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Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors

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Abstract

Aims

We aim to construct a comprehensive global database of litter decomposition rate (*k* value) estimated by surface floor litterbags, and investigate the direct and indirect effects of impact factors such as geographic factors (latitude and altitude), climatic factors (mean annual tempePlrature, MAT; mean annual precipitation, MAP) and litter quality factors (the contents of N, P, K, Ca, Mg and C:N ratio, lignin:N ratio) on litter decomposition.

Methods

We compiled a large data set of litter decomposition rates (*k* values) from 110 research sites and conducted simple, multiple regression and path analyses to explore the relationship between the *k* values and impact factors at the global scale.

Important findings

The *k* values tended to decrease with latitude (LAT) and lignin content (LIGN) of litter but increased with temperature, precipitation and nutrient concentrations at the large spatial scale. Single factor such as climate, litter quality and geographic variable could not explain litter decomposition rates well. However, the combination of total nutrient (TN) elements and C:N accounted for 70.2% of the variation in the litter decomposition rates. The combination of LAT, MAT, C:N and TN accounted for 87.54% of the variation in the litter decomposition rates. These results indicate that litter quality is the most important direct regulator of litter decomposition at the global scale. This data synthesis revealed significant relationships between litter decomposition rates and the combination of climatic factor (MAT) and litter quality (C:N, TN). The global-scale empirical relationships developed here are useful for a better understanding and modeling of the effects of litter quality and climatic factors on litter decomposition rates.

Keywords: climatic factors • geographic factors • litter decomposition rate • litter quality • path analysis • terrestrial ecosystems

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Introduction

Litter decomposition plays an important role in carbon (C) cycling in terrestrial ecosystems (Aerts 2006; Field *et al.* 1998; Shiels 2006). One noteworthy feature of litter decomposition is the variability of litter decomposition rate (*k*) among ecosystems and under different climatic conditions. To accurately predict the amount of C released through the litter decomposition, this variability must be accountable and well documented (Liski *et al.* 2003). So far, it is still not entirely clear how *k* values distribute at the large spatial scale and, more importantly, which factors are critical in controlling the litter decomposition globally.

Litter decomposition of plant species has been studied for decades, especially at site levels (e.g. Aerts 1997; Gholz *et al.* 2000; Olson 1963). Factors that regulate *k* values have been identified as (i) climatic factors such as mean annual temperature (MAT), mean annual precipitation (MAP) and annual actual evapotranspiration (AET) (Aerts 1997; Berg *et al.* 2000; Dyer *et al.* 1990; Meentemeyer and Berg 1986; Moore 1986; O'Neill *et al.* 2003); (ii) litter quality, e.g. nitrogen content (N) (Yavitt and Fahey 1986), carbon:nitrogen ratio (C:N) (Edmonds 1980; Berg and Ekbohm 1991), lignin content (LIGN) (Gholz *et al.* 1985) and lignin:N ratio (LIGN:N) (Aerts 1997; Waring and Schlesinger 1985); (iii) vegetation and litter

types (Gholz *et al.* 1985, 2000; Prescott *et al.* 2000) and (iv) geographical variables such as LAT and altitude (ALT) (Aerts 1997; (Silver and Miya 2001). While these studies provide very helpful information for our understanding of control on litter decomposition, the results are mostly site specific, based on small-scale laboratory and field experiments, and difficult to extrapolate to the large spatial scales.

Several litter decomposition studies have been conducted at the large spatial scales on leaf litter (Aerts 1997; Dyer *et al.* 1990; Meentemeyer 1978; Swift *et al.* 1979), woody debris (Yin 1999) and root litter (Silver and Miya 2001). The results indicated that at the large scales, most single factors only account for <50% of variation in the *k* values. The combination of several factors explains better in most cases. For example, Dyer *et al.* (1990) analyzed the data from published studies and found that first-year litter mass loss is well correlated with AET at the global scale. In the tropical systems, ~78% of the litter decomposition variation can be explained by AET and LIGN, whereas in the boreal systems, AET and N can explain ~16% only. Using a very comprehensive leaf litter database, Aerts (1997) demonstrated that AET is the most important regulator and accounts for 46% of the *k* value variation. Yin (1999) suggested that substrate quality and microbial growth rates exert a great constraint on the wood litter *k* values. Silver and Miya (2001) synthesized the global pattern of root litter *k* values extracted data from experiments using buried litterbag. But results of root litter decomposition rates from these buried litterbags studies could be quite different from surface floor litterbags incubation. Therefore, an updated database including leaf, woody and root litter is necessary to develop the patterns and controlling factors on litter decomposition at the global scale.

This study was designed to construct a comprehensive database of *k* values estimated by surface floor litterbags incubation and investigate the direct and indirect effects of climatic and litter quality factors and the relative importance of these variables on litter decomposition rates at the global scale. We first collected litter decomposition data from published papers, estimated the *k* values and developed a global *k* value database. Based on this database, we then tried to seek general patterns of *k* values along LAT, across vegetation and litter types. We further examined the relationships of *k* values and the regulating factors, especially the relative importance of these factors, at the global scale.

