Global pattern and drivers of stable residue size from decomposing leaf litter

Renshan Li [a], Xingyi Guo [a], Jianming Han [a], Qingpeng Yang [b,c,*], Weidong Zhang [b,c,*], Xin Yu [d], Xinkuan Han [a], Longchi Chen [b,c], Xin Guan [b,c], Zhangquan Zeng [e], Huixia Yang [f], Silong Wang [b,c]

[a] College of life Science, Luoyang Normal University, Luoyang 471934, China
[b] Huitong Experimental Station of Forest Ecology, CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Shenyang 110016, China
[c] Huitong National Research Station of Forest Ecosystem, Huitong 418307, China
[d] Fujian Provincial Key Laboratory of the Development and Utilization of Bamboo Resources, Sanming University, Sanming 365000, China
[e] Hunan Academy of Forestry, Hengshan Research Station of Forest Ecosystem, Changsha 410004, China
[f] Liaoning Institute of Forest Management, Dandong, Liaoning 118002, China

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ABSTRACT

Stable residue from decomposing leaf litter is related to humus buildup in the forest floor and thus to the accumulation of carbon in the soil organic layer (OLC). However, the global pattern and controls of stable residue size remains poorly understood. Herein, the spatial pattern of stable residue size and its association with a series of potential drivers were evaluated by synthesizing available data worldwide. The results showed that stable residue size had a significant and positive correlation with the litter initial nitrogen (N) and lignin concentrations, and a negative correlation with the initial manganese concentration. Larger stable residues were found from decomposing broadleaf litter *vs.* coniferous litter. The decomposition of green leaf litter produces an equal amount of stable residue as that of brown litter. Stable residue size correlated quadratically with mean annual temperature and latitude, and linearly with mean annual precipitation. Methodological factor also matters, because stable residue size decreased as field incubation time increased. The boosted regression tree model indicated that litter initial traits have the most explanative ability for the variance in stable residue size. We highlighted that litter initial traits exert a predominant role over climate in shaping the stable residue size globally. Our findings are beneficial for a more accurate prediction of global-scale OLC accumulation.

1. Introduction

Leaf litter, which represents over 50% of net primary production in terrestrial ecosystems that is returned to the soil, has been characterized as a main source of soil carbon (C), especially in the upper organic layers (Cebrian, 1999; Wardle et al., 2004; De Marco et al., 2018). Decomposition prevents litter-derived C from accumulating; therefore, the contribution of litter to soil C sequestration is highly dependent on the amount of the litter that can remain during decomposition (Berg, 2017). Most plant litter cannot decompose completely, but will create a stable residue that adds to soil organic matter (SOM) when the decomposition rate approaches very nearly zero at the late stage (Berg 2000; Currie et al. 2010; Yang et al., 2018). Therefore, evaluating the size and exploring the controls of stable residue is essential to accurately predict

the accumulation rate of C in organic layers (OLC), which is of particular importance under climate change scenarios (Berg 2017).

Over past decades, decomposition has increasingly been described with asymptotic multi-pool models, whereby the stable residue size can be estimated (Berg and Matzner, 1997; Hobbie et al., 2012; Li et al., 2022). In comparison with the more frequently used single pool model that assumes a complete decomposition of the litter (Olson, 1963), multi-pool models are equal or better in fitting the decomposition data (Hobbie et al., 2012; Riggs et al., 2015). Although extensive research has been conducted, the controlling factors of the stable residue after litter decomposition remain controversial. Stable residue size was often positively related to litter initial lignin concentration as late-stage decomposition is dominated by lignin degradation (Osono and Takeda, 2005; Hobbie et al. 2012). However, stable residue formation is

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sometimes predominantly affected by litter initial N concentration, because of the N inhibition of lignolytic enzymes or the recombination of N and many litter constituents that create more recalcitrant compounds (Berg et al., 2014; Li et al., 2022). It is also reasonable to expect a relationship of litter manganese (Mn) or calcium (Ca) with stable residue size, because Mn is essential for the production of manganese peroxidase (MnP), an important lignin-degrading enzyme, and Ca is an important constituent of cell walls of white rot fungi that are capable of decaying lignin (Keiluweit et al., 2013; Berg and McClaugherty, 2014). However, the existing evidence is both for and against these metal elements as controls (Berg et al., 2013; Virzo De Santo et al., 2009; Lovett et al., 2016; Yang et al., 2018). Climate is also proposed to be a determinant of stable residue size because of its key role in shaping microbial decomposition (Harmon et al., 2009). Nevertheless, literature has shown that climate may or may not serve as a driver of stable residue size (Berg and Meentemeyer, 2002; Berg, 2014). Such a discrepancy could be attributed to the different lignin-degrading microflora with different request for, or tolerance to, nutrients and climate, depending on the substrate and/or site (Virzo De Santo et al., 2009).

Large-scale synthesis, which integrates multiple ecosystem types, can reveal the spatial pattern and controls of stable residue size, and effectively reconcile these divergent views. Historically, Berg and colleagues have synthesized the size and controlling factors of stable residue for some temperate and boreal forest ecosystems. Based on decomposition studies particularly in Europe, Berg et al. (2013) found that the stable residue size varied from 0 to 57% of initial litter mass depending on the initial concentration of Mn in the litter. In a more recent review, Berg and Lönn (2022) found that the decomposition of Scots pine and Norway spruce needle litter in Sweden left a stable residue of approximately 19% and 26%, respectively, of the initial mass on average, and its variation could be explained by both climate and litter initial traits. These studies clearly advanced our understanding of the contribution of litter decomposition to OLC accumulation at the continental scale, but offered limited information on whether these laws are globally applicable. In addition, we know surprisingly little about the relative contribution of each driver to stable residue production.

To address this knowledge gap, we synthesized the available data from published leaf litter decomposition studies worldwide, which have calculated the stable residue size using multi-pool models. The aim of this study was to assess the size of stable residue after leaf litter decomposition, as well as determining how it is influenced by a series of potential factors, at the global scale. Specifically, the following aspects were determined: (1) What are the global-scale patterns of stable residue size? (2) How do litter traits and climate factors modulate stable residue size? (3) Are the differences in methodology a source of variance in stable residue; and (4) what is the relative importance of these factors in regulating stable residue worldwide.

