Soil Biology and Biochemistry 204 (2025) 109751

Contents lists available at ScienceDirect

Soil Biology and Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Time-varying associations between absorptive fine roots and leaf litter decomposition across 23 plant species

Lili Dong [a,b,*], Björn Berg [c], Yiqi Luo [d], Hongtao Zou [b], Tao Sun [a]

[a] CAS Key Laboratory of Forest Ecology and Silviculture, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, 110016, China
[b] College of Land and Environment, Shenyang Agricultural University, Shenyang, 110866, China
[c] Departments of Forest Sciences, University of Helsinki, Helsinki, 00014, Finland
[d] School of Integrative Plant Science, Cornell University, Ithaca, NY, USA

ARTICLE INFO

Keywords:
Decomposition
Carbon cycling
Absorptive fine roots
Leaf litter
Soil carbon
Biogeochemical models

ABSTRACT

Litter decomposition is the first step for soil organic matter (SOM) formation. By transferring carbon, nutrients and energy from plant to soil, litter decomposition maintains soil fertility and soil health in terrestrial ecosystems. The dominant factors regulating leaf litter and fine root decomposition rates affect how plant biomass is decomposed into new products (such as CO2), contribution to the basic scientific research and beyond, into the realms of land management and global change policy. Litter chemistry, such as the high nitrogen (N) concentration in recently senesced tissues, is related to higher rates of leaf litter decomposition. However, it is unclear whether long-term decomposition of fine roots is coordinated with leaf litter decomposition, based on the initial chemical traits of these tissues. Here we followed the decomposition of leaf litter and absorptive fine roots (the distal three root-branch orders) across 23 species over five years in a temperate grassland. We found that decomposition rates of absorptive fine roots were significantly correlated with those of leaf litter in the initial stage, across grassland species. However, this tight coordination between leaf litter and fine root decomposition diverged with time. Absence of correlation between leaf and fine root decomposition in later stages of decomposition arose partly because of dissimilar tissue chemistry of absorptive fine roots and leaf litter, and partly because of the different driving factors for decomposition of absorptive fine roots and leaf litter. Our results suggest that the chemical traits could predict the fate of fine roots vs. leaf litter in the early stage of decomposition but may be not valid during the later decomposition stage or for explaining the trajectory of long-term decomposition, when the accumulated recalcitrant compounds were more influential in the decomposition process.

1. Introduction

Plant litter is a dominant source of soil humus and organic matter. Decomposition of plant litter is the first step in the formation of soil organic matter (SOM) and thus a critical process influencing soil fertility and soil health (Cotrufo et al., 2015; Lehmann et al., 2020). Several studies have emphasized litter chemistry as the dominant factor to drive litter decomposition, both at local and regional scales (Minerovic et al., 2018; Jackrel et al., 2019; Berg and McClaugherty, 2020). A meta-analysis has demonstrated that functional traits such as concentrations of nitrogen (N), lignin (acid-unhydrolyzable residue–AUR) and other indices of litter chemistry may explain large variation in leaf litter decomposition rates among tree species (Cornwell et al., 2008; Zhang et al., 2024). Also, driving factors may change from an early, carbohydrate-regulated stage to the lignin-dominated one, the latter often encompassing the main part of litter tissues (*e.g.* Berg and McClaugherty, 2020). Whether the relative decomposability of different tissue types (*e.g.* leaf litter or fine roots) represent the whole plant still is not clear. Further, we still do not know if the same chemical traits predict decomposition rates across herbaceous species.

Plant chemistry has been related to ecological processes on the ecosystem level and allows us to elaborate how their effects differ among plant species as regards the process of litter decomposition (Reich et al., 2003; Lin et al., 2020). 'Plant Economics Spectrum' (PES), which reflects

This article is part of a special issue entitled: SOM 2024 conference published in Soil Biology and Biochemistry.

* Corresponding author. College of Land and Environment, Shenyang Agricultural University, Shenyang, 110866, China.
E-mail address: donglili329@163.com (L. Dong).

https://doi.org/10.1016/j.soilbio.2025.109751
Received 21 November 2024; Received in revised form 12 February 2025; Accepted 15 February 2025
Available online 18 February 2025

cost-benefit tradeoff in resource acquisition, provides a useful framework for examining the relationship between plant tissue chemistry and litter decomposition, especially between the chemical resistance spectrum and litter decomposition (Reich, 2014; Burton et al., 2020). The PES is based on the well-supported theory that plants have a plant specific, e.g. fast or slow, investment strategy in carbon and nutrient elements' cycling and other ecological processes. For example, this theory argues that 'fast' species with high N and phosphorus (P) have 'fast' leaves, 'fast' roots and 'fast' decomposition, whereas 'slow' species with high AUR have 'slow' leaves, 'slow' roots and 'slow' decomposition (Freschet et al., 2012; Reich, 2014). Thus, chemical properties such as high or low concentrations of N, P or AUR should be correlated among plant species or tissue types (Wright et al., 2004). The 'Root Economics Spectrum' (RES) for fine roots across herbaceous and dwarf shrub species has high-lighted the existence of a strong covariation among elements and chemical compounds such as water-solubles and N, as well as ratios, such as C:N, AUR:N, influencing root decomposition rates (Roumet et al., 2016). Therefore, understanding the relationships between above- and belowground chemical traits would be important for understanding the strength of an effect of species on decomposition rate and thus their relative contributions to SOM formation.

In the present study, we used the absorptive fine roots, defined as the first three distal branch orders, hereafter called 'fine roots' (Sun and Mao, 2011; McCormack et al., 2014; Dong et al., 2020) to investigate if the correlations among elements and chemical compounds between leaf litter and fine roots should support observed differences in decomposition rates among species; whether decomposition patterns and rates of leaf litter and fine roots of herbaceous plants follow the same prediction as that given for tree species within this framework.

Short-term studies in most terrestrial environments normally do not reveal any dynamics in the later stages of decomposition (Berg and McClaugherty, 2008; Harmon et al., 2009). Most studies that have correlated litter decomposition rates for below- and above-ground rela-tionships have focused on the early decomposition stage, normally less than 40–50% accumulated mass loss, a level often reached after less than two years' decomposition. The results from such studies have been either positive (Wang et al., 2010; Birouste et al., 2012; Freschet et al., 2012), or have had none or just a weak correlation (Hobbie et al., 2010; Ma et al., 2016). A basic question to ask before initiating such a study is what we mean with the concept decomposition rate, how it should be calculated, over what time period and up to what decomposition level. Some recent long-term studies have found that the conventional single exponential model often overestimates long-term decay rates because of leaching or a higher rate in the early stage (Berg, 2014; Trevathan-Tackett et al., 2020; Adams and Neumann, 2024).

The decomposition rates in the early stage are dominated by decomposition of easily degradable carbohydrates and in the late stage by the degradation of AUR, requiring different populations of microorganisms and other sets of enzymes (Dong et al., 2020, 2022). Also, the regulation of enzyme activity may depend on concentrations of specific elements. For example, manganese (Mn) is an important element to promote the synthesis of manganese peroxidase, playing a crucial role in degradation of lignin in the late, lignin-dominated stage (Berg and McClaugherty, 2020; Zhang et al., 2024). N has a strong positive effect (Melillo et al., 1982) and its role is inverted in late as compared to the early stage partly due to N inhibits ligninase synthesis and reacting with lignin residues to form stable compounds, or partly because N accelerates the accumulation of microbial necromass to cover the residue and be difficult to decompose (Sun et al., 2024). Our objective was to assess how the relationship between decomposition rates of fine roots and leaf litter changes over the very early and the entire decomposition process and identify the chemical compounds and elements controlling decomposition rates of fine roots vs. leaf litter at the very early and the entire decomposition stages. Further, we have aimed at evaluating the potential contributions of decomposing leaf litter and fine roots on SOM formation.

