Science
AAAS

The Global Stoichiometry of Litter Nitrogen Mineralization
Stefano Manzoni, *et al.*
Science **321**, 684 (2008);
DOI: 10.1126/science.1159792

Science (print ISSN 0036-8075; online ISSN 1095-9203) is published weekly, except the last week in December, by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005.

Copenhagen. It is supported by funding agencies in Denmark (Forskningsrådet for Natur og Univers), Belgium (Fonds National de la Recherche Scientifique), France (Institut Polaire Française and Institut National des Science l'Univers/CNRS), Germany (AWI), Iceland (Rannís), Japan (Ministry of Education, Culture, Sports, Science and Technology), Sweden (Polarforskningssekretariatet), Switzerland (Der Schweizerische Nationalfonds) and the United States (NSF, Office of Polar Programs).

Supporting Online Material
www.sciencemag.org/cgi/content/full/1157707/DC1
Materials and Methods
Tables S1 and S2
Data

12 March 2008; accepted 12 June 2008
Published online 19 June 2008;
10.1126/science.1157707
Include this information when citing this paper.

The Global Stoichiometry of Litter Nitrogen Mineralization

Stefano Manzoni,[1] Robert B. Jackson,[2] John A. Trofymow,[3] Amilcare Porporato[1]*

Plant residue decomposition and the nutrient release to the soil play a major role in global carbon and nutrient cycling. Although decomposition rates vary strongly with climate, nitrogen immobilization into litter and its release in mineral forms are mainly controlled by the initial chemical composition of the residues. We used a data set of ~2800 observations to show that these global nitrogen-release patterns can be explained by fundamental stoichiometric relationships of decomposer activity. We show how litter quality controls the transition from nitrogen accumulation into the litter to release and alters decomposers' respiration patterns. Our results suggest that decomposers lower their carbon-use efficiency to exploit residues with low initial nitrogen concentration, a strategy used broadly by bacteria and consumers across trophic levels.

Plant residues deposited to the soil are subject to biological degradation (*1*–*3*). During this process, litter carbon (C) is respired to CO_2 while providing energy to the decomposers, whereas nutrient concentrations generally increase (*4*). Nutrients in mineral forms are taken up by the decomposers (immobilized) and thus accumulate in the litter. Typically, net nitrogen (N) release in mineral forms (ammonium and nitrate) from a given plant residue (net mineralization) only occurs after N concentration reaches a critical value (*1*). Knowledge of this threshold and how it is related to biogeochemical or climatic factors is essential to predict the patterns of nutrient cycling in natural and agricultural settings (*4*–*6*), to improve our understanding of ecosystem stoichiometry (*7*, *8*), and to constrain biogeochemical models (*9*). The biological degradation of litter is mainly carried out by microbial decomposers, including bacteria and fungi, and their grazers, which have higher N:C values compared with most litter types (*1*). This creates a high N demand, and, even though a considerable fraction of assimilated C is respired, the decomposers often still require some inorganic N uptake during at least the early phases of decomposition. The decomposer N:C and the respiration rate (complementary to the carbon-use efficiency) define the actual nutrient requirement of the decomposers (*9*–*11*). Although the decomposer N:C ratios have been observed to be relatively constant across ecosystems and litter types, the causes of patterns of variation in carbon-use efficiency are still unclear.

We analyzed litter decomposition data including the temporal evolution of both carbon and nitrogen, as measured in litterbags left to decompose in field conditions (*12*) or from chemical analysis of large branches and logs along decomposition chronosequences. On the basis of 55 litter types classified by initial N concentrations ranging from 0.03% to 3% (*13*), we show that the carbon-use efficiency tends to increase with higher initial substrate N:C ratio, which corresponds to a more-efficient nitrogen use and a less-efficient carbon use for N-poor substrates (i.e., litter with low N concentration and low N:C). In turn, low carbon-use efficiencies allow net mineralization to occur early during decomposition, even in relatively N-poor residues.

The dynamics of net N immobilization, accumulation, and mineralization have been described mathematically with mass balance equations (*9*, *11*, *14*). We developed a general set of such equations that allows us to obtain universal analytical curves of N accumulation and release during decomposition, when the decomposer characteristics can be assumed relatively constant in time (*13*). Specifically, the general expression for the fraction of initial litter nitrogen content, n, as a function of the fraction of remaining carbon content in the litter sample, c, can be written independently of the specific decomposition model as

$$n(c) = c\frac{r_B}{r_{L,0}} + \left(1 - \frac{r_B}{r_{L,0}}\right)c^{\frac{1}{1-e}} \qquad (1)$$

where $r_{L,0}$ is the initial litter N:C ratio, r_B is the decomposer biomass N:C, and e is the decomposer carbon-use efficiency (i.e., amount of C in new biomass per unit C decomposed). Thus, the N dynamics are represented in terms of the fraction of remaining litter C content, avoiding any explicit account of the temporal variability of decomposition rates caused by climatic factors or nutrient limitation. On the basis of data from 15 data sets containing observations at more than 60 sites worldwide (table S1), this universal representation of N immobilization and release curves appears to be valid across diverse terrestrial ecosystems and with different initial litter N:C values.

During decomposition, the fraction of remaining N and lost C move along the curves from left to right at a speed dictated by biogeochemical and environmental conditions (Fig. 1). All the curves show slower N loss than C loss, meaning that N tends to accumulate, and the N:C ratio of the litter increases throughout decomposition. Where the curves increase with respect to the initial condition, not only is N retained more efficiently than C, but net immobilization occurs. At the point on each curve where n is maximal, immobilization ends and net mineralization begins. Conversely, if the curve decreases monotonically there is no initial net immobilization, as in Fig. 1, A and B. The maximum of the N release curve thus corresponds to the litter critical N concentration, which can be expressed analytically in terms of N:C ratio as a function of the decomposer characteristics, $r_{CR} = e \cdot r_B$ (*9*, *10*). In general, the lower r_{CR} is, the earlier N release occurs, even in N-poor residues. Moreover, when $r_{CR} < r_{L,0}$, net release occurs from the beginning of decomposition. Conversely, if r_{CR} is high, large amounts of mineral N have to be immobilized to increase the litter N concentration to its critical value.

