve to test the assumptions built into each. Testing each model also serves to test the conceptual views of decomposition processes that each model represents.

Unfortunately, data available from LIDET study sites were insufficient to provide the detailed climate drivers used in some of the original model formulations. For example, GENDEC was developed to use daily observations of litter moisture and temperature values, which were not collected for these experiments. To control for the effects of incomplete climate data on the present modeling study, a common climate driver was used in all models (DEFAC, Figure 2). This climate driver is described in detail by Parton *et al.* [1987] and incorporates the effects of (1) the ratio of monthly precipitation to potential evapotranspiration and (2) monthly average soil temperature, on decay rates. Although this aggregate approach might affect some models more than others, it does provide a common basis for application. Detailed explanations of model development, structure, and validation are published elsewhere, but an overview of each model follows.

2.2.1. CENTURY. The CENTURY soil organic matter model originally was designed to calculate litter decay in prairie ecosystems (Figure 1a) [Parton *et al.*, 1987]. This model explicitly identifies five pools of organic matter: (1) a labile litter fraction (X_1), (2) a structural litter component (X_2), (3) microbial biomass (X_4), (4) a soil organic matter fraction with slow turnover (X_5), and (5) a very recalcitrant soil organic matter (SOM) pool (X_6). Flow rates of carbon from pools are modified by an abiotic climatic factor (DEFAC) that re-

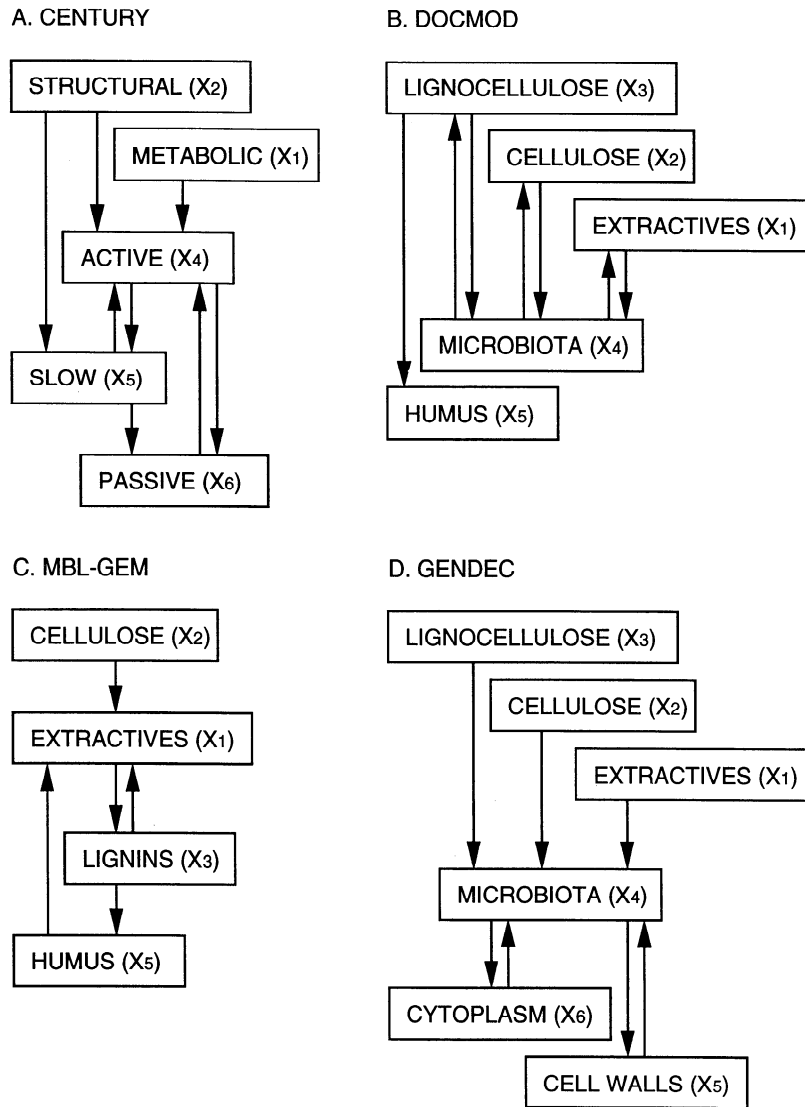


Figure 1. Carbon flow diagrams for models (a) CENTURY, (b) Dissolved Organic Carbon Model (DOCMOD), (c) Marine Biological Laboratory General Ecosystem Model (MBL-GEM), and (d) General Decomposition Model (GENDEC).

duces decomposition under less than optimal environmental conditions. Also, carbon and nitrogen dynamics are closely coupled so that low nitrogen availability can constrain rates of carbon turnover. The flow of carbon from each dead organic matter pool (C_s , substrate $s = 1, 2, 4, 5, 6$) is calculated as follows:

$$dC_s/dt = -k_s C_s S_{MT} N_s \quad (1)$$

where k_s is the maximum decay rate for substrate s , and S_{MT} and N_s are scalar multipliers representing the effects of climate and nitrogen limitations, respectively.

Plant residue is divided into structural and metabolic material as a function of the initial lignin:nitrogen ratio of the litter. The structural material is resistant to decomposition and includes lignin, cellulose, and hemicellulose. The metabolic fraction is readily decomposable. Maximum decay rates of 4.5 and 18.5 yr^{-1} are used for structural and metabolic materials, respectively. The decomposition rate of the structural material is further modified as a function of lignin:cellulose ratio, with

lower decomposition rates at higher ratios. The model assumes that lignin is transferred directly to a slowly cycling organic matter pool when structural material is decomposed (a 30% loss of carbon through respiration accompanies this flow). Microbial biomass in the surface litter is created from the metabolic and nonlignin structural material with a microbial growth efficiency of 45% (that is, 55% of the carbon is lost as CO_2). A maximum loss rate of 7.3 yr^{-1} is assumed for microbiota (60% as CO_2) with dead microbial material (cell walls, etc.) being transferred to the slow organic matter pool. The maximum loss rate of slow soil organic matter is 2 yr^{-1} (55% as CO_2). All decomposition flows are controlled by the abiotic decomposition factor that is the product of soil temperature and soil moisture limitations (DEFAC). The model runs on a weekly time step.

Nitrogen flows in the model follow carbon flows and are equal to the product of the carbon flow and N:C ratio of the recipient pool. The C:N ratio of microbes is assumed to be a lin-

car function of nitrogen content of the material being decomposed; it increases from 12 to 22 as the nitrogen content of litter decreases from 2% to 0.1%. The C:N ratio of slow SOM is equal to C:N ratio of surface microbes plus 6 (these ratios were determined by fitting the model to rates of litter decay:nitrogen mineralization observed in other experiments). The C:N ratio of structural material is fixed at 150, while the C:N ratio of metabolic residue varies with the overall nitrogen content of the litter. Nitrogen associated with the carbon lost as microbial respiration is mineralized and flows into a soil mineral pool ($\text{NO}_3 + \text{NH}_4$). Immobilization of nitrogen from the soil occurs if carbon flow requires additional nitrogen to maintain the specified C:N ratio; the carbon flow is set to zero where there is no mineral nitrogen available. The decomposition of structural material usually results in nitrogen immobilization, while turnover of microbes and slow SOM mineralizes nitrogen.

2.2.2. DOCMOD. The DOCMOD model was developed to simulate the combined processes of litter decay, humification, and leaching in humid forested regions [Currie and Aber, 1997] and includes the following five pools of organic matter: (1) an extractable litter fraction (X_1), (2) unprotected holocellulose (X_2 , cellulose + hemicelluloses), (3) lignocellulose (X_3), (4) microbial biomass (X_4), and (5) a soil humic pool (X_5). Carbon flow from each litter pool (C_s , substrate $s = 1, 2, 3$) occurs through the exponential decay of each pool, modified according to climate:

$$dC_s/dt = -k_s C_s S_{MT} \quad (2)$$

where k_s is the decay rate of substrate s , and S_{MT} is the scalar multiplier representing the effect of climate limitations. For the purposes of the present study, climate effects were represented by the value of DEFAC (previously discussed). The model operates on a monthly time step (Figure 1b).

The three litter fractions in this model are defined by proximate carbon-fractionation analysis of whole litter, i.e., as extractable, acid-soluble ("holocellulose") and acid-insoluble ("lignin") materials [Ryan et al., 1990]. All of the acid-insoluble material, together with an equivalent amount of

acid-soluble material, is allocated to the lignocellulose pool and represents a recalcitrant litter fraction. All of the remaining acid-soluble material is allocated to the unprotected holocellulose pool. Decay coefficients k_s are calculated at each iteration, based on the litter lignocellulose index (LCI) [which equals lignin + (lignin + holocellulose)], because LCI changes as decomposition proceeds [Aber et al., 1990]. The mass loss from each litter pool is multiplied by the microbial production:respiration ratios for each litter type to estimate microbial growth. Microbial turnover in each month is equal to 63% of microbial biomass production [Gregorich et al., 1991], with dead microbial mass allocated to the litter pools according to the chemical composition of the microbiota. Each month, a quantity equal to one third of the mass lost from the lignocellulose pool through decomposition is transferred to the humus pool. For the purposes of the current exercise, the humus pool undergoes insignificant decay over a 2-year span.

Nitrogen pools and transfers are linked to carbon pools and fluxes (Figure 1b). Nitrogen in plant litter is associated with lignocellulose and extractable materials. The lignocellulose pool has a C:N ratio equal to the C:N ratio of overall litter; the remainder of the nitrogen in litter is allocated to the extractives pool [Aber et al., 1984]. All but two nitrogen transfers are calculated as the product of carbon transfer and the N:C ratio of the source pool. The exceptions are immobilization of nitrogen by the lignocellulose pool and sequestering of nitrogen in humus, although the latter process is insignificant over the short time frame addressed in this exercise. Immobilization of nitrogen in the lignocellulose pool is controlled by the initial concentration of nitrogen in this pool at the start of each year; low values drive immobilization, while high values result in mineralization [Aber and Melillo, 1982; Aber et al., 1984; McClagherty et al., 1985; White et al., 1988; Johnson, 1992]:

$$I = 0.014 - 0.95 N_{lc} \quad (3)$$

where I is the amount of nitrogen immobilized per unit of lignocellulose and N_{lc} is the nitrogen concentration of the lignocellulose pool. With microbial turnover, nitrogen is transferred to the pools of extractives and cellulose [Aber et al., 1984] and indirectly to the lignocellulose pool via (3). Exogenous nitrogen, together with any nitrogen mineralized during short-term decay, enters a soil mineral pool that is available for immobilization.

