Root and leaf decomposition become decoupled over time: implications for below- and above-ground relationships

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Summary

1. Studies elucidating patterns and mechanisms of decomposition are moving from a leaf-centred view towards a whole-plant perspective, in which root and leaf decomposition differs among species, yet this prediction has so far received mixed empirical support.

2. Here, we examined the rates and temporal dynamics of decomposition of absorptive fine roots (the distal two root-branch orders) and leaf litter by measuring mass loss across 10 subtropical and temperate tree species, and CO_2 efflux across 18 tree species in a 15-month laboratory incubation experiment.

3. Eight of 12 initial chemical traits were positively correlated between roots and leaf litter (Pearson's *r* range of 0·48–0·82). However, mass loss and respiration rates between roots and leaf litter were correlated only in the first 3 months, but unrelated in the subsequent 12 months. This was due to root decomposition rates slowing down after the first 3 months.

4. The disparity in decomposition rates between roots and leaf litter was mainly due to the higher chemical recalcitrance of roots and suggests that roots and leaf litter need to be considered separately when evaluating their role in plant–soil feedbacks. A better understanding of whole-plant ecological strategies is needed to quantify the impact roots vs. leaves on detrital processes.

Key-words: absorptive fine roots, carbon cycling, fine root decomposition, litter chemistry, plant functional traits, plant–soil feedback, whole-plant economics spectrum, woody plants

Introduction

Studies elucidating patterns and mechanisms of litter decomposition are progressively moving from a leaf-centred to a whole-plant perspective (Wardle *et al.* 2004; Hobbie *et al.* 2010; Freschet *et al.* 2013). Among those that examined the possibility of using leaf litter decomposition rates to predict root decomposition rates, some showed a positive correlation in decomposition rates between roots and leaves (Wang, Liu & Mo 2010; Birouste *et al.* 2012; Freschet, Aerts & Cornelissen 2012), others found no or a weak correlation (Hobbie 1996; Vivanco & Austin 2006; Hobbie *et al.* 2010). These contrasting reports highlight the highly uncertain nature of the relationship between root and leaf litter decomposition.

Positive correlations between root and leaf litter decomposition are one of the predictions of whole-plant economics theory (Reich *et al.* 2003; Freschet *et al.* 2010; Liu *et al.* 2010; Reich 2014). This theory argues that 'fast' species have 'fast' leaves, 'fast' roots and 'fast' decomposition rates, whereas 'slow' species have 'slow' leaves, 'slow' roots and 'slow' decomposition rates (Freschet, Aerts & Cornelissen 2012; Reich 2014). However, whether root and leaf litter decomposition of woody plants follow the predictions of this framework is poorly understood. Therefore, our first objective was to investigate whether rates of root and leaf litter decomposition are correlated across tree species and whether such correlations are driven by similarities in chemical traits that influence decomposition rates of roots vs. leaf litter.

Limited appreciation of temporal changes in decomposition may have obscured the reported relationship between

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root and leaf decomposition. Many decomposition studies estimated a single decay constant and compared this constant between root and leaf litter decomposition (e.g. Freschet *et al.* 2013). However, different decay rates may occur at different stages of decomposition (Berg & McClaugherty 2008; Herrmann & Prescott 2008; Bray, Kitajima & Mack 2012; Zhu, Yang & He 2013; Treseder *et al.* 2014). In our previous studies, we found that both root and leaf litter showed relatively fast mass loss (22% and 43%, respectively) during the first year of field decomposition (Fan & Guo 2010; Xiong *et al.* 2013), but in the second year, root decomposition slowed down substantially and lost <3% of remaining mass in contrast with a high mass loss rate of 20% in leaf litter (Fan & Guo 2010; Xiong *et al.* 2013). This temporal disparity may affect the relationship between root and leaf litter decomposition, but few studies have examined the phenomenon. Therefore, our second objective was to assess how root and leaf decomposition relationship changes over different phases of decomposition.