The litter decomposition observations and Eq. 1 can be used to study the patterns of variation of the litter r_{CR} and decomposer characteristics. Using the analytical N release curve provides a theoretical underpinning to previous estimates of the onset of mineralization based on regressions of field observations (*4*, *15*) and offers robust estimates of r_{CR} and the decomposer parameters, e and r_B. In particular, r_B does not vary systematically along gradients of organic matter and litter N:C and typically remains in the range of 0.07 to 0.2 [or C:N between 5 and 15 (*7*, *16*, *17*)]. We thus assumed an average value of $r_B = 0.1$ and fitted the remaining free parameter, e, for each litter type (*13*). For given values of r_B and e and applying a nonlinear transformation of Eq. 1, all observations of litter C and N content collapse well onto a single 1:1 curve (Fig. 2 and fig. S1), showing that the variation of e alone explains most of the variability in the data.

We assessed how r_{CR} and e, which are simply proportional when r_B is a constant, respond to changes in climatic variables and initial litter conditions. Parton *et al.* (*18*) and Moore *et al.* (*15*) noted that the N release patterns observed in two

[1]Civil and Environmental Engineering Department, Duke University, Durham, NC 27708, USA. [2]Department of Biology and Nicholas School of the Environment, Duke University, Durham, NC 27708, USA. [3]Canadian Forest Service, Pacific Forestry Centre, Victoria, BC V8Z 1M5, Canada.

*To whom correspondence should be addressed. E-mail: amilcare@duke.edu

continental-scale decomposition experiments do not depend on climatic variables. Our analysis, which includes many additional data sets (table S1), not only confirms the lack of a significant correlation between r_{CR} and mean annual precipitation or temperature but also reveals a significant power law relationship between r_{CR} and $r_{L,0}$ (Fig. 3A). This result shows that decomposers of low-N residues are able to begin mineralization even when the litter N concentration is still relatively low. In fact, for a given r_B, lower values of r_{CR} imply lower values of e (i.e., higher fractions of respired C), indicating that some decomposers with low energetic efficiency may be able to decompose low-N litter without necessarily having to immobilize much inorganic N. A low r_{CR} (and low e) also explains the low N immobilization observed during decomposition of N-poor wood (*19*). Apparently, decomposers are able to use the limited but relatively reliable N bound to organic compounds, thus reducing their dependence on the less-reliable or less-accessible inorganic pool. Nevertheless, because estimated values of r_{CR} are generally higher than $r_{L,0}$ (data points above the dashed line in Fig. 3A), some degree of immobilization remains necessary. For a given $r_{L,0}$, the variability in r_{CR} might be attributed to site effects. In fact, a trend for higher N accumulation in litters from sites with higher soil N:C ratios has been reported (*15*), although there are not enough data to test for such an effect globally.

Lastly, the pattern of decline in e as a function of $r_{L,0}$ appears to be independent of possible changes in r_B (shaded area in Fig. 3A). Remarkably, a similar pattern has also been observed [Fig. 3B; see also (*13*)] at different time scales and trophic levels in bacterial cultures (*20*), in aquatic bacteria (*21*), and in terrestrial and aquatic grazers (*22*–*25*). The generality of such a result hints at a common mechanism of carbon utilization across diverse ecosystems and trophic levels, where carbon "waste" occurs under restricted nutrient availability. From a metabolic perspective, the observation of low e may be related to regulation of catabolic reactions in low-nutrient conditions to maintain a stable cellular composition (*20*, *21*) or to increased C throughput by the decomposers or decomposer food web for obtaining N from recalcitrant substrates (*17*, *26*). A better understanding of the causes of this behavior is of fundamental interest and could reveal the constraints on decomposer community functioning under N-poor conditions, an important goal for improving biogeochemical modeling. In biogeochemical models of soil and litter, the carbon-use efficiency of decomposers is generally assumed constant or to decrease with substrate N:C, in agreement with our results (*14*, *17*, *27*). However, our estimates are generally lower than the efficiency values typically assumed, suggesting that current models might underestimate the heterotrophic respiration flux per unit mass of decomposed litter or organic matter.

In summary, the N-release patterns of decomposing litter appear to be regulated by the initial chemical composition of the litter and the stoichiometric requirements of the decomposers (Fig. 1). In particular, the critical N:C ratio, below which net immobilization occurs, is uncorrelated with climatic variables but strongly correlated with initial litter chemistry (Fig. 3A). Because decom-

