Biogeochemistry (2012) 108:395–411
DOI 10.1007/s10533-011-9607-x

Decomposition pathways of ^{13}C-depleted leaf litter in forest soils of the Swiss Jura

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Received: 14 October 2010 / Accepted: 27 April 2011 / Published online: 24 May 2011

Abstract Decomposition of leaf litter and its incorporation into the mineral soil are key components of the C cycle in forest soils. In a ^{13}C tracer experiment, we quantified the pathways of C from decomposing leaf litter in calcareous soils of a mixed beech forest in the Swiss Jura. Moreover, we assessed how important the cold season is for the decomposition of freshly fallen leaves. The annual C loss from the litter layer of 69–77% resulted mainly from the C mineralization (29–34% of the initial litter C) and from the transfer of litter material to the deeper mineral soil (>4 cm) by soil fauna (30%). Although only 4–5% of the initial litter C was leached as dissolved organic carbon (DOC), this pathway could be important for the C sequestration in soils in the long term: The DOC leached from the litter layer was mostly retained (95%) in the first 5 cm of the mineral soil by both physico-chemical sorption and biodegradation and, thus, it might have contributed significantly to the litter-derived C recovered in the heavy fraction (>1.6 g cm^{-3}) at 0–4 cm depth (4% of the initial litter C). About 80% of the annual DOC leaching from the litter layer occurred during the cold season (Nov–April) due to an initial DOC flush of water-soluble substances. In contrast, the litter mineralization in winter accounted for only 25% of the annual C losses through CO_2 release from the labelled litter. Nevertheless, the highest contributions (45–60%) of litter decay to the heterotrophic soil respiration were observed on warm winter days when the mineral soil was still cold and the labile litter pool only partly mineralized. Our ^{13}C tracing also revealed that: (1) the fresh litter C only marginally primed the mineralization of older SOM (>1 year); and (2) non-litter C, such as throughfall DOC, contributed significantly to the C fluxes from the litter layer since the microbial biomass and the DOC leached from the litter layer contained 20–30% and up to 60% of unlabelled C, respectively. In summary, our study shows that significant amounts of recent leaf litter C (<1 year) are incorporated into mineral soils and that the cold season is clearly less important for the litter turnover than the warm season in this beech forest ecosystem.

Keywords Stable isotopes · Litter contribution · Soil CO_2 effluxes · Dissolved organic carbon · Priming effect · Winter · Beech forest

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Introduction

The litter layer links the above- and belowground C cycle and is the C pool with the fastest turnover rates in forest soils. Although recent leaf litter (<1 year) generally accounts for less than 5% of the total amount of organic C in forest soils (Potter and Klooster 1997), its mineralization can contribute temporally up to 40% (Subke et al. 2004; Cisneros-Dozal et al. 2006) and annually more than 20% (Rey et al. 2002; Sulzman et al. 2005) to soil respiration. Moreover, the input of labile litter C may affect the soil respiration indirectly by priming the mineralization of older, stable soil-organic matter (SOM) (Kuzyakov et al. 2000; Fontaine et al. 2007). A substantial fraction of litter-derived C is leached from decomposing litter (Hagedorn and Machwitz 2007). In the mineral soil, this 'new' dissolved organic carbon (DOC) might be effectively stabilized by the interaction with mineral surfaces (Neff and Asner 2001; Kalbitz and Kaiser 2008). Finally, litter C is transformed into SOM and can persist for years or even decades, for instance occluded in aggregates (Swanston et al. 2005; Six et al. 2002). All of these processes in and directly below the litter layer may respond particularly sensitive to climatic changes due to the high lability of the litter C pool and the very high temperature and moisture variability in soils at the surface (Borken et al. 2003; Cisneros-Dozal et al. 2006; Joos et al. 2010). Therefore, the rates at which leaf litter is decomposed and transformed into different fractions of SOM are important parameters in soil carbon models (e.g. Yasso; Liski et al. 2005).

For a large number of ecosystems, litter bags have been used to estimate the control of the mass loss from litter by litter quality, decomposer communities and climatic conditions (e.g. Hättenschwiler et al. 1999; Moore et al. 1999; Liski et al. 2003). However, only a few field studies, tracking the fate of ^{13}C or ^{14}C labelled litter, have investigated the different pathways of litter decomposition; including mineralization, leaching, and transformation into SOM (e.g. Bird and Torn 2006; Fröberg et al. 2009; Rubino et al. 2010).

Using isotopes to track litter-derived C has several advantages over litter bags, such as: (1) litter-feeding soil fauna is not excluded from the decomposition process; (2) the downward transport of litter-derived C can be followed; and (3) the momentary litter-derived CO_2 effluxes can be measured, providing an insight into short-term dynamics of litter mineralization. Recent tracer studies indicate that the fate of litter C may differ considerably in different forest ecosystems. For instance, while mineralization was the most important decomposition pathway in a French beech forest (Ngao et al. 2005), the fraction of litter C transported to the mineral soil was twice as high as the fraction respired as CO_2 in an Italian poplar forest (Rubino et al. 2010).

Information about litter C dynamics is especially sparse for forests with calcareous bedrock as most studies on the cycling of litter-derived C have been conducted in acidic forest soils (e.g. Subke et al. 2004; Fröberg et al. 2007). One common characteristic of calcareous soils is that they have thin organic layers, which indicate a rapid loss of incoming litter due to a high level of biological activity (Scheu 1997; Walthert et al. 2004). Results from microcosm studies suggest that, in base-rich soils, large amounts of fresh leaf litter are incorporated into the mineral soil by macrofauna within a few months (Scheu 1997; Bonkowski et al. 1998). Without using an isotopic label, however, it is not possible to determine how quantitatively important this pathway is.

Although in deciduous forests, most leaf litter falls in autumn, little is known about the fate of this fresh litter C over the winter months. Is the litter preserved due to the cold temperatures or partly mineralized due to its high decomposability? Litter bag studies suggest that substantial amounts of freshly fallen litter C may already be lost in winter (e.g. Heim and Frey 2004). The C losses observed in these studies, however, probably resulted largely from an initial DOC flush, which has been found to occur in several leaching experiments (Hagedorn and Machwitz 2007; Hansson et al. 2010). The biodegradation of this 'wintertime' DOC in the mineral soil might be small as the soil microbial activity is low. Thus, the cold season could be an important period for the transport of litter-derived DOC to the mineral soil where it may be stabilized through interactions with mineral surfaces.

In this study, we present results from a litter manipulation experiment in which, at the beginning of the cold season, ^{13}C-labelled beech leaves were added to two adjacent forest soils with pH values of 7.5 and 5.9. The main goal of our ^{13}C-tracer study was to quantify the different pathways of litter-

derived C in base-rich soils during 1 year: its release as CO_2, its leaching as DOC, its incorporation into the microbial biomass and its transport to the mineral soil. In particular, we aimed to assess: (1) the fate of freshly fallen litter C during the cold season; (2) the contribution of mineralization and leaching of litter C to the C fluxes in forest soils throughout the year; (3) the retention of litter-derived C in the mineral soil; and (4) whether fresh litter C primes the decomposition of older soil C.