Microbial growth is primarily limited by the availability of decomposable carbon substrates. This is affected through calculation of microbial production as the product of mass loss in each carbon fraction and the production:respiration ratio for the fraction. Nitrogen limitation of microbial growth can occur if litter is high in labile material (extractives) and either the nitrogen content of litter is low ($\leq 0.8\%$) or mineral nitrogen supply is low. When nitrogen limitation of microbial growth occurs, mass is still lost from each litter fraction but the carbon is assumed to be mineralized to CO_2 . This reduces the transfer of carbon to the pools representing microbiota and, subsequently, microbial products.

The net loss of mass from the system occurs through CO_2 efflux and leaching of dissolved organic matter (DOM). For the purposes of this exercise, we are concerned only with total mass loss, so the distinction between carbon outputs is not important.

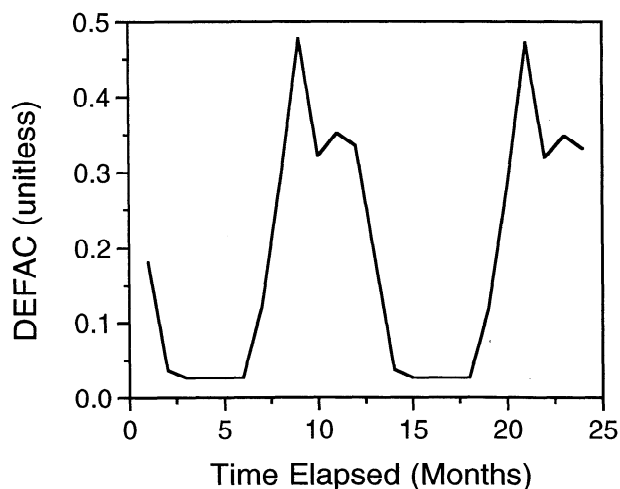


Figure 2. Monthly values of climate driver (DEFAC) used to drive decay rates in the Wisconsin simulations (study began on November 3, 1980).

2.2.3. MBL-GEM. The decomposition module in MBL-GEM is described by *Rastetter et al.* [1991] (Figure 1c) and consists of four organic carbon pools and associated nitrogen pools: (1) extractives (X_1 , hot water and dichloromethane), (2) cellulose (X_2 , acid soluble), (3) lignin (X_3 , acid insoluble), and (4) humus (X_5 , older soil organic matter). The C:N ratios of all but the extractives pool are constant. Organic matter enters the extractives pool from a variety of sources, and thus the C:N ratio of the extractives pool may change through time, asymptotically approaching the overall C:N ratio of materials entering from other pools.

Transformations among the carbon fractions are controlled by temperature, soil moisture, nitrogen availability, microbial efficiency, and the lignocellulose index (LCI):

$$T_{ij} = d_{ij} b_{ij} S_{MT} C_i [\exp(-a_i \text{LCI})] N_m / (k_{ij} + N_m) \quad (4)$$

where T_{ij} is the transformation of carbon from pool i to pool j , d_{ij} is a rate constant (month^{-1}), b_{ij} is the microbial substrate utilization efficiency (unitless), S_{MT} is the scalar multiplier representing the effect of climate limitations (with values of DEFAC used in these simulations), a_i is LCI shielding parameter (unitless), LCI is lignocellulose ratio (unitless), C_i is the amount of carbon in pool i (g C m^{-2}), N_m is the inorganic nitrogen availability (g N m^{-2}), and k_{ij} is the half-saturation constant for nitrogen immobilization (g N m^{-2}). The value of a_i is zero when pool i is either lignin or humus, and k_{ij} is zero for transformations where there is a net mineralization of nitrogen. Losses as CO_2 associated with transformation T_{ij} equal $T_{ij} (1 - b_{ij})/b_{ij}$. Nitrogen is lost from pool i at a rate $R_i T_{ij}$ and is gained by pool j at a rate $R_j T_{ij}$, where R_i and R_j are the N:C ratios of pools i and j , respectively. In the case where pool j is extractives, R_j is the N:C ratio of organic matter transformed into extractives, not of extractives. Thus the N:C ratio of the extractives pool is variable, as determined by the N:C ratios of incoming materials.

2.2.4. GENDEC. The GENDEC model is described in detail by *Moorhead and Reynolds* [1991] and recognizes six pools of carbon and nitrogen, including (1) labile plant compounds (X_1), (2) holocellulose (X_2 , cellulose + hemicellulose), (3) resistant plant compounds (X_3 , lignins), (4) live microbial biomass (X_4), (5) dead microbial cell walls (X_5), and (6) dead microbial cytoplasm (X_6). Nitrogen flows are assumed to balance calculated carbon flows, given the N:C ratios of decomposing materials (Figure 1d). The loss of carbon from each dead organic matter pool (C_s , $s = 1, 2, 3, 5, 6$) is a function of moisture and temperature conditions and N limitation:

$$dC_s/dt = -k_s C_s S_{MT} N_s \quad (5)$$

where k_s is the intrinsic decay rate coefficient for substrate s and S_{MT} and N_s are scalar multipliers representing climatic and nutrient controls, respectively. The total quantities of carbon and nitrogen available for microbial use consist of the sum of all losses from dead organic matter pools, while available nitrogen also includes mineral forms. The model runs on a daily time step.

Microbial dynamics are modeled as four processes: (1) growth, (2) respiration, (3) death, and (4) net mineralization or immobilization of nitrogen (see below). Microbial growth and respiration are driven by total carbon losses from the litter, assuming a carbon assimilation efficiency of 60% and the rest is lost as CO_2 . Microbial mortality consists of two parts, a frac-

tion of the standing biomass ($0.1\% \text{ d}^{-1}$) and a fraction (20%) of daily growth [*Parnas*, 1975].

The flow of carbon from nutrient-limited substrates (such as cellulose) is controlled by the availability of nitrogen from other sources. This is because the internal nitrogen content of such pools is insufficient to meet microbial needs in association with potential carbon losses (based on k and S_{MT}). This effect is given by the scalar N_s in (5) and is determined by balancing carbon and nitrogen requirements of the decomposer microorganisms. In essence, decay is not limited by the relative availability of either carbon or nitrogen when the C:N ratio of the microbiota is equal to the product of the microbial assimilation efficiency and the C:N ratio of the litter pool. If this product is larger than the microbial C:N ratio, the system is N limited; otherwise, the system is limited by carbon. Potential net immobilization and mineralization of nitrogen also are calculated according to (5), based on estimates of nitrogen deficiency or excess.

2.3. Calibration Study

An initial suite of simulations was performed to verify that a common set of data could provide needed parameter values and driving variables for all models and that all models exhibited reasonable behavior within these restrictions. This served as a calibration suite of simulations in which a single climate scalar (DEFAC) was substituted for the various representations of climatic effects on decomposition included in original model formulations (previously discussed). Data from a field study of decomposing sugar maple leaves (*Acer saccharum*) in a Wisconsin maple forest [*Aber et al.*, 1984] were used for this exercise. Existing information was sufficient to provide initial values of state variables and parameters for all models, as well as to compare simulations to actual litter decay patterns. The primary goal of this calibration exercise was to ensure that each model reasonably matched the observed pattern of litter mass loss over time given the common climate driver (DEFAC). In addition, observations of carbon fractions and total nitrogen content of decaying litter, available from the Wisconsin study, were used to explore finer details of model behavior that were not possible with the less complete information provided by the LIDET field experiment (see below).

2.4. Intersite Simulations

Two litter types (*Drypetes glauca* and *Triticum aestivum*; a tropical broadleaf foliage and grassland cereal crop, respectively) and four sites (Arctic Tundra, Harvard Forest, Jornada, and Luquillo) were selected for simulations. These litters have among the highest and lowest C:N and N:lignin ratios of the litter types used in the LIDET study, and the selected sites encompass the range of climatic conditions included in the LIDET study. Chemical characteristics of the litter were used to provide initial state variables and parameters for the models (Table 1), assuming an initial quantity of $100 \text{ g litter C m}^{-2}$. Because mineral nitrogen availability may influence litter decay, two sets of simulations were conducted with each litter type on each site. The first set of simulations included no source of nitrogen other than the litter. The second set included an additional pool of 2 g N m^{-2} for use by decomposers, as if a pool of mineral nitrogen was available from surrounding

Table 1. Chemical Characteristics of Litter Used in Simulations

Litter Characteristic	Species		
	<i>Acer saccharum</i>	<i>Drypetes glauca</i>	<i>Triticum aestivum</i>
Extractives ^a , %	44.8	48.00	10.65
Acid Solubles, %	43.1	42.55	72.75
Acid Insolubles, %	12.1	9.45	16.60
N, g per 100 g C	1.66	3.97	1.21

^aAll values based on ash-free mass.

soils. Climate controls on decay rates in all models were incorporated by the use of the scalar (DEFAC).

3. Results and Discussion

3.1. Preliminary Simulations: Sugar Maple Decay in Wisconsin

Sugar maple leaves decomposed very rapidly in Wisconsin during the warm months of the study and more slowly during the cooler periods (Figure 3; note that field incubations started on November 3, 1980). Moreover, patterns of cumulative mass loss and a cumulative measure of the climate scalar used to drive models were similar (Figure 3), verifying a close relationship between litter decay at this site and climate regime. All four models produced patterns of mass loss that were similar to observations (Figure 4a), suggesting that these models were comparable with respect to overall litter mass dynamics and responses to climate. Litter C:N ratios also were similar between observations and simulations (Figure 4b), although litter nitrogen content was more variable among models. These comparisons between model simulations and experimental observations suggest that our knowledge of mass loss during decay is more precise than our understanding of nitrogen dynamics.