Materials and methods

Data extraction

We extracted litter decomposition data from incubation studies using surface litterbags. To ensure the comparability of environmental variables among studies, results from laboratory or buried litterbags studies were excluded (for *k* values estimated by buried bags, see Silver and Miya 2001). The resultant database included 70 published studies at ~110 sites ranging from 38°S to 69°N (see supplemental data Appendix 1 online). Original data from publications in the literature, which were either actual litter mass (grams) or normalized litter mass (i.e. starting with one unit in the beginning of the experiments), were digitized from figures or extracted directly from tables at each measurement time. In the case that the actual litter mass was presented in the original papers, we first normalized it by converting the starting litter mass to 1, and then calculated *k* values. The decomposition rate was calculated using a first-order exponential decay function (Olson 1963; Silver and Miya 2001;Wieder and Lang 1982):

$$y = e^{-kt}, \quad (1)$$

where *y* is the percent mass remaining at a time point and *t* is the time elapsed since the beginning of litter decomposition experiments (year). In a few publications where the *k* values and coefficient of determination (R^2) of the model were presented, we directly incorporated the *k* and R^2 values into our database.

To develop the relationship of *k* value with its regulating variables, accessory variables were also extracted from the publications. Those were geographic variables (i.e. LAT, ALT), climatic variables (i.e. MAT, MAP) and litter quality variables (i.e. N, C:N, LIGN, LIGN:N, and P, K, Ca and Mg). We calculated the total nutrient (TN) contents by summarizing N, P, K, Ca and Mg. We classified vegetation types into broadleaved forest (BF) (including hardwood mixed forest), coniferous forest (CF), grassland (GL), broadleaved and conifer mixed forest (MF), rain forest (RF), shrub land (SL), swamp forest (SW) and tundra (TU). Litter types were divided into broadleaved (BL), bark (BAR), branch (BRA), conifer needle (CN), grass (G), moss (M), root (R) and woody (W). The longest experiment included in this study lasted 5 years (Gholz *et al.* 2000).

Data analysis

To examine the relationships between the estimated *k* values and the accessory variables, we conducted both simple and multiple regression analyses. The simple regression was used to identify the pattern (e.g. linear or nonlinear) of the relationship of *k* values with individual variables. Since some of these variables were correlated, we used multiple regression analysis to construct a best regression equation of *k* values with statistically significant variables. Stepwise method was used to select and keep significant variables in the equation. Path analysis was conducted to examine the relative importance of these accessory variables on *k* values. We constructed a path network including all these statistically significant variables and calculated the direct and indirect path coefficients (McClendom 2002). All data analyses were conducted with SAS software (SAS Institute Inc., Cary, NC).

Results and discussion

The database of litter decomposition rate derived in this study includes 293 *k* values from the 70 studies ranging from 0.006 to

4.993 g g^{-1} yr^{-1}. The *k* values were well estimated by the first-order exponential decay function similar to many of the other studies (Wieder and Lang 1982). The majority of the coefficient of determination (R^2) was within the range of 0.8–1.0 in this study (Fig. 1c). Less than 2% of the data sets (i.e. 5 out of 293) could not be adequately described by the exponential decay function. The 293 *k* values had a left-skewed distribution with a medium of 0.300 g g^{-1} yr^{-1} and a mean of 0.581 g g^{-1} yr^{-1} (Fig. 1a). The distribution was well described by $f = 0.0045 + 4.191ke^{-4.81k}$, where *f* is the frequency and *k* is the litter decomposition rate. Since the majority of the litter decomposition studies compiled in this paper used leaf material (243 out of the 293 *k* values), we plotted a frequency distribution of the *k* values for leaf litter only, which had a distribution similar to that with all the *k* values (Fig. 1b). Our estimations of *k* value were consistent to other studies. For example, Gholz *et al.* (2000) estimated that *k* values of litter decomposition rate ranged from 0.032 to 3.734 from arctic tundra to tropical rain forest after 5 years. It is understandable that our estimated leaf litter *k* values were smaller than root litter *k* values compiled by Silver and Miya (2001) that range from 0.03 to >7.0 g g^{-1} yr^{-1}.

The broad variation in estimated *k* values was largely attributable to the differences in geographical locations, climatic conditions and litter quality, which are discussed below.