Materials and methods

Study site

The litter experiment was established in a mixed beech forest at 680 m a.s.l. on the steep south-facing slope (24°) of the Lägeren mountain close to Zurich (47°28′40.8″ N, 8°21′55.2″). At this Swiss CarboEurope research site (CH-Lae), the net-ecosystem CO_2 exchange has been measured routinely since 2004 using the eddy covariance method and soil respiration since 2006 using closed soil-chamber systems (Ruehr et al. 2010; Etzold et al. 2010). The site is on the geological transition between Jurassic limestone and Tertiary molasse sediments (Heim et al. 2009). The mean annual temperature is 8.4°C and the mean precipitation is 930 mm. The litter experiment was performed on two soil types 200 m apart. One of the soils was a Rendzic Leptosol (or Rendzina; pH 7.5) and the other a Haplic Cambisol (pH 5.9), according to the World Reference Base of Soil Resources (IUSS Working Group WRB 2007). The bedrock of both soils was marl, but overlaid with limestone debris in the Rendzina. Both soils had mull-type organic layers indicative for a high biological activity. The properties of the topsoils (0–10 cm) are given in Table 1. Beech and Norway spruce dominated on both sites, but only the Rendzina was covered by a dense herb layer of wild garlic (*Allium ursinum* L.) in spring.

Labelled litter experiment

After leaf fall in mid November 2007, we replaced the native litter layer with ^{13}C-labelled beach leaves (750 g m^{-2}, $\delta^{13}C = -40.8‰$, C/N = 28) in plots of 50 × 50 cm. The labelled litter originated from the final harvest of an open-top chamber experiment in Switzerland where beech trees were fumigated with ^{13}C-depleted CO_2 for four consecutive years (Hagedorn et al. 2005). Nearby each 'soil + litter' treatment (<1 m), an identical surface area was left without any litter layer for the 'bare soil' treatment. Here, polystyrene shreds were added to mimic a litter layer and its impact on soil moisture and temperature. Both treatments were applied in five replicates to each of the two soil types, which were arranged within a radius of 10 m. The 'soil + litter' plots and the 'bare soil' plots were enclosed within acrylic glass frames (height 12 cm), which were inserted 2 cm into the forest floor and covered with a polyethylene net (mesh size = 0.7 × 0.3 mm) to prevent litter loss due to wind and inputs of fresh litter. In order to recognize the ^{13}C signal of litter-derived CO_2 better, we minimized root respiration by digging a 30 cm deep trench around each plot. A plastic sheet was inserted to prevent external root ingrowths. Vegetation growth within the frames was suppressed by periodically weeding.

Soil CO_2 efflux and its $\delta^{13}C$

Soil CO_2 effluxes were measured bi-weekly with the chamber of a portable infrared gas analyzer (Li-8100, LI-COR Inc., Lincoln, NE, USA). This was placed on permanently installed PVC collars (5 cm high, 20 cm diameter), inserted to 2 cm depth. The measurements started 1 month before litter addition and were always carried out between 11 am and 4 pm.

On ten sampling dates, the $\delta^{13}C$ of the soil respiration ($\delta^{13}C_{resp}$) was determined using the static closed soil chamber approach (e.g. Ohlsson et al. 2005). The collars were closed with a plastic lid and one gas sample was collected from each chamber after a certain closure time, varying between 8 and 40 min. The closure time was estimated from the previous CO_2-efflux measurement to obtain an increase in the CO_2 concentration of about 400 ppm. The concentrations and the $\delta^{13}C$ of ambient CO_2 needed to calculate the $\delta^{13}C$ of soil-respired CO_2 were determined from gas samples taken next to each collar immediately after they were closed. The gas samples were taken with a syringe through a septum in the lid and injected into glass vials (12 ml) previously evacuated and closed with an airtight rubber septum. Their ^{13}C ratios and the CO_2 concentrations were then analyzed with a Gasbench

Table 1 Properties of the top 0–10 cm of soil

	pH ($CaCl_2$)	Particle-size distribution (%)			Bulk density (g cm^{-3})	C_{org} (%)	C/N	C_{org} pool (kg m^{-2})	$\delta^{13}C_{org}$ (‰)
		250–2000 μm	2–250 μm	<2 μm					
Rendzina	7.5 (0.1)	25 (2)	21 (3)	54 (5)	0.91 (0.03)	3.9 (0.3)	12.0 (0.1)	3.6 (0.2)	−27.2 (0.2)
Cambisol	5.9 (0.1)	23 (4)	35 (2)	42 (3)	0.94 (0.6)	2.8 (0.5)	11.3 (0.5)	2.6 (0.1)	−26.7 (0.2)

Five soil cores (5 cm diameter) were taken from both soil types. The values are means ± standard errors

II, connected to a mass spectrometer Delta Plus (both Thermo Finnigan Mat, Bremen, Germany).

The temperatures in the air, in the litter layer and at soil depths of 5 cm and 10 cm were measured using a Licor thermocouple for each sampling location at the same time as the CO_2 effluxes. To record soil temperatures continuously, temperature loggers (ibuttons, Maxim Integrated Products DS1922L, USA) were installed in three replicates per treatment at a soil depth of 10 cm.

DOC fluxes

Throughfall was sampled 1.5 m above the forest floor using PE funnels (Ø 11 cm) connected to 1.5-L PE bottles. The water percolating through the litter layer was captured with zero-tension lysimeters (13 × 17 cm PVC boxes), equipped with four openings (Ø 1 cm) to allow soil animals to feed on the litter. Suction plates (Ø 5.5 cm) made of borosilicate glass (pore size P5; Schmizo, Zofingen, Switzerland) were used to collect the soil solution at depths of 5 cm and 10 cm (only 'soil + leaves'), applying a constant suction of 400 hPa with a vacuum pump (EcoTech, Bonn, Germany). The soil water was collected in 0.5 l bottles buried in the soil. The water samples were collected after every larger rain event to minimize biodegradation of DOC. All water samples were passed through 0.45-μm cellulose-acetate filters (Schleicher & Schuell, ME25), pooled on a monthly base and refrigerated until analysis. This did not alter the DOC concentrations. HCl suprapur (30%) was added to all samples to remove inorganic C. Samples were then analyzed for DOC concentrations, employing a TOC/TN analyzer (TOC-V, Shimadzu Corporation, Tokyo, Japan). In addition, the molar UV absorptivity at 285 nm in the DOC was measured using a Cary 50 UV-spectrophotometer (Varian, Palo Alto, USA). Aliquots (50–80 ml) were freeze-dried to determine the $\delta^{13}C$ of the DOC. Here, the addition of 5 mg of K_2SO_4 per sample facilitated the recovery and the weighing of the dissolved organic matter after freeze-drying.

Sampling and chemical analyses

Soil and litter samples

One year after the litter addition, the litter that remained on the soil surface was collected, cleaned to remove mineral particles and dried at 60°C for analysis. Subsequently, a soil core (Ø 5 cm) 10 cm in length was taken from each plot, frozen and divided into layers 2 cm thick with a hacksaw. The first two layers (0–2 cm, 2–4 cm) were physically fractionated into different SOM pools, while the soils from the other depths were freed from the roots, dried at 60°C and sieved (<2 mm) for total pool estimates.

Physical fractionation

Soils were fractionated into the light fraction (LF) and the heavy fraction (HF). At first, the dried soil samples were suspended in a sodium-polytungstate solution with a density of 1.6 g cm^{-3} (Kaiser and Guggenberger 2007). After decanting the floating fraction (free LF), the suspension was ultrasonicated at 270 J ml^{-1} (HD3200, Bandelin, Zurich, Switzerland) to yield the occluded LF (Roscoe et al. 2000). To reduce the number of samples, the occluded LF and the free LF were combined. Samples of the LF and the HF were dried at 60°C, weighed and milled with a ball mill. Prior to the C analysis, all soil samples were additionally fumigated with acidic vapour for 8 h to remove inorganic C (Walthert et al. 2010).

