The Global Stoichiometry of Litter Nitrogen Mineralization
Stefano Manzoni, et al.
Science 321, 684 (2008);
001: 10.1126/science.1159792

The following resources related to this article are available online at
www.sciencemag.org (this information is current as of August 1, 2008):

Updated information and services, including high-resolution figures, can be found in the online version of this article at:
http://www.sciencemag.org/cgi/content/full/321/5889/684

Supporting Online Material can be found at:
http://www.sciencemag.org/cgi/content/full/321/5889/684/DC1

This article cites 23 articles, 3 of which can be accessed for free:
http://www.sciencemag.org/cgi/content/full/321/5889/684#otherarticles

This article appears in the following subject collections:
Geochemistry, Geophysics
http://www.sciencemag.org/cgi/collection/geochem_phys

Information about obtaining reprints of this article or about obtaining permission to reproduce this article in whole or in part can be found at:
http://www.sciencemag.org/about/permissions.dtl
The Global Stoichiometry of Litter Nitrogen Mineralization

Stefano Manzoni,1 Robert B. Jackson,2 John A. Trofymow,3 Amilcare Porporato
* stamp correspondence should be addressed. E-mail: amilcare@duke.edu

Plant residues deposited to the soil are subject to biological degradation (1-3). During this process, litter carbon (C) is respired to CO2, 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 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 5% (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

\[ n(c) = \frac{r_B}{r_{CR}} + \left(1 - \frac{r_B}{r_{CR}}\right)e^{-r_e c} \]  

where \( r_{CR} \) is the initial litter N:C ratio, \( r_B \) is the decomposer biomass N:C, and \( r_e \) 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, \( r_{CR} = \rho r_B / g(y, 10) \). In general, the lower \( r_{CR} \), the earlier N release occurs, even in N-poor residues. Moreover, when \( c r < k_0 \), net release occurs from the beginning of decomposition. Conversely, if \( r_B \) 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 \( r_B \) 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 \( r_B \) and the decomposer parameters, \( \omega \) and \( r_B \). In particular, \( a_B \) 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 \( a_B = 0.1 \) and fitted the remaining free parameter, \( c \), for each litter type (13). For given values of \( a_B \) and \( c \) 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 \( c \) alone explains most of the variability in the data.

We assessed how \( r_{CR} \) and \( \omega \), 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
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 con-elation 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 Jitter, 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-
poorer N:C ratio is relatively constant, this pattern results in higher heterotrophic respiration per unit area (Fig. 3A). The dashed curve indicates points where \( r_{C:B} = r_{L:C} \); 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 \( N:C (r_S) \) and consumer \( N:C (r_B) \) at different trophic levels (Reciprocal, terrestrial plant residue decomposers (this study); \( + \), marine bacteria (22); \( - \), terrestrial plant residue decomposers (this study); \( \cdot \), terrestrial insects (23); and \( \times \), aquatic insects (24)). The solid line is a linear least square fit of the log-transformed \( e \) and \( r_{S:B} \) \( e = 0.45 \times r_{S:B}^{0.66}, R = 0.72; \ P < 0.0001 \).

References and Notes

13. See supporting materials on Science Online.
31. This research was supported by Department of Energy (DOE) Forest-Atmosphere Carbon Transfer and Storage project (FACT-I), NSF DEB0235425 and C2T191, 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 LIDET experiment was provided by Climate Change and Ecosystem Processes Network of the National Canadian Forest Service and Natural Resources Canada Panel on Energy Research Development. We also thank G. Katal, D. Richter, and two anonymous reviewers for useful comments.

Supporting Online Material

www.sciencemag.org/cgi/content/full/294/5548/889/DC1
Materials and Methods
Fig S1
Table S1
29 April 2008; accepted 1 July 2008
10.1126/science.1159792