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Mineralisation, leaching and stabilisation of ^{13}C-labelled leaf and twig litter in a beech forest soil

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Abstract. Very few field studies have quantified the different pathways of C loss from decomposing litter even though the partitioning of C fluxes is essential to understand soil C dynamics. Using 0.75 kg m^{-2} of ^{13}C-depleted leaf (δ^{13}C = −40.8 ‰) and 2 kg m^{-2} of twig litter (δ^{13}C = −38.4 ‰), we tracked the litter-derived C in soil CO_2 effluxes, dissolved organic C (DOC), and soil organic matter of a beech forest in the Swiss Jura. Autotrophic respiration was reduced by trenching. Our results show that mineralisation was the main pathway of C loss from decomposing litter over 1 yr, amounting to 24 and 31 % of the added twig and leaf litter. Contrary to our expectations, the leaf litter C was mineralised only slightly (1.2 times) more rapidly than the twig litter C. The leaching of DOC from twigs amounted to half of that from leaves throughout the experiment (2 vs. 4 % of added litter C). Tracing the litter-derived DOC in the soil showed that DOC from both litter types was mostly removed (88–96 %) with passage through the top centimetres of the mineral soil (0–5 cm) where it might have been stabilised. In the soil organic C at 0–2 cm depth, we indeed recovered 4 % of the initial twig C and 8 % of the leaf C after 1 yr. Much of the ^{13}C-depleted litter remained on the soil surface throughout the experiment: 60 % of the twig litter C and 25 % of the leaf litter C. From the gap in the ^{13}C-mass balance based on C mineralisation, DOC leaching, C input into top soils, and remaining litter, we inferred that another 30 % of the leaf C but only 10 % of twig C could have been transported via soil fauna to soil depths below 2 cm. In summary, over 1 yr, twig litter was mineralised more rapidly relative to leaf litter than expected, and much less of the twig-derived C was transported to the mineral soil than of the leaf-derived C. Both findings provide some evidence that twig litter could contribute less to the C storage in these base-rich forest soils than leaf litter.

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1 Introduction

Litterfall represents the major nutrient flux in temperate forests and often accounts for more than half of the annual C input to soils (Meentemeyer et al., 1982; Perruchoud et al., 1999). How much the aboveground litter contributes to the soil C pool in the long term depends considerably on the rate at which its C is either mineralised to CO_2 or incorporated into mineral soils through soil fauna and dissolved organic C (DOC) (Rubino et al., 2010).

Decay rates of litter are related to climatic conditions (Liski et al., 2003), but they can also vary significantly between litter materials at the same forest site (Moore et al., 1999). Here, C/N ratios and lignin concentrations have often been found to be the best predictor of C losses from litter (e.g. Heim and Frey, 2004; Hagedorn and Machwitz, 2007). Ligneous tissues of twigs with low N contents are, therefore, supposed to be much more resistant to microbial decay than leaf litter, even though different kinds of fungi have proved to be very effective in the degradation of woody tissues (Griffith and Body, 1991).

Based on this mechanistic concept, most soil C models assume clearly slower decay and transformation rates for twig than for leaf litter (Liski et al., 2005; Carrasco et al., 2006; Scott et al., 2006). However, only a few studies have compared the decomposition pathways of twigs and leaves in the field, even though fine woody litter contributes about 30 % to annual litterfall in temperate forests (Thürig et al., 2005). Litterbag studies in China and along a climatic gradient in

Table 1. Properties of the top 0–10 cm of soil. Five soil cores (5 cm in diameter) were taken from both soil types. The values are means ± standard errors.

	pH	Particle-size distribution (%)			Fine-earth bulk	C_{org}	C/N	C_{org} pool	$\delta^{13}C_{org}$
	($CaCl_2$)	250–2000 µm	2–250 µm	< 2 µm	density (g cm^{-3})	(%)		(kg m^{-2})	(‰)
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)

Finland found that leaf and needle litter lost about twice as much C as twig litter (Guo et al., 2007; Vávřová et al., 2009). By contrast, very small differences in C losses from litterbags were observed between beech leaves and spruce branchlets on a Rendzina soil in Switzerland (Hättenschwiler et al., 1999).

Particularly little is known about the translocation of twig-derived C to mineral soils. For instance, we are not aware of any study that has measured DOC leaching from decomposing twigs in the field. Leaching of DOC from leaf litter can contribute to 10–30 % of total C losses from litter (Magill and Aber, 2000; Hagedorn and Machwitz, 2007), and might be important for the C transport to mineral soils, where it is either immobilized by microbes or adsorbed on mineral surfaces (Kalbitz and Kaiser, 2008). Incubation studies suggest that, after the loss of the water-soluble fraction, DOC leached from litter derives predominantly from degradation products of lignin (Kalbitz et al., 2006). Consequently, lignin-rich litter such as twigs should have a particularly high potential to release DOC in later stages of decomposition. Several studies have indeed observed enhanced DOC fluxes below decaying coarse woody debris (Yano et al., 2005; Zalamea et al., 2007; Kahl, 2008). Moreover, more twig-derived DOC might be retained in mineral soils than leaf-derived DOC since the high-molecular-weight, lignin-derived components of DOC, the so-called "hydrophobic" DOC fractions, have a higher affinity for mineral surfaces than the "hydrophilic" fractions with fewer functional groups (Kaiser and Guggenberger, 2000).