To this purpose we made a five-year decomposition study covering absorptive fine roots and leaf litter of 23 species, encompassing mostly herbaceous and dwarf shrub species in a temperate steppe (Inner Mongolia, China) and calculated decomposition rates using two negative exponential decomposition models and an asymptotic model. We also measured 16 initial litter chemical traits, which previously have been shown to influence litter decomposition rates at different stages. Based on the predictions of 'Whole-Plant Economics Spectrum' theories, we tested three hypotheses on the correlations between decomposition rates of fine roots and leaf litter: (i) that initial chemical traits should be correlated between fine roots and leaf litter across species; (ii) that decomposition rates should be correlated between fine roots and leaf litter, namely species with high decomposition rates for leaf litter should have high decomposition rates for fine roots, and species with low decomposition rates for leaf litter should have low rates for fine roots; (iii) decomposition rates of fine roots and leaf litter would be driven by similar chemical traits in either initial or the entire long-term decomposition.

2. Materials and methods

2.1. Site description

The study site is located in the Erguna River Basin, in northeastern Inner Mongolia in China (50°10′46.1″N; 119°22′56.4″E), on a relatively flat land with the most typical loamic haplic chernozem soil. Mean annual precipitation (MAP) is 360 mm, of which more than 70% falls during the growing season from June to August and mean annual temperature (MAT) is −2.4 °C (1957–2019). The site is located in the research area of Erguna Research Station at an experimental site that has been fenced since 2013 to prevent grazing. More information about the site can be found in Dong et al. (2019, 2020). Six randomized blocks (10 m × 10 m), with a distance of at least 5 m between each one, were selected for the litter decomposition study.

2.2. Collection of fine roots and leaf litter

Absorptive fine roots and leaf litter were collected when they turned to be withered and senescent from a long-term experimental site in a temperate steppe. In short, fine root and leaf litter samples were taken from 23 species at the site and sorted into four functional groups encompassing five grasses, nine forbs, five legumes and four dwarf-shrub species (woody plants) (Table 1). The senescent leaf litter of the 23 species was manually collected from the grassland site in September 2015. After removing the petioles and cutting samples into <3-cm long pieces, 8.0 g of oven-dried (65 °C × 48 h) leaf litter of each species was placed in each nylon-net bag (litterbag) measuring 15 cm × 10 cm with a mesh size of 40 μm, which allows microbial decomposers to enter the litterbags but prevents litter fragments from falling out.

Firstly, we found the target species through the above-ground canopy, then we anchored the linking target specie root. The fresh roots of 23 species were collected from the locked soil blocks using a custom-made trowel. Secondly, the soil was carefully removed from the block to get the intact root branching systems, which were washed in tap water to allow us to distinguish and pick the distal absorptive fine roots. Finally, the roots were air-dried. The first three distal branch-order roots of each species were combined and classified as absorptive fine roots, from now and onwards called fine roots. To determine the moisture of the air-dried litter and fine roots we dried subsamples at 65° for 48 h to constant mass. Then, 4.0 g of the fine roots were placed in each nylon-net bag, measuring 10 × 5 cm, with a 40 μm mesh size.

2.3. Experimental design, decomposition study and sampling of litterbags

In late September 2015, we placed litterbags per litter type (fine roots and leaf litter from 23 species) in each block for nine successive

Table 1
Taxonomic list of the 23 grassland species used in this study.

Species	Genus	Family	C_3/C_4	Abbreviation	Functional Group
Leymus chinensis	*Leymus*	*Gramineae*	C_3	*L.c.*	Grasses
Stipa baicalensis	*Stipa*	*Gramineae*	C_3	*S.b.*	Grasses
Cleistogenes squarrosa	*Cleistogenes*	*Gramineae*	C_4	*C.s.*	Grasses
Achnatherum sibiricum	*Achnatherum*	*Gramineae*	C_3	*A.s.*	Grasses
Koeleria macrantha	*Koeleria*	*Gramineae*	C_3	*K.m.*	Grasses
Carex duriuscula	*Carex*	*Cyperaceae*	C_3	*C.d.*	Forbs
Carex pediformis	*Carex*	*Cyperaceae*	C_4	*C.p.*	Forbs
Allium tenuissimum	*Allium*	*Liliaceae*	C_3	*A.t.*	Forbs
Allium mongolicum	*Allium*	*Liliaceae*	C_4	*A.m.*	Forbs
Polygonum divaricatum	*Polygonum*	*Polygonaceae*	C_3	*P.d.*	Forbs
Dysphania aristata	*Dysphania*	*Amaranthaceae*	C_4	*D.a.*	Forbs
Klasea centauroides	*Klasea*	*Compositae*	C_3	*K.c.*	Forbs
Thalictrum squarrosum	*Thalictrum*	*Ranunculaceae*	C_3	*T.s.*	Forbs
Pulsatilla turczaninovii	*Pulsatilla*	*Ranunculaceae*	C_3	*P.t.*	Forbs
Thermopsis lanceolata	*Thermopsis*	*Leguminosae*	C_4	*T.l.*	Legumes
Vicia sepium	*Vicia*	*Leguminosae*	C_3	*V.s.*	Legumes
Medicago ruthenica	*Medicago*	*Leguminosae*	C_3	*M.r.*	Legumes
Medicago falcata	*Medicago*	*Leguminosae*	C_3	*M.f.*	Legumes
Lespedeza bicolor	*Lespedeza*	*Leguminosae*	C_3	*L.b.*	Legumes
Artemisia dracunculus	*Artemisia*	*Compositae*	C_4	*A.d.*	Woody
Artemisia frigida	*Artemisia*	*Compositae*	C_3	*A.f.*	Woody
Potentilla bifurca	*Rosaceae*	*Rosales*	C_3	*P.b.*	Woody
Kochia prostrata	*Kochia*	*Amaranthaceae*	C_4	*K.p.*	Woody

samplings during the five years of decomposition, resulting in a total of 2484 litterbags (six blocks × 23 species × two litter types × nine samplings). Leaf litterbags were fastened on the ground using pegs after removing all grass. Root litterbags were buried in the soil at a depth of 10 cm.

At each sampling, litterbags of both leaf litter and fine roots for each species were retrieved from the six blocks, with two samplings (May and September) for the first four years (from 2016 to 2019), and one sampling in September in the following year 2020. After sampling, the litter samples were air-dried before removal of mineral soil particles and debris, then oven-dried at 65 °C for 48 h. The residual mass was weighed individually for each litterbag. Ash was determined by combustion in a muffle furnace at 550 °C for 4 h for each litter type and sampling. Ash contents (mean of 2.6%) was subtracted from the remaining litter mass and we have used ash-free organic matter in the calculations.