The sampling bias of fine roots may have further added uncertainty to the reported coordination (or lack of it) between root and leaf decomposition. The majority of root decomposition studies used all roots <2 mm in diameter (so-called fine roots) to investigate the root–leaf decomposition relationship (Hobbie *et al.* 2010; Birouste *et al.* 2012; Freschet *et al.* 2013). However, within the 'fine root' group, only the most short-lived and metabolically active absorptive fine roots are functionally comparable to leaves as resource acquisition organs (Guo *et al.* 2008; Xia, Guo & Pregitzer 2010; McCormack *et al.* 2015). These absorptive fine roots, composed of first two to three distal branch orders in woody species, have been observed to decompose more slowly than long-lived transport fine roots (fourth order and above, McCormack *et al.* 2015) (Fan & Guo 2010; Goebel *et al.* 2011; Xiong *et al.* 2013). Most importantly, the proportions of absorptive and transport fine roots vary substantially among species (Wang *et al.* 2006; Kubisch, Hertel & Leuschner 2015). Thus, root decomposition studies lumping together these two functionally different fine roots may lead to the results that differ from using only absorptive fine roots, and the magnitude of such difference may vary markedly across species. To overcome this problem, we only used absorptive fine roots for root decomposition in our study.

We tested two hypotheses on the relationship between root and leaf litter decomposition: (i) according to the predictions of 'whole-plant economics spectrum theories', initial chemical traits should be correlated between roots and leaf litter across species, such that species producing 'fast' leaves will also produce 'fast' roots; and (ii) this 'fast-slow' strategy should show strong afterlife effects: species with fast decomposition rates in leaf litter should have fast decomposition rates in roots, and species with slow decomposition rates in leaf litter should also have slow rates in roots. We sampled absorptive fine roots and leaf litter of 18 tree species from subtropical and temperate forests in

China. Roots and leaf litter were incubated in the laboratory for 15 months, during which litter decomposition rates (mass loss rates and CO_2 efflux rates) were repeatedly measured. In addition, we measured 12 initial litter chemical traits that have previously been shown to influence litter decomposition rates.

Materials and methods

SAMPLING OF ROOTS AND LEAF LITTER

Absorptive fine roots and leaf litter were sampled from a subtropical site and a temperate site in eastern China. The subtropical site was located in the Heshan Hilly Land Interdisciplinary Experimental Station (22°40′N, 112°50′E) of the South China Botanical Garden of Chinese Academy of Sciences in Guangdong Province. Mean ± SD annual temperatures was 21·7 ± 0·6 and mean ± SD annual precipitation was 1556 ± 773 mm. The soil is Acrisol (FAO-UNESCO 1988). Twelve subtropical species were sampled from monoculture plantations established in 1984 (Table 1). More information of the site can be found in Li *et al.* (2001) and Xiong *et al.* (2008). The temperate site was located at Maoershan Forest Research Station (45°21′N, 127°30′E) of the Northeast Forestry University in Heilongjiang province. Mean annual temperature was 3·9 ± 0·7 °C and mean annual precipitation was 644 ± 156 mm. The soil is loamy Hap-Boric Luvisol (FAO-UNESCO 1988). More information of this site can be found in Wang *et al.* (2006). Six temperate tree species were sampled from the monoculture plantations established in 1986. In total, 18 species from 10 families were sampled, including nine evergreen broadleaved species, three deciduous broadleaved species, five evergreen coniferous species and one deciduous coniferous species (Table 1).

Fresh leaf litter was collected with litter traps in October to November from each plantation. After removing the petioles, leaf litter was cut into pieces (2 cm × 3 cm) and air-dried before laboratory incubation. Root samples were collected from soil blocks (30 cm × 30 cm × 30 cm) that were excavated at a distance of 1 m from the tree trunk of the target species. During root collection, the soil was carefully removed from the block to expose the main lateral root branches, and the intact root branching systems were sampled. We then washed these root branching systems in deionized water, and picked the distal two root-branch orders off the branching root system until 30 g fresh weight of root material was obtained. Collected root samples were then air-dried and stored under the room temperature. We used live roots because we do not have reliable methods to identify the dead roots at specific stages of decomposition (e.g. undecomposed dead roots or <5% decomposed dead roots) and to sample them in sufficient quantity (Hobbie *et al.* 2010).

