



Estimating the critical N:C from litter decomposition data and its relation to soil organic matter stoichiometry



G.I. Ågren^{a,*}, R. Hyvönen^a, S.L. Berglund^a, S.E. Hobbie^b

^a Department of Ecology, Swedish University of Agricultural Sciences, P.O. Box 7044, SE-750 07 Uppsala, Sweden

^b Department of Ecology, Evolution and Behavior, University of Minnesota, Saint Paul, MN 55108, USA

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ABSTRACT

Carbon (C) and nitrogen (N) interact strongly during decomposition of litters with repercussions for stoichiometry of soil organic matter (SOM). A characteristic parameter describing this interaction is the critical N:C ratio, r_c , i.e. the litter N:C ratio at which net N mineralisation commences. We show here how r_c can be estimated from time series of decomposition and use four large data bases to investigate how environment and litter properties determine r_c . We find that r_c increases with increasing initial litter N:C and N fertilisation. The critical N:C responds also to large scale variations in environment but it is not clear which environmental variable drives this variability. With increasing r_c we find an increase in SOM N:C. SOM N:C increases more rapidly than r_c , which can be explained if the decrease in substrate quality during decomposition is taken into account.

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1. Introduction

Carbon (C) and nitrogen (N) interact strongly during decomposition of litters with repercussions for the mass and stoichiometry of soil organic matter (SOM). Much attention has, therefore, been devoted to understand and predict the consequences of this interaction. The question in most studies has been how the C–N interaction regulates the rate of release of C and N from litters and SOM, and it has been extensively shown that there is a strong positive correlation between N:C in litters and the rate of litter mass loss (e.g. Melillo et al., 1982; Hobbie, 2005; Cornwell et al., 2008). As a consequence, N:C or N:lignin is often used as an index of quality or decomposability of litter (e.g. Aerts, 1997). On top of litter quality, climate plays a major role for decomposition rates (e.g. Aerts, 1997). Other environmental factors such as a possible interaction between physical and chemical litter properties and the decomposer community also contribute to modifying rates.

However, C and N differ in one important respect in that the mass of C is constantly decreasing while in initially N-poor litters the mass of N will increase up to some critical N:C ratio (r_c) and thereafter decrease; in sufficiently N-rich litter this decrease will

commence immediately. This relation between C and N is well established both empirically (e.g. Aber and Melillo, 1980; Moore et al., 2006, 2011; Parton et al., 2007; Manzoni et al., 2008) and theoretically (Ågren and Bosatta, 1998). The relation is simple and depends on only three system properties: (i) initial N:C ratio of the litter (r_0), (ii) N:C ratio of the decomposer community (r_d), and (iii) carbon-use efficiency or production-to-assimilation ratio of the decomposer community (e_0); the critical N:C ratio can be shown to be the product of e_0 and r_d ($r_c = e_0 r_d$) (Ågren and Bosatta, 1998). An important aspect of this relation is that it is independent of the rate of decomposition; i.e. climate plays no role to the extent that it does not affect r_d or e_0 (see Discussion). Although the masses of C and N in the decomposer biomass are small compared with SOM C and N (3 and 5%, respectively, in the data from Cleveland and Liptzin, 2007), the decomposer stoichiometry is important because decomposers are the gateway through which SOM is processed and therefore leave a strong imprint on SOM stoichiometry. The overall SOM stoichiometry will then be determined by a balance between plant material that has still escaped decomposers and material that has been processed to different degrees. On top of that, there can also be purely chemical processes that attach or detach N from C skeletons.

A problem with the parameters coupling C and N is the strong negative correlation between r_d and e_0 observed in estimates and predicted by theory (Manzoni et al., 2008, see also below), making

* Corresponding author. Tel.: +46 18 672449.
E-mail address: goran.agren@slu.se (G.I. Ågren).

Table 1

Summary of litter data properties in the four data bases. In the BI, CCNHA, and LIDET data bases the same litter has been used in all samples of a litter type whereas in the SWECON data base the same litter type has been collected in different years and at different location, initial N concentrations show then the range of concentrations.

