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RESEARCH ARTICLE

Plant litter chemistry controls coarse-textured soil carbon dynamics

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Abstract

1. As soils store more carbon (C) than the Earth's atmosphere and terrestrial biomass together, the balance between soil C uptake in the form of soil organic matter (SOC) and release as CO_2 upon its decomposition is a critical determinant in the global C cycle regulating our planet's climate. Although plant litter is the predominant source of C fuelling both soil C build-up and losses, the issue of how litter chemistry influences this balance remains unresolved.
2. As a contribution to solving that issue, we traced the fate of C during near-complete decomposition of ^{13}C-labelled leaf and root litters from 12 plant species in a coarse-textured soil. We separated the soil organic carbon into mineral-associated organic matter (MAOM) and particulate organic matter (POM) pools, and investigated how 14 litter chemical traits affected novel SOC formation and native SOC mineralization (i.e. the priming effect) in these soil fractions.
3. We observed an overall net increase in SOC due to the addition of litter, which was stronger for root than for leaf litters. The presumed stable MAOM-C pool underwent both substantial stabilization and mineralization, whereas the presumably less stable POM-C pool showed substantial stabilization and reduced mineralization. Overall, the initial increase in soil C mineralization was fully counterbalanced by a later decrease in native soil C mineralization. POM-C formation as well as MAOM-C formation and mineralization were positively related to the initial litter lignin concentration and negatively to that of the nitrogen leachates, whereas the opposite was observed for POM-C mineralization.
4. *Synthesis*. Our results highlight the importance of litter chemical traits for SOC formation, and stabilization, destabilization and mineralization. In our coarse-textured soil, the amount of MAOM-C did not change despite large C fluxes through this pool. The litter chemical traits that drove these processes differed from those frequently reported for fine-textured soils far from mineral-associated C saturation. To account for these discrepancies, we propose an

integrative perspective in which litter quality and soil texture interactively control soil C fluxes by modulating several SOC stabilization and destabilization mechanisms. Irrespective, our results open new critical perspectives for managing soil C pools globally.

KEYWORDS
carbon cycle, carbon saturation, decomposition, mineral-associated organic matter, particulate organic matter, plant litter traits, priming effect, soil organic matter

1 | INTRODUCTION

Predominantly fuelled by plant litter, soils store more than twice the amount of carbon (C) contained in the Earth's atmosphere and terrestrial biomass together (Lehmann & Kleber, 2015). By decomposing litters, soil organisms drive the formation of new soil organic matter (Cotrufo et al., 2013; Lehmann & Kleber, 2015) (SOM) and the mineralization of litter C and subsequent CO_2 release into the atmosphere (Kuzyakov, 2010; Perveen et al., 2019). Stimulated by fresh litter, decomposer communities may also accelerate native soil organic C (SOC) decomposition (priming effect; Kuzyakov, 2010; Liang et al., 2018; Perveen et al., 2019). In combination, these processes contribute to regulate the Earth's climate as well as to the capacity of soils to support ecosystem functioning and provide ecosystem services (Lavallee et al., 2020; Lehmann & Kleber, 2015).

It was supposed for some time that the inherent chemical properties of substrates added to soils determined their persistence. Over the last few decades, though, the view has emerged that the rate at which organic matter (OM) decomposes depends on its accessibility to decomposer organisms and the physicochemical environment in which they operate (Lehmann & Kleber, 2015; Schmidt et al., 2011). Substrates that can be rapidly decomposed (typically referred to as 'labile') may nevertheless persist for long a long time in soils when not accessible to decomposers, and inversely, substrates previously believed to resist decomposition (i.e. 'recalcitrant') have been shown to decompose fairly well under appropriate conditions (Klotzbücher et al., 2011, 2016; Marschner et al., 2008).

Long-term SOC sequestration, for centuries and more (Lavallee et al., 2020), occurs as plant litter and/or microbial decomposition products (hereafter 'biopolymers') associate with soil minerals forming mineral-associated organic matter (MAOM; Kleber et al., 2015; von Lützow et al., 2006). Organic matter in this fraction is protected from microbial degradation via several mechanisms, including its sorption onto mineral surfaces (Kleber et al., 2015; von Lützow et al., 2006), inclusion in nanometre- to micrometre-sized micro-aggregates (Chenu & Plante, 2006; Hatton et al., 2012), and co-precipitation with metal (Fe and Al) oxides (Kleber et al., 2015; von Lützow et al., 2006). Carbon stabilization in the MAOM fraction is limited, however, by soil texture, that is, the amount of fine particles (clay + fine silt; i.e. <20 μm) that provide mineral surfaces for OM sorption, and function as nuclei for novel micro-aggregate formation (Lehmann et al., 2007; Totsche et al., 2018). Extensive OM occupation of reactive mineral sites brings this soil fraction close to its theoretical maximum C storage capacity, which Hassink (1997) refers to as the maximum capacity to preserve C. In view of inherent limitations when exclusively focusing on fine particles to quantify a soil's capacity to sequester C (see Matus, 2021; Stewart et al., 2009), we hereafter refer to mineral-associated (rather than 'soil') C saturation when considering the theoretical maximum C storage capacity related to a soil's fine particle fraction.

In contrast, the C contained in the particulate organic matter (POM), spanning a continuum of physically uncomplexed, partly decomposed litters to recalcitrant and mineral-free compounds, has shorter residence times, but still builds up over decades when physically protected from microbial degradation, for instance by occlusion in larger aggregate structures (Gregorich et al., 2006). For this fraction, no clear limits on C storage have yet been identified (Lavallee et al., 2020). Therefore, despite widespread focus on long-term MAOM-C sequestration and its potential in view of climate change mitigation, a more integrative 'whole-soil' (MAOM + POM) approach to C storage is urgently needed (Barré et al., 2017).

The recently developed framework of SOM formation and stabilization (Microbial Efficiency-Matrix Stabilization, MEMS; Cotrufo et al., 2013) holds that litters with high contents of labile (i.e. easily degradable) compounds enhance SOM formation more than those rich in recalcitrant compounds as the former are more efficiently converted to microbial biomass and metabolic products, which are believed to be the principal SOM precursors (Miltner et al., 2012; Ludwig et al., 2015; but see Angst et al., 2021). This superior efficiency is of particular relevance for SOM accumulation when the stabilization capacity of the soil matrix is high. Yet, observations that roots contribute disproportionally to SOC stocks (Clemmensen et al., 2013; Kätterer et al., 2011; Rasse et al., 2005), despite their higher recalcitrance relative to leaf litters, raises some questions. Whether this high contribution of roots provides a challenge to the MEMS framework or, alternatively, points to other mechanisms enhancing root-derived SOC stocks, can be debated. For instance, predominantly labile root exudates (Berhongaray et al., 2019; Lavallee et al., 2018; Sokol et al., 2019), as well as root-associated fungi (Clemmensen et al., 2013), may favour the formation of root-derived SOC relative to leaf-derived SOC. The immediate proximity of root litters and root exudates to soil minerals has also been suggested to favour the rapid stabilization of root decomposition products (Lavallee et al., 2018; but see Rasse et al., 2005). Laboratory studies

incubating dead litters, thus excluding root exudation and litter-soil proximity as potential explanations, have found no effect of litter type (leaves vs. roots) on SOC (Steffens et al., 2015), nor enhanced incorporation of litter C in the SOC for root compared to leaf litters (Hu et al., 2016). These latter observations, then, raise questions about the microbial efficiency pillar of the MEMS framework.

Apart from playing a central role in SOC formation, the input of fresh OM can also stimulate native SOC decomposition (positive 'priming effect') by alleviating energy constraints on microbial activity and biomass (Fontaine et al., 2011; Kuzyakov, 2010). Native SOC mineralization is often reduced when nitrogen (N) is in sufficient supply as this may reduce the need for N mining (Chen et al., 2014; Fontaine et al., 2011). While priming has been studied extensively, its persistence up to complete decomposition of OM inputs—a recent meta-analysis reported that few studies only lasted longer than half a year (Luo et al., 2016), its control by litter quality, as well as its significance for different SOC fractions (e.g. MAOM-C vs. POM-C) are poorly understood.

Current theory holds that OM persists in soils as long as it is shielded from microbial attack. As a corollary, the protective capacity of organo-mineral complexes against microbial degradation of OM should reduce priming in the MAOM fraction relative to the POM fraction. Consistent with this expectation, in a grassland transect study, Chen et al. (2019) found SOM stabilization through organo-mineral interactions to significantly reduce the priming effect. Specifically, priming was inversely related to the soil's capacity to provide C protection (high molar Fe/Al oxides and exchangeable Ca to SOC ratios) and occlusion in micro-aggregates (see Rasmussen et al., 2007 for corresponding results). High clay + silt content also reduced C priming. In contrast, priming scaled positively with the proportion of C in macro-aggregates (see Tian et al., 2016 for similar findings of priming in distinct aggregate size classes). The protective capacity of organo-mineral complexes appears limited, though. No protection provided by the soils' Fe and Al oxides nor by its clay content appeared in a large-scale study by Perveen et al. (2019) including 35 contrasting soils. In addition, root exudates are able to destabilize MAOM (Keiluweit et al., 2015), both via the direct (acid-driven) destabilization of organo-mineral complexes, as well as indirectly via enhanced (microbial) enzyme secretion (Jilling et al., 2021). In combination, these results suggest that OM in organo-mineral associations may indeed provide SOC with some protection against microbial attack, but also indicate that not all OM in the MAOM fraction is irreversibly bound.