2. Materials and methods

2.1. Data extraction and assembly

We searched the Web of Science (https://www.webofscience.com/wos/woscc/basic-search) for the peer-reviewed decomposition studies reporting the size of stable residue. The keyword "litter decomposition" was first used to search all the published litter decomposition works, and the keywords "stable residue" or "asymptotic" or "multi-pool" or "limit value" were applied to determine the target literature. The "limit value" was employed as a key word, because some relevant studies did not use stable residue size to exhibit the mass remains when decomposition approached a rate of nearly zero, but the limit value was used to show the percentage that the litter has lost at that time. Stable residue size was calculated as1 minus the "limit value" (Hobbie et al., 2012). The reference lists of relevant literature were also carefully scanned to avoid possible omissions.

These studies were then screened and identified manually based on

the following criteria: (1) Experiments were conducted with brown litter or green leaf litter; (2) field incubation that used litter bags or containers were performed; (3) time-series litter mass loss was determined by multiple retrieval of litter bags or containers at intervals of given periods; (4) the stable residue size or limit value was calculated by fitting asymptotic models to decomposition data (e.g., Eqs. (1) and (2)).

$$X = A + (1 - A)e^{-kt} \tag{1}$$

$$L = m(1 - e^{-kt/m}) \tag{2}$$

where X and L are the proportions of the initial mass remaining and lost, respectively, after a time period t of decomposition; k is the initial decomposition rate; and A and m stand for the stable residue and limit value, respectively.

Only stable residue from decomposing litter was considered in this study, and the k values calculated from these models were not regarded. For the data presented graphically in the source papers, we assessed them using the Origin Digitizer Tool (version 9.0; OriginLab, Northampton, MA, USA). There were also observations that appeared more than once in the target literature. For example, many observations reported by Berg and colleagues in their papers [e.g. Berg et al. (1996) and Davey et al. (2007)] were also included in their DELILA II data base (Litter Decomposition website https://149.156.165.8/deco/). The duplicate records were carefully removed, making the same observation that originated from different papers was included only once in our dataset. A list of the data sources can be found in Appendix 1. Finally, 474 observations of stable residue size were obtained and were further divided depending on species functional type (broadleaf species *vs.* coniferous species) or litter senescence degree (brown litter *vs.* green leaf). Study sites were partitioned into three climate zones based on latitude (23.5° < subtropical ≤ 35°, 35°< temperate ≤ 55°, boreal greater than 55°; Shen et al., 2019).

We focused on three categories of factors that might affect the stable residue size, including litter initial traits (e.g., initial concentrations of N, lignin, Mn, and Ca in litters), experimental factors (e.g., mesh size and incubation time), and climate factors [e.g., latitude, altitude, mean annual temperature (MAT), and mean annual precipitation (MAP)]. Some values were missing for these factors, because not all the information was provided in the source papers. For litter bags with varied mesh in the upper and lower side, we refer to mesh size (expressed as mm^2) of the upper side. The collected data for each single calculated stable residue size and the relevant geographical position, climate, methodology, and litter initial traits was listed in Appendix 2. The number of the stable residue size for different biomes, functional types, and litter senescence degrees was listed in Table S1 (Appendix 3).

2.2. Statistical analysis

One-way analysis of variance (ANOVA) was used to test whether stable residue size shows a significant difference between species functional types, litter senescence degrees, and climate zones. The differences in the initial concentrations of N, lignin, Mn, and Ca in litter between broadleaf litter and coniferous litter or brown litter and green leaf were also assessed using one-way ANOVA. Linear regression analyses were used to determine the relationship between stable residue size and litter initial N, lignin, Mn, and Ca concentration, as well as latitude, altitude, MAT, MAP, mesh size, and incubation time. Linear regression analyses were also used to test the relationship between MAT or MAP and litter initial N, lignin, and Mn concentration. Moreover, a boosted regression tree (BRT) was employed to explore the relative influence of the affecting factors mentioned above on stable residue size. All the statistics were performed with the R software (v.4.0.1, R Core Team, 2021).

3. Results

The stable residue size in our dataset spanned a range of 0–68.2% of the initial litter biomass, with an average of 26.2%. The decomposition of broadleaf litters produced marginally significantly ($P = 0.07$) larger stable residues (27.3%) than that of coniferous litters (24.7%) (Fig. 2). Stable residue size showed no significant difference after the decomposition of brown litter and green leaf litter (Fig. 2). Stable residue size in temperate (27.7%) and boreal (25.2%) zones were significantly higher than those in subtropical (19.5%) zones, while no significant difference in stable residue size was found between temperate and boreal zones (Fig. 2).

The initial N and Ca concentrations of broadleaf litter were 58.8% and 65.6% higher (both $P < 0.01$) than those of coniferous litter, respectively (Fig. S1, Appendix 3). The initial lignin concentration of broadleaf litter (237.7 mg g^{-1}) was significantly lower than that of coniferous litter (274.4 mg g^{-1}) (Fig. S1, Appendix 3). The initial concentrations of lignin, Mn, and Ca of brown litter were significantly higher than those of green leaves by 43.0%, 107.7%, and 202.7%, respectively (Fig. S1, Appendix 3). The initial N concentration showed no remarkable difference between brown litter and green leaf litter. Stable residue size was correlated positively with initial concentrations of N ($R^2 = 0.133$; $P < 0.01$) and lignin ($R^2 = 0.124$; $P < 0.01$) in litter (Fig. 3 a and b), but negatively with litter initial Mn concentration ($R^2 = 0.077$; $P < 0.01$) (Fig. 3 c). However, no correlation was observed between the litter initial Ca concentration and stable residue size (Fig. 3 d).

