

Decomposition processes: modelling approaches and applications

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Abstract

Decomposition is a fundamental ecosystem process, strongly influencing ecosystem dynamics through the release of organically bound nutrients. Decomposition is also a complex phenomenon that can be modified by changes in the characteristics of the decaying materials or prevailing environmental conditions. For these reasons, the impacts of local, regional or global environmental changes on the quality and turnover of dead organic matter are of considerable interest. However, realistic limits to the complexity, as well as temporal and spatial scales, of experimental studies restrict their usefulness in extrapolating long-term or large-scale results of simultaneous environmental changes. Alternatively, many simulation models have been constructed to gain insight to potential impacts of anthropogenic activities. Because structure and approach determine the strengths and limitations of a model, they must be considered when applying one to a problem or otherwise interpreting model behaviour. There are two basically different types of models: (1) empirical models generally ignore underlying processes when describing system behaviour, while (2) mechanistic models reproduce system behaviour by simulating underlying processes. The former models are usually accurate within the range of conditions for which they are constructed but tend to be unreliable when extended beyond these limits. In contrast, application of a mechanistic model to novel conditions assumes only that the underlying mechanisms behave in a consistent manner. In this paper, we examine models developed at different levels of resolution to simulate various aspects of decomposition and nutrient cycling and how they have been used to assess potential impacts of environmental changes on terrestrial ecosystems.

Keywords: Decomposition; Ecosystem modelling; Enzyme models

1. Introduction

Decomposition is comparable in importance to primary production as a fundamental ecosystem process. In fact, an ecosystem needs only producers and decomposers (as biological components) to exist indefinitely, and some extreme environments support few other trophic entities,

e.g. the Antarctic Dry Valleys (Cathey et al., 1981; Parker and Simmons, 1985). Nonetheless, decomposers typically receive less attention from scientific investigators than plants or other heterotrophic groups.

Decomposition is a composite phenomenon in which many different processes contribute to the degradation of complex organic compounds (Fig. 1; see also Swift et al., 1979). Theoretically, these processes ultimately reduce organic materials to

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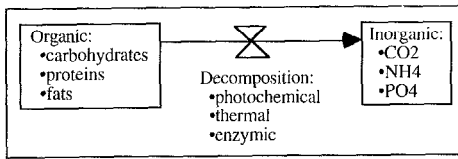


Fig. 1. Conceptual model of processes responsible for litter decay.

their inorganic constituents. Of particular importance to ecosystem dynamics is the release of organically bound nutrients, e.g. nitrogen and phosphorus, which then can be utilized by plants.

Organic matter decay can be viewed from many levels of resolution, e.g. an ecosystem process, a property of saprophytic community dynamics, an extension of decomposer microorganism physiology and nutrition, or as a composite biochemical process based on enzyme kinetics. In this paper reference is made to a hierarchical framework, emphasizing relationships between levels of resolution, insights provided within levels, and applications to specific questions (Table 1). Biomass dynamics of microbial communities, net respiratory output, etc., are included in the knowledge that taxonomic, methodological, and interpretive problems limit understanding of soil microbiota at the community, population, species and individual levels (Klopatek et al., 1993). In spite of such difficulties, decomposition and concomitant nutrient cycling processes are central to many environmental management scenarios, e.g. maintenance of site fertility, reclamation following disturbance, determining sustainable harvest regimes, and assessing long-term system responses to global changes. In this paper, the development of models at different

Table 1
Hierarchical perspectives of decomposition processes; level of interest and associated context

Level of interest	Context
Biosphere	Changing climate, CO ₂ , UV-B
Ecosystem	Energy and nutrient cycles
Community	Plant-microbial interactions
Population	Microbial growth
Physiological	Microbial physiology
Sub-cellular	Extracellular enzymes

levels of resolution is used to examine various aspects of decomposition and nutrient cycling.

2. Types of models

Many mathematical models have been constructed to simulate litter decay, and a brief critique of common mathematical techniques is provided by Weider and Lang (1982). A more general scheme (Reynolds and Leadley, 1992) classified models according to the underlying conceptual approach. This classification system clarifies the strengths and limitations inherent in different modelling strategies and, thus, provides valuable insights for potential management applications.

Reynolds and Leadley recognize two fundamentally different categories, viz. empirical and mechanistic models. Empirical models describe the behaviour of a system at a particular hierarchical level of interest, without examining underlying processes. For this reason, such models often are very accurate predictive tools within the range of system behaviour for which they are developed, but their utility in exploring processes on other sites, for other systems, or in response to changing environmental conditions is highly problematical. In contrast, mechanistic models reproduce system behaviour by simulating underlying processes. The application of mechanistic models to conditions other than those for which they were developed assumes that the underlying processes behave in a consistent manner.

Many models incorporate elements of empirical and mechanistic approaches. For example, semi-mechanistic models include a mix of mechanistic and empirical approaches at a given hierarchical level of interest. These models offer potential for extrapolation because they explicitly incorporate some of the biological underpinnings of the process.

Because structure and approach determine the limitations of a model, they must be considered when applying one to a problem or interpreting model behaviour.

2.1. Empirical approaches

In general, decomposing materials lose mass as they decay and negative exponential models often

are used to describe this pattern (Weider and Lang, 1982):

$$\text{Mass}_t = \text{Mass}_0 \cdot e^{-kt} \quad (1)$$

where the litter mass remaining after some time interval (t) is calculated as a function of the original mass and a decay rate coefficient (k). Without knowledge of the underlying mechanisms, the importance of environmental factors can be used empirically to modify this pattern. For example, the rate of litter mass loss is affected by temperature and moisture conditions. Temperature effects often are described by an exponential equation or Q_{10} function. On the other hand, moisture effects are more complicated, maximum decay rate occurs at some optimum moisture condition and declines as moisture conditions diverge from this optimum (Bunnell and Scoullar, 1975). Usually, the effects of moisture and temperature are included in models by scaling the estimated decay rate (Eq. 1) according to temperature and moisture responses (Andr n and Paustian, 1987).