Here, we traced the fate of ^{13}C-enriched leaf and root litters from 12 herbaceous plant species, that is, a total of 24 litters of contrasting chemistry (Figure S1) until near-complete disappearance of litter residues with the aim to test the overall effect of litter input and chemistry on SOM (i.e. POM and MAOM) formation, stabilization and destabilization by incubating them in a sandy-loam soil near mineral-associated C saturation. We expected (i) new SOC to mainly accumulate in the POM fraction (Castellano et al., 2015; Stewart et al., 2009), and this accumulation to be primarily driven by recalcitrant plant compounds, in particular lignin (Cotrufo et al., 2015). We expected novel MAOM formation, in contrast, to be limited and driven by labile plant compounds (Cotrufo et al., 2013, 2015). As a corollary, we expected more novel SOC formation (through POM-C) for root than for leaf litters. We further expected (ii) to observe a positive priming effect on the whole-soil level (Kuzyakov, 2010; Perveen et al., 2019), but less so for litters with high initial N and N leachate content, as this may reduce the need for N mining (Chen et al., 2014; Fontaine et al., 2011). In contrast, as priming occurs through the alleviation of microbial energy constraints, easily degradable C sources, in particular C leachates, were expected to enhance priming in the early decomposition phase. As organo-mineral complexes may protect OM from SOM decomposers to some extent, we expected to observe priming mainly in the POM fraction.

2 | MATERIALS AND METHODS

2.1 | Production of ^{13}C–^{15}N labelled plant material

Twelve herbaceous species (*Bituminaria bituminosa*, *Brachypodium phoenicoides*, *Bromus erectus*, *Bromus madritensis*, *Clinopodium nepeta*, *Crepis foetida*, *Dactylis glomerata*, *Daucus carota*, *Medicago minima*, *Picris hieracioides*, *Tordylium maximum* and *Trifolium angustifolium*), representative of southern France Mediterranean old-field succession, were selected on the basis of contrasting life histories (five annuals, two biennials and five perennials), taxonomic groups (Poaceae, Fabaceae, Lamiaceae, Apiaceae and Asteraceae) and functional traits both above- and below-ground (Figure S1; Birouste et al., 2012). Seeds from these species were collected in August 2014 and set to germinate in September for 3 weeks. Seedlings were then transplanted to pots filled with a nitrogen-poor soil containing <1 g kg^{-1} inorganic carbon (the same soil as used for litter incubation, as described below) at a density of 200 individuals per m^2. Pots were placed in an air-tight glasshouse under natural light conditions with automated air-cooling (temperature allowed to fluctuate between 15 and 28°C), irrigation, air humidity control and CO_2 injection. Plants were grown under a $^{13}CO_2$-labelled atmosphere for 5 months by automated injection of 4 at% ^{13}C-CO_2 each time the chamber CO_2 concentration fell below 440 ppm. Soil released ^{12}C-CO_2 was responsible for temporal variation in the chamber ^{13}C-CO_2 concentration, with accumulation of ^{12}C-CO_2 inversely correlated with CO_2 fixation by plants and the intensity of photosynthesis. Measures made at mid-experiment indicated that the ^{13}C-CO_2 concentration in the chamber varied from 1.2 at% at dawn at the peak of overnight soil CO_2 accumulation to 1.4 at% in early afternoon at the peak of plant CO_2 fixation, providing a fairly constant concentration of ^{13}C-CO_2 of 1.27 at% (±0.05 SE) along the day. Pots underwent monthly addition of a ^{15}N solution (50/50 nitrate/ammonium in the form of 10 at% ^{15}N $Ca[^{15}NO_3]_2Na$ and $^{15}NH_4Cl$) in increasing amounts from 2 to 8 g N m^{-2} for a total of 18 g N m^{-2}. During the last month, irrigation was reduced step-by-step to induce plant senescence. None of the plant species had started to produce reproductive organs. At the end of the senescence period, plants were harvested and sorted into leaf, stem, tap roots and fine roots (i.e. all roots except tap roots, corresponding

here to roots of the three most distal orders). Root samples were carefully cleaned with water before sorting. All material was air-dried at 25–30°C. Leaf and fine-root material was subsequently considered as litter and used in trait analyses and decomposition experiments.

Leaf and fine-root samples were measured for ^{13}C and ^{15}N concentrations on a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd.). Three subsamples were used to assess the homogeneity of the labelling among leaves of the same species and fine roots of the same species. Although this varied among species, leaf litter showed an average enrichment of 2.56 at% ^{13}C (ranging from 2.19 to 2.82) and 6.49 at% ^{15}N (ranging from 5.00 to 8.32) and fine-root litter showed an average enrichment of 2.50 at% ^{13}C (ranging from 2.35 to 2.64) and 6.32 at% ^{15}N (ranging from 4.80 to 7.60).

2.2 | Litter trait measurements

A set of 14 chemical traits was measured on the leaf and fine-root litter subsamples from our 12 species (Figure S1). This included the concentrations of carbon (C) and five nutrients, nitrogen (N), phosphorus (P), magnesium (Mg), calcium (Ca) and manganese (Mn), the concentrations of water-soluble compounds, hemicellulose, cellulose, lignin and condensed tannins, and the concentrations of C, N and P in litter leachates. Specifically, C and N were measured on a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd.). P, Mg, Ca and Mn were measured, after acid mineralization, by plasma emission spectrometry (ICP-MS, Thermo Scientific iCAP Q, Thermo Fisher Scientific GmbH, Germany). The concentrations of water-soluble compounds, hemicellulose, cellulose and lignin were obtained by the van Soest method (van Soest, 1963) with a Fibersac 24 fibre analyser (Ankom). Condensed tannins were measured according to the acid butanol method (Coq et al., 2010; Waterman & Mole, 1994). Litter leachates were obtained by extracting 0.5 g of litter (air-dried and cut in 1 cm long pieces) in 30 ml of distilled water for 30 min on an end-over-end shaker (20 rpm at 20°C), then filtered at 0.45 µm. Total C and N concentrations in the extracts were analysed using an automated TOC-TN analyser (Shimadzu, TOC-Vcph, Japan). Total P concentration was determined colorimetrically after digestion with sulphuric acid and hydrogen peroxide (35 min at 100°C and 2 h at 360°C) by the molybdenum blue method, with an autoanalyser (Evolution II; Alliance Instrument). Litter leachates correspond to easily accessible compounds at early stages of the litter incubation and can influence the microbial decomposer community stoichiometry and nutrient limitation (Fanin et al., 2013).

2.3 | Litter incubation experiment

The soil used for litter incubation, excavated in Villefort (France; 44°43′N, 3°92′E), was a brunisol developed on a schist parent material (https://www.geoportail.gouv.fr/donnees/carte-des-sols). The soil was sieved at 5 mm, spread in trays, and humidified to induce germination of the seed bank. After 2 weeks, the germinated seeds were manually removed and the soil was air-dried until constant mass, then sieved at 2 mm and homogenized. Sets of subsamples were used for soil physicochemical characterization and to estimate soil residual humidity (oven-dried at 105°C) and soil field capacity. The soil had a pH of 7 and a sandy-loam texture [9% clay (<2 µm), 17% fine silt (2–20 µm), 9% coarse silt (20–50 µm), 12% fine sand (50–200 µm) and 53% coarse sand (200–2000 µm)]. The soil had C and N concentrations of 15 and 1.1 $g\,kg^{-1}$, respectively, a P availability of 0.035 $g\,kg^{-1}$ Olsen-P and a cation exchange capacity of 7.75 $cmol\,kg^{-1}$. Total soil C was considered equivalent to SOC since the soil did not contain significant amount of inorganic carbon.

Hassink (1997) proposed that the theoretical value of C saturation of a soil can be calculated as: 4.09 + 0.37 (% fine silt + clay). For the soil used in this study, the theoretical value for C saturation is therefore 13.7 $g\,C\,kg^{-1}$. This figure is, theoretically, the maximum amount of stable SOC (SSOC) that can be retained by organo-mineral interactions with fine silt and clay particles, referred hereafter as the (theoretical) mineral-associated C saturation. In our coarse-textured soil, the (initial) C in the MAOM fraction was 12.9 $g\,C\,kg^{-1}$ (with minimal and maximal values of 11.9 and 14.0 $g\,C\,kg^{-1}$ respectively) representing 86% ± 7% of total SOC, a value close to that of Angers et al. (2011), who estimated that the actual SSOC concentration of a soil represents ~85% of total SOC. Considering the theoretical value for C saturation of our soil calculated above, the soil used in this study has reached: $[1-(13.7-12.9)/13.7]\times 100 = 94.2\%$ of its theoretical C saturation level (with minimal and maximal values of 86.5% and 101.8% respectively). The C saturation level of our soil surpassed 90% whatever the calculation method used (see text S1).