MICROCOSMS AND INCUBATION

We incubated collected leaf litter and root samples using microcosms in the laboratory. Microcosms were made of capped PVC containers (7 cm × 7 cm × 6 cm). Air-dried subsamples of roots and leaf litter were oven-dried for 48 h at 65 °C to a constant weight, before weighing and sealing these plant materials into the PVC containers. For leaf litter, 3·00 g (±0·1 mg) dry weight was placed on 50 g quartz sands in each container. For roots, 1·00 g (±0·1 mg) dry weight was placed on 50 g quartz sands due to the labour-intensive work required to collect sufficient amount of absorptive fine roots. Each litter type of each species had 24 replicates (6 L harvests and four replicates for each harvest). To initiate incubation, water content in the quartz sands was adjusted to

Table 1. Taxonomic list of 18 studied tree species

Species	Family	Growth form	Abbreviation	Site
Acacia auriculiformis	**Fabaceae**	**Evergreen broadleaf**	**Acau**	**Subtropical**
Acacia crassicarpa	**Fabaceae**	**Evergreen broadleaf**	**Accr**	**Subtropical**
Acacia mangium	**Fabaceae**	**Evergreen broadleaf**	**Acma**	**Subtropical**
Cinnamomum burmannii	**Lauraceae**	**Evergreen broadleaf**	**Cibu**	**Subtropical**
Cunninghamia lanceolata	**Taxodiaceae**	**Evergreen conifer**	**Cula**	**Subtropical**
Fraxinus mandshurica	Oleaceae	Deciduous broadleaf	Frma	Temperate
Juglans mandshurica	Juglandaceae	Deciduous broadleaf	Juma	Temperate
Larix gmelinii	Pinaceae	Deciduous conifer	Lagm	Temperate
Machilus chinensis	**Lauraceae**	**Evergreen broadleaf**	**Mach**	**Subtropical**
Michelia macclurei	**Magnoliaceae**	**Evergreen broadleaf**	**Mima**	**Subtropical**
Phellodendron amurense	**Rutaceae**	**Deciduous broadleaf**	**Pham**	**Temperate**
Picea asperata	Pinaceae	Evergreen conifer	Pias	Temperate
Pinus elliottii	**Pinaceae**	**Evergreen conifer**	**Piel**	**Subtropical**
Pinus koraiensis	Pinaceae	Evergreen conifer	Piko	Temperate
Pinus massoniana	Pinaceae	Evergreen conifer	Pima	Subtropical
Schima superba	**Theaceae**	**Evergreen broadleaf**	**Scsu**	**Subtropical**
Schima wallichii	Theaceae	Evergreen broadleaf	Scwa	Subtropical
Sterculia lanceolata	Sterculiaceae	Evergreen broadleaf	Stla	Subtropical

Species with mass loss measurement are indicated in bold.

60% of water-holding capacity. Litter in each container was inoculated with microbes by spraying 5 mL of soil suspension over the litter. The soil suspension was prepared by dispersing 900 g soil (top 5 cm of mineral soil sampled from the plantation where each litter was collected) in 4000 mL de-ionized water and letting sit for 10 min before use. The lid of each container was fitted with a three-way stopcock to keep the container aerobic and for CO_2 sampling. All containers were incubated in the laboratory incubator (BPS-250CL; Yiheng, Shanghai, China)under dark conditions with constant temperature (25 °C) and soil moisture (60% water-holding capacity) (Wetterstedt, Persson & Ågren 2010). To maintain constant soil moisture, we set the incubator at 82% relative humidity and added distilled water at regular intervals (containers were weighted weekly).

MEASUREMENT OF RESPIRATION RATES AND LITTER MASS LOSS RATES

Litter respiration rates were measured for all 18 species, but mass loss rates were measured only for 10 species (Table 1) because for the other eight species, we were not able to collect enough root mass for repeated mass sampling. Before CO_2 sampling, the PVC containers were left open without lids and placed under a fume hood for 10 min for complete CO_2 exchange. During CO_2 sampling, the containers were capped with lids and sealed with the three-way stopcocks. Headspace gas of 10 mL was collected using syringes fitted with a three-way stopcock at 0 and 15 min after container sealing, assuming that the CO_2 concentration inside the container increased linearly during containers sealing (Karhu *et al.* 2010; Wetterstedt, Persson & Ågren 2010). The CO_2 concentrations in gas samples were analysed within 24 h with a CO_2 chromatograph (HP 5890; Agilent Technologies, Palo Alto, CA, USA) equipped with a flame ionization detector (FID). The CO_2 flux for each measurement period was multiplied by the gas volume of the containers and divided by the litter dry weight to obtain the respiration rates (mg of CO_2-C respired per gram of dry mass during each measurement period). Litter respiration rates were measured monthly after the incubation was initiated, and the values for each time interval were summed to calculate cumulative respiration for the month 0–3, month 4–15 and month 0–15.