Quadratic correlations were found between stable residue size and latitude or MAT ($R^2 = 0.040$ and 0.042, respectively, and both $P < 0.01$). MAP showed a positive linear correlation with stable residue size ($R^2 = 0.018$; $P < 0.01$) (Fig. 4). Litter initial N concentration ($R^2 = 0.037$; $P < 0.01$) increased and that of litter Mn ($R^2 = 0.018$; $P < 0.05$) decreased linearly with MAP (Fig. S2, Appendix 3). Moreover, there was a marginal significant positive correlation ($R^2 = 0.013$; $P = 0.059$) between litter initial lignin concentration and MAP (Fig. S2, Appendix 3). MAT showed no correlations with litter initial concentrations of N and Mn,

but was correlated significantly and negatively with litter initial lignin concentration ($R^2 = 0.142$; $P < 0.01$) (Fig. S2, Appendix 3). The influence of methodological factors was also considered. Stable residue size showed no relationship with mesh size of litter bags, but was negatively correlated with incubation time ($R^2 = 0.015$; $P < 0.05$) (Fig. 5).

Taking advantage of the BRT model, the respective contributions of the above mentioned factors to explaining the variation in stable residue size were evaluated (Fig. 6). These factors together explained 81.16% of the variation in stable residue size. The relative influence of these factors was in the sequence of litter N (31.7%) > litter lignin (15.6%) > litter Mn (12.7%) > litter Ca (10.5%) > latitude (6.6%) > MAP (6.0%) > incubation time (5.3%) > MAT (4.8%) > altitude (3.6%) > mesh size (3.3%).

4. Discussion

More than 95% of the observations of our dataset showed a stable residue size larger than 0, illustrating that leaf litter generally remains a stable fraction after decomposition (Fig. 2). This stable fraction will add to the SOM, take part in humus buildup in the forest floor, and contribute to OLC accumulation (Berg and Meentemeyer, 2002; Berg, 2014). However, the magnitude of the contribution was highly variable considering the wide range covered by the stable residue size globally (Appendix 2). We found that litter initial traits, climate, and methodology were all associated with the variance in stable residue size. These findings are explained in more depth below.

4.1. Stable residue size as controlled by litter initial traits

Litter initial traits controlled the size of stable residue worldwide, with litter having higher N and lignin concentrations or lower Mn concentration producing larger stable residues during decomposition (Fig. 3 a, b, and c). These results were consistent with previous small-scale findings (Berg and Meentemeyer, 2002; Sun et al., 2019; Virzo De Santo et al., 2009), suggesting the straightforward control of these
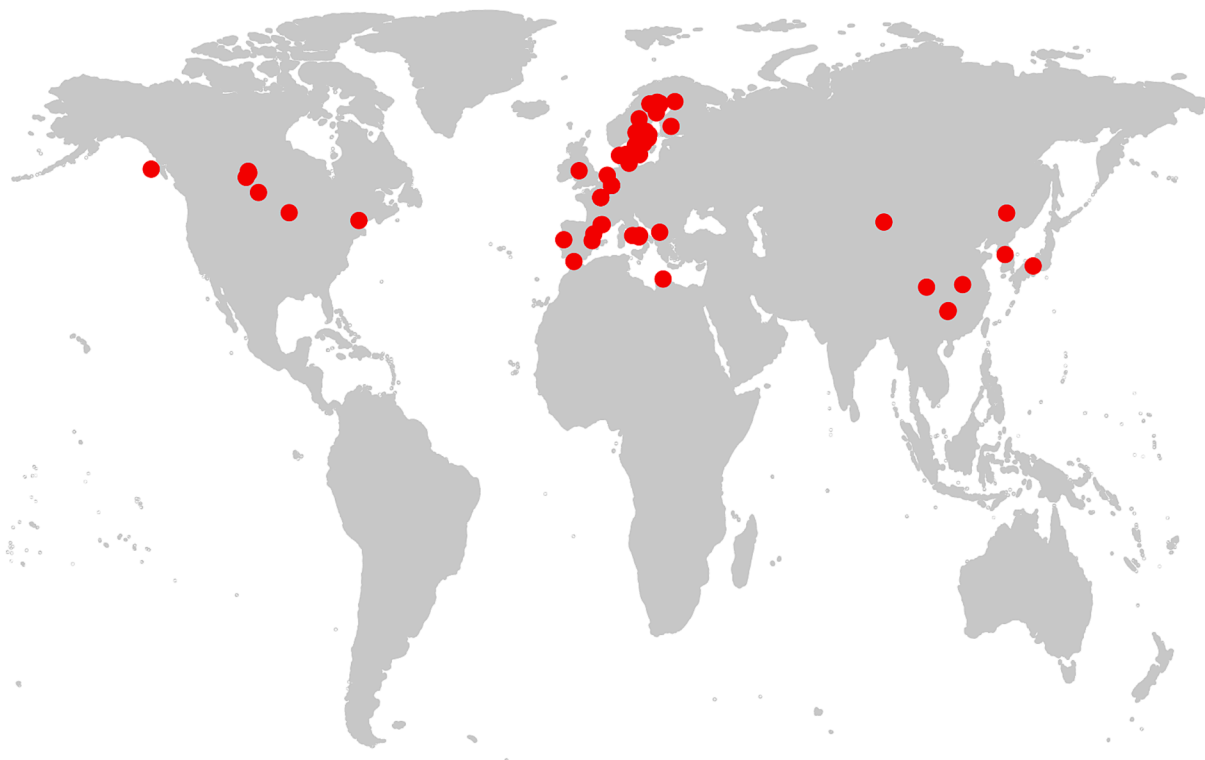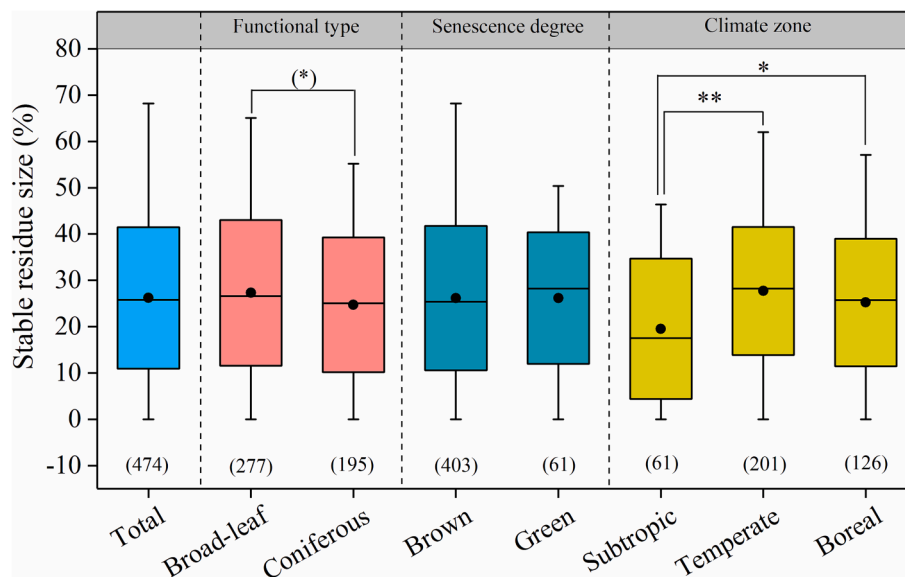

Fig. 1. Distribution of leaf litter decomposition studies that have reported the stable residue size or limit value around the world.