Leaf litter and fine-root litter from each of the 12 species were cut in 1 cm^2 and 1 cm long pieces, respectively, thoroughly homogenized and 12 samples of 0.4 g were weighed for each of the 24 litter materials. Each of these samples was thoroughly mixed with 50 g of air-dried, 2 mm sieved soil and transferred to a 80 ml jar in two steps to allow the placement of a polyester mixed bed ionic resin capsule (PST1; Unibest) in the centre of the jar. Fifteen jars of bare soil were prepared in the same way. This resulted in 303 jars, representing three replicates of four sequential harvests of 24 types of soil-litter mixtures and one bare soil. At the start of the experiment, soils were brought to 80% field capacity using distilled water and jars were closed with pierced lids allowing gas exchanges. Soil humidity decreased only moderately during the course of the incubation. The microcosms were kept in a dark chamber at 25°C for the whole duration of the experiment. Three replicates of control soil without litter input were harvested to measure soil C and ^{13}C at% concentration and conduct soil fractionation. Then, three replicates of each type of jar were harvested at four time steps, that is, after 10, 38, 157 and 367 days. Upon harvest the content of jars was spread on plates to dry at a temperature of 25°C. Subsamples of soil (including litter fragments) were analysed for C concentrations and ^{13}C at% on a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd.). Litter

decomposition dynamics were assessed on a 10 g subsample of incubated soil-litter mixture by manually sorting litter pieces remaining in the soil. Litter samples were ground with a ball mill and measured for C and N concentrations using an elemental analyser (CHN model EA1108; Carlo Erba Instruments).

2.4 | Soil fractionation

Both control soils and soils in which litter had decomposed for 1 year were fractionated. No litter fragments were taken from the latter soils prior to fractionation. As at that moment on average 97% of the initial litter C had decomposed, all remaining litter residues must have undergone strong decomposition, and should be considered as POM. Soil samples (6 g) were fractionated via a physical fractionation procedure as described in detail in Golchin et al. (1994). Briefly, soils were separated into a light particulate organic matter fraction (POM; <1.6 g cm^{-3}) and a dense mineral-associated organic matter fraction (MAOM; >1.6 g cm^{-3}) (Lavallee et al., 2020). The POM was isolated in two steps. First, soils were suspended in 25 ml of a sodium iodide (NaI) solution with a density of 1.6 g cm^{-3} within a 50 ml polypropylene centrifugation tube (Sarstedt AG & Co). The tubes were gently shaken manually 20 times with an end-over-end movement and centrifuged during 35 minutes at 8000 RPM. The free light fraction floating on top of the NaI solution was then aspirated with a filtration unit and rinsed with 200 ml of distilled water on a 0.45 µm filter. The remaining soil was resuspended with ~25 ml NaI and 12 glass beads (6 mm diameter) were added into the tubes. The latter were then capped, shaken for 1 h on a reciprocal shaker to destroy macro- and large micro-aggregates, and centrifuged 35 min at 8000 RPM to liberate the occluded organic matter. The light fraction floating on top of the NaI solution was recovered and rinsed with 200 ml of distilled water on a 0.45 µm filter. Following the POM removal, the residual soil remaining at the bottom of the tube was resuspended with ~30 ml of distilled water to rinse the remaining dense fraction (i.e. MAOM). The tubes were capped again, vigorously shaken manually for 1 min to fully resuspend the residue, and centrifuged 15 min at 8000 RPM after which the water was removed with the aspiration unit. The rinsing procedure was repeated twice for a total of three rinsings. The cleaned fractions were oven-dried at 60°C. The dried weight of the POM and MAOM fractions were measured and their C concentrations and ^{13}C at% were analysed on a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd.).

2.5 | Community level physiological profiles

The community level physiological profile (CLPP) of the soil microbial community was assessed on approximately 22 g of air-dried soil from all harvested microcosms using the MicroResp™ system (Macaulay Scientific Consulting; Campbell et al., 2008). These soil sub-samples were homogenized and checked in order to ensure an even distribution of remaining litter fragments within MicroResp DeepWell Microplates. CLPP can be used to derive information on functional or metabolic diversity and to indicate shifts in microbial community structure and functioning (Bending et al., 2002). About 0.45 g of air-dried soil including remaining litter fragments was incubated in triplicate in 96-DeepWell Microplates (Fisher Scientific E39199) together with a solution containing 1.5 mg C of ^{15}C substrates (except for the low-soluble phenolic acids and cellulose, for which 0.75 mg C g^{-1} soil was added), so as to reach 80% of field capacity. This was repeated for three C substrates, namely the caffeic, syringic and vanillic phenolic acids that correspond to lignin subunits. Gel detection plates were prepared as recommended by the manufacturer with 1% Oxoid Agar, 12.5 µg ml^{-1} Cresol red, 150 mM KCl and 2.5 mM NaHCO3. After an initial 2 h pre-incubation step at 25°C in the dark to account for the lag period, each microplate was covered with a detection plate using a silicone gasket (MicroResp™). The assembly was secured with a clamp and incubated for four additional hours. Optical density at 590 nm (OD590) was measured in detection wells before and after incubation using a Victor 1420 Multilabel Counter (Perkin Elmer). Final OD590 were normalized using pre-incubation OD and converted to substrate-induced respiration (SIR) rates expressed in µg $C\text{-}CO_2$ g^{-1} air-dried soil h^{-1}. The mean values for the triplicate wells were used for further data analyses.

2.6 | Calculations

Decomposition rate constants (k) and limit values (A) were calculated from the equation:

$$LMR = A + (1 - A) \times e^{-kt}, \quad (1)$$

where LMR is the litter mass remaining and t is the time (days).

The amount of C in the initial litter (hereafter 'initial litter C' [g]) was calculated as litter mass (0.4 g) multiplied by the initial litter C concentration, and varied between litter types and species (see Figure S1).

The amount of C remaining in the decomposing litter (hereafter 'remaining litter C' [g]) at time t_n was calculated as the product of the litter mass remaining and its C concentration at harvest t_n.

Litter C loss at time t_n was expressed as initial litter C minus remaining litter C at harvest t_n.

The total litter-derived C remaining in the microcosm (hereafter 'litter-derived C' [g], i.e. remaining litter C + litter-derived SOC) at time t_n was assessed using the isotopic mixing model:

$$\text{Litter-derived C (g)} = (\delta_{treat} - \delta_{cont}) / (\delta_{litter} - \delta_{cont}) \times [\text{microcosm C}] \times MM, \quad (2)$$

where δ_{treat} and δ_{cont} represent the $\delta^{13}C$ of the microcosm (mix of soil and remaining litter) under litter treatment and in the control soil at harvest t_n respectively. δ_{litter} represents the $\delta^{13}C$ of the initial litter. [microcosm C] represents the C concentration in the microcosm (mix of soil and remaining litter) at harvest t_n (g g^{-1}) and MM is the initial dry

mass (50 g) of soil in the microcosm that was assumed to remain fairly constant during the incubation (<1% difference across microcosms and time if considering litter addition and C loss via respiration).

The amount of C in microcosm soil that originated from initial litter C (hereafter 'litter-derived SOC' (g)) at time t_n was calculated by subtracting remaining litter C (g) at harvest t_n from litter-derived C (g) at harvest t_n.

The amount of litter C respired from the microcosm (hereafter 'respired litter C' (g)) at time t_n was obtained by subtracting remaining litter C (g) at harvest t_n and litter-derived SOC (g) at harvest t_n from initial litter C (g).

The amount of litter C decomposed in the microcosm (hereafter 'decomposed litter C' (g)) at time t_n was obtained by subtracting the remaining litter C (g) at harvest t_n from the remaining litter C (g) at harvest t_{n-1}. The litter C loss and the litter C decomposed at any time t_n only differ in terms of time period assessed, which is relative to t_0 and t_{n-1} respectively.

The rates of litter C loss, respired litter C and litter-derived SOC between two consecutive harvests were calculated by estimating the difference between harvest t_n and t_{n-1} and expressing it per day of the period $t_n - t_{n-1}$.

An estimate of C transfer efficiency (TE) from litter to soil across the entire incubation year was calculated as TE = 1 − (litter respired C/litter C loss), where the ratio represents the proportion of litter C respired as a fraction of the litter C loss (see also Figure S6).

The amount of native C remaining in the microcosm soil (hereafter 'native SOC' (g)) at time t_n was calculated as:

$$\text{Native SOC (g)} = [\text{microcosm C}] \times \text{MM - remaining litter C} - \text{litter-derived SOC}, \quad (3)$$

where [microcosm C] represents the C concentration in the microcosm (mix of soil and remaining litter) at harvest t_n ($g\,g^{-1}$), MM is the initial dry mass (50 g) of soil in the microcosm and remaining litter C and litter-derived SOC are measured at harvest t_n. Note that at t_0, the term 'remaining litter C–litter-derived SOC' equates the initial litter C.

Priming refers to changes in the mineralization of native soil C driven by fresh C supply (Kuzyakov, 2010). The amount of primed C, that is, the amount of native SOC decomposed following fresh organic matter addition relative to the amount without such addition, at time t_n was calculated as the native SOC at harvest t_n in the control microcosms that had not received litter, minus the amount of native C remaining at harvest t_n in the microcosms where we added litter:

$$\text{Primed C (g)} = \text{native SOC}_{\text{cont}} - \text{native SOC}_{\text{treat}} \quad (4)$$

with positive values indicating higher soil C loss with litter addition. The primed POM-C and primed MAOM-C were calculated in the same way, by replacing whole-soil native SOC_{cont} and native SOC_{treat} by their POM and MAOM fractions respectively.