To measure litter mass loss rates, containers were harvested 1, 3, 5, 8, 11 and 15 months after incubation. Four replicate containers for each litter type of each species were collected at each harvest. The adhering quartz particles were removed from litter surface before litter was oven-dried at 65 °C to a constant weight, and litter dry mass was weighted.

CHEMICAL ANALYSES

Root and leaf litter samples were ground into fine powder (<0·25 mm) using a SPEX 8000-D mixer mill (SPEX, Edison, NJ, USA) before chemical analyses. Initial total C and N concentrations were determined with an elemental analyzer (Vario Microcube; Elementar, Hanau, Germany). The initial total Ca, K, P, Fe, Mg, Mn, S and Zn concentrations were measured with an ICP-MS analyzer (Elan DRC-e; PerkinElmer, Norwalk, CT, USA) after digesting the samples in HF and $HClO_4$ solution. Concentrations of organic soluble fraction (OSF), acid-soluble fraction (ASF) and acid-insoluble fraction (AIF) were determined following Ryan, Melillo & Ricca (1990). Briefly, a sub-sample weighing 0·5 g (m_0) was extracted with aqueous acetone (2 × 25 mL 70%, 30 min) with the residues extracted with aqueous methanol (2 × 25 mL 50%, 30 min). The residues after extractions were freeze-dried, weighed (m_1) and then digested in 50 mL of sulphuric acid (72%) for 3 h followed by filtration. The residues were washed repeatedly with de-ionized water during filtration until pH was 7·0 (± 0·1) and were again freeze-dried and weighed (m_2). OSF, ASF and AIF were calculated as $(m_0–m_1)/m_0$, $(m_1–m_2)/m_0$ and m_2/m_0, respectively. The three fractions combined equal to the original mass of samples (i.e. m_0). Among them, OSF is considered to consist of wax, sugars and other organic soluble materials, ASF includes cellulose and hemicellulose and AIF includes lignin and other recalcitrant chemicals which are difficult to be decomposed (Ryan, Melillo & Ricca 1990).

STATISTICAL ANALYSIS

Chemical traits and decomposition rates were log_{10}-transformed to meet the assumptions of normality and homogeneity of variance when necessary. The differences in chemical traits, mass loss and mass remaining between roots and leaf litter were analysed

using paired sample *t*-tests with each species as a pair (the root and leaf litter of each species is a pair). Bivariate correlations between root and leaf chemical traits were evaluated by Pearson's correlation. And the relationship between roots and leaf litter in mass loss and C loss (cumulative respiration) was analysed by standardized major axis regressions (SMA) (Warton *et al.* 2006). We used SMA regressions because, in contrast to simple linear regression, they do not assume a unidirectional effect of one parameter over the other (i.e. SMA minimize the areas of the triangles formed by the observations and the line).

The effect of leaf litter decomposition rate and decomposition stage on the root decomposition rate was analysed by linear mixed model with restricted maximum likelihood. The response variable (root mass loss rates or respiration rates) was log_{10} transformed. Decomposition rate of leaf litter and decomposition stage were designated as fixed effects and species as random effects. In this case, the significant interaction between leaf litter decomposition rate and decomposition stage (leaf litter × stage) meant that the decomposition stage would have significant influence on the on the relationship between root and leaf litter decomposition.

Moreover, the relationship between mass loss and initial chemical traits was first assessed via linear regressions and then forward stepwise regressions in which the trait was included if partial $P < 0.05$. Furthermore, each of the selected models was checked for collinearity among the significant variables as determined by the variation inflation factor (set to a limit of VIF < 4), and the collinear variables which lowered most the fit of the model was excluded from the subsequent model. The results of stepwise regression were reported as adjusted R^2 to allow comparison between models with a different number of explanatory variables. SMA and mixed-effects model were performed in the R 3.0.0 statistical platform (R Core Team 2014) with the package *smatr* (Warton *et al.* 2012) and *nlme* (Pinheiro *et al.* 2015), respectively. All other statistical analyses were performed using SPSS software (version 13.0; SPSS Inc., Chicago, IL, USA).