Microbial biomass

We used the chloroform-fumigation extraction to determine the microbial biomass in the mineral soil at

0–2 cm depth and in the litter layer 4, 8 and 12 months after litter addition (Brookes et al. 1985). Soil samples were taken with a corer (Ø 2 cm) and within 5 h after soil sampling, roots were removed and ten grams of fresh soil and five grams of litter was fumigated for 24 h with $CHCl_3$ and then extracted for 1 h with 50 ml of 0.25 *M* K_2SO_4. Meanwhile, a second sample was extracted without fumigation. The organic C content in the extracts was determined with a TOC analyzer (TOC-500, Shimadzu Corporation, Tokyo, Japan). The microbial C was then calculated from the difference between the fumigated and the unfumigated extracts, assuming an extraction efficiency (K_{ec}) of 0.45 (Wu et al. 1990). For the isotope analysis, the extracts were freeze-dried.

The concentrations and the isotope ratios of C and N in the soil and freeze-dried samples were measured with an elemental analyzer (Euro EA 3000, HEKAtech, Germany) coupled to an isotope ratio mass spectrometer (Delta V Advantage, Thermo, Germany).

Calculations and statistics

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

Gas samples from each soil chamber represented a mixture of ambient CO_2 and cumulated soil-respired CO_2. The $\delta^{13}C$ of soil respired CO_2 ($\delta^{13}C_{resp}$) was calculated as follows (see Subke et al. 2004):

$$\delta^{13}C_{resp} = (\delta^{13}C_{chamber} \times CO_{2chamber} - \delta^{13}C_{ambient} \times CO_{2ambient})/(CO_{2chamber} - CO_{2ambient}) \quad (1)$$

Litter-derived C

The contribution of labelled litter C (f_{litter}) to soil-C fluxes and pools was calculated for each plot individually using the following mixing model:

$$f_{litter} = (\delta^{13}C_{soil+litter} - \delta^{13}C_{control})/(\Delta^{13}C); \quad (2)$$

where $\delta^{13}C_{soil+litter}$ is the $\delta^{13}C$ of the C fluxes and pools in the 'soil + litter' treatment, $\delta^{13}C_{control}$ is the corresponding ^{13}C signature measured in the adjacent 'bare soil' plot and $\Delta^{13}C$ is the difference in the $\delta^{13}C$ between the bulk litter (−40.8‰.) and the soil organic C (SOC; −26.7 to −27.8‰). This approach assumes that isotopic fractionation of ^{13}C was minimal, or at least the same, in the litter layer and the mineral soil during both C mineralization and DOC production (e.g. Schweizer et al. 1999; Santruckova et al. 2000; Fröberg et al. 2007).

Modeling CO_2 effluxes

The relation between soil CO_2 effluxes and soil temperature was fitted with the temperature function proposed by Fang and Moncrieff (2001):

$$CO_{2\,soil} = a \times (T - T_{min})^b; \quad (3)$$

where *T* is the soil temperature at a depth of 10 cm, and T_{min}, *a*, and *b* are parameters derived from non-parametric curve fits (Origin 7.1, OriginLab, USA). The annual C losses through CO_2 release from soils were estimated using the daily soil temperatures as input variables in Eq. 3 fitted to each plot separately.

It was not possible to fit the litter-derived CO_2 effluxes to a reasonable temperature function because the litter C pool declines with time. Alternatively, most ^{13}C-tracer studies simply interpolate the flux rates between the measurements without taking the temperature into consideration (e.g. Ngao et al. 2005; Bird and Torn 2006). In this study, however, we employed a new approach to model litter-derived CO_2 effluxes more accurately by using the temperature dependency of litter-free soils and by incorporating the declining decomposability of the litter C. The temperature sensitivity of the mineral-soil respired CO_2 was estimated by fitting Eq. 3 to the flux rates in the 'bare soil' treatment. Assuming that the mineralization of 'new' litter C and mineral-soil C are equally temperature sensitive, we scaled Eq. 3 to the litter-derived CO_2 effluxes at the beginning of January by linear transformation:

$$CO_{2\,litter} = a \times (T - T_{min})^b \times S \quad (4)$$

The transformation factor *S* was the theoretical ratio of litter-derived CO_2 and mineral soil-derived CO_2 at identical soil and air temperatures. The litter-derived CO_2 effluxes in January were selected as reference values because they contributed most to the soil respiration. Using the air temperature in Eq. 4, we calculated theoretical flux values for all sampling days. The ratio (factor *P*) between the measured litter-derived fluxes and the theoretical values

describes then the change in the mineralization potential of the litter C pool relative to the reference measurements. Therefore, P can be used as a correction factor in Eq. 4:

$$CO_{2\,litter} = a \times (T - T_{min})^{b} \times S \times P \quad (5)$$

After linearly interpolating P between the sampling days and using the daily air temperatures in Eq. 5, we estimated the daily C losses from the litter through CO_2 release for every plot individually, and thus we could calculate the total mineralization of litter C during both the cold and the warm season.

The model for litter-derived CO_2 neglects that the sensitivity of microbial respiration to temperature probably depends on the substrate quality, and thus might be different for leaf litter and SOM in the mineral soil (Conant et al. 2008; Kammer et al. 2009; Craine et al. 2010). To test the robustness of the model to this uncertainty, we continuously varied the parameters T_{min} and b of Eq. 5 to obtain temperature sensitivities equivalent to Q_{10} values of 2–3, which is the common range of Q_{10} values in early stages of leaf litter decomposition (Fierer et al. 2005; Conant et al. 2008). The variation in the temperature sensitivity changed the estimated values for effluxes of litter-derived CO_2 by maximally ±8% as compared to our model ($Q_{10} = 2.5$). This uncertainty was smaller than the variability in CO_2 effluxes between different plots. Moreover, the temperature sensitivity had only negligible influence on the seasonal dynamic of the estimated CO_2 effluxes as the correction factor P in Eq. 5 also accounted for seasonal effects on litter mineralization. The model outcome, therefore, is relatively robust against variations in the temperature sensitivity used.

DOC fluxes

In comparison to the CO_2 effluxes, the approach to determine the cumulated fluxes of DOC below the litter layer and at depths of 5 and 10 cm was straightforward as the DOC in soil water was permanently captured using lysimeters. The DOC concentrations were measured in the collected soil water and the fluxes of DOC were then calculated by linking the DOC concentrations to water fluxes simulated with the COUP model (Jansson and Karlberg 2001). The organic C content and the particle-size distribution of different soil layers were used among other variables to parameterize the model. The climatic input variables—air temperature, precipitation, vapour pressure, wind speed and net radiation—were all recorded at a nearby meteorological station 100 m away.

Statistics

Differences in C fluxes between the two litter treatments and the two soil types were tested with linear mixed effect models using the nlme package from the statistic software R version 2.8.1 (Pinheiro et al. 2008). By including random effects for the 'plot group' and for each single 'litter plot', the models accounted for both the split unit design of the experiment and the repeated measurement structure. In all final models, normality and homoscedasticity of the residuals were verified visually with diagnostic plots and, when necessary, the dependent variable was log transformed.

