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RESEARCH ARTICLE

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Litter carbon and nutrient chemistry control the magnitude of soil priming effect

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Abstract

1. Plant litter inputs can promote the decomposition of soil organic matter (OM) through the priming effect (PE). However, whereas leaf litter chemistry has long been identified as the primary driver of litter decomposition within biomes worldwide, little is known about how litter chemical traits influence the occurrence and strength of the PE.
2. Here, we studied the effects of 15 co-occurring C_3 leaf litters of contrasting chemistry on C_4 soil respiration by analysing changes in ^{13}C natural abundance during early and later stages of litter decomposition (up to 125 days).
3. Besides an apparent PE of 16% in the first 3 days, soil C respiration was increased by 24% on average with leaf litter addition in the initial stage of decomposition (4–26 days) and by 8% at later stages (27–125 days). Most interestingly, soil PE related well to initial litter chemistry and the dominant factors influencing the magnitude of the PE changed with decomposition stage. In the early stage of decomposition, litter leachate C content and litter hemicellulose concentration were positively correlated with the strength of the PE, whereas tannin concentration was negatively associated with soil PE. Together, tannin and hemicellulose explained half of the observed variation in the PE (R^2 = 0.58). In the later phase of decomposition, lignin and lignin:N ratios were negatively related to the PE, whereas Ca, K and Mg concentrations were positively related to the PE; lignin alone gave the best prediction of the PE (R^2 = 0.58) at later decomposition stages.
4. Our findings provide evidence that the magnitude and direction of the PE is influenced by the chemistry of OM inputs and suggest that, as decomposition proceeds differently among litter of contrasting chemistry, litters can also have variable effect on soil PE through time. The predictive power of litter chemical traits on soil PE opens new perspectives for improving our mechanistic

understanding of soil PE and improving our abilities to model soil C dynamics at variable scales.

KEYWORDS
^{13}C natural abundance, C_4 soil, carbon mineralization, litter chemistry, litter decomposition, soil organic carbon, soil priming effect

1 | INTRODUCTION

Soils contain the largest reservoir of carbon (C) in terrestrial ecosystems (Lin, Zhu, & Cheng, 2015), the size and stability of which depend on the balance between C inputs from plant litter and C outputs from soil organic C (SOC) mineralization (Averill & Hawkes, 2016). SOC mineralization is influenced by microbial activities, which are usually nutrient or energy limited in most soils. Leaf litter inputs to soil can release this limitation and stimulate SOC mineralization rates (Kuzyakov, 2010; Wang, Wang, He, Liu, & Wu, 2014), a phenomenon known as "the priming effect (PE)" (Kuzyakov, 2010; Zhang & Wang, 2012).

Plant litter decomposition plays an important role in regulating C and nutrient cycling in soil systems (Cornwell et al., 2008; Freschet et al., 2013). Litter decomposition is determined by three main factors: climate, litter quality and decomposer organisms (Bradford et al., 2017; Coûteaux, Bottner, & Berg, 1995; García-Palacios, Mckie, Handa, Frainer, & Hättenschwiler, 2016). While it is well accepted that climate is the predominant factor controlling litter decomposition at the global scale (Aerts, 1997; Makkonen et al., 2012; Zhou et al., 2008), litter quality, which generally varies with plant species, was viewed as the critical factor in determining litter decomposition within biomes (Cornwell et al., 2008). Litter chemistry correlates broadly with initial rates of litter decomposition (Melillo, Aber, & Muratore, 1982; Schmidt et al., 2011). Leaf litter chemical properties that stimulate decomposition rates include low lignin concentrations, high concentrations of nitrogen (N) and cations (potassium: K; calcium: Ca; and magnesium: Mg) and low tannin concentrations (Hättenschwiler, Coq, Barantal, & Handa, 2011; Makkonen et al., 2012; Paudel et al., 2015; Zhang, Hui, Luo, & Zhou, 2008).

The importance of plant litter for SOC decomposition has long been recognized (Broadbent & Bartholomew, 1949; Sparling, Cheshire, & Mundie, 1982). Over the past several decades, empirical evidence has been growing that the PE plays a crucial role in regulating SOC decomposition and in predicting the responses of soil ecological processes to global change (Fontaine, Bardoux, Abbadie, & Mariotti, 2004; Sullivan & Hart, 2013). However, the strength, direction and duration of the PE can be controlled by multiple factors, including soil physico-chemical properties, the amount and quality of organic substances present in the soil, and microbial community structure and activity (Blagodatskaya & Kuzyakov, 2008; Kuzyakov, 2010; Luo, Wang, & Smith, 2016). Owing to difficulties associated with disentangling all these influences, the response of SOC decomposition to litter addition remains controversial. Divergent results have been reported, with stimulatory (Luo et al., 2016; Zhang & Wang, 2012), inhibitory (Kuzyakov & Bol, 2006; Potthast, Hamer, & Makeschin, 2010) or no effects (Nottingham, Griffiths, Chamberlain, Stott, & Tanner, 2009; Wang et al., 2014; Zhang, Wang, & Wang, 2013) on SOC decomposition rates. Several hypotheses have been proposed to explain these inconsistent PEs associated with the input of litter (Blagodatskaya & Kuzyakov, 2008; Fontaine, Mariotti, & Abbadie, 2003; Kuzyakov, Friedel, & Stahr, 2000). Generally, positive PEs could be induced due to increased microbial biomass and associated microbial production of extracellular enzymes, whereas negative PEs might be caused by the toxic effects of litter to micro-organisms and preferential litter utilization by micro-organisms (Kuzyakov et al., 2000; Xiao, Guenet, Zhou, Su, & Janssens, 2014; Zhang et al., 2013). More specifically, the balance in microbial competition between micro-organism communities specialized in the decomposition of easily degradable organic compounds and those feeding on polymerized SOC may further explain differences in soil PE (Fontaine et al., 2003). In this context, the chemical composition of fresh litter inputs could be a critical driver of SOC degradation by regulating the balance between different functional types of soil microbial communities (Fang, Nazaries, Singh, & Singh, 2018; Fanin, Hättenschwiler, & Fromin, 2014). Despite this, the relationship between litter chemistry and PEs remains largely unexplored.