Species	Litter types ^a	r_0 (mg N/g C)
BI		
<i>Acer rubrum</i> (red maple)	W, B	1.8, 9.0
<i>Acer saccharum</i> (sugar maple)	F (b), R	16.6, 33.4
<i>Populus grandidentata</i> (aspen)	F (b)	16.6
<i>Quercus alba</i> (white oak)	F (b)	16.8
<i>Quercus rubra</i> (red oak)	F (b)	16.4
<i>Pinus strobus</i> (white pine)	F (b), R, W	8.8, 18.6, 0.8
<i>Tsuga canadensis</i> (hemlock)	F (b), B	16.6, 6.0
CCNHA		
<i>Acer saccharum</i> (sugar maple)	F (b,g)	9.0, 36.4
<i>Betula</i> (birch)	W	1.8
<i>Pinus strobus</i> (white pine)	F (b)	19.8
<i>Quercus ellipsoidalis</i> (northern pin oak)	F (b, g)	19.8, 50.6
<i>Schizachyrium scoparium</i> (little bluestem)	F (b)	6.6
Filter paper		0
LIDET		
<i>Acer saccharum</i> (sugar maple)	F (b)	17.0
<i>Schizachyrium gerardi</i> (big bluestem)	F (b), R	13.4, 16.8
<i>Drypetes glauca</i>	F (b), R	42.7, 16.3
<i>Pinus elliottii</i> (slash pine)	F (b), R	7.3, 17.5
<i>Pinus resinosa</i> (red pine)	F (b), R	17.5, 26.7
<i>Quercus prinus</i> (Chestnut oak)	F (b)	21.5
<i>Thuja plicata</i> (western redcedar)	F (b)	13.4
<i>Triticum aestivum</i> (wheat)	F (b)	7.8
SWECON		
<i>Betula pubescens</i> (downy birch)	F (g)	34.8
<i>Picea abies</i> (Norway spruce)	F (b, g)	8.4–36.6, 17.0
<i>Pinus contorta</i> (lodgepole pine)	F (b, g)	6.8–8.4, 21.0
<i>Pinus sylvestris</i> (Scots pine)	F (b, g)	5.8–22.8, 30.2

^a F = foliage, R = roots, W = wood, B = bark, b = brown/senesced material, g = green material; b if not indicated.

it difficult to separate them. Manzoni et al. (2008) circumvented this problem by assigning a fixed value to r_d and attributed responses to initial litter N:C in decomposition patterns to changes in decomposer carbon-use efficiency. However, decomposer N:C ratios vary at least by a factor of 4 (Cleveland and Liptzin, 2007; Li et al., 2012) or maybe even by a factor of 10 or more (Xu et al., 2013), which indicates that the assumption of the same r_d for all systems is an oversimplification. Similarly, an assumption of a constant e_0 is not warranted as large variability in carbon-use efficiency has been observed (Manzoni et al., 2012).

We will in this paper use four large data bases to investigate the problem of estimating the parameters r_d and e_0 (r_0 is known). Our hypothesis is that the property, which can be estimated with accuracy, is the critical N:C ratio (r_c), not its components (r_d and e_0). This leaves open the possibility that decomposer communities can respond to the substrate N:C and environment by changing their carbon-use efficiency as well as their own N:C. Fortunately, as we will show, r_c is a useful system property, which can be used to predict N:C in SOM. The data will also allow us to investigate possible home-field advantages (but here in terms of differences in stoichiometry between a native and a foreign site), i.e. decomposition of litter is faster in the native site than in a foreign site (Freschet et al., 2012a). In contrast to Parton et al. (2007) and Manzoni et al. (2008) we do not need to split data according to initial N:C (r_0) in our analyses but can apply the same method to all data.

2. Data

We will use time series of decomposition data from four different data bases (Table 1). By “data point”, we mean the properties of a single litter sample at a single point in time in the time

series. By “data set”, we mean all data points for a specific type of litter at the same site. When litters have been placed at different positions in the soil or different mesh sizes of litter-bags have been used, we treat these as different data sets. By “data base” we mean all the data sets from a specific investigation using identical methods for all data sets. All data have been obtained with similar methods, such that each data set can be viewed as an independent sample of the relations between r_c and other system properties. A short description of the data bases and associated soil data is as follows:

BI (Aber et al., 1984): These data are from a litter-bag decomposition study with 12 litter types decomposed at 5 closely located forest communities on Blackhawk Island in the Wisconsin River, U.S.A. In the study, different mesh sizes of litter-bags and different placements of the litter-bags were tested. Data consist of 60 data sets where each data point is the average of 4 replicate samples, for a total of 480 data points. The study extends over 732 days with 7 or 12 sampling occasions. Nitrogen concentrations are on a mass basis. Data on SOM N:C in the F + H layer or the A1 horizon are from Pastor et al. (1984).