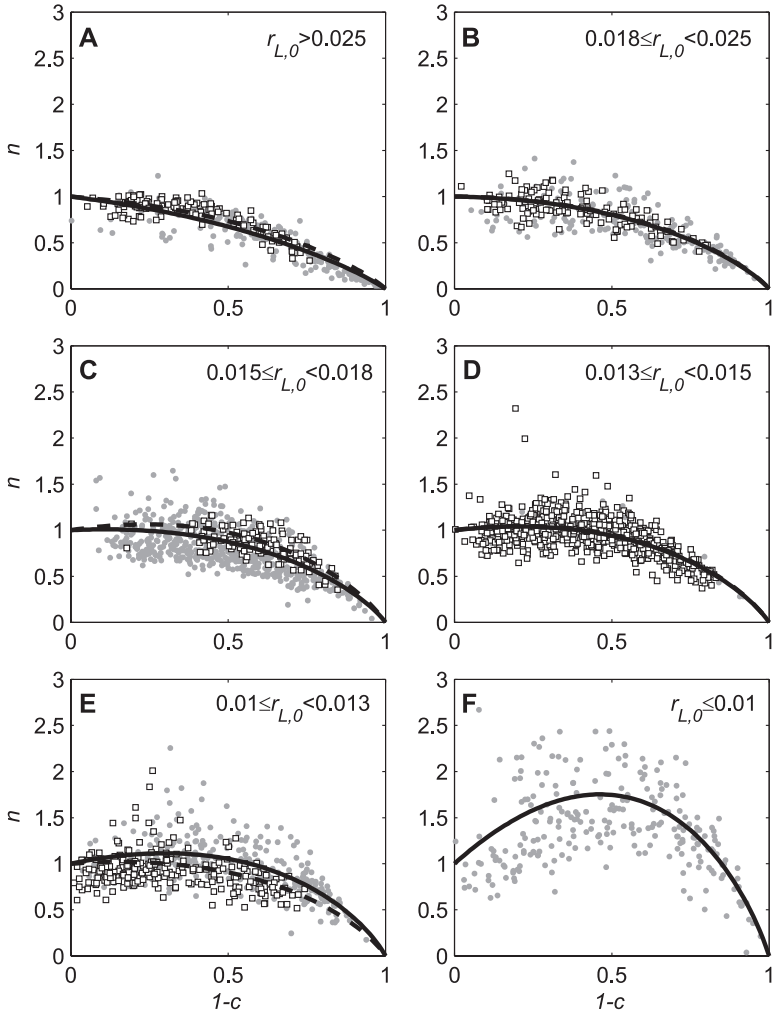

Fig. 1. Nitrogen release patterns across litter types. (**A** to **F**) Observed and modeled fractions of initial nitrogen, $n = N_L(t)/N_L(0)$, as a function of the decomposed fractions of initial carbon, $1 - c = 1 - C_L(t)/C_L(0)$, for leaf litter with decreasing values of $r_{L,0}$. Data and analytical N release curves for the LIDET data set (*18*, *28*, *29*) are represented by ● and solid lines; data from the CIDET data set (*12*, *15*), by □ and dashed lines.

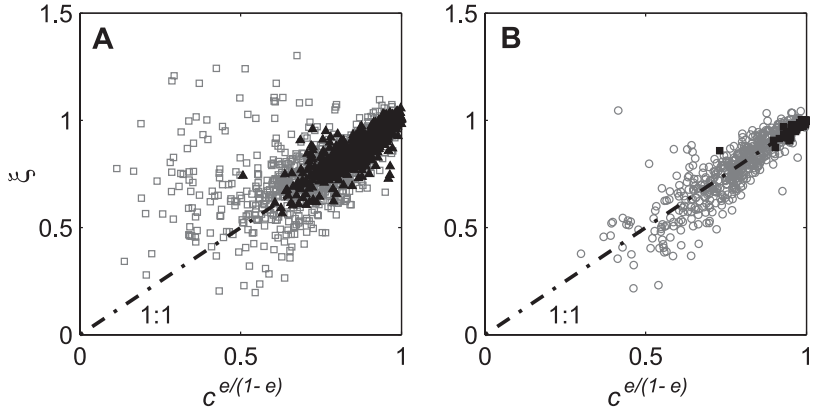

Fig. 2. Normalized representation of the nitrogen release curves. Plots of the normalized variable $\xi = (r_L - r_B)/(r_{L,0} - r_B)$ (eq. S5) against $c^{e/(1-e)}$ for litters of different origin [(**A**) broadleaved tree and shrub leaves, □, and conifer needles, ▲; (**B**) grass leaves, ○, and woody residues, ■], showing that the analytical N release curves (Eq. 1) fitted to the data with the only free parameter e is able to capture most of the variability in all litter types.

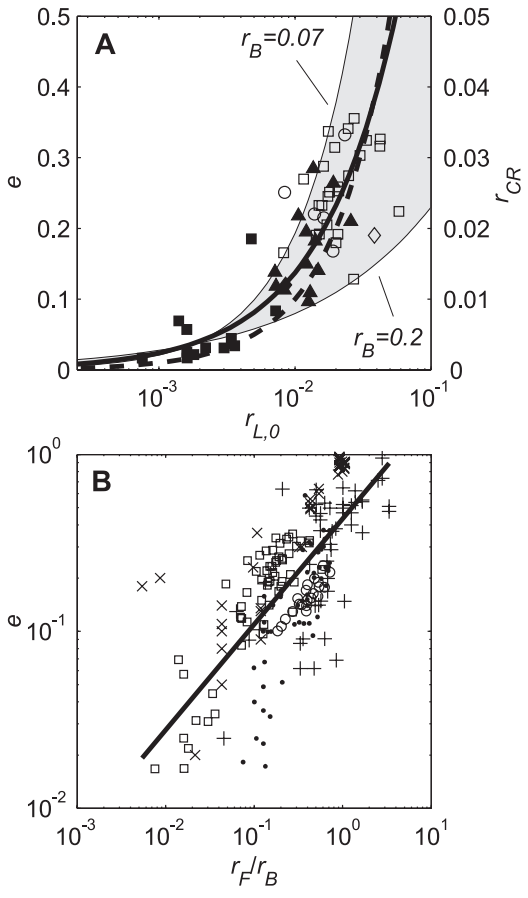

Fig. 3. Effect of litter quality on decomposer stoichiometry. (**A**) Decomposer efficiency, *e* (left), or r_{CR} (right) as a function of $r_{L,0}$ when r_B = 0.1. Symbols indicate different litter types as in Fig. 2; ◇ and ◆ refer to a decomposing log (r_B = 0.122) and the underlying soil (r_B = 0.135), respectively [data elaborated after (*16*, *30*)]. The solid line is a linear least square fit of the log-transformed r_{CR} and $r_{L,0}$ ($r_{CR} = 0.45 \times r_{L,0}^{0.76}$; $R = 0.88$; $P < 0.0001$). The shaded area shows the effects on *e* of different r_B around 0.1 (solid line). The dashed curve indicates points where $r_{CR} = r_{L,0}$: Litter points above this curve need to immobilize N; points below release N since the beginning of decomposition. (**B**) Estimates of *e* as a function of the ratio between food source N:C (r_F) and consumer N:C (r_B) at different trophic levels: □, terrestrial plant residue decomposers (this study); +, marine bacteria (*21*); ○, terrestrial larvae (*25*); ●, terrestrial insects (*23*); and ×, aquatic insects (*24*). The solid line is a linear least square fit of the log-transformed *e* and r_F/r_B [$e = 0.43 \times (r_F/r_B)^{0.60}$; $R = 0.72$; $P < 0.0001$].

poser N:C ratio is relatively constant, this pattern suggests that the decomposer communities are able to adapt partially to low-nitrogen substrates (i.e., low $r_{L,0}$) by decreasing their C-use efficiency and thus the critical N:C of the litter (Fig. 3A). Such a pattern has been observed in aquatic environments and at other trophic levels (*21*–*25*) and appears to be a universal response of decomposers in nutrient-poor conditions (Fig. 3B). Decreasing efficiency results in higher heterotrophic respiration per unit mass of litter humified or unit nutrient released, suggesting that the soil carbon cycle is likely more open than currently thought.