The net C balance ($mg\,C\,g^{-1}$ soil) was calculated as the litter-derived SOC minus the primed C. For the POM and MAOM fractions, the net C balance was calculated as the POM-C minus primed POM-C and MAOM-C minus primed MAOM-C respectively. For these calculations, litter-derived SOC, POM-C, MAOM-C, primed C, primed POM-C and primed MAOM-C were expressed as $mg\,C\,g^{-1}$ soil.

In order to provide scaled numbers more appropriate to the comparison with other studies, all of the indices described above were expressed per initial C content of native soil or per initial litter C content.

2.7 | Statistical analysis

All statistics were computed using R version 3.6.3 (www.r-project.org). We used model averaging (using the 'MuMIn' package version 1.43.15) to assess the influence of the predictors (i.e. chemical traits) on the independent variables. For each independent variable, the set of predictors was reduced based on a priori knowledge of the role of chemical traits in soil processes (Section 2.8). We performed model averaging on the set of models whose AICc values were similar to that of the best model (i.e. $\Delta AICc \leq 3$) to avoid unnecessarily restricting the number of potentially informative models yet keep their number lower than that of the number of predictors. We verified the robustness of our reported results by also running all analyses for $\Delta AICc \leq 2$, which hardly affected the results. Problems of collinearity were minimized by omitting predictors from the analysis when Pearson correlations were larger than 0.7 (Dormann et al., 2013) (Table S5). All predictors were centred and divided by their standard deviation prior to the linear modelling. Differences between leaf and root litters were assessed using pair-wise *t*-tests.

2.8 | Litter chemical trait predictors

Litter chemical traits were used to predict observed patterns allowing generalization beyond species identity effects. Litter type (i.e. leaf vs. root litters) was not included as predictor in the linear models we constructed as it co-varied with the majority of litter chemical traits (see Figure S1). Total C concentration was omitted as predictor as its variation among species was approximately an order of magnitude lower than that of all other chemical traits (see Figure S1). Predictors were chosen based on reported effects in the literature on all our dependent variables. In order to limit the number of model parameters, ratios and interactions between chemical traits were also omitted. Retained predictors were as follows:

Decomposition rate: cellulose (Bhatnagar et al., 2018; López-Mondéjar et al., 2016), hemicellulose (López-Mondéjar et al., 2016), lignin (Hobbie et al., 2006; Klotzbücher et al., 2011; Stewart et al., 2015), tannins (Coq et al., 2010), water-soluble compounds (WSCs), containing (among others) compounds that are easily assimilated, and the nutrients nitrogen (N) (Ochoa-Hueso et al., 2020; Talbot & Treseder, 2012; Zhang et al., 2008), phosphorus (P) (Cornelissen & Thompson, 1997; Ochoa-Hueso et al., 2020) and their leachates (as well C leachates), as well as calcium (Ca) (Hobbie et al., 2006; Zhang et al., 2008), magnesium (Mg) and manganese

(Mn) (Ochoa-Hueso et al., 2020). The same predictors were used for the decomposed litter-C and the respired litter-C.

Priming: priming is sensitive to the quality of the fresh organic matter added (Di Lonardo et al., 2017; Lyu et al., 2019; Shahbaz et al., 2017), and diminishes with increasing soil nutrient availability, including N, P, Ca and Mg (Liu et al., 2018). To test for the effect of C quality, we included hemicellulose and cellulose, lignin, tannins and C leachates. To test for the effect of nutrient availability, N and P and their leachates, as well as Ca, Mg and Mn were further retained as predictors. Identical predictors were retained for whole-soil priming as well as that of the particulate organic matter (POM) and mineral-associated organic matter (MAOM) fraction.

Soil organic matter (SOM) formation: recent conceptual advances suggest that high quality litters enhance efficient soil organic matter (SOM) formation relative to low quality litters containing relatively high concentrations of recalcitrant compounds, particularly when the soil mineral matrix has a high organic matter stabilization capacity (Cotrufo et al., 2013), but see (Castellano et al., 2015; Huang et al., 2019). C as well as the nutrients N, P, Ca, Mg and Mn (as well as others not presently assessed) co-limit microbial decomposition and mediate the activity of certain exoenzymes (Ochoa-Hueso et al., 2020). Furthermore, Ca^{2+}, Mg^{2+} and Mn^{2+} cations may be involved in SOM stabilization via polyvalent cation bridging (von Lützow et al., 2006; Wiesmeier et al., 2019). For the litter-derived SOC, the POM-C and the MAOM-C, we included the same predictors as for decomposition rate (above). The same predictors were also used to model net-C balance.

3 | RESULTS

3.1 | Litter C decomposition and respiration

An average of 97% (±2.5 SE) of the initial litter C was decomposed after 367 days (Figure 1a, Figure S2), with small but highly significant (Table S2) differences between leaf and root litters, whose initial litter C was 98% (±1.7 SE) and 95% (±2.0 SE) decomposed respectively. In the first half year (only), the graminoids decomposed more slowly than the legumes and forbs (Figure S2), most likely due to their higher cellulose (and hemicellulose) but lower water-soluble compound concentrations (Figure S3), which controlled the litter C decomposition in that period (Table S3). As the calculation of the remaining litter C is constrained by the difficulty of identifying remaining partially decomposed litter fragments, this number likely represents an upper bound. This limited precision notwithstanding, the estimated decomposition rates indicated that by decomposing the litters in highly favourable conditions, our 1-year incubation effectively simulated multi-year decomposition in the field (Table S4). Leaf litters ($k = 0.162\,g\,g^{-1}\,day^{-1}$) decomposed faster than root litters ($k = 0.091\,g\,g^{-1}\,day^{-1}$; $t_{11} = 3.840$, $p = 0.003$; Table S2). Similarly, at each harvest but the first, significantly more leaf litter C than root litter C was respired (Figure 1b). Cumulatively, after 1 year, the amount of the initial respired litter C for leaf and root litters was 77% (±4.3 SE) and 66% (±6.6 SE) respectively. The respired litter C did not vary significantly at any moment among the three plant functional groups (all $p > 0.05$).

3.2 | SOC formation

New SOC formation, representing the balance between litter-derived biopolymers entering the SOC pool and C leaving it as respired CO_2 (Figure 1b), occurred rapidly initially but diminished subsequently (Figure 1c). This new SOC represented a substantial part of the initial litter C, ranging from 18% to 45% after 1 year, and was significantly higher for root than for leaf litter (Figure 1c, Table S2). At most harvests, less novel SOC was formed by the graminoids than by the legumes and forbs, even though this effect vanished for the leaf litters and weakened for the root litter at the end of the year (Figure S4). As for the decomposed litter C, variation across all litters were likely due to differences in cellulose, hemicellulose and water-soluble compound concentrations (Figure S3), as these controlled the formation of novel litter-derived SOC (Table S3).

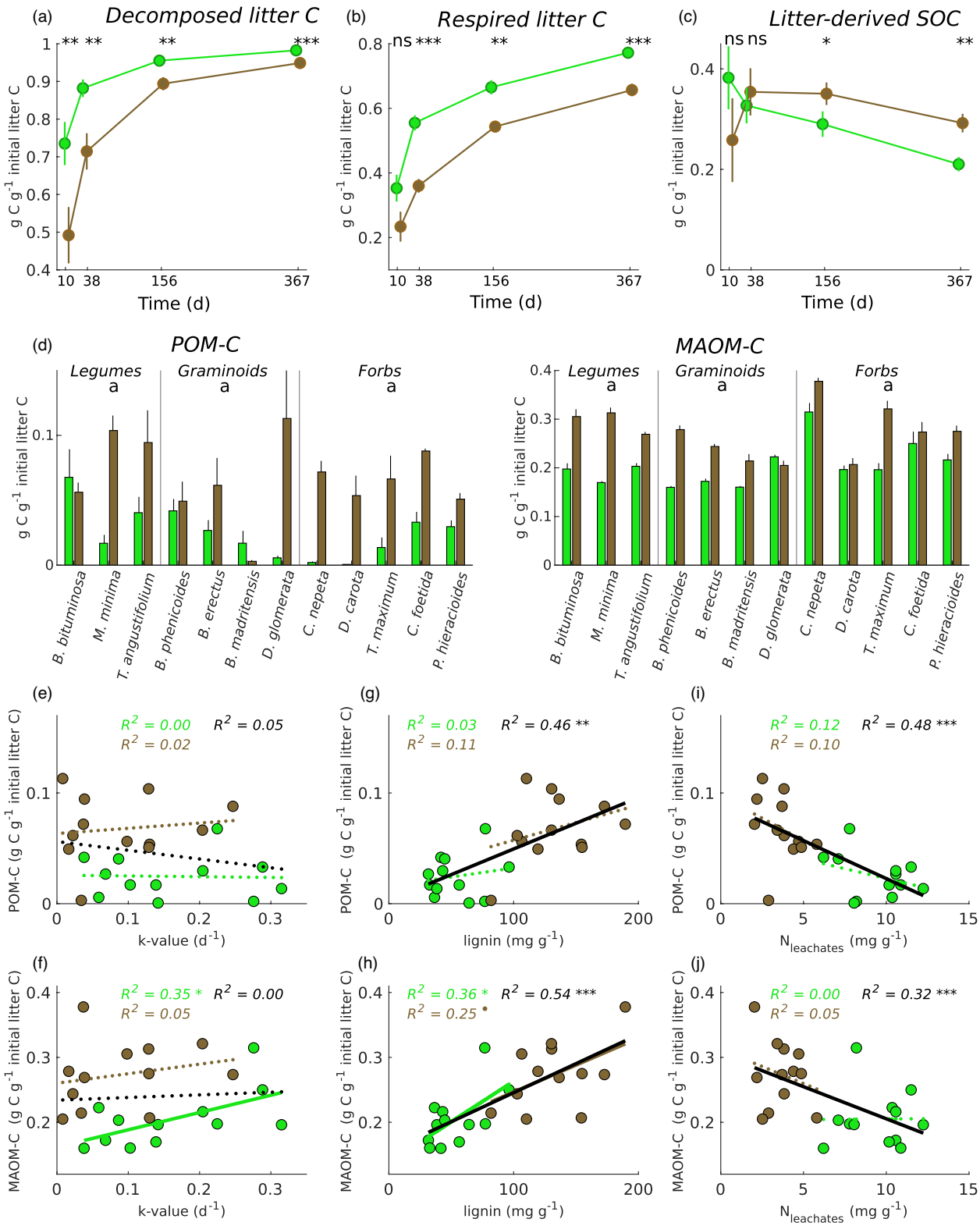
Soil fractionation at near-complete litter decomposition (day 367) showed that litter-derived POM-C represented between 0.001 and $0.11\,g\,C\,g^{-1}$ of initial litter C, and litter-derived MAOM-C between 0.16 and $0.38\,g\,C\,g^{-1}$ of initial litter C, depending on litter type, species identity and chemical composition (Figure 1d, Table S2). Differences among plant functional groups, though, were not significant (Figure S5).