Fig. 2. Comparison of stable residue size after leaf litter decomposition (percentage of initial litter mass) among different functional types, senescence degrees, and climate zones. Number of samples is indicated by the number enclosed in brackets. Significant difference between two columns is represented by (*) ($P < 0.10$), * ($P < 0.05$) or ** ($P < 0.01$).
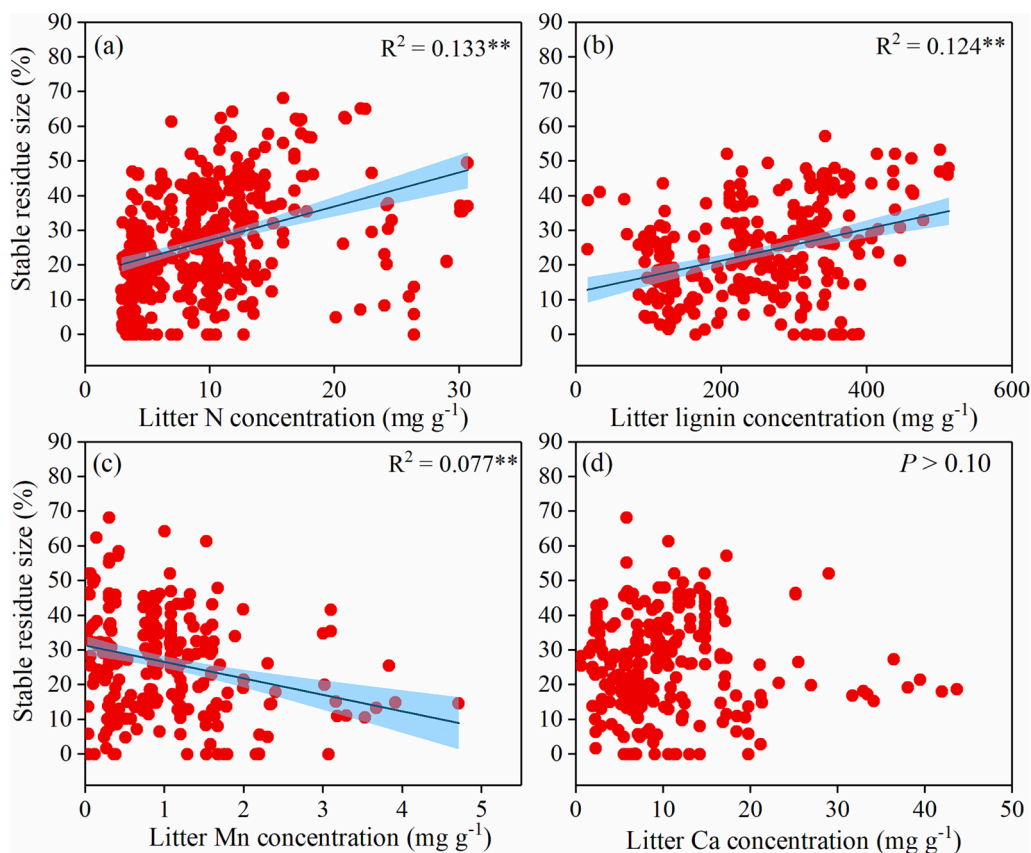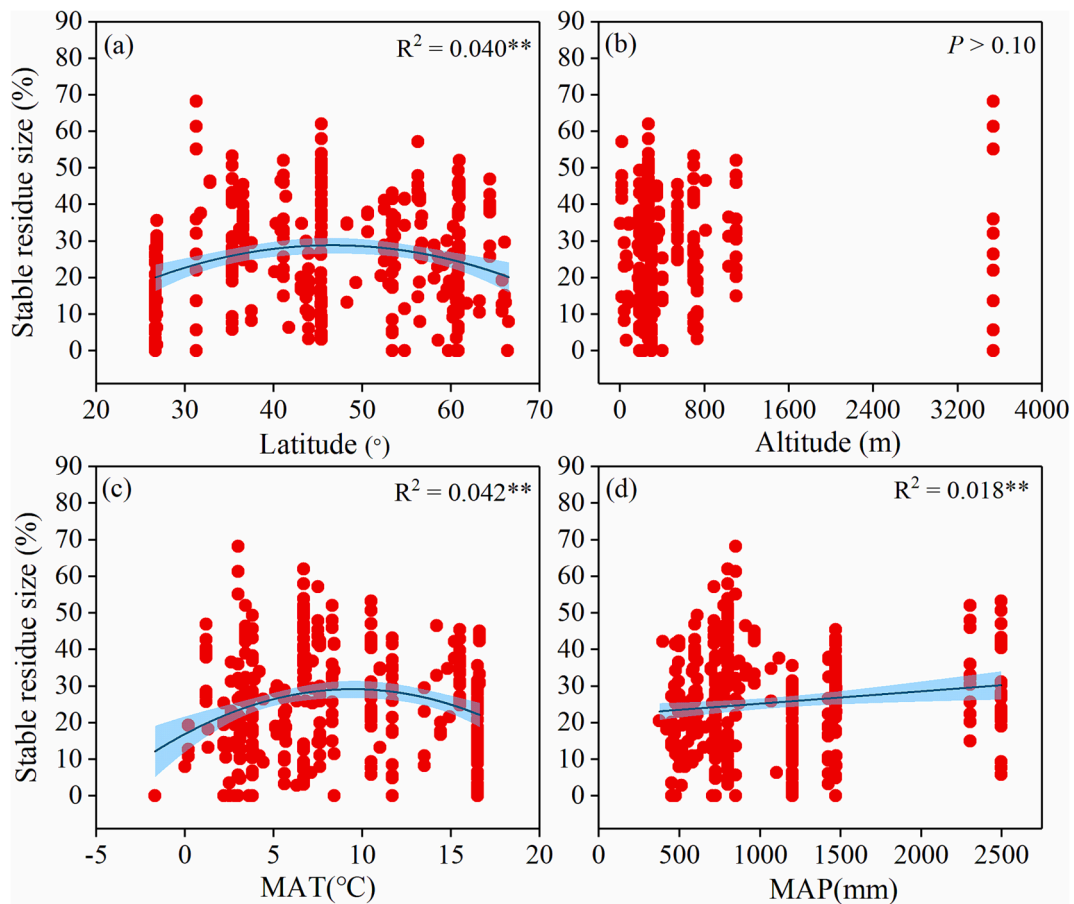