In the last decade, several studies have taken advantage of isotopically labelled litter to investigate not only the mass loss but also the pathways of decomposition of leaf, needle and root litter (e.g. Bird and Torn, 2006; Fröberg et al., 2009; Rubino et al., 2010). Isotopic labels allow the estimation of litter contributions to soil respiration as well as the tracking of litter-derived C from the forest floor to mineral soils. We have found, however, no study which has applied this powerful approach to assess C fluxes from decomposing twig litter. Thus, the fate of twig-derived C is still very uncertain: is it mainly respired back to the atmosphere or does it contribute significantly to the long-term storage of C in forest soils?

The aim of this study was to compare the decomposition pathways of leaf and twig litter in a mixed beech forest in the Swiss Jura mountains. Over the course of 1 yr, we measured CO_2 production, DOC leaching, and translocation of C from ^{13}C-depleted leaves and twigs originating from young beech trees from a four-year CO_2 enrichment experiment. The specific objectives of our study were: (1) to test the general assumption that fine-woody litter decomposes much more slowly than non-woody litter; (2) to assess the contribution of decaying twigs and leaves to soil respiration and DOC fluxes in forest soils; and (3) to estimate how much of the leaf and twig litter is incorporated into mineral soils, and thus might contribute to the long-term storage of C in "base-rich" forest soils.

2 Materials and methods

2.1 Study site description

The experimental site is in a mixed beech forest on the relatively steep (on average 24°) south-facing slope of the Lägeren mountain (680 m a.s.l.). This hill range is situated about 20 km NW of Zurich (47°28′40.8″ N, 8°21′55.2″ E) and belongs to the easternmost part of the Jura mountain range. As a contribution to the CarboEurope IP, net-ecosystem CO_2 exchange and soil respiration have been measured routinely there for several years (Etzold et al., 2010; Ruehr et al., 2010). The mean annual temperature is 8.4 °C and mean annual precipitation is 930 mm. The litter experiment was carried out on two soil types 200 m apart and with different parent materials. One of the soils is a Rendzic Leptosol (Rendzina) overlying limestone debris and the other a Haplic Cambisol on a bedrock of marl. The properties of the topsoils (0–10 cm) are presented in Table 1. Both soils have mull-type organic layers indicative of a high level of biological activity, but the pH and soil organic C content of the topsoils are higher in the Rendzina than in the Cambisol. The overstory vegetation is more diverse on the Rendzina where, in addition to beech (*Fagus sylvatica* L.) and spruce trees (*Picea abies* (L.) Karst.) growing on both soils, also ash (*Fraxinus excelsior* L.) and maple trees (*Acer pseudoplatanus* L.) occur. In 2007, the annual litterfall was larger on the Rendzina (330 g C m^{-2}) than on the Cambisol (230 g C m^{-2}), but consisted of about 70 % leaf litter and of 30 % fine woody litter in both soils (N. Ruehr, personal communication, 2009).

2.2 Labelled litter experiment

The litter experiment started in November 2007, lasted for 1 yr, and included three different litter treatments. In plots of 50×50 cm, the native litter layer was replaced either through ^{13}C-labelled beech leaves (isotope ratio (δ^{13}C) = −40.8 ‰; referred to as "soil + leaves"), ^{13}C-labelled twigs (δ^{13}C = −38.4 ‰; "soil + twigs"), or polystyrene shreds ("bare soil"). The later was used to mimic a litter layer and its impact on soil moisture and temperature. To recover the isotopic label for both litter types equally well, we added larger amounts of twigs (2 kg m^{-2}) than of leaves (0.75 kg m^{-2}) since the woody litter was expected to decompose much more slowly. The labelled litter originated from six-year-old beech trees of a CO_2 enrichment experiment in Switzerland, in which trees had been exposed to ^{13}C-depleted CO_2 for four years (Hagedorn et al., 2005). The twigs had diameters ranging from 1 to 8 mm (4 mm on average), and were cut into pieces 4 to 8 cm in length.

In both soils, each litter treatment was replicated five times. The replicates were arranged in five groups within a radius of 10 m, each consisting of the three different treatments. The distance between the litter plots within a group was about 1 m. The litter plots were framed with acrylic glass (12 cm height) 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. To amplify the ^{13}C signal of litter-derived CO_2 we minimized autotrophic respiration by digging a 30 cm deep trench around each plot 6 months before the start of the experiment. A plastic sheet was inserted to prevent lateral root ingrowths. Vegetation growth on the plots was suppressed by periodically weeding.

At intervals of two months, the soil water content was determined gravimetrically within the trenched area and adjacent to it, showing that the trenching had negligible effects on soil moisture. The reason might have been lateral water fluxes along the slope. We cannot rule out, however, that decaying roots and a reduced plant uptake of nutrients after the trenching affected decomposition of SOM and litter. But this artefact was probably small. In an accompanying experiment at the same site, increased N additions (+55 kg ha^{-1} yr^{-1}) had no influence on SOM mineralisation and only slightly reduced the mineralisation of litter and the leaching of DOC (F. Hagedorn, personal communication, 2011).

2.3 Soil CO_2 effluxes and its δ^{13}C

Soil CO_2 effluxes were measured with a portable infrared gas analyzer (Li-8100, LI-COR Inc., Lincoln, NE, USA) at bi-weekly intervals between October 2007 (one month before litter addition) and November 2008. The chamber of the IRGA was placed on permanently installed PVC collars (5 cm high, 20 cm in diameter), inserted into the soils to a depth of 2 cm.