References and Notes

1. B. Berg, C. A. McClaugherty, *Plant Litter: Decomposition, Humus Formation, Carbon Sequestration* (Springer, Berlin, 2003).
2. M. J. Swift, O. W. Heal, J. M. Anderson, *Decomposition in Terrestrial Ecosystems*, vol. 5 of *Studies in Ecology* (Univ. of California Press, Berkeley, 1979).
3. S. A. Waksman, *J. Agric. Sci.* **14**, 555 (1924).
4. J. D. Aber, J. M. Melillo, *Can. J. Bot.* **60**, 2263 (1982).
5. G. Seneviratne, *Biol. Fertil. Soils* **31**, 60 (2000).
6. B. Berg, G. Ekbohm, *Ecology* **64**, 63 (1983).
7. C. C. Cleveland, D. Liptzin, *Biogeochemistry* **85**, 235 (2007).
8. R. W. Sterner, J. J. Elser, *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere* (Princeton Univ. Press, Princeton, NJ, 2002).
9. S. Manzoni, A. Porporato, *Soil Biol. Biochem.* **39**, 1542 (2007).
10. G. I. Ågren, E. Bosatta, *Theoretical Ecosystem Ecology: Understanding Element Cycles* (Cambridge Univ. Press, Cambridge, 1996).
11. E. Bosatta, H. Staaf, *Oikos* **39**, 143 (1982).
12. J. A. Trofymow, CIDET, "The Canadian Intersite Decomposition Experiment (CIDET): Project and site establishment report," *Tech. Rep. No. BC-X-378* (Pacific Forestry Centre, Victoria, Canada, 1998).
13. See supporting materials on *Science* Online.
14. W. J. Parton, D. S. Schimel, C. V. Cole, D. S. Ojima, *Soil Sci. Soc. Am. J.* **51**, 1173 (1987).
15. T. R. Moore, J. A. Trofymow, C. E. Prescott, J. Fyles, B. D. Titus, *Ecosystems* (*New York*) **9**, 46 (2006).
16. S. C. Hart, *Ecology* **80**, 1385 (1999).
17. H. W. Hunt *et al.*, *Biol. Fertil. Soils* **3**, 57 (1987).
18. W. Parton *et al.*, *Science* **315**, 361 (2007).
19. O. N. Krankina, M. E. Harmon, A. V. Griazkin, *Can. J. For. Res.* **29**, 20 (1999).
20. J. B. Russell, G. M. Cook, *Microbiol. Rev.* **59**, 48 (1995).
21. P. A. del Giorgio, J. J. Cole, *Annu. Rev. Ecol. Syst.* **29**, 503 (1998).
22. J. J. Elser *et al.*, *Nature* **408**, 578 (2000).
23. W. J. Mattson, *Annu. Rev. Ecol. Syst.* **11**, 119 (1980).
24. T. J. Pandian, M. P. Marian, *Freshw. Biol.* **16**, 93 (1986).
25. F. Slansky, P. Feeny, *Ecol. Monogr.* **47**, 209 (1977).
26. J. M. Craine, C. Morrow, N. Fierer, *Ecology* **88**, 2105 (2007).
27. W. B. McGill, H. W. Hunt, R. G. Woodmansee, J. O. Reuss, in *Terrestrial Nitrogen Cycles: Processes, Ecosystem Strategies and Management Impacts*, F. E. Clark, T. Rosswall, Eds. (Ecological Bulletins, Stockholm, 1981), vol. 33, pp. 49–115.
28. M. E. Harmon, Long-Term Ecological Research (LTER) Intersite Litter Decomposition Experiment (LIDET), Forest Science Data Bank code TD023, Corvallis, OR, 2007, www.fsl.orst.edu/lter/data/abstract.cfm?dbcode=TD023.
29. H. L. Gholz, D. A. Wedin, S. M. Smitherman, M. E. Harmon, W. J. Parton, *Glob. Change Biol.* **6**, 751 (2000).
30. S. C. Hart, G. E. Nason, D. D. Myrold, D. A. Perry, *Ecology* **75**, 880 (1994).

31. This research was supported by Department of Energy (DOE) Forest-Atmosphere Carbon Transfer and Storage project (FACT-1), NSF DEB 0235425 and 0717191, and DOE PER 64242-0012346. LIDET data sets were provided by the Forest Science Data Bank, a partnership between the Department of Forest Science, Oregon State University, and the U.S. Forest Service Pacific Northwest Research Station, Corvallis, Oregon. Significant funding for these data was provided by the NSF Long-Term Ecological Research program (DEB-02-18088). Funding for the CIDET experiment was provided by Climate Change and Ecosystem Processes Network of the Canadian Forest Service and Natural Resources Canada Panel on Energy Research Development. We also thank G. Katul, D. Richter, and two anonymous reviewers for useful comments.