CCNHA (Hobbie, 2008): These data are from a litter-bag experiments in the Cedar Creek Natural History Area, Central Minnesota, U.S.A. with 8 substrates of which one is filter paper and two are green leaves at 8 sites. The sites included 2 old fields and 6 forest sites. Within each site there was a control treatment and a nitrogen fertiliser treatment. The data consist of 128 data sets with in general 6 harvests of 6 replicates, for a total of 4608 data points. Nitrogen concentrations are on a mass basis. The study extends over 1763 days with 7 sampling occasions. Data on SOM N:C in the surface 10 cm of soil in the control plots are from Keeler et al. (2009).

LIDET (Harmon, 2010): From the data collected by the Long-term Intersite Decomposition Experiment Team we have used the 12 litter types that have been decomposed in litter-bags at 27 sites distributed from Alaska to Panama and the Caribbean Islands. The data consists of 263 data sets with in general 4 replicates of each observation, for a total of 10,374 data points. The study extends over 102–3730 days with 2–11 sampling occasions. Nitrogen concentrations and masses are on ash-free bases. No corresponding soil data are available.

SWECON (Berg et al., 1991a,b): These litter-bag data were collected during the SWECON project (Persson, 1980) and consists of 4 litter types decomposed at 13 sites ranging from northern Sweden to Central Europe. The same type of litter has been collected in many similar stands, in some cases also in fertiliser trials. The initial properties of a litter type vary therefore slightly. Data consists of 107 data sets, where each data point is obtained from mixing the content of 20 replicate litter-bags, or a total of 1048 data points. The study extends over 160–1983 days with 3–18 sampling occasions. Nitrogen concentrations are on a mass basis. Data on SOM N:C in the H layer from three sites are from Lundmark et al. (1982).

For conversion of mass/organic matter to C we assume 50% C concentration; none of the studies have reported C concentrations. The use of N concentrations on a total mass basis in three of the data bases and on an ash-free mass basis in one data base is no problem for our purposes as we only use N:C ratios for our calculations, where both N and C concentrations are equally affected by the choice of total mass versus ash-free mass as the basis. All values are expressed on mass basis.

3. Theory

Consider a litter cohort with initial mass of C (C_0) and initial mass of N (N_0); $r_0 = N_0/C_0$. During decomposition the mass of C

decreases such that at time t a fraction $g(t)$ remains (Fig. 1A) while at the same time the N:C ratio, $r(t)$, increases, Fig. 1B. The process is assumed to occur in the presence of an external N source, such that decomposers can maintain their N:C ratio, r_d . This gives rise to the typical pattern of an increasing mass of N in the litter with time until the critical N:C ratio, r_c , is reached and at which point the mass of N in the litter starts to decrease (Fig. 1C). This pattern can be explained from the three parameters: (i) r_0 , the initial N:C ratio in the litter; (ii) r_d , the N:C ratio of the decomposers; and (iii) e_0 , the carbon-use efficiency (CUE) or production-to-assimilation ratio of the decomposers with $r_c = e_0 r_d$.

In addition, rate parameters are required to fully describe the C and N dynamics during decomposition. In the simplest approach, rates are simply proportional to the mass of C (exponential decay) but more advanced approaches take into account a decreasing litter quality and hence decreasing rates with degree of decomposition, e.g. the continuous-quality theory (Ågren and Bosatta, 1998). However, the following relation, which does not explicitly contain rate parameters and is valid both when litter quality is assumed constant and when litter quality is allowed to change during decomposition, can be derived (Ågren and Bosatta, 1998, solving for $r_d = f_N/f_C$ in (3.38) and (4.51))

$$r_d = \frac{r(t) - r_0 g(t)^{e_0/(1-e_0)}}{1 - g(t)^{e_0/(1-e_0)}} \quad (1)$$

In what follows we will for simplicity just write r and g instead of $r(t)$ and $g(t)$.

The problem of the correlation between the parameters r_d and e_0 can be understood if we consider (1) in the limit of small e_0 . Then

$$g^{e_0/(1-e_0)} \approx 1 + \frac{e_0}{1-e_0} \ln g \approx 1 + e_0 \ln g$$

We also approximate $r - r_0 g^{e_0/(1-e_0)} \approx r$. Inserting these approximations in Equation (1) gives

$$r_d = \frac{r}{-e_0 \ln g} \quad (2)$$

or

$$e_0 r_d = r_c = -\frac{r}{\ln g} \quad (3)$$

As we will show, $r/\ln g$ is approximately constant during decomposition. It is, therefore, not possible to estimate e_0 and r_d separately from this type of data; the parameter that can be estimated is instead r_c . We will, therefore, rewrite Equation (1) as

$$r_c = e_0 \frac{r - r_0 g^{e_0/(1-e_0)}}{1 - g^{e_0/(1-e_0)}} \quad (4)$$

We will now use the data from the four different data bases with Equation (4) to estimate r_c ; Fig. 1D shows four examples with one data set from each of the data bases to illustrate the calculations. The right hand side of Equation (4) requires, in addition to the measured values (r , r_0 , and g), a value for e_0 . We use a value of 0.25, but other values give similar estimates of r_c (see below) and this value therefore cannot be used for other calculations. For each data set we calculate an average r_c for the time series (Fig. 1D); all r_c values referred to below are such average values. However, because of the sensitivity in the estimate of r_c to values of g close to 1, we