Global pattern of k values across LAT

The estimated *k* values tended to decrease with LAT (Fig. 2). The relationship between *k* values and LAT (without distinction of north from south latitude) was described by $k = -0.0169\,\mathrm{LAT} + 1.212$ with $R^2 = 0.15$ ($P < 0.001$, Fig. 2a). Higher variability in *k* values was shown in the low LAT (between 10°N and 10°S) compared with that in the high LAT,

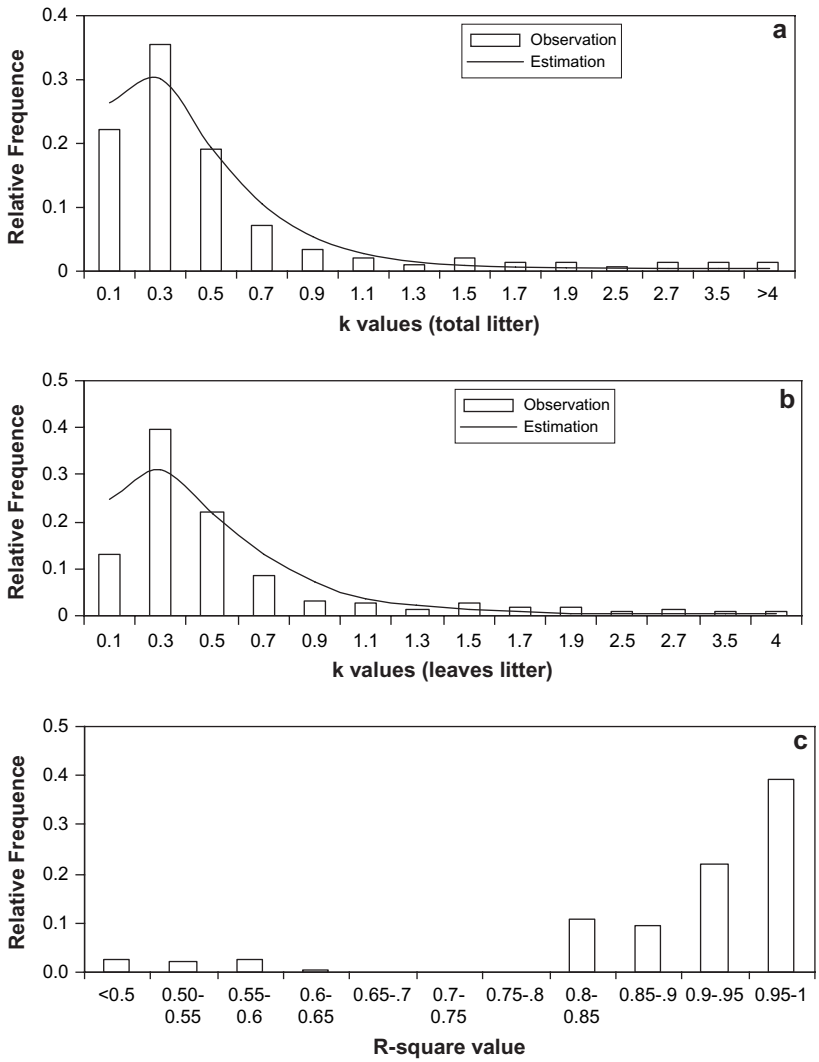

Figure 1 Frequency distributions of *k* values for the whole database (a), for the subset of the database with leaf litter only (b) and for the coefficient of determination R^2 (c). The medium of the *k* values for both the whole database and the data set of leaf litter is 0.3 g g^{-1} yr^{-1}. Majority of the R^2 values is >0.8, indicating that the first-order decay function can be realistically used to describe the litter decomposition process.

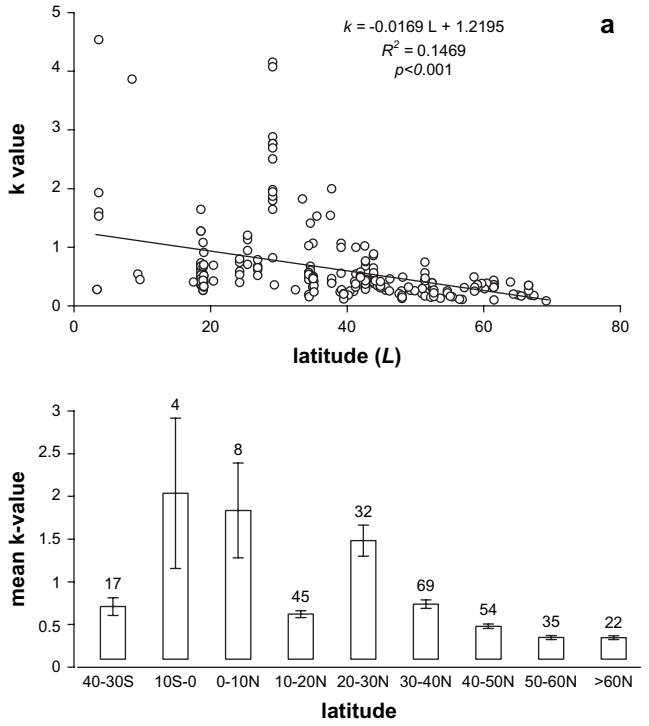

Figure 2 Variation of *k* values with LAT and global pattern of litter decomposition rates (*k* values) across LAT. Data at the top of column were numbers of *k* values. Overall, *k* values decrease with LAT with high variability in low latitudinal regions.