Supporting Online Material

www.sciencemag.org/cgi/content/full/321/5889/684/DC1
Materials and Methods
Fig. S1
Table S1

29 April 2008; accepted 1 July 2008
10.1126/science.1159792

Regulation of CD45 Alternative Splicing by Heterogeneous Ribonucleoprotein, hnRNPLL

Shalini Oberdoerffer,[1] Luis Ferreira Moita,[2]* Daniel Neems,[1] Rui P. Freitas,[2]* Nir Hacohen,[2,3] Anjana Rao[1]†

The transition from naïve to activated T cells is marked by alternative splicing of pre-mRNA encoding the transmembrane phosphatase CD45. Using a short hairpin RNA interference screen, we identified heterogeneous ribonucleoprotein L-like (hnRNPLL) as a critical inducible regulator of CD45 alternative splicing. HnRNPLL was up-regulated in stimulated T cells, bound CD45 transcripts, and was both necessary and sufficient for CD45 alternative splicing. Depletion or overexpression of hnRNPLL in B and T cell lines and primary T cells resulted in reciprocal alteration of CD45RA and RO expression. Exon array analysis suggested that hnRNPLL acts as a global regulator of alternative splicing in activated T cells. Induction of hnRNPLL during hematopoietic cell activation and differentiation may allow cells to rapidly shift their transcriptomes to favor proliferation and inhibit cell death.

It is estimated that greater than 75% of genes yield alternative transcripts, contributing to considerable functional diversity within the genome (*1*, *2*). SR (serine-arginine rich) proteins are key positive regulators of alternative splicing that bind enhancer sequences on nascent tran-

Supporting Online Material for

The Global Stoichiometry of Litter Nitrogen Mineralization

Stefano Manzoni, Robert B. Jackson, John A. Trofymow, Amilcare Porporato*

*To whom correspondence should be addressed. E-mail: amilcare@duke.edu

Published 1 August 2008, *Science* **321**, 684 (2008)
DOI: 10.1126/science.1159792

This PDF file includes:

Supporting Online Materials and Methods

1 Carbon-nitrogen relationships in decomposing litter

The relationship between the carbon and nitrogen contents in decomposing plant residues has been extensively studied for its importance in controlling nutrient availability in natural and managed ecosystems (*1-4*). Early studies recognized a linear relationship between N concentration and mass (or carbon) loss (*5-7*), suggesting that N accumulates while C is lost from the litter. N accumulation depends on three main factors: i) microbial immobilization during growth, ii) bonding of N to aromatic compounds, and iii) chemical fixation of external N (e.g., soil inorganic N or added N from fertilization) to low-N fresh litter (*8*). N immobilization by decomposers is generally considered the predominant accumulation factor during the initial and more active phase of decomposition, until mass loss reaches about 70% (*1*). Chemical fixation of inorganic N may be important in sites with large sources of exogenous inorganic N (e.g., fertilization, fallow fields), while here we will focus on natural ecosystems where the primary external sources of N are from canopy throughfall and atmospheric deposition. In general, N losses from the plant residues are controlled by both biological and physical factors. However, leaching of organic compounds is typically less important than biological decomposition (*9*) and the predominant pathway of N loss is through decomposer mineralization by the decomposers and subsequent leaching of N in inorganic forms.

Since here we focus on natural systems where physical processes do not significantly affect the stoichiometry of residue decomposition, we can consider the predominant biological factors only. Waksman (*10*) was among the first to recognize that the nutrient requirements of the decomposer community had to be met before the organic matter in the soil releases the nutrients necessary for plant growth. Also the linear relationship between carbon and nitrogen contents in decomposing litter can be explained by considering the stoichiometric requirements of the decomposers (*7*), as clearly formalized by earlier mathematical models based on the balance of C and N assimilated into the biomass (*11, 12*). Similar concepts are today embedded in most biogeochemical and ecosystem models (*13-16*), and we will build on such a theoretical basis to derive a general N-release curve.

2 Litter decomposition data

We used litter decomposition data from the LTER Long-term Intersite Fine Litter Decomposition Experiment, LIDET (*17-19*) and the Canadian Intersite litter Decomposition Experiment, CIDET (*20-22*). Both experiments are based on long-term reciprocal litterbag studies of decomposition and nutrient mineralization in widely different climatic conditions and using chemically different plant residues. In the present work, data on leaf decomposition for all species with >15 observations were used. Wetland and desert sites, where abiotic nutrient loss pathways are likely to be predominant (*23, 24*), were excluded. For this analysis, replicate measurements at the same site were averaged, and data points showing a gain of mass or N concentrations higher than five times the initial concentration were considered as outliers. The LIDET litter mass data were converted into C remaining using linear regressions of C

concentrations measured within the same experiment. Observations of N remaining as a function of C lost from LIDET and CIDET experiments are shown in Fig. 1 in the main text.

To make a more comprehensive assessment and to cover a larger range of initial litter N:C we added other datasets to our analysis, including both fine litter and wood decomposition data (denoted by ■), with N:C ratios as low as $r_{L,0} \approx 7\times10^{-4}$ (Table S1). We selected datasets with at least two years of both litter mass (or carbon) and nitrogen decomposition of fine litter using the litterbag technique, or based on chronosequence studies in the case of long-term wood decomposition. To have series that were representative of the whole decomposition process, we only considered decomposition datasets with mass loss greater than 40% and >15 data points for any individual litter type (regardless of the site) in the case of fine litter. Lacking detailed temporal measurements of wood decomposition, we also considered several chronosequence studies, even though they provided series of only four to seven data points. Despite their low number, in fact, these points are highly representative, as they generally cover mass losses from zero to more then 70% and integrate both intra- and inter-annual climatic variability. In the chronosequence studies where mass loss data were not reported, we used wood density as a proxy.

Litter mass was converted to C mass using reported C concentrations, or, when no information was available, assuming a C concentration of 50% (mass of C per unit dry weight of litter). Slight errors or temporal changes in this conversion factor (e.g., *25*) would not significantly change the N release patterns.