Although several studies have assessed the effect of litter addition on SOC decomposition, prior PE studies utilized a small number of plant litters (Kuzyakov, 2010; Wang et al., 2014). Commonly tested litters were typically ^{13}C-labelled plant materials such as ryegrass, wheat straw and green leaves instead of actual plant litters (Blagodatskaya & Kuzyakov, 2008; Fontaine et al., 2003) and poorly represented the global diversity of litter chemistry. Consequently, to the best of our knowledge, no studies have yet directly investigated the influence of contrasting litter chemistry on the magnitude and direction of the PE. Additionally, as litter decomposition processes change with time (Berg & McClaugherty, 2008; Bray, Kitajima, & Mack, 2012), the influence of the decomposing litter on microbial communities also changes (Fanin, Hättenschwiler, Chavez Soria, & Fromin, 2016), with likely effects on the magnitude of the PE (Luo et al., 2016). Therefore, it is crucial to gain a better understanding of the dynamics of the PE and the dominant factors controlling the PE at different stages of decomposition (García-Palacios, Maestre, Kattge, & Wall, 2013; Zhang et al., 2016).

The overall objective of this study was to determine the influence of leaf litter chemistry on the strength of the PE at both the initial and intermediate stages of litter decomposition.

To do so, we studied the ^{13}C isotopic signature of CO_2 respired from microcosms where leaf litters of 15 C_3 plant species with contrasting chemical composition were added to a C_4 soil. We hypothesized that the magnitude of the PE would vary with the chemistry of litter species and differ among decomposition stages. Specifically, assuming that the nutritional competition and balance between microbial communities control the PE (Fontaine et al., 2003), we further hypothesized that litters with high concentrations of easily degradable C compounds (e.g., litter C leachates, cellulose and hemicellulose) would mostly induce increases in PE in the initial stages of decomposition, as they are likely to stimulate micro-organisms specialized in degrading easily degradable SOC, whereas litters with high recalcitrant compound content (e.g., lignin) would increase the PE in later stage of decomposition, as they are more likely to stimulate micro-organisms specialized in degrading recalcitrant SOC. Alternatively, following the co-metabolism concept, we hypothesized that the rate of litter decomposition and therefore the access of microbial communities to litter compounds would essentially drive the PE, leading to similar prediction of a positive relationship between easily degradable C compounds and PE in the initial stage of decomposition but negative relationship between the concentration of recalcitrant compounds and the PE at later stages of decomposition.

2 | MATERIALS AND METHODS

2.1 | Sampling of soil and leaf litter

The soil used in this study was collected from the plough layer (0–20 cm) of an agricultural site that has been planted with a C_4 maize crop for over 20 years at the experimental station of Heilongjiang Academy of Agricultural Science (45°69'N, 126°62'E), near Harbin, Heilongjiang Province, northeast China. Local mean annual temperature is 4.5°C and annual precipitation is 569 mm. The soil is a clay loam (43% sand, 22% silt, 35% clay) with a pH of 6.9. Soil C and N concentrations were 17.3 and 1.5 g/kg, respectively, corresponding to a C:N ratio of 11.6. The $\delta^{13}C$ value of C_4 maize soil was −15.8‰. The soil was air-dried, thoroughly homogenized and passed through a 2-mm-mesh sieve. Visible plant debris and stones were carefully removed by hand.

We collected freshly senesced leaf litter from 15 common and relatively abundant tree species in a subtropical forest characterized by a wide range of life strategies, carbon chemistry (Table 1) and nutrient content (Supporting Information Table S1) at the Huitong Natural Research Station of Forest Ecosystem (26°40'–27°09'N, 109°26'–110°08'E) in the Hunan Province, central China. Local mean annual temperature and precipitation are 16.5°C and 1,200 mm. Only freshly senesced, undamaged leaf litter was picked, whereas leaves with visible signs of herbivory, abrasions, fungal attacks or leaves that were still green were excluded. The litter was pooled by species and dried at 35°C immediately after collection.

2.2 | Experimental set-up and soil incubation

We used the natural abundance difference in $\delta^{13}C$ values of C_3 plant leaf litters and C_4 soil to separate leaf-derived CO_2 from soil-derived CO_2. The equivalent of 150 g dry soil was weighed into a 1-L Mason jar and adjusted to 60% water-holding capacity by adding distilled water. Leaf litter samples were ball-milled into fine powder and homogenized by passing through a 0.25-mm-mesh sieve. We added ground litter rather than chopped litter, because we were mostly interested in differences in litter chemistry, rather than in aspects of litter morphology, size or anatomy that could (a) affect the homogeneity of litter distribution within the soil in the microcosms and create non-optimal contact between soil and litter, and (b) interact with litter chemistry in a non-systematic way and thereby obscure the potential effect of litter chemical compounds on soil PE. Prior to litter addition, all soils were pre-incubated at 25°C for 10 days.

After pre-incubation, litter powder was added to the soil and throughly mixed. The amount of added litter C was calculated separately for each species so as to represent 5% of the SOC concentration (corresponding to 0.25–0.43 g of litter material; Supporting Information Table S2). The amount of litter C added to the soil (75 g C m^{-2} $year^{-1}$, considering a soil depth of 10 cm) corresponded to a realistic yearly input of litter in local tree plantations (e.g. *Cunninghamia lanceolata* forest; Ning et al., 2009). Three analytical replicates were included for each leaf litter. Soils without litter addition were also included as controls. Two holes were punched in the Mason jar lids and installed with bulkhead connectors (SMC, KQ2E06-00A; Singapore). Polyurethane tubes (TU-0604; SMC, USA) were used for linking the bulkhead connectors with a manual valve (VHK2-06F-06F; SMC, Japan). The manual valve remained open during incubation, but was kept closed between sampling periods. All incubations were conducted in a laboratory incubator (SPX-500; Jiangnan, Ningbo, China) at a constant temperature of 25°C for 125 days.

2.3 | Analysis of CO_2 fluxes

Gas samples were sampled from jars on days 1, 3, 7, 10, 15, 26, 61, 90 and 125 after the incubation began. To make sure that there was no CO_2 at the start of the CO_2 flux measurements, we removed CO_2 inside each jar before gas sampling by circulating CO_2-free air, which was generated using an air compressor (ACO-318; Hailea, Guangdong, China) pumped through a soda lime column for 2 min. Then, jars were immediately sealed by closing the manual valve. Due to the faster CO_2 release from soil in the initial stages of decomposition than at later stages, gas was collected 12 (early stage) or 24 hr (later stage) after sealing using a portable gas sampling pump (01 L-D; Delin, Dalian, China) and stored in a pre-evacuated gas sampling bag (LB-201-0.2; Delin). The CO_2 concentration and $\delta^{13}C$ were analysed by a High-precision Isotopic CO_2 Cavity Ring-Down Spectrometer (Picarro G2131-i Analyzer; Picarro, Inc., Santa Clara, CA, USA).

