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Global-Scale Similarities in Nitrogen Release Patterns During Long-Term Decomposition

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Litter decomposition provides the primary source of mineral nitrogen (N) for biological activity in most terrestrial ecosystems. A 10-year decomposition experiment in 21 sites from seven biomes found that net N release from leaf litter is dominantly driven by the initial tissue N concentration and mass remaining regardless of climate, edaphic conditions, or biota. Arid grasslands exposed to high ultraviolet radiation were an exception, where net N release was insensitive to initial N. Roots released N linearly with decomposition and exhibited little net N immobilization. We suggest that fundamental constraints on decomposer physiologies lead to predictable global-scale patterns in net N release during decomposition.

Litter decomposition converts the products of photosynthesis to inorganic components and stable soil organic matter. Decomposition releases more carbon (C) annually than fossil fuel combustion (1, 2), and it represents the primary source of nutrients for plants,

and both nutrients and energy for microbes, over biological time scales (3, 4). This is particularly true for the supply of nitrogen (N), which lacks a notable geologic input and is commonly a limiting element to plant growth (5). Internal recycling of N from litter decomposition thus provides a key resource for ecosystem productivity.

Litter decomposition is a lengthy process generally requiring years to decades for completion, and considerable N remains in litter after the initial decomposition phase (6–8). The vast majority of decomposition studies have been conducted over short time periods (<5 years), and at local scales using site-specific litters (9–11), making cross-site comparisons difficult. The lack of long-term broad-scale studies on litter decomposition and nutrient release inhibits our ability to accurately predict ecosystem C balance and response to environmental change at regional and global scales. The Long-Term Intersite Decomposition Experiment (LIDET) was a 10-year effort encompassing most of the world's biomes designed to deter-

mine long-term controls on decomposition and nutrient immobilization or mineralization. The study used several leaf and root litters that differed in chemical quality, with a core set of five to six leaf litters and three root litters that were decomposed at all sites (12). This data set is unique in that it encompasses the global array of climatic conditions (Table 1), includes a wide range of soil types and associated soil microbial community compositions, and was carried out over an unprecedented time span. Our goal was to use the LIDET core litter data set (1) from upland terrestrial sites to determine which combination of climate, initial litter chemistry, and site-specific characteristics (e.g., those derived from edaphic conditions and decomposer biota) best predict long-term patterns in litter N dynamics during decomposition (1, 10, 12–14). The data set included seven biomes, each with at least two replicate sites ($n = 21$ sites). We used mean annual temperature and precipitation, actual evapotranspiration, and the climatic decomposition index (CDI) as potential predictors of decomposition rates and N dynamics (Table 1). The CDI incorporates seasonality in temperature and moisture and has been shown to be well correlated with decomposition rates over 1 to 5 years (1). The core litters were chosen to encompass a wide range of C:N ratios, and concentrations of N, lignin, and other secondary compounds (Table 1, table S2).

CDI was the best predictor of decomposition rates globally (correlation coefficient $r^2 = 0.68$). Leaf and root litter decomposition were slowest in the cold, dry regions, such as boreal forest and tundra, and fastest in the warm, moist tropical forests (Fig. 1). A notable exception was the rapid leaf litter decomposition rate in arid-zone perennial grasslands despite a CDI of 0.11 (Fig. 1C); these ecosystems may have been affected by ultraviolet (UV) radiation (15–17) in addition to climate.

Unlike patterns in mass loss, net N immobilization and release in leaf litter were strongly

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Table 1. Climate data for the seven biomes used in this study. The mean time to the initiation of net N release (TNET) is given in years for each leaf litter species and biome and was calculated using the best-fit equation to determine the point of maximum net N immobilization (18). Mean

precipitation (PPT), temperature (TMP), actual evapotranspiration (AET), and the climatic decomposition index (37) are shown. TRAE, *Triticum aestivum*; PIRE, *Pinus resinosa*; THPL, *Thuja plicata*; ACSA, *Acer saccharum*; QUPR, *Quercus prinus*; DRGL, *Drypetes glauca*.