To estimate the contribution of litter-derived CO_2, the ^{13}C signature of the soil CO_2 effluxes ($\delta^{13}C_{resp}$) was determined with the closed soil-chamber method on ten sampling dates (e.g. Ohlsson et al., 2005). Depending on the CO_2 efflux, the soil collars were hermetically sealed for 8–40 min with a lid, allowing for a CO_2 increase of 430 ± 11 ppm. At the end of the accumulation period, one gas sample was taken from each chamber with a syringe through a septum in the lid and injected into glass vials (volume of 12 ml, Exetainer gas testing vials, Labco Limited, High Wycombe, UK), which had been previously closed with airtight rubber septa and evacuated with a vacuum pump to 2×10^{-2} hPa. In addition, gas samples were collected next to each collar immediately after they had been closed (ambient air). The gas samples were analysed for both the CO_2 concentration and the δ^{13}C within 1–3 days after sampling using a Gasbench II, coupled with an isotope ratio mass spectrometer Delta Plus (both Thermo Finnigan Mat, Bremen, Germany). More details on the IRMS system employed in this study as well as tests of the leak tightness of the glass vials can be found in Joos et al. (2008).

To correct for the contamination of chamber CO_2 with ambient CO_2, $\delta^{13}C_{resp}$ was calculated with the following mixing model (see Subke et al., 2004):

$$\delta^{13}C_{resp} = (\delta^{13}C_{chamber} \cdot [CO_2]_{chamber} - \delta^{13}C_{ambient} \cdot [CO_2]_{ambient}) / ([CO_2]_{chamber} - [CO_2]_{ambient}), \quad (1)$$

where $[CO_2]$ is the concentration and δ^{13}C the isotopic composition of CO_2 in the ambient air and in the soil chamber. We preferred this simple mixing model to conventional Keeling plots of five or more data points, as it requires only two gas samples to estimate $\delta^{13}C_{resp}$, which reduced the accuracy of the estimate only slightly but allowed the measurement of more replicates in the field. Previous tests showed that the use of two instead of five gas samples affected the values of $\delta^{13}C_{resp}$ in single plots by on average ±0.39 ‰ within the same range in CO_2 concentrations. This difference was of the same magnitude as the error of the intercept extrapolation in the Keeling plots. Moreover, in the same litter experiment, Kammer et al. (2011) found very similar estimates for litter-derived CO_2 when the values of $\delta^{13}C_{resp}$ were either derived from simple mixing models or from high-resolution Keeling plots (1200 data points) using a quantum cacade laser-based spectrometer.

2.4 Water, litter and soil sampling

Throughfall was sampled 1.5 m above the forest floor with one PE funnel (Ø 11 cm) next to each plot group. In each plot, soil water was collected below the litter layer with zero-tension lysimeters (13×17 cm PVC boxes). Four openings (Ø 1 cm) on the bottom of the zero-tension lysimeters allowed soil animals to feed on the litter. Soil water at a soil depth of 5 cm was sampled with suction plates (Ø 5.5 cm) made of borosilicate glass (pore size P5; Schmizo, Zofingen,

Switzerland) to which a continuous suction of −400 hPa was applied with a vacuum pump (EcoTech, Bonn, Germany). Both the lysimeters and the suction plates were installed on the downhill side of the litter plots. The soil water was continuously collected in 0.5 l bottles, which were buried in the soil and emptied after every larger rain event.

At the start of the experiment, a small part of the added labelled litter (2.5 g of leaf litter and 10 g of twig litter) was placed in litterbags (10 × 10 cm; polypropylene) with mesh sizes of 1 mm. After 1 yr, the bags (one per plot) were collected from the forest floor and the litter that remained was cleaned to remove mineral particles, dried at 60 °C for chemical analysis and at 105 °C to determine the dry mass. The same procedure was applied to the unconfined labelled litter that remained on the surface. Subsequently, a soil core (Ø 5 cm) 10 cm in length was taken from each plot, frozen and divided into 2 cm thick layers with a hacksaw. The soil samples were freed from roots, dried at 60 °C and sieved (<2 mm).

2.5 Chemical analysis

All water samples were passed through 0.45-µm cellulose-acetate filters (Schleicher & Schuell, ME25), pooled on a monthly base and refrigerated until analysis. To remove inorganic C, HCl suprapur (30 %) was added to all samples. DOC concentrations were determined with a TOC/TN analyzer (TOC-V, Shimadzu Corporation, Tokyo, Japan). The UV absorptivity at 285 nm in the DOC was measured using a Cary 50 UV-spectrophotometer (Varian, Palo Alto, USA). Aliquots of 50–80 ml were freeze-dried to determine the δ^{13}C of the DOC. To facilitate the weighing of the freeze-dried dissolved organic matter, 5 mg of K_2SO_4 was added to each sample.

