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The partitioning of litter carbon fates during decomposition under different rainfall patterns: a laboratory study

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Abstract During litter decomposition, three major fates of litter carbon (C) are possible: emission as carbon dioxide (CO_2) into the atmosphere, leaching of dissolved organic carbon (DOC), and translocation and transformation into soil organic carbon (SOC). Soil moisture, one of the key drivers of litter decomposition, is predicted to change in the future due to shifts in precipitation patterns. We explored the effects of low, medium and high rainfall intensities on the partitioning of litter carbon fates in a 6-month long laboratory experiment. We tracked carbon in ^{13}C-labeled tulip poplar litter in a laboratory mesocosms by measuring respiration rates, dissolved organic carbon in the leachate, and soil organic carbon at the end of the experiment. Mesocosms with the same three rainfall intensities but without leaf litter were also set up. Leaching of labile carbon caused priming, but the effect was stronger in the low intensity treatment. Transport of litter-derived carbon also differed: in high intensity treatment there was more total carbon in the surface soil and more litter-derived carbon in in the deep soil layers. The cumulative CO_2 efflux was not significantly different. Our results highlight that extreme rainfall events, as projected by most climate models, may lead to altered carbon cycling in temperate forest soils.

Keyword Extreme rainfall event · Litter carbon partitioning · Carbon transport · Priming effect · Temperate forest

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Introduction

Leaf litter decomposition is a key component in nutrient cycling and a major source of soil organic carbon. The decaying surface litter is exposed to physical, chemical and biological processes, including fragmentation, leaching, microbial growth as well as being consumed by saprophagous invertebrates. Litter carbon, translocated into the soil can undergo a variety of transformations (Cotrufo et al. 2015; Rubino et al. 2010; Soong et al. 2015), most of which are

microbially mediated. Eventually, carbon can be lost to the atmosphere as CO_2, to a lesser extent as CH_4 or volatile organic compounds (VOC), or as dissolved organic carbon (DOC) in deeper soil or in runoff. Carbon retained in the soil can be incorporated to microbial biomass and eventually form soil organic matter (SOM), which consists of a variety of organic substances continuously transformed by the decomposer food web (Lehmann and Kleber 2015). The fates and rates of belowground carbon transformations depend on substrate chemistry, the structure of the soil food web, and various abiotic factors, including soil texture, pH, temperature and moisture. Changes in these conditions can shift the balance between carbon storage and release with possible consequences at ecosystem scale or even globally (Jackson et al. 2017; Schmidt et al. 2011).

Litter decomposition rate is affected by a multitude of factors including substrate quality (Hu et al. 2018; Prescott 2010), diversity and activity of soil biota (Ayres et al. 2006; Di Lonardo et al. 2018), and climatic variables such as temperature, moisture and actual evapotranspiration (Berg 2000; Cortez 1998). Soil moisture is influenced by amount, frequency, intensity, duration, and timing of rainfall events. Increased frequency and intensity of intense rainfall events, has already been appearing even in places where total precipitation was decreasing (Trenberth 2011). Projections by global circulation models (GCM) are consistent that there would be an increase in frequency of intense rainfall events both globally (Beier et al. 2012; Trenberth 2011) and regionally in the Northeastern United States (Hayhoe et al. 2006).

Extreme precipitation regimes profoundly alter hydrological processes even in mesic systems (Knapp et al. 2008), yet most studies manipulating precipitation regimes have focused on changing total amounts of precipitation through water addition or removal (Beier et al. 2012; Wu et al. 2011); rainfall frequency and intensity have been less studied. Lensing and Wise (2007) found that litter under ambient condition decayed faster than either low-rainfall or high-rainfall treatments and attributed the results to more variability in intensity and timing of rainfall events at ambient conditions. In a prairie ecosystem, increased rainfall variability resulted in litter with a higher C:N ratio and a lower decay rate, leading to altered carbon cycling (Schuster 2016). Intense wetting and drying cycles were shown to translocate more carbon from the O horizon to the mineral layer (Hentschel et al. (2007). At the ecosystem level, Lee et al. (2004) estimated that CO_2 flux from heterotrophic respiration could total 5–10% of the annual net ecosystem production after an intense rainstorm. Despite the potential importance of high intensity rainfall events in soil carbon cycling, the effect of such extreme events on the fate of litter carbon during decomposition is still not well understood.

Adding labile litter C during the initial phase of litter decomposition may stimulate the mineralization in the native soil, causing a microbial priming effect, in which addition of an easily decomposable substrate leads to increased mineralization rate of the native soil (Kuzyakov 2010; Kuzyakov et al. 2000). Crow et al. (2009) and Sulzman et al. (2005) found aboveground C input from leaf litter to be an efficient C source, inducing priming effect due to increased microbial biomass or activity. Different rainfall patterns could affect the fates of easily decomposable litter carbon, thus altering the magnitude of priming effect, and eventually soil carbon stocks.

Although it is generally expected that different rainfall patterns lead to altered soil carbon fluxes (Harper et al. 2005; Knapp et al. 2002), quantifying litter carbon fates into CO_2, soil organic matter, and DOC is challenging. The application of ^{13}C isotopes provides a useful tool for exploring the fates of litter carbon during decomposition. For example, Bird et al. (2008) used ^{13}C labeled root and needle to accurately quantify labeled C in different soil organic matter fractions in a forest soil; with ^{13}C labeled leaf litter, studies yielded a better estimate of litter carbon partitioning and found mineralization of litter carbon to be the major pathway of carbon loss (Kammer et al. 2011; Rubino et al. 2010).

We performed a lab experiment to partition litter carbon fates in different manipulated rainfall patterns. To achieve this, we incubated ^{13}C-labeled leaf litter in direct contact with the soil and thereafter partitioned the fate of litter-carbon into SOC, CO_2 and leachate-DOC based on ^{13}C mass balance. Varying rainfall intensity treatments with different frequencies were simulated while total amount of precipitation was kept constant. We hypothesized that high intensity rainfall will lead to (1) less litter mass loss because of lower microbial activity caused by less frequent rainfall events, (2) more carbon loss as DOC, (3) more litter carbon transport to deeper soil, and (4) less priming

effect due to less C input and more labile C leaching as stated by (1) and (2). To our knowledge, this is the first decomposition study in which litter mass loss has been budgeted in terms of CO_2 efflux to the atmosphere, C input to the soil to form soil organic matter, and DOC leached out of soil system under different rainfall patterns. This represents an important step towards a deeper understanding of soil carbon cycling under changing precipitation, especially the increase of extreme events.