3 Carbon-use efficiency of consumers and aquatic decomposers

Fig. 3A in the main text shows a clear trend of increasing decomposer carbon-use efficiency with increasing initial N content of the litter. This trend is consistent with observations of carbon-use efficiency in decomposers from aquatic environments and consumers at higher trophic levels [Fig. 3B, see also (*26*)]. In order to compare data from different environments and trophic levels, we considered growth efficiencies only (biomass growth over ingested substrate) and normalized the food source N:C ratios (r_F) by the decomposer or consumer N:C ratio (r_B), using values reported in the literature. We assumed average N:C ratios of 0.23 and 0.18 for marine bacteria (*27, 28*) and insects (*29*), respectively. Specific values for terrestrial larvae were reported by Slansky and Feeny (*30*). Food N concentrations were converted to N:C ratios assuming a C content of 50% in case only the N percentage was given. Since data for aquatic insects only account for the assimilation efficiency (*31*), the corresponding data points in Fig. 3B (indicated by ×) may overestimate the actual growth efficiency.

4 Model description

In this section we derive an analytical model of the N release curve as a function of remaining C in the litter explicitly based on the mass stoichiometry of the decomposers. Let us denote the total carbon and nitrogen mass contents per litterbag by C_L and N_L, respectively, and their N:C ratio as r_L. Litter carbon is decomposed at a rate D, a fraction e of which is used by decomposers, $G=e\cdot D$, while the fraction 1-e is lost through respiration, $R_B=(1-e)D$ (where the parameter e is often called decomposer efficiency,

(*16*)). Note that, according to the above definition, the respiration R_B accounts for all C losses due to decomposer activity associated with the decomposition flux D, and thus integrate at the annual time scale a variety of short-term respiratory processes (possibly occurring at different trophic levels in the detrital food web) that are not explicitly accounted for. Since our goal is to analyze the patterns of plant litter decomposition across litter types and climatic gradients, we also neglect explicit treatment of microbial succession and other trophic groups, and assume that the decomposer N:C ratio r_B, and the efficiency e are constant in time and representative of the whole decomposer community. As shown later, the specific value of r_B can vary in a wide range without changing the main patterns in the results. This allows us to compute the net mineralization M as the difference between the total nitrogen made available by decomposing litter, $D \cdot N_L/C_L = D \cdot r_L$, and the N needed by the decomposer to assimilate C at a rate G with constant r_B, that is $e \cdot r_B \cdot D$. Accordingly, we obtain

$$M = D\left(r_L - r_{CR}\right), \tag{S1}$$

where $r_{CR}=e \cdot r_B$ is the critical N:C ratio. When litter N:C is below the critical value, immobilization is necessary; otherwise net N mineralization occurs (*13*). The mass balance equations for C_L and N_L in a single litter cohort can thus be written as

$$\frac{dC_L}{dt} = -R_B \tag{S2}$$

$$\frac{dN_L}{dt} = -M = -\frac{R_B}{\left(1-e\right)}\left(r_L - r_{CR}\right). \tag{S3}$$

Combining Eqs. S2 and S3 yields

$$\frac{dN_L}{dC_L} = \frac{r_L - r_{CR}}{1-e}\ . \tag{S4}$$

Eq. S4 can be solved in terms of the normalized variables $c=C_L(t)/C_L(0)$ and $n=N_L(t)/N_L(0)$, with the condition $n(c=1)=1$, leading to the fundamental Eq. 1 describing the N release curve of a single litter cohort as an implicit function of time. Eq. 1 can be also written in normalized form as (Figs. 2 and S1)

$$\xi = \frac{r_L - r_B}{r_{L,0} - r_B} = c^{\frac{e}{1-e}}. \tag{S5}$$

Eq. 1 is equivalent to other formulations derived for a lumped model (*11*) and in the context of a more complex continuum-quality decomposition model (*16*). Here it has been derived for a lumped model controlled by a generic decomposition function D, suggesting that the N release curve depends little on the specific choice of model structure and formulation. Notably, Eq. 1 does not depend on the decomposition function D, which typically includes the effects of both N limitation and environmental conditions

on microbial activity (*13*). Accordingly, even if low availability of inorganic N during the early decomposition phase decreases the rates of litter degradation, it does not alter the basic decomposer stoichiometry. Also, environmental variables such as water availability and temperature affect the C and N temporal dynamics in Eqs. S2 and S3 (*17, 22*), but not litter stoichiometry evolution (Eq. S4) or the N release curve, as confirmed by experimental evidence (*20, 24*). This feature allows us to use Eq. 1 to model global N immobilization and release patterns across litter types and climatic conditions.

Fitting Eq. 1 to observations of litter C and N contents provides estimates of the decomposer N:C, r_B, and efficiency, e. However, as already noted by Ågren and Bosatta (*16*), their product (i.e., r_{CR}) is the primary factor controlling the shape of the N release curves, preventing an independent estimate of r_B and e solely based on Eq. 1. Hence, we assume a constant decomposer N:C, and use Eqs. 1 and S5 to estimate the decomposer efficiency e from least square regression of the observations (Figs. 1, 2, S1). The efficiency e is finally converted to r_{CR} from the definition as $r_{CR}=e \cdot r_B$ (both parameters are shown in Fig. 3A). We tested the sensitivity of the model by choosing r_B =0.07, 0.1, and 0.2 (i.e., decomposer C:N equal to 15, 10, and 5, respectively; see Fig. 3A). The higher and intermediate values of r_B are typical of soil and litter microbial biomass N:C (*32-34*), while the smaller one is more typical of purely fungal biomass (*1, 35*). As shown in Fig. 3A, even if we hypothesize a negative trend of r_B from 0.2 to 0.07 with decreasing $r_{L,0}$ (as it would occur from a soil to N-poor plant litter), such variation could not balance the decrease of r_{CR} and thus offset the decrease in efficiency. This proves that such efficiency decrease with $r_{L,0}$ is robust to possible shifts in decomposer composition across litter types.

We used two different regression methods to obtain e: numerical type I nonlinear least square fitting of Eq. 1 using the relative C and N concentrations c and n (as in Fig. 1), and analytical type II regression of the log-transformed normalized form of the N release curve (Eq. S5, Figs. 2 and S1). The values of e estimated from the two methods did not differ significantly; however, the reported estimates of e and r_{CR} are all based on the first regression method.