The primary goal of simulating the decomposition of sugar maple leaves for the Wisconsin study was to ensure that all models would provide reasonable patterns of mass loss given a common climate driver (discussed previously). However, detailed litter chemistry data from the Wisconsin study also permitted a closer examination of model behavior than possible with LIDET data. While simulated mass loss patterns for sugar maple leaves were similar to observations, changes in litter carbon chemistry during decomposition showed greater differences both among simulations and between model output and experimental results (Figure 5). This is consistent with differences between observed and simulated values of litter nitrogen.

Differences in simulated litter chemistry can be attributed to the various mechanisms by which models estimated litter decay. For example, CENTURY underestimated lignin losses and overestimated losses of extractives, while GENDEC overestimated net loss of cellulose and underestimated net loss of extractives. Because both models showed reasonably close correspondence to observed mass loss and have similar decay rate coefficients for litter constituents, differences in the sizes of particular substrate pools resulted from the different ways in which decomposition products were allocated among various

pools. In GENDEC, dead microbial materials were assumed to consist of 85% extractives and 15% recalcitrants but to contain no acid-soluble (cellulosic) fraction. If this allocation scheme was changed to include an acid-soluble component of microbial products, it would compensate for the discrepancy between observations and simulations and still remain consistent with reported chemical attributes of microbiota. In CENTURY, the entire quantity of recalcitrant structural materials (lignins) in litter was transferred directly to the slow soil pool (X_5) without the production of any soluble by-products of decomposition. The addition of a small transfer from lignins to an extractives pool, as included in MBL-GEM, would bring model simulations more in line with observations. Differences between DOCMOD simulations and experimental observations were relatively small, although the model tended to overestimate quantities of extractives and cellulose while underestimating lignin pool size. Although DOCMOD includes the secondary production of acid-insoluble compounds as a product of decomposition, the rate of this transformation is very slow. With respect to litter carbon pools, MBL-GEM output followed observations very closely.

Perhaps the most important result of these simulations is that while the phenomenon of litter mass loss can be simulated in a reasonably accurate manner in a number of ways, closer evaluation of litter chemistry during decay suggests that mechanisms included within the different models may not fully capture the dynamics of decay. However, crude analyses of chemical fractions of litter (e.g., extractives, acid solubles and acid insolubles) yield no insight to the origins of these materials, i.e., whether they are unaltered components of the original plant litter, microbial products, or some combination of plant and microbial compounds. Thus it is impossible to evaluate the relative accuracy of the various models or reasons why model results differed from observations. Clearly, further study of litter chemistry during decomposition is needed.

In summary, this exercise demonstrated that a modest set of decomposition and climate data could provide needed param-

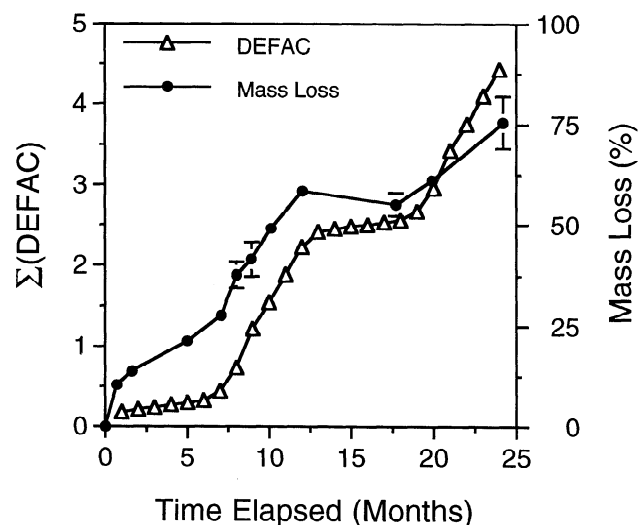


Figure 3. Cumulative values of climate scalar (DEFAC) and mass loss (percent) of leaf litter (*Acer saccharum*) during litter decay in Wisconsin (study began on November 3, 1980).

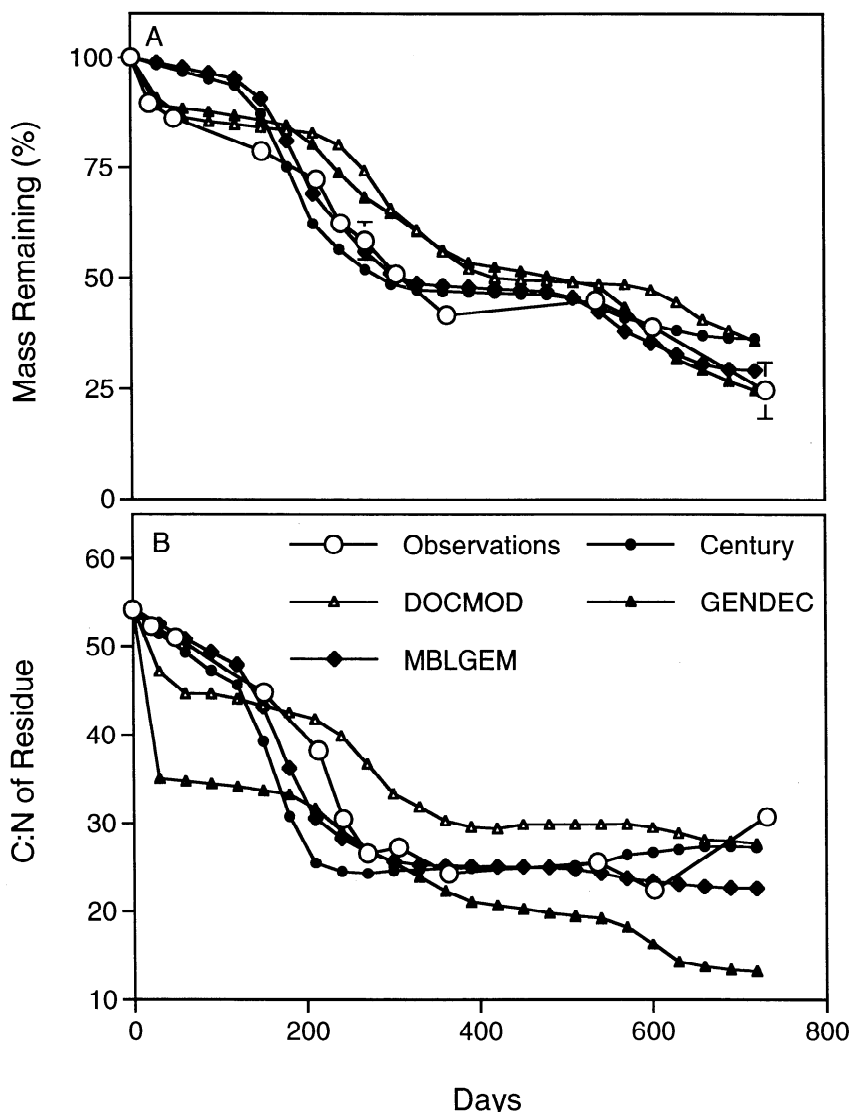


Figure 4. Comparisons between model simulations and observed litter decay patterns (study began on November 3, 1980): (a) litter C:N ratio and (b) litter mass remaining. Symbols denote observations, open circles; CENTURY, solid circles; DOCMOD, open triangles; MBL-GEM, solid diamonds; and GENDEC, solid triangles.

ters and drivers for these models of litter decay. Results also revealed some ramifications of underlying assumptions and structural features of these models, by examining the finer details of carbon chemistry dynamics, that were not apparent in gross patterns of litter mass loss. This suggests that care be used in the interpretation of gross model output, even when output apparently matches observations.

3.2. LIDET Experiments

In contrast to the study of sugar maple litter decay in Wisconsin, no a priori expectations existed for the decomposition patterns of litter used in the LIDET study. This is because the incubation of *Drypetes* and *Triticum* litter on arctic tundra, tropical rain forest, eastern deciduous forest, and warm desert sites represents novel combinations of litter type and site. For example, the *Drypetes* leaf litter used in this study is derived

from a tropical hardwood tree not capable of growing at the other sites. While these combinations may be unrealistic (or extremely improbable), they provide a stringent test for models that estimate litter decay on the bases of climatic and litter quality characteristics. Moreover, this novel set of conditions may be more likely to reveal biases in modeling approaches resulting from site and litter considerations used in initial model development.