The C and N concentrations and the δ^{13}C in litter, 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). The long-term precision of the δ^{13}C measurements was ±0.07 ‰. Both the fresh and the decomposed litter were additionally analysed for: (1) hot water extractables by extracting 1 g of milled sample three times with 25 ml of hot (85 ± 5 °C) water and once with cold water (15 min each); (2) phenolics by applying the Folin-Denis colorimetric method to the water extracts (Swain and Hillis, 1959); (3) Klason lignin. The Klason lignin was the residue of milled litter after it had been extracted with hot water and ethanol, hydrolyzed with 3 ml of 72 % sulphuric acid for 1 h at 30° C and, after addition of 84 ml water, autoclaved for 1 h at 120 °C. (4) The soluble lignin was estimated from the UV absorbance of the hydrolisate at 205 nm (Dence, 1992).

The microbial biomass in the litter layer was analysed 4 and 12 months after litter addition using the chloroform-fumigation extraction (Brooks et al., 1985). Briefly, 5 g of fresh litter was fumigated for 24 h with $CHCl_3$ and then extracted with 50 ml of 0.25 *M* K_2SO_4. The microbial C and N were calculated from the differences in the C and N concentrations between these extracts and additional extracts from non-fumigated samples.

2.6 Meteorological measurements

Thermocouples connected to the portable IRGA were used to measure the temperatures in the air, in the litter layer, and at soil depths of 5 cm and 10 cm for each sampling location at the same time as the measurements of the CO_2 effluxes. In addition, soil temperatures were recorded continuously with temperature loggers (ibuttons, Maxim Integrated Products DS1922L, USA) installed in three replicates per treatment at a soil depth of 10 cm. Moreover, a meteo station 100 m away from the experimental site recorded air temperature, soil moisture at depths of 5, 10, 30 and 50 cm, air humidity, wind speed and net radiation, all with intervals of 30 min. Precipitation was measured at an eddy covariance flux tower 80 m away.

2.7 Calculations and statistics

2.7.1 Litter-derived C

The contribution of labelled litter C (f_{litter}) to soil-C fluxes and pools was calculated for each plot individually as follows:

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

where $\delta^{13}C_{soil+litter}$ is the δ^{13}C of the investigated C flux/pool in the "soil + litter" treatment, $\delta^{13}C_{control}$ is the δ^{13}C of the same C flux/pool in the adjacent "bare soil" plot or of the throughfall DOC (for DOC leaching from the litter layer), $\delta^{13}C_{litter}$ is the δ^{13}C of the bulk litter (−40.8 ‰ and −38.4 ‰) and $\delta^{13}C_{SOC}$ is the δ^{13}C of the SOC in the top soil (0–10 cm) of the investigated plot measured at the end of the experiment. Means and standard errors of f_{litter} were calculated from the five replicates of each treatment. This approach is based on the assumption that isotopic fractionation of ^{13}C was minimal, or at least the same, in the litter layer and the mineral soil during both C mineralisation and DOC production (e.g. Schweizer et al., 1999; Santruckova et al., 2000; Fröberg et al., 2007). Moreover, it neglects that there still might have been CO_2 from autotrophic respiration as the soils were only trenched to 30 cm depth. Several studies have found that autotrophic respiration is depleted in ^{13}C by on average 4 ‰ relative to δ^{13}C of SOM in top soils (Bowling et al., 2008). To test the robustness of f_{litter} to this uncertainty, we assumed contributions of autotrophic respiration to mineral soil-derived CO_2 of 10–30 % and varied the parameters in Eq. (2) to obtain values for f_{litter} of 0.1–0.5. This sensitivity test showed that Eq. (2) could have overestimated f_{litter} of soil CO_2 effluxes by 3–9 %.

2.7.2 DOC fluxes

The vertical fluxes of DOC below the litter layer and at a depth of 5 cm were estimated by multiplying the DOC concentrations by water fluxes simulated with the COUP model (Jansson and Karlberg, 2004). The model was parameterized using the organic C content, the particle-size distribution of different soil layers, and several other parameters. The input variables were air temperature, precipitation, vapour pressure, wind speed and net radiation. Finally, soil moisture data were used to validate the model.

2.7.3 Modeling CO_2 effluxes

The temperature dependency of the soil CO_2 effluxes was fitted with the following equation (see Fang and Moncrieff, 2001):

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

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).

However, it was not possible to fit the litter-derived CO_2 effluxes to a simple temperature function since the litter C pool declines with time. For modeling C respired from added litter, we thus used the temperature dependency of CO_2 effluxes in the "bare soil" treatment and scaled this function to the litter-derived C effluxes at the beginning of January by linear transformation:

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

where the transformation factor S is the theoretical ratio of litter-derived CO_2 and mineral soil-derived CO_2 at identical soil and air temperatures. We selected the values in January as a reference because litter contributed most to the soil respiration on this sampling date. In a next step, the mineralisation potential of litter C was expressed as the ratio between measured and theoretical (no change in C pool) litter-derived CO_2 fluxes, which were calculated with Eq. (4) for all sampling days. This ratio (factor P) was used as a correction factor:

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

To estimate the daily C losses from the litter through CO_2 release, we interpolated P between the sampling days and used the air temperature as input variable. The mineralisation rates were calculated as the ratio of the respired CO_2-C and the initial amount of litter C.

2.7.4 Statistics

Differences in C fluxes and C pools between the litter treatments were tested with linear mixed effect models using the nlme package from 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. Beside the litter type, soil and time were used as fixed factors. 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. For some analysis, the data set was divided into the measurements made in winter and into those made during the warm season. Winter was defined as the period from the start of the experiment at the end of November 2007 until the start of budburst of trees at end of April 2008.