TABLE 1 Initial litter chemistry of the 15 subtropical tree species incubated in this study

			Initial litter C quality (g/kg)						
Species	**Family**	**Growth form**	**C leachates**	**Lignin**	**Cellulose**	**Hemicellulose**	**Tannin**	**Lignin:N**	**C**
Cyclobalanopsis glauca	Fagaceae	Evergreen broadleaf	47.5 ± 1.6	129.9 ± 6.1	155.4 ± 6.3	145.8 ± 1.1	303.9 ± 3.3	34.2 ± 1.5	381.8 ± 11.2
Castanopsis hystrix	Fagaceae	Evergreen broadleaf	27.3 ± 0.5	95.0 ± 2.9	167.9 ± 4.1	188.7 ± 6.1	273.7 ± 2.8	30.6 ± 1.1	310.1 ± 8.3
Cunninghamia lanceolata	Taxodiaceae	Evergreen conifer	21.8 ± 0.7	137.5 ± 3.8	211.5 ± 12.7	39.1 ± 4.4	196.9 ± 4.8	34.4 ± 3.5	399.6 ± 13.2
Liquidambar formosana	Hamamelidaceae	Deciduous broadleaf	41.9 ± 1.0	134.9 ± 5.0	100.5 ± 5.2	59.3 ± 4.0	523.1 ± 12	32.9 ± 2.0	405.4 ± 15.3
Yulania denudata	Magnoliaceae	Deciduous broadleaf	49.9 ± 2.6	113.2 ± 6.0	214.5 ± 3.4	140.5 ± 5.8	58.7 ± 0.4	30.6 ± 0.9	365.6 ± 7.6
Michelia macclurei	Magnoliaceae	Evergreen broadleaf	31.4 ± 0.8	129.2 ± 2.5	128 ± 2.2	156.3 ± 3.4	568.8 ± 14.4	36.9 ± 1.0	347.8 ± 11.0
Machilus pauhoi	Lauraceae	Evergreen broadleaf	62.8 ± 1.8	116.2 ± 2.1	205.4 ± 12.2	168.3 ± 1.7	198.7 ± 6.0	38.7 ± 1.6	298.5 ± 4.9
Osmanthus fragrans	Oleaceae	Evergreen broadleaf	66.8 ± 4.0	127.2 ± 5.0	73.7 ± 11.6	117.9 ± 8.3	34.5 ± 3.0	37.4 ± 1.5	437.1 ± 8.5
Phoebe zhennan	Lauraceae	Evergreen broadleaf	31.4 ± 0.8	165 ± 0.8	110.9 ± 1.7	170.8 ± 6.7	423.6 ± 3.6	50.0 ± 0.5	329.4 ± 5.8
Pinus massoniana	Pinaceae	Evergreen conifer	45.4 ± 1.1	120 ± 2.8	242.7 ± 13.8	164.5 ± 3.6	196 ± 6.5	34.3 ± 1.5	352.7 ± 5.2
Paulownia fortunei	Scrophulariaceae	Deciduous broadleaf	88.2 ± 3.6	98.4 ± 2.7	250.2 ± 2.5	227.5 ± 14.0	43.7 ± 1.9	22.9 ± 0.9	425.4 ± 3.9
Quercus laevis	Fagaceae	Deciduous broadleaf	62.7 ± 0.6	86.6 ± 3.5	182 ± 11.9	74.4 ± 6.6	291.7 ± 5.7	16.7 ± 0.3	519.0 ± 7.4
Quercus variabilis	Fagaceae	Deciduous broadleaf	55.7 ± 2.6	177.2 ± 1.0	98.1 ± 5.4	125.4 ± 12.7	285.5 ± 4.4	43.2 ± 1.0	411.5 ± 11.0
Symplocos laurina	Symplocaceae	Evergreen broadleaf	17 ± 1.8	158 ± 3.3	73.1 ± 2.7	110.1 ± 9.0	269.2 ± 4.7	42.7 ± 0.9	373.9 ± 4.5
Schima superba	Theaceae	Evergreen broadleaf	37 ± 1.1	112.6 ± 5.1	142 ± 7.2	125 ± 9.0	494.9 ± 12.9	24.5 ± 1.6	455.3 ± 6.0

2.4 | Measurement of litter chemistry

The ground leaf litter was analysed for C, N, phosphorus (P), litter C leachates, lignin, hemicellulose, cellulose and tannin using standard methods. Briefly, C and N concentrations were determined using a CN elemental analyser (ElementarVario, Hanau, Germany). To determine litter C leachates, 2 g litter powder samples were extracted with 60 ml deionized water, by shaking them on a reciprocal shaker for 30 min. The resulting solution was filtered and then analysed using a TOC analyser (Vario TOC cube; Elementar Analysis system GmbH, Langenselbold, Germany). Lignin, hemicellulose and cellulose (300 mg litter samples) were measured according to the National Renewable Energy Laboratory Procedure (Sluiter et al., 2008). In brief, we used a two-step acid hydrolysis to fractionate the litter into easily quantified forms. The hydrolysis liquid was used to quantify the cellulose and hemicellulose by high-performance liquid chromatography (Agilent-1260; Agilent Technologies, Santa, Clara, CA, USA). Two fractionate forms of lignin (acid-insoluble material and acid-soluble material) were measured by UV–Vis spectroscopy (Lambda 25; PerkinElmer, Singapore). Tannins were determined by an acid–butanol assay as described by Hagerman (2011). The initial total P, Ca, K, Mg and Mn concentrations were measured using inductively coupled plasma mass spectroscopy (ICP-MS) (Elan DRC-e; PerkinElmer, Norwalk, CT, USA) after acid digestion of litter samples with H_2SO_4 and $HClO_4$ solution.

2.5 | Calculations and statistical analysis

CO_2-C efflux was calculated as follows:

$$R=\frac{C\times V\times M\times 273.15}{22.4\times(273.15+T)\times W\times t}, \quad (1)$$

where R is the CO_2-C efflux (μg C g^{-1} soil day^{-1}); C is the measured CO_2 concentration (ppm); V is the effective volume of a 1-L Mason jar (L); M is the molar mass of C (12 g/mol); 22.4 (L) is the molar volume of an ideal gas at 1 atm and 273.15 K; W is the gram dry weight of the soil; t is the time of CO_2 accumulation (days); and T is the incubation temperature (25°C).