The remaining mass (%) at each sampling (M_r) was divided by the initial mass (M_i) giving us ($M_r/M_i \times 100$). Litter mass loss (%) was calculated as (M_i - M_r)/$M_i \times 100$.

2.4. Chemical analysis

Subsamples of pre-decomposed leaf litter and fine roots from 23species were ground with a ball mill to obtain a uniform particle size for all the following chemical analysis.

Initial total C and N concentrations were determined by combustion using an elemental analyzer (Vario Microcube Analyzer; Elementar Analysensysteme GmbH, Germany). Initial total P, potassium (K), calcium (Ca), magnesium (Mg) and manganese (Mn) were measured using an ICP analyzer (Elan DRC-e; PerkinElmer, Norwalk, CT, USA), following digestion in HF and $HClO_4$.

Some carbon compounds were analyzed including non-structural carbohydrates (NSC, mainly simple sugars and soluble starch), neutral detergent solubles (NDS, mainly wax, amino acids, protein and lipids) (Van Soest, 1963, 1967), cellulose and hemicellulose (the acid-hydrolyzable fraction, AHF), acid-unhydrolyzable residue (AUR, mainly lignin). NDS, cellulose, hemicellulose and AUR contents were analyzed using the fiber analysis method of Van Soest (1963, 1967) using different solvent elutions on an ANKOM 2000i fiber analyzer (ANKOM Technology, Macedon NY, USA). NSC was extracted in a sequence of extractions in 80% ethanol solution for soluble sugars, followed by 9.2 mol/L $HClO_4$ for detection of starch, both sugar and starch were measured by anthrone-H_2SO_4 colorimetry. The sum of sugars and starch were calculated as NSC contents.

Some secondary metabolites (Sun et al., 2018) including total phenols, condensed tannin (CT), and total alkaloids (TA) were also detected in this research, because which have been proven to inhibit decomposition due to thei bitter taste and complex molecular structures (Northup et al., 1998). Total phenols (TPH) contents were determined colorimetrically using the Folin-Ciocalteau reagent following the technique of Marigo (1973). The contents of condensed tannins and total alkaloids was analyzed using commercial chemical assay kits (Comin Biotechnology Co., Ltd. Suzhou, China) according to the acid-butanol method and acid-dye colorimetry, respectively (Waterman and Mole, 1994; Coq et al., 2010).

2.5. Decomposition model selection

Decomposition rates are generally calculated based on the negative exponential decomposition equation (Olson, 1963). Sometimes the single exponential model is inappropriate, especially for long-term decomposition data (Minderman, 1968; Wieder and Lang, 1982) and a double exponential equation is more realistic (e.g. Lousier and Parkinson, 1976). When decomposition appears not to proceed beyond a certain point, an asymptotic model sometimes provides a better fit (Sridhar et al., 2002; Wieder and Lang, 1982). We calculated the decomposition rates by fitting the proportion of remaining mass over time to three negative exponential decomposition models (Hobbie, 2008):

single exponential

$$\text{model}, X_t \Big/ X_0 = e_s^{-kt} \quad \text{(Eq. 1)}$$

double exponential

$$\text{model}, X_t \Big/ X_0 = C\, e_1^{-kt} + (1 - C)\, e_2^{-kt} \quad \text{(Eq. 2)}$$

asymptotic decomposition

$$\text{model}, X_t \Big/ X_0 = A + (1 - A)\, e_a^{-kt} \quad \text{(Eq. 3)}$$

where X_t is the remaining amount of the initial mass X_0 remaining at time t (year), and k_s is the decay constant in the single-exponential model. In the double exponential model, C is the fraction of the initial mass that decomposes with decomposition rate k_1, while the remaining fraction (1-C) decomposes with decomposition rate k_2. In the asymptotic

model, A is the calculated fraction of remaining mass when decomposition rate is zero in the late stage of decomposition, while (1 - A) is the mass fraction that decomposes at a measurable rate and k_a is the rate at time zero. Note that models (1) and (2) are constrained so the initial mass at time zero becomes 1.

We fit all the data collacting from 9 samplings likein 6 blocks (replication) across 23 species to the models, just as fitting each individual decomposition curve per species to each model. In addition to the coefficient of determination (R^2) in fitting data, we used Akaike's information criterion (AIC) and Akaike weights (w_r) to compare different decomposition models across species. The model with the lowest AIC value has the best support in the data and is closest to the unknown truth (Burnham and Anderson, 2002). To compare three models across 23 grassland species, Akaike weights (w_r) were calculated as:

$$w_r = \frac{e^{\frac{-\Delta AIC_r}{2}}}{\sum_{r=1}^{R} e^{\frac{-\Delta AIC_r}{2}}} \quad \text{(Eq. 4)}$$

ΔAIC = AIC of each model – the lowest AIC of the model, which is the difference in AIC values between a model r and the best model with the lowest AIC value, and R is the number of models being compared (here $R = 3$). The Akaike weight (w_r, $w_1+w_2+w_3 = 1$) of model r can be interpreted as the probability that model r is the best model of all three candidate models given the data set used for model testing. The model with higher w_r is better in explaining data than the other candidate models (Table S1, Supporting information). If the w_r in any case was not significant difference among the candidate models (6 replication per species for each model), we conclude that the models were indistinguishable in their abilities to describe the decomposition data.

For all species (n = 23) the Akaike weights (w_r) calculated by the AIC criterion showed that the single exponential, double exponential and asymptotic models had on average 22, 13 and 65% probability, respectively, of being the best-fit model for our leaf litter-data; for fine roots we obtained the probability of 9, 21 and 70%, respectively, for the models (Table S1). This suggest that the asymptotic model (Eq. (3)) was the most suitable one for our data set.

2.6. Statistical analysis

The asymptotic decomposition model had lower AIC and hence higher w_r than the single exponential model in nearly all cases, and was equally good as the double exponential model in most cases but had less parameters (Table S1). In the present study, we selected the asymptotic decomposition model to estimate decomposition rate k_a and the asymptotic value A for the data analyses. We used results from the asymptotic model: (i) to determine whether leaf litter and fine root decomposition rates were correlated across grassland species using Pearson's regression analysis (n = 23); (ii) to determine which chemical traits that influence above-*versus* below-ground decomposition, we compared both k_a and the asymptote (A) of leaf litter and fine roots to their initial chemical traits using linear regressions. Furthermore, correlations between fine roots and leaf litter chemical traits were analyzed by busing multiple stepwise regressions (n = 23); (iii) to analyze the interspecific variation in decomposition rates of leaf litter and fine roots across species using one-way analysis of variance (ANOVA). We ran Non-metric Multi Dimensional Scaling (NMDS) analysis for the sixteen chemical litter traits to visualize the variation in litter quality among different species. Here the litter with more NSC, NDS, and other labile-C compounds are defined as high quality, with more cellulose and polyphenols (e.g. lignin, tannin and their degradation products) and other recalcitrant C compounds are considered as low quality. In NMDS, the projection direction of different spots (species) and rays (sixteen chemical traits) on the X- or Y-axis represent the strength of the variable in driving the spatial distribution and would reflect the correlation of chemical traits between leaf litter and fine root. Statistically significant differences were set with P values < 0.05. Most analyses were performed using SPSS 19.0 for Windows (SPSS Inc., Chicago, IL, USA). NMDS statistical analyses were performed with the open-source statistical environment 'R', version 3.5.1 (R Development Core Team, 2018) using the package vegan.