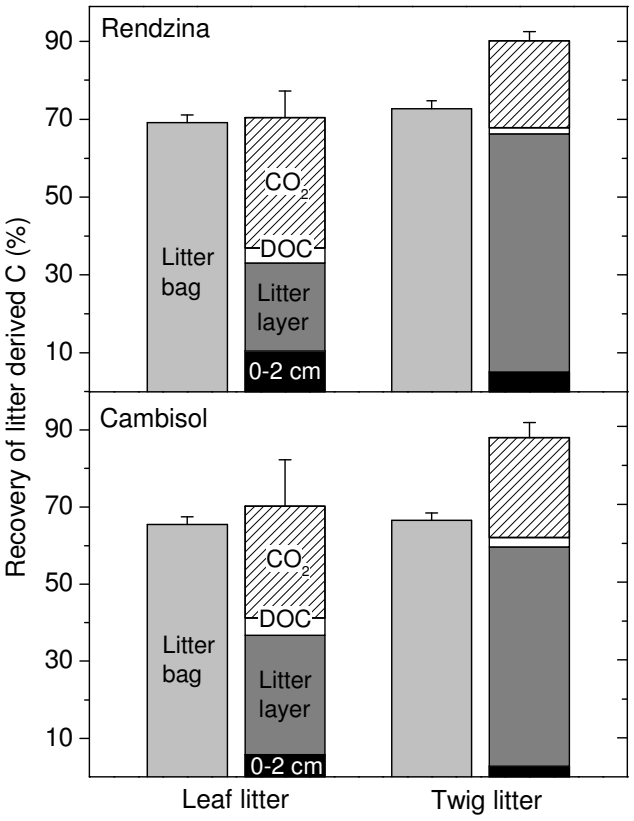

Fig. 1. Total recovery of the ^{13}C-labelled litter C in litterbags and in different C fluxes and C pools after 1 yr of decomposition. Means and standard errors of five replicates.

3 Results

3.1 Changes in the mass and quality of the litter

The amount of litter C that remained in litterbags after 1 yr of decomposition ranged from 66 to 73 % (Fig. 1). It was larger on the Rendzina than on the Cambisol (lme soil effect: $F = 12.1$, $p < 0.01$), and it was slightly but not significantly larger for twig than for leaf litter (69.5 % vs. 67.5 %; lme litter effect: $F = 2.7$, $p = 0.12$). In contrast, the proportion of the ^{13}C-labelled litter recovered in the litter layer (not

Table 2. Selected parameters of leaf and twig litter at the beginning and after 1 yr of decomposition. Litter of both soil types are combined as their chemical parameters differed only marginally. The values are means ± standard errors. The number of replicates is ten for all parameters of litter quality and six for microbial C/N.

Litter	Time	C/N	Hot water-soluble substances ($mg\,g^{-1}$)	Fraction of phenols in water solubles (%)	Lignin* ($mg\,g^{-1}$)	$\delta^{13}C_{org}$ (‰)	Microbial C/ Microbial N
Leaf	fresh	28 (1)	247 (7)	25 (1)	340 (9)	−40.8 (0.2)	9.2 (0.3)
Twig	”	95 (2)	127 (5)	10 (0)	280 (2)	−38.4 (0.1)	12 (0.3)
Leaf	1 yr	20 (1)	66 (4)	10 (1)	530 (8)	−40.4 (0.2)	5.4 (0.3)
Twig	”	51 (6)	72 (8)	6 (1)	420 (20)	−38.3 (0.5)	10 (0.4)

* Klason lignin + soluble lignin.

confined in litterbags) was twice (Cambisol) and three times (Rendzina) as large for twig litter (57–61 %) as it was for leaf litter (23–31 %; Fig. 1).

The C/N ratio of both the bulk litter and the litter microbial biomass increased over the course of the experiment and was clearly wider in the twig than in the leaf litter (Table 2). At the beginning of the experiment, concentrations of hot water-soluble substances were twice as large in the leaf as in the twig litter, but equally small in both litter types after 1 yr. Surprisingly, the lignin concentrations (Klason lignin + soluble lignin) were about 20 % lower in the twig than in the leaf litter (Table 2). Over 1 yr, they increased by a factor of 1.5 in both litter types. Only an insignificant increase in the δ^{13}C of the litter material (+0.1–0.4 ‰) was observed.

3.2 Contribution of litter C to SOC

At the end of the experiment, slight shifts by 0.2–0.5 ‰ ($p < 0.01$) in the δ^{13}C of SOC indicated that recent litter C contributed 2–5 % to the C pools at 0–2 cm depth, corresponding to about 4 % of the initial twig C and to about 8 % of the initial leaf C (Fig. 1). However, no significant litter effect on the δ^{13}C of SOC was observed at depths below 2 cm.