Supporting Figures and Tables

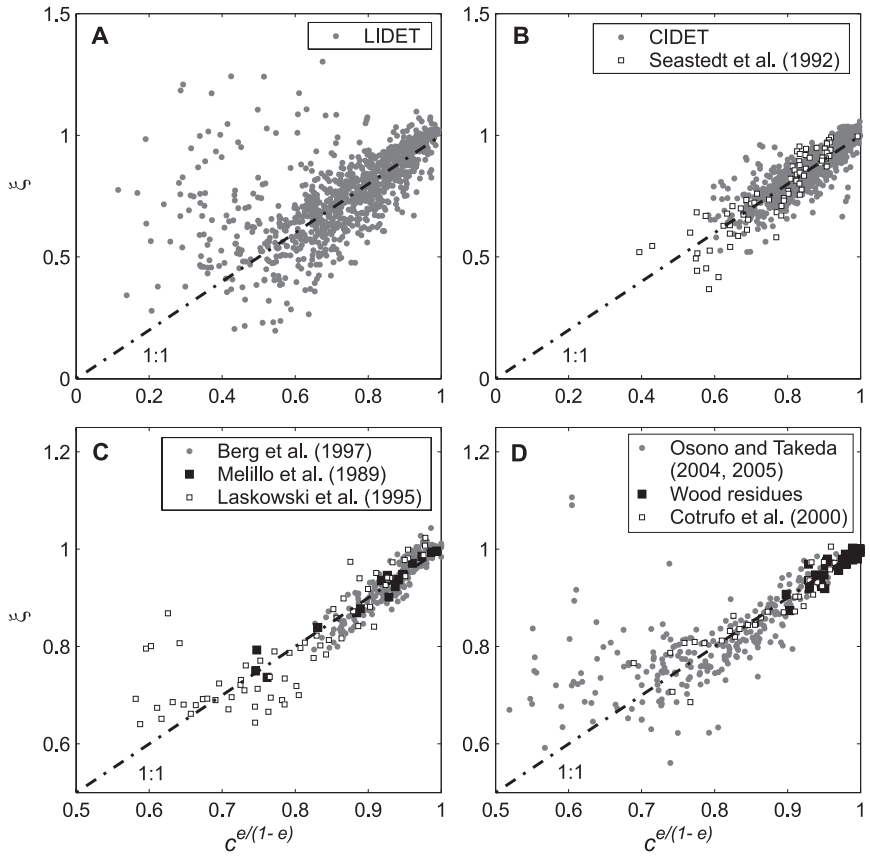

Fig. S1. Plots of the normalized variable ξ (Eq. S5) against $c^{e/(1-e)}$ for each dataset analyzed. As in Fig. 2, the analytical N release curves are fitted to the data with the only free parameter e. Dataset information and correlation statistics of the normalized variables are reported in Table S1.

Tab. S1. Characteristics of the selected datasets.

Dataset reference	Experiment type [*]	Litter type [†]	Number of species	Number of data points	$r_{L,0}$ range ($\times 10^{-3}$)	$\frac{C_L(0)}{N_L(0)}$ range	R [‡]
Lambert et al. (*36*)	CS	■	1	7	3.0	332	0.88
Foster and Lang (*37*)	CS	■	2	12	1.4-1.6	625-714	0.90
Edmonds (*38*)	LB	■	2	9	4.8-7.2	139-209	0.87
Sollins et al. (*39*)	CS	■	3	12	1.6-2.2	454-625	0.92
Melillo et al. (*40*)	LB	▲	1	16	7.1	140	0.98
Seastedt et al. (*41*)	LB	○	1	71	38.8	25.8	0.89
Means et al. (*42*)	CS	■	1	5	1.6	620	1.00
Busse (*43*)	CS	■	1	5	0.7	1327	0.97
Laskowski et al. (*44*)	LB	□, ▲	2	67	13.7-27.2	36.7-73.2	0.82
Berg et al. (*45*)	LB	▲	3	211	9.3-11.6	86-107.5	0.93
CIDET (*21*)	LB	○, □, ▲	10	1076	12.1-25.8	38.8-82.5	0.87
Kankrina et al. (*46*)	CS	■	3	13	3.4-3.6	277-294	0.94
Cotrufo et al. (*47*)	LB	□	2	32	18.2-31.3	32-55	0.91
Osono and Takeda (*48, 49*)	LB	□, ▲	14	260	10.6-58.1	17.2-94.3	0.65
LIDET (*18, 19*)	LB	○, □, ▲	9	987	8.3-42.4	23.6-120.9	0.60

[*] LB: litterbag method; CS: chronosequence study.

[†] ○, grass leaves; □, broadleaved tree and shrub leaves; ▲, conifer needles; ■, woody residues (symbols as in Figs. 2 and 3).

[‡] R: Pearson correlation coefficients between ξ and $c^{e/(1-e)}$ for each dataset (Eq. S5, Figs. 2 and 1S); all correlations are highly significant ($P<0.0001$, except datasets from Lambert (*16*), $P<0.01$, and Busse (*23*) and Edmonds (*18*), $P<0.005$).