Materials and methods

Experimental design

To explore the effects of rainfall intensity and role of leaf litter in soil carbon cycling, a 6-month long experiment was set up in laboratory soil columns. Rainfall was simulated at three intensities; low (LOW), medium (MED) and high (HIGH). Leaf litter was added to half of the columns (LOW+, MED+, HIGH+) while soil surface in the other half remained bare (LOW−, MED−, HIGH−). The following variables were measured regularly during the experiment: CO_2 efflux, $\delta^{13}C$ of respired CO_2, leachate volume, total dissolved organic carbon (DOC) and $\delta^{13}C$ in the leachate. Air temperature and soil moisture were continuously monitored. Initial and final C and $\delta^{13}C$ in litter and soil, the latter at different depths, were analyzed. Detailed descriptions for each of these measurements are given below.

Soil columns

To detect measurable changes in soil carbon content we used medium size mesocosms (in our case diameter: 19 cm, height: 25 cm), which are often used in soil ecology and biogeochemistry experiments (Crumsey et al. 2015; Paul et al. 2012; Setälä et al. 1990). Taking undisturbed soil columns of this size from forests is challenging due to the high density of roots. As a compromise between undisturbed and completely homogenized soils, we recreated soil horizons with homogenized soils following the so-called 'simulated forest floor' approach proposed by Huhta and Setälä (1990). Specifically, soils from a 150-year forest stand at the Smithsonian Environmental Research Center (SERC) were collected in September 2016 from the top 0 to 10 cm (surface soil) and from the deeper (20–40 cm) mineral layer (subsurface soil) for this laboratory study. SERC is located along the western shore of Chesapeake Bay in Edgewater, MD (38° 53′ N, 76° 33′ W) with a mean annual precipitation of 1146 mm and the mean annual temperature of 13 °C (Correll et al. unpublished data). The forest is dominated by tulip poplar (*Liriodendron tulipifera*), sweet gum (*Liquidambar styraciflua*), oaks (*Quercus* spp.), American beech (*Fagus grandifolia*), and hickories (*Carya* spp.) (Pitz et al. 2018). The soil type is Collington (Typic Hapludult), with fine sandy loam at the surface and sandy clay loam below the B_t horizon (NRCS 2015). Clay content increases with depth from 12.6% in the A horizon to 24–31% in the B_{t1}–B_{t2} horizons (NEON 2019) which starts at 25 cm (Yesilonis et al. 2016). No carbonate accumulation has been detected in SERC forest soils (Ma et al. 2013).

Both soil layers were sieved through a 4 mm sieve with roots, leaves and occasional pebbles from historical alluvial deposition removed. A total of 18 soil columns were reconstructed in transparent acrylic columns, with a diameter of 19 cm (Supplementary Fig. 1). At the bottom of the columns, a 10 cm deep clean gravel layer was added to prevent anaerobic conditions. The gravel was covered with 2 mm mesh and topped with 2.85 kg and 6.00 kg of surface and subsurface soil, respectively, amounting to 25 cm high soil column with 10 and 15 cm soil layers. Bulk densities of surface and subsurface layers were 0.80 g cm^{-3} and 1.41 g cm^{-3}, respectively. These values were similar to those measured in the field in a nearby soil pit: 0.78 g cm^{-3} and 1.42 g cm^{-3} at 0–10 cm and 20–30 cm depths, respectively. Initial carbon contents at 0–10 cm and 10–25 cm in the column were 4.1% and 0.5%, and $\delta^{13}C$ were − 27.3‰ and − 26.0‰, respectively.

7.0 g (dry mass) of tulip poplar (*L. tulipifera*) leaf litter was placed on the soil surface in half of the soil columns, equaling to 233 g m^{-2}. Tulip poplar makes up 30–70% of total litter input at SERC forests (Szlavecz et al. 2018). The amount used in the experiment is at the upper end of this range. To follow the fate of leaf litter carbon, dual-isotope-labeled (^{13}C and ^{15}N) litter was used as described in Bernard et al. (2015). Briefly, tulip poplar saplings were grown in a large (2.4 m × 2.4 m × 2.4 m) growth chamber continuously supplied with 1000‰ (2.19 atom%) $^{13}CO_2$ and (98% ^{15}N) ammonium nitrate ($^{15}NH_4{}^{15}NO_3$)

fertilizer. In the fall, leaves were allowed to naturally senesce and fall. To ensure relatively homogeneous litter quality and level of enrichment, leaves were broken up by hand, sieved through an 8-mm sieve with petioles removed. Carbon content and $\delta^{13}C$ of enriched leaf litter were 43.2% and 244.2‰, respectively.

During the experiment, air temperature and relative humidity were monitored continuously by Maxim's iButton (Maxim Integrated, San Jose, California, USA). ECH_2O EC-5 moisture sensors (METER Group, Pullman, Washington, USA) were installed at 8 cm depth to monitor volumetric water content (VWC).

Rainfall treatments

In this experiment, both the frequency and intensity of rainfall were manipulated, while total amount delivered through the entire experimental period, remained constant. Rather than arbitrarily create extreme conditions, we used local, historical precipitation data from SERC and surrounding weather stations to derive the intensity and frequency of the three (LOW, MED, HIGH) rainfall treatments. Fifteen-minute precipitation data from US Custom House in Baltimore (1984–1999) (https://www.ncdc.noaa.gov/cdo-web/datatools) was used to determine rainfall intensity. Frequency of heavy rainfall events was derived from daily precipitation data from US Naval Academy (1894–1976) (https://www.ncdc.noaa.gov/cdo-web/datatools) in Annapolis, Maryland and SERC (2002–2013). Supplementary Table1 demonstrates how low and high intensity rainfall treatments in our experiment are comparable to historical precipitation data. Low-intensity treatment had average 15-min rainfall intensity (4.2 mm h^{-1}) and average frequency of rainfall events (once per 3.5 days). The high-intensity treatment had top 1% of 15-min rainfall intensity (28.2 mm h^{-1}) and top 1% of frequency of rainfall events (once per 14.0 days) respectively. In the high-intensity rainfall event, 1200 ml (42.3 mm) deionized water was added to column in 1.5 h. In the low-intensity rainfall event, 300 ml (10.6 mm) water was added to column in 2.5 h.

The medium-intensity rainfall treatment was alternating between low and high intensity rainfall treatments in a 2-week interval. As a result, during a 4-week period, the high-intensity treatment received two heavy rainfall events, the low-intensity treatment received eight smaller rainfall events, and the medium-intensity treatments received four rainfall events with low intensity in the first 2 weeks, followed by one heavy rainfall event with high intensity.

There were three rainfall manipulations and two leaf litter manipulations with three replicates in each combination for a total of 18 columns. The six treatments hereafter are labeled as LOW+ (low intensity-litter added), LOW− (low intensity-no litter), MED+ (medium intensity-litter added), MED− (medium intensity-no litter), HIGH+ (high intensity-litter added), and HIGH− (high intensity-no litter).