3.3 CO_2 effluxes

The addition of leaf litter ($0.75\,kg\,m^{-2}$) and twig litter ($2\,kg\,m^{-2}$) to bare soils had distinct positive effects on soil CO_2 effluxes throughout the experiment (lme contrast: bare soil vs. soil + litter, $F = 140.2$, $p < 0.001$; Fig. 2). Moreover, the CO_2 efflux was significantly larger in plots with twig litter than in those with leaf litter (+25 %; lme without bare soil: $F = 29.0$, $p < 0.001$). Using the strong dependency of the soil CO_2 effluxes on the temperature at a depth of 10 cm ($R^2 = 0.85$–0.97; Eq. 3), we estimated that total C losses from the soils ranged from $575\,g\,m^{-2}\,yr^{-1}$ in the bare Cambisol to $1038\,g\,m^{-2}\,yr^{-1}$ in the Rendzina with a twig layer (Table 3). Here, it is important to note that the litter layer was mostly wet throughout the summer 2008 with frequent rain

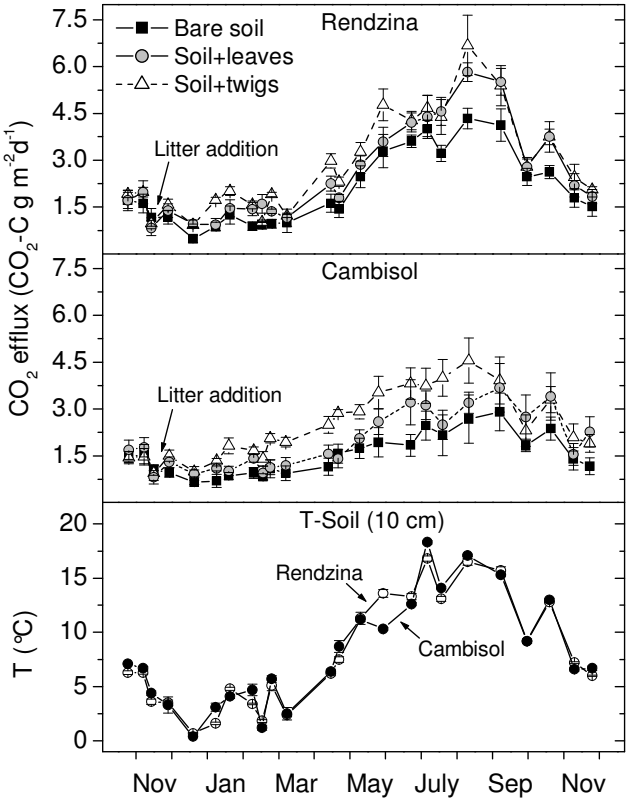

Fig. 2. Seasonal course of the soil CO_2 effluxes in the Rendzina and the Cambisol and of the soil temperature at a depth of 10 cm. The values are the means of five replicates ± standard error.

and the soil moisture at a depth of 10 cm rarely dropped below 15 vol-% (about 55 % relative soil water content), which is the threshold for water limitation on soil respiration at our site (Ruehr et al., 2010). Thus, no correlation between soil CO_2 effluxes and soil moisture was observed.

The ^{13}C signature of CO_2 respired from the bare soils varied between −23 and −28 ‰ over the course of the experiment (Fig. 3), and was on average −25.1 ‰ in the Rendzina

Table 3. Total C loss from forest soils through CO_2 and cumulated DOC fluxes below the litter layer and in the mineral soil at a depth of 5 cm during the course of the litter experiment (November 2007–2008). The values are the means of five replicates ± standard errors.

Soil	Treatment	CO_2 release ($g\,CO_2$-C m^{-2})	DOC litter layer ($g\,DOC\,m^{-2}$)	DOC at 5 cm ($g\,DOC\,m^{-2}$)
Rendzina	Bare soil	803 (71)	–	8.9 (1.8)
	+ Leaves (0.75 $kg\,m^{-2}$)	973 (52)	20.4 (3.5)	11.7 (1.2)
	+ Twigs (2 $kg\,m^{-2}$)	1038 (59)	21.8 (4.6)	12.4 (1.3)
Cambisol	Bare soil	575 (106)	–	9.2 (1.9)
	+ Leaves (0.75 $kg\,m^{-2}$)	683 (128)	21.5 (1.8)	8.5 (1.5)
	+ Twigs (2 $kg\,m^{-2}$)	888 (94)	29.1 (4.7)	9.8 (1.4)

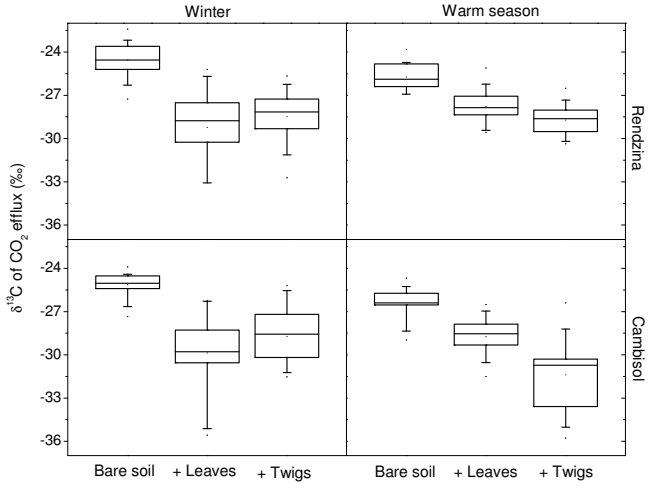

Fig. 3. Variability in the δ^{13}C of the soil CO_2 efflux. Each box shows the median value, the quartiles and the 2.5 %- and 97.5 %-quantiles of 25 single measurements in the winter (November 2007–April 2008) and in the warm season (April 2008–November 2008).