Results

CO_2 effluxes

The soil respiration showed a pronounced seasonal pattern (Fig. 1), largely following the soil temperature at a depth of 10 cm ($R^2 = 0.85$–0.97; Eq. 3). No relationship, however, was found between soil CO_2 effluxes and soil water contents. This indicates that soil moisture ranging from 25 to 40 vol.% at a depth of 10 cm was not a limiting factor for microbial activity in mineral soils throughout the experiment. While no significant site effect ($p = 0.25$) on soil respiration was observed in winter (Nov 07–April 08), the soil CO_2 effluxes were, on average, 50% higher in the Rendzina than in the Cambisol ($p < 0.001$) during the warm season (April 08–Nov 08). Cumulated over 1 year, the mineral soils from the trenched plots lost 600–900 g C m^{-2} through microbial respiration (Fig. 2).

The natural ^{13}C abundance in mineral soil-derived CO_2 ranged from −24.0‰ to −27.5‰ in both the Rendzina and the Cambisol (Fig. 3a), indicating that the dissolution of carbonates contributed negligibly to the soil CO_2 effluxes. The addition of ^{13}C-depleted

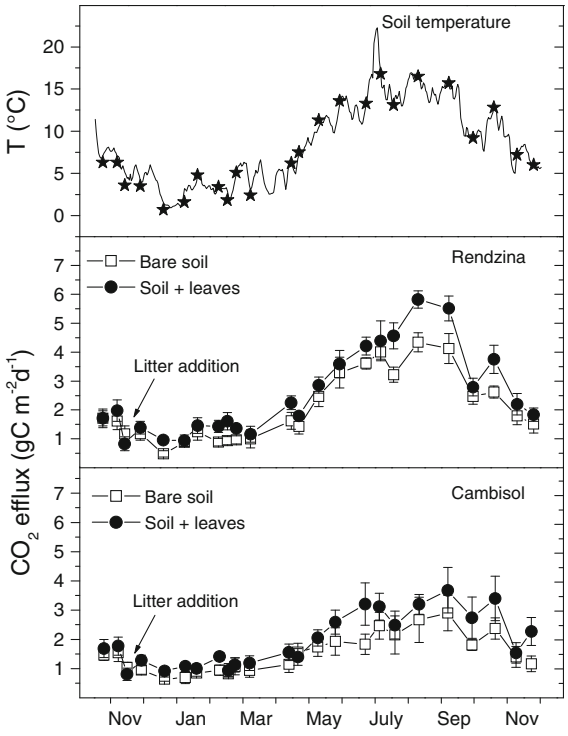

Fig. 1 Seasonal course of the soil temperature at a depth of 10 cm and of the heterotrophic soil respiration in the Rendzina and the Cambisol. The stars are the mean soil temperatures during the CO_2-efflux measurements. The CO_2 effluxes are the means of five replicates (±standard error)

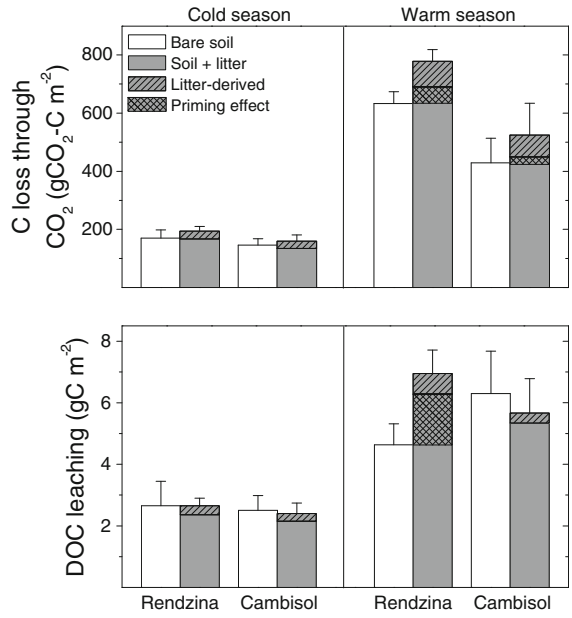

Fig. 2 C loss through CO_2 release and leaching of DOC at a depth of 5 cm in the 'bare soil' and the 'soil + litter' treatments, cumulated over the warm and the cold season. The crossed area indicates positive priming effects of the added litter on the mineralization and the leaching of 'old' C (>1 year) in the mineral soil. All values are means of five replicates (±standard error)

leaves ($\Delta^{13}C = -13.6‰$) enhanced CO_2 effluxes significantly (Fig. 1; $p < 0.001$), and decreased the ^{13}C ratio of soil-respired CO_2 by 1.2–8.4‰ relative to the 'bare soil' (Fig. 3a). The only exception was the sampling in December at air temperatures of −4°C when no litter-derived CO_2 effluxes were observed. Three weeks later, however, at air temperatures of 6°C and soil temperatures of about 1°C, the contribution of leaf litter to soil-respired CO_2 (f_{litter}) peaked at 60% in the Rendzina and 45% in the Cambisol (Fig. 3b). Subsequently, f_{litter} declined continuously to about 10% at the end of the experiment in November.

The seasonal pattern of the litter mineralization was less pronounced than that of the soil respiration (Fig. 4): The highest litter-derived CO_2 effluxes in winter were only 25% lower than the peaking fluxes in summer, despite differences in air temperatures of 13°C. In comparison, the peaks in total soil-respiration rates differed by a factor of 2.5 between the seasons (Fig. 1). Soil type had a minor effect on the mineralization rates of the litter C. They were slightly (−15%), but not significantly ($p = 0.17$), lower in the Cambisol than in the Rendzina.

The annual C losses of the litter, estimated by applying the temperature dependency of the CO_2 effluxes in the 'bare soil' treatment ($R^2 = 0.91$; $Q_{10} = 2.5$; see Eqs. 3 and 5), were 33.5 ± 4.5% in the Rendzina and 29.0 ± 3.3% in the Cambisol. Mineralization during the five winter months accounted for 25% of the annually respired litter C (Table 2; Fig. 4).

Fractions of soil-respired CO_2 that originated from priming effects were calculated as the difference between cumulated C losses through CO_2 release from the 'soil + litter' treatment and the sum of C losses from the litter layer and the 'bare soil' treatment (Fig. 2). These differences were small in winter, indicating that the litter layer had no effect on the CO_2 release from the mineral soil. During the warm season, however, the litter layer increased the SOM mineralization slightly, but not significantly (+7%, $p = 0.21$).

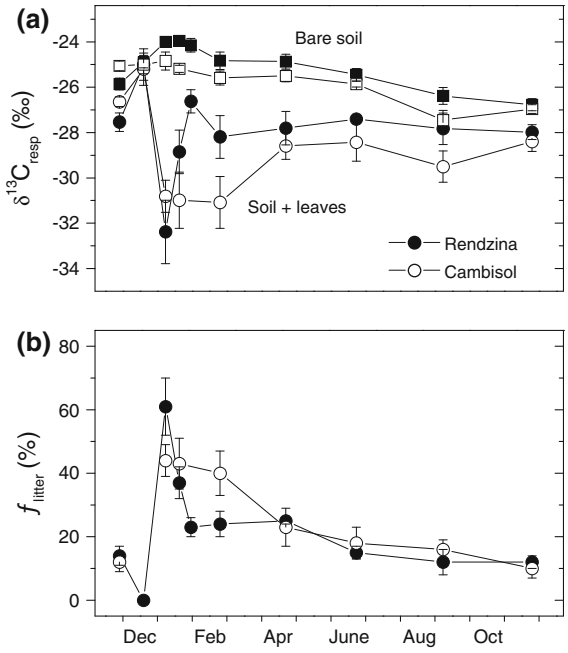

Fig. 3 **a** ^{13}C signatures of soil CO_2 effluxes ($\delta^{13}C_{resp}$), and **b** contributions of litter-derived C to the heterotrophic soil respiration (f_{litter}). The values are the means of five replicates (±standard error)