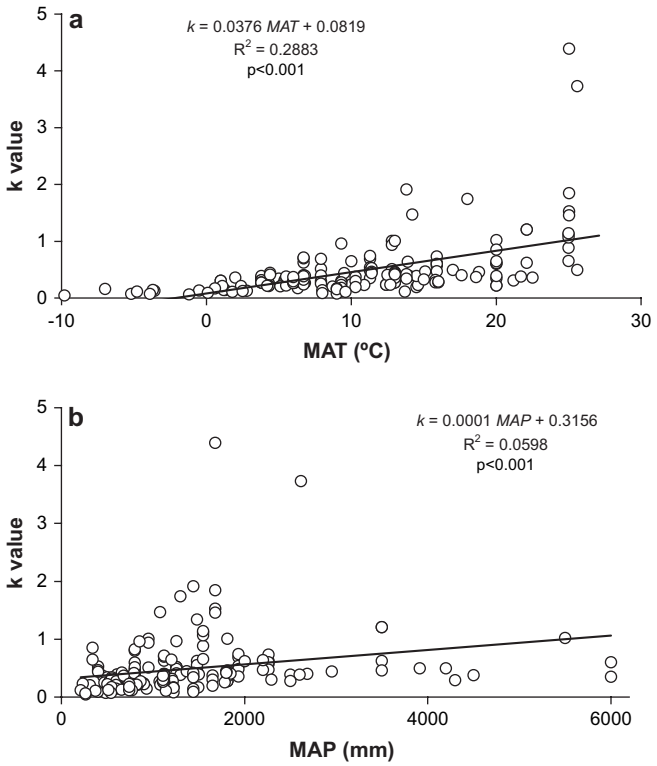

Figure 3 Variation of *k* value with MAT (a) and MAP (b). The *k* values increase with both MAT and MAP.

presumably due to high variance among climatic conditions and species diversity in the low LAT plus small sample size in this region. A similar negative correlation of *k* values with LAT was reported for buried root litter (Silver and Miya 2001). Further path analysis in this study showed that the correlation between *k* values and LAT, however, largely resulted from its indirect effect on *k* values via latitudinal variations in MAT, MAP and vegetation-associated changes in TN or C:N. The direct effect of ALT on *k* values was small and not significant (data not shown). ALT influenced *k* values indirectly via affecting MAT, MAP vegetation types or litter quality. Considering that climatic factors change less with ALT than with LAT, the influence of ALT change on litter decomposition could be weaker than that of LAT change.

To further investigate how *k* values changed with LAT, we averaged *k* values for each interval of 10 degrees of LAT from 40°S to 69°N. In general, *k* values at the equator were the highest and decreased with LAT toward both the south and north poles. However, the averaged *k* value in the 10–20°N regions was much lower than those in the adjacent regions, largely due to aridity (Gholz *et al.* 2000, Fig. 2b). This region was primarily occupied by tropical thorn scrub, semi-desert or desert plants. Unfavorable surface conditions in this region and the concentration of litter in discontinuous areas could also hinder the development of the surface decomposer community (Couteaux *et al.* 1995), leading to lower litter decomposition rates.

Temperature and precipitation effects on k values

Variation in *k* values along the LAT likely resulted, at least partially, from geographical differences in temperature and precipitation. We plotted *k* values against MAT and MAP. In general, *k* values linearly increased with MAT with $k = 0.0376\ MAT + 0.0819$, $R^2 = 0.29$ ($P < 0.001$, Fig. 3a), since favorable temperature conditions stimulated activities of the decomposer community such as fungi and soil fauna and thereby accelerated the litter decomposing. The *k* values were also significantly correlated with MAP ($P < 0.01$, Fig. 3b) with an even smaller R^2 compared with MAT. Most of the *k* values were derived from the decomposition studies in regions where MAP was <2000 mm. Higher variability in *k* values was found in areas where MAP was between 1000 and 2000 mm. A combination of MAT with MAP accounted for 30% of the variation in *k* values (Table 1). At the global scale, to the extent that our database covers, MAT was evidently more important than MAP in regulating litter decomposition (Fig. 3a versus 3b). Nevertheless, water availability could become the dominant factor in influencing litter decomposition at local scales, particularly in desert or semi-arid regions where water was the primary limiting factor (Couteaux *et al.* 1995). Even in a region where MAP was high, seasonal drought could limit litter decomposition. In Canada, for example, Moore *et al.* (1999) reported that AET is significantly correlated to litter decomposition rates at the forest sites due to water deficit in summer.