Litter-derived POM-C did not correlate with decomposition rate, and MAOM-C only weakly, but positively for leaf litter (Figure 1e,f). Differences in litter-derived MAOM-C (and POM-C, albeit only across litter types; Figure 1g) were strongly positively correlated with litter lignin concentration (Figure 1h), but negatively to concentrations in hemicellulose and N leachates (Figure 1i,j, Table S3).

3.3 | Primed SOC

At the whole-soil level, strong positive priming appeared limited to the early incubation phase before subsequently turning negative, and remaining so for root litters (Figure 2a, Figure S6). Cumulated over 1 year, the priming effect was not significant, but tended to be positive for leaf litters ($0.003\,g\,C\,g^{-1}$ initial soil C) and negative for root litters ($-0.009\,g\,C\,g^{-1}$ initial soil C, Figure 2a,d, Table S2), with large differences between species (Figure S6). The primed SOC did not scale (systematically) with any of the litter chemical traits measured (Table S3) nor vary significantly ($p > 0.05$) with plant functional groups (Figure S6).

In terms of soil fractions, litter input generally induced positive priming from the MAOM fraction ($0.059\,g\,C\,g^{-1}$ initial soil C; Figure 2c) yet negative priming from the POM fraction ($-0.062\,g\,C\,g^{-1}$ initial soil C; Figure 2b), with large species-specific differences in both fractions (Figure 2b,c). For comparison, over 1 year, the control soil lost 0.0537 g MAOM-C g^{-1} initial soil C and 0.1106 g POM-C g^{-1}



initial soil C. Priming from both fractions was negatively correlated with each other ($R^2 = -0.86$, $p < 0.001$). The initial concentrations in litter lignin and N leachates controlled the priming of both POM-C and MAOM-C (the latter significant for N leachates only) (Figure S7, Table S3) albeit in opposite ways; increasing concentrations of N-rich leachates decreased positive MAOM-C priming but lowered the negative POM-C priming.

3.4 | Net SOC balance

Our estimates of the SOC balance in POM and MAOM revealed strongly contrasting patterns among the 24 litters (Figure 2), with the largest net SOC gain being about five times larger than the largest loss (Figure 2h). For MAOM, the C gain from SOC formation was mostly cancelled out by positive priming in about half of

FIGURE 1 Litter carbon fate. The proportion of (a) decomposed litter C, (b) respired litter C and (c) litter-derived soil organic carbon (SOC) for leaf and root litters (green and brown colour respectively) across 1 year. The rate of litter-derived SOC formation turns negative for leaf and root litters from day 38 and 156, respectively, onward. (d) After 1 year, a smaller proportion of the initial litter C was retrieved in the POM (left panel) than in the MAOM fraction (right panel) across all 12 plant species. Root litter contributed more strongly to both POM-C and MAOM-C than did leaf litter (Table S2), but novel C storage was independent of plant functional group for each soil fraction ($F_{2,21} = 1.090$, $p = 0.354$, $F_{2,21} = 2.256$, $p = 0.130$ for POM-C and MAOM-C, respectively, ANOVA type III). (e) Whereas the POM-C was independent of the litter decomposition rate k, (f) leaf litter-derived but not root litter-derived MAOM-C correlated significantly with decomposition rate k. (g) Whereas initial litter lignin concentrations drove POM-C only across litter types, (h) it did so both within as well as across litter types for the MAOM-C. Both (i) POM-C and (j) MAOM-C varied significantly with initial litter N leachate concentrations across but not within litter types. Error bars (in a–d) indicate standard errors. '.', '*', '**' and '***' represent significant leaf–root differences (a–d) and Pearson correlations (e–j) with $p < 0.10$, 0.05, 0.01 and 0.001 respectively. Solid but not dotted lines represent significant correlations (e–j).

the litters (Figure 2c,g); consequently, the net MAOM-C balance was not significantly different from zero ($p > 0.05$). However, as the POM-C replenishment was typically larger than priming-induced C loss (Figure 2b,f), and on average positive ($t_{23} = 5.075$, $p < 0.001$), the net effect of decomposing litter on total soil SOC remained positive ($t_{23} = 7.110$, $p < 0.001$), except for leaf litter from three species (Figure 2h).

On average, the quantitatively realistic leaf and root litter input simulated here increased the total soil C stock by 4% and 8% (relative to its initial C content) respectively; both increases were significantly larger than zero ($t_{11} = 3.593$, $p = 0.002$ and $t_{11} = 7.595$, $p < 0.001$ respectively) and differed significantly from each other (Table S2). This differential effect of leaf and root litters was associated with the higher concentration in lignin and lower concentration in N leachates of root litters as compared to leaf litters (Figures S1 and S8). However, the total soil C stock did not vary significantly among functional groups for either leaf or root litters.

4 | DISCUSSION

As fresh litter deposition simultaneously drives novel SOC formation and the mineralization of native SOC, we studied both processes as well as their cumulative effect in terms of the net SOC balance as ^{13}C labelled leaf and root litters from 12 grassland species were incubated for 1 year. Specific to our study, our incubated soils were coarse textured and near their theoretical mineral-associated C saturation level. Out of 14 litter chemical traits, the initial litter lignin and N leachates concentrations consistently appeared as predictors for the formation of novel MAOM-C and POM-C as well as in the mineralization of native SOC in both soil fractions.

4.1 | Recalcitrant litter compounds drive novel MAOM-C and POM-C formation

We expected novel SOC formation to primarily accumulate in the POM fraction and to mainly be driven by recalcitrant plant compounds, in particular lignin. Novel MAOM formation, in contrast, was expected to be limited and driven by labile plant compounds. Correspondingly, we expected root litters to enhance novel SOC formation as POM-C relative to leaf litters. These expectations were only partially confirmed. At near-complete litter decomposition (day 367), the amount of initial litter C recovered in the MAOM fraction was substantially larger than that in the POM fraction. The integration of novel C into the MAOM fraction despite it being near its theoretical mineral-associated C saturation (but see below) may indicate that the new C was adsorbed onto other organic molecules already in direct contact with mineral surfaces, forming an organo-mineral complex organized into multilayers or zonal structures (Kleber et al., 2007). Novel C may also have become incorporated in the MAOM fraction through entrapment in micro-aggregates (Totsche et al., 2018) or via co-precipitation with aluminium (Al) and iron (Fe) hydroxides (Kleber et al., 2015). In our low clay soils, a considerable amount of decomposition products may have become entrapped in newly formed small (<53 μm), but not larger, micro-aggregates (Schweizer et al., 2019). Co-precipitation with Al and Fe was likely moderate in our soils, however, in view of the rather small molar Al/C and Fe/C ratios (Table S5) (Nierop et al., 2002) and the pH (=7) of our soils (Rasmussen et al., 2018). In view of its low content, the contribution of exchangeable Ca (Rasmussen et al., 2018; Rowley et al., 2018) to our soil's SOC stabilization potential was likely low, but that of short-order range minerals may have been more extensive. Our soil-texture derived theoretical C saturation may thus (moderately) underestimate our soil's true C storage potential. A substantial proportion of litter-derived C that was recovered in the almost C saturated MAOM fraction may indicate that the newly decomposed OM had competitively displaced native OM compounds in the organo-mineral complexes (Kaiser & Kalbitz, 2012).