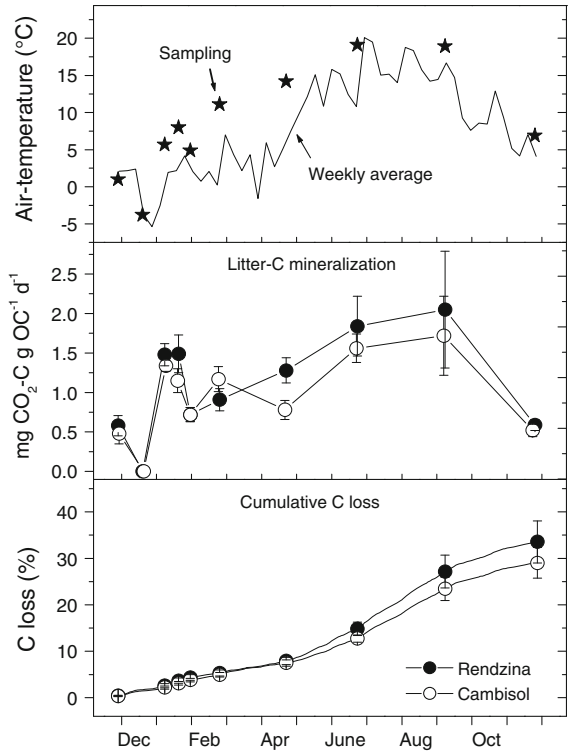

Fig. 4 Air temperature, rates of litter-C mineralization and cumulative C loss through CO_2 release from the labelled leaves. Please note that the mineralization rates represent the CO_2-effluxes measured in the field, whereas the cumulative C losses were modeled with Eq. 5 using the mineralization rates as input variables. All values are the means of five replicates (±standard error)

DOC leaching and retention

Litter layer

The leaching of DOC from the litter layer significantly differed from the seasonal course of CO_2 effluxes. About 80% of the annual fluxes of litter-derived DOC occurred during the five winter months, mainly due to an initial DOC flush (Fig. 5). Subsequent to the first leaching cycle, the fluxes of litter-derived DOC dropped to values about eight times lower and then remained in a narrow range throughout the experiment. The ^{13}C ratio of the DOC leached from the labelled litter layer increased by 6–7‰ over the course of the experiment (Fig. 6). Thus, up to 60% of this DOC originated from non-litter C. For 1 year, the leaf litter lost 13–16 g C m^{-2} through DOC leaching. This amount corresponds to 4–5% of its initial C pool (Table 2) and to 11–16% of the litter C respired as CO_2. The DOC release from the litter did not depend on the soil type throughout the experiment (Fig. 5; $p = 0.27$). The DOC of the first leaching cycle was characterized by an approximately 40% lower molar UV absorptivity compared to the subsequently leached DOC, with absorptivity values ranging from 220 to 300 l cm^{-1} mol^{-1} (data not shown).

Mineral soil

The DOC fluxes, cumulated over 1 year and averaged for both soils, declined from 22 g DOC m^{-2} $year^{-1}$ under the litter layer, to 9 and 6.5 g DOC m^{-2} $year^{-1}$ at soil depths of 5 and 10 cm, respectively. The contribution of litter-derived DOC to mineral-soil DOC was largest in early winter, when it was 17–24% but it then dropped to a relatively constant value of about 10% in the Rendzina and about 5% in the Cambisol (Figs. 5 and 6). Thus, only small amounts of labelled litter DOC were recovered in the mineral soil (at 5 cm: 0.8 g DOC m^{-2} $year^{-1}$; at 10 cm: 0.4 g DOC m^{-2} $year^{-1}$; Fig. 5). This finding

Table 2 Different pathways of litter-derived C

Period	CO_2	C fluxes (% of initial litter C)			C pools (% of initial litter C)		
		DOC Oi	DOC 5 cm	DOC 10 cm	LF 0–2 cm	HF 0–2 cm	Litter layer
Rendzina							
Winter	7.9 (0.8)	2.9 (0.6)	0.08 (0.0)	0.06 (0.0)			
1 year	33.5 (4.5)	3.8 (0.7)	0.26 (0.1)	0.15 (0.0)	3.3 (1.3)	7.2 (2.0)	22.6 (3.3)
Cambisol							
Winter	7.5 (0.7)	3.7 (0.2)	0.08 (0.0)	0.07 (0.0)			
1 year	29.0 (3.3)	4.6 (0.3)	0.17 (0.1)	0.12 (0.0)	3.7 (1.3)	2.0 (1.6)	31.0 (10)

The C fluxes were either modeled (CO_2) or cumulated (DOC) over five winter months and over the entire year. The litter C that remained in the litter layer or was incorporated in either the light fraction (LF < 1.6 g cm^{-3}) or the heavy fraction (HF) of the mineral soil at 0–2 cm depth was determined 1 year after litter addition. The values are means and standard errors from five plots

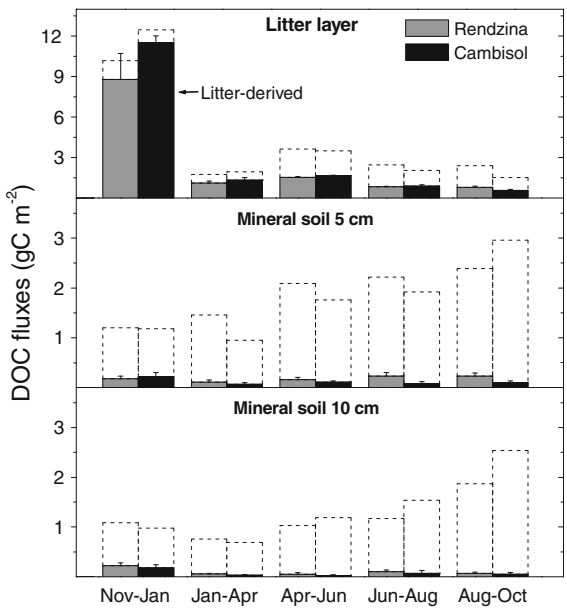

Fig. 5 DOC fluxes at three different depths. The entire *bar* represents the total DOC flux, which consists of litter-derived DOC (*filled part*) and non-litter DOC (*dashed line*). The values are the means of five replicates (±standard error)

indicates that most DOC (93–98%) leached from the litter layer was retained in the top centimeters of the soil profile.

While there was no soil-type effect on DOC fluxes from the mineral soil itself ($p = 0.69$), twice times as much litter-derived DOC was recovered at depths of 5 and 10 cm in the Rendzina than in the Cambisol (Fig. 5). This suggests a stronger retention of 'new' litter DOC in the slightly acidic mineral soil. The fact that the DOC fluxes at 5 cm in the 'bare soil' did not differ significantly from those in the 'soil + litter' treatment from November to April ($p = 0.71$) shows that, in winter, the litter layer barely stimulated the DOC production in the mineral soil (Fig. 2). During the warm season, the litter effect on the leaching of native DOC in the mineral soil depended on the soil type ($P_{\text{litter} \times \text{soil}} < 0.01$; Fig. 2): The fluxes of 'old' DOC in the 'soil + litter' plots were clearly higher (+35%) than in the 'bare soil' plots in the Rendzina, but slightly lower in the Cambisol (−15%).