Fig. 3. Relationships between stable residue size and litter initial concentration of nitrogen (a), lignin (b), manganese (c), and calcium (d). The 95% confidence intervals are indicated by the shaded areas. ** $P < 0.01$.

litter traits on stable residue size. Amongst these traits, the initial litter N concentration had the most explanative ability for the variation in stable residue size (Fig. 6). Litter N concentration has been inversely related to the rate of OLC sequestration, because high-N litter decomposes and is lost more rapidly (Finzi et al. 1998; Vesterdal et al. 2008; Mueller et al., 2015). The present study provided evidence of higher litter N

concentration benefiting OLC accumulation, as indicated by the larger stable residues left after decomposition (Fig. 3 a).

Species functional types also accounted for the variation in stable residue size. The stable residue size from decomposing broadleaf litter was over 10% larger than that from decomposing coniferous litter (Fig. 2), possibly because of the higher N concentration in the former

Fig. 4. Relationships among stable residue size and latitude (a), altitude (b), mean annual temperature (c), and mean annual precipitation (d). The 95% confidence intervals are indicated by the shaded areas. ** $P < 0.01$.
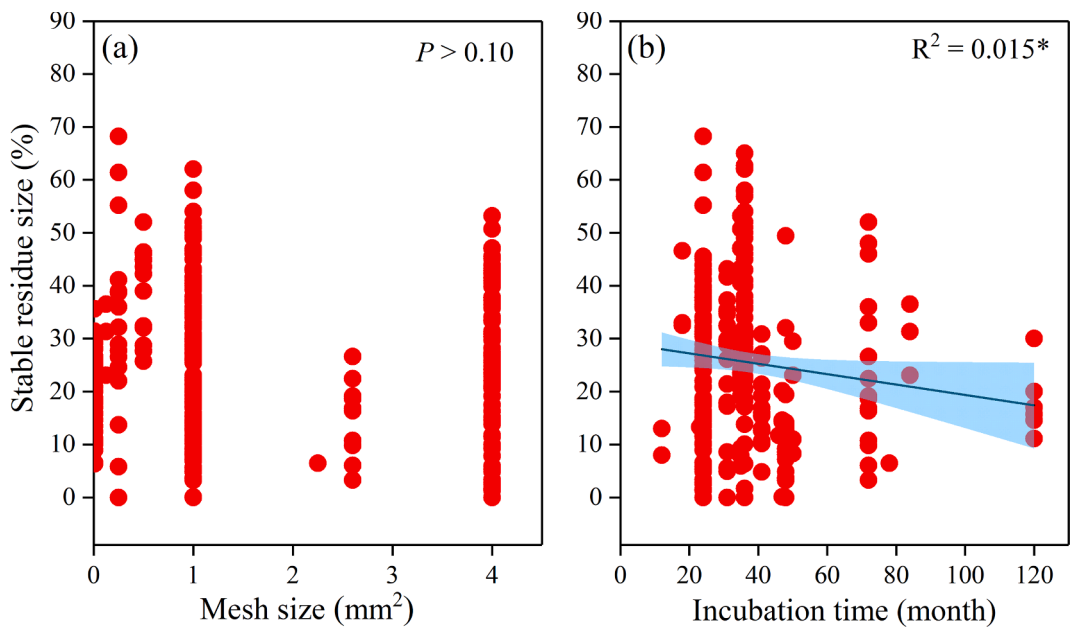
Fig. 5. Relationships between stable residue size and mesh size of the litter bags (a) and incubation time in the field (b). The 95% confidence intervals are indicated by the shaded areas. * $P < 0.05$.

than in the latter (Fig. S1, Appendix 3). This finding was not surprising considering that coniferous species are often characterized by a more conservative life strategy and store fewer nutrients in their foliage than broadleaf ones (Zukswert and Prescott, 2017). Litter inherits a significant part of leaf functional features and should parallel foliage in terms of the nutrient concentration (Freschet et al. 2010; Reich, 2014; Lin
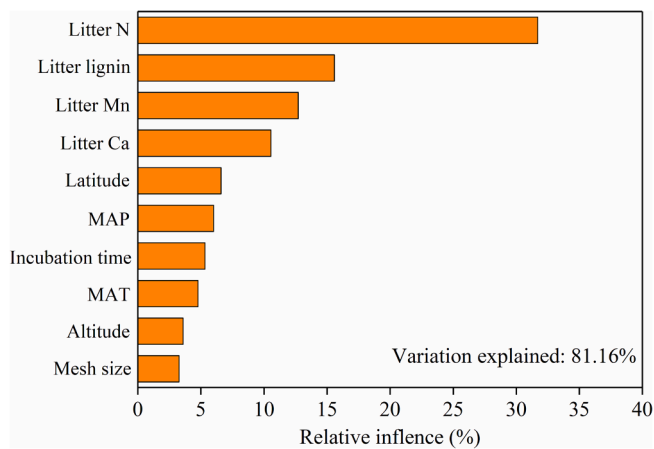
Fig. 6. Relative influence of different predictors in explaining the variation in stable residue size based on the boosted regression tree model. Abbreviations: N, nitrogen; Mn, manganese; Ca, calcium; MAP, mean annual precipitation; MAT, mean annual temperature.

et al., 2020). In this circumstance, forests dominated by broadleaf species might contribute more than those dominated by coniferous species to OLC accumulation. This conclusion makes sense particularly considering that the litterfall in broadleaf forests is larger than that in coniferous forests worldwide (Shen et al., 2019).