Biome	Mean annual PPT (mm)	Mean annual TMP (°C)	Climatic decomposition index (CDI)	Mean AT (mm)	TRAE 0.38% N TNET	PIRE 0.58% N TNET	THPL 0.62% N TNET	ACSA 0.80% N TNET	QUPR 1.02% N TNET	DRGL 1.98% N TNET
Arid grassland	331	13.0	0.11	1490	—	—	—	—	—	—
Humid grassland	807	9.8	0.30	1138	3.5	3	3.9	1.75	1.6	0.25
Tundra	788	-6.0	0.09	589	9.5	7.6	6.4	2.6	1.6	0.5
Boreal forest	750	0.0	0.12	830	6.4	4	4	2.6	1.3	0.5
Coniferous forest	1840	11.2	0.27	1058	3.8	2.6	2.2	1.4	0.7	0.25
Deciduous forest	1485	8.8	0.32	1070	1.85	1.1	0.9	0.8	0.33	0.2
Tropical forest	3210	23.6	0.78	1429	0.4	0.6	0.35	0.5	0.2	0.1

controlled by initial tissue N concentrations regardless of climate, other litter quality parameters, or site characteristics. A single, continuous nonlinear regression derived from the data explained 77% of the variability in net N immobilization and release as a function of initial leaf litter N concentrations and mass remaining for all forested biomes, humid grasslands, and tundra ecosystems (Fig. 2) (18). Patterns in net N immobilization and release were clearly delineated into four categories based on the initial leaf litter N concentrations (Table 1): high N (1.98% N, *Drypetes glauca*), intermediate N (1.02% N, *Quercus prinus*), low N [0.58 to 0.80% N, *Pinus resinosa* (decomposed at all but four sites), *Thuja plicata*, *Acer saccharum*], and very low N (0.39% N, *Triticum aestivum*). Litter high in initial N content had the best fit to the equation ($r^2 = 0.91$), although we could still explain 47% of the variation with the low-N litter that had the poorest fit. Leaf litters with intermediate to high initial N concentrations showed little or no net N immobilization, defined as the fraction of original N > 1 (Fig. 2, A and B). Substantial net N release started when ~40% of the mass was lost. The maximum fraction of original N immobilized increased as the initial N concentration decreased to low and very low levels (Fig. 2, A to D). There was also a general pattern of increased variance of the fraction of N remaining as the initial N content of the leaf litter decreased. On average, 170% of the initial N was immobilized (net) in the litter with very low initial N, and net N release occurred only after 60% of the mass had been lost.

These data demonstrate that fundamental constraints on microbial physiology lead to predictable patterns in net N immobilization and release during long-term decomposition. Patterns in net N immobilization and release have been shown to be related to the initial N concentration of specific leaf litters (19, 20), but these relations were thought to be dependent upon climate, other litter chemical characteristics (7), edaphic conditions (21, 22), or microbial community composition (23, 24). Theoretically the C:N ratio should dominantly control net N