Initial litter lignin concentration drove the formation of both novel MAOM-C and POM-C. Although lignins are no longer believed to resist decomposition in the long term (Marschner et al., 2008), their consistent effect indicates that they may nonetheless contribute substantially to POM-C and MAOM-C formation (Huang et al., 2019; Kallenbach et al., 2016). The 'recalcitrance' of lignins and other acid-unhydrolyzable residues select for decomposer communities with lignolytic activities (Figure S9; Wickings et al., 2012). As the extracellular enzymatic repertoire of fungi surpasses that of bacteria (Datta et al., 2017), these communities were likely fungi dominated. This feedback induces different C recycling and anabolic processes, likely favouring fungal biomass, which is thought to contribute disproportionately to MAOM-C formation (Kleber

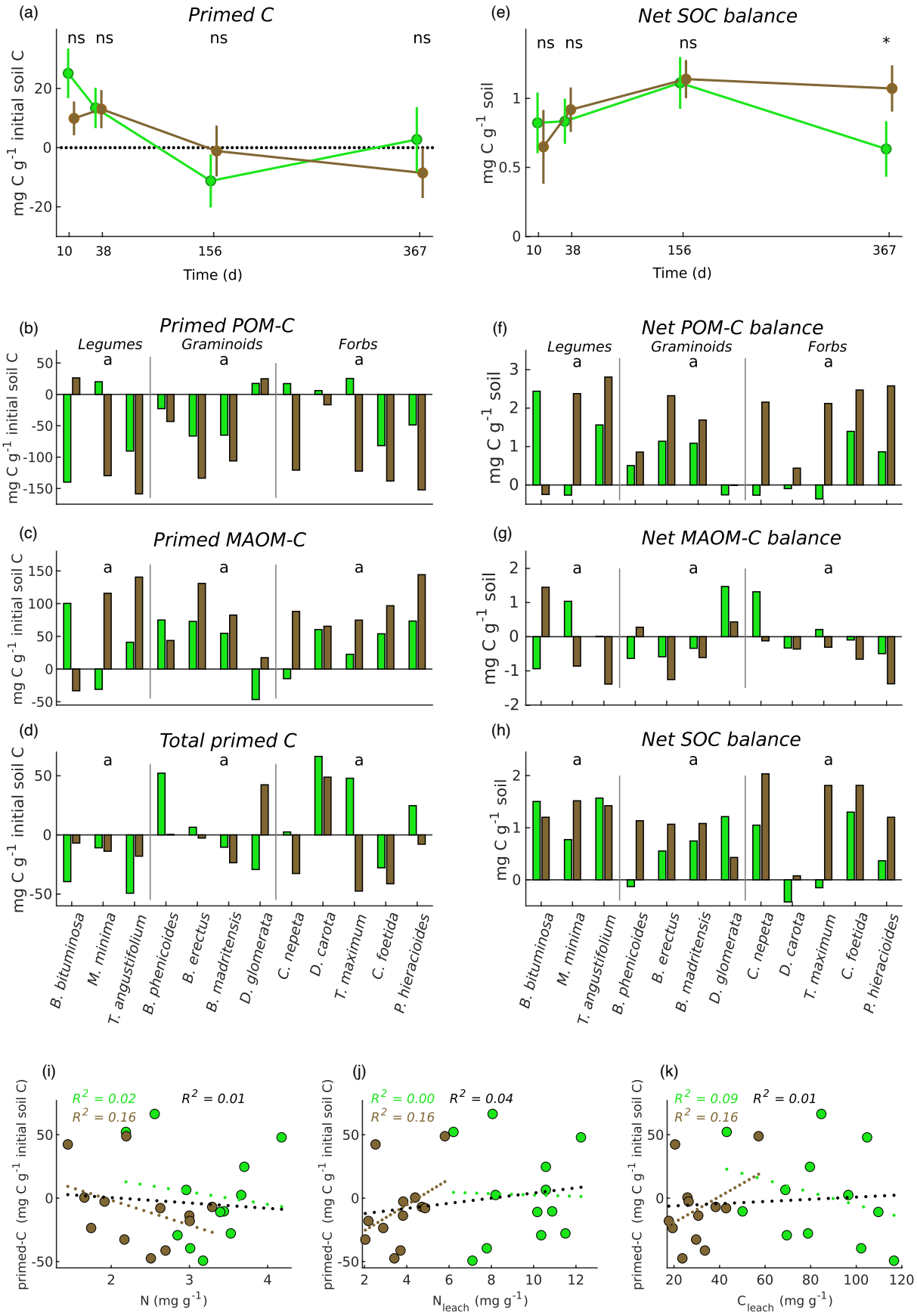


FIGURE 2 The priming effect and the net C balance. (a) Whole-soil primed C for leaf and root litters (green and brown colour respectively) over 1 year. Leaf–root differences never reached significance. Error bars indicate standard errors. (b–d) Primed POM-C, primed MAOM-C and whole-soil primed C (= primed POM-C + primed MAOM-C) over 1 year for all 12 plant species and litter types. Primed POM-C was more negative for root litters (−89 mg C g^{-1} initial soil C) than for leaf litters (−36 mg C g^{-1} initial soil C; Table S2). No other effect of litter type or plant functional type was found (all $p > 0.05$; ANOVA type III). (e) Net C balance (= litter-derived SOC gains − Primed SOC losses) over 1 year. Across SOC gains and losses, root litter decomposition increased SOC concentration more than leaf litter after 1 year. (f–h) The net C balance of the near-complete litter decomposition after 1 year reveals large differences among species, yet is overall positive for the POM fraction (f) and the whole soil (h), but neutral for the MAOM fraction (g). The difference between leaf and root litters was significant for net POM-C (0.65 and 1.63 mg C g^{-1} soil respectively) and net whole-soil SOC (0.70 and 1.23 mg C g^{-1} soil respectively), but not for net MAOM-C (Table S2). No effect of plant functional type was found (all $p > 0.05$; ANOVA type III). Neither N nor the N and C leachates predicted the primed C (i–k). '*' and 'ns' represent significant ($p < 0.05$) and non-significant ($p > 0.05$) leaf–root differences (a, e). None of the Pearson correlations (i–k) were significant, as indicated by the dotted lines.

et al., 2007; Ludwig et al., 2015; Miltner et al., 2012). In addition, or alternatively, lignin-derived phenols' strong sorptive affinity (Hernes et al., 2013) may favour their direct stabilization (i.e. without prior conversion into microbial biomass) in MAOM (Sokol et al., 2019). In comparison, degradation products of the more labile litter compounds may have been preferentially subject to microbial recycling, thereby augmenting litter C respiration, and concurrently reducing the transfer to litter C to the soil, relative to lignin-rich litters (Geyer et al., 2016) (Figure S10, Table S3).

In contrast to the positive influence of litter lignin concentration on MAOM-C and POM-C formation, high N leachates concentrations were associated with reduced MAOM-C and POM-C formation. Immediately, but only briefly available N-rich leachates that modify decomposer community stoichiometry and relieve nutrient limitation (Fanin et al., 2013) may favour lignin degradation at early stages of the litter decomposition process (Figure S10) and thereby limit the direct stabilization of their derived phenols.

Our results bring perspective to the hypothesized relation between litter quality and SOC formation efficiency in the MEMS framework (Cotrufo et al., 2013, 2015; Liang et al., 2018). One pillar of the MEMS framework concerns the importance of the decomposer substrate use efficiency (CUE when considering C as substrate), with efficiency being defined as the amount of microbial biomass production relative to the amount of substrate assimilated (which is partitioned into a microbial biomass production and a mineralization component). A high efficiency, as commonly observed for labile litters, implies relatively little C-CO_2 loss relative to microbial biomass production, with the latter deemed of primary importance following reports that a dominating part of stabilized SOC is of microbial origin (Mambelli et al., 2011; Miltner et al., 2012; but see Angst et al., 2021). Although we did not assess the incorporation of litter C into microbial biomass, about 11% more litter C was respired from (labile) leaf litters than from (recalcitrant) root litters. Consequently, the denominator in the CUE calculation was larger for the leaf than root litters, perhaps due to enhanced microbial recycling (as suggested above). In a recent re-evaluation of existing data, Angst et al. (2021) found microbial necromass to constitute about 39% of the silt- and clay-sized MAOM. They also found lignin to be about twice as abundant in the silt-sized MAOM than in the clay-sized MAOM, which may help explain our results, since our soils contained about twice as much fine silt (and thrice as much fine + coarse silt) as clay particles. At the least, our results call into question the generality of one pillar of the dually-motivated MEMS framework and are consistent with the view that the relation between litter quality and SOM formation efficiency may be inverted when the soil mineral matrix is near C saturation with reduced stabilization capacity (Castellano et al., 2015). Under such conditions, often observed in surface soils, the effect of labile compounds on SOC formation may only be transient (novel SOC formation was stimulated by the nutrient-rich water-soluble compounds initially; Table S3), or largely overcome by that of recalcitrant litters at the later decomposition stages. As we neither manipulated the mineral-associated soil C saturation nor used different soils, however, it remains to be seen if and to which extent our findings are effectively related to our soil's C saturation and/or soil type, more generally.