3. Results

3.1. Initial tissue chemistry of leaf litter and fine roots

Initial chemical composition differed considerably among species and between the main groups of leaf litter and fine roots (Table S2). Initial concentrations of the nutrients N, P, K, Ca, Mg and the compounds total phenols (TP), condensed tannins (CT), and total alkaloids (TA), neutral detergent solubles (NDS, mainly wax, amino acids, protein and lipids) were significantly lower in fine roots than in leaf litter for most of the species (P at least <0.05), except for P in the subgroup legumes and Ca and Mg in the subgroup grasses, which had much higher concentrations in fine roots than in leaf litter (Table S2). There was no difference in P concentrations within the legumes' group and none for cellulose and hemicellulose in the grasses' group. Also, concentrations of Mn and AUR were significantly higher in fine roots than in leaf litter (n = 23, P at least <0.05) (Table S2).

As regards average concentrations, those for non-structural carbohydrates (NSC, mainly simple sugars and soluble starch) for all grasses (five species) and forbs (nine species) were significantly lower in fine roots than in the corresponding leaf litter ((Table S2, $P < 0.05$), while for legumes and woody plants (dwarf shrubs) there was a large variation in NSC concentrations among the fine roots and leaf litter.

Seven out of the 16 chemical traits, namely concentrations of N, Ca, K, NDS, NSC, hemicellulose and condensed tannins were positively and significantly correlated between fine roots and leaf litter (Table 2, $P < 0.05$), with the correlation coefficients ranging from 0.462 for condensed tannin to 0.808 for hemicellulose (Table 2, $P < 0.001$).

3.2. General decomposition patterns for leaf litter and fine roots

Leaf litter and fine roots showed similar general patterns for remaining mass with time (Fig. 1). Both the groups of combined litter showed a tendency for the remaining mass to approach an asymptote with time – with a tendency to more mass loss for leaf litter. The average cumulative mass loss in the first three years of incubation reached about 72% for leaf litter and about 65% for fine roots. After five years, the average cumulative mass loss for all leaf litter was about 83%, leaving 17% of the litter as remaining mass. For fine roots the average cumulative mass loss was 72%, leaving 28% as remaining mass. The average calculated asymptote based on remaining mass was 15.7% for leaf litter and 20.4% for fine roots.

The four functional species showed differences in average cumulative mass loss. After five years, the cumulative mass loss for leaf litters averaged 83, 80, 82 and 68 %, respectively, for grasses, forbs, legumes and woody shrubs and for fine roots 62, 77, 70 and 57%, respectively (Fig. S1). The average leaf litter asymptotes for the functional groups, namely grasses, forbs, legumes and woody plants, were 11, 17, 18 and 17%, respectively, and for fine roots the values were 15, 21, 23 and 26%, respectively (Fig. 5, shown as the A value). Across functional groups, the average cumulative mass loss was significantly higher for most leaf litter than for fine roots throughout the five years of decomposition ($P < 0.01$; Fig. S1). Woody shrubs lost mass significantly slower than the other groups both for leaf litter and fine roots ($P < 0.01$; Fig. S1).

3.3. Leaf litter and fine roots – decomposition relationships

We have used the asymptotic model to explore the relationships for k_a and asymptote for both leaf litter and fine roots. For species and groups, the asymptotic model gave initially high mass-loss rates with k_a

Table 2
Initial tissue chemistry by functional groups for fine roots and leaf litter and their correlations coefficient across 23 grassland species (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$). Note: NSC, non-structural carbohydrates (lowmolecular sugars and starch); NDS, neutral detergent solubles, including NSC; AHF, the acid-hydrolyzable fraction, sum of cellulose and hemicellulose; AUR, the acid-unhydrolyzable residue; TPH, total phenols; CT, condensed tannin; TA, total alkaloids.

Chemical traits	Leaf litter				Mean (n = 23)	Fine roots				Mean (n = 23)	Correlations
	Grasses	Forbs	Legumes	Woody		Grasses	Forbs	Legumes	Woody		R^2 (n = 23)
Nutrients (mg/g) and some ratios											
C:N	20.79	20.28	15.12	17.43	19.09	41.39	39.8	18.99	33.74	35.44	**0.511***
AUR:N	1.42	2.04	2.02	3.42	2.01	22.20	13.69	4.75	12.27	13.88	0.186
N (%)	2.09	2.26	3.19	2.59	2.42	0.98	1.12	2.43	1.42	1.38	**0.703*****
P	1.68	2.25	1.61	2.52	2.01	0.89	1.20	1.84	0.61	1.19	0.142
K	15.47	21.32	11.56	22.11	17.98	5.58	10.23	6.51	14.13	8.72	**0.692*****
Ca	3.77	10.59	11.98	11.24	9.22	6.36	8.43	4.50	4.09	6.69	**0.563****
Mg	1.22	2.43	4.96	9.89	3.38	1.94	2.12	2.36	2.21	2.13	0.179
Mn	0.06	0.05	0.05	0.05	0.06	0.17	0.13	0.07	0.08	0.14	0.354
Carbon Fraction (%)											
NSC	8.64	16.05	12.63	7.34	12.64	2.19	19.70	12.77	3.08	12.28	**0.475***
NDS	40.69	63.39	72.36	76.07	60.78	22.72	49.92	53.62	34.17	42.29	**0.742*****
Cellulose	26.43	15.91	12.19	9.59	17.17	28.10	20.17	19.59	34.04	23.42	0.320
Hemicellulose	29.92	15.99	9.27	7.61	17.29	28.58	15.20	13.08	17.64	18.37	**0.808*****
AHF	57.34	31.45	21.36	17.34	35.46	56.47	35.45	32.85	51.65	41.79	
AUR	2.96	4.70	6.06	8.85	4.95	20.60	14.71	11.48	16.64	15.73	0.080
Ash	1.79	0.80	1.09	1.33	1.29	2.20	3.53	2.25	2.95	2.80	0.09
Secondary Metabolites (mg/g)											
TPH	6.85	10.89	11.47	11.65	10.07	5.63	7.40	4.78	9.24	6.62	0.328
CT	0.06	0.19	0.94	1.60	0.45	0.04	0.05	0.04	0.61	0.10	**0.462***
TA	0.77	1.12	0.78	0.51	0.90	0.16	0.27	0.16	0.02	0.19	0.336

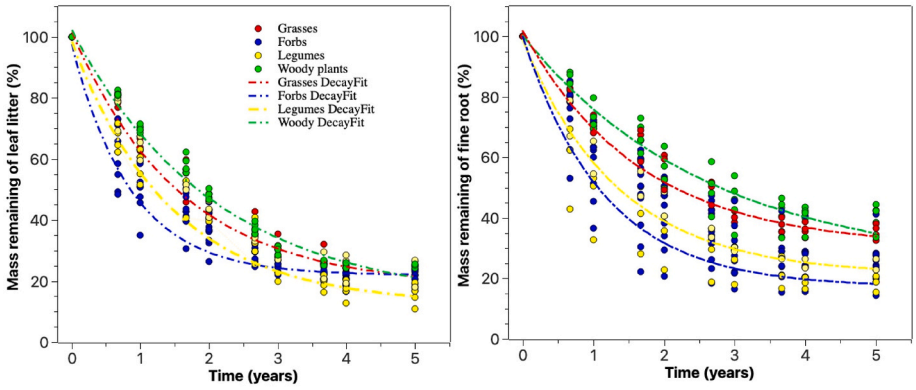

Fig. 1. Remaining mass (%) of leaf litter and fine roots across 23 species in a grassland ecosystem, here distinguished by functional groups. The decomposition experiment was conducted at a common grassland site in Inner Mongolia, China and had a duration of five years.