Results

INITIAL CHEMISTRY OF ROOTS AND LEAF LITTER

Initial chemical traits differed between roots and leaf litter across 18 species (Tables 2 and S1, Supporting information). Concentrations of OSF, Ca, K and Mn were significantly lower in roots than in leaf litter across 18 species ($P < 0.05$), while concentrations of AIF, N, Fe and Zn were significantly higher in roots than in leaf litter ($P < 0.05$).

No significant differences were found for concentrations of ASF, P, Mg and S between roots and leaf litter.

Eight of 12 chemical traits (concentrations of ASF, AIF, N, Ca, K, P, Mg and S) were positively correlated between roots and leaf litter ($P < 0.05$) (Table 2), with the correlation coefficients ranging from 0.48 (for P) to 0.82 (for N).

PATTERNS OF LITTER DECOMPOSITION RATES

Across the 10 species, mass remaining was significantly higher in roots than in leaf litter throughout the 15-month incubation ($P < 0.01$; Fig. 1). At the end of the incubation, mass loss of leaf litter averaged at 37% across 10 species with the lowest in *A. crassicarpa* (28%) and the highest in *P. amurense* (50%); mass loss of roots averaged at 25% across 10 species with the lowest in *A. auriculiformis* (20%) and the highest in *P. amurense* (39%).

Mass loss rates were positively correlated between roots and leaf litter during the first 3 months ($R^2 = 0.81$; Fig. 2a), but were uncorrelated in the subsequent 12 months ($P = 0.07$; Fig. 2b). Averaged across 10 species, the mass loss in the first 3 months of total mass loss over the entire incubation accounted for 68% in roots and 55% in leaf litter. These high proportions of mass loss represented by the first 3 months led to the correlated total mass loss across the 15-month incubation between roots and leaf litter ($R^2 = 0.75$; Fig. 2c). Similar to mass loss, respiration rates were highly correlated between roots and leaf litter in the first 3 months across 18 species ($R^2 = 0.61$), but uncorrelated thereafter (Fig. 3). For both mass loss and respiration rate, a significant interaction occurred between the leaf–root correlation and the decomposition stage ($P < 0.01$) (Table 3), suggesting that the relationship between root and leaf decomposition changed over time.

THE RELATIONSHIP BETWEEN DECOMPOSITION RATE AND INITIAL CHEMISTRY

The decomposition rates of roots and leaf litter were predicted by different initial chemical traits. In the first
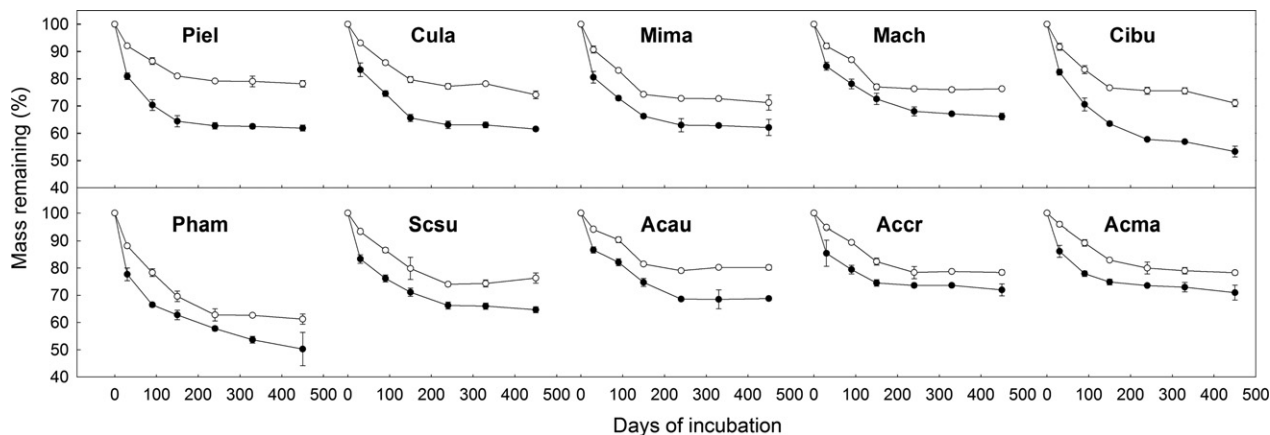
Table 2. Initial tissue chemistry (means ± SE) for roots and leaf litter and their correlations across 18 tree species (*$P < 0.05$, **$P < 0.01$).