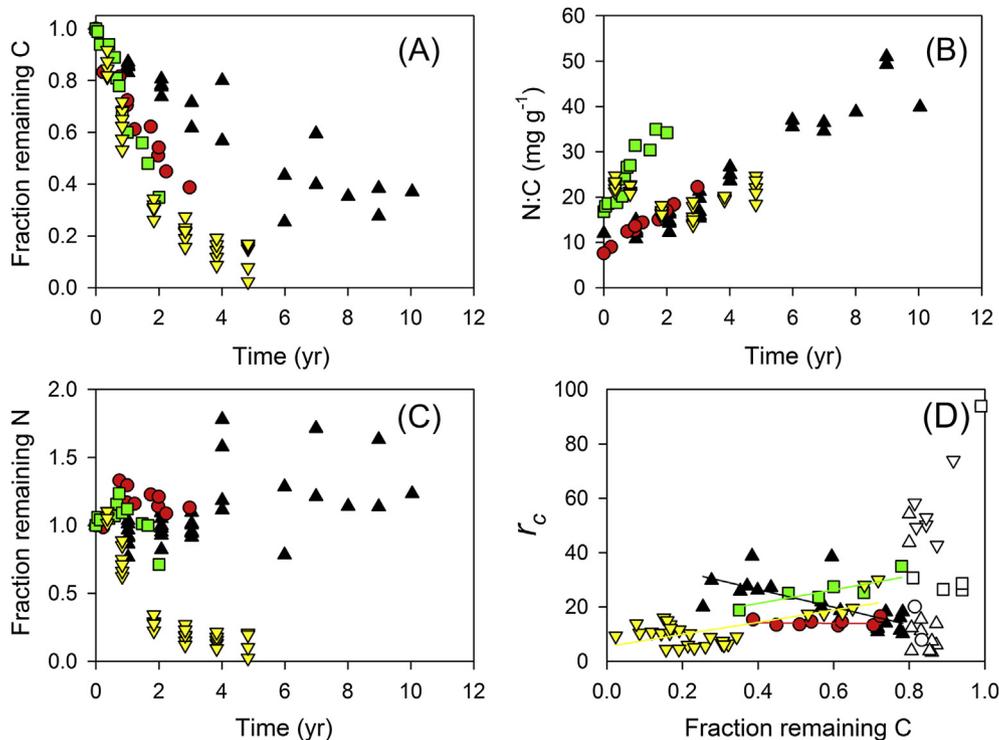


Fig. 1. Four data sets with C and N dynamics during decomposition. (■) = *Quercus alba* leaves from BL. (▼) = Green *Acer saccharum* leaves from CCNHA. (▲) = *Pinus resinosa* needles from LIDET. (●) = *Pinus sylvestris* needles from SWECON. (A) Fraction remaining C (g) as a function of time. (B) N:C mass ratio (r) as a function of time. (C) Fraction of initial N remaining as a function of time (rg). (D) Critical N:C ratio as a function of fraction remaining C (g) estimated from Equation (4). Solid symbols are included in the calculation of slopes. Open symbols with the same shapes are from the same data set but not included in the calculation of the slopes ($g > g_c = 0.8$). For each data set an average r_c is calculated using the values corresponding to the solid symbols. The line (■) has a slope of 31.0, the line (▼) a slope of 22.5, the line (▲) a slope of -32.6, and the line (●) a slope of 1.27.

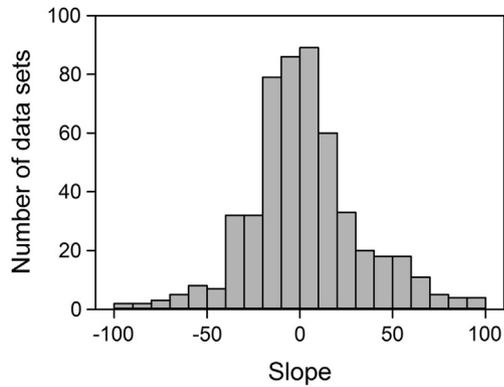


Fig. 2. Frequency distribution of slopes of regressions of critical N:C (r_c) versus fraction remaining C (g) where 23 data sets with absolute values of slopes >100 are excluded. Total number of data sets = 518. $e_0 = 0.25$ and $g_c = 0.8$.

will exclude data where g is larger than some cut-off value g_c . Inspection of Equation (4) shows that for g above 0.8–0.9, uncertainty in g rapidly affects the estimate of r_c . We use $g_c = 0.8$ as a default value.