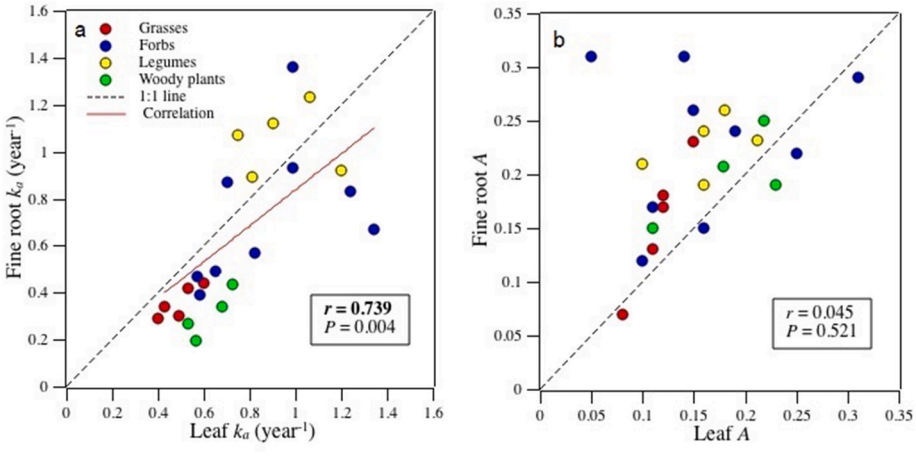

Fig. 2. Relationships between decomposition rates (k_a) and asymptotes (A) of leaf litter and fine roots by Pearson's regression analysis (r). Both k_a and A were calculated using the asymptotic model. The 23 species are given as functional groups and shown in different colours. The asymptote is the fraction of residual mass of the initial one. For comparison of rates we refer to the 1:1 line.

ranging between 0.39 and 1.34 year^{-1} for leaf litter and for fine roots between 0.27 and 1.38 year^{-1} (Fig. 5).

We investigated the decomposition relationships using k_a and 1st-year mass loss for both leaf litter and fine roots and found that they differed greatly both among and within functional groups (Fig. 2; Fig. S2). A general trend is that the values for both k_a and 1st-yr mass loss were lower for fine roots than for leaf litter. Fine roots' decomposition rates (k_a) were positively correlated with those of leaf litter across species (n = 23); a higher initial decomposition rate for fine roots corresponded to a higher rate for leaf litter across species (Fig. 2a, $r = 0.739$, $P = 0.004$). In terms of the early-stage decomposition process, the 1st-year mass loss for leaf litter (r = 0.634, $P < 0.001$) was positively correlated to that of the fine roots across species (Fig. S2). The first-year mass loss ranged from 23.3 to 65% for leaf litter and from 19.8 to 67.3% for fine roots, covering a main part of the entire mass loss during decomposition.

Grasses and woody species had lower decomposition rates (k_a) for fine roots than for leaf litter, cf. the 1:1 line ($P < 0.05$; Fig. 2a). For some of the legumes and forbs, k_a was located above the 1:1 line, with higher rates for fine roots than for leaf litter ($P < 0.05$, Fig. 2a). The legumes'

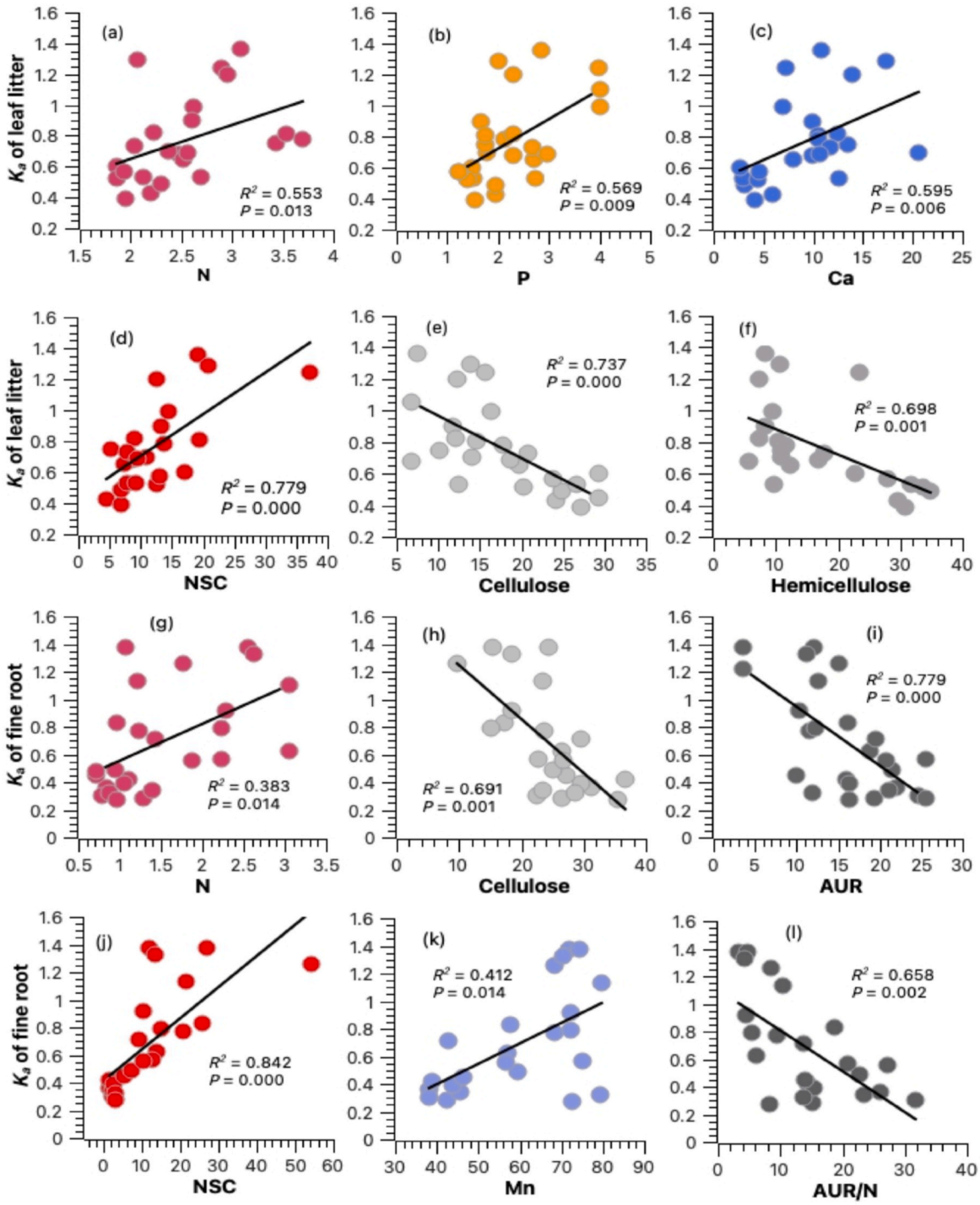

Fig. 3. Linear relationships between decomposition rates (k_a) and predictors for decomposition of leaf litter (upper panel) and of fine roots (lower panel). The six predictors of decomposition were shown for leaf litter and fine roots due to the statistical significance as the best single predictors ($P < 0.05$ in all cases).

and forbs' groups had high decomposition rates for both fine roots and leaf litter ($P < 0.01$) followed by the groups for woody plant and grasses (Fig. 2a).