Table 1 Regressions of litter decomposition with geographic, climatic factors and litter quality variables

Variable/regression	*n*	R^2
Climatic/geographic factors		
$k = 0.0016 + 0.0447$ MAT	163	0.288**
$k = -0.065 + 0.0001$ MAP + 0.044 MAT	163	0.300**
$k = -0.4744 + 0.0081$ LAT + 0.0586 MAT	163	0.301**
$k = -0.353 + 0.0063$ LAT − 0.00005 MAP + 0.06 MAT	163	0.305**
Litter quality variables		
$k = 0.946 - 0.011$ LIGN:N	141	0.131**
$k = -0.131 + 0.268$ TN	68	0.388**
$k = -2.307 + 0.029$ C:N + 0.524 TN	68	0.702**
$k = -2.132 + 0.031$ C:N − 0.006 LIGN:N + 0.495 TN	68	0.733**
Combination		
$k = -0.308 + 0.026$ MAT + 0.205 TN	68	0.467**
$k = -2.484 + 0.026$ MAT + 0.0287 C:N + 0.461 TN	68	0.781**
$k = -2.935 + 0.0003$ MAP + 0.021 MAT + 0.0315 C:N + 0.516 TN	68	0.805**
$k = -4.131 + 0.023$ LAT + 0.063 MAT + 0.032 C:N + 0.517 TN	68	0.875**

n is the number of data points included in each of the regression analyses, and R^2 is the coefficient of determination for the regression line. **Represents significant at $\alpha = 0.01$ level. See see supplemental data Appendix 1 for description of abbreviations for LA, MAT, MAP, LIGN:N, TN and C:N.

MAT and MAP accounted for 72–87% of the variation in litter mass remaining at 18 forest research sites in Canada. However, along the transect of 14 stands of Norway spruce (*Picea abies* (L.) Karst.) in Sweden (from 56–66°N), where locally collected needle litter was incubated, Berg *et al.* (2000) reported that there is virtually no relationship between AET (with a range between 371 and 545 mm) and first-year litter mass loss. Similarly, Dyer *et al.* (1990) found that AET and N can only account for ~16% of the variability of litter decomposition rates in the boreal systems. The low coefficients of determination (i.e. $R^2 < 0.30$) in our study indicate that temperature or moisture alone cannot independently explain the global-scale variability of litter decomposition rates.

Variation of k values in vegetation types and litter types

Averaged *k* values in different vegetation types ranged from 1.3 g g^{-1} yr^{-1} in rain forests to 0.18 g g^{-1} yr^{-1} in tundra. The *k* value was ranked in a descending order as RF > SW >BF > MF >GL > SL > CF > TU (Fig. 4a). Litter decomposition in the RF floors was >7-fold faster than that in the TU floors. Variations in litter decomposition rates were mainly caused by the differences in associated litter quality, microclimates, soil properties and microbial community composition (Gholz *et al.* 2000; Zhang *et al.* 2000). In general, rain forests or broadleaved forests distributed at low LAT where MAT and MAP were high.

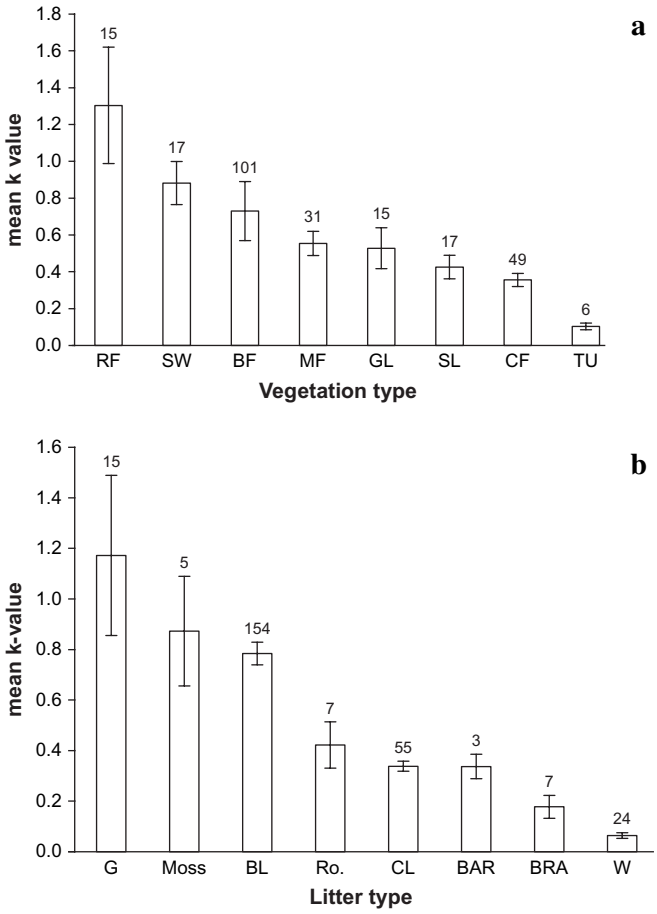

Figure 4 Variation of *k* value with different vegetation types (a) and litter types (b) at the global scale. Data at the top of column are the number of statistical *k* values. Vegetation types include rain forest (RF), swamp (SW), broadleaved forest (BF), mixed forest (MF), grassland (GL), shrub land (SL), coniferous forest (CF) and tundra (TU). Litter types include grass leaf (G), moss (M), broadleaved litter (BL), roots (R), conifer needles (CL), bark (BAR), branch (BRA) and woody litter (W).

