The Global Stoichiometry of Litter Nitrogen Mineralization

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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

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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-
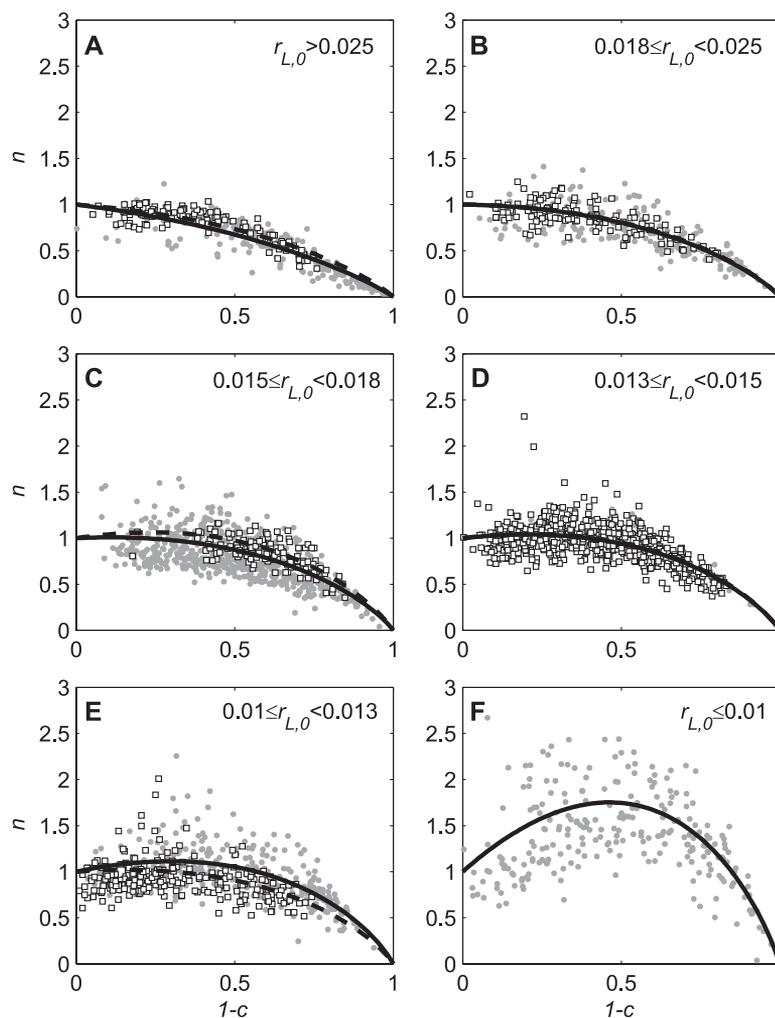

Fig. 1. Nitrogen release patterns across litter types. (**A** to **F**) Observed and modeled fractions of initial nitrogen, $n = N_L(t)/N_L(0)$, as a function of the decomposed fractions of initial carbon, $1 - c = 1 - C_L(t)/C_L(0)$, for leaf litter with decreasing values of $r_{L,0}$. Data and analytical 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.
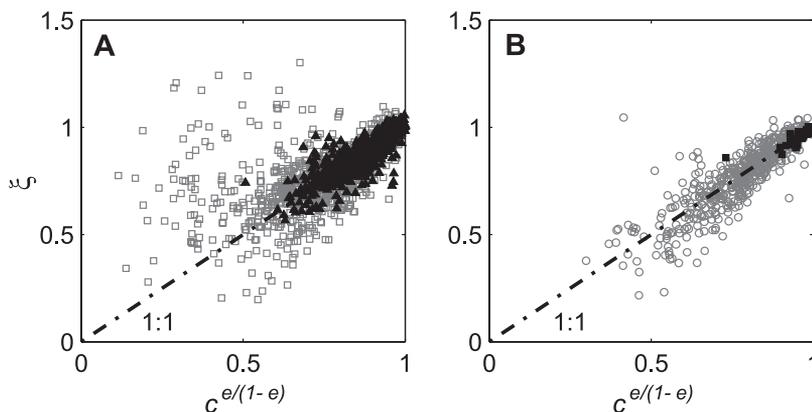
Fig. 2. Normalized representation of the nitrogen release curves. Plots of the normalized variable $\xi = (r_L - r_B)/(r_{L,0} - r_B)$ (eq. S5) against $c^{e/(1-e)}$ for litters of different origin [(**A**) broadleaved tree and shrub leaves, □, and conifer needles, ▲; (**B**) grass leaves, ○, and woody 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 [$e = 0.43 \times (r_F/r_B)^{0.60}$; $R = 0.72$; $P < 0.0001$].
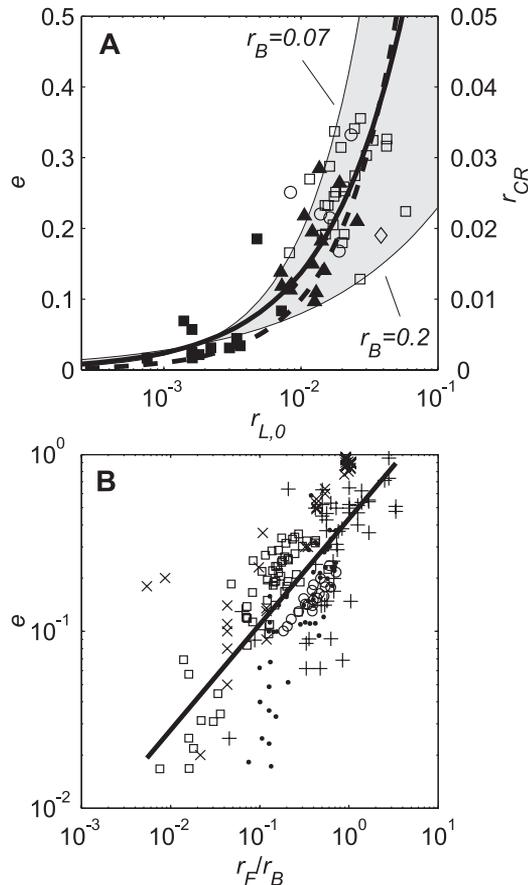
poser N:C ratio is relatively constant, this pattern suggests that the decomposer communities are able to adapt partially to low-nitrogen substrates (i.e., low $r_{L,0}$) by decreasing their C-use efficiency and thus the critical N:C of the litter (Fig. 3A). Such a pattern has been observed in aquatic 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.

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Regulation of CD45 Alternative Splicing by Heterogeneous Ribonucleoprotein, hnRNPLL

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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-