The asymptote values were not correlated between fine roots and leaf litter across the 23 species (Fig. 2b, n = 23, r = 0.045, $P = 0.521$), but the asymptotes for most of the species were higher for fine roots than for leaf litter as those of fine roots located above the 1:1 line (Fig. 2b), indicating that the contribution of fine roots to SOM formation was greater than that of leaf litter.

3.4. Initial chemistry vs decomposition rates and asymptotes of leaf litter and fine roots

Initial concentrations of N and NSC were significantly and positively correlated with k_a for both leaf litter and fine roots (Fig. 3); the pre-decomposition NSC content was the best predictor of k_a for leaf litter among those predictors assessed, explaining 78% of variation in k_a for leaf litter (Figs. 3d), and 84% for fine roots (Fig. 3j). Cellulose and hemicellulose were significantly and negatively ($P < 0.001$) correlated with k_a for leaf litter (Fig. 3e and f). For fine roots there was a negative correlation with concentrations of cellulose ($P < 0.001$) (Fig. 3h). Further, k_a for leaf litter was significantly and positively related to concentrations of P and Ca, explaining 57% and 59% of the variation (Fig. 3b and c), respectively. For fine roots k_a was positively correlated to Mn, explaining 41% of the variation (Fig. 3k). Initial AUR concentrations and the AUR/N ratios were negatively correlated with k_a only for fine roots (Fig. 3i and l), explaining 78% and 66% of the variation, respectively, whereas no relationship was observed for leaf litter.

When we related the 1st-yr mass loss to the 16 traits, the pattern obtained for k_a was mainly repeated (Fig. S3). Concentrations of P and NSC gave significant and positive relationships, whereas cellulose gave a negative one. For fine roots, concentrations of P and NSC gave positive relationships, whereas cellulose gave a negative one as well as AUR and AUR/N (Fig. S3).

The contents of N and NDS were significantly and positively related to the residual mass, defined by the asymptote, explaining 49% and 62% of the variation residual mass for leaf litter and fine-roots, respectively, suggesting more residual mass for species at higher initial N and NDS (Fig. 4a and b, n = 46, $P < 0.05$). AUR concentrations and AUR/N ratios and other traits showed no association with the asymptote, not for leaf litter and not for fine roots (Fig. 4c and d).

4. Discussion

4.1. Coupled decomposition of fine roots and leaf litter in the early stage

Consistent with our first hypothesis, several initial traits were positively correlated between fine roots and leaf litter, including C/N ratio and concentrations of N, K and C-based compounds, such as NSC, NDS, hemicellulose and CT (condensed tannins). These results thus appear to support the whole-plant economics spectrum framework in which a set of chemical compounds in leaf litter match those of fine roots in a given ecosystem, in our case a grassland site. Initial litter chemistry has previously been recognized as a major factor controlling decomposition rate and has been suggested to explain a large part of the variability in early-stage litter decomposition rates (Strickland et al., 2009; Berg and McClaugherty, 2020).

The concept mass loss encompasses both leaching and microbial decomposition and with high concentrations of both NSC and NDS, both leaching and microbial decomposition are reasonable in our study. For example, the legumes' group had the highest concentrations of more readily decomposed carbon compounds (NSC) and relatively labile C among the four functional groups (Table 2) and were generally located at the high-quality end of the NMDS axes giving a high mass-loss rate (Fig. 6). In contrast, grasses and woody species had the lowest decomposition rates because of their higher concentrations of AHF (hemicellulose plus cellulose) and AUR, which were generally located at the low-quality end of the NMDS axes (Fig. 6) thus as more recalcitrant in comparison to the readily decomposed soluble compounds. These results indicate that nutrients of legumes and forbs litter were preferentially utilized by microorganisms leading to a fast mass loss due to their higher N contents and C quality; these may be the most important indicators to develop sustainable management practices within species and genus for improving soil quality, thus mitigating grassland degradation (Lehmann

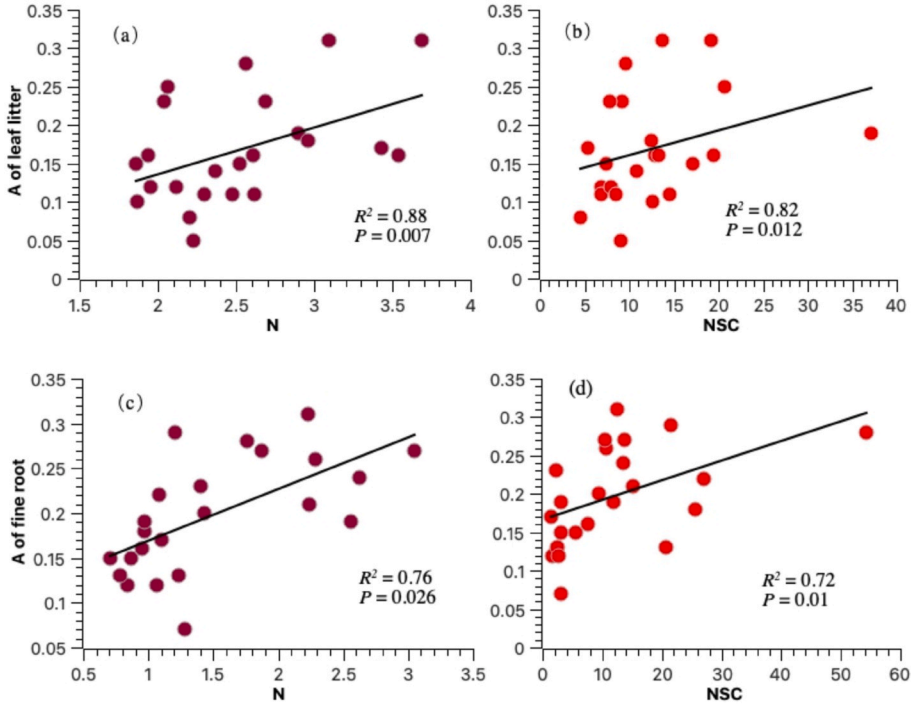

Fig. 4. Linear relationships between the asymptotic values (A) and initial chemical traits are given in long-term decomposition in grassland.