Not all types of materials decay at the same rate even under identical climatic regimes, but knowledge of underlying chemistry is needed to predict these patterns. Plant materials consist of many different types of compounds, each of which decays at a particular rate (Minderman, 1968). Often, for convenience, these compounds are placed into three general classes of materials; polar and non-polar extractives (soluble component) decay very rapidly and have high nutrient contents; acid-soluble fractions (cellulose and hemicellulose) decay rapidly if nutrients are available but decay slowly otherwise; acid-insoluble fractions (lignins) decay slowly at all times. The decay rate of a material can be more accurately estimated when its chemical composition is known.

These general relationships between decomposition, litter quality and climate are so ubiquitous and well-known that many studies of litter decay do not examine other factors. Some models are based solely on these relationships, for example, Meentemeyer (1978) developed a very simple equation to calculate the amount of litter loss over time:

$$\text{Loss} = a + b \cdot \text{AET} + c \cdot \text{AET}/L \quad (2)$$

where AET is actual evapotranspiration, L is lignin content of the litter and a , b and c are model parameters. Another empirical model was developed by Melillo et al. (1982), in which mass loss is an exponential function of time (Eq. 1) and the decay rate coefficient varies with initial lignin and nitrogen content of the litter:

$$-k = d \cdot (\text{lignin}/\text{nitrogen})^f \quad (3)$$

where d and f are model parameters. The primary strength of such empirical models is their ability to predict system behaviour accurately within the range of data for which they were developed. The models developed by Meentemeyer and Melillo and colleagues were based on data collected in closed-canopy, mesic, temperate forests; they have been used very successfully to describe litter decay in such ecosystems.

Although the Meentemeyer model describes litter decay well in many ecosystems, it does not hold for others (Whitford et al., 1981; Schaefer et al., 1985). Surface litter loses mass far too rapidly in the northern Chihuahuan Desert, USA, to be consistent with Meentemeyer's equation (Fig. 2); Schaefer et al. (1985) found that litters high in lignin content decayed faster than those with low lignin content (note negative slope of regression in Fig. 2). This contradiction of Meentemeyer's model illustrates the key limitation of empirical models, i.e. often they are inaccurate when used beyond the range of data for which they were developed.

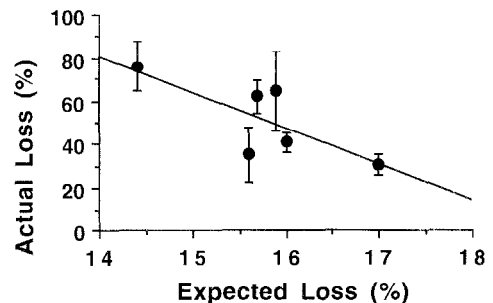


Fig. 2. Actual vs. expected mass losses of various litter types in the northern Chihuahuan Desert, New Mexico, USA; $R^2 = 0.571$ (data from Schaefer et al., 1985).

2.2. Mechanistic models

More mechanistic models have been developed to simulate litter decay (Bosatta and Ågren, 1991), although the common ones are actually semi-mechanistic in structure (McGill et al., 1981; Van Veen et al., 1984; Parton et al., 1987; Stroo et al., 1989; Moorhead and Reynolds, 1991; Rastetter et al., 1992). In most cases, decomposer microorganisms are identified as driving litter decay, and attention is directed toward linking decay processes to attributes of microbial physiology. Thus, the effects of moisture and temperature regimes on litter decay result largely from alterations in microbial activity. Temperature affects decay in three basic ways: (1) microbial activities are very limited in frozen soils or at temperatures exceeding 40–50°C; (2) activity rates generally increase from low temperatures (above 0°C) to a maximum at about 30–40°C; and (3) short-term freezing-thawing events often cause high turnover in microbial biomass (Morley et al., 1983). In a comparable manner, moisture availability has at least three effects: (1) microbial activities are very limited in dry soils (< -1.5 MPa) and in very moist or saturated soils when anaerobic conditions develop, (2) activity rates generally increase to some maximum at an intermediate level of moisture, and (3) rapid changes in moisture levels, such as rain following a dry period, increase microbial turnover (Kieft et al., 1987).

Decomposition rates are affected by nutrient and lignin content of litter. Different materials decompose at contrasting rates because they are degraded differentially by catabolic enzymes produced by saprophytic organisms (Linkins et al., 1984). However, few studies have attempted to quantify enzymic activities or relate these activities to litter decay. In general, most semi-mechanistic models divide decaying materials into sub-classes of compounds. A common scheme is one identifying soluble, holocellulose, and lignin fractions of litter. Decomposition then is estimated with a three-component exponential equation:

$$dC/dt = C_1e^{-k_1t} + C_2e^{-k_2t} + C_3e^{-k_3t} \quad (4)$$

where the combined loss of solubles (C_1), holocellulose (C_2) and lignins (C_3) defines the overall loss of litter (C).

Linking carbon and nutrient dynamics of the decomposition process is readily explained on the basis of microbial physiology. For example, the flow of C from nutrient-limited substrates (such as cellulose) is controlled by the availability of N from other sources because the internal N content of such nutrient-limited pools is insufficient to meet microbial needs in association with potential C losses. Therefore, actual C losses from such materials are limited by balancing system C and N availabilities with microbial needs (Parnas, 1975, 1976; Bosatta and Berendse, 1984):

$$(C/N)_l \times e = (C/N)_m \quad (5)$$

where e is the carbon assimilation efficiency of the microbiota, and $(C/N)_l$ and $(C/N)_m$ are the C/N ratios of litter and microbiota, respectively. If $(C/N)_l \times e > (C/N)_m$, then microbial growth is limited by nitrogen availability. Conversely, if $(C/N)_l \times e < (C/N)_m$, then growth is limited by carbon availability. This is true for any essential nutrient. Add to this relationship the fact that some organic compounds can be more readily degraded than others, and it defines the fundamental way in which litter quality controls decomposition. When mineral forms of nutrients are also considered, this equation can be expanded to estimate net immobilization or mineralization potentials (Moorhead and Reynolds, 1991).