Our evaluation of the LIDET field experiments consists of two parts: in the first, we elucidate the general behavior of these models as a group, in comparison to actual litter decay, while in the second, we examine the performances of individual models. Field data provided by the LIDET experiment consisted of litter mass loss and C:N ratio of the remaining litter at 12 and 24 months for three sites (Arctic Tundra, Harvard Forest, and Jornada) and litter mass after 4, 8, 12, and 15 months of decay at Luquillo. More detailed litter chemistry at-

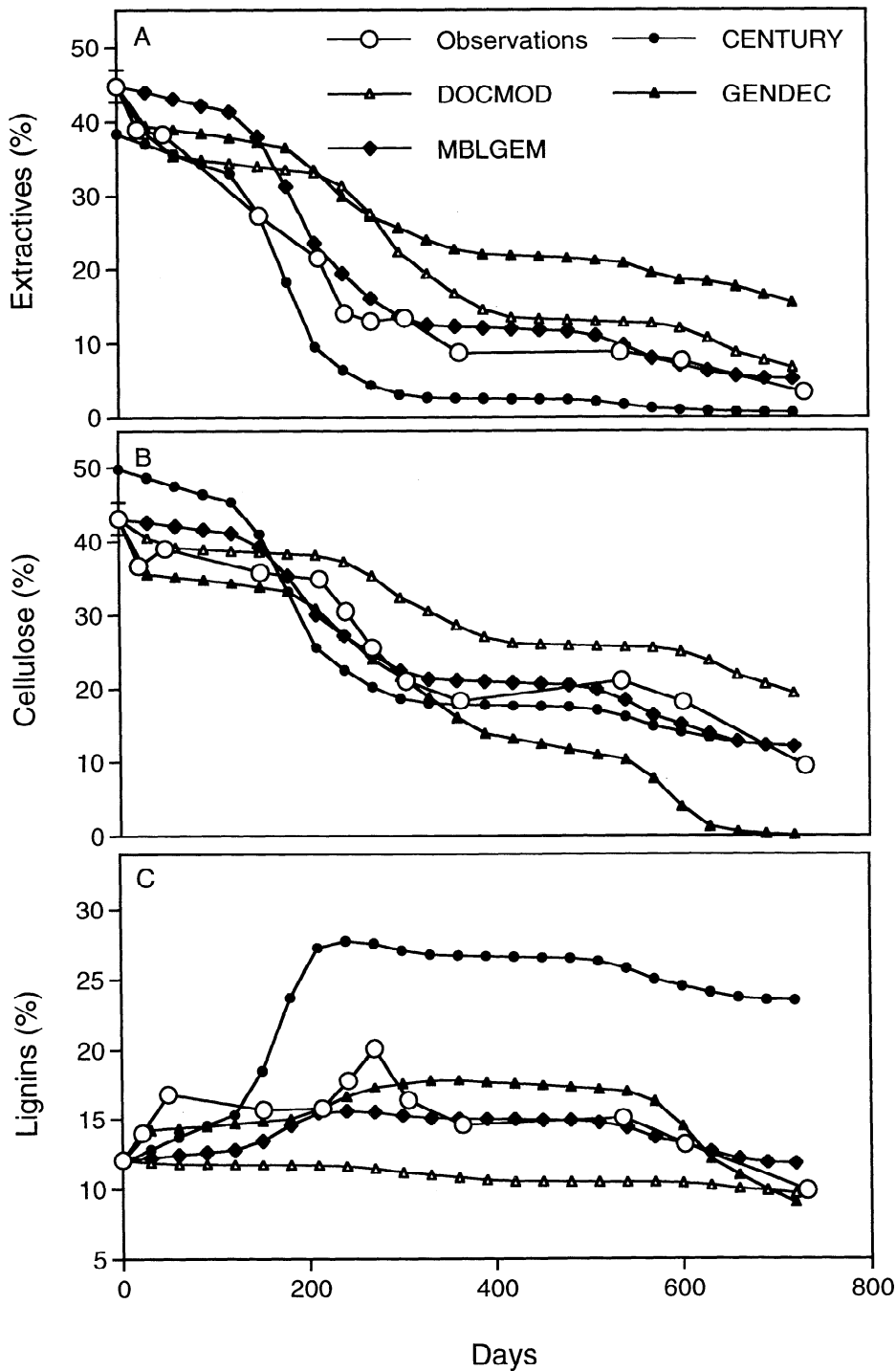


Figure 5. Carbon fractions remaining in sugar maple leaf litter over time (study began on November 3, 1980): (a) extractives, (b) acid solubles, and (c) acid insolubles. Symbols denote observations, open circles; CENTURY, solid circles; DOCMOD, open triangles; MBL-GEM, solid diamonds; and GENDEC, solid triangles.

tributes are not currently available for these experiments. Also, climatic and edaphic data for study sites were limited (previously mentioned and see below).

3.2.1. General model behaviors: mass losses. Decomposition varied with site and litter quality. Both simulated and observed mass losses were highest in warm, moist environ-

ments (Luquillo and Harvard Forest) than in cold (Arctic Tundra) or dry (Jornada) sites. In addition, simulated and observed decay was more rapid for *Drypetes* than *Triticum* (Figures 6 and 7), consistent with evidence from other studies suggesting that the higher nitrogen and lower lignin content of *Drypetes* (Table 1) would result in more rapid decomposi-

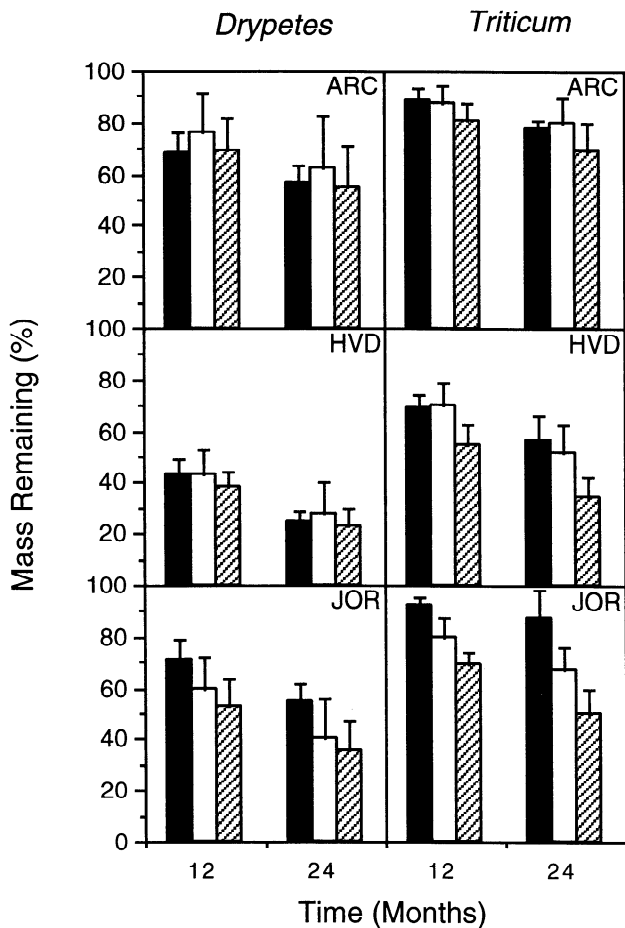


Figure 6. Mass of litter remaining (percent) after 12 and 24 months field incubation for (top) Arctic Tundra (ARC), (middle) Harvard Forest (HVD), and (bottom) Jornada (JOR), and (left) *Drypetes* and (right) *Triticum*. Solid bars denote observed means (+standard error), open bars represent the mean of model predictions at low nitrogen availability (+standard error), and hatched bars denote mean of model predictions at high nitrogen availability (+standard error).

tion [e.g., Melillo et al., 1982, 1989]. For simulations, increasing the availability of mineral nitrogen stimulated the mass loss of *Triticum*, the low-quality litter, more than *Drypetes*. This was expected because most model formulations treat *Drypetes* as less limited by nitrogen availability than *Triticum*. Unfortunately, mineral nitrogen availabilities at these sites were not known and thus could not be used to aid in evaluating model output.

3.2.1.1. Site effects: Observed mass losses for both litter types were greatest at Luquillo, intermediate at Harvard Forest, and lowest at the Arctic Tundra and Jornada sites (Luquillo > Harvard Forest > Arctic Tundra ≈ Jornada), although decay rates were similar at Arctic Tundra and Jornada. By comparison, mass loss rates estimated by our models were also highest at Luquillo and intermediate at Harvard Forest (Luquillo > Harvard Forest > Jornada > Arctic Tundra) but lower at Arctic Tundra than Jornada. Differences between model output and observations were greatest at the Jornada, where models overestimated losses (Figure 6), and at Luquillo, where models underestimated losses (Figure 7).

In this modeling study, differences between sites were represented solely by the climate scalar (DEFAC). At Jornada, overestimates of decomposition may have resulted from an unrealistically favorable climate scalar, which averaged 0.114 over the 24-month simulation period (possible values for DEFAC range between 0 and 1.0). Strong limitations to decomposition at the soil surface are imposed by microclimatic conditions in this warm desert, which include temperatures that frequently exceed 60°C and a prevailing lack of available moisture. Conditions favorable for decomposer organisms at the soil surface may be frequent, following summer convection storms, but are so brief in duration that little biological activity occurs [Moorhead and Reynolds, 1989, 1991]. Therefore an average monthly climate scalar may artificially inflate estimated decay.

In contrast to Jornada, models underestimated decomposition at Luquillo, where it is possible that the climate scalar was too restrictive. Values for DEFAC averaged 0.661 over the 15-month simulation period, although warm and moist conditions at the soil surface may be closer to optimum for decay during much of the time. At the Harvard Forest and Arctic Tundra sites, smaller differences existed between observations and simulations. At Arctic Tundra, extremely cold temperatures throughout most of the year limited decomposition in models (DEFAC averaged 0.047). In contrast, mass losses were substantial and very similar between observations and simulations at Harvard Forest, possibly because many of the data used in the development of these decomposition models were derived from studies of litter decay in similar, mesic forests. Also, our calibration exercise with sugar maple litter in Wisconsin (previously discussed) may have predisposed subsequent simulations to closely match litter decay at Harvard Forest.

Obviously, many other factors have been shown to affect decomposition, and differences among sites with respect to

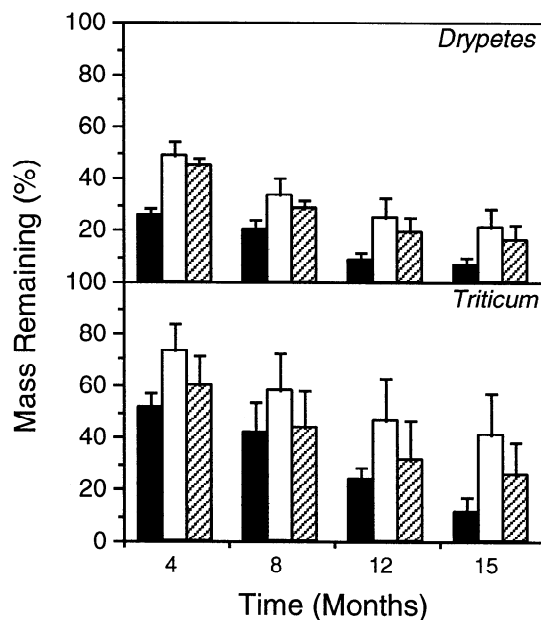


Figure 7. Mass of litter remaining (%) after 12 and 24 months field incubation at Luquillo for (top) *Drypetes* and (bottom) *Triticum*. Bars are same as in Figure 6.

these factors may have contributed to divergences between simulations and observations. However, the focus of the current study was limited to those controls on litter decay addressed by these general models.