The critical N:C ratio is also an important predictor of the long-term development of SOM N:C. If we assume a constant litter input rate and a constant initial litter N concentration, the steady state N:C in SOM (N_{ss}/C_{ss}) becomes, when we disregard quality changes during decomposition (Ågren and Andersson, 2012, page 129)

$$\frac{N_{ss}}{C_{ss}} = r_c + (1 - e_0)r_0 \quad (5)$$

Since the initial N:C ratio of litter (r_0) generally is small compared to the critical N:C ratio (r_c), the SOM N:C will tend towards r_c . When we include the effects of a declining litter quality, we get a different expression

$$\frac{N_{ss}}{C_{ss}} = \frac{r_c}{1 - \beta\eta_{11}e_0} + \left(1 - \frac{e_0}{1 - \beta\eta_{11}e_0}\right)r_0 \quad (6)$$

where β is a parameter describing how the decomposers' rate of use of the litter changes with litter quality and η_{11} a parameter describing the rate of quality decline during decomposition (Ågren and Bosatta, 1998, page 59). Note that in the limit of $\eta_{11} = 0$ or $\beta = 0$ (no effects of litter quality) Equation (6) equals Equation (5). With standard parameter values ($\beta = 7$, $\eta_{11} = 0.36$, $e_0 = 0.25$), the soil N:C will be 2.70 r_c or 0.68 r_d when we neglect the term in r_0 . Thus, although the critical N:C will be the same, irrespectively if quality changes are considered or not, inclusion of quality changes leads to a considerably higher N:C ratio in the soil.

4. Results

A first condition for the use of Equation (4) is that r_c is constant during decomposition. Fig. 2 shows the slopes of the regressions of r_c versus g for all data sets with $|\text{slope}| < 100$ and cut-off value, $g_c = 0.8$; this excludes 23 data sets with $|\text{slope}| > 100$ and 17 data sets where no slopes could be calculated because all g -values were larger than g_c . The average slope is 2.5 with a standard deviation of 30.3 and thus the average slope taken over all data sets was not significantly different from 0. The assumption that r_c is independent of degree of decomposition was therefore not rejected.

We have also tested the robustness of our calculations by using a different cut-off value, $g_c = 0.9$, and different decomposer efficiencies, $e_0 = 0.15$ and 0.35, Table 2. The average slopes are still close to 0 (2.2, 4.0, –0.8) with similar standard deviations (33.3,

Table 2

Regressions between r_c 's or slopes estimated with different parameters. Regressions are of the form $y = ax + b$, where x is the value with $g_c = 0.8$ and $e_0 = 0.25$ (standard values) and y the corresponding value with alternative parameters. Values in parentheses are SE.

Parameters	Regression	r^2
r_c		
$g_c = 0.9, e_0 = 0.25$	$y = 1.02 (0.02)x - 0.31 (0.32)$	0.89
$g_c = 0.8, e_0 = 0.15$	$y = 1.00 (0.01)x - 0.93 (0.29)$	0.91
$g_c = 0.8, e_0 = 0.35$	$y = 0.94 (0.01)x + 1.54 (0.28)$	0.91
Slope		
$g_c = 0.9, e_0 = 0.25$	$y = 0.87 (0.03)x + 0.18 (0.91)$	0.62
$g_c = 0.8, e_0 = 0.15$	$y = 1.03 (0.02)x + 1.55 (0.47)$	0.90
$g_c = 0.8, e_0 = 0.35$	$y = 0.86 (0.01)x - 2.83 (0.34)$	0.92

32.8, 27.1); one more data set with a slope around –800 has been excluded. The estimated r_c -values remain practically the same for all other tested parameter combinations, suggesting that the method is, indeed robust; the slopes of the regressions of r_c from different estimations are close to 1 and the intercepts small relative to typical values of r_c . The slopes are somewhat more sensitive to the choice of parameters but with increasing g_c and e_0 the slopes decrease, pointing to more stable estimates of r_c .