Mass balance equations were used to separate leaf-derived CO_2 from soil-derived CO_2:

$$C_L=C_t\frac{(\delta_t-\delta_S)}{(\delta_L-\delta_S)} \quad (2)$$

$$C_S=C_t-C_L \quad (3)$$

where C_t is the total CO_2-C from soil respiration ($C_t = C_L + C_S$) during the considered time period, C_L is the amount of C derived from C_3 litter, C_S is the amount of C derived from C_4 soil, δ_t is the $\delta^{13}C$ value of CO_2 emitted from jars containing soil–litter mixtures, and δ_L and δ_s are the $\delta^{13}C$ values of C_3 litter material and C_4 soil, respectively.

Soil cumulative production of CO_2 (T, mg C/kg soil) at early and later stages of decomposition was calculated by the following equation:

$$T=\sum_{i=1}^{n}(R_i+R_{i+1})/2\times(t_{i+1}-t_i) \quad (4)$$

where R_i and R_{i+1} are soil CO_2 efflux at ith and (i + 1)th incubation time (mg C kg^{-1} day^{-1}), respectively; t_{i+1}–t_i is the interval between the ith and (i + 1)th incubation time (day); and n is the number of incubation times.

Mean daily soil CO_2 production (mg C kg^{-1} soil day^{-1}) at early and later stages of decomposition was then calculated by dividing T by the number of days in each stage.

The proportion of litter C decomposition (L_d, %) was calculated using the following equation:

$$L_d=(T_d/M_d)\times 100 \quad (5)$$

where T_d is the cumulative CO_2 (mg C/kg) efflux from litter during the incubation period and M_d is the amount of litter C added to soil (mg C/kg).

The early stage of litter decomposition was defined here as the phase presenting a sharp decrease in CO_2 efflux with time (i.e., for all litters, from the first to the 26th day after the start of the incubation), whereas the late phase of decomposition was characterized by relatively stable, lower CO_2 efflux rates (as observed for all litters 61, 90 and 125 days after the start of the incubation). This trend was highly conserved across all 15 species allowing the delineation of the same early versus later phase of decomposition for all 15 litters (Supporting Information Figure S1).

It is generally considered that the initial flush of CO_2 occurring during the first 3 days after new C input mainly results from an increased turnover or pool substitution of soil microbial biomass (Blagodatskaya & Kuzyakov, 2008; Kuzyakov, 2010). This "apparent" PE occurring during the first 3 days of incubation was therefore omitted from PE calculations for the early stage of decomposition (0–26 days) so as to consider only the "real" PE. The PE induced by litter addition on SOC decomposition was expressed as the % change compared to CO_2-C released from the control. The magnitude of PE during the considered time period (t) was calculated using the following equation:

$$PE(\%)_{[t]}=100\times(CO_2-C_{\text{treatment }t}-CO_2-C_{\text{control }t})/CO_2-C_{\text{control }t} \quad (6)$$

where CO_2-$C_{treatment}$ is the accumulated amount of total emitted CO_2 derived from C_4 soil in the litter-amended soil and CO_2-$C_{control}$ is the amount of CO_2 emitted from the control soil. The absolute change in decomposition of SOC following addition of litter was also calculated by subtracting CO_2-$C_{control}$ from CO_2-$C_{treatment}$.

The difference in PE between early and later phases of decomposition was tested across all litter species using paired t tests. A correlation analysis was carried out, to test collinearity among litter traits. To determine how well variation in multiple aspects of litter chemistry explained variation in the PE, the relationships between leaf litter chemical properties, litter decomposition and the PE were assessed using hierarchical multiple linear regressions. The introduction of "added litter mass" as a covariate with precedence in hierarchical multiple

linear regression analyses was necessary to correct for the potentially confounding influence of variable added litter mass (litter input was based on a similar total litter C addition across species). Models with lowest Akaike information criterion (AICc) were retained. All data met the requested assumptions of these parametric tests. Statistical analyses for all data were carried out using SPSS version 16.0 (SPSS Inc., Chicago, IL, USA).

3 | RESULTS

3.1 | Litter decomposition and relationship with litter chemistry

The 15 common species used in this study exhibited a broad range of leaf litter chemistry properties (Table 1, Supporting Information Table S1). Lignin and lignin:N ratio ($r = 0.86$, $p < 0.001$), P and K ($r = 0.78$, $p < 0.001$), and Ca and Mg ($r = 0.74$, $p < 0.01$) were highly correlated (Supporting Information Table S3). At the initiation of the experiment, these litters all displayed a high carbon decomposition rate (i.e., high litter-derived CO_2 fluxes) that decreased quickly and markedly in the initial stages of litter decomposition (0–26 days) and then remained low during later stages of litter decay (27–125 days) (Figure 1, Supporting Information Table S4). The fraction of added litter C decomposed over the entire incubation period was 24% averaged across all 15 species with the lowest for *Phoebe bournei* (15%) and the highest for *Machilus pauhoi* litter (41%) (Figure 2). On average, 65% of the decomposition occurred in the early stage. Initial litter chemistry properties related only poorly to early and later stage leaf litter decomposition (Table 2). Whether in univariate or multivariate analyses, only Mn concentration explained some variation in litter decomposition in the early stage (negative relationship; $R^2 = 0.33$, $p = 0.03$), whereas N concentration explained some variation in litter decomposition in the later stage (negative relationship; $R^2 = 0.28$, $p = 0.04$) (Tables 2 and 3).