Surprisingly, the stable residue size from decomposing green leaf was comparable to that from decomposing brown litter at the global scale (Fig. 1), despite their contrasting initial traits (Fig. S1, Appendix 3). This phenomenon was likely a consequence of the lower lignin and Mn concentrations in green leaves compared with those in brown litter, which might work to counteract the modulation in late-stage decomposition, resulting in an unchanged stable residue size. Determining the stable residue size after green leaf decomposition is important, because ongoing climate change might lead to large abnormal leaf falls before senescence via frequently extreme climate events, such as hurricanes, tropical storms, and freezes (IPCC, 2013; Yang et al., 2014; Li et al., 2021). Our findings thus showed a neutral influence of possibly increased green leaf input on OLC accumulation. Nevertheless, the records of green leaf decomposition are limited at this stage, and it seems that a definitive conclusion is difficult to formulate. Therefore, the effects of abnormally shed litter decomposition on OLC accumulation still requires further attention.

4.2. Climate factors affecting stable residue size

Stable residue size showed a hump-shaped relationship with MAT, resulting in a similar latitudinal trend in stable residue size (Fig. 4 a and c). Temperature has been negatively related to stable residue size previously, owing to its vital thermal role in late stage decomposition (Harmon et al. 2009; Berg et al., 2010 and 2022). Our results that stable residue size in the subtropical zone was lower than that in temperate and boreal zones supported this trend. However, we cannot exclude the possibility that temperature has conveyed part of its influence to the stable residue size via affecting litter initial lignin concentration (Fig. S2, Appendix 3). These findings provided an important explanation for the lower SOM content in low than in high latitude regions (Wang et al. 2018). Interestingly, from temperate zones to colder boreal zones, stable residue size did not increase, but decrease slightly. This phenomenon could be partly attributed to the changed litter trait in boreal regions, which has compensated for the temperature reduction. Most boreal cases were for coniferous litters, the decomposition of which tends to produce fewer stable residues for its lower N concentration as compared with the broadleaf cases, which were mainly from temperate areas (Table S1, Appendix 3).

MAP can also affect stable residue size. In America, Harmon et al. (2009) found that decomposition was more extensive and yielded fewer stable residues in wetter regions, where the decomposers are favored. However, a different scenario was observed in the current study, where litter decomposition in rain-rich areas produced relatively large stable residues compared with that in dry regions (Fig. 4 d), indicating amazing moisture inhibition of late-stage decomposition. The most likely explanation is that the litter trait has acted in linking MAP to stable residue size, because the litter in our dataset responded to increasing MAP with an increased N concentration and a decreased Mn concentration (Fig. S2, Appendix 3). The positive relationship of MAT with litter N concentration was also reported in earlier reviews based on board-scale synthesis (Liu et al., 2006; Yuan and Chen, 2009).

4.3. Influence of litter initial traits vs. Climate

At the global scale, our findings showed that litter initial traits prevail over climate in regulating stable residue size (Fig. 6). Although litter initial traits were climate-dependent to some extent, little of the variation in litter initial traits can be explained by climate (Fig. S2, Appendix 3), indicating a minor indirect influence of climate on the stable residue size. Moreover, the weaker climate dependence of stable residue size could also be a result of the decreased response of decomposition to climate variation and the increased response to litter trait variation in the near-humus stages (Berg and Meentemeyer, 2002). Occurring primarily at the late stage, lignin decomposition was also found to be more explained by litter N concentration than by temperature (Duboc et al., 2014). The reduced response of late stage decomposition to climate variation, in fact, is somewhat unexpected for the following reasons. Climate (i.e., temperature) matters more than litter initial traits in determining early stage decomposition at the broad scale (Aerts, 2006). It is reasonable to expect that temperature remains the major controller of late stage decomposition and of stable residue size, because litter components remaining at late stage (e.g., lignin) are more recalcitrant and their decomposition should have a stronger temperature dependence (Davidson and Janssens, 2006). This inconsistency likely results from the fact that the response of recalcitrant substrates to climate change is confounded by factors other than intrinsic molecular recalcitrance, such as sorptive interactions with soil minerals and the soil water content, weakening the explanative ability of temperature (Kleber, 2010; Duboc et al., 2014).

4.4. How do methodological differences matter?

The mesh size of litter bags, which controls the access of fauna decomposers of different body sizes, might represent contrasting fauna effects on decomposition and confound the relationship between stable residue size and the controlling factors (Li et al., 2022). Despite theoretical and empirical evidence of a positive fauna effect on decomposition (Coq et al., 2010; Frouz, 2018), stable residue size in the present study remained constant as the mesh size varied (Fig. 5 a). This result did not support the view that soil fauna have a general effect on late-stage decomposition and stable residue size, differing greatly from a previous study by Li et al. (2022), who claimed that litter decomposition responded to mesofauna presence with a decrease in stable residue size. This discrepancy can be attributed to the climate-dependent pattern of the fauna effect. The effect of soil fauna on litter decomposition varies depending on the density, diversity, and activity, which are all associated with climate, leading to a greater fauna effect at warmer and wetter climates (Lin et al., 2019; Peña-Peña and Irmler, 2018; Hättenschwiler and Jørgensen, 2010; Meyer et al., 2011). Unlike the study of Li et al. (2022), which was carried out in a subtropical area, most cases included in our synthesis occurred in temperate and boreal regions, where the late-stage decomposition might be weakly shaped by soil fauna because of thermal or hydrological limitation. In supporting our explanation, García-Palacios et al. (2016), who studied temperate forests, also

reported a minor role of soil fauna in regulating C loss during late stage decomposition.