Soil columns were constructed in December 2016. To minimize the disturbance effect, soil columns were kept intact for 3 months, then deionized water was added gradually to raise soil moisture to field capacity. Addition of tulip poplar as well as rainfall manipulation started four months after soil column construction. When VWC was over 35% for over half of the soil columns, the amount of water addition was reduced proportionally for all soil columns to avoid complete saturation and anoxic conditions. The total amount of water added during the entire experiment was 8700 ml per column, which is equivalent to 306.8 mm precipitation.

CO_2 flux measurements

CO_2 flux was measured daily and more frequently before and after rainfall events, with a total of 3663 measurements made. Static chamber method was used to determine CO_2 fluxes. A PVC lid assembled with a CO_2 sensor (GMP 343, Vaisala, Vantaa, Finland) was placed on the experimental columns. CO_2 concentrations in the headspace were recorded every second for 6 min. Then CO_2 concentration was averaged in 30 s intervals to account for the fluctuation of readings from sensors, especially when flux was low. Gas flux rate was calculated as:

$$F = \frac{dC}{dT} * \frac{V}{S}$$

where F is the gas flux in mg m^{-2} h^{-1}, C is the mole concentration in μmol m^{-3}, T is time, V is the volume of headspace, and S is the area of the soil surface in the chamber. dC/dT can be estimated as slopes of fitted lines between CO_2 concentrations and time.

$\delta^{13}C$ of respired CO_2

In addition to frequent CO_2 flux measurements, $\delta^{13}C$ of respired CO_2 was determined monthly for a total of five campaigns for LOW+ and HIGH+ treatments. When taking $\delta^{13}C$ measurement, an airtight lid with septa was placed on top of the plastic column. At each sampling event a series of 60 ml gas samples was taken from the headspace, and transferred to Cali-5-Bond air and gas sampling bags (Calibrated Instruments Inc., McHenry, Maryland, USA). Following the protocols by Cotrufo et al. (2014) and Ngao et al. (2005), three gas samples were taken in the first campaign. To improve the *y* intercept, a fourth sampling point was added in the subsequent campaigns. Depending on CO_2 efflux rate, the period between the first and last samplings varied between 0.5 and 2 h to allow sufficient concentration increase in the headspace. CO_2 concentration and $\delta^{13}C$ of CO_2 was determined by a cavity ring-down spectroscopic carbon isotope analyzer (Picarro G2101-i, Picarro Inc., Santa Clara, California, USA) connected to an automated sampling manifold (Picarro A0311). We used keeling plots to calculate $\delta^{13}C$ of respired CO_2 (Brand and Coplen 2012). We occasionally dropped a data point because of poor quality data from the analyzer. In every case, the slope was based on ≥ 3 observations. For a slope to be determined as a quality data point, the R^2 had to be greater than 0.80.

To gain insight on how $\delta^{13}C$ of respired CO_2 and the proportion of CO_2 derived from leaf litter would change over time after rainfall events, four time points were selected for gas sampling. Only high (HIGH+) and low (LOW+) intensity litter treatments were sampled because medium (MED+) alternates between the two rainfall events. In LOW+, $\delta^{13}C$ of respired CO_2 was measured immediately after (T_{L1}), 4 h (T_{L2}), 1 day (T_{L3}), and 3.5 days (T_{L4}) after rain event. In HIGH+, $\delta^{13}C$ of respired CO_2 was measured immediately after (T_{H1}), 2 days (T_{H2}), 7 days (T_{H3}), and 14 days after rain event (T_{H4}) (Supplementary Fig. 2).

Due to technical reasons, in weeks 3–4, $\delta^{13}C$ of respired CO_2 was only measured in one column per treatment and in weeks 7–8, two columns were measured in each treatment. For the following three campaigns of measurements in weeks 11–12, 17–18, and 23–24, all three columns in each treatment were measured.

Leachate collection

Leachates were collected from a funnel beneath the gravel layer of the soil column using plastic bottles within 8 h after rainfall events. Thirty milliliters subsamples were immediately passed through 0.45 µm glass fiber filters, acidified with phosphoric acid, and stored at 4 °C for later isotope and concentration analyses.

Litter collection and soil sampling

At the end of the experiment, all recognizable litter residues were collected from the soil surface. Litter was oven dried at 70 °C, weighed to determine mass loss during the experiment, and ground to powder for subsequent analyses. Soil columns were divided into five depths: 0–2, 2–6, 6–12, 12–18, and 18–25 cm. Subsamples from each depth were oven dried at 70 °C to constant weight and ground for later isotope analyses. Gravimetric water content (GWC) was determined by drying subsamples from each depth at 105 °C until constant mass, as well as for recovery of dry soil mass and soil carbon.

Stable isotope analyses of soils, leaves, and DOC

The C content and stable isotope compositions of soils and leaves before and after incubation, and DOC collected at several stages of decomposition were analyzed at the UC Davis Stable Isotope Facility (Davis, California, USA). Leaves were analyzed for ^{13}C, ^{15}N isotope and C content using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Soils were analyzed for ^{13}C, ^{15}N isotope and C content using an Elementar Vario EL Cube or Micro Cube elemental analyzer (Elementar Analysensysteme GmbH, Hanau, Germany) interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer. DOC was analyzed for ^{13}C and concentration using an O.I. Analytical Model 1030 TOC Analyzer (Xylem Analytics, College Station, TX) interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer utilizing a GD-100 Gas Trap Interface (Garden Instruments). Samples were acidified and purged with helium off-line to remove all dissolved inorganic carbon. Stable isotope ratio of C was expressed using delta (δ) notation:

$\delta^{13}C_{sam} = [R_{sam}/R_{std} - 1] * 1000‰$, where R_{sam} is the isotope ratio ($^{13}C/^{12}C$) in the samples, and R_{std} is the isotope ratio in the standard, which is Pee Dee Belemnite (PDB) for C.

Calculations

SOC-C

The fraction of litter-derived C in the different soil layers f_s can be obtained by applying a two-source mixing model (Balesdent et al. 1987) of the difference in δ values between the soil with litter (δ_s) and the average of no litter treatment soil (δ_n) at the end of the experiment, according to:

$$f_s = \frac{\delta_s - \delta_n}{\delta_l - \delta_n}$$

where δ_l is the $\delta^{13}C$ value of the litter sample. We assumed the $\delta^{13}C$ values of the litter-derived C incorporated into SOM is equivalent to the $\delta^{13}C$ values of the bulk litter. The amount of carbon from leaf litter at different layers M_{l-s} was calculated as:

$$M_{l-s} = M_{s-s} \times (1 - GWC) \times C_{carbon-s} \times f_s$$

where M_{s-s} is the mass of soil, $C_{carbon\text{-}s}$ is carbon content (g/g) of soil.