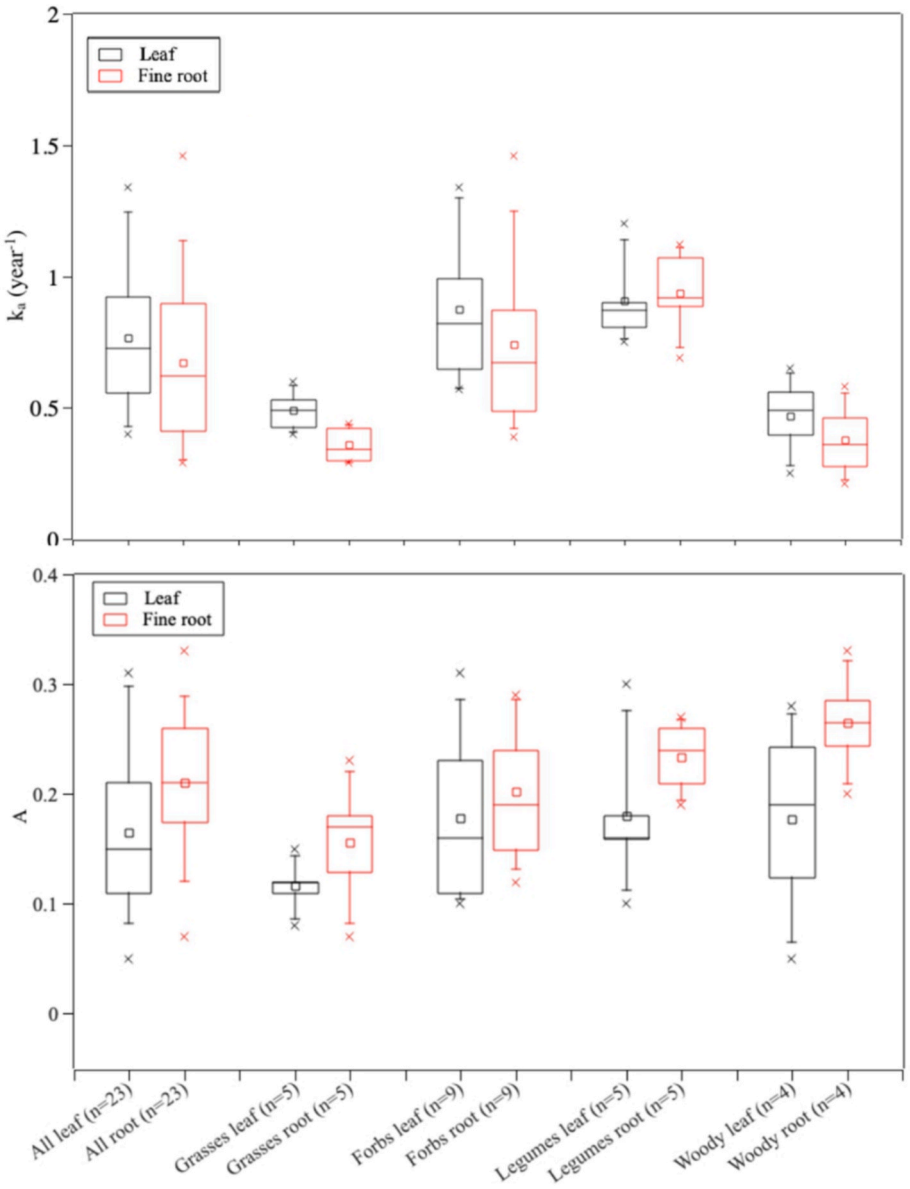

Fig. 5. Decomposition rates (k_a) and the asymptote (A) of leaf litter and fine roots according to functional groups based on 23 grassland species. Box plots represent median, first and third quarters and the whiskers on the boxes represent the 95% intervals. Mean ratios are displayed as squares, the minimum and maximum values are displayed as crosses. n is number of species.

et al., 2020; Parr et al., 2024).

Consistent with our second hypothesis, decomposition rates of fine roots and leaf litter co-vary in the early decomposition stage because of the similar chemical factors, e.g. initial concentrations of N and NSC, which were the best predictors for both leaf litter and fine roots' decomposition rates, followed by concentrations of P, Ca and Mn (Fig. 3). These results are consistent with previous reports suggesting that litter elements such as N, P, Ca and Mn, as well as carbon fractions influence litter decomposition rates (Keiluweit et al., 2015; Chomel et al., 2016; Sun et al., 2018, 2024; See et al., 2019). The positive associations of Ca in leaf litter and Mn in fine roots with decomposition, may be ascribed to their catalytic or biological roles for organic matter decomposition (Lovett et al., 2016; Rowley et al., 2018; Zhang et al., 2024). For example, Grossman et al. (2020) have reported that Ca was positively related to the extent of litter mass loss as Ca is an essential component of the fungal cell wall and can increase the growth of white-rot fungi (Berg et al., 1996). Decomposition rates increased in fine roots with relatively high Mn concentration because of the importance of Mn for the degradation of lignin via manganese peroxidase (MnP) and redox cycling (Hofrichter, 2002). These results appear to support the plant economics spectrum (PES) framework in which a set of chemical compounds in leaf litter match those of fine roots in a given ecosystem, in our case a grassland site, indicating that those with high decomposition rates in leaf litter will have high decomposition rates in fine roots (Reich, 2014). This study can help make the PES predictive in that some of those traits, which are aligned between root and leaf tissue, are also associated with relative decomposition rates. For instance, N, NSC, and cellulose all have significant, explanatory, and consistent effects on k_a for both leaf and root tissue (Fig. 3). This suggests a consistent pattern in which plant parts that are richer in N and NSC (and poorer in cellulose) lose mass more quickly in the early decomposition stages. This may be due to a coordinated ecological strategy between above- and belowground plant C and nutrient investment (Freschet et al., 2013; Li et al., 2022). Our results indicate some common leaf and root chemical traits, linking tissue chemistry to affect plant litter decomposition thus a first step for soil organic matter formation (Vleminckx et al., 2021).

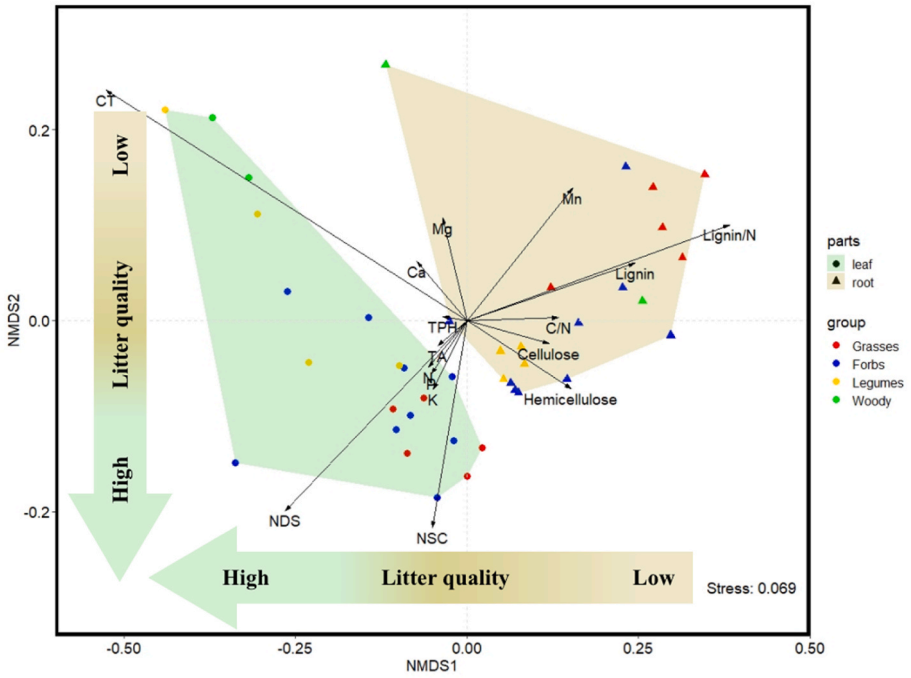

Fig. 6. Nonmetric multidimensional scaling (NMDS) ordination based on Bray–Curtis similarity matrices depicting litter chemical traits. Leaf litter and fine roots are grouped by polygons (leaf litter in green; fine roots in yellow). High quality is defined as substrate with high concentrationns of soluble carbon compounds. The Stress value = 0.069 indicated that the NMDS model is well fitted.