3.2.1.2. Effects of litter quality and mineral nitrogen: The higher-quality litter (*Drypetes*) decayed more rapidly than the lower quality litter (*Triticum*) at all sites, both in the experiments and simulations. While the availabilities of mineral nitrogen were not known for the sites in this study, we wished to explore the possible impacts of different nitrogen levels on simulations. This was because other experiments have shown that decomposer microorganisms immobilize nitrogen from adjacent soils [Parker et al., 1984; Holland and Coleman, 1987], including the additions of mineral nitrogen [Marion et al., 1987], and that nitrogen additions may stimulate decomposition of nutrient-poor substrates [Berg et al., 1975]. Thus portions of the following discussion are speculative, but simulation results may be viewed as representing decomposition under conditions of limited and unlimited availability of mineral nitrogen.

In general, increasing the availability of mineral nitrogen increased the simulated mass loss of *Triticum*, the low-quality litter, more than *Drypetes*, but the relative effect of this treatment varied between sites. When nitrogen availability was increased in Jornada simulations, models overestimated mass losses even more than without the additional nitrogen. Because increased nitrogen availability will only increase simulated litter decay as climate permits, this response in model behavior is consistent with the view that an unrealistically favorable climate driver may have enhanced estimated decomposition (discussed previously). Conversely, differences between observations and model output at Luquillo were reduced by increasing nitrogen availability in simulations, suggesting that the climate scalar may not have been the only factor contributing to underestimates of litter decay at the site.

At the Arctic Tundra, fertilization had approximately equal impacts on simulated decay of both litter types although *Triticum* should respond more than *Drypetes*. However, decay was so slow at this site that the simulated addition of mineral nitrogen would stimulate a small increase in cellulose turnover for both litters. At Harvard Forest, simulated patterns of litter decay, without additional mineral nitrogen, were very close to observations. The addition of nitrogen produced overestimates of mass loss for both litter types. While this may suggest that model formulations, climate driver, and assumptions about nitrogen availability were particularly accurate for the site, it also is possible that our calibration exercise (previously discussed) influenced subsequent model behavior for Harvard Forest.

3.2.2. General model behaviors: nitrogen dynamics. In addition to litter mass loss patterns, the LIDET study also provided several observations of nitrogen content of decaying litter (Figure 8). Overall, simulated nitrogen content was lower than observed in *Drypetes* litter and higher than observed for *Triticum* (Figure 8), but many differences existed between combinations of site, litter type, nitrogen availability, and date. For instance, simulations with higher nitrogen availability at Luquillo and Arctic Tundra showed closer correspondence to observed mass loss and nitrogen content of remaining *Drypetes* litter (Figures 6-8). The opposite pattern

existed for Jornada, where estimated mass loss and litter nitrogen content were generally closer to observations without additional nitrogen (Figures 6 and 8).

Some patterns of litter decay appeared to coincide with particular site attributes. At Jornada, soil nutrient concentrations are very low [e.g., Gutierrez and Whitford, 1987], so the addition of an external pool of mineral nitrogen in simulations was probably unrealistic and drove decay and nitrogen immobilization even further beyond observed values. The same was true for the Arctic Tundra site, where model predictions overestimated nitrogen content of *Triticum* litter at higher nitrogen availability, consistent with overestimates of litter mass loss. The Arctic Tundra site also has extremely low levels of nitrogen availability [Giblin et al., 1991; Shaver et al., 1992],

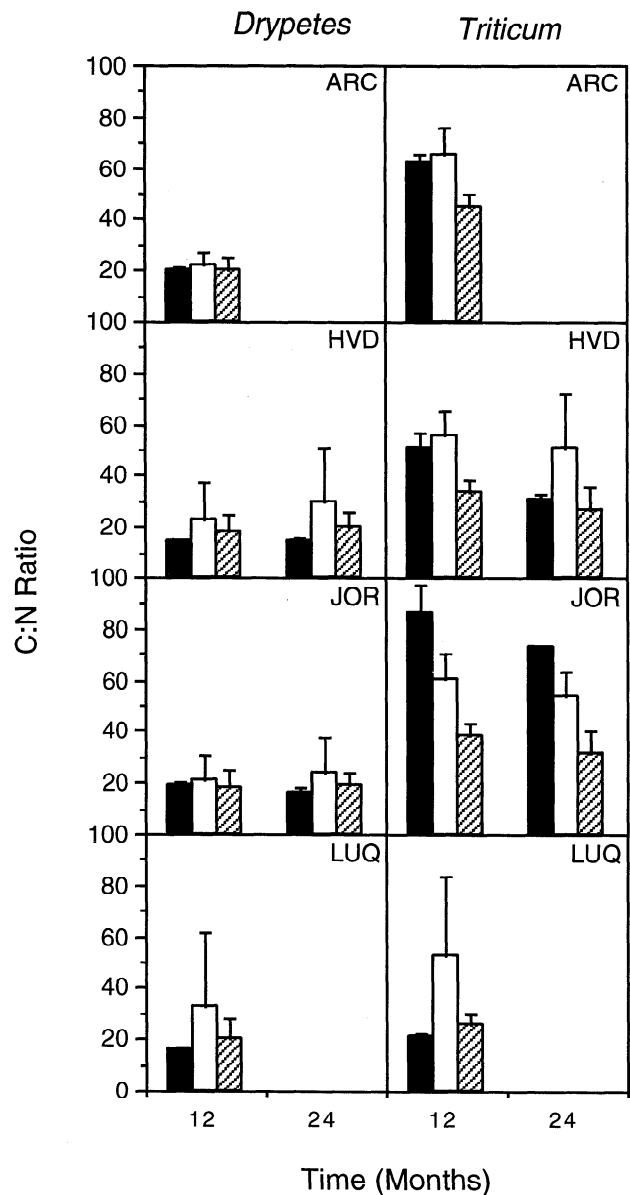


Figure 8. C:N ratio of litter remaining after 12 and 24 months field incubation for (top to bottom) Arctic Tundra (ARC), Harvard Forest (HVD), Jornada (JOR), and Luquillo (LUQ) and (left) *Drypetes* and (right) *Triticum*.

so exogenous supplies of nitrogen are not likely to support litter decay.

At Luquillo, the actual nitrogen content of both litter types was very close to predictions when simulations included the availability of mineral nitrogen. This is consistent with patterns of simulated mass loss, in that predictions were closer to observations when additional nitrogen was included in model runs. At Harvard Forest, model predictions of litter nitrogen content more closely matched observations when nitrogen availability was increased, but this pattern varied with litter type and over time. Such inconsistencies are difficult to explain with the limited data available for this study.

3.2.3. Individual model behaviors. More details of individual model behaviors were revealed by the study of sugar maple litter decay in Wisconsin (discussed earlier) than could be ascertained with LIDET results because of the greater resolution of litter chemistry in the former experiment. However, model behaviors with different litter types and contrasting climatic regimes and levels of nitrogen availability offered by the LIDET simulation studies revealed different sensitivities of models to these controlling factors (Table 2).

3.2.3.1. Site effects on mass loss: Models usually showed greater litter decay at sites with higher temperatures and moisture availabilities (e.g., Luquillo), for higher-quality litter (*Drypetes*), and when mineral nitrogen availability was increased. However, overall differences in model output between sites generally were larger than differences associated with litter type or nitrogen availability, suggesting that climatic factors exerted the greatest control on all simulations. Differences in sensitivity to climate were apparent between models despite the fact that the same climate driver (DEFAC) was used in all cases. This emphasizes the point that although climate probably was the strongest control on model behavior, other factors (e.g., litter quality and nitrogen availability) exerted different levels of control within different models.

Three models, CENTURY, DOCMOD, and MBL-GEM, exhibited similar patterns of decomposition with site, tending to overestimate litter decay at Jornada and underestimate decay at Luquillo (Figures 9-11). Differences between simulations and observations were larger for GENDEC, which demonstrated less sensitivity to climate drivers. This may be because GENDEC was designed to utilize daily climate drivers, which is an important consideration in desert ecosystems [Moorhead and Reynolds, 1991, 1993b], but such resolution of soil climate data was unavailable for the LIDET study. Three of the four sites chosen for this simulation study represent the most extreme climates included in the LIDET study (arctic tundra, hot desert, and tropical rain forest). DEFAC appears to underestimate climatic controls in these cases, leading to overestimates of mass loss in the desert and tundra and underestimates of decomposition in the rain forest.