Leachate-C

The fraction of leachate derived from litter f_l can be estimated by:

$$f_l = \frac{\delta_{s-l} - \delta_{n-l}}{\delta_l - \delta_{n-l}}$$

where δ_{s-l} is $\delta^{13}C$ of DOC from litter treatment soils, $\delta_{n\text{-}l}$ is $\delta^{13}C$ of DOC from no litter treatment soils, and δ_l is the $\delta^{13}C$ value of the litter sample. We assumed that the $\delta^{13}C$ values of the litter-derived leachate are equivalent to the $\delta^{13}C$ values of the bulk litter. The amount of carbon from leaf litter in DOC was calculated as the sum of litter carbon in leachate M_{l-l}:

$$M_{l-l} = V \times C_{carbon-l} \times f_l$$

where V is volume of leachate, and $C_{carbon\text{-}l}$ is the concentration of DOC.

CO_2-C

The amount of carbon from leaf litter in CO_2 (M_{CO_2}) was calculated from mass balance:

$$M_{CO_2} = M_{carbon-loss} - \sum M_{l-s} - \sum M_{l-l}$$

where $M_{carbon\text{-}loss}$ was calculated as the difference between litter carbon before and after incubation.

Priming effect

To account for priming effect, the fraction of litter-derived CO_2 over the CO_2 respired f_{CO_2} can be estimated by:

$$f_{CO_2} = \frac{\delta CO_{2_s} - \delta CO_{2_n}}{\delta CO_{2_l} - \delta CO_{2_n}}$$

where δCO_{2_s} is the $\delta^{13}C$ value of respired CO_2 from the soil with leaf litter, δCO_{2_n} is the $\delta^{13}C$ value of respired CO_2 from no litter treatment soil, which is estimated as δ value of initial soil at surface, and δCO_{2_l} is the $\delta^{13}C$ value of respired CO_2 from labeled litter. We assumed that no isotopic fractionation is associated to the respiration process ($\delta CO_{2_l} = \delta_l$, $\delta CO_{2_n} = \delta_n$).

Priming effect (*PE*) was calculated as the difference between CO_2 efflux from soil with and without litter of the same rainfall treatment at the same time (Kuzyakov 2010; Kuzyakov et al. 2000):

$$PE = (1 - f_{CO_2}) \times E_l - E_n$$

where E_l and E_n are CO_2 efflux from soil with and without litter addition, respectively.

In our calculations, no isotope fractionation is assumed, i.e. litter-derived CO_2, SOC, and DOC is assumed to be the same as bulk litter C. While this assumption may not be valid, similar approach is commonly used both in the laboratory and in the field to follow litter carbon to soil (Fahey et al. 2011; Kammer et al. 2011; Rubino et al. 2010) and soil food web (Eissfeller et al. 2013; Soong et al. 2016; Zieger et al. 2015).

Statistical analysis

All statistical analyses were conducted using R version 3.3.3. P values below 0.05 were considered significant and those between 0.05 and 0.1 were

considered nearly significant. One-way ANOVA was used to evaluate effect of rainfall on litter mass loss, cumulative CO_2 efflux, and different components of recovered litter carbon in litter treatment soils. Two-way ANOVA was used to evaluate effects of both depth and litter on $\delta^{13}C$ and carbon content of soil. Effects of litter and rainfall on total volume and carbon mass of leachate, and carbon content at 0–2 cm depth were also evaluated by two-way ANOVA. Mixed effect models were conducted using the *lme4* package (Bates et al. 2015) to assess rainfall effect on priming effect. Priming effect was compared between T_{L1} and T_{H1} (right after water addition), and between T_{L3} and T_{H2} (1 day and 2 days after water addition respectively). Column number was treated as random effect, sampling weeks, sampling time (whether T_{L1} and T_{H1} or T_{L3} and T_{H2}), and rainfall were treated as fixed effects. The significance of factors was tested using likelihood ratio test following the order listed above.

Mixed effect models were also run to evaluate effects of sampling weeks, sampling time, and rainfall on proportion of CO_2 from leaf litter, with data from first campaign excluded due to lack of replicates. The significance of factors was tested using likelihood ratio test following the order listed above. Linear regression model was run to explore the relationship between DOC concentration and volume of leachate.

Results

Litter mass loss and recovery of litter carbon

After 6 months, tulip poplar leaf litter lost 67.3 ± 3.2% mass in control rainfall treatment, 64.7 ± 3.2% in medium rainfall treatment, and 60.8 ± 3.4% in extreme rainfall treatment. Litter mass loss showed no significant difference among three rainfall treatments.

Based on mass balance, about half of litter carbon (48.1 ± 1.5%) was respired as CO_2, with remaining leaf litter (30.6 ± 1.8%) and soil carbon (21.3 ± 1.2%) mostly comprising the other half (Fig. 1a). Only a small fraction (0.02 ± 0.01%) of litter carbon ended up as DOC. A comparison between the high (HIGH+) and low (LOW+) intensity rainfall treatments (Fig. 1b) reveals that more litter carbon was recovered under HIGH+ at 2–6 cm, 6–12 cm, 12–25 cm soil depths and in DOC. Details of each litter carbon pathway are discussed later.

CO_2 efflux

After each rainfall event, mesocosms with litter addition exhibited a CO_2 pulse (Fig. 2) followed by a rapid decrease as the leaf litter dried. Apart from the pulses, CO_2 efflux decreased over time in both litter and no litter treatments (Fig. 2). The cumulative CO_2 efflux during the entire incubation period were 3927.1 ± 189.6 mg, 3489.3 ± 164.7 mg, and 3599.3 ± 176.0 mg C-CO_2 for LOW+, MED+, and HIGH+ treatments, respectively; the results were not significantly different. Similar to CO_2 flux, the contribution of CO_2-C from leaf litter peaked after each rain event and decreased until the next (Fig. 3; Table 1, $p < 0.001$), as evidenced by $\delta^{13}C$ of respired CO_2 (Supplementary Fig. 3). The contribution of litter carbon to CO_2-C decreased over time (Fig. 3; Table 1, $p < 0.001$).

Priming effect initially increased, peaked in weeks 17–18 and decreased afterwards. The effect was higher in the LOW+ than in HIGH+ treatments (Fig. 4, Table 1, $p = 0.047$).