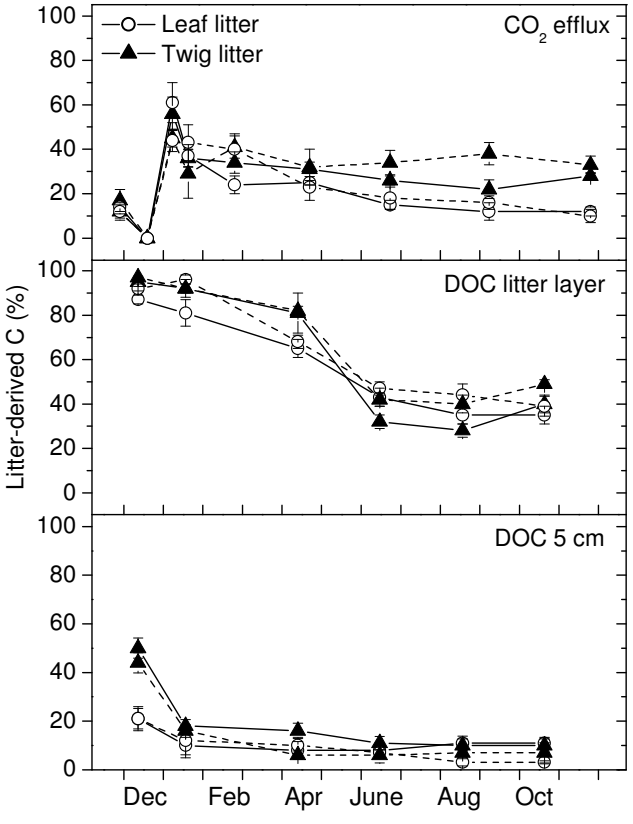

Fig. 4. Contribution of litter-derived C to the soil CO_2 effluxes and to the DOC leached from the litter layer and from the mineral soil at a depth of 5 cm. Means and standard errors of five replicates in the Rendzina (solid line) and the Cambisol (dashed line).

and −25.9 ‰ in the slightly acidic Cambisol. The small difference in the δ^{13}C of CO_2 between the two soils indicates that the dissolution of carbonates was a negligible source of CO_2 in the Rendzina. The decomposition of ^{13}C-depleted leaves ($\Delta^{13}C = -13.6$ ‰) and twigs ($\Delta^{13}C = -11.2$ ‰) decreased the ^{13}C ratio of soil CO_2 effluxes on average by 4.5 ‰ in winter and by 2.5 ‰ over the warm season (lme contrast: bare soil vs. soil + litter, $F = 54.2$, $p < 0.001$; Fig. 3).

The fraction of litter-derived C in the soil CO_2 effluxes (f_{litter}) peaked at 45–60 % in January (Fig. 4) when the litter was still fresh and the soil temperature (1 °C) lower than the air temperature (6 °C). Three weeks before, however, no litter decomposition had been observed at air temperatures clearly below 0 °C. While f_{litter} in the "soil + leaves" plots declined continuously with increasing time of decomposition to about 10 % at the end of the experiment, no significant time effect on f_{litter} was found in the "soil + twigs" plots from February to November (lme time effect for this period: $F = 1.9$, $p = 0.13$). As a consequence, f_{litter} was not dependent on the litter type in winter (lme litter effect: $F = 0.1$, $p = 0.79$), but was considerably larger for twigs than for leaves over the warm season independent of the soil type ($F = 31.2$, $p < 0.001$). In agreement with this temporal pattern, twig-derived C was mineralised 40 % more slowly than leaf-derived C in

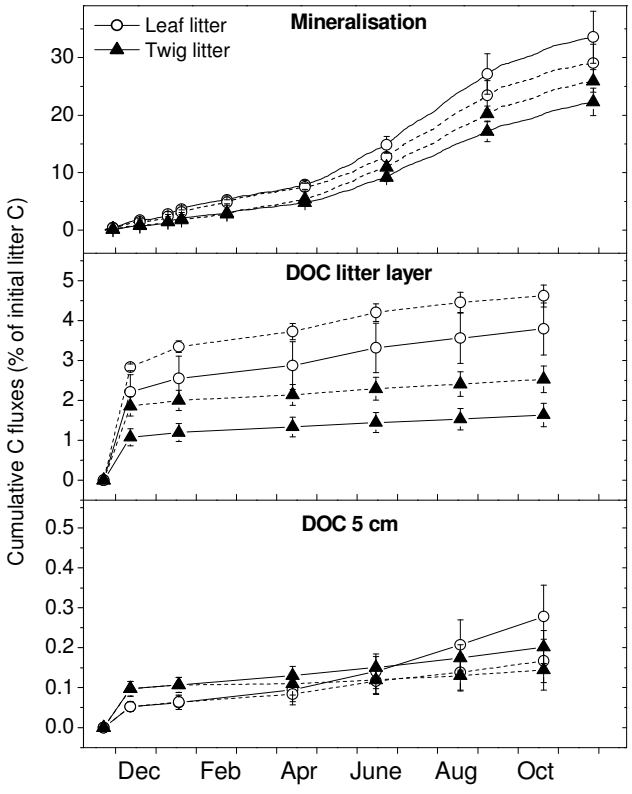

Fig. 5. Seasonal dynamics of litter-derived C respired as CO_2, leached as DOC from the litter layer and recovered in the DOC at a depth of 5 cm. The solid line represents the Rendzina and the dashed line the Cambisol. The values are the means of five replicates ± standard error.