Table 2. Relative Sensitivities of Individual Models to Controlling Factors

Model	Site	Litter Quality	N Availability
GENDEC	lowest	highest	high
DOCMOD	highest	low	lowest
MBL-GEM	moderate	high	highest
CENTURY	moderate	inconsistent	moderate

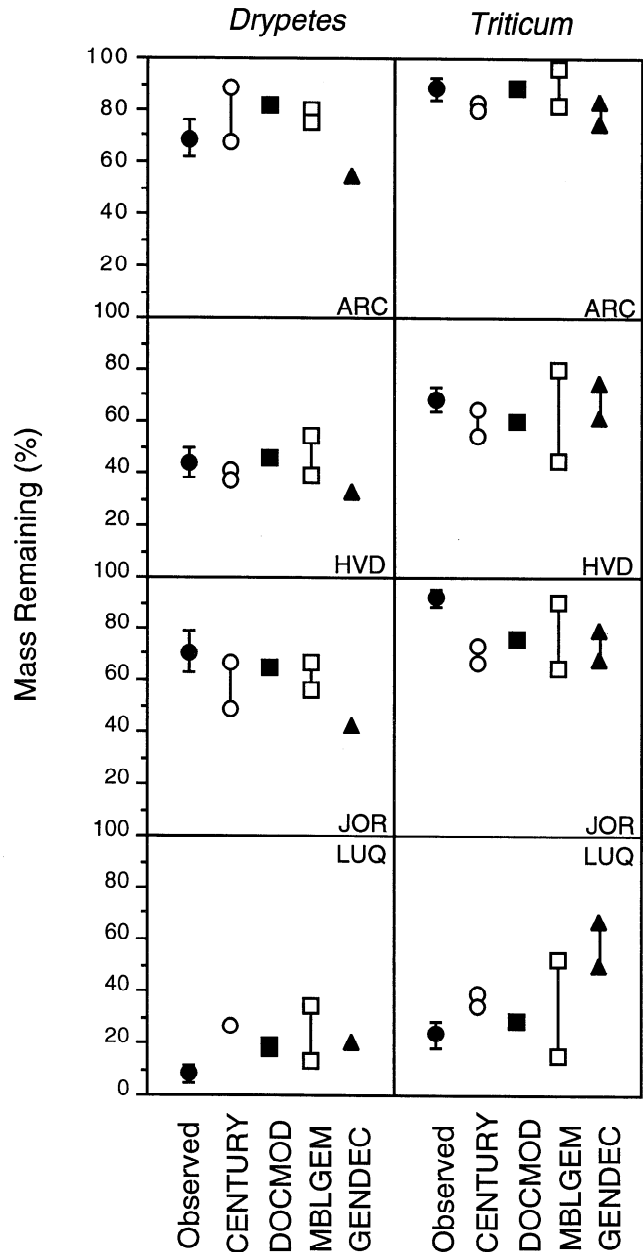


Figure 9. Mass of litter remaining (percent) after 12 months field incubation for (top to bottom) Arctic Tundra (ARC), Harvard Forest (HVD), Jornada (JOR), and Luquillo (LUQ) and (left) *Drypetes* and (right) *Triticum*. Upper values denote low nitrogen availability, while lower values equal high nitrogen availability.

3.2.3.2. Litter quality effects on mass loss: All models demonstrated an effect of litter quality on decay; that is, the higher-quality litter type (*Drypetes*) usually decayed more rapidly for simulations at all sites (Figures 9-11). This was expected because *Drypetes* has nearly 5 times as much extractive material and about half as much cellulose or lignin than *Triticum*. Extractives have a high rate of mass loss relative to the other two carbon fractions, so all models predicted a more rapid initial loss of *Drypetes*. Also, organic nitrogen released during simulated decay stimulates the degradation of cellulose

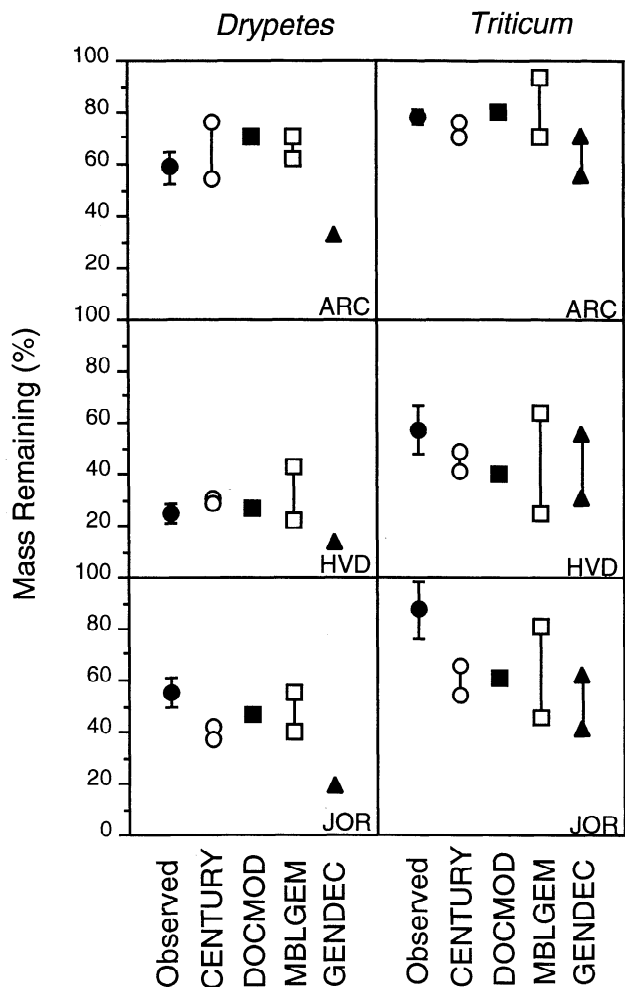


Figure 10. Same as Figure 9, but for 24 months field incubation.

in some models, so this effect was stronger in *Drypetes*, the litter containing the most nitrogen. For these reasons, *Drypetes* usually lost mass more rapidly in simulations than *Triticum*, but there was considerable difference in model sensitivity to litter quality (Table 2); GENDEC was most sensitive, followed by MBL-GEM, DOCMOD, and then CENTURY. For example, GENDEC predicted a difference of 38% in mass remaining for the two litter types after 12 months at Jornada (without additional mineral nitrogen), while MBL-GEM predicted a 24% difference; DOCMOD and CENTURY estimated differences of 11% and 8%, respectively. This pattern existed for most sites, although CENTURY estimated large differences between mass losses of litter types at Harvard Forest and Luquillo and small differences at Arctic Tundra and Jornada. In fact, CENTURY actually estimated more rapid decay of *Triticum* than *Drypetes* at Arctic Tundra, when mineral nitrogen was absent, in spite of the higher quality of *Drypetes* (Figure 9).

Differences in model behaviors with respect to litter quality reflect differences in how the models transform carbon compounds and link carbon and nitrogen flows. For example, CENTURY balances carbon and nitrogen flows according to the microbial C:N ratio, but the C:N ratio of the microbial pool

may vary between 12 and 22 [Parton *et al.*, 1987]. This imposes less limitation on decay than a more conservative microbial C:N ratio, such as the fixed value used in GENDEC (C:N = 10). Also, CENTURY was the only model used in this study that does not explicitly divide the structural components of litter into separate pools of cellulosic and recalcitrant (primarily lignin) compounds. Instead, flows of cellulosic materials are routed to the active soil pool while lignin is transferred to the slow soil pool (Figure 1a), according to a function based on the overall lignin:cellulose ratio of the litter.

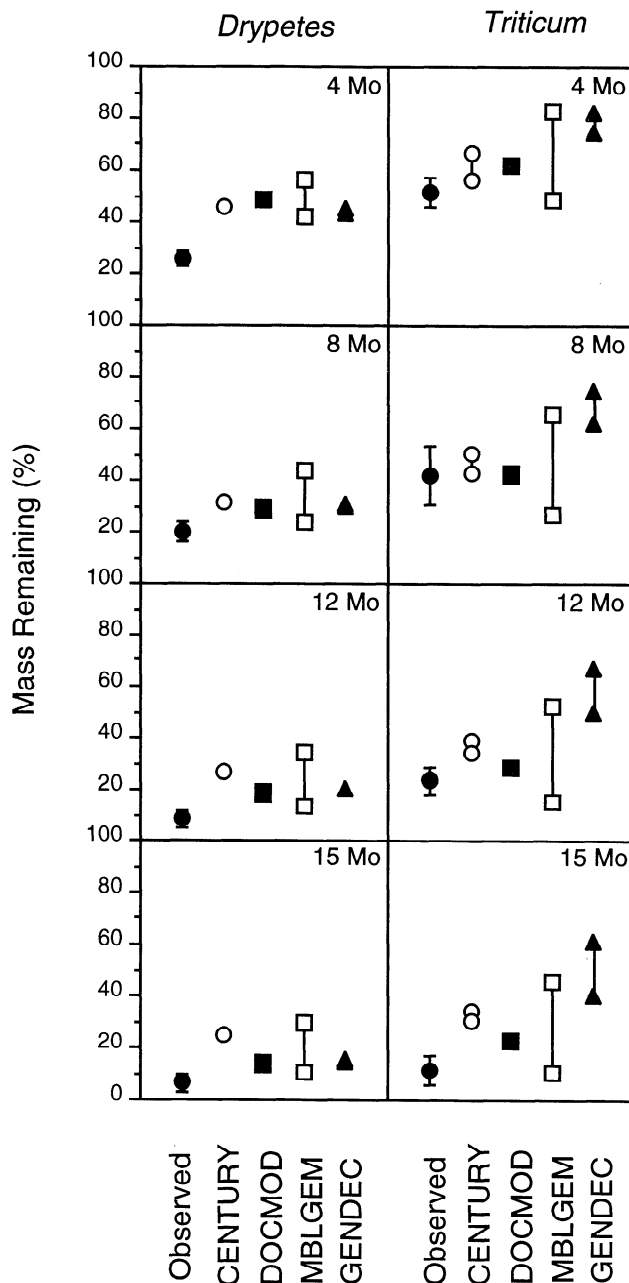


Figure 11. Mass of litter remaining (percent) at Luquillo after (top to bottom) 4, 8, 12, and 15 months incubation for (left) *Drypetes* and (right) *Triticum*. Upper values denote low nitrogen availability, and lower values equal high nitrogen availability.

However, this relationship was developed from a range of litter types that did not include the quality extreme represented by *Drypetes* [Parton et al., 1987]. Perhaps this contributed to large variations in estimates of *Drypetes* decay by CENTURY.