Soil organic carbon (SOC)

The effects of depth and litter on $\delta^{13}C$ and $\delta^{15}N$ of soil carbon and soil carbon content at the end of experiment were evaluated using two-way ANOVA (Supplementary Fig. 4). For $\delta^{13}C$, depth ($F_{4,80} = 108.2$, $p < 0.001$), litter ($F_{1,80} = 160.6$, $p < 0.001$), and interaction ($F_{4,80} = 136.8$, $p < 0.001$) effects were all significant. Litter treatment soils had a more positive $\delta^{13}C$ value than no litter treatment soils ($p < 0.001$). Similar results were obtained for $\delta^{15}N$ (Supplementary Fig. 5). Litter had no effect on total carbon content.

One-way ANOVA was performed to evaluate the effect of rainfall on $\delta^{13}C$, $\delta^{15}N$ of soil and soil carbon content in litter treatment soils after incubation at different depths separately. For $\delta^{13}C$, rainfall effect was significant at all depths, except at 0–2 cm. In HIGH+ rainfall treatment, $\delta^{13}C$ of soil carbon was higher at 6–12, 12–18, and 18–25 than either MED+ or LOW+ intensity treatment (Supplementary Table 2, $p < 0.05$ for all of the comparisons). At 2–6 cm depth, both HIGH+ and MED+ soils had a

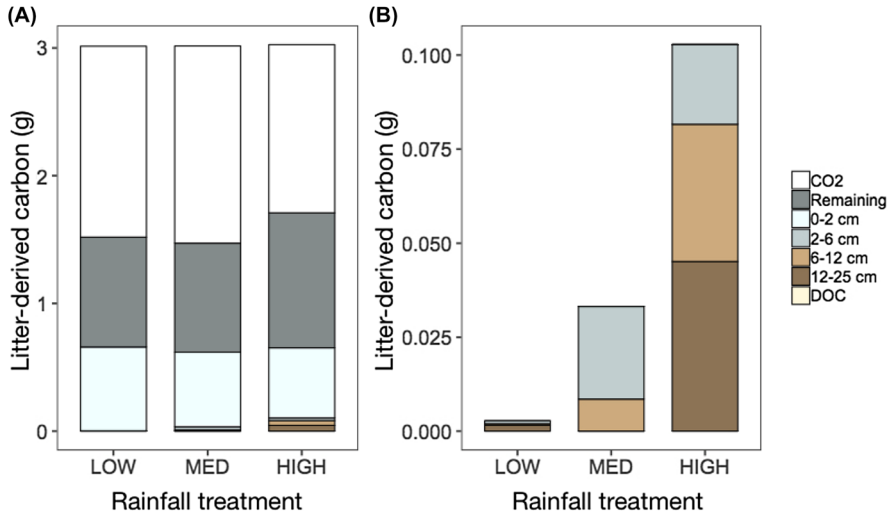

Fig. 1 Litter-derived carbon in all components (**a**) and deeper soil (**b**) in different treatments. Plot B is an enlarged part of plot A, with just deeper soil included. Note the small contribution of litter carbon to DOC

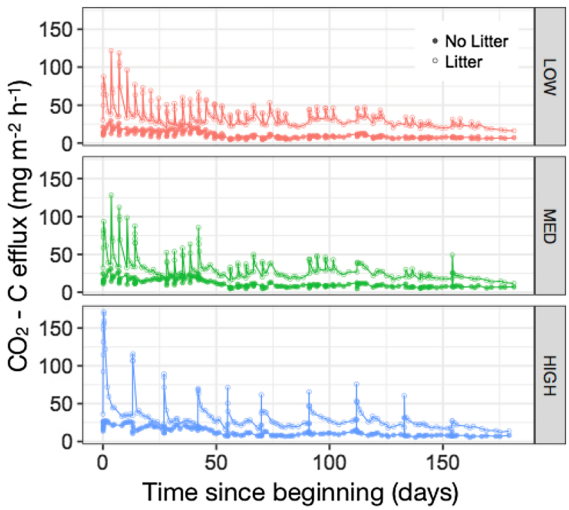

Fig. 2 CO_2 efflux during lab experiment in different rainfall treatments. Each peak indicates a rainfall application. Each point is the mean of three replicate measurements

higher $\delta^{13}C$ than LOW+ soils (Fig. 5a, Supplementary Table 2, $p < 0.001$ for both cases). Rainfall effect on $\delta^{15}N$ of soil at different depths was similar to the effect on $\delta^{13}C$ (see Supplementary Table 3 for details). Rainfall effect was only significant on soil carbon content at 0–2 cm ($F_{2,6} = 7.9$, $p = 0.021$). Soil carbon content at 0–2 cm was significantly higher in HIGH+ than either LOW+ ($p = 0.022$) or MED+ ($p = 0.053$) treatments (Fig. 5b). Carbon content of litter addition soils were higher than no litter treatment soils only at 0–2 cm and only under high intensity rainfall ($p = 0.019$).

Similarly, one-way ANOVA was used to evaluate vertical distribution of litter-derived carbon at the end of the experiment. At 0–2 cm there was no statistical difference among rainfall treatments. More litter carbon was detected at 2–6 cm, both in HIGH+ and MED+ than in LOW+ treatments ($p < 0.001$ for both cases). HIGH+ maintained a significant effect in the remaining depths ($p < 0.05$ for all of the comparisons), while MED+ and LOW+ were not different (Table 2).

Carbon stocks that describe the amount of carbon in the soil profile, have been calculated at the end of the experiment (Supplementary Table 4). As expected, carbon stocks varied by depth. Neither litter nor rainfall treatment affected total carbon stocks, which is not surprising, given that compared to the total amount of initial carbon in the soil column (120.6 g), the carbon addition in the leaf litter treatment was relatively small (3.0 g), more than 50% of which has been lost as CO_2 carbon.

Dissolved organic carbon (DOC)

Both volume and total carbon of leachate varied depending on treatments (Table 3). Both litter ($F_{1,12} = 166.1$, $p < 0.001$) and rainfall ($F_{2,12} = 4.6$, $p = 0.034$) effects on total volume were significant, while interaction ($F_{2,12} = 0.4$, $p = 0.649$) was not. More leachate was collected in litter than no litter treatment ($p < 0.001$), and more leachate was collected in HIGH than LOW treatment ($p = 0.029$) (Supplementary Fig. 6). There existed a negative