As a result, the litter was decomposed more easily in those regions than in other regions. In contrast, coniferous forests, such as Taiga, usually distributed at high LAT where low MAT and/or MAP slowed down litter decomposition. Furthermore, soil acidity in coniferous forests was usually higher than that in broadleaved forests or grasslands, thus limited microbe activities (Gholz *et al.* 2000).

Estimated *k* values also varied with litter types and decreased in order as G > M > BL > R > CN > BAR > BRA > CW (Fig. 4b). In general, leaf litter from herbaceous species was decomposed more easily than that from trees. Differences in *k* values among various litter types were mainly due to variance in litter quality. Litter with high concentration of phenolics (tannin and LIGN) and low concentration of N were generally decomposed slowly (Lambers *et al.* 1998). CW, BRA, BAR and CN, for example, had a higher lignin concentration and a higher C:N and was decomposed more slowly than BL and GL.

Variation of k values with litter quality

Litter quality in this study was indicated by eight variables: C:N, N, LIGN and LIGN:N and concentrations of P, K, Ca and Mg. Litter decomposition rates increased with N, P, K, Ca and Mg (Fig. 5a–e, respectively) but decreased with C:N (Fig. 5f), LIGN (Fig. 5g) and LIGN:N (Fig. 5h). All those simple correlations were statistically significant except the one between *k* values and C:N ($P > 0.05$, Fig. 5f). TN alone explained 38.8% variation in *k* values, more than any other individual variables. A combination of TN and C:N accounted for 70.2 % of the variation of *k* values (Table 1). Similar results were reported by Stohlgren (1988a, 1988b). These results, together with many others, supported that initial concentrations of N, LIGN in plant litter and LIGN:N could be good predictors of litter decomposition rates in many ecosystems (Aber and Melillo 1980; Bryant *et al.* 1998; Melillo *et al.* 1982; Stohlgren 1988a, 1988b; Taylor *et al.* 1989).

Interactive effects of geographic factor, climate and litter quality on litter decomposition

It has long been demonstrated that climatic factors and initial litter quality interactively regulate litter decomposition processes (Gholz *et al.* 2000; Meentemeyer 1978). Based on the multiple regression analysis, we found that combined geographic and climatic factors (including LAT, MAT and MAP) accounted for 30.5% of variation of *k* values, whereas litter quality variables (including C:N, LIGN, LIGN:N and TN) collectively accounted for 73.3%. When we combined climatic