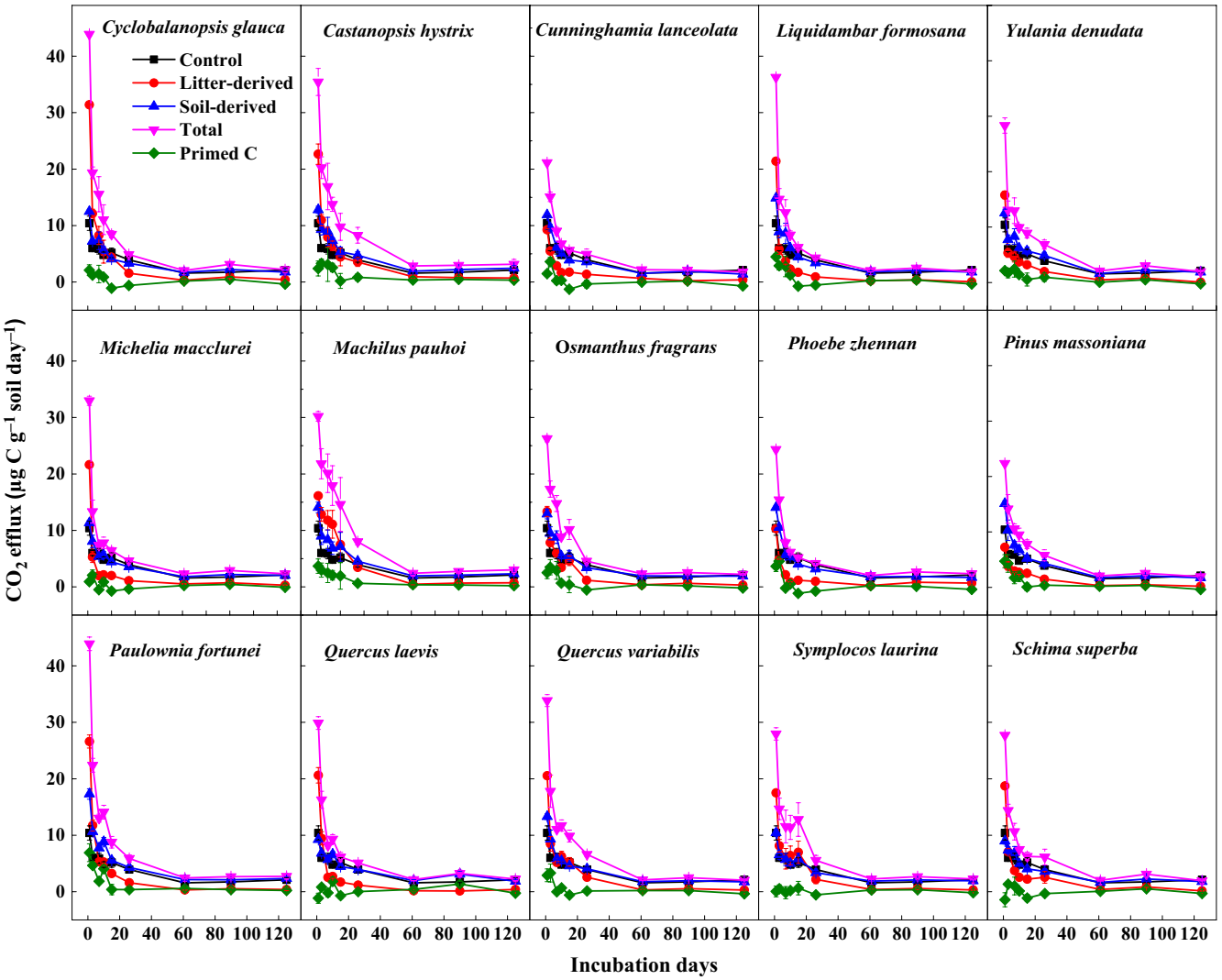

FIGURE 1 CO_2 effluxes from soil control (black lines with squares), plant-derived CO_2 (red lines with circles), soil-derived CO_2 (blue lines with triangles), total CO_2 (pink lines with inverted triangles) and priming of soil organic C (green lines with diamonds) during 125 days of incubation

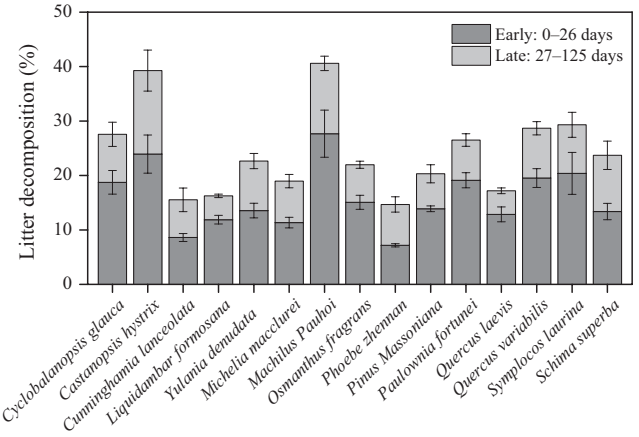

FIGURE 2 Cumulative fraction of added plant litter released as CO_2 during two stages of decomposition. Bars are means of three replicates ±1 *SE*

3.2 | CO_2 production and PE

Over the 125-day incubation period, mean daily CO_2 production from the control soil was 4 mg C kg^{-1} soil day^{-1}, but 8 mg C kg^{-1} soil day^{-1} from the soil with leaf litter. This ranged from 6 (*Phoebe zhennan*) to 11 mg C kg^{-1} soil day^{-1} (*M. pauhoi*) (Figure 3).

Across the 15 species, the magnitude of PE (*c.* 1 mg C kg^{-1} soil day^{-1}) at the early stage of decomposition was significantly higher than at the later stage (*c.* 0.2 mg C kg^{-1} soil day^{-1}; $p < 0.001$). Overall, in the first 26 days, added leaf litters significantly stimulated the decomposition of SOC by 24% on average, which was threefold higher than in the 27- to 125-day period (8% on average). Leaf litter addition induced additional SOC decomposition as compared to the control soil for all 15 species in the early stage of incubation (4–26 days) and all but two species in the later stage (27–125 days) (Figure 3). Nevertheless, the magnitude of this PE varied strongly among treatments. The PE ranged from 4% to 51% in the early stage of incubation and from a 7% reduction to a 25% enhancement in the later stage of incubation (Figure 3).

3.3 | Relationships between PE and leaf litter chemistry

Initial leaf litter chemistry and PE were significantly related, although these relationships differed among earlier and later stages of decomposition (Table 2). In the early stage of litter decomposition, the PE was positively related to the amount of litter C leachates and litter hemicellulose concentration and related negatively to tannin concentration (Table 2, Figure 4). In the later stage of litter decomposition, lignin and to a lesser extent the lignin:N ratio were related negatively to the PE, whereas K, Ca and Mg concentrations were positively related to the PE (Table 2, Figure 4). However, the PE was not related to initial N or P concentrations in either the early or later stage of decomposition. Additionally, the added litter mass only had a marginally significant effect on early PE ($R^2 = 0.20$, $p = 0.09$) and no significant effect on later PE ($R^2 = 0.00$, $p = 0.82$). Considering all litter traits together, the combination of tannin and hemicellulose concentrations appeared most relevant to explain the PE in the early stage of decomposition ($R^2 = 0.58$, $p = 0.006$), whereas lignin concentration was the single best explanatory variable in the later stage ($R^2 = 0.58$, $p = 0.001$) (Table 3).