4.2 | Contrasting priming effects in the MAOM and POM fraction

We expected priming to be positive on the whole-soil level, and this native SOC mineralization to be less for litters high in initial N and N leachate content (by reducing the need for N mining) and to be enhanced by easily degradable C sources in the early decomposition phase. Relative to the different soil fractions, we expected to observe priming mainly in the POM fraction but much less so in the MAOM fraction. Again, these expectations were only partially corroborated by the data. In our litter-soil incubations, on average, following the expected typical SOC over-mineralization early on (Kuzyakov, 2010), the priming effect subsequently turned negative, and eventually became statistically indistinguishable from zero. These dynamics emphasize the importance of examining priming over longer periods than currently done, as it may qualitatively and quantitatively change our view on the effect of litter deposition on native SOM decomposition (see also Zhang et al., 2017). As our microcosm experiment simulated multi-year in situ decomposition outcomes, however, it remains to be investigated how these priming dynamics are altered as fresh litters are deposited to the soil before the (near complete) decomposition of previously added litter material (Hamer & Marschner, 2005; Wang

et al., 2019). If such a novel deposition re-energizes decomposer communities, our results do not contrast the notion that priming contributes to native SOC losses in natural ecosystems (Perveen et al., 2019). Alternatively, and speculatively, the observed initial positive priming may reflect the (over) mineralization and exhaustion of relatively easy degradable SOC, causing medium- to long-term negative priming. In this case, repeated novel litter deposition may increasingly exhaust a soil's easily degradable SOC leading to a less positive, and maybe even vanishing priming effect. Hamer and Marschner's (2005; experiment 4) study, in that regard, suggests that both mechanisms may be operative, but in a soil-dependent manner.

In contrast to our expectation, across 1 year, the litter addition had instigated C over-mineralization in the MAOM fraction yet under-mineralization in the POM fraction. The loss of MAOM-C, although surprising since it is commonly considered more stable than POM-C (Lavallee et al., 2020), underlines its dynamic equilibrium with the soil solution (Kleber et al., 2007, 2015), and indicates that younger, more sorptive compounds may displace older, previously adsorbed OM (Kaiser & Kalbitz, 2012). In our microcosms, this dynamic was likely enhanced by the experimentally induced disturbances to the soils, and its significance under natural, relatively undisturbed conditions requires testing. Previous work has indicated that root systems, through their exudates, may destabilize MAOM (Keiluweit et al., 2015), both through the exudates' acidity as well as by increasing microbial enzyme secretion (Jilling et al., 2021). As in our microcosms root exudates were absent, it seems likely that increased enzyme secretion following litter deposition either liberated organic C from the organo-mineral complexes or led to the destabilization of small aggregates in the MAOM fraction.

The negative correlation between the priming from the MAOM and POM fractions indicate an opposite behaviour of these fractions, as also observed with respect to their C stabilization (Stewart et al., 2009), perhaps with transfer between these two fractions. Such a transfer may occur if desorbed OM, rather than being entirely mineralized, is rapidly used by micro-organisms and further protected from decomposition by occlusion into aggregates, whose formation is stimulated by increased litter-induced microbial activity (Six & Paustian, 2014), particularly in surface soils where micro-sites are saturated with OM (Angers, 1998; Tisdall & Oades, 1982).

In contrast to our expectation, the measured initial litter traits did not explain the priming on the whole-soil level. Also unexpected, the priming of POM-C decreased with initial litter lignin concentration, and enhanced by the initial litter N leachate concentration. The negative impact of the latter on the MAOM-C priming did follow our expectation. Decreasing positive MAOM-C priming with increasing N-rich leachates likely indicates a reduced microbial N-mining (Fontaine et al., 2011), whereas its lowering of the negative POM-C priming may imply a reduced transfer of native soil C from MAOM to POM. Importantly, the negative correlation between the primed POM-C and MOAM-C indicates that litter input may affect native SOC far more than currently highlighted by assessments of bulk SOC, at least in soils near C saturation. In such (mostly) coarse-textured soils, the dynamic nature of the equilibrium characterizing MAOM in the soil solution (Kleber et al., 2007, 2015) may be enhanced relative to fine-textured soils as relatively more OM is bound to the outer, weaker binding zones of the organo-mineral complexes (Kleber et al., 2007).

Our results suggest that failure to take into account soil type may render management strategies to enhance long-term C sequestration inadvertently counter-productive. They further indicate that potential for C storage in coarse-textured soils may lie in an efficient management of medium-term C storage in the POM pool (Barré et al., 2017), as its C storage capacity is less limited, if at all, than that of the long-term MAOM pool (Cotrufo et al., 2019; Lavallee et al., 2020).

4.3 | Net SOC storage in soils close to C saturation is limited to the POM fraction

Despite the commonly acknowledged central role of litter in soil organic matter dynamics, surprisingly little data are available on its effects on the relative 'input–output' balance (Liang et al., 2018). Our expectation, in that regard, was that litter addition would enhance SOC accrual mainly through gains in the POM fraction. This expectation was largely confirmed (albeit through different pathways than anticipated; see above). In our soils close to their theoretical mineral-associated C saturation limit, the consistent C gain from SOC formation in the MAOM fraction was mostly cancelled out by positive priming, so that on average, the net balance for MAOM-C did not differ significantly from zero. In contrast, the mostly negative POM-C priming added to the POM-C formation, rendering the net POM-C, and consequently overall net SOC positive. These results confirm previous assumptions that any gain in soil C occurs as POM once the MAOM fraction is saturated with organic matter (Castellano et al., 2015; Cotrufo et al., 2019; Hassink, 1997; Stewart et al., 2009).

The net SOC gain for root litters was twice as large as that for leaf litters, which is consistent with previous findings that most SOC is root derived (Kätterer et al., 2011; Rasse et al., 2005). Our present findings highlight that the larger contribution of below-ground versus above-ground plant material to SOC holds in the absence of root exudation. In fact, as expected from the effects of litter chemistry on both SOC formation and priming, this differential effect of leaf and root litters was associated with the higher concentration in lignin and lower concentration in N leachates of root litters as compared to leaf litters (Figures S1 and S8). The absence of a plant functional-group effect on total SOC stocks after 1 year, despite initial differences in litter-derived SOC formation, may be due to smaller differences in these two litter traits than observed between leaf and root litters (Figure S3). Overall, the mostly positive but variable effect of plant litters on the balance between carbon formation and destabilization is key for our understanding of plant effects on the global C cycle and must be extended to effects of living plants, including root exudation processes.

4.4 | Litter chemistry effects on soil carbon storage and priming: A potential way forward

Mineral-associated soil C saturation modifies the relation between litter quality and SOC stabilization (Castellano et al., 2015), but it remains unclear how. We offer an integrative perspective to that effect linking litter quality, microbial decomposition and a number of well-documented SOC stabilization and destabilization mechanisms consistent with our data (Figure 3). Following numbers in the text, from **(1)** to **(13)** refer to processes illustrated in Figure 3. In soils far from mineral-associated C saturation (Figure 3b), a substantial part of decomposition products associates with native organo-mineral complexes (grey dots) varying in sorption strength (the darker the grey the stronger bound) and mineral surfaces (brown lines) or, especially in acidic soils, co-precipitate with Al and/or Fe oxides (Rasmussen et al., 2018) **(1)**. In neutral to alkaline soils, as in our soils, the released decomposition products more likely associate with clay and calcium (Rasmussen et al., 2018; Rowley et al., 2018). These decomposition products may replace some weakly bound native organic matter (light grey dots) through sorption–desorption (back- and forth arrows, scaled to rate; Guggenberger & Kaiser, 2003; Kaiser & Kalbitz, 2012; Kleber et al., 2015) **(2)**. As labile litter stimulates the 'in vivo' pathway more effectively than recalcitrant litters (Cotrufo et al., 2013), most newly formed SOC is rapidly stabilized as MAOM as sufficient mineral binding sites are available. Primed C losses (CO_2 leaving the soil—red arrows) are presumably primarily of POM-C origin (unbound and aggregated grey dots) as most MAOM-C is bound **(3)**. With progressing decomposition (Figure 3c), the proportion of recalcitrant litter compounds increases and the decomposer community becomes more fungi dominated, leading to overall more recalcitrant decomposition products (including microbial necromass; brown dots) that associate with native organo-mineral (and -metal) complexes and mineral surfaces **(4)**. These decomposition products may replace some previously bound decomposition products from the initial decomposition stage (back-and forth arrows) that often reveal a weaker sorptive affinity (Sokol et al., 2019) **(5)**. At this decomposition stage, the proportion of litter-derived recalcitrant compounds may increase in the soil, favouring aggregation, and thus, increasing POM-C formation **(6)**. The rates of processes **(4)–(6)** should be greater for lignin-rich litters, which release a higher proportion of recalcitrant compounds with strong sorptive affinity (Kaiser & Zech, 1997).