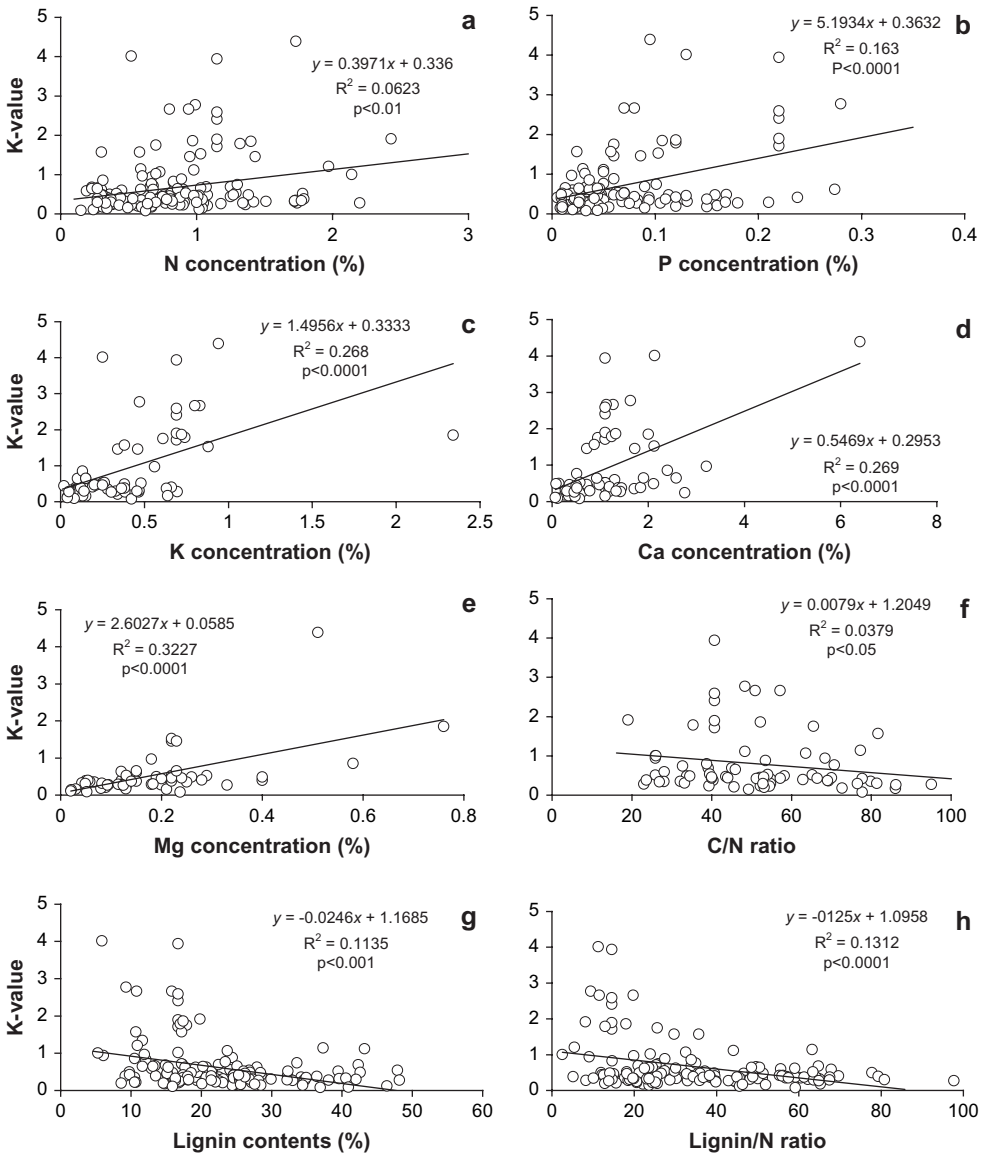

Figure 5 Variation of *k* value with initial litter quality variables. The *k* values are positively correlated with nutrient concentrations of N, P, K, Ca and Mg but negatively with C:N ratio, LIGN and lignin:N ratio.

factors with litter quality variables, three of them (i.e. MAT, C:N and TN) accounted for 78.1% of the variation in the *k* values. With the additional variable of LAT, 87.5% of variation in the *k* values could be explained (Table 1). Thus, our regression analysis showed that MAT, C:N, TN and LAT are major factors co-regulating litter decomposition process. These results were consistent with some previous studies. For example, Moore *et al.* (1999) found that MAT, MAP and LIGN:N explain 73% of the variation in mass remaining for 11 litter types across 18 forest sites. Similar results were also found by Silver and Miya (2001) who synthesized litter decomposition using buried litterbags. In contrast, Dyer *et al.* (1990) reported that climate clearly dominates the patterns of mass loss rates at large regional scales. Our study indicated that both climatic factors and litter quality were important in regulating leaf litter decomposition process in the surface litterbags.

Direct and indirect effects on k values

We further conducted a path analysis to examine the direct and indirect effects of five significant variables (i.e. LAT, MAT, MAP, C:N and TN) on *k* values. The path network of the five regulating variables with the *k* value was displayed in Fig. 6. LAT influenced litter decomposition mainly through its indirect effects associated with changes in MAT, MAP, TN and C:N in different LATs. As expected from global temperature distribution, LAT had a strong influence on MAT with an indirect path coefficient of –0.684, reflecting that LAT had a negative effect on *k* values via MAT. LAT had smaller path coefficients with MAP, C:N and TN. MAT further propagated its influences on *k* values both directly and indirectly through changes in litter quality variables of C:N and TN. The indirect effects of LAT on *k* values were through changes in MAP and then through litter quality variables. Among all the five regulating factors, MAT was the most important one in influencing *k* values both directly and indirectly. Our path analysis showed that the direct path coefficient of MAT to *k* values was $P_{MAT-k} = 0.781$. In addition, MAT also indirectly affected *k* values via its associated changes in MAP, TN and C:N. In contrast, MAP had a minor direct effect on *k* values. Indirect effects of MAP on litter decomposition at the global scale were primarily through changes in C:N. Both TN and C:N had significant influences on litter decomposition. The path coefficient of TN to *k* values (P_{TN-k}) was 1.192 (Fig. 6), the largest among all the path coefficients. C:N, which was significantly correlated to TN, had a path coefficient of −0.728, also strongly affected the *k* value (P_{CN-k}=0.922). Although both TN and C:N had strong direct effects on *k* values, the large negative correlation between the two variables suggested possible partial substitution of one by the other in indicating litter quality. Nonetheless, the combination of TN and C:N can explain more variability in *k* values than any one of them.

Comparison with other studies on litter decomposition

Compared with several other studies on litter decomposition at the large spatial scales (e.g. Aerts 1997; Dyer *et al.* 1990;