Trait	Leaf litter	Roots	Correlation coefficient
Organic soluble fraction (OSF, %)	26·34[a] ± 1·92	9·48[b] ± 1·04	−0·14
Acid-soluble fraction (ASF, %)	38·60 ± 2·43	36·58 ± 1·75	0·50*
Acid-insoluble fraction (AIF, %)	36·06[a] ± 1·79	53·94[b] ± 2·05	0·51*
Nitrogen (N, mg g^{-1})	11·17[a] ± 0·96	17·49[b] ± 1·27	0·82**
Calcium (Ca, mg g^{-1})	14·34[a] ± 2·28	8·75[b] ± 1·01	0·60**
Potassium (K, mg g^{-1})	3·89[a] ± 0·61	1·03[b] ± 0·16	0·60**
Phosphorus (P, mg g^{-1})	0·69 ± 0·20	1·01 ± 0·14	0·48*
Ferrum (Fe, mg g^{-1})	0·36[a] ± 0·04	2·21[b] ± 0·30	−0·01
Magnesium (Mg, mg g^{-1})	1·41 ± 0·27	1·77 ± 0·14	0·77**
Manganese (Mn, mg g^{-1})	0·33[a] ± 0·08	0·08[b] ± 0·01	0·09
Sulphur (S, mg g^{-1})	1·95 ± 0·19	2·33 ± 0·18	0·50*
Zinc (Zn, mg g^{-1})	0·07[a] ± 0·01	0·23[b] ± 0·06	−0·14

Different letters in the same row indicate significant differences ($P < 0.05$) between roots and leaf litter

Fig. 1. Mass remaining (mean ± SE, $n = 4$) of roots (open circles) and leaf litter (solid circles) during 15 months of incubation.
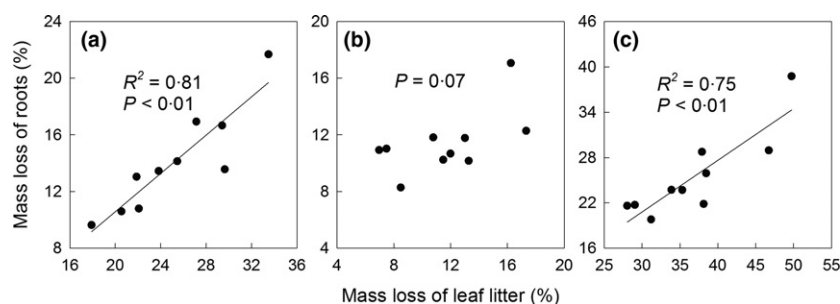

Fig. 2. Relationships of cumulative mass losses between roots and leaf litter in the month 0–3 (a), month 4–15 (b) and month 0–15 (c).

3 months of incubation, except ASF and P concentrations, OSF, AIF, Mg and Mn concentrations were only significantly related to the mass loss rates of roots, whereas Ca concentration was only related to the leaf litter (Table 4). In the subsequent 12 months, ASF, AIF and Ca concentrations were significantly related to the mass loss rates of both roots and leaf litter (Table 4). Several additional traits, such as N, P and Mg concentrations were only significantly related to the mass loss rates root, whereas K concentration was only related to the leaf litter (Table 4). In stepwise regressions, ASF concentration ($R^2_{adj} = 0.75$) was the only selected factor explaining the variation of leaf litter mass loss in the first 3 months of incubation, and Ca concentration ($R^2_{adj} = 0.56$) was the only selected factor in the subsequent 12 months (Table 5). However, Ca concentrations were highly positively related to ASF in leaf litter ($r = 0.90$). For roots, AIF concentration was selected as the factor to explain root mass loss in both early ($R^2_{adj} = 0.72$) and later stages ($R^2_{adj} = 0.75$) (Table 5).

Discussion

According to the whole-plant economics theory, root and leaf litter decomposition should vary in coordination across species (Freschet *et al*. 2010; Liu *et al*. 2010; Freschet, Aerts & Cornelissen 2012; Reich 2014). However, our study showed that decomposition rates between roots and leaf litter were correlated only in the first 3 months but unrelated at the later stage of decomposition, suggesting that this root–leaf coordination was transient and did not hold for the majority of root and leaf litter mass.