3.2.3.3. Mineral nitrogen effects on mass loss: The addition of mineral nutrients has been demonstrated to enhance litter decay under nutrient-limited conditions (previously discussed), but nitrogen availability was not known for these sites. However, comparisons of field observations with model responses to different nitrogen regimes provide an indirect evaluation of model behavior. Overall, model responses to simulated mineral nitrogen availabilities were consistent with expectations; that is, predicted decay was greater at higher mineral nitrogen availability, and litter with low nitrogen content (*Triticum*) responded more than the high-quality litter (*Drypetes*) for three of four models, namely, CENTURY, GENDEC, and MBL-GEM. In contrast, mineral nitrogen availability exerts no control over litter mass loss in DOCMOD (Figures 9-11). Interestingly, predictions by DOCMOD were within the range of estimates produced by the other models, questioning the value of more detailed attention to coupled carbon and nitrogen flows, at least with regard to mass loss.

With regard to the other models, the effect of mineral nitrogen availability was largest in MBL-GEM simulations, probably because it influenced a variety of transformations that immobilize nitrogen, i.e., the rate of cellulose loss to extractives, lignin to humus, and sometimes extractives to lignin and extractive to extractives (depending on internal nitrogen concentrations). In the simulations presented here, the effect of inorganic nitrogen on the transformation of extractives to either lignin or extractives occurred only for the first few months of decay for *Triticum*. The transformation of lignin to humus is a slow process and plays only a minor role in these simulations. Thus the most important effect of inorganic nitrogen was on the loss rate of cellulose, increasing it eightfold for the high-N simulations over rates in the low-N simulations (for *Triticum*). This difference accounts for most of the range in total carbon remaining between the high-N and low-N predictions (Figures 9-11).

The behavior of CENTURY was less intuitive, showing the greatest effect of nitrogen availability on *Drypetes* decay at Arctic Tundra and Jornada sites, with *Triticum* decay responding more at Harvard Forest and Luquillo. It is difficult to interpret these results, given the initial differences in litter quality (Table 1). However, model responses may have been affected by the scheme of allocating carbon flows from the structural pool of *Drypetes* litter (as previously discussed) and the controls that nitrogen availability exerts on these flows, further exacerbated for the extreme environments represented by Arctic Tundra and Jornada.

3.2.3.4. Litter nutrient dynamics: The nitrogen content of decomposing litter was consistent with predicted patterns of mass loss for most models; that is, nitrogen content usually increased with loss of mass (Figures 12 and 13). For example, because GENDEC loses carbon only through microbial respiration and has no mechanism for the loss of other elements, C:N ratios are entirely determined by loss of carbon and the amounts of materials remaining in the various model pools

(each has a fixed C:N ratio). Similar patterns existed for other models for the same reasons (e.g., CENTURY and DOCMOD). However, MBL-GEM estimated rather low nitrogen concentrations for *Drypetes* and *Triticum* at both Jornada and Luquillo, in the absence of mineral nitrogen availability, even though mass losses were substantial; about 52% of *Triticum* litter mass remained after 12 months incubation at Luquillo, but the C:N ratio of this litter was 97:1 (approximating the original C:N ratio of this litter type; see Table 1). It appears that a substantial amount of nitrogen was mineralized by

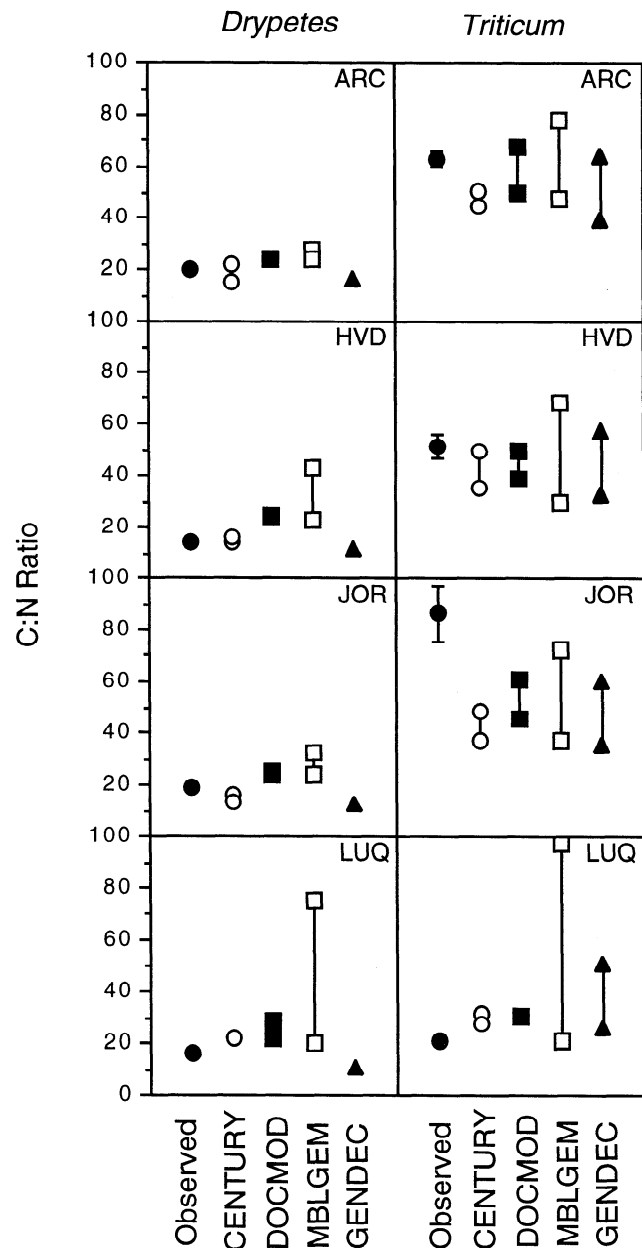


Figure 12. C:N ratio of litter remaining after 12 months field incubation for (top to bottom) Arctic Tundra (ARC), Harvard Forest (HVD), Jornada (JOR), and Luquillo (LUQ) and (left) *Drypetes* and (right) *Triticum*. Upper values denote low nitrogen availability, and lower values equal high nitrogen availability.

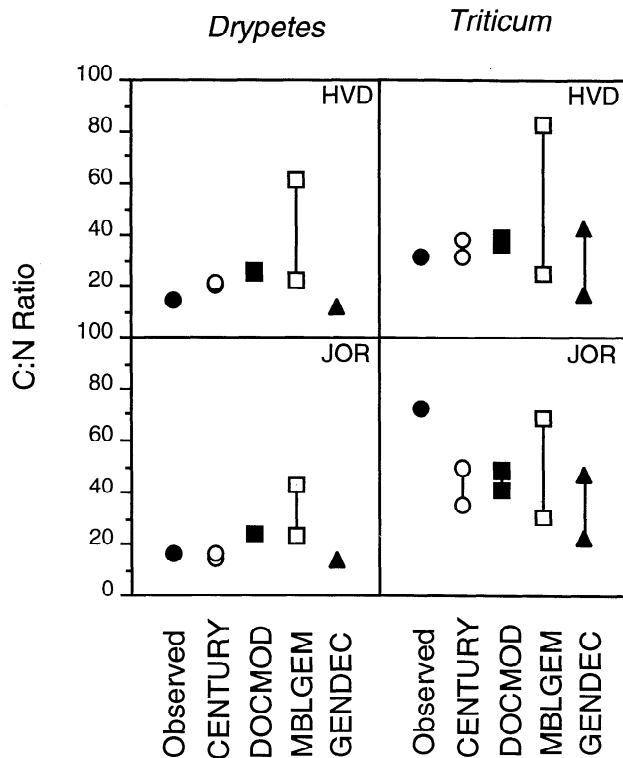


Figure 13. Same as Figure 12, but for 24 months field incubation.

MBL-GEM, in spite of the overall, low nitrogen content of remaining litter.

Although DOCMOD includes no response of litter mass loss to mineral nitrogen availability, there were differences in the C:N ratios of remaining materials. Thus the impact of nitrogen limitations on decomposition in this model is manifested as controls on microbial nitrogen dynamics.

4. Conclusions and Recommendations

In summary, simulated litter decay was more responsive to climate (as a driver) than litter quality or mineral nitrogen availability. These results are consistent with more empirical models of litter decay, such as that by *Meentemeyer* [1978], in which climatic factors exert stronger control on decay rates than litter quality. However, *Meentemeyer's* model has been shown to be inaccurate for environmental conditions exceeding those for which it was developed [*Whitford et al.*, 1981; *Schaefer et al.*, 1985], which is a common limitation to such empirical models [cf. *Reynolds and Leadley*, 1992]. The more mechanistic models used in the present study should approximate litter decay more accurately for novel combinations of litter quality and site because underlying mechanisms were included in model formulation. In fact, differences between simulated and observed mass losses were fairly modest (Figures 6 and 7), most observed means falling within ± 1 standard deviation of the means of model predictions.

Models demonstrated sensitivities to two aspects of litter quality: proximate carbon fractions and nitrogen content. In general, simulated litter decay increased with litter nitrogen

content and decreased with litter lignin content, as predicted by many simpler empirical models. However, models also exhibited interactions between litter nitrogen content and mineral nitrogen availabilities, although empirical data were not available to test this response. The nitrogen content of remaining detritus in the LIDET studies, in conjunction with the detailed litter chemistry data available from the Wisconsin study, revealed some inadequacies in our understanding of nutrient controls on decomposition, material transformations during decay, and other relationships between decomposer systems and nutrient cycling in their "host" ecosystems. The observations provided by the LIDET field studies emphasized this point.

The combination of experimental and modeling analyses in the LIDET study provides a unique opportunity for achieving a greater working knowledge of decomposition, because the empirical data are being collected in a manner that facilitates comparison and provide a consistent basis for extrapolating model behavior across sites and litter types. However, the LIDET study was designed specifically to examine the effects of initial litter quality and prevailing site conditions on long-term changes in litter mass and quality. Although this permits extrapolating beyond limitations of earlier, general models [e.g., *Meentemeyer*, 1978], it still includes restrictions imposed by the experimental design. The scope and resolution of the empirical data limit the level of mechanism that can be included in models, and insights that can be gained to short-term changes in litter chemistry and nitrogen dynamics. In short, the LIDET data are too coarse in temporal and chemical resolution to address these issues, despite providing greater insights to broad-scale patterns of litter decay.