Dynamics of the microbial community are incorporated in many of the more mechanistic decomposition models, with microbial growth, death (and subsequent decay) and mineralization processes variously included. Turnover of the microbial pool is very important because the release of nutrients from dead microbial biomass can stimulate the decay of nutrient-limited substrates or otherwise result in the net mineralization of nutrients. One of the most detailed descriptions of microbial dynamics was incorporated in a model developed by Paustian and Schnürer (1987) which focussed entirely on the growth dynamics of decomposer fungi. In this approach, the dynamics and characteristics of the fungal community were interpreted with respect to decay processes.

The major strength of these more mechanistic models is the confidence with which they can be applied to novel situations or conditions for which

they were not developed. For example, semi-mechanistic models of decomposition processes (Parton et al., 1987; Moorhead and Reynolds, 1991; Rastetter et al., 1991) have been used, apparently successfully, for situations very different from those upon which they were based (Burke et al., 1989; Schimel et al., 1990; Rastetter et al., 1992; Moorhead and Reynolds, 1993; Ojima et al., 1993). The major drawback to greater mechanism is the complexity of the resulting model, requiring more data to define parameters and greater attention to interpreting model behaviour.

2.3. Enzyme-based modelling

Recently, a new type of model has been developed to describe litter decay, based on the activities of extracellular enzymes. Since micro-organisms accomplish decay by producing enzymes that catalyze the degradation of substrates in their immediate environment, decomposition rates should be directly related to the activity of key classes of enzymes (Sinsabaugh et al., 1991). However, models expressing litter decay as a function of extracellular enzyme activities have been restricted largely to the degradation of dissolved organic materials in aquatic environments (Chróst, 1991). Only Sinsabaugh et al. (1991) have attempted to relate enzyme activities to mass loss of plant litter in terrestrial systems.

Preliminary analyses of published data show that litter mass loss rates are correlated with the activities of extracellular enzymes (Fig. 3), and this relationship can be used as a statistically-based model of litter decay (Sinsabaugh et al., 1994). Although such a model is empirical at the level of enzyme activity, enzyme activity is the primary biological mechanism underlying litter degradation (the latter representing a higher, hierarchical level phenomenon). The potential uses of enzyme-based decomposition models are only now being explored.

3. Model applications

Models are developed for a variety of reasons, including use in the synthesis of data, identifying areas of uncertainty, testing and formulating hypotheses, and evaluating conceptual relationships. However, models are also applied to ques-

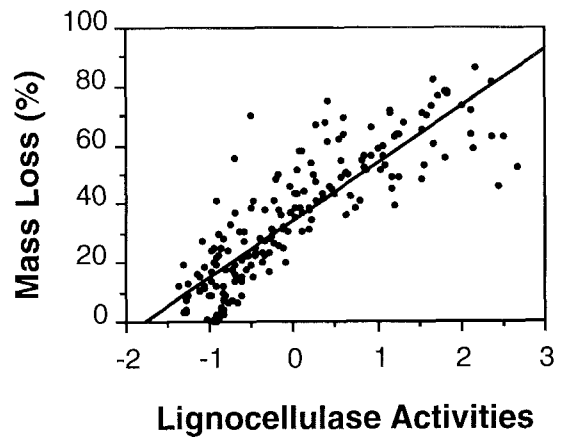


Fig. 3. Relationship between litter mass loss and a cumulative measure of extracellular lignocellulase degradative enzyme activities associated with the litter. Data derived from a suite of published studies; $R^2 = 0.732$ (from Sinsabaugh et al., 1994).

tions of interest to resource managers and may be used to help formulate policy decisions.

3.1. Decomposition as an isolated process

Litter decay is important to studies of soil erosion and site fertility, because surface litter layers dissipate raindrop energy, slow surface water movements, absorb water, minimize wind erosion and serve as a major source of nutrients. Decomposition models have been developed and used to simulate litter decay or nutrient cycling processes independent of other aspects of ecosystem behaviour. Obviously, many of the simple empirical models, like those formulated by Meentemeyer (1978) and Melillo et al. (1982, 1989), have limitations but can be used to estimate litter turnover and mineral nutrient release under different climatic conditions and altered litter quality, as determined by their driving variables. However, caution is necessary when extrapolating beyond the conditions for which these models were developed. In contrast, more mechanistic models offer greater potential for exploring novel conditions, and have been used to extrapolate the effects of global climatic changes and of anthropogenic activities on litter decay and nutrient cycling.

One of the ways in which a number of global changes, such as climate, atmospheric CO_2 , and

UV-B intensity, may affect ecosystems is by modifying nutrient cycles (Graham et al., 1990; Reynolds et al., 1995). Decomposition rates change in response to changing physical factors, litter characteristics, and decomposer communities. In addition, nutrient and energy dynamics are so tightly linked in terrestrial ecosystems that soil organic matter dynamics and site fertility should be affected by changes in litter decay (van de Geijn and van Veen, 1993). However, only recently have studies begun to investigate these topics (Wedin and Tilman, 1990).

The effects of temperature and moisture conditions on litter decay rates are well known. For these reasons, the effects of climate changes on decomposition are not difficult to evaluate. All other factors being constant, shifts in temperature and moisture patterns drive predictable changes in decomposition rates. Results of several simulation studies examining the potential effects of changing climate on decomposition and nutrient cycles generally support this view (Pastor and Post, 1988; Schimel et al., 1990; Rastetter et al., 1992; Moorhead and Reynolds, 1993; Ojima et al., 1993). Moorhead and Reynolds (1995) showed that decomposition and nitrogen dynamics in a tussock tundra soil responded to changes in moisture and temperature regimes in a predictable fashion, but uncertainties in projected soil climatic regimes limited the reliability of model results (Table 2). Similarly, other studies link a range of model behaviours to uncertainties in predicted climate changes (Schimel et al., 1990; Ojima et al., 1993), although simulated decay patterns are consistent with fluctuations in temperature and moisture regimes.