References

1. B. Berg, C. A. McClaugherty, *Plant litter. Decomposition, humus formation, carbon sequestration* (Springer, 2003), pp. 286.
2. G. Seneviratne, *Biology and Fertility of Soils* **31**, 60 (Apr, 2000).
3. P. M. Vitousek, R. W. Howarth, *Biogeochemistry* **13**, 87 (1991).
4. S. A. Waksman, F. G. Tenney, K. R. Stevens, *Ecology* **9**, 126 (1928).
5. J. D. Aber, J. M. Melillo, *Canadian Journal of Botany-Revue Canadienne De Botanique* **60**, 2263 (1982).
6. B. Berg, G. Ekbohm, *Ecology* **64**, 63 (1983).
7. J. D. Aber, J. M. Melillo, *Canadian Journal of Botany-Revue Canadienne De Botanique* **58**, 416 (1980).
8. C. E. Prescott, in *Nutrient acquisition by plants. An ecological perspective* H. BassiriRad, Ed. (Springer-Verlag, Berlin Heidelberg, 2005), vol. 181, pp. 347.
9. B. Michalzik, K. Kalbitz, J. H. Park, S. Solinger, E. Matzner, *Biogeochemistry* **52**, 173 (Jan, 2001).
10. S. A. Waksman, *Journal of Agricultural Science* **14**, 555 (Oct, 1924).
11. E. Bosatta, H. Staaf, *Oikos* **39**, 143 (1982).
12. H. Parnas, *Soil Biology & Biochemistry* **7**, 161 (1975).
13. S. Manzoni, A. Porporato, *Soil Biology & Biochemistry* **39**, 1542 (Jul, 2007).
14. W. B. McGill, H. W. Hunt, R. G. Woodmansee, J. O. Reuss, in *Terrestrial nitrogen cycles. Processes, ecosystem strategies and management impacts* F. E. Clark, T. Rosswall, Eds. (Ecological Bullettins, Stockholm, 1981), vol. 33, pp. 49-115.
15. W. J. Parton, D. S. Schimel, C. V. Cole, D. S. Ojima, *Soil Science Society of America Journal* **51**, 1173 (Sep-Oct, 1987).
16. G. I. Ågren, E. Bosatta, *Theoretical ecosystem ecology. Understanding element cycles* (Cambridge University Press, Cambridge, United Kingdom, 1996), pp. 234.
17. H. L. Gholz, D. A. Wedin, S. M. Smitherman, M. E. Harmon, W. J. Parton, *Global Change Biology* **6**, 751 (Oct, 2000).
18. M. E. Harmon, LTER Long-term Intersite Decomposition Experiment (LIDET), Forest Science Data Bank, code TD023, Corvallis, OR, 2007. www.fsl.orst.edu/lter/data/abstract.cfm?dbcode=TD023.
19. Long-term Intersite Decomposition Experiment Team (LIDET), "Meeting the challenges of long-term, broad-scale ecological experiments" *Publication 19* (LTER Network, 1995).
20. T. R. Moore, J. A. Trofymow, C. E. Prescott, J. Fyles, B. D. Titus, *Ecosystems* **9**, 46 (Feb, 2006).
21. J. A. Trofymow, CIDET, "The Canadian Intersite Decomposition Experiment (CIDET). Project and Site Establishment Report" *Tech. Report No. BC-X-378* (Pacific Forestry Centre, 1998).
22. J. A. Trofymow *et al.*, *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **32**, 789 (May, 2002).
23. A. T. Austin, L. Vivanco, *Nature* **442**, 555 (Aug, 2006).
24. W. Parton *et al.*, *Science* **315**, 361 (Jan, 2007).

25. C. M. Preston, J. A. Trofymow, L. B. Flanagan, *Canadian Journal of Soil Science* **86**, 235 (Apr, 2006).
26. R. W. Sterner, J. J. Elser, *Ecological stoichiometry. The biology of elements from molecules to the biosphere* (Princeton University Press, Princeton and Oxford, 2002), pp. 439.
27. J. C. Goldman, D. A. Caron, M. R. Dennett, *Limnology and Oceanography* **32**, 1239 (Nov, 1987).
28. J. C. Goldman, M. R. Dennett, *Marine Biology* **109**, 369 (1991).
29. J. J. Elser *et al.*, *Nature* **408**, 578 (Nov, 2000).
30. F. Slansky, P. Feeny, *Ecological Monographs* **47**, 209 (1977).
31. T. J. Pandian, M. P. Marian, *Freshwater Biology* **16**, 93 (Feb, 1986).
32. C. C. Cleveland, D. Liptzin, *Biogeochemistry* **85**, 235 (Sep, 2007).
33. J. P. Schimel, J. M. Gulledge, J. S. Clein-Curley, J. E. Lindstrom, J. F. Braddock, *Soil Biology & Biochemistry* **31**, 831 (Jun, 1999).
34. S. C. Hart, *Ecology* **80**, 1385 (Jun, 1999).
35. H. Staaf, B. Berg, *Canadian Journal of Botany-Revue Canadienne De Botanique* **60**, 1561 (1982).
36. R. L. Lambert, G. E. Lang, W. A. Reiners, *Ecology* **61**, 1460 (1980).
37. J. R. Foster, G. E. Lang, *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **12**, 617 (1982).
38. R. L. Edmonds, *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **17**, 499 (Jun, 1987).
39. P. Sollins, S. P. Cline, T. Verhoeven, D. Sachs, G. Spycher, *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **17**, 1585 (Dec, 1987).
40. J. M. Melillo *et al.*, *Plant and Soil* **115**, 189 (Apr, 1989).
41. T. R. Seastedt, W. J. Parton, D. S. Ojima, *Canadian Journal of Botany-Revue Canadienne De Botanique* **70**, 384 (Feb, 1992).
42. J. E. Means, P. C. Macmillan, K. Cromack, *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **22**, 1536 (Oct, 1992).
43. M. D. Busse, *Soil Science Society of America Journal* **58**, 221 (Jan-Feb, 1994).
44. R. Laskowski, M. Niklinska, M. Maryanski, *Ecology* **76**, 1393 (Jul, 1995).
45. B. Berg, C. A. McClaugherty, M. Johansson, "Chemical change in decomposing litter can be systematized with respect to the initial chemical composition of the litter" *Tech. Report No. 74* (Swedish University of Agricultural Sciences, 1997).
46. O. N. Krankina, M. E. Harmon, A. V. Griazkin, *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **29**, 20 (Jan, 1999).
47. M. F. Cotrufo, M. Miller, B. Zeller, in *Carbon and nitrogen cycling in European forest ecosystems* E. D. Schulze, Ed. (Springer-Verlag, Berlin Heidelberg, 2000), vol. 142, pp. 500.
48. T. Osono, H. Takeda, *Ecological Research* **19**, 593 (Nov, 2004).
49. T. Osono, H. Takeda, *Ecological Research* **20**, 41 (Jan, 2005).