A surprising result was the negative associations of cellulose and hemicellulose with k_a as well as to the 1st -year mass loss in the early phase. These findings are inconsistent with previous research, which suggesting that cellulose has a positive correlation with decomposition rates in tree species (Ostertag and Hobbie, 1999; Ma et al., 2016; Sun et al., 2013). A possible explanation is that the cellulose and hemicellulose are partly protected polymers and generally covered by and encrusted in lignin, which must first be depolymerized by extracellular enzymes prior to assimilation (Boerjan et al., 2003). The slow decomposition of lignin residues limits microbes' access to cellulose and hemicellulose, which means that cellulose and hemicellulose can only be decomposed after lignin is removed (Berg et al., 2000; Pauly and Keegstra, 2008). Another explanation is that the negative associations of AHF with decomposition rate may be ascribed to the fact that decomposition of cellulose and hemicelluloses are complex processes and require the formation of extracellular enzymes (Eriksson et al., 1990; Dong et al., 2022). Moreover, the extracellular enzyme activities as important indicators of soil quality play crucial role in regulating SOM formation to maintain grassland soil health.

In the perspective of an early stage dominated by soluble and readily available compounds, concentrations of cellulose, hemicelluloses and lignin may be considered as relatively recalcitrant compounds and less readily decomposed given their complex molecular structure in comparison to NCS (sugar and starch). The complex molecular compounds from litter residues combined with environmental and biological regulators predominate soil aggregation and organic matter formation. The molecular structure of biomass and organic material has long been considered to determine long-term decomposition rates (Berg and McClaugherty, 2020). For instance, complex molecules (such as lignins or plant lipids), although decomposing slowly and predicted to persist in soils as humic polymers have been shown to turn over more rapidly than the bulk of the organic matter (Grandy and Neff, 2008). However, labile compounds, such as sugars in plant litter, although they lose mass fast, can persist through microbial decomposition not for weeks but for decades in soil (Schmidt et al., 2011). We therefore cannot extrapolate the initial stages of litter decomposition to explain the soil organic formation and persistence of plant-derived organic compounds in soils for long time.

4.2. *Decoupled residual mass of fine roots vs leaf litter in long-term decomposition*

The residual mass at the asymptote was not related to most of the initial elements and compounds, except for the positive association with the concentrations of N and NSC (Fig. 4a and b). That the residual mass defined by the asymptote increases with increasing initial N concentration has been reported for e.g. forest litter (Berg and McClaugherty, 2020). That high N concentration has a reversed role as compared to the early stage and takes the role of a stabilizing agent for the residual litter has been well documented (Sun et al., 2024).

The impact of N and litter C quality on the formation and turnover of microbial products has been investigated in our previous research following a microbial residue proxy, such as amino sugars (Sun et al., 2024). These main components of microbial cell walls tend to be formed rapidly and accumulate in SOM in the presence of substrates richer in N, suggesting that the substrate quality is a determining factor affecting the accumulation of microbial products (necromass proxied as amino sugar) (Liang et al., 2007). Previous research has reported that higher N and labile components such as NSC are easily taken up by microorganisms and then efficiently converted to microbial biomass and necromass, which covers the surface of litter residues, being difficult to decompose, but tending to facilitate the formation of stable soil aggregate (Cotrufo et al., 2013, 2015). However, we did not find any relationship between initial AUR concentration and the residual asymptotic mass, not for leaf litter and not for fine roots although lignin is the second most abundant plant-derived organic substance after cellulose, representing up to 30% of plant litter C (Boerjan et al., 2003). For our grassland substrates the lignin concentrations were on average just 5% for leaf litter and c. 15% for fine roots (Table 2). In fact, molecular structures alone do not control long-term litter decomposition and SOM stability in herbaceous plant-dominated communities, while environmental and biological controls, such as different temperature, moisture, and different

microbial decomposer between fine root in soil and leaf litter decomposition on the top of soil, may predominate in long-term decomposition due to their different below and above-ground soil environment (Freschet et al., 2013; Berg and McClaugherty, 2020).

4.3. Potential contributions to SOM formation

The asymptotic remaining mass (A), for fine roots on average 20.4% were higher ($p < 0.05$) than for leaf litter, with an average of 15.8%, showing that fine roots give a higher residual mass as compared to leaf litter. Thus, the average asymptotic fine-root residue was 67% higher than that of leaf litter, suggesting that the decomposition of fine roots may contribute to 60% more than that of leaf litter in organic matter accumulation in soil. Further, it has been reported that microbial formation of stable soil carbon is more efficient from belowground (fine root) than aboveground (leaf litter) inflows (Sokol and Bradford, 2019). In addition, some research has reported that the absorptive fine roots are more conductive than leaf litter to trigger formation of stable C in soil aggregate to improve soil quality by secreting root exudates and interacting with higher soil microbial activity and diversity (Chari and Taylor, 2022; Liang et al., 2023). Last but not least, the decomposition rates of fine roots for most species were much lower than those of leaf litter (Fig. 5), indicating that the fine root with longer turnover time and higher contents of recalcitrant compounds probably facilitate to soil humus accumulation in grassland.

5. Conclusions

We have demonstrated that fine-root decomposition mirrored leaf litter decomposition in the early stage of litter decomposition, and that the main positively influencing factors were concentrations of N and labile C compounds (NSC and NDS), while hemicellulose, cellulose and AUR showed a rate-dampening effect on early-stage decomposition of herbs' species. However, the decomposition patterns of fine roots and leaf litter decoupled in long-term decomposition. Our results suggest that the whole-plant economics framework could be used to predict the fates of fine roots *vs*. leaf litter in the early stage of long-term decomposition but may not be valid over time when lignin or microbial necromass interacted in the process. Our results may support the view that natural selection in a grassland favors plant communities with coordinated nutrient and carbon investment strategies in both above- and below-ground, but showed a time-dependent association in this long-term ecological process to maintain the sustainable development of a grassland ecosystem.

CRediT authorship contribution statement

Lili Dong: Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Björn Berg:** Writing – review & editing, Validation, Methodology, Conceptualization. **Yiqi Luo:** Writing – review & editing, Visualization, Validation, Supervision. **Hongtao Zou:** Validation, Resources. **Tao Sun:** Validation, Supervision, Resources, Project administration.

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.

Acknowledgments

We acknowledge the valuable help from all the staff of the Erguna Forest-Steppe Ecotone Ecosystem Research Station of IAE, CAS. The funding for this research was supported by the National Key R&D Program of China (2022YFD2201300), the CAS (Chinese Academy of Sciences) Project for Young Scientists in Basic Research (YSBR-108), the International Partnership Program of Chinese Academy of Sciences (151221KYSB20210005), International Postdoctoral Exchange Fellowship Program from Postdoctoral Science Foundation of China (Grant Number 2020032), and Liaoning Outstanding Youth Project (2024JH3/10200035) to L.D.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2025.109751.

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