COUPLED ROOT–LEAF LITTER DECOMPOSITION IN THE EARLY STAGE

As hypothesized, most (eight out of 12) measured initial chemical traits were positively correlated between roots and leaf litter, including ASF and AIF(indicative of C quality, Xiong *et al*. 2013) and elements like N, P, Ca, K, Mg and S (indicative of litter stoichiometry or other unidentified aspects of litter decomposability) (Table 2). These findings are consistent with the literature that reported positive correlations between roots and leaf litter in N and P concentrations (Kerkhoff *et al*. 2006), and in C quality traits such as hemicellulose and cellulose concentrations (Birouste *et al*. 2012). These correlated traits may indicate coordinated ecological strategies between above- and below-ground in plant C and nutrient economy (Freschet *et al*. 2010; Liu *et al*. 2010; Reich 2014).

Furthermore, the positive correlations in initial chemical traits did translate into a strong correlation in decomposition rates between roots and leaf litter in the first 3 months. This finding seems to support the whole-plant economics spectrum framework in which 'fast' leaves match 'fast' roots and 'slow' leaves match 'slow' roots (Freschet, Aerts & Cornelissen 2012; Reich 2014).
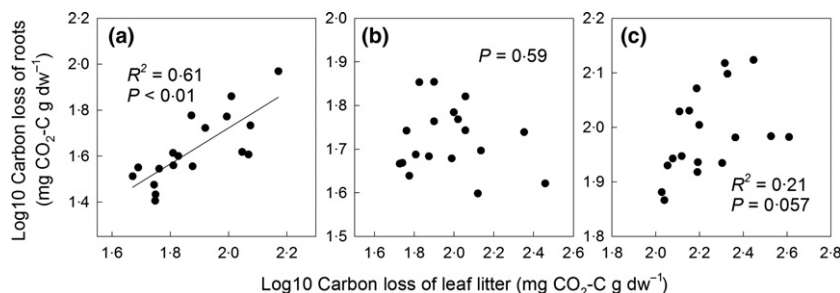
Fig. 3. Relationships of cumulative carbon losses between roots and leaf litter in the month 0–3 (a), month 4–15 (b) and month 0–15 (c).

Table 3. Results of mixed-model analysis for the relationships between root and leaf litter decomposition during the entire experimental stages

	Root mass loss rate		Root respiration rate	
Source	$F_{1, 7}$	P	$F_{1, 15}$	P
Leaf litter	29·16	<0·01	12·70	<0·01
Stages	1·25	0·30	5·83	0·03
Leaf litter × stages	12·44	<0·01	22·38	<0·01

Table 4. Coefficients (R^2) of linear regressions between mass loss and initial chemical traits in roots and leaf litter at two decomposition stages.

	The first 3 months		The last 12 months	
Trait	Leaf litter	Roots	Leaf litter	Roots
OSF	0·303 (−)	**0·637** (+)	0·018 (−)	0·192 (+)
ASF	**0·774** (+)	**0·401** (+)	**0·539** (+)	**0·686** (+)
AIF	0·213 (−)	**0·755** (−)	**0·521** (−)	**0·780** (−)
N	0·001 (−)	0·162 (+)	0·088 (+)	**0·566** (+)
Ca	**0·531** (+)	0·247 (+)	**0·606** (+)	**0·549** (+)
K	0·039 (+)	0·005 (+)	**0·441** (+)	0·005 (−)
P	**0·484** (+)	**0·736** (+)	0·370 (+)	**0·760** (+)
Fe	0·143 (+)	0·061 (+)	0·236 (+)	0·038 (−)
Mg	0·280 (+)	**0·510** (+)	0·384 (+)	**0·630** (+)
Mn	0·001 (−)	**0·566** (+)	0·003 (+)	**0·630** (+)
S	0·020 (−)	0·148 (+)	0·098 (+)	**0·557** (+)
Zn	0·001 (+)	0·190 (+)	0·069 (−)	0·017 (+)

Significant regressions ($P < 0·05$) were indicated in bold. Positive and negative correlations indicated by symbols of (+) and (−), respectively.

However, mass loss in the first 3 months of incubation (early-stage decomposition) represented only a small portion of total litter mass: an average of 20% in leaf litter and 17% in roots. Thus, whether this 'afterlife' effect of initial chemical traits extends to the entire decomposition process requires validation from later stages of decomposition.