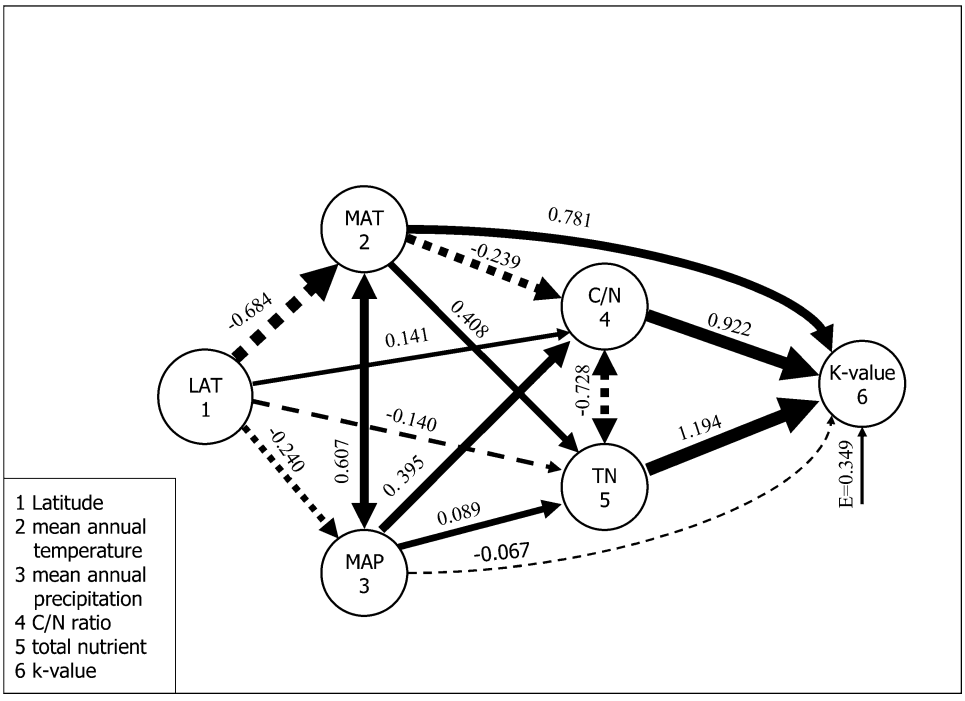

Figure 6 Path analysis shows direct and indirect effects on litter decomposition rates (*k* values). Solid lines represent positive effects and dotted lines represent negative effects. See see supplemental data Appendix 1 online for description of abbreviations LAT, MAT, MAP, TN and C:N ratio.

Silver and Miya 2001), this study synthesized more recent published data and included all different litter types. But it should not be considered an exhaustive review of litter decomposition, since a lot of information is believed to exist in early or 'gray' literature. Due to the limitation of the data availability, more leaf litter was included in the database than other litter types. Another potential limitation of our database, as in any other data synthesis, was that individual studies might use slightly different litter decomposition protocols, such as different litterbag mesh sizes and incubation times. Nonetheless, the present study has improved our understanding on global litter decomposition and is unique in at least the following four aspects. (i) An updated global database was compiled including different leaf, woody and root litter decomposition data (Table 1). Among the 70 studies used in this study, ~27 were published after 1996. The new data reflect the most recent understanding on litter decomposition process; (ii) many studies have identified important factors regulating litter decomposition, but seldom evaluated relative importance of these factors in regulating litter decomposition. Using the path analysis, we found that litter quality was the most important direct regulator of litter decomposition. Other factors, such as MAT and MAP, also affected litter decomposition either directly or indirectly via affecting litter quality; (iii) this study confirmed that at the global scale, litter decomposition could be well modeled by a combination of climatic, litter quality and geographic variables, although independently, no variable could account for >40% variation in litter decomposition rates. The high coefficient of determination (R^2 = 0.875) indicates that it might be adequate to estimate global litter decomposition rates in global geochemical models based on this statistical model; and (iv) we found that k values were the highest at the equator and decreased with LAT toward both the south and north poles. The k values also varied with litter types. The patterns of litter decomposition rates resulted from species compositions which determine litter quality and LAT which determines climatic variables.

In conclusion, we developed a comprehensive global database of aboveground k values by synthesizing published litter decomposition data and investigated the relative importance of regulating variables on litter decomposition rates among different ecosystems at the global scale. Our results improved our understanding of litter decomposition in several aspects. First, we demonstrated that k values tended to decrease with LAT and LIGN but increased with temperature, precipitation and nutrient concentrations. With combination of LAT, MAT, C:N and TN accounted for 87.54% of the variation in the litter decomposition rates. This result indicates that the climatic factors and litter quality are important direct regulators of litter decomposition at the global scale. Second, path analysis showed that LAT affected k values by indirect effects through MAT and MAP but less through litter quality. MAT and MAP affected litter decomposition directly as well as indirectly via effecting litter quality on litter decomposition rates. Third, our study confirmed that a first-order exponential decay function can be used to adequately describe decomposition process in the majority of cases. Last, plant ecology is now entering on a phase where global data sets are gathered together (Moles *et al.* 2007). Building a general pattern at large scales not only extended the results of small-scale studies but also provided more new information such as global mean and variation of litter decomposition rate here. Given the complex inter-relationships among the factors that influence litter decomposition rates, the comprehensive analysis of litter decomposition with litter quality and climatic variables is very useful for model development to project future rate of terrestrial C sequestration and for prediction of ecosystem C dynamics in response to natural or experimental perturbations.

Supplementary data

Supplementary data is available at *Journal of Plant Ecology* online.

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