Aside from climatic and CO₂ effects, the potential impacts of other disturbances and stresses on decomposition are being examined with simulation models. For example, Moorhead and Callaghan (1994) recently explored the potential effects of increasing UV-B levels on litter degradation and soil organic matter dynamics. Many organic polymers, including plant lignins, are susceptible to photochemical degradation so that increasing UV-B levels may stimulate litter turnover. This could affect soil organic matter pools because plant lignin constitutes a significant por-

Table 2

Results of varying climate regime, i.e. average soil water content (% dry soil wt.), season length (days) and maximum summer temperature (°C), on simulated annual turnover of litter nitrogen by decomposer microbiota in an arctic, tussock tundra soil (from Moorhead and Reynolds, in press)

Water (%)	Annual turnover (gN · m ⁻² · year ⁻¹)		
	Maximum summer temperature/season length		
	7°C, 93 days	9°C, 113 days	11°C, 133 days
200	3.79	5.02	6.43
250	4.18	5.53	7.09
300	4.55	6.02	7.71
400	5.16	6.83	8.74
500	5.54	7.32	9.37
600	5.62	7.43	9.50
700	5.39 ^a	7.12	9.11
750	5.17	6.83	8.74
800	4.88	6.46	8.27
900	4.19	5.54	7.10
1000	3.39	4.49	5.76

^aCurrent conditions.

tion of SOM (Stott et al., 1983). Data from desert ecosystems suggest that photochemical degradation of exposed litter is significant in hot, dry environments; this is consistent with the direct relationship between decay rate and lignin content of surface litter reported by Schaefer et al. (1985; Fig. 2).

Moorhead and Callaghan (1994) used the CENTURY model (Parton et al., 1987) to project the effects of increasing UV-B intensity on litter decay and SOM pool sizes by increasing the decay rate of lignin and allocating the increased carbon flow from litter lignin to use by microorganisms (Fig. 4). A set of 20-year simulations with a 25% increase in lignin turnover produced end-of-year quantities of lignin and holocellulose in residual litter that were 64 and 32% lower than control values, respectively. The size of the active, slow and passive soil pools decreased ≤0.7, 3.9 and 2.5%, respectively. The greatest impact of increased lignin degradation was accelerated litter turnover and loss of carbon from the system via microbial respiration, with modest impact on soil organic matter pools. This does not imply that

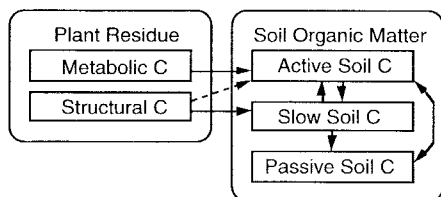


Fig. 4. Carbon flow diagram for the CENTURY model, describing litter decay (Parton et al., 1987). Dashed arrow indicates modification to simulate photodegradation of lignins in plant litter exposed at the soil surface.

changes in surface accumulations of litter are unimportant because erosion patterns and short-term nutrient dynamics are closely related to litter decay. As yet, no experimental studies have tested these results.

3.2. Decomposition in an ecosystem context

Decomposition is only a part of whole ecosystem behaviour, so studies of decay processes in isolation from other ecological processes should be viewed with skepticism. For example, Pastor and Post (1988) evaluated potential effects of climate changes on forest ecosystems and noted that vegetation composition depends in part on soil nitrogen availability. In turn, changes in vegetation composition can alter soil nitrogen availability (Wedin and Tilman, 1990).

Pastor and Post (1988) identified decomposition as a process that links plant community composition and soil nutrient status. Therefore, any factor that modifies litter quality or quantity, or decomposition rates, affects patterns of decay and nutrient mineralization. In a recent evaluation of elevated CO_2 effects on terrestrial ecosystems, Reynolds et al. (1995) noted that litter quality may change with CO_2 levels because the C/N ratios of at least some plants change with CO_2 enrichment (Coûteaux et al., 1991; Lambers, 1993). In addition to the direct effects of elevated CO_2 on the chemistry of particular species, plant community composition may change as a result of shifts in competitive interactions among species, thus altering overall litter characteristics. Whatever the cause, changes in litter quality would be expected to affect decomposition.

The effects of litter quality on decay patterns have been examined in a multitude of experimental and simulation studies (Reynolds et al., 1995). Moreover, these effects are predictable; decay rates decrease with increasing lignin content, and increase with nutrient concentration (Parton et al., 1987; Moorhead and Reynolds, 1991). The greatest challenge in applying such models to a changing world is predicting the changes in litter quality. Schimel et al. (1990), Rastetter et al. (1992) and Ojima et al. (1993) are among those who include changing litter quality as a dynamical component of their modeling studies, but do not address explicitly the mechanisms responsible for this change. Rastetter et al. (1992), in particular, emphasize the point that nutrient availabilities ultimately will limit ecosystem responses to changes in climate and CO_2 .

Other anthropogenic impacts further complicate the evaluation of the effects of climate, changes in CO_2 , etc., on the decomposition and nutrient cycling processes. For example, the results of a temperate grassland model (Thornley et al., 1991) suggest that combined CO_2 and N fertilization from human activities have synergistic effects on ecosystem carbon dynamics. Burke et al. (1991) also indicate that the effects of other human impacts are likely to diminish our ability to detect ecosystem responses to global changes. Clearly, the predictive capacities of ecosystem models are limited by their abilities to incorporate and integrate the important driving variables. Nevertheless, Ågren et al. (1991) conclude that several models of forest and grassland ecosystems provide realistic predictions of responses to climate change because these models explicitly link key plant and decomposer processes.

3.3. Experimental and modelling interface

At the least, uncertainties in projected changes in climate and litter quality limit the confidence with which models can predict future patterns of decomposition and nutrient cycling. Nor is it easy to conduct validation experiments that adequately represent realistic temporal and spatial dimensions, or capture the complexities of, ecological systems. However, a spatially-based climosequence of contiguous sites can be used as a sur-

rogate for temporal changes in climatic characteristics at a particular site while retaining the ecological features of the system. For example, Tate (1992) offers a soil climosequence in tussock grasslands of New Zealand as a surrogate for temporal changes in soil carbon dynamics accompanying probable climatic change for this ecosystem type. These grassland climates range in mean annual temperature from 2–10°C and total annual precipitation from 350–5000 mm, respectively. The relationship between soil carbon content and temperature-precipitation factors across this sequence of sites suggests that global warming would increase C-turnover in these soils in a manner that is consistent with expected effects of temperature and moisture conditions on decay processes.