Fig. 3 shows the relation between the average r_c for each data set (default e_0 and g_c) and initial substrate N concentration (r_0). There is considerable scatter in the estimates of r_c such that there is no relation between r_c and r_0 when all data sets are used (Fig. 3A). However, when an average r_c for a litter type is used (Fig. 3B), there is a significant positive relationship ($P < 0.01$) between r_c and r_0 , although the correlation is not significant for the BI and LIDET data bases, likely as a result of the strong influence of a few individual data sets.

Fig. 4 shows the pairs of r_c 's from the same site and the same substrate in the fertilised versus control plots. Virtually all values from the fertilised plots are higher than those from control plots. The regression line through these data have, however, a slope less than 1 indicating that the effect of fertilisation is strongest for sites and litter types leading to the smallest r_c .

When we plot SOM N:C for a site against the average r_c for the litter type collected at the same site, we find, including all data bases, a positive correlation ($P < 0.05$) between these two variables (Fig. 5).

Apart from effects of initial litter N concentration, we also expect site conditions to have other effects on r_c . Our data bases are not complete factorial experiments. It is, therefore, not practical to use standard ANOVA methods because of the large number of missing values. We have instead chosen to look at the average coefficients of variations (CV) in r_c -values when they are calculated over litter types or over sites, Table 3. The larger CV for sites than litter type in the BI and CCNHA data indicate that litter type means more than site conditions for determining r_c whereas the LIDET data indicate equal weight for both factors; the SWECON data are not suitable for this type of analysis.

5. Discussion

Our analysis shows that it is possible with confidence to estimate the critical N:C ratio, r_c , from the relation between carbon mass loss and N:C ratios in litter decomposition data. It is also clear that r_c increases with increasing initial litter N:C (r_0), Fig. 3. Moore et al. (2006, 2011), using a different methodology and a different data base but with a narrower range of r_0 , obtained relationships between r_c and r_0 similar to our result. Increasing r_c is also connected to an increasing SOM N:C, Fig. 5, and thus an increase in soil N. With increasing r_0 the decomposers will therefore be exposed to

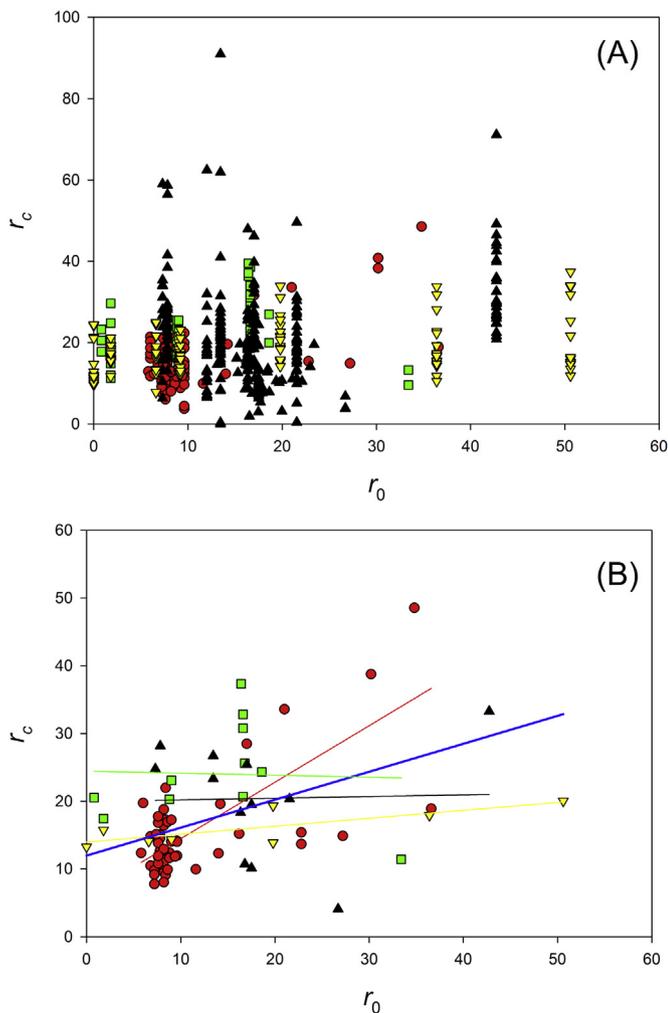


Fig. 3. Relations between critical N:C ratio (r_c) and initial litter N:C ratio (r_0). (A) Graphs of all data sets with one point from LIDET at $r_0 = 7.8$ and $r_c = 170$ not shown. Multiple values of r_c at one r_0 reflect differences among sites for this litter type. (B) Mean r_c for a litter type (averaged over sites). Thin lines are regressions within a data base, thick line the regression across all data bases, $r^2 = 0.25$ ($P < 0.01$). (■) = BI. (▼) = CCNHA. (▲) = LIDET. (●) = SWECON.