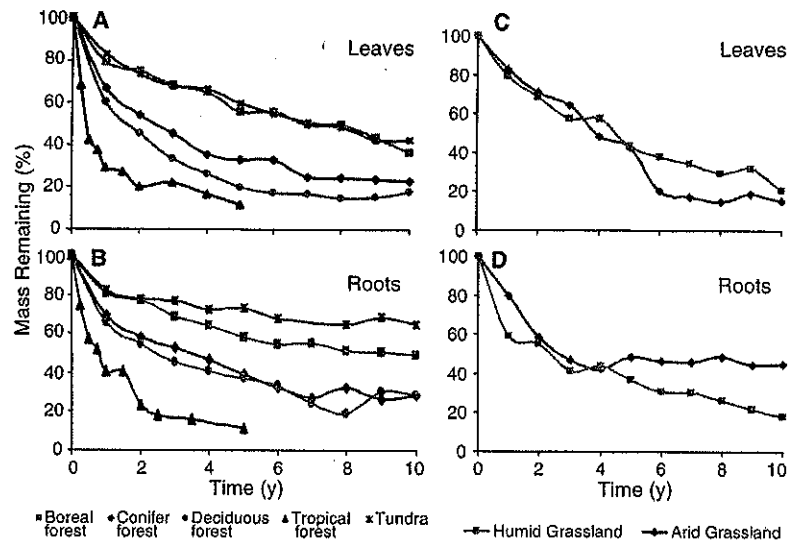


Fig. 1. Average mass remaining as a function of time for LIDET core leaf ($n = 5$ to 6 species) and root ($n = 3$ species) litters decomposed in 21 sites. (A) Leaf litter decomposed in forest and tundra biomes; (B) root litter decomposed in forest and tundra biomes; (C) leaf litter decomposed in humid and arid grasslands; (D) root litter decomposed in humid and arid grasslands. Each species and litter type was decomposed in replicate bags and collected at multiple time points. Results show that leaf and root litter decomposition rates generally increase as the CDI increases (Table 1). In arid grasslands, leaf litter decomposed more rapidly than expected (based on the CDI), possibly due to photodegradation.

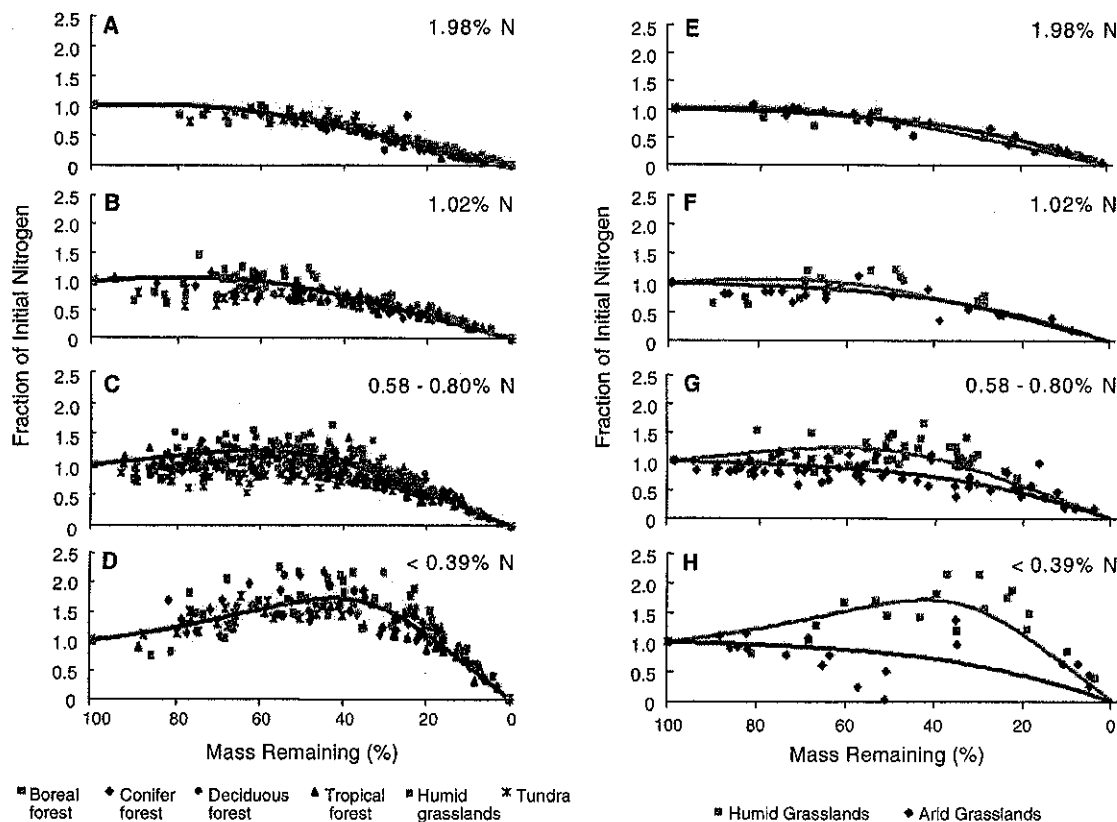
release during litter decomposition because microbial decomposers should only release N when their N requirements have been met. At low C:N ratios (e.g., high N concentrations), decomposers meet their N requirements directly from the litter. At higher initial C:N ratios, net immobilization typically occurs as microbes access N exogenous to the litter and convert it to microbial biomass or exoenzymes [e.g., (25)]. Immobilization of exogenous N is presumably controlled by N availability in the environment. Patterns in net N release and immobilization should thus be dependent upon the relative C:N ratios of the decomposer organisms and the substrate, as well as N availability in the environment. Here we show that leaf litter N dynamics can be predicted at broad spatial and long temporal scales based only on the initial litter

N concentration and the mass remaining during decomposition.