A suite of modelling studies focussing on the central prairie regions of the USA also may be interpreted as examining a climosequence extending from the warmer, drier, southwest shortgrass prairies to the cooler, wetter, northeast tallgrass prairies (Parton et al., 1987; Burke et al., 1989; Schimel et al., 1990; Burke et al., 1991; Ojima et al., 1993). In general, soil organic matter pools increase with increasing rainfall and decreasing temperature. Schimel et al. (1990) and Ojima et al. (1993) specifically modify climate drivers to assess potential impacts of climate change on these ecosystems; decomposition was related most closely to temperature. Unfortunately, neither these models nor observations of Tate's (1992) tussock grassland toposequence explicitly include changes in litter quality due to changes in plant community composition, a likely consequence of climate change for many ecosystems.

Aside from uncertainties in projected changes in climate and litter quality, differential behaviours and sometimes conflicting predictions of various decomposition models reduce our confidence in their output. A broadly based set of integrated experimental and modelling studies is being conducted to address these uncertainties simultaneously. The Long-Term, Intersite Decomposition Experiment Team (LIDET) is monitoring the decay of various litters (a total of 31 different types) on 21 sites throughout North America. A detailed description of the LTER sites is provided by Van Cleve and Martin (1991). The types of lit-

Table 3

Chemical characteristics of litter examined within the long-term, intersite decomposition study (LIDET), sponsored by the USA Long-Term Ecological Research (LTER) program

Species	Lignin (%)	Nitrogen (%)
<i>Acer saccharum</i> (leaves)	16.64	0.87
<i>Ammophila breviligulata</i> (leaves)	19.26	0.74
<i>Betula lutea</i> (leaves)	26.71	1.63
<i>Bouteloua eriopoda</i> (leaves)	14.39	0.98
<i>Bouteloua gracilis</i> (leaves)	9.84	0.97
<i>Ceanothus greggii</i> (leaves)	14.59	1.35
<i>Cornus nuttallii</i> (leaves)	0.36	0.99
<i>Drypetes glauca</i> (leaves)	9.48	1.98
<i>Drypetes glauca</i> (roots)	17.92	0.93
<i>Fagus grandifolia</i> (leaves)	26.93	0.93
<i>Gonystylus bancanus</i> (wood)	24.63	0.32
<i>Kobresia myosuroides</i> (leaves)	11.72	1.10
<i>Larrea tridentata</i> (leaves)	10.93	2.13
<i>Liriodendron tulipifedra</i> (leaves)	10.10	0.80
<i>Myrica cerifer</i> (leaves)	27.81	2.03
<i>Pinus ellioti</i> (leaves)	27.47	0.49
<i>Pinus ellioti</i> (roots)	33.82	0.79
<i>Pinus resinosa</i> (leaves)	26.51	0.72
<i>Pinus strobus</i> (leaves)	21.72	0.70
<i>Populus tremuloides</i> (leaves)	21.17	0.78
<i>Pseudotsuga menzesii</i> (leaves)	25.00	0.90
<i>Quercus prinus</i> (leaves)	25.36	1.14
<i>Rhododendron macrophyllum</i> (leaves)	18.13	0.54
<i>Robinea pseudoacaia</i> (leaves)	24.89	2.48
<i>Schizachyrium gerardi</i> (leaves)	12.04	0.67
<i>Schizachyrium gerardi</i> (roots)	15.66	0.67
<i>Schizachyrium scoparium</i> (leaves)	16.02	0.69
<i>Spartina alternifolia</i> (leaves)	6.86	0.76
<i>Thuja plicata</i> (leaves)	21.04	0.72
<i>Triticum aestivum</i> (leaves)	17.72	0.52
<i>Voshysia ferragenea</i> (leaves)	19.85	1.98

ter being examined include a broad range of litter quality characteristics (Table 3), and the study sites represent climatic conditions ranging from tropical rain forests through arctic tundra, including deserts, grasslands, and temperate forests (Table 4). Four decomposition models (Fig. 5) are being used to simulate litter decay in this study, to gain insight to the limitations imposed by model structure on their abilities to capture the dynamics of interactions between climate and litter quality.

3.4. Insights provided by enzyme models

The activities of extracellular enzymes can be

Table 4

Field sites, ecosystem types and locations for the long-term, intersite decomposition study (LIDET), sponsored by the USA Long-Term Ecological Research (LTER) program

Site	Ecosystem	Location
Andrews LTER	Temperate rain forest	Oregon, USA
Arctic Lakes LTER	Arctic tundra	Alaska, USA
Baro Colorado Island	Tropical rain forest	Baro Colorado Island, Panama
Bonanza Creek LTER	Boreal forest	Alaska, USA
Blodgett Research Forest	Conifer forest	California, USA
Cedar Creek LTER	Tallgrass prairie	Minnesota, USA
Central Plains LTER	Shortgrass steppe	Colorado, USA
Coweeta LTER	Eastern deciduous forest	North Carolina, USA
Curlew Valley	Sagebrush steppe	Utah, USA
Florida State University	Slashpine forest	Florida, USA
Guanica State Forest	Dry tropical forest	Puerto Rico
Hubbard Brook LTER	Eastern deciduous forest	New Hampshire, USA
Harvard Forest LTER	Eastern deciduous forest	New York, USA
Jornada LTER	Warm desert	New Mexico, USA
Juneau, Alaska	Temperate rain forest	Alaska, USA
Kellogg LTER	Temperate agriculture	Michigan, USA
Konza LTER	Tallgrass prairie	Kansas, USA
La Selva Station	Tropical rain forest	Costa Rica
Loch Vale Watershed	Subalpine forest	Colorado, USA
Luquillo LTER	Subtropical rain forest	Puerto Rico
Monte Verde	Evergreen cloud forest	Costa Rica
Niwot Ridge LTER	Alpine tundra	Colorado, USA
North Inlet LTER	Estuarine marsh	South Carolina, USA
Northern Lakes LTER	Temperate lakes	Wisconsin, USA
Olympic National Park	Temperate rain forest	Washington, USA
Santa Margarita Reserve	Coastal chaparral	California, USA
Sevilleta LTER	Desert grassland/shrubland	New Mexico, USA
Virginia Coast LTER	Barrier islands	Virginia, USA

used to develop models of particular decomposition and nutrient cycling processes. For example, analyses of *Eriophorum vaginatum* (arctic sedge) tussocks provided parameters for a Michaelis-Menten model of phosphatase activities in an Alaska tussock tundra (Moorhead et al., 1993). This model was used to simulate seasonal phosphatase activities in the soils of this phosphorus-limited ecosystem. Results suggested that amounts of P released from decaying organic matter varied widely over the course of the summer and that phosphatase activities associated with living roots of *E. vaginatum* were capable of exceeding the annual plant demand for P. Clearly, the level of specificity afforded by enzymic studies permits focussing on selected aspects of decomposition and nutrient cycling. It also provides insights into broader questions.