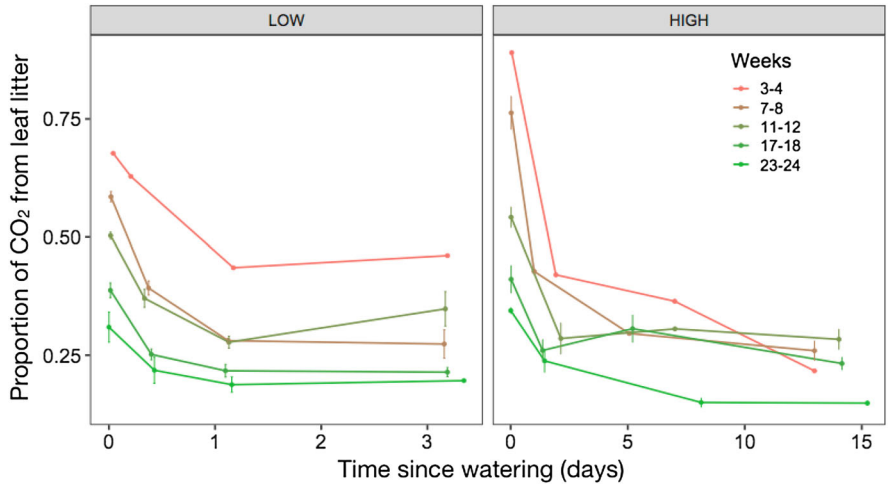

Fig. 3 Temporal change of proportion of CO_2 from leaf litter after different rainfall treatments. Error bars represent standard error. Note the different scales of the x-axes. In the first campaign data are available only for one column in each treatment

Table 1 Results of mixed effect models testing the effects of rainfall on proportion of CO_2 from leaf litter (Prop) and priming effect (PE) (mg m^{-2} h^{-1})

	Weeks		Time		Rainfall	
	χ^2	P	χ^2	P	χ^2	p
Prop	28.56	< 0.001	109.33	< 0.001	0.69	0.406
PE	46.40	< 0.001	3.45	0.063	3.95	0.047

Because the data in the first campaign only had one replicate, it was excluded for this statistical analysis

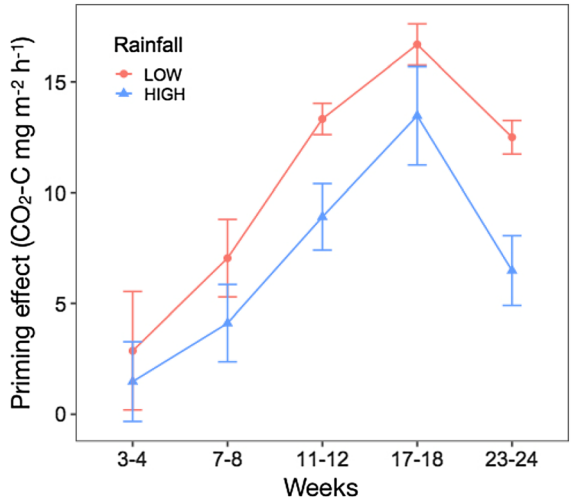

Fig. 4 Temporal change of priming effect in different rainfall treatments. Priming effect was calculated as the difference of CO_2 efflux from soils with and without litter. The means were calculated from four time points after rainfall application across all columns measured with $\delta^{13}C$ of respired CO_2 (Total N = 96). Error bars represent standard error

exponential relationship between DOC concentration and volume ($R^2 = 0.63$, $p < 0.001$, Supplementary Fig. 7). Similar to total volume, both litter ($F_{1,12} = 55.4$, $p < 0.001$) and rainfall ($F_{2,12} = 2.2$, $p = 0.030$) effects on carbon leached were significant, while interaction ($F_{2,12} = 0.2$, $p = 0.796$) was not. More carbon leached in litter than no litter treatment ($p < 0.001$), and more carbon leached in HIGH than LOW rainfall treatment ($p = 0.026$) (Fig. 6).

$\delta^{13}C$ of DOC showed different patterns for HIGH+ and LOW+ treatments (Fig. 7b). After first rain event there was a pulse in HIGH+, followed by a fast decrease; still, $\delta^{13}C$ of DOC remained consistently higher than base line ($\delta^{13}C$ from no litter treatment soils). In LOW+, at first $\delta^{13}C$ was not significantly different from base line, then progressively increased exceeding the base line in the second half of the experiment. Patterns of $\delta^{13}C$ in MED+ were in between HIGH+ and LOW+ treatments. Total carbon leached from leaf litter were 0.07 ± 0.03 mg, 0.38 ± 0.14 mg, and 1.87 ± 0.80 mg for LOW+, MED+, and HIGH+ treatments respectively, with nearly significant ($p = 0.079$) difference between HIGH+ and LOW+ (Fig. 7a).

Discussion

Although there was a reverse trend between rainfall intensity and litter mass loss, the difference was not significant. Leaf litter did not decompose more slowly

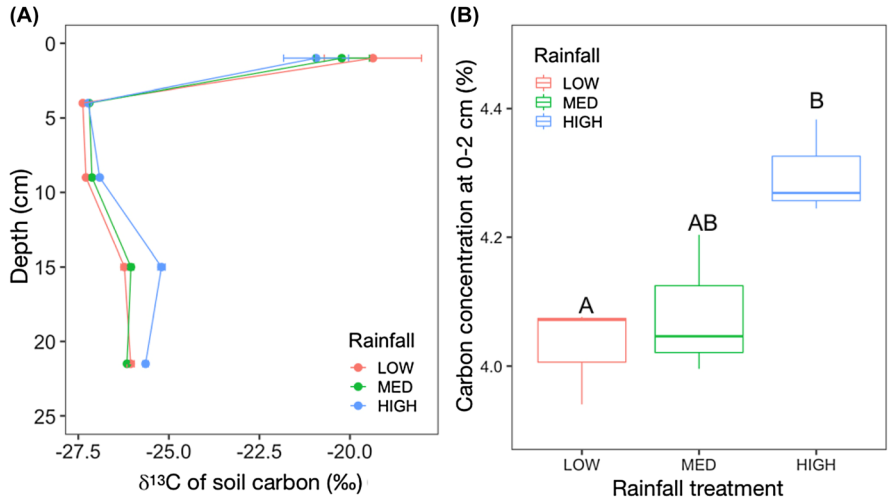

Fig. 5 $\delta^{13}C$ of soil carbon in the soil profile (**a**) and carbon content at 0–2 cm (**b**) in litter addition treatments. Error bars represent standard error. When error bars are not visible they are smaller than the symbol. In plot B, treatments with different letters are significantly different. In plot A, ANOVA tests were all significant except at 0–2 cm, and details of p values are in Supplementary Table 2

Table 2 Litter carbon recovered at different depths in the soil column (mg)

Depth (cm)	Rain intensity		
	LOW	MED	HIGH
0–2	657.0 ± 106.0^a	587.0 ± 54.0^a	551.0 ± 40.9^a
2–6	0.8 ± 0.7^a	24.6 ± 2.8^b	21.2 ± 0.4^b
6–12	0.4 ± 0.4^a	8.5 ± 3.4^a	36.5 ± 5.5^b
12–18	*0^a	1.6 ± 1.6^a	29.3 ± 3.6^b
18–25	2.1 ± 2.1^a	*0^a	15.8 ± 3.6^b

Different superscript letters represent significant difference at p = 0.05 level (One-way ANOVA, Tukey's post-hoc test)

*Zero values mean that the litter treatment soil was lower than that that of the corresponding value in bare soil

at high rainfall intensity; thus the results do not support our first hypothesis. Our second, third, and fourth hypotheses were supported: high intensity rainfall resulted in higher carbon content in leachate (although the effect was nearly significant), more litter carbon in deeper soil and weaker priming effect.