Microbial C

The amount of microbial C (mg g^{-1} SOC) at a depth of 0–2 cm did not differ significantly between either the soil types ($p = 0.43$) or the 'bare soil' and the 'soil + litter' treatment ($p = 0.55$; Table 3). While in the litter layer the proportion of microbial C almost doubled from winter to summer (Table 3), the microbial C in the mineral soil decreased by about 30% from the cold to the warm season.

The ^{13}C ratios of the microbial biomass were about 4‰ higher than those of the light fraction (LF; <1.6 g cm^{-3}) and about 2.5‰ higher than those of the heavy fraction (HF; >1.6 g cm^{-3}) at a depth of 0–2 cm (Fig. 7). In the litter layer, the microbial ^{13}C shift relative to the bulk litter ranged from 5 to 6.5‰ throughout the experiment. Under the assumption that the native ^{13}C enrichment of microbial C on litter was at most 4‰ (see above microbial C vs. LF), we estimated that roughly more than 10–20% of the C assimilated by microbes in the litter layer did not originate from the labelled litter (Table 3). In the microbial biomass of the mineral soil at 0–2 cm

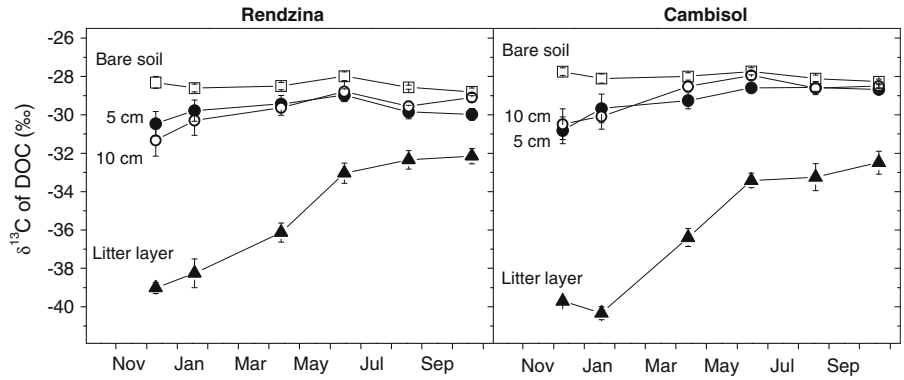

Fig. 6 ^{13}C signature of the DOC leached from the litter layer and the mineral soil at depths of 5 cm (bare soil, soil + leaves) and 10 cm (soil + leaves). The values are the means of five replicates (±standard error)

Table 3 Microbial biomass C and its proportion, derived from the 'new' litter C determined in the litter layer and the mineral soil (0–2 cm) using chloroform-fumigation extraction

Soil	Sample	Microbial C (mg g^{-1} SOC)			Litter-C fraction (%)		
		March	July	Nov	March	July	Nov
Rendzina	Litter layer	18 (1)	33 (1)	28 (1)	80 (2)	92 (3)	82 (5)
	0–2 cm (below litter)	36 (3)	24 (2)	27 (1)	5 (1)	9 (4)	3 (6)
	0–2 cm (bare soil)	39 (3)	26 (2)	26 (4)	–	–	–
Cambisol	Litter layer	21 (3)	36 (3)	24 (3)	88 (3)	90 (4)	80 (5)
	0–2 cm (below litter)	64 (2)	21 (0)	30 (5)	3 (4)	5 (3)	7 (4)
	0–2 cm (bare soil)	41 (12)	18 (1)	27 (6)	–	–	–

The samples were collected 4, 8 and 12 months after litter addition. The values are means and standard errors from three plots

depth, the fraction of litter-derived C ranged from 3 to 9% on all three sampling dates (Table 3). Hence, 1–2 g m^{-2} of litter C was incorporated into the microbial biomass at 0–2 cm depth, corresponding to about 0.5% of the total litter C added.

New C in different SOC pools

At the end of the experiment, the $\delta^{13}C$ of the litter collected from the soil surface was slightly, but not significantly, higher than the $\delta^{13}C$ of the initially added litter in both soils (−40.4‰ vs. −40.8‰; $p = 0.22$). The fraction of added leaf C that remained in the litter layer after 1 year was on average 23% in the Rendzina and 31% in the Cambisol (Table 2).

The $\delta^{13}C$ values in both the LF and the HF of the mineral soil at 0–2 cm depth were shifted slightly, but significantly, by the addition of litter ($p < 0.001$; Fig. 7). One year after litter addition, about 3.5% of the initial litter C was stored in the LF at 0–2 cm depth (Table 2), where it contributed 6% to the total

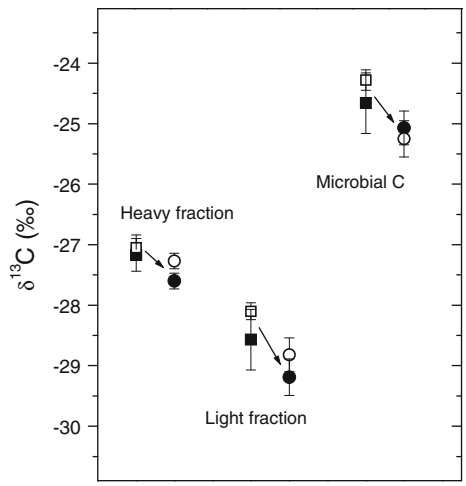

Fig. 7 Shift in the ^{13}C signature of different SOM fractions (0–2 cm) 1 year after the litter addition. The *squares* are the 'bare soil', the *circles* are the 'soil + litter' treatment, the *filled symbols* are the Rendzina and the *open symbols* are the Cambisol. The values are the means of five replicates (±standard error)

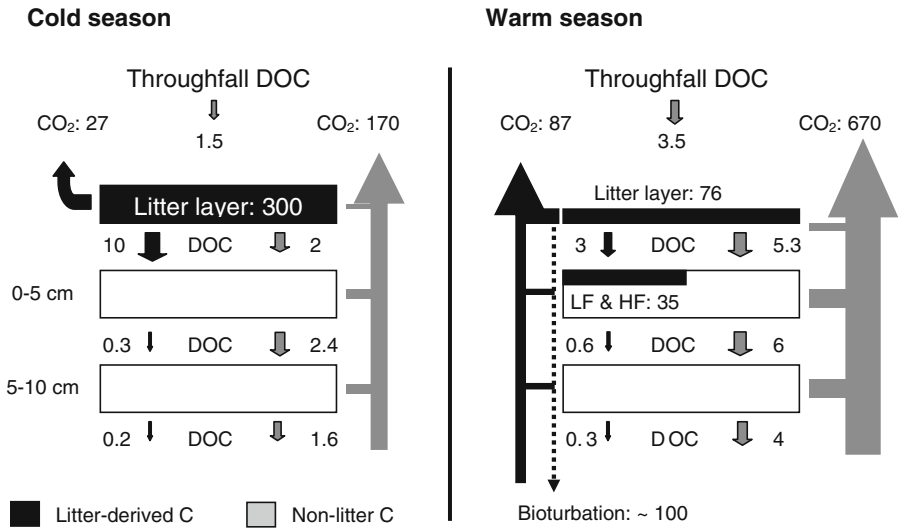

Fig. 8 C fluxes and C pools (g C m^{-2}) from added leaf-litter C and non-litter C, cumulated over the cold (Nov 07–April 08) and the warm season (April 08–Nov 08). The values are the means of five replicates in the Rendzina

C pool of the LF. The HF at 0–2 cm depth contained two times more 'old' C than the LF, and stored 7% of the initial litter C pool in the Rendzina and 2% in the Cambisol. No significant change in the ^{13}C signature, however, was observed at 2–4 cm depth in either the HF or the LF (data not shown).