Increasing amounts of labile carbon have been observed in plant rhizospheres associated with elevated CO₂ and may stimulate microbial activities which influence nutrient availabilities (Norby et al., 1986; O'Neill et al., 1987; Conroy et al., 1992; Comins and McMurtrie, 1993). Following a 3-year in situ CO₂ fumigation experiment in tussock tundra (Alaska, USA; Hilbert et al., 1987; Grulke et al., 1990), assays of below-ground enzymic activities detected increased activity of the alternate oxidase pathway in plant roots and mycorrhizae, increased phosphatase activity on root and mycorrhizae surfaces and in surrounding soils, increased cellulase activities on mycorrhizae surfaces, and reduced cellulase activities in surrounding soils (Linkins, unpublished data). These changes in phosphatase activities were used to modify the phosphatase model developed by

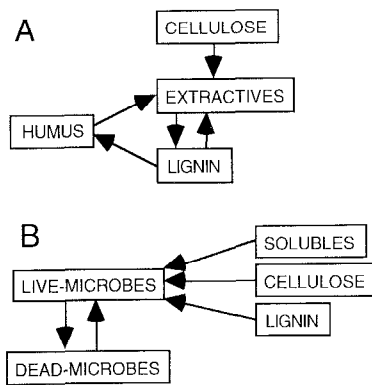


Fig. 5. Carbon flow diagrams for litter decay models used within a long-term, intersite decomposition study (LIDET), sponsored by the USA Long-Term Ecological Research (LTER) program; A, GEM (Rastetter et al., 1991); B, GENDEC (Moorhead and Reynolds, 1991) (see also CENTURY, Fig. 4).

Moorhead et al. (1993) to simulate phosphorus dynamics of tussock tundra. Similarly, changes in cellulase activities were used to modify the tussock tundra decomposition model developed by Moorhead and Reynolds (1993). Behaviours of the modified models suggest that nitrogen release from decaying organic matter was sensitive to the rate of cellulose decay; the observed reduction in cellulase activity in organic soil at doubled CO_2 reduced simulated annual nitrogen turnover. The effects of a concurrent increase in cellulase activity associated with rhizomorphs of mycorrhizae are less certain, but probably represent a localized increase in nitrogen release. An observed increase in phosphatase activities of root surfaces at higher CO_2 increased (roughly) the amount of associated phosphorus mineralization proportionally. Similar effects were found for roots, mycorrhizae, and organic soil horizons. Arctic plants appear to respond to elevated CO_2 by stimulating phosphatase activities of roots and mycorrhizae, and cellulase activity of mycorrhizae. Changes in enzyme activities within nearby soils suggest that carbon exudation from plant roots may inhibit cellulase activities (and thus nitrogen release) but stimulate phosphatase activities.

Enzymic assays can be used to develop or

modify models to reflect changes in decomposition or nutrient cycling processes. In addition to focussing on the activities of particular suites of enzymes, changes in the relative activities of suites of enzymes also provide insight to microbial community dynamics. For example, Sinsabaugh and Moorhead (1994) developed a model that compares the relative activity levels of carbon-acquiring versus nutrient-acquiring enzymes as a means of evaluating controls on decomposition. Similar approaches could be used to examine plant-decomposer, or plant-mutualist interactions.

4. Conclusions

Decomposition is a key ecological process that controls nutrient availabilities to plants in terrestrial ecosystems. Traditional studies of ecosystem dynamics and current research focussing on the impacts of global changes on ecosystems emphasize the link between producer and decomposer subsystems. For example, Leadley and Reynolds (1992), modelling plant responses of tussock tundra, concluded that increasing temperature, season length, moisture availability, and CO_2 level will have little impact on plant productivity unless nutrient availabilities also change. Experimental data from a variety of studies corroborate this conclusion and recent modelling efforts are beginning to link above- and below-ground responses of ecosystems to changes in climate, CO_2 and other disturbances.

The value of a model to any particular study depends on the match between study goals and model formulation. Recent evaluations of ecosystem models (Leadley and Reynolds, 1992) and arctic decomposition models (Moorhead and Reynolds, 1995), emphasize the relative strengths and weaknesses of modelling approaches suggested by Reynolds and Leadley (1992). In summary, empirical models are easy to formulate, require few data for development or use, and generally are very accurate within the range of conditions for which they are built. The greatest limitation to empirical models is their unreliability for novel conditions. Mechanistic models tend to be more applicable to novel situations because

they incorporate biological processes underlying the phenomenon of interest explicitly. However, they also are more complex, requiring more types of information (e.g. underlying physiological processes) to develop and use. Moreover, interpretation of model behaviour can be difficult for complex models.

Acknowledgements

Financial support for this work was provided by National Science Foundation grant BSR-9108329, United States Department of Agriculture National Research Initiative Program grant 92-37101-7569, and United States Department of Energy Office of Health and Environmental Research grant DE-FG05-92ER61493.