Longer incubation time was associated with a smaller stable residue size in the present study (Fig. 5 b). Therefore, sufficient incubation time that guarantees that decomposition can reach the late stage is essential for a reliable estimation of stable residue size (Berg et al., 2010; Hobbie et al., 2012). In this case, some previous records of stable residue size might have involved the risk of being overestimated because of inadequate incubation time. However, our findings do not necessarily imply a time-taking, long incubation for all studies on stable residue size, because the time needed for the decomposition to reach the late stage depends on litter traits and climate (Berg et al., 2010; Hobbie et al., 2012; Li et al., 2022). The time standard of field incubation that is linked to different litter species and climate zones thus deserves further attention.

5. Conclusion

Taking advantage of available data worldwide, we explored how the stable residue from decomposing leaf litter is modulated by potential factors, as well as their relative importance. Overall, globally stable residue size can be modulated by both litter initial traits and climate. Litter with higher N and lignin concentrations or a lower Mn concentration leaves larger stable residues after decomposition, contributing more to OLC accumulation. Climate also played a role in determining stable residue size; however, the climatic influences can be distorted by litter initial traits. Therefore, litter initial traits have stronger power than climate in predicting the input of litter-derived C to the soil. Soil fauna does not affect stable residue size, challenging the view that soil fauna prevents soil C accumulation by stimulating litter decomposition. Moreover, an inadequate field incubation time can cause bias to the estimation of stable residue size. Collectively, our study provides new insight into the global-scale relationship between leaf litter decomposition and OLC accumulation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.catena.2023.107390.

References

Aerts, R., 2006. The freezer defrosting: global warming and litter decomposition rates in cold biomes. J. Ecol. 94, 713–724.

Berg, B., 2000. Litter decomposition and organic matter turnover in northern forest soils. For. Ecol. Manag. 133, 13–22.

Berg, B., 2014. Decomposition patterns for foliar litter — A theory for influencing factors. Soil Biol. Biochem. 78, 222–232.

Berg, B., 2017. Decomposing litter; limit values; humus accumulation, locally and regionally. Appl. Soil Ecol. 123, 494–508.

Berg, B., Ekbohm, G., Johansson, M.B., McClaugherty, C., Rutigliano, F., Virzo De Santo, A., 1996. Maximum decomposition limits of forest litter types; a synthesis. Can. J. Bot. 74, 659–672.

Berg, B., Matzner, E., 1997. Effect of N deposition of plant litter and soil organic matter in forest ecosystems. Environ. Rev. 5, 1–25.

Berg, B., Meentemeyer, V., 2002. Litter quality in a north European transect versus carbon storage potential. Plant Soil 242, 83–92.

Berg, B., Davey, M.P., De Marco, A., Emmett, B., Faituri, M., Hobbie, S.E., Johansson, M.B., Liu, C., McClaugherty, C., Norell, L., Rutigliano, F.A., Vesterdal, L., Virzo De Santo, A., 2010. Factors influencing limit values for pine needle litter decomposition: a synthesis for boreal and temperate pine forest systems. Biogeochemistry 100, 57–73.

Berg, B., Erhagen, B., Johansson, M.B., Vesterdal, L., Faituri, M., Sanborn, P., Nilsson, M., 2013. Manganese dynamics in decomposing needle and leaf litter — a synthesis. Can. J. For. Res. 43, 1127–1136.

Berg, B., Lönn, M., 2022. Long-term effects of climate and litter chemistry on rates and stable fractions of decomposing Scots pine and Norway spruce needle litter—A synthesis. Forests 13, 125.

Berg, B., McClaugherty, C., 2014. Plant litter: decomposition, humus formation, carbon sequestration. Springer, New York.

Cebrian, J., 1999. Patterns in the fate of production in plant communities. The American Naturalist 154 (4), 449–468.

Coq, S., Souquet, J.M., Meudec, E., Cheynier, V., Hattenschwiler, S., 2010. Interspecific variation in leaf litter tannins drives decomposition in a tropical rain forest of French Guiana. Ecology 91, 2080–2091.

Currie, W.S., Harmon, M.E., Burke, I.C., Hart, C., Parton, J.W., Silver, W., 2010. Cross-biome transplants of plant litter show decomposition models extend to a broader climatic range but lose predictability at the decadal time scale. Glob. Change Biol. 16, 1744–1761.

Davey, M.P., Berg, B., Emmett, B.A., Rowland, P., 2007. Decomposition of oak leaf litter is related to initial litter Mn concentrations. Can. J. Bot. 85, 16–24.

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173.

De Marco, A., Esposito, F., Berg, B., Zarrelli, A., De Santo, A.V., 2018. Litter inhibitory effects on soil microbial biomass, activity, and catabolic diversity in two paired stands of Robinia pseudoacacia L. and Pinus nigra Arn. Forests 9, 766.

Duboc, O., Dignac, M.F., Djukic, I., Zehetner, F., Gerzabek, M.H., Rumpel, C., 2014. Lignin decomposition along an Alpine elevation gradient in relation to physicochemical and soil microbial parameters. Global Change Biol. 20, 2272–2285.

Finzi, A.C., Van Breemen, N., Canham, C.D., 1998. Canopy tree-soil interactions within temperate forests: species effects on soil carbon and nitrogen. Ecol. Appl. 8, 440–446.

Freschet, G.T., Cornelissen, J.H.C., van Logtestijn, R.S.P., Aerts, R., 2010. Substantial nutrient resorption from leaves, stems and roots in a sub-arctic flora: what is the link with other resource economics traits? New Phytol. 186, 879–889.

Frouz, J., 2018. Effects of soil macro- and mesofauna on litter decomposition and soil organic matter stabilization. Geoderma 332, 161–172.

García-Palacios, P., Shaw, E.A., Wall, D.H., Hättenschwiler, S., 2016. Temporal dynamics of biotic and abiotic drivers of litter decomposition. Ecol. Lett. 19, 554–563.

Harmon, M.E., Silver, W.L., Fasth, B., Chen, H., Burce, I.C., Parton, W.J., Hart, S.C., Curric, W.S., 2009. Long-term patterns of mass loss during the decomposition of leaf and fine root litter: an intersite comparison. Glob. Change Biol. 15, 1320–1338.

Hättenschwiler, S., Jørgensen, H.B., 2010. Carbon quality rather than stoichiometry controls litter decomposition in a tropical rain forest. J. Ecol. 98, 754–763.