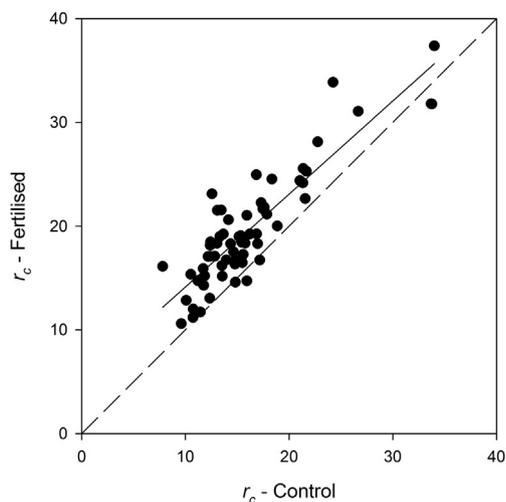


Fig. 4. Relation between r_c for the same litter type at the same sites but from control versus fertilised plots. The regression is $y = 5.17 + 0.90x$, $r^2 = 0.78$ ($P < 0.01$). The dashed line is the 1:1 line.

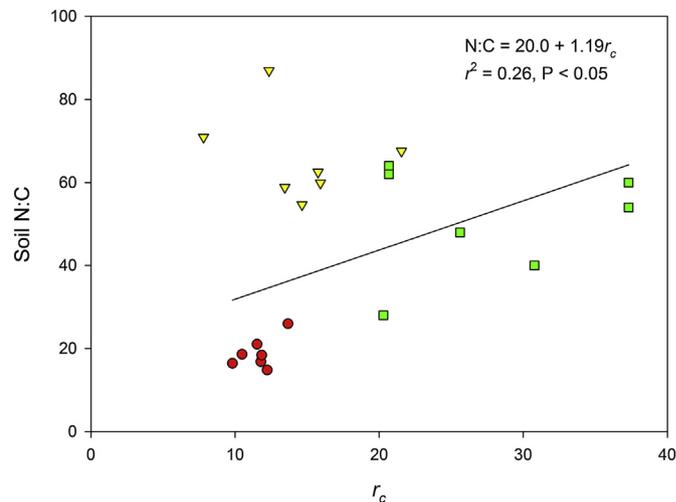


Fig. 5. Relation between SOM N:C and the average r_c for the litters from the same site. (■) = BI. (▼) = CCNHA. (●) = SWECON. SOM N:C unavailable for LIDET. The two highest values for SOM N:C from CCNHA were excluded from the regression.

increasing N availability in both the fresh litter and in SOM. It is, therefore, not clear if the connection between r_c and r_0 is a direct one, one mediated via SOM, or a combination of the two. The CCNHA fertilisation experiment also shows that increasing availability to N through external additions increases r_c (Fig. 4). There is also a barely significant ($P < 0.05$) trend of increasing r_c with soil inorganic N in this experiment (data from Hobbie (2005) not shown). These r_c estimates are from a short-term period, just 10 months, and soil inorganic measurements were made at a different time, so we do not want to emphasise this result too much. The conclusion is, however, that we should expect r_c to respond to both N concentration in the substrate and N availability in the environment. We cannot from this study determine if such an N effect arises from an increase in r_d or e_0 .

When we consider the BI data there is clearly less difference in r_c among different sites than among different substrates suggesting that the dominant factor for determining r_c is substrate properties, Table 3. If site effects were strong, we would expect r_c of litters decomposing at the site of collection to differ from r_c at foreign sites. However, this is not the case for BI and CCNHA litters. On the other hand, with the LIDET data, substrate and environment play approximately similar roles, Table 3. A major difference between BI/CCNHA and LIDET is the geographical spread of the experimental sites. Although there is large variability in soil N mineralisation within the BI experiment, the physical climate is the same (Pastor et al., 1984). The physical climate can modify decomposer properties and increasing temperature seems to decrease decomposer carbon-use efficiency, e_0 (Manzoni et al., 2012). Since $r_c = e_0 r_d$ it is possible that when r_c is estimated over a large temperature gradient, a temperature effect might enter through e_0 although a test of r_c against annual site temperature with LIDET data reveals no trend (data not shown, $R^2 = 0.011$, $n = 257$). A further complication arises from the interaction between e_0 and N availability, which

Table 3
Coefficients of variation (CV) for r_c -values.

Data	All	Species	Site
BI ^a	0.26	0.10	0.21
CCNHA	0.32	0.22	0.27
LIDET ^b	0.58	0.48	0.46

^a r_c Values averaged over treatments within a site.