3.4 | Relationships between litter decomposition and PE

Leaf litter decomposition rate was positively related to the PE during the early stage of litter incubation ($R^2 = 0.29$, $p = 0.04$; Figure 5a),

TABLE 2 Strength (R^2) and significance (p) of linear regressions between initial leaf litter chemical traits and leaf litter decomposition and priming effect during two decomposition stages

	Early stage				Later stage			
	Litter decomposition		Priming effect		Litter decomposition		Priming effect	
Trait	R^2 (+/–)	*p*-value	R^2 (+/–)	*p*-value	R^2 (+/–)	*p*-value	R^2 (+/–)	*P*-value
Litter C leachates	0.078 (+)	0.078	**0.298** (+)	0.035	0.049 (–)	0.429	0.241 (+)	0.063
Lignin	0.038 (+)	0.489	0.139 (–)	0.171	0.016 (–)	0.656	**0.584** (–)	0.001
Cellulose	0.009 (+)	0.734	0.254 (+)	0.056	0.006 (+)	0.782	0.235 (+)	0.067
Hemicellulose	0.193 (+)	0.094	**0.342** (+)	0.022	0.268 (+)	0.060	0.166 (+)	0.132
Tannin	0.108 (–)	0.233	**0.361** (–)	0.012	0.008 (–)	0.746	0.102 (–)	0.246
Lignin:N	0.000 (–)	0.960	0.006 (–)	0.786	0.022 (+)	0.595	**0.389** (–)	0.013
N	0.102 (–)	0.246	0.190 (–)	0.104	**0.284** (–)	0.041	0.021 (+)	0.604
P	0.017 (+)	0.644	0.006 (+)	0.791	0.068 (–)	0.347	0.234 (+)	0.068
Ca	0.219 (+)	0.08	0.042 (+)	0.466	0.035 (+)	0.506	**0.354** (+)	0.019
K	0.001 (–)	0.922	0.004 (–)	0.821	0.130 (–)	0.187	**0.312** (+)	0.031
Mg	0.06 (+)	0.371	0.022 (+)	0.602	0.001 (+)	0.773	**0.396** (+)	0.012
Mn	**0.331** (–)	0.025	0.085 (–)	0.293	0.135 (–)	0.178	0.238 (–)	0.065

Bold value denotes statistically significant relationship between litter decomposition (or priming effect) and litter initial traits.

TABLE 3 Outcome of determination of stepwise regressions between initial litter chemical properties and litter decomposition and priming effect at two decomposition stages. The strength (R^2) and significance (p) of models with lowest *AICc* are displayed

	Model					
	Early stage			Later stage		
	Traits	R^2	p	Traits	R^2	p
Litter decomposition	Mn	0.331	0.025	N	0.284	0.041
Priming effect	Tannin	0.361	0.018	Lignin	0.584	0.001
	Tannin; hemicellulose	0.575	0.006			

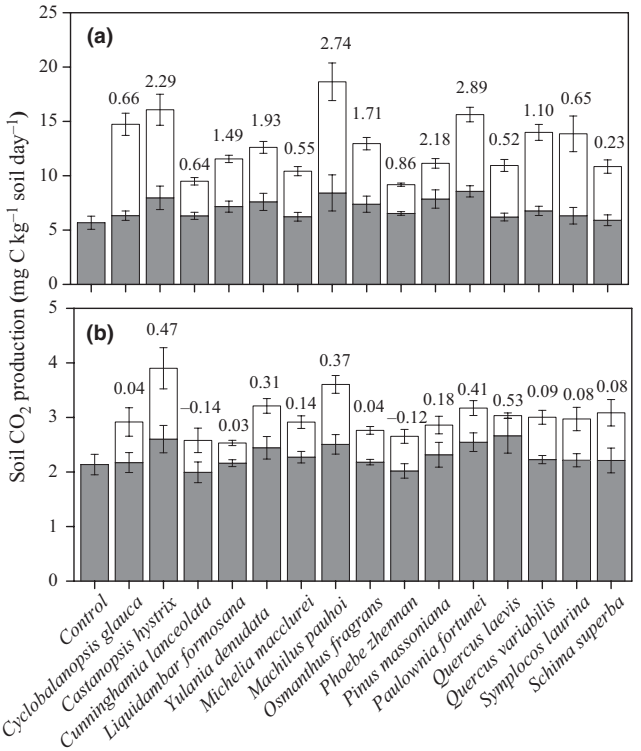

FIGURE 3 Mean daily SOM-derived CO_2 (grey bar), leaf litter-derived CO_2 (white bar) and CO_2 associated with the PE (data above the bars) in soils amended with litter at early stage (0–26 days) (a) and later stage (27–125) (b) of decomposition. Bars are means of three replicates ±1 *SE*

that is when the largest part of the PE occurred (76% averaged across all species), but there was no relationship between decomposition rates and PE in the later stage (p = 0.28; Figure 5b). Over the entire period of decomposition, litter decomposition rate was positively related to the PE (R^2 = 0.32, p = 0.03; Figure 5c).

4 | DISCUSSION

Our findings provide evidence that the magnitude and direction of the PE is influenced by the chemistry of organic matter (OM) inputs. In particular, the relative proportion of different C compounds in litter input, such as litter C leachates, hemicellulose, lignin and tannins, can have substantial influence on the soil PE. Importantly, as decomposition proceeds differently among litters of contrasting chemistry, litters can also have variable effects on soil PE over time. In this context, our results also suggest that in the medium term, litter compounds unrelated to the C resource, such as cation content (Ca, K, Mg), might also influence the magnitude of the soil PE.

4.1 | Variation in soil PE with litter addition and decomposition stages

In line with previous studies showing that different kinds of substrates can trigger PE to different extents (Blagodatskaya & Kuzyakov, 2008; Luo et al., 2016), we demonstrated here that different litters with contrasting chemistry also trigger variable PEs. The addition of leaf litter generally stimulated the decomposition of native SOC although in a few instances we also observed inhibiting effects or no effect of inputs on native SOC mineralization rates (Blagodatskaya & Kuzyakov, 2008; Kuzyakov, 2010; Wang et al., 2014; Zhang & Wang, 2012).