This modeling study demonstrated a general correspondence between approaches commonly used to simulate decomposition and actual patterns of litter decay. These models included more mechanisms than previously used in such broad-scale simulations, suggesting patterns of litter chemistry and nutrient dynamics. Data from the LIDET experiment will provide a basis for altering model parameters and structure to be more consistent with observed patterns of long-term decay. However, these simulations also revealed the potential value of additional data. For example, higher temporal resolution of microclimate and litter chemistry, in addition to an assessment of mineral nutrient availability for a particular site, will be needed to gain a more precise understanding of decomposition. However, such data must be collected within a broad context of site and litter quality characteristics to provide an adequate basis for extending the current LIDET study.

Acknowledgments. We wish to thank D. Schaefer, J. Lodge, A. Ricca, J. Melillo, J. Laundre, and J. Anderson for providing climate data from the Arctic Tundra, Jornada, Luquillo Forest, and Harvard Forest LTER sites used in these simulations. Support for this work was provided by a National Science Foundation grant BSR-9108329.

References

- Aber, J. D., and J. M. Melillo, Nitrogen immobilization in decaying hardwood leaf litter as a function of initial nitrogen and lignin content, *Can J. Bot.*, 60, 2263-2269, 1982.
- Aber, J. D., C. A. McLaugherty, and J. M. Melillo, Litter decomposition in Wisconsin forests - Mass loss, organic-chemical constituents and nitrogen, School of Nat. Resour., Univ. of Wis., Madison, 1984.

- Aber, J. D., J. M. Melillo, and C. A. McLaugherty, Predicting long-term patterns of mass loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. *Can. J. Bot.*, *68*, 2201-2208, 1990.
- Berg, B., L. Karenlampi, and A. K. Vuom, Comparisons of decomposition rates measured by means of cellulose, in *Fennoscandian Tundra Ecosystems, Part 1, Plants and Microorganisms*, edited by F. E. Wielgolaski, pp. 261-267, Springer-Verlag, New York, 1975.
- Berg, B., et al., Litter mass loss rates in pine forests of Europe and Eastern United States: Some relationships with climate and litter quality, *Biogeochemistry*, *20*, 127-159, 1993.
- Burke, I. C., C. M. Yonker, W. J. Parton, C. V. Cole, K. Flach, and D. S. Schimel, Texture, climate, and cultivation effects on soil organic matter content in U.S. grassland soils, *Soil Sci. Soc. Am. J.*, *53*, 800-805, 1989.
- Currie, W. S., and J. D. Aber, Modeling leaching as a decomposition process in humid, montane forests, *Ecology*, *78*, 1844-1860, 1997.
- Giblin, A. E., J. J. Nadelhoffer, G. R. Shaver, J. A. Laundre, and A. J. McKerrow, Biogeochemical diversity along a riverside toposequence in arctic Alaska, *Ecol. Monogr.*, *61*, 415-435, 1991.
- Gregorich, E. G., R. P. Voroney, and R. G. Kachanoski, Turnover of carbon through the microbial biomass in soils with different textures, *Soil Biol. Biochem.*, *23*, 799-805, 1991.
- Gutierrez, J. R., and W. G. Whitford, Chihuahuan desert annuals: Importance of water and nitrogen, *Ecology*, *68*, 2032-2045, 1987.
- Harmon, M. E., G. A. Baker, G. Spycher, and S. E. Greene, Leaf-litter decomposition in the Picca/Tsuga forests of Olympic National Park, Washington, U.S.A., *For. Ecol. Manage.*, *31*, 55-66, 1990.
- Holland, E. A., and D. C. Coleman, Litter placement effects on microbial and organic matter dynamics in an agroecosystem, *Ecology*, *68*, 425-433, 1987.
- Johnson, D. W., Nitrogen retention in forest soils, *J. Environ. Qual.*, *21*, 1-12, 1992.
- Long-Term Intersite Decomposition Experiment Team (LIDET), Meeting the challenge of long-term, broad-scale ecological experiments, *Publ. No 19*, Long-Term Ecological Research Network Off., Seattle, Wash., 1995.
- Marion, G. M., P. C. Miller, and C. H. Black, Competition for tracer ¹⁵N in tussock tundra ecosystems, *Holarctic Ecol.*, *10*, 230-234, 1987.
- McLaugherty, C. A., J. Pastor, J. D. Aber, and J. M. Melillo, Forest litter decomposition in relation to soil nitrogen dynamics and litter quality, *Ecology*, *66*, 266-275, 1985.
- Meentemeyer, V., Macroclimate and lignin control of litter decomposition rates, *Ecology*, *59*, 465-472, 1978.
- Melillo, J. M., J. D. Aber, and J. F. Muratore, Nitrogen and lignin control of hardwood leaf litter decomposition dynamics, *Ecology*, *63*, 621-626, 1982.
- Melillo, J. M., J. D. Aber, A. E. Linkins, A. Ricca, B. Fry, and K. J. Nadelhoffer, Carbon and nitrogen dynamics along the decay continuum: Plant litter to soil organic matter, *Plant Soil*, *115*, 189-198, 1989.
- Minderman, G., Addition, decomposition and accumulation of organic matter in forests, *J. Ecol.*, *56*, 355-362, 1968.
- Moorhead, D. L., and J. F. Reynolds, Mechanisms of surface litter decomposition in the northern Chihuahuan desert: A reinterpretation, *J. Arid Environ.*, *16*, 157-163, 1989.
- Moorhead, D. L., and J. F. Reynolds, A general model of litter decomposition in the northern Chihuahuan Desert, *Ecol. Modell.*, *59*, 197-219, 1991.
- Moorhead, D. L., and J. F. Reynolds, Effects of climate change on decomposition in arctic tussock tundra: A modeling synthesis, *Arct. Alp. Res.*, *25*, 403-412, 1993a.
- Moorhead, D. L., and J. F. Reynolds, Changing carbon chemistry during decomposition of creosotebush fine litter in the northern Chihuahuan Desert, *Am. Midl. Nat.*, *130*, 83-89, 1993b.
- Ojima, D. S., W. J. Parton, D. S. Schimel, J. M. O. Scurlock, and T. G. F. Kittel, Modelling the effects of climatic and CO₂ changes on grassland storage of soil-C, *Water Air Soil Pollut.*, *70*, 643-657, 1993.
- Olson, J. W., Energy storage and the balance of producers and decomposers in ecological systems, *Ecology*, *44*, 322-331, 1963.
- Parker, L. W., P. F. Santos, J. Phillips, and W. G. Whitford, Carbon and nitrogen dynamics during decomposition of litter and roots of a Chihuahuan desert annual, *Lepidium lasiocarpum*, *Ecol. Monogr.*, *54*, 339-360, 1984.
- Parnas, H., Model for decomposition of organic material by microorganisms, *Soil Biol. Biochem.*, *7*, 161-169, 1975.
- Parton, W. J., D. S. Schimel, C. V. Cole, and D. S. Ojima, Analysis of factors controlling soil organic matter levels in Great Plains Grasslands, *Soil Sci. Soc. Am. J.*, *51*, 1173-1179, 1987.
- Rastetter, E. B., M. G. Ryan, G. R. Shaver, J. M. Melillo, K. J. Nadelhoffer, J. E. Hobbie, and J. D. Aber, A general model describing the responses of the C and N cycles in terrestrial ecosystems to changes in CO₂, climate, and N deposition, *Tree Physiol.*, *9*, 101-126, 1991.
- Rastetter, E. B., R. B. McKane, G. R. Shaver, and J. M. Melillo, Changes in C-storage by terrestrial ecosystems - How C-N interactions restrict responses to CO₂ and temperature, *Water Air Soil Pollut.*, *64*, 327-344, 1992.
- Reynolds, J. F., and P. W. Leadley, Modeling the response of arctic plants to climate change, in *Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective*, edited by F. S. Chapin III et al., pp. 413-438, Academic, San Diego, Calif., 1992.
- Ryan, M. G., J. M. Melillo, and A. Ricca, A comparison of methods for determining proximate carbon fractions of forest litter, *Can. J. For. Res.*, *20*, 166-171, 1990.
- Schaefer, D., Y. Steinberger, and W. G. Whitford, The failure of nitrogen and lignin control of decomposition in a North American desert, *Oecologia*, *65*, 382-386, 1985.
- Shaver, G. R., W. D. Billings, F. S. Chapin III, A. E. Giblin, K. J. Nadelhoffer, W. C. Oechel, and E. B. Rastetter, Global change and the carbon balance of arctic ecosystems, *Bioscience*, *42*, 433-441, 1992.
- Trofymow, J. A., C. M. Preston, and C. E. Prescott, Litter quality and its potential effect on decay rates of materials from Canadian forests, *Water Air Soil Pollut.*, *82*, 215-226, 1995.
- Vitousek, P. M., Beyond global warming: Ecology and global change, *Ecology*, *75*, 1861-1876, 1994.
- White, D. L., B. L. Haines, and L. R. Boring, Litter decomposition in Southern Appalachian Black locust and pine-hardwood stands: Litter quality and nitrogen dynamics, *Can. J. For. Res.*, *18*, 54-63, 1988.
- Whitford, W. G., V. Meentemeyer, T. R. Seastedt, K. Cromack Jr., D. A. Crossley Jr., P. Santos, R. L. Todd, and J. B. Waide, Exceptions to the AET model: Deserts and clear-cut forests, *Ecology*, *62*, 275-277, 1981.

W. S. Currie, Appalachian Laboratory, University of Maryland, Frostburg, MD 21532

M. E. Harmon, Department of Forest Science, Oregon State University, Corvallis, OR 97331

D. L. Moorhead, Department of Biological Sciences, University of Toledo, Toledo, OH 43606

W. J. Parton, Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523

E. B. Rastetter, The Ecosystems Center Marine Biological Laboratory, Woods Hole, MA 02543

(Received March 13, 1998; revised October 9, 1998; accepted November 13, 1998.)