Discussion

Tracing ^{13}C in litter-derived C provided a more detailed insight into the pathways of decomposing beech leaves than the analyses of net C fluxes in the litter layer and in the mineral soil. For instance, total DOC fluxes changed only slightly from the litter layer to the soil depth of 5 cm from spring to autumn (Figs. 5 and 8). This would suggest that processing of litter-derived DOC in the mineral soil was negligible. In contrast, the tracking of ^{13}C-labelled litter revealed that, during the warm season, 80–90% of the DOC leached from the litter was retained in the mineral soil, and 90–95% of the DOC at the depth of 5 cm originated from the mineral soil itself. Thus, the DOC turnover was much greater than expected from the net fluxes. We also found that 'external' non-litter C contributed significantly to the C fluxes from the litter layer since the microbial biomass contained 10–20% of unlabelled C and the DOC leached from the litter layer up to 60% (Table 3; Figs. 5 and 6). Similar fractions of non-litter C were recently observed in C fluxes from ^{14}C-labelled litter in a hardwood forest (Fröberg et al. 2009). Our study suggests that one source of this non-litter C was throughfall DOC, which amounted to 5 g C m^{-2} $year^{-1}$, and thus corresponded to the non-litter C observed in the DOC leached from the litter layer. The fraction of unlabelled C in the microbial biomass, however, indicates an input of non-litter C to the litter layer of more than 15 g m^{-2} $year^{-1}$, which probably originated from the deposition of pollen and other particulate organic matter. Throughfall measurements in German beech forests by LeMellec et al. (2010) have shown that particulate organic matter can exceed DOC inputs.

Pathways of litter decomposition

After 1 year of decomposition, 29–34% of the litter-derived C had returned as CO_2 to the atmosphere and 4–5% had been leached as DOC (Table 2, Fig. 4). The sum of both fluxes was within the range of the annual C losses (24–44%) from beech leaves observed in litterbag studies in Switzerland (Hättenschwiler et al. 1999; Heim and Frey 2004). In both soils, we recovered 70% of the labelled leaf litter C by summing up across all fluxes and pools that had been measured throughout the experiment (Table 2, Fig. 8). We attribute the missing litter C in the mass balance mainly to the transfer of leaf material by soil animals into deeper soil horizons. This was observed in a lab experiment on calcareous

soils by Scheu (1997), who found that earthworms removed more than 30% of beech leaves within 3 months. Consequently, the export of leaf litter by soil fauna probably equalled the loss via mineralization and exceeded the leaching of 'new' DOC from the litter layer, as well as the incorporation of 'new' C into the mineral soil at a depth 0–2 cm (Table 2, Fig. 8). Therefore, in beech forests with mull-type organic layers, bioturbation is the dominant transport pathway of 'new' litter C into the mineral soil, while leaching seems to be less important than in coniferous ecosystems with thick organic layers (e.g. Neff and Asner 2001; Hagedorn et al. 2008; Kalbitz and Kaiser 2008).

Our finding that the pathways of litter C differed only slightly between the Rendzina and the Cambisol (Table 2) suggests that the pH values of 7.5 and 5.9 are both within the optimum range for microbial decay of leaf litter and activity of the soil fauna. Thus, our study provides no support for the general assumption that litter decomposition is positively linked to the pH value associated with a higher species diversity of the decomposer community (Vesterdal 1997; Schaefer et al. 2009).

Seasonal dynamics in mineralization and leaching

The mineralization and the leaching of litter C differed greatly not only quantitatively, but also in their seasonal dynamics. While respiration during the five winter months accounted for only 25% of the annual C loss through CO_2 from the litter (Table 2; Figs. 4 and 8), the DOC leaching in the cold season was 80% of the annual leaching losses (Table 2, Fig. 5). This result suggests that mineralization and leaching from litter are not basically linked, which goes along with the findings of several lab studies that CO_2 and DOC production correlate only slightly (Magill and Aber 2000; Park et al. 2002; Hagedorn and Machwitz 2007). The large DOC fluxes in early winter probably resulted from the flushing out of water-soluble substances by heavy rainfall. The initially leached DOC had a low molar UV absorptivity, indicating that it comprised largely substances with a low-molecular weight and not microbially degraded aromatic compounds (Dilling and Kaiser 2002). Although such peaking DOC concentrations have already been observed under litter layers following the autumn leaf fall (Park and Matzner 2003), we cannot rule out that in our litter experiment, the DOC flush was intensified by the drying of the litter before its application (see Fröberg et al. 2007).

In several tracer studies, measuring litter-derived CO_2 effluxes between spring and autumn, the litter fractions of soil respiration (f_{litter}) have been observed to decline quickly with increasing time after litter addition (Rochette et al. 1999; Subke et al. 2004; Joos et al. 2010). Our one-year experiment starting in winter only partly confirms this pronounced temporal pattern (Fig. 3). The highest values for f_{litter} (up to 60%) were indeed measured in winter when the most labile components of the leaf litter were still available, while during the warm season, more than 5 months after the litter addition, f_{litter} was always below 30%. Our results, however, also revealed that in winter, f_{litter} considerably depends on the gradient between air and soil temperatures. The highest values for f_{litter} were observed on warm winter days when air temperatures exceeded 5°C but the temperatures in the mineral soil were still close to zero degrees. In comparison, in November and December, a very cold (0–1°C) or frozen litter layer on soils with temperatures above 3°C only contributed negligibly to soil respiration despite the very fresh litter C (Fig. 3). Modeling the seasonal C losses through CO_2 from both the added litter and the mineral soil, taking these very cold periods into account, resulted in clearly higher C losses from the litter in the warm season than in the cold season (Figs. 2 and 8) and only slightly lower values for f_{litter} (13% vs. 15%). Thus, the warm season was much more important for the litter turnover than the cold season.

Here, it should be noted that the litter layer was mostly wet throughout the summer 2008 with frequent rains and the soil moisture never dropped below critical values of 15 vol.% at which soil respiration starts to decrease at our research site (Ruehr et al. 2010). Nevertheless, we may have slightly overestimated the cumulated C losses from the litter in summer because we measured the litter-derived CO_2 effluxes only on a few sampling days. Thereby, we ignored the few periods (at most 20 days in total) when the litter layer was dried out, and thus the microbial activity on surface litter was reduced (Cisneros-Dozal et al. 2006; Joos et al. 2010). However, our ^{13}C-based estimates of litter

mineralization are in line with those from a litterbag study in Switzerland in which beech leaves were found to have lost 24–40% of their initial weight after 1 year, but only 1–9% during the initial six winter months (Heim and Frey 2004).

We assume that the litter C respired over the winter months originated largely from labile leaf compounds such as hydrophilic substances because: (1) the cumulated C losses through CO_2 release in winter of about 8% agreed well with the fraction of water-soluble components in beech leaves (Vesterdal 1997; Zeller et al. 2000); and (2) the mineralization rates declined by 30% from January to April despite a temperature increase of 9°C (Fig. 4), indicating the loss of the most labile compounds. Over the warm season, however, the decrease in the litter C pool was only slightly reflected in the litter-derived CO_2 effluxes. In particular, in late summer and in autumn, the recycling of litter C (<1 year) already incorporated into the mineral soil by DOC leaching, microbes or invertebrates might have been a significant CO_2 source (Fig. 8). At the last sampling in November, for instance, we observed that f_{litter} was about 15% in two litter plots where the litter layer had completely disappeared.