^b One outlier with $r_c = 170$ not included.

leads to an increase in e_0 with increasing initial litter N:C (Ågren et al., 2001; Berglund and Ågren, 2012). The interaction between environment and substrate is, therefore, complicated (Freschet et al., 2012b).

A challenge arising from this study is how to separate r_c into e_0 and r_d . The most straight-forward way and possibly the only one applicable to long-term litter-bag studies is direct measurements of the decomposer N:C ratios, r_d , along with measurements of litter mass losses and nutrient determinations. Techniques for measuring decomposer carbon-use efficiency suitable for large-scale investigations are lacking (see review of techniques in Manzoni et al., 2012).

The eight data sets with green litters deviate systematically from the data sets with brown litters. As can be seen in Fig. 1D, the data with the green litter from CCNHA decline from high estimated values of r_c to values typical for all litters at the end of the observation period (small g). Such a decline is observed for all green litters and show that they deviate in some respect from the standard model of C–N interactions. To understand this behaviour we have used a simple pool model with two pools of different qualities and initial N:C ratios. The C loss is exponential from both pools and the N dynamics follow Equation (1). The only combination of qualities and initial N:C ratios that predicts the observed result is when the high quality pool also has the low N:C ratio. Green litters differ from senesced, brown litters by having higher N:C ratios but also higher starch contents. Our interpretation is, therefore, that it is the high starch content, high quality but low N:C, of the green litters that causes this different behaviour. The reason that this behaviour has not been observed earlier is, we believe, that almost all litter decomposition studies are performed with senesced, brown litters. It is also possible that green leaves systematically start out with a decomposer community with different properties (e_0 , r_d) because they are dominated by a phyllosphere community. Green litters could be important in some ecosystems; it might therefore be necessary to consider modifying existing models of litter decomposition to account for their unique properties.

We have calculated the relationship between SOM N:C and decomposer N:C from two studies covering a wide range of terrestrial ecosystems (Cleveland and Liptzin, 2007; Li et al., 2012). From Li et al. we find a positive correlation (SOM N:C = $-9.0 + 1.3$ Decomposer N:C, $P < 0.001$, recalculated from their C:N) between the two variables but no correlation in Cleveland and Liptzin (SOM N:C/Decomposer N:C = 0.61). The latter value for SOM N:C/Decomposer N:C is close to 0.68 that was predicted with reference parameter values for decomposition with quality changes, Equation (6). However, SOM N:C should increase as $2.70 r_c$, but the data from our data sets give a shallower slope of 1.19. This indicates that factors, other than those included in our analysis so far need to be taken into account when predicting SOM N:C from decomposer properties. One such factor is the contribution to SOM from other litter types with different initial N concentrations. Fine roots tend to be lower in N:C than leaves (Liu et al., 2010) and woody tissues are definitely lower in N:C. Another factor can be the contribution to SOM from protected, undecomposed plant tissues and how this is handled in measurements of SOM N:C (von Lützwow et al., 2006; Schmidt et al., 2011). However, analysing the consequences of including all litter types is beyond the scope of this paper. An additional difficulty is that relations such as Equations (5) and (6) are assuming SOM N:C to be in steady state with respect to litter input, a condition that is unlikely to be satisfied in almost any single data set or site. This can be particularly problematic if the current stand is planted at a site with previously different vegetation; this might explain the outliers in Fig. 5 for CCNHA, where changes in land use have occurred.

Development of ecosystems involves changes both within and among species that, if uninterrupted by disturbances, in the long run tend to drive toward stronger nutrient limitation (Wardle et al., 2009). In that perspective, our results represent a negative feedback that should retard the development towards increasing nutrient limitation. With increasing nutrient limitation, the litter produced will become less nutrient-rich, lowering r_0 . This will lower the critical N:C, which promotes a shift towards earlier N mineralisation and decreased stock of N in SOM; hence proportionally more N will be in the vegetation.

A further development of this analysis might take into account that r_c ought to increase with the age of the litter. Since N:C increases during decomposition, taking one and the same substrate but using different times as starting points for calculating the decomposition process, would be equivalent to analysing different substrates with different initial N:C ratios, r_0 . The increase in r_c with r_0 that we have shown then means that, the more degraded the substrate has become, the larger will be the predicted r_c when it is used as initial point. This should result in negative slopes of r_c versus remaining C, Fig. 1D. That this is not observed indicates that other factors intervene during decomposition; maybe a decrease in carbon-use efficiency, e_0 , with decreasing substrate quality.

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