While the PE is generally defined as a short-term change in the turnover of soil OM caused by comparatively moderate treatment of the soil (Kuzyakov et al., 2000), the temporal dynamics of the PE has been rarely estimated (Kuzyakov, 2010). In a recent meta-analysis, Luo et al. (2016) observed significant positive PEs that strongly decreased over time but persisted up to 100 days after adding complex C substrates (such as plant litter) to soil. Our results support this and other results (Fontaine et al., 2011; Zhang & Wang, 2012) showing long-term effects of complex substrate additions on the soil PE. They further confirm across a range of litters with contrasting chemistry that the magnitude of the PE generally decreases predictably with time (Luo et al., 2016; Zhang et al., 2013). Among litter species, the significant relationship between litter decomposition and soil PE may suggest that faster litter decomposition rates trigger larger C accessibility to micro-organisms and therefore increase the PE. For all litters, the much faster decomposition rate in the initial compared to the later stages of decomposition also relates to the much stronger PE observed in the first 26 days of litter incubation. Previous studies have indeed shown that, as litter decomposition proceeds, labile fractions are quickly exhausted and recalcitrant C compounds like lignin and cellulose remain (Bray et al., 2012; Wickings, Grandy, Reed, & Cleveland, 2012; Yue et al., 2016). The C return on investment in lignolytic enzymes is hypothesized to be low

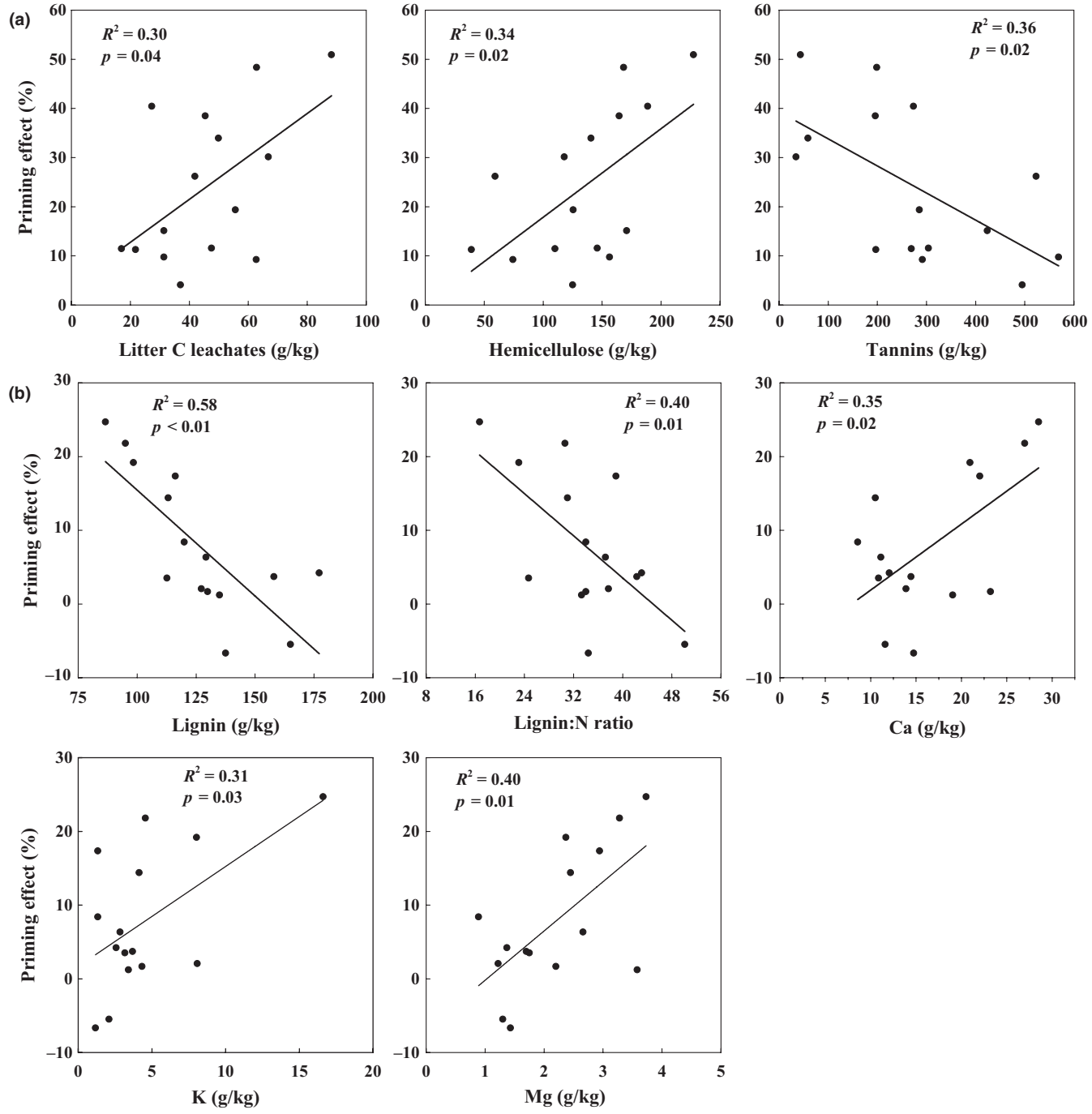

FIGURE 4 Relationships between priming effect and litter chemistry at early stage (a) and later stage (b) of decomposition. Strength (R^2) and significance (p) of linear regressions are displayed when significant

(Talbot & Treseder, 2012), therefore limiting the growth and activity of microbial communities feeding on lignin and potentially explaining the decrease in soil PE occurring in the later stage of decomposition.

4.2 | Leaf litter chemistry control on soil PE

In support of our overarching hypothesis, leaf litter chemistry strongly influenced the magnitude of the soil PE. The positive relationship between soil PE and the concentrations of litter C leachates and hemicellulose in the initial stages of decomposition may be mainly explained by the co-metabolism concept, resulting from stimulated microbial growth and enzyme production induced by the utilization of litter easily degradable C compounds (i.e., C leachates and hemicellulose), with consequences for both the decomposition of litter and native SOC (Kuzyakov et al., 2000; Qiao et al., 2013; Xiao et al., 2014). While lignin has conventionally been considered as a recalcitrant compound that protects hemicellulose and cellulose from degradation by microbes (Austin & Ballaré, 2010;