References

- Ågren, G.I., R.E. McMurtrie, W.J. Parton, J. Pastor and H.H. Shugart, 1991. State-of-the-art of models of production-decomposition linkages in conifer and grassland ecosystems. *Ecol. Appl.*, 1: 118–138.
- Andr n, O. and K. Paustian, 1987. Barley straw decomposition in the field: a comparison of models. *Ecology*, 68: 1190–1200.
- Bosatta, E. and G.I. Ågren, 1991. Dynamics of carbon and nitrogen in the organic matter of the soil: a generic theory. *Am. Nat.* 138: 227–245.
- Bosatta, E. and F. Berendse, 1984. Energy or nutrient regulation of decomposition: implications for the mineralization-immobilization response to perturbations. *Soil Biol. Biochem.*, 16: 63–67.
- Bunnell, F.L. and K.A. Scoullar, 1975. ABISKO II — A computer simulation model of carbon flux in tundra ecosystems. In: T. Rosswall and O.W. Heal (Eds.), *Structure and Function of Tundra Ecosystems*. *Ecol. Bull. (Stockholm)*, 20: 425–448.
- 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 Sci. Soc. Am. J.*, 53: 800–805.
- Burke, I.C., T.G.R. Kittel, W.K. Laurenroth, P. Snook, C.M. Yonker and W.J. Parton, 1991. Regional analysis of the central Great Plains. *Bioscience*, 41: 685–692.
- Cathey, D.D., B.C. Parker, G.M. Simmons, Jr. and W.H. Youngue, Jr., 1981. Artificial substrates in southern Victoria Land lakes of Antarctica. *Hydrobiologia*, 85: 3–16.
- Chr st, R.J. (Ed.), 1991. *Microbial Enzymes in Aquatic Environments*. Springer, New York.
- Co teaux, M.-M., M. Mousseau, M.-L. C l rier and P. Bottner, 1991. Increased atmospheric CO₂ and litter quality: decomposition of sweet chestnut leaf litter with animal food webs of different complexities. *Oikos*, 61: 54–64.
- Comins, H.N. and R.E. McMurtrie, 1993. Long-term response of nutrient-limited forests to CO₂ enrichment — equilibrium behaviour of plant-soil models. *Ecol. Appl.*, 3: 666–681.
- Conroy, J.P., P.J. Milham and E.W.R. Barlow, 1992. Effect of nitrogen and phosphorus availability on the growth response of *Eucalyptus grandis* to high CO₂. *Plant Cell Environ.*, 15: 843–847.
- Graham, R.L., M.G. Turner and V.H. Dale, 1990. How increasing CO₂ and climate change affect forests. *Bio-Science*, 40: 575–587.
- Grunke, N.E., G.H. Riechers, W.C. Oechel, U. Hjelm and C. Jaeger, 1990. Carbon balance in tussock tundra under ambient and elevated atmospheric CO₂. *Oecologia*, 83: 485–494.
- Hilbert, D.W., T.I. Prudhomme and W.C. Oechel, 1987. Response of tussock tundra to elevated carbon dioxide regimes: analysis of ecosystem CO₂ flux through nonlinear modelling. *Oecologia*, 72: 466–472.
- Kieft, T., L. Srooker and M.K. Firestone, 1987. Microbial biomass response to a rapid increase in water potential when dry soil is wetted. *Soil Biol. Biochem.*, 19: 119–126.
- Klopatek, C.C., E.G. O'Neill, D.W. Freckman, C.S. Bledsoe, D.C. Coleman, D.A. Crossley, E.R. Ingham, D. Parkinson and J.M. Klopatek, 1993. The Sustainable Biosphere Initiative: A Commentary from the U.S. Soil Ecology Society, 12 pp.
- Lambers, H., 1993. Rising CO₂, secondary plant metabolism, plant-herbivore interactions and litter decomposition — theoretical considerations. *Vegetatio*, 104: 263–271.
- Leadley, P.W. and J.F. Reynolds, 1992. Long-term response of an arctic sedge to climate change — A simulation study. *Ecol. Appl.*, 2: 323–340.
- Linkins, A.E., J.M. Melillo and R.L. Sinsabaugh, 1984. Factors affecting cellulase activity in terrestrial and aquatic ecosystems. In: M.H. Klug and C.A. Reddy (Eds.), *Current Perspectives in Microbial Ecology*. American Society of Microbiology, pp. 572–579.
- Meentemeyer, V., 1978. Macroclimate and lignin control of litter decomposition rates. *Ecology*, 59: 465–472.
- 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., J.D. Aber, A.E. Linkins, A.R. Turner, B. Fry and K.J. Nadelhoffer, 1989. Carbon and nitrogen dynamics along the decay continuum: plant litter to soil organic matter. In: M. Clarholm and L. Bergstr m (Eds.), *Ecology of Arable Land*. Kluwer, Dordrecht, pp. 53–62.
- McGill, W.B., H.W. Hunt, R.G. Woodmansee and J.O. Reuss, 1981. PHOENIX. A model of the dynamics of carbon and nitrogen in grassland soils. *Ecol. Bull. (Stockholm)*, 33: 49–115.
- Minderman, G., 1968. Addition, decomposition and accumulation of organic matter in forests. *J. Ecol.*, 56: 355–362.