Partition of litter carbon in our experiment (Fig. 1) is comparable to other studies in forest ecosystems in that mineralization of litter to CO_2 contributed the most, followed by litter carbon transported to mineral soil (Kammer et al. 2011; Ngao et al. 2005), and leaching of DOC from litter was minimal (Fröberg et al. 2007, 2009). Rainfall events directly affect decomposition rates by wetting the substrate and stimulating microbial activity. Large fluctuations in precipitation result in extreme wet and dry cycles of the leaf litter. In our experiment, litter mass loss tended to decrease with increasing rainfall intensity. In the low-intensity treatment, litter stayed more consistently moist than in the extreme treatment, resulting in an overall higher decomposition rate. Medium treatment lies between control and extreme treatments. Extreme rainfall variability has been tied to slower decomposition of several grassland species (Walter et al. 2013). Drought induced by longer intervals between rainfall events inhibited microbial activity, resulting in lower decomposition rate in a temperate grassland (Bloor and Bardgett 2012).

Table 3 Total volume (TV) of leachate and total carbon (TC) leached during the experiment

	LOW+	MED+	HIGH+	LOW−	MED−	HIGH−
TV (ml)	866.0 ± 172.0	1120.0 ± 83.7	1152.0 ± 44.3	0	91.8 ± 67.9	243.0 ± 64.4
TC (mg)	43.8 ± 7.8	45.9 ± 4.0	58.1 ± 6.2	0	7.5 ± 4.4	14.0 ± 2.6

Under low intensity-no litter treatment no leaching occurred

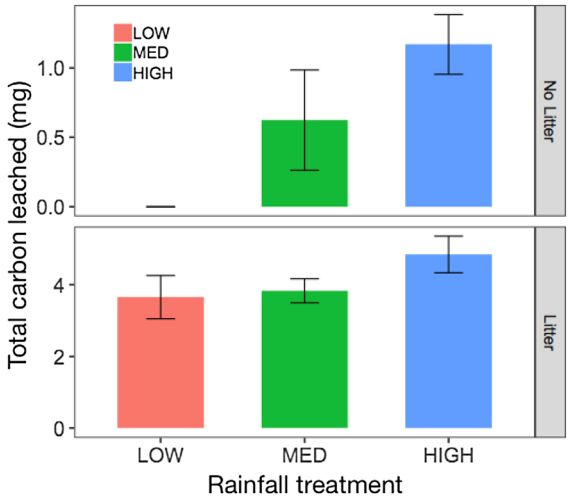

Fig. 6 Total carbon leached from columns in different treatments. Error bars represent standard error. No carbon leached from control, no litter treatment. Two-way ANOVA shows both rainfall ($p = 0.026$) and litter ($p < 0.001$) effects were significant while interaction ($p = 0.796$) was not. Error bars represent standard error

Litter drove the trend of CO_2 efflux

The pulse-like events of rapidly increasing CO_2 right after rainfall application (Fig. 2) is a microbial response to increased water and nutrients (Borken et al. 2003), and it is referred to as "Birch effect" (Birch 1964). Litter drove the trend of CO_2 efflux, especially right after watering, which is supported by a rather high proportion of leaf litter-derived CO_2-C (Fig. 3). Similarly, leaf litter dominating CO_2 pulses have been observed after rain and water addition in the field (Cisneros-Dozal et al. 2007). Given that in in our experiment there was no root respiration, and fungal biomass was likely low, the high contribution of litter carbon to total CO_2 flux was expected.

Leaf water moisture and the contribution of leaf litter to total soil respiration has been shown to be linearly correlated (Lee et al. 2004), indicating a dependence of biological activity on leaf litter wetness as well. In our experiment the wetting–drying cycles of leaf litter and associated microbial activity is reflected in the short-term dynamics both in the total CO_2 efflux and the proportion of litter-derived carbon. The decreasing trend of these variables throughout the experiment can be due to the decrease in labile carbon substrate and, or change in microbial community composition (Borken and Matzner 2009), or carbon use efficiency (Soong et al. 2015). At a more advanced stage of decomposition leaf litter becomes relatively enriched in recalcitrant chemical components (Berg 2000). Ma et al. (2019) incubated surface soils from SERC forests and showed a consistent decrease in fungal/bacterial ratio between the first and sixth month of the experiment. Repeated analysis of the litter residue along with microbial community composition and activity can provide better insight to the

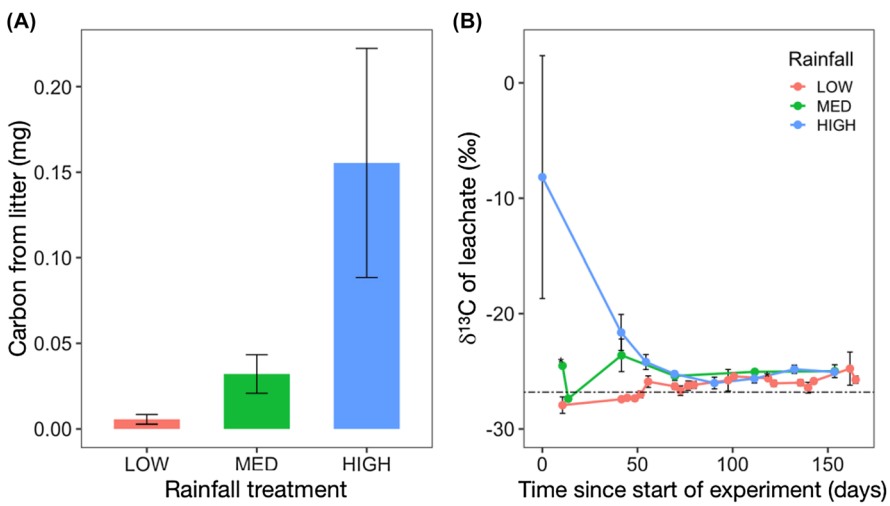

Fig. 7 Carbon recovered from leaf litter in DOC (N = 3) (**a**), and temporal change of $\delta^{13}C$ of DOC from litter addition columns in different rainfall treatments (**b**). Dashed line in plot B represents the mean $\delta^{13}C$ of DOC collected from no litter treatment columns throughout the experiment (N = 8). Error bars represent standard error. *Only one of the three replicates produced leachate. In other cases, where error bars are not seen, the symbols are larger than the error bars

underlying mechanisms of changing carbon fluxes over time.