In soils close to mineral-associated C saturation (Figure 3d), fewer mineral binding sites and organo-mineral (and -metal) complexes are available, leading to a rapid increase in the concentration of labile litter-derived decomposition and microbial products in the soil solution (a 'bottleneck effect'), which are ultimately mineralized **(7)**, or bind predominantly to the weaker binding outer zone of organo-mineral complexes (Kleber et al., 2007) **(8)**, destabilizing and replacing the weakly bound fractions of the native MAOM **(9)**. The rates of processes **(7)** and **(8)** are likely higher for labile compared to recalcitrant litters due to their faster release and weaker sorptive affinity of the decomposition products (Sokol et al., 2019). Our observed enhanced respiration of litter-C of the more labile leaf litters relative to root litters (Figure 1a) is consistent with this proposition (process **7**). In the absence of MAOM-C time series, the proposed enhanced rate of (**8**) for labile litters cannot be confirmed, but their initial faster SOC formation (Figure 1c), driven by the easy degradable water soluble compounds (Table S3), are suggestive thereto. Process **(9)** is likely increasingly stimulated in soils approaching mineral-associated C saturation (Khandakar et al., 2021) as the ratio between weaker bound to stronger bound ('outer zone' light grey circles and 'inner zone' dark grey circles respectively; Figure 3d) organic matter may decrease. This leads to substantial MAOM destabilization that can cause native SOC losses via priming **(10)**, as observed in our soils (Figure 2c). Similar to processes occurring in soils far from mineral-associated C saturation, decomposition products of the more recalcitrant litter compounds become more abundant in the soil solution as decomposition progresses (Figure 3e), which associate with native organo-mineral (and -metal) complexes and mineral surfaces **(11)**, and may replace some previously bound decomposition products from labile litter compounds **(12)**, and may favour aggregation and increasing POM-C formation **(13)**. The rates of processes **(11)–(13)** are expected to be higher for lignin-rich litters (same as in soils far from mineral-associated C saturation); the positive effects of lignin (across 1 year) on novel POM-C and MOAM-C formation (Figure 1g,h, Table S3) are consistent with, albeit not conclusive for, the propositions for process (**11**, **13**). However, overall, the rates of process (**12**) are likely lower than in soils far from mineral-associated C saturation, because less labile litter-derived compounds bound to organo-mineral complexes in the earlier phase of decomposition (Figure 3d). However, POM-C formation may be enhanced **(13)**, resulting from limiting binding sites, and thus, lower rates of process **(11)**. As most MAOM is entrapped in aggregates (Hatton et al., 2012), soil aggregation likely modulates the rates of **(1)–(13)** by modifying microbial decomposer access to organic matter and hence microbial community structure, abundance and activity (Wilpiszeski et al., 2019), as well as through its effect on gas and liquid fluxes (Ebrahimi & Or, 2016).

5 | CONCLUSIONS

In the coarse-textured soil near mineral-associated C saturation we studied here, decomposing litters increased SOC concentration through two processes (Figure 3 'synthesis', Section 4.4). First, new litter-derived C was stabilized into POM and MAOM, and second, there was less native soil POM-C mineralization than in the absence of decomposing litters. Of all litter chemistry characteristics measured, lignin and N leachate concentrations were the best predictors of these two processes. Since root litter chemistry differed systematically from leaf litter chemistry, root litter contributed twice as much to SOM than leaf litter on average, which corroborates earlier findings (Kätterer et al., 2011; Rasse

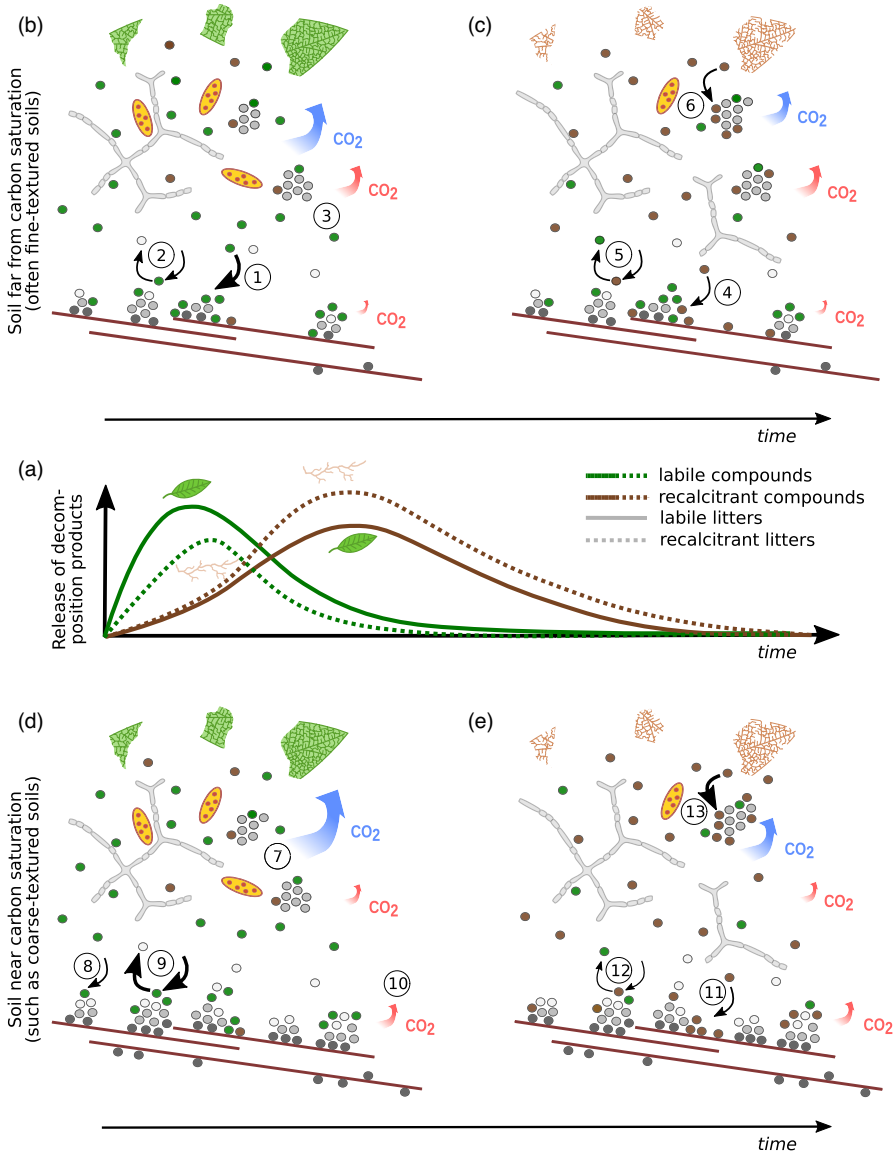


FIGURE 3 A renewed perspective on the influence of litter chemistry on soil carbon storage and priming. Initial litter chemistry is likely to have persistent effects during litter decomposition, although differently between soils of different soil mineral-associated carbon saturation (b, c unsaturated and d, e saturated). See main text, for more details on the proposed mechanisms, numbered here from (1) to (13) on the figure. (a) After litter input to the soil, plant-derived degradation products are progressively released into the soil solution. Labile compounds (green lines; early peak) are released faster than recalcitrant compounds (brown lines; later peak). The relative abundance of labile versus recalcitrant compounds and the rapidity of their release varies with the initial litter quality (as exemplified by leaf vs. root litter: solid vs. dotted lines respectively). Thus, the amount of rapidly released labile versus slowly released recalcitrant compounds (colour coded) scales with the initial litter quality (line-style coded); more labile compounds are released initially but less recalcitrant compounds are released later on for labile litters than for recalcitrant ones. (b–e) Independent of soil C saturation, bacterial (yellow ellipses) and fungal (light grey lineal structures) decomposers rapidly mineralize part of the labile compounds (blue arrows, scaled to rate) of fresh litter material (panels b and d, corresponding to the green lines in a) and leaving behind mostly labile litter-derived decomposition (and bacterial-dominated microbial) products (green circles). In a later decomposition stage (panels c and e, corresponding to the brown lines in a) mineralization rates diminish and more recalcitrant litter-derived decomposition (and fungi-dominated microbial) products (brown circles) are released.

et al., 2005). Our findings that litters have opposite effects on native soil MAOM-C and POM-C, and of common predictors of SOC formation and priming, emphasize the potentially complex interplay between OM stabilization and destabilization processes and call for further integration in the study of these processes within and between C pools, and how they vary over time. Furthermore, whereas our findings do not rule out that priming is an important cause of substantial SOC loss in natural ecosystems (Perveen et al., 2019), they point to a dynamic balance in the soil between co-occurring positive and negative priming effects (see Section 4.2 above). Regardless, even in our soil that was likely close to its mineral-associated C saturation, the balance between SOC gains via formation and losses due to priming was predominantly positive, albeit limited to the POM fraction. Finally, the consistent key

role played by lignin and soluble N-containing compounds in these processes brings perspective to the recently suggested conceptual framework of SOM formation (Cotrufo et al., 2013, 2015), according to which labile compounds favour SOM formation relative to recalcitrant compounds in soils with high matrix stabilization capacity. A main reason for the diverging findings may be fundamental differences among soil types. Indeed, in our coarse-textured soils near their mineral-associated C saturation, recalcitrant lignin-rich litters rather than labile ones most efficiently drove novel SOC formation, indicating that the efficiency with which microbes decompose litter does not unequivocally translate into SOC accrual, as previously proposed for finer-textured soils. As about 80% of the Earth's soils contain less than 30% clay (Shangguan et al., 2014), and are thus prone to mineral-associated C saturation, our findings imply that soil management strategies targeted at enhancing C storage to help mitigating climate change and promote sustained ecosystem functioning need to account explicitly for differences in soil types and should focus more specifically on medium-term C storage (Barré et al., 2017) and its interplay with long-term stabilization and destabilization processes.

AUTHOR CONTRIBUTIONS

Grégoire T. Freschet conceived the experiment, with input from Catherine Roumet, Stephan Hättenschwiler, Alison D. Munson and Nathalie Fromin. Malo Y. Bourget, Vincent Poirier, Grégoire T. Freschet and Catherine Roumet performed the experiment and ran the analyses. Raoul Huys and Grégoire T. Freschet analysed the data. Raoul Huys and Grégoire T. Freschet wrote the first draft of the paper. All authors contributed to the writing of the paper.

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CONFLICT OF INTEREST

The authors declare no competing interests.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data used in this study are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.m63xsj45g (Huys et al., 2022).

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SUPPORTING INFORMATION

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

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