- Moorhead, D.L. and T. Callaghan, 1994. Potential effects of increasing UV-B radiation on litter decay and site fertility. *Biol. Fertil. Soil*, 18: 19–26.
- Moorhead, D.L. and J.F. Reynolds, 1991. A general model of litter decomposition in the northern Chihuahuan Desert. *Ecol. Model.*, 59: 197–219.
- Moorhead, D.L. and J.F. Reynolds, 1993. Effects of climate change on decomposition in arctic tussock tundra: a modelling synthesis. *Arct. Alpine Res.*, 25: 403–412.
- Moorhead, D.L. and J.F. Reynolds, 1995. Modelling decomposition in arctic ecosystems. In: J.F. Reynolds and J.D. Tenhunen (Eds.), *Landscape Function: Implications for Ecosystem Response to Disturbance, A Case Study in Arctic Tundra*, Ch. 17. Ecological Studies Series. Springer, New York, in press.
- Moorhead, D.L., C.A. Kroehler, A.E. Linkins and J.F. Reynolds, 1993. Dynamics of extracellular phosphatase activities in *Eriophorum vaginatum* tussocks. *Arct. Alpine Res.*, 25: 50–55.
- Morley, D.R., J.A. Trofymow, D.C. Coleman and C. Cambardella, 1983. Effects of freeze-thaw stress on bacterial populations in soil microcosms. *Microb. Ecol.*, 9: 329–340.
- Norby, R.J., E.G. O'Neill and R.J. Luxmoore, 1986. Effects of atmospheric CO₂ enrichment on the growth and mineral nutrition of *Quercus alba* seedlings in nutrient poor soil. *Plant Physiol.*, 82: 83–89.
- Ojima, D.S., W.J. Parton, D.S. Schimel, J.M.O. Scurlock and T.G.F. Kittel, 1993. Modelling the effects of climatic and CO₂ changes on grassland storage of soil-C. *Water Air Soil Pollut.*, 70: 643–657.
- O'Neill, E.G., R.J. Luxmoore and R.J. Norby, 1987. Elevated atmospheric CO₂ effects on seedling growth, nutrient uptake and rhizosphere bacterial populations of *Liriodendron tulipifera* L. *Plant Soil* 104: 3–11.
- Parker, B.C. and G.M. Simmons, Jr., 1985. Paucity of nutrient cycling and absence of food chains in the unique lakes of Southern Victoria Land. In: W.R. Siegfried, P.R. Condy and R.M. Laws (Eds.), *Antarctic Nutrient Cycles and Food Webs*. Springer, New York, pp. 238–244.
- Parnas, H., 1975. Model for decomposition of organic material by microorganisms. *Soil Biol. Biochem.*, 7: 161–169.
- Parnas, H., 1976. A theoretical explanation of the priming effect based on microbial growth with two limiting substrates. *Soil Biol. Biochem.*, 8: 139–144.
- 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 Sci. Soc. Am. J.*, 51: 1173–1179.
- Pastor, J. and W.M. Post, 1988. Response of northern forests to CO₂-induced climate change. *Nature*, 334: 55–58.
- Paustian, K. and J. Schnürer, 1987. Fungal growth response to carbon and nitrogen limitation: a theoretical model. *Soil Biol. Biochem.*, 19: 613–620.
- 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 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.
- Rastetter, E.B., R.B. Mckane, G.R. Shaver, J.M. Melillo, 1992. Changes in C-storage by terrestrial ecosystems — How C-N interactions restrict responses to CO₂ and temperature. *Water Air Soil Pollut.*, 64: 327–344.
- Reynolds, J.F. and P.W. Leadley, 1992. Modelling the response of arctic plants to climate change. In: F.S. Chapin, III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver and J. Svoboda (Eds.), *Physiological Ecology of Arctic Plants: Implications of Climatic Change*. Academic Press, San Diego, CA, pp. 413–438.
- Reynolds, J.F., P.R. Kemp, B. Acock, J.-L. Chen and D.L. Moorhead, 1995. Limitations and uncertainties in modeling the effects of elevated CO₂ on plants and ecosystems. In: H.A. Mooney and G.W. Koch (Eds.), *Terrestrial Ecosystem Response to Elevated Carbon Dioxide*. Physiological Ecology Series. Academic Press, Orlando, FL, in press.
- Schaefer, D., Y. Steinberger and W.G. Whitford, 1985. The failure of nitrogen and lignin control of decomposition in a North American desert. *Oecologia*, 65: 382–386.
- Schimel, D.C., W.J. Parton, T.G.F. Kittel, D.S. Ojima and C.V. Cole, 1990. Grassland biogeochemistry: links to atmospheric processes. *Clim. Change*, 17: 13–25.
- Sinsabaugh, R.L. and D.L. Moorhead, 1994. Resource allocation to extracellular enzyme production: a model for nitrogen and phosphorus control of litter decomposition. *Soil Biol. Biochem.*, 26: 1305–1311.
- Sinsabaugh, R.L., R.K. Antibus and A.E. Linkins, 1991. An enzymic approach to the analysis of microbial activity during plant litter decomposition. *Agric. Ecosyst. Environ.*, 34: 43–54.
- Sinsabaugh, R.L., D.L. Moorhead and A.E. Linkins, 1994. The enzymic basis of plant litter decomposition: emergence of an ecological process. *Appl. Soil Ecol.*, 1: 97–111.
- Stott, E., G. Kassin, W.M. Jarrell, J.P. Martin and K. Haider, 1983. Stabilization and incorporation into biomass of specific plant carbons during biodegradation in soil. *Plant Soil*, 70: 15–26.
- Stroo, H.F., K.L. Bristow, L.F. Elliott, R.I. Papendick and G.S. Campbell, 1989. Predicting rates of wheat residue decomposition. *Soil Sci. Soc. Am. J.*, 53: 91–99.
- Swift, M.J., O.W. Heal and J.M. Anderson, 1979. Decomposition in terrestrial ecosystems. *Studies in Ecology*, Vol. 5. University of California Press, Berkeley, CA, 372 pp.
- Tate, K.R., 1992. Assessment, based on a climosequence of soils in tussock grasslands, of soil carbon storage and release in response to global warming. *J. Soil Sci.*, 43: 697–707.
- Thornley, J.H.M., D. Fowler and M.G.R. Cannell, 1991. Terrestrial carbon storage resulting from CO₂ and nitrogen fertilization in temperate grasslands. *Plant Cell Environ.*, 14: 1007–1011.
- Van Cleve, K. and S. Martin, 1991. Long-term ecological research in the United States: a network of research sites. LTER Publication No. 11, Long-Term Ecological Research Network Office, Seattle, WA.

- Van de Geijn, S.C. and J.A. Van Veen, 1993. Implications of increased carbon dioxide levels for carbon input and turnover in soils. *Vegetatio*, 104: 283–292.
- Van Veen, J.A., J.N. Ladd and M.H. Frissel, 1984. Modelling C and N turnover through the microbial biomass in soil. *Plant Soil*, 76: 257–274.
- Wedin, D.A. and D. Tilman, 1990. Species effects on nitrogen cycling: a test with perennial grasses. *Oecologia*, 84: 433–441.
- Whitford, W.G., V. Meentemeyer, T.R. Seastedt, K. Cromack, Jr., D.A. Crossley, Jr., P. Santos, R.L. Todd and J.B. Waide, 1981. Exceptions to the AET model: deserts and clear-cut forests. *Ecology*, 62: 275–277.
- Wieder, R.K. and G.E. Lang, 1982. A critique of the analytical methods used in examining decomposition data obtained from litter bags. *Ecology*, 63: 1636–1642.