Hobbie, S.E., Eddy, W.C., Buyarski, C.R., Adair, C.E., Ogdahl, M.L., Weisenhorn, P., 2012. Response of decomposing litter and its microbial community to multiple forms of nitrogen enrichment. Ecol Monogr. 82, 389–405.

IPCC, 2013: Climate change 2013: The physical science basis. In Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change; Cambridge university, USA, 2013.

Keiluweit, M., Nico, P.S., Sarginci, M., Harmon, M., Pett-Ridge, J., Kleber, M. 2013. Is biotic manganese oxidation driving long-term litter decomposition? Oregon State University, Dr Thesis. pp. 96–128 (Chapter 3).

Kleber, M., 2010. What is recalcitrant soil organic matter? Environ. Chem. 7, 320–332.

Li, R.S., Zhang, Y.Z., Yu, D., Wang, Y., Zhao, X.X., Zhang, R.H., Zhang, W.D., Wang, Q.K., Xu, M., Chen, L.C., Wang, S.L., Han, J.M., Yang, Q.P., 2021. The decomposition of green leaf litter is less temperature sensitive than that of senescent leaf litter: An incubation study. Geoderma 381, 114691.

Li, R.S., Yang, Q.P., Guan, X., Chen, L.C., Wang, Q.K., Wang, S.L., Zhang, W.D., 2022. High quality litters with faster initial decomposition produce more stable residue remaining in a subtropical forest ecosystem. Catena 213, 106134.

Lin, D.M., Wang, F., Fanin, N., Pang, M., Dou, P.P., Wang, H.J., Qian, S.H., Zhao, L., Yang, Y.C., Mi, X.C., Ma, K.P., 2019. Soil fauna promote litter decomposition but do not alter the relationship between leaf economics spectrum and litter decomposability. Soil Biol. Biochem. 136, 107519.

Lin, D.M., Yang, S.F., Dou, P.P., Wang, H.J., Wang, F., Qian, S.H., Yang, G.R., Zhao, L., Yang, Y.C., Fanin, N., 2020. A plant economics spectrum of litter decomposition among coexisting fern species in a subtropical forest. Ann. Bot-London 125, 145–155.

Liu, C.J., Berg, B., Kutsch, W., Westman, C.J., Ilvesniemi, H., Shen, X.H., Shen, G.R., Chen, X.B., 2006. Leaf litter nitrogen concentration as related to climatic factors in Eurasian forests. Global Ecol. Biogeogr. 15, 438–444.

Lovett, G.M., Arthur, M.A., Crowley, K.F., 2016. Effects of calcium on the rate and extent of litter decomposition in a northern hardwood forest. Ecosystems 19, 87–97.

Meyer, W.M., Ostertag, R., Cowie, R.H., 2011. Macro-invertebrates accelerate litter decomposition and nutrient release in a Hawaiian rainforest. Soil Biol. Biochem. 43, 206–211.

Mueller, K.E., Hobbie, S.E., Chorover, J., et al., 2015. Effects of litter traits, soil biota, and soil chemistry on soil carbon stocks at a common garden with 14 tree species. Biogeochemistry 123, 313–327.

Olson, J.S., 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44, 322–331.

Osono, T., Takeda, H., 2005. Limit values for decomposition and convergence process of lignocellulose fraction in decomposing leaf litter of 14 tree species in a cool temperate forest. Ecol Res. 20, 51–58.

Peña-Peña, K., Irmler, U., 2018. Nitrogen and carbon losses from decomposing litter in natural and agroecosystems of two different climate regions of Brazil. Eur. J. Soil Biol. 86, 26–33.

Reich, P.B., 2014. The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. J. Ecol. 102, 275–301.

Riggs, C.E., Hobbie, S.E., Cavender-Bares, J., Savage, J.A., Wei, X., 2015. Contrasting effects of plant species traits and moisture on the decomposition of multiple litter fractions. Oecologia 179, 573–584.

Shen, G.R., Chen, D.M., Wu, Y., Liu, L., Liu, C.J., 2019. Spatial patterns and estimates of global forest litterfall. Ecosphere 10, e02587.

Sun, T., Cui, Y.L., Berg, B., Zhang, Q.Q., Dong, L.L., Wu, Z.J., Zhang, L.L., 2019. A test of manganese effects on decomposition in forest and cropland sites. Soil Biol. Biochem. 129, 178–183.

Vesterdal, L., Schmidt, I.K., Callesen, I., et al., 2008. Carbon and nitrogen in forest floor and mineral soil under six common European tree species. For. Ecol. Manag. 255, 35–48.

Virzo De Santo, A., De Marco, A., Fierro, A., Berg, B., Rutigliano, F.A., 2009. Factors regulating litter mass loss and lignin degradation in late decomposition stages. Plant Soil 318, 217–228.

Wang, Q.K., Liu, S.E., Tian, P., 2018. Carbon quality and soil microbial property control the latitudinal pattern in temperature sensitivity of soil microbial respiration across Chinese forest ecosystems. Global Change Biol. 24, 2841–2849.

Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Puttern, W.H., Wall, D. H., 2004. Ecological linkages between aboveground and belowground biota. Science 304, 1629–1633.

Yang, Q.P., Xu, M., Chi, Y.G., Zheng, Y.P., Shen, R.C., Wang, S.L., 2014. Effects of freeze damage on litter production, quality and decomposition in a loblolly pine forest in central China. Plant Soil 374, 449–458.

Yang, Q.P., Li, R.S., Zhang, W.D., Zheng, W.H., Wang, Q.K., Chen, L.C., Guan, X., Xu, M., Wang, S.L., 2018. Decomposition of harvest residue needles of different needle ages in a Chinese fir (*Cunninghamia lanceolata*) plantation. Plant Soil 423, 273–284.

Yuan, Z.Y., Chen, H.Y.H., 2009. Global trends in senesced-leaf nitrogen and phosphorus. Global Ecol. Biogeogr. 18, 532–542.

Zukswert, J.M., Prescott, C.E., 2017. Relationships among leaf functional traits, litter traits, and mass loss during early phases of leaf litter decomposition in 12 woody plant species. Oecologia 185, 305–316.