Net N release started when the average C:N ratio of the leaf litter was less than 40 (a range of 31 to 48). This is somewhat lower than in a 6-year decomposition study across Canada (C:N = 55) (22). The Canadian study used a narrower range of initial litter N and reported no relation between initial N concentration and rates of net N release. However, when net N release and immobilization are examined per unit of mass remaining, results were similar to the LIDET study.

As with mass loss, there was one exception to the pattern of net N release from the LIDET study. In arid-zone perennial grasslands, leaf litters with low and very low initial N concentrations showed a linear trend of net N release

Fig. 2. Fraction of original litter N remaining as a function of the leaf litter mass remaining for tundra, grassland, and forest biomes. (A) to (D) include all biomes except arid grasslands; (E) to (H) compare arid and humid grasslands. Data are divided into litter high in initial N (A and E), intermediate initial N (B and F), low initial N (C and G), and extremely low initial N (D and H). The lines on the graphs show the best-fit model for describing the pattern of fraction of original N as a function of the initial N concentration of the litter (18). Model results match the observed data and show that net N immobilization, defined as an absolute increase in N concentration of the litter, is highest for the leaf litter with very low initial N concentration and decreases to minimal values for high initial N concentration of leaf litter. Leaf litter in arid grasslands was an exception showing no N immobilization in the low and very low N litters.



with little or no net N immobilization (Fig. 2, E and F). The pattern of net N release versus mass remaining for arid grasslands could be described by an equation with no effect of initial litter N concentration (18) (Fig. 2, E to H). This contrasts with the results from humid grasslands that exhibited increasing net N immobilization as the initial N concentration of the leaf litter decreased (Fig. 2, E to H). Leaf litters decomposed faster in humid grasslands than in arid grasslands during the early stages of decomposition, but decomposition increased more rapidly in arid grasslands after the first 3 to 5 years to a level equivalent to that of deciduous forests (Fig. 1). This was surprising given that the CDI for arid grasslands is <50% that of the humid grassland and deciduous forest biomes. The effect was not seen for root tissues, which were decomposed below ground and decayed faster in humid grasslands than in arid grasslands (Fig. 1D). The rapid increase in leaf litter decomposition during the later stages of decomposition and the linear net N release regardless of initial N concentration in arid grasslands may be caused by photodegradation. Arid grasslands typically have less than 100 g m⁻² of standing live and dead plant tissues, whereas humid grasslands have more than 400 g m⁻² above-ground plant biomass that intercepts most of the

solar radiation before it gets to the surface leaf litter (26). Studies conducted during the early stages of decomposition (1 to 3 years) in arid grasslands have produced conflicting results regarding the effects of UV radiation on decomposition processes (15, 27, 28). However, recent studies suggest that where biotic decomposition is not favored (such as high litter lignin:N ratio and low moisture availability typical of arid grasslands), the abiotic process of photodegradation may predominate (16). This mechanism could explain the lack of a strong correlation between N concentration and decomposition, as well as the absence of net N immobilization at these sites.

Contrary to patterns of net N immobilization and release with mass loss, the time required to initiate net N release (TNET) was sensitive to initial tissue chemistry and climate. The TNET was inversely correlated with initial litter N and CDI ($r^2 = 0.77, P < 0.01$) (Table 1). The relation with CDI reflects the climatic controls on decomposition rate. The humid tropical biome had the lowest TNET values, ranging from 0.5 year for very low initial N litter to less than 0.1 year for high initial N litter. In the tundra and boreal forest biomes, it took more than 7 years for net N release to occur in litter with very low initial N, but only 0.5 year for net N