Retention and stabilization of litter DOC in the mineral soil

The ^{13}C values showed a strong decline in litter-derived DOC from the litter layer to the mineral soil at depths of 5 and 10 cm (Figs. 5 and 6), indicating an effective retention of this 'new' DOC within the first centimeters of the mineral soil. The 'new' C accounted, on average, for only 10% of the DOC flux at 5 cm, which implies that most of the DOC leached below 5 cm originated from the mineral soil itself. Comparable strong retentions of ^{13}C- and ^{14}C-labelled litter DOC have been observed for both mineral soils (Fröberg et al. 2009) and organic layers (Fröberg et al. 2007; Müller et al. 2009), but the mechanisms behind them remain uncertain.

Our results provide evidence that both physico-chemical sorption and biodegradation contributed significantly to the DOC retention. We found that DOC was retained not only in the warm season but also in winter, and thus also when microbial activity was low, which suggests that sorption processes played a crucial role. The enhanced DOC retention in the Cambisol (Fig. 5), which was possibly due to a stronger sorption to soil minerals at lower pH values (Tipping 2002), supports this conclusion. On the other hand, the fact that the initially flushed DOC, which contained the largest hydrophilic fraction, was more strongly retained (98%) than the DOC subsequently leached (70–95%) suggests that DOC was also taken up by microbes since hydrophilic DOC has a lower affinity to mineral surfaces than hydrophobic DOC and is also more biodegradable (Kaiser and Guggenberger 2000; Kalbitz et al. 2003). Indeed, on all three sampling dates, we found small but detectable fractions of 'new' litter C in the microbial biomass of the mineral soil at a depth of 0–2 cm (1–2 g C m^{-2}; Table 3 and Fig. 7). At the end of the winter, this new microbial C probably originated from litter-derived DOC since it appears very likely that the cold temperatures prevented the transport of litter material by invertebrates. Assuming that 50% of the litter-derived DOC assimilated by the microbial biomass was lost as CO_2 (Six et al. 2006), a rough mass balance indicates that 20–40% of the litter DOC could have been biologically immobilized in the two soil types at a depth of 0–2 cm during the winter months.

The retention of litter-derived DOC in the mineral soil either by microbial immobilization or by physico-chemical interactions represents an important stabilization mechanism for SOM (Kaiser and Guggenberger 2000; Kalbitz and Kaiser 2008). At the end of our experiment, the heavy soil fraction at 0–2 cm depth did indeed comprise 4% new C in the Rendzina and 2% new C in the Cambisol. Although these fractions seem small, they corresponded to 25 g m^{-2} of new litter C in the Rendzina and 7 g m^{-2} in the Cambisol, which is in the range of the total DOC amount retained in the mineral soil (12–15 g DOC m^{-2} $year^{-1}$). In the long-term, this pathway could contribute significantly to C sequestration in soils.

No priming of native C mineralization

Labile litter C may stimulate the mineralization of older stable SOM (Fontaine et al. 2007; Nottingham et al. 2009), but in our study we found only slight support for such a priming effect (Fig. 2). No priming occurred in winter, while during the warm season the

leaf litter enhanced the SOM mineralization slightly but not significantly (+7%). These small priming effects fit in the findings of Subke et al. (2004) that the litter layer had no effect on the mineralization of 'old' SOM in forest soils where the root respiration was excluded by girdling. In contrast, Sulzman et al. (2005) reported that, after 6 years of additional leaf litter input, the mineralization of older C, calculated from the difference in soil CO_2 effluxes between double litter plots and control plots, was significantly stimulated (+20–30%). In our experiment, the incorporation of leaf litter into the mineral soil by soil fauna probably did not start before summer, and most litter-derived DOC was retained in the uppermost soil (Fig. 8). Hence, the contact of 'new' labile C with older SOM was largely restricted to the first centimeters of the soil during most of the experiment. This part of the soil probably made only a minor contribution to the totally respired CO_2, which, in turn, might explain the insignificant response of mineral soil-derived CO_2 to the fresh C source. Moreover, the addition of litter did not alter the microbial biomass of the mineral soil (Table 3), which could have affected the mineralization of SOM (e.g. Nottingham et al. 2009). The marginal effect of litter on microbes is underlined by the small fractions of recent litter C recovered in the microbial C at a depth of 0–2 cm (3–9%, Table 3). This is further supported by the results from a ^{14}C tracer study on the Oak Ridge Reservation, where 1–4 year old litter was only a small C source (<10%) for microbes in the mineral soil (Kramer et al. 2010).

Recent tracer-based studies suggest that the supply of fresh DOC, such as throughfall DOC or rhizodeposits, can enhance the mobilization of native DOC in the first centimeters of the soil (Hagedorn et al. 2008; Müller et al. 2009). Our results, however, give a controversial picture: No priming effect was observed in winter (Fig. 2), while during the warm season, the leaching of native DOC in the mineral soil was increased under the litter layer in the Rendzina (+35%), but slightly reduced relative to the 'bare soil' in the litter plots of the Cambisol (−15%). Here, we cannot clarify whether the priming effect on DOC leaching indeed depends on the soil type possibly due to a different availability of nutrients (Fontaine et al. 2003), or if the different responses can simply be attributed to the spatial heterogeneity of the DOC leaching.

Conclusions

Using ^{13}C-labelled litter yielded insights into the fate of decomposing leaf litter in a mixed beech forest in the Swiss Jura. We quantified three main pathways of litter-derived C, which all corresponded to about 30% of the initial litter C pool: Litter-C mineralization, transfer of litter material to the deeper mineral soil (>4 cm depth) by soil fauna, and litter C remaining on the soil surface. Only 4–5% of the added litter C, however, was leached as DOC. Our study also shows that in these types of forest soils with high pH values: (1) the greatest contribution of fresh leaf litter to the soil respiration can be expected on warm winter days when the mineral soil is still cold and the labile litter pool is only partly mineralized; (2) about 25% of the annual litter mineralization and 80% of the litter-derived DOC leaching occurred during winter (Nov–April); (3) about 95% of the DOC leached from the litter layer was retained in the first centimeters of the mineral soil, probably due to both physico-chemical sorption and biodegradation; (4) 'external' non-litter C contributed significantly to the C fluxes from the litter layer; and (5) fresh fallen litter did not prime the mineralization of old SOM.

Acknowledgments We would like to thank Simone Ackermann, Dominik Bornhauser, Noureddine Hajjar, David Hiltbrunner, Roger Köchlin, Dimitri Malsam, Christian Merkli and Alois Zürcher (all WSL) for assistance in the field and laboratory; Ursula Graf (WSL), Mathias Saurer and Rolf Siegwolf (PSI, Villigen) for analyzing the stable isotopes; and Philipp Vock and his team from the Forest Enterprise Wettingen for their kind cooperation. We are also grateful to Nadine Rühr, Lydia Gentsch (ETH, Zurich) and Christoph Hüglin (EMPA, Dübendorf) for providing us with meteorological data for our site and Silvia Dingwall for accurately proof-reading the manuscript. This study was funded by the Swiss National Science Foundation (Grant No. 205321–112021).

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