Higher intensity rainfall transported litter carbon to deeper soil

Consistent with previous laboratory studies (Fröberg et al. 2007, 2009), litter carbon loss as DOC was small. Some carbon, percolating through the soil column, remains as SOM via various mechanisms (Hagedorn et al. 2015; Kaiser and Guggenberger 2000), as was the case in our experiment. The DOC collected at the bottom does not necessarily mean carbon loss from the system. Our soil column was 25 cm tall; in the field processing and retaining DOC can continue further down in the soil profile.

DOC ranged from 2.5 to 37.5 mg L^{-1}, and the result is within the range of DOC concentrations measured in situ in B horizon of temperate forest soils (Michalzik et al. 2001). Leaf litter layer can prevent water from evaporation, leading to more leachate collected under litter treatment columns. Compared to medium and high intensity rainfall treatments, smaller amount of water was applied to low intensity treatment in a relatively longer time frame in a single rainfall event, so water percolated through a drier soil column more slowly, with less leachate collected.

Due to dilution and less contact time with soil (McDowell and Wood 1984), a higher volume of water resulted in a lower DOC concentration. Despite the lower [DOC], the greater volume of leachate yielded more cumulative carbon loss in high intensity rainfall columns (Fig. 6), in agreement with field observations (Bernal et al. 2002; Eimers et al. 2008; Hinton et al. 1997).

The higher $\delta^{13}C$ of DOC in HIGH+ (Fig. 7b) indicates that more litter carbon was transported to deeper horizons under high intensity rainfall, supporting our third hypothesis. Rapid water movement induced by high intensity rainfall can weaken the interactions of DOC with soil minerals and microbial processing, leading to translocation of litter carbon to deeper soil (Hagedorn et al. 2000; Kaiser and Guggenberger 2005; Kaiser and Kalbitz 2012), which is also supported by $\delta^{15}N$ results. While the leachate was not analyzed, most likely labile, water soluble substances contributed to the high value of $\delta^{13}C$ at the early stages of decomposition (Berg 2000; Berg and Lundmark 1987; Cotrufo et al. 2015; Soong et al. 2015). While $\delta^{13}C$ remained above the baseline (no litter treatment soils) throughout the experiment, the source of the litter carbon in the later stages would require further analyses. For example, carbon could have been directly leached out from the leaves or from the soil by desorption and dissolution of $SO^{13}C$ (Kaiser and Kalbitz 2012).

Litter carbon transported to deeper horizons can contribute to stable soil organic carbon formation. If subsoil has higher clay content, as is the case in our forests (NEON 2019; Yesilonis et al. 2016), dissolved carbon can be effectively retained (Kaiser and Guggenberger 2000; Mikutta et al. 2007) and form stable SOC (Cotrufo et al. 2015; Ma et al. 2019).

Carbon accumulation at the surface soil

In the absence of bioturbation and mixing, the main mechanisms of carbon transfer from surface litter to soil are leaching (DOC) and subsequent microbial stabilization as well as physical transfer of litter particles adding to the POM fraction. The relative importance of these processes changes during decomposition along with changes in litter chemistry, but both are important in new SOM formation (Cotrufo et al. 2015). In our experiment increased litter carbon loss via DOC, combined with a lower priming effect in the high intensity rainfall may account for higher soil carbon content at surface soil. A 5-year tulip poplar litter addition experiment at SERC old forests indicated a significant carbon input as coarse particulate organic matter (cPOM) to surface soil (Ma et al. 2014, 2019). High intensity rainfall may further promote fragmentation by physically damaging leaves, but this needs to be tested experimentally.

The temporal change in priming effect needs further investigation. Priming effect in litter incubation experiments has been shown to be highest in the first couple of weeks and has been associated with the addition of highly available C pool from leaf litter (Chao et al. 2019; Zhang and Wang 2012). At the same time, this labile carbon source, carried downward as DOC, can be incorporated to SOC with high efficiency at early stages of litter decomposition (Cotrufo et al. 2015). Moreover, the intensity and mechanisms of priming effect are highly dependent on the chemistry and amount of added C and on the microbial biomass and community composition (Blagodatskaya and Kuzyakov 2008). Unlike many incubation

experiments with stable laboratory conditions, in our case carbon input to the soil happened in pulses, e.g. via rainfall events presumably triggering changes in microbial activity. With the early loss of labile compounds, both the amount and quality of the added carbon likely changed over time. Increase of PE over time, followed by decrease has been detected before (Blagodatskaya and Kuzyakov 2008). However, to properly interpret the observed temporal patterns in our case, several additional parameters, such as microbial community biomass and composition, enzyme activities and DOM chemistry need to be monitored (Kuzyakov 2010).

In summary, our ^{13}C tracer experiment clearly shows that change of precipitation patterns will alter the relative importance of litter carbon fates. High intensity rain events lead to an increase of labile litter carbon in DOC, which may contribute for the increase of DOC in forest watersheds (Bernal et al. 2002); at the same time may lead to carbon accumulation in deeper soil.

Conclusions

The projected increases of both extreme rainfall events and amount of precipitation (Trenberth 2011) will affect all terrestrial ecosystems regardless of their hydrological status (Knapp et al. 2008). In mesic systems, where water is less limiting, the excess amount of water is expected to be lost via runoff while in between rain events these ecosystems are predicted to experience water stress more frequently (Knapp et al. 2008). Changes in hydrology and soil water dynamics alters carbon fluxes on the forest floor and belowground. While in terms of absolute amount, high intensity rainfall did not affect soil carbon stocks, the greater vertical movement of water carried approximately 30 times more litter carbon through the soil profile compared to ambient (low intensity) conditions. In the field where runoff is also a major pathway of water during extreme rainfall events, the vertical transport of litter carbon may not be as intense as in the lab, but over time this may still account for a significant SOM increase in deeper soil. Field experiments are needed to test whether the laboratory findings apply to *in-situ* conditions, where both the forest floor and surface soil are structurally more complex and diverse. The surface soil is covered with a variety of leaf litter types with different leaf chemistry and thus decomposability. Additional carbon sources are present in the forms of fine roots and dead bodies and droppings of soil invertebrates. Both diversity and abundance of microorganisms are higher, which translates to higher carbon transformation rates. Especially importantly, earthworms and plant roots can create preferential flow, which can transport carbon to even deeper in the soil. All these drivers are dynamic, and their relative importance changes daily, seasonally, and during extreme conditions in the field. However, despite excluding other important carbon sources and hydrologic pathways, our experiment highlights that changing precipitation patterns will alter soil carbon cycling processes in systems where water usually does not limit biological activity.

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