DECOUPLED ROOT AND LEAF LITTER DECOMPOSITION AT THE LATER STAGE

From the 4th to the 15th month, neither mass loss rates nor CO_2 release rates were correlated between roots and

Table 5. Selected traits and coefficients of determination of step-wise regressions between mass loss and initial chemical traits in roots and leaf litter at two decomposition stages

	Model				
	The first 3 months			The last 12 months	
Litter type	Traits	R^2_{adj}	P	Traits	R^2_{adj}	P
Leaf litter	ASF	0·746	0·001	Ca	0·556	0·008
Roots	AIF	0·724	0·001	AIF	0·753	0·001
	AIF; OSF	0·874	0·014	AIF; Ca	0·934	0·004

leaf litter. And this trend should continue because roots and leaf litter differ so markedly in chemistry and decomposition rate (see more discussions below). Therefore, the mid-stage and late-stage decomposition may not be correlated between roots and leaf litter. Thus, the whole-plant economics framework may not be valid for predicting the fates of roots vs. leaf litter during the entire decomposition process (Hobbie *et al.* 2010; but see Freschet, Aerts & Cornelissen 2012). Our second hypothesis was therefore not supported.

The lack of correspondence between root and leaf litter decomposition after the early stage can mainly be explained by chemical recalcitrance and slow decomposition rates in roots. Beginning the fourth month of incubation, root decomposition slowed substantially, losing only 8% of total litter mass from the 4th to 15th month, averaged across 10 species. In contrast, leaf litter decomposition largely followed the initial trend, losing 17% of total mass during this stage. The rapid slowing down in root decomposition beginning the fourth month may be due to the exhaustion of root labile C in the first 3 months, given that C fractions representing more labile C (e.g. OSF and ASF) are much lower in roots (46% of total mass) than in leaf litter (64%). In the later stage, root decomposition rates were very low and negatively correlated with AIF concentrations (indicative of recalcitrant C fractions) (Fan & Guo 2010; Xiong *et al.* 2013), whereas leaf litter decomposition rates were much higher and positively correlated with Ca concentrations, which were highly correlated to ASF (a labile C fraction) (Table 5).

Although the differences of ASF and AIF between roots and leaf litter appeared to be most reasonable to explain the decoupled root–leaf decomposition at the later stage, the specific chemical compounds contained in these C fractions remain poorly understood. Emerging evidence suggests that roots may contain more secondary compounds than leaf litter, such as higher condensed tannins, bound phenols and lignin phenols, all of which may inhibit decomposition (Wang *et al.* 2015; Xia, Talhelm & Pregitzer 2015). We do not yet know whether these recalcitrant molecular phenolic compounds would fall into AIF (Wang *et al.* 2015). Future studies should better understand the specific compounds responsible for the low root decomposition rates in the later stage. Preferably, long-term root decomposition studies in the field similar to that of Herrmann & Prescott (2008) for wood decomposition are needed to understand both the patterns of root decomposition and the chemical mechanisms underlying these patterns.

Decoupled root–leaf decomposition found here seems to contradict a recent study showing a strong positive correlation between root and leaf litter decomposition (Freschet, Aerts & Cornelissen 2012). However, the positive correlation between roots and leaves reported in Freschet, Aerts & Cornelissen (2012) was mainly driven by systematic differences between herbs and woody species as woody species had more recalcitrant tissue chemistry in both roots and leaf litter than herbacious species. When examined separately, neither woody group nor herbaceous group showed strong correlation between root and leaf decomposition (Freschet, Aerts & Cornelissen 2012).

Conclusions

We demonstrated that decomposition of roots and leaf litter in 18 tree species were coordinated only in the very early stage (the first 3 months of incubation, and with mass loss <20% of total litter mass), but became decoupled after the exhaustion of limited amount of liable C in roots. The decoupled decomposition between roots and leaf litter for more than 80% of total mass in our study, together with previous studies showing slow root decomposition in different tree species, suggest that root decomposition does not mirror leaf litter decomposition, particularly among woody species. In the future, a better understanding of whole-plant ecological strategies is needed to quantify the impact roots vs. leaf litter on detrital processes.

Acknowledgements

Data accessibility

All data used in this article are present in the article and its supporting information.

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Table S1. Species in this study, and values of 12 initial chemical traits for 18 tree species.