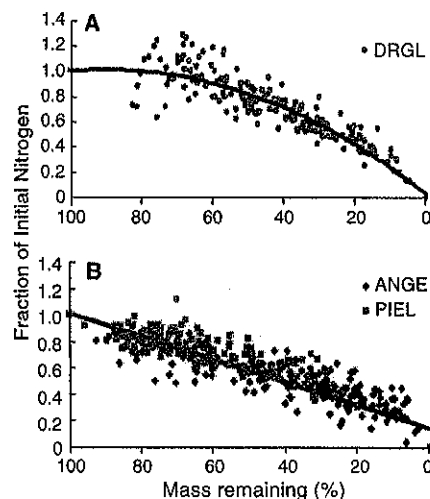


Fig. 3. Fraction of original root litter N remaining as a function of the litter mass remaining for *Drypetes glauca* root litter (A), and *Andropogon gerardi* and *Pinus elliotii* root litter (B), decomposing at the LIDET sites. Net N immobilization was minimal for decomposing root litter, with N being released as soon as decomposition of root litter starts. The equation for the DRGL roots is $y = -0.0001x^2 + 0.0221x + 0.0192, r^2 = 0.90$; the relation for the PIEL and ANGE roots is $y = 0.0087x + 0.1409, r^2 = 0.87$.

release from litter high in initial N. The TNET was at least 50% faster for most leaf litters decomposed in temperate deciduous forests when compared to coniferous forests and humid grasslands, all with similar CDIs (Table 1). Within a given CDI level, other factors such as edaphic conditions or decomposer communities may contribute to the differences observed (29, 30). At the highest leaf litter N concentrations, all biomes experienced net N release during the first year of decomposition.

Root litter N followed a linear pattern with mass remaining (Fig. 3) and could best be described by two equations. The first was for *D. glauca* roots, which demonstrated a small amount of net N immobilization early in decomposition for a range of sites, possibly due to slightly higher concentrations of nonpolar extractives and slightly lower acid extractable carbohydrates concentrations than the other species (table S2). The second equation described net N release for the pine and grass roots that did not immobilize N during decomposition. A comparison of litter N dynamics during decomposition of pine and grass roots with leaf litter of similar initial N concentration (Figs. 2 and 3) showed that N was released from roots much more rapidly than from leaf litter. Roots released N as soon as litter decomposition was initiated (C:N ratio > 50). Microbial decomposers in the soil may have greater access to moisture, organic matter, and mineral N than microbes involved in leaf litter decomposition at the soil surface, which would facilitate net N release during decomposition (31). Similar patterns in net N release in roots have been described for native root litter decomposed in situ in grasslands (32), temperate broadleaf forests (33), temperate conifer forests (34), and moist and humid tropical forests (35, 36).

Our data show that the initial N concentration of leaf litter is a dominant driver of net N immobilization and release during long-term litter decomposition at a global scale. This occurs regardless of climate, other litter chemical properties, edaphic conditions, or soil microbial communities. Our data also show that N can be released early in decomposition from high-quality litters in environments that support low decomposition rates. The time required to initiate net N release was predicted from the initial N of the litter and the CDI across biomes, but required more site information within a given CDI. Roots generally lost N linearly with mass loss during decomposition. Because N release during decay plays a fundamental role in net ecosystem production, improved understanding of the controls on net N release during decomposition is likely to greatly improve our ability to predict terrestrial C dynamics at global and regional scales.

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Supporting Online Material

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Water Solubility in Aluminous Orthopyroxene and the Origin of Earth's Asthenosphere

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Plate tectonics is based on the concept of rigid lithosphere plates sliding on a mechanically weak asthenosphere. Many models assume that the weakness of the asthenosphere is related to the presence of small amounts of hydrous melts. However, the mechanism that may cause melting in the asthenosphere is not well understood. We show that the asthenosphere coincides with a zone where the water solubility in mantle minerals has a pronounced minimum. The minimum is due to a sharp decrease of water solubility in aluminous orthopyroxene with depth, whereas the water solubility in olivine continuously increases with pressure. Melting in the asthenosphere may therefore be related not to volatile enrichment but to a minimum in water solubility, which causes excess water to form a hydrous silicate melt.

Earth's asthenosphere is often assumed to roughly coincide with the low-velocity zone, a layer of reduced seismic velocities and increased attenuation of seismic waves. The low-velocity zone usually begins at a depth

of 60 to 80 km below the oceans and ends around 220 km (1). Below continental shields, the upper boundary is depressed to 150 km. The seismic characteristics of the low-velocity zone could be easily explained by the presence of a small frac-