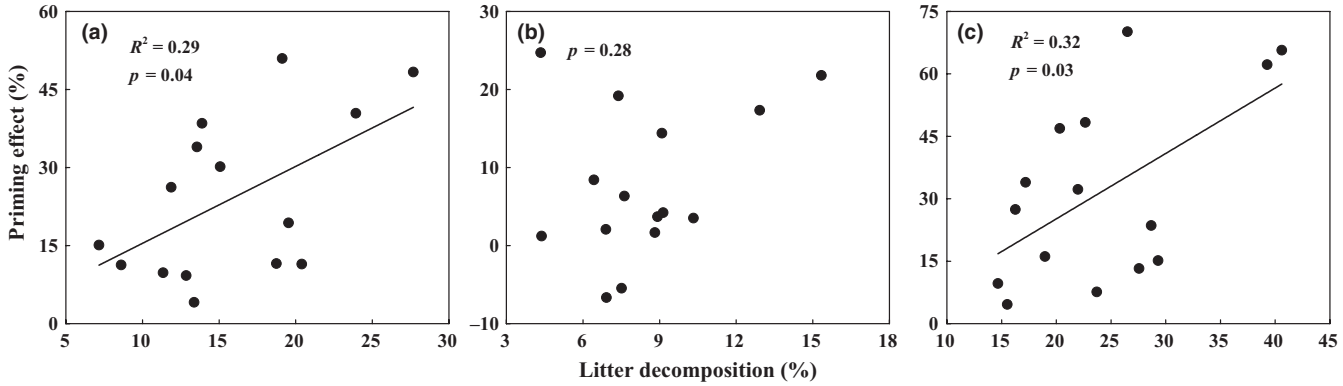

FIGURE 5 Relationships between litter decomposition and priming effect during days 0–26 (a), days 27–125 (b) and days 0–125 (c). Strength (R^2) and significance (p) of linear regressions are displayed when significant

Hall, Silver, Timokhin, & Hammel, 2015; Talbot & Treseder, 2012), unshielded hemicellulose is generally abundant in the early stages of decomposition. Therefore, this unshielded hemicellulose may have provided microbial communities with an easily accessible C source and thereby stimulated the soil PE in the early stage of decomposition, until the unshielded portions were exhausted. In contrast, the concentration of tannins was negatively associated with the PE in the early decomposition stage, possibly resulting from the inhibitory effect of tannins on soil enzyme activity, thus impeding SOC mineralization (Chomel et al., 2016; Liu et al., 2017), before tannin compounds were further degraded by soil microbial communities in the later stage of decomposition (Joanisse, Bradley, Preston, & Munson, 2007; Makkonen et al., 2012; Ushio, Balser, & Kitayama, 2013).

In support for our alternative hypothesis, a negative relationship between lignin and the PE was observed in the later stage of litter decomposition. As litter decomposition proceeds, the chemical composition of litter changes; labile C compounds are exhausted whereas recalcitrant litter compounds such as lignin tend to accumulate (Berg & McClaugherty, 2008; Coûteaux et al., 1995; Hall et al., 2015). A large proportion of lignin in litter would therefore correspond to a lower amount of decomposition by-products in the form of accessible C substrate at later stages of decomposition that may explain the lower soil PE. The substantial PE observed in the later stage of decomposition suggests nonetheless that other complex C sources may still be available for microbial communities (Luo et al., 2016) or that additional mineralization of SOC by the microbial community induced by earlier inputs persists after all easily accessible C substrates have been used (Fontaine et al., 2011).

Interestingly, the lack of a relationship between the soil PE and initial leaf litter N and P concentrations contrasts with previous studies that suggested that high soil N and P availability can decrease the soil PE (Fontaine et al., 2011; Wang et al., 2014). This lack of effect could be due to the already high availability of N (inorganic N = 132 mg/kg) and P (available p = 70 mg/kg) in the (chemically fertilized) agricultural soil used in our experiment, preventing any effect of additional N and P from litter on microbial stoichiometry and therefore on litter decomposition (Freschet, Aerts, & Cornelissen, 2012) and the PE (Luo et al., 2016). In contrast, we found a strong positive influence of several cation concentrations (Ca, K and Mg) on the soil PE in the later stage of litter decomposition. The positive influence of these cations could be linked to their role in relieving a potential deficiency of our experimental soil in such elements, thereby favouring long-term microbial growth, activity and litter decomposition (Cornelissen & Thompson, 1997) and stimulating SOC decomposition rates. However, given the strong correlation between Ca and Mg, their relative influence on later PE cannot be disentangled.

Finally, we acknowledge that our work, using only one homogeneous sample of litter per species, demonstrates the effect of between-species litter chemistry effects and does not represent the natural variability of within-species litter chemistry effects on soil PE, which precludes comparisons among species. Additionally, the use of ground litter was not entirely representative of the effect of typical litter input on soil PE and may have increased soil PE as compared to entire or coarsely chopped litter. For example, Nottingham et al. (2009) found that chopped and ground maize added to soil caused similar increases in the soil CO_2 efflux, but that ground maize caused a larger PE than chopped maize. Nonetheless, our methodological choice allowed us to establish important links between litter chemical quality and PE.

5 | CONCLUSIONS

We demonstrated here that leaf litter chemical traits (litter C leachates, hemicellulose, tannin and lignin, or even Ca, K and Mg) and litter decomposition rate strongly influence the magnitude and direction of the PE. Additionally, the dominant factors that control soil PE were different during contrasting stages of decomposition. While the lack of data on microbial biomass and community composition does not allow us to draw conclusions about the mechanisms behind the observed patterns, we note that these results are consistent with the idea that the access of microbial communities to litter-derived compounds (as controlled by litter decomposition rate) plays a role in driving the PE at early and intermediate stages of decomposition. A potential positive effect of high concentrations of recalcitrant compounds in litter, such as lignin, on the PE at later stages of decomposition was not observed. However, our results did not cover the entire period of litter decomposition and

do not exclude that microbial competition (e.g. the balance between different functional types of soil microbial communities mediated by litter chemistry effects) could become dominant at the latest stages of decomposition and eventually persist after the complete disappearance of litters (Fontaine et al., 2011). While this study demonstrated the potentially important effect of litter chemistry on the PE, further experiments using temporally explicit approaches are critically needed to explore the role of microbial biomass and community composition in mediating these effects. Moreover, soils with different properties should also be considered to further strengthen the validity of such experimental results across a range of soils and ecosystems.

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AUTHORS' CONTRIBUTION

W.D.Z. and S.L.W. designed the experiment. L.C. performed the experiment and led the writing of the manuscript with contributions from G.T.F., and F.A.D., L.C., Y.Y.L. and W.D.Z. analysed the data. X.Y., W.H.Z., X.G., Q.P.Y. and L.C.C. were involved in fieldwork and laboratory analysis. All authors contributed to revisions of the manuscript.

DATA ACCESSIBILITY

The data associated with this paper are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.b4s71jj (Chao et al., 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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