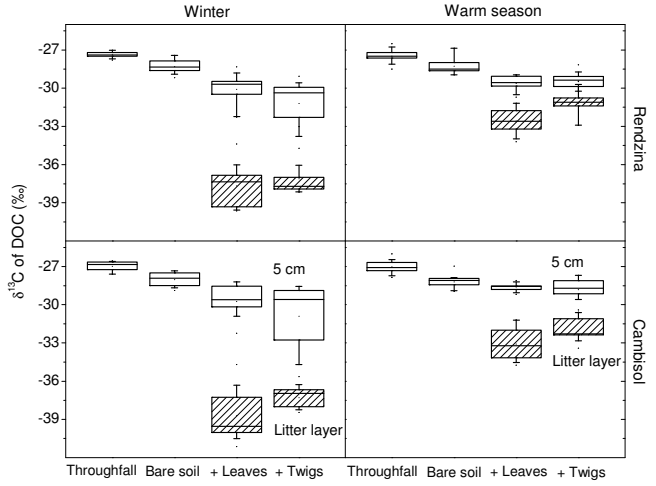

Fig. 6. Variability in the δ^{13}C of the DOC leached from both the litter layer and the mineral soil at a depth of 5 cm as well as the δ^{13}C of throughfall DOC. Each box shows the median value, the quartiles and the 2.5 %- and 97.5 %-quantiles of 15 single measurements in the winter (November 2007–April 2008) and in the warm season (April 2008–November 2008).

winter, but only 15 % more slowly over the warm season. By modelling CO_2 effluxes from litter between measurements (Eq. 5), we estimated that, after 1 yr, the twig litter had lost 22–26 % of its initial C through CO_2 and the leaf litter 29–34 % (Fig. 5).

3.4 DOC fluxes

The total fluxes of DOC dropped from 20–29 g DOC m^{-2} yr^{-1} below the litter layer to 9–12.5 g DOC m^{-2} yr^{-1} at a soil depth of 5 cm, with only marginal differences between the twig and leaf litter treatments, as well as between the two soil types (Table 3). The ^{13}C tracing revealed that litter-derived C contributed to, on average, 70 % of the DOC leached from the litter layer but to only 11 % of the DOC leached from mineral soils (Figs. 4 and 6). Therefore, litter-derived DOC was mostly retained (88–96 %) in the top centimetres of the soil profile and most of the DOC at a depth of 5 cm originated from "older" SOM.

The seasonal dynamics of litter-derived DOC were very similar for both litter types. An initial flush of DOC from the litter layer, associated with heavy rainfalls in early winter, was followed by clearly lower and constant leaching rates throughout the rest of the experiment (Fig. 5). The leaching rates, however, were much lower for twig than for leaf litter during both the initial DOC flush and the subsequent leaching cycles ($p < 0.001$). Over 1 yr, the twig litter lost 1.5–2.5 % of its initial C pool through leaching of DOC, whereas the leaf litter lost 4–5 % of its C through this pathway.

In contrast to the DOC leaching below the litter layer, the amount of litter-derived DOC detected in mineral soils was not significantly lower for twig than for leaf litter (−20 %; lme litter effect: $F = 1.4$, $p = 0.26$; Fig. 5). Consequently, less DOC leached from twigs was retained when it passed through the uppermost mineral soil than DOC leached from leaves. Furthermore, less litter-derived DOC was recovered in the mineral soils of the Cambisol than in those of the Rendzina (−40 %; lme soil effect: $F = 7.9$, $p < 0.05$).

We assessed the quality of litter-derived DOC using the UV absorbance at 285 nm of soil water, which was corrected for throughfall DOC with a simple mixing model. The correction was necessary since throughfall DOC had a clearly lower UV absorptivity than the litter-derived DOC (on average 200 vs. 300 l mol^{-1} cm^{-1}). Moreover, the large difference of δ^{13}C in the DOC (litter layer) between the winter and the warm season indicates a large contribution of throughfall to the DOC leached from the litter layer especially after the green up of trees in spring (Fig. 6). The UV absorptivity of litter DOC greatly increased during the course of the experiment and peaked in summer at 350–450 l mol^{-1} cm^{-1} (Fig. 7). The twig-derived DOC also had a lower UV absorptivity (−15 %) than the leaf-derived DOC throughout the experiment (lme litter effect: $F = 0.5$, $p < 0.001$).

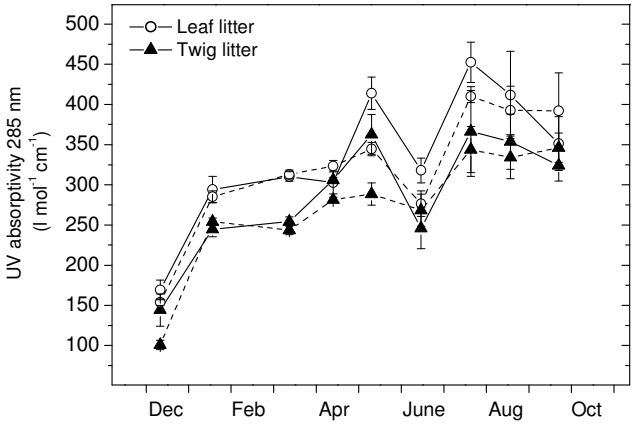

Fig. 7. Specific UV absorptivity of litter-derived C leached from the forest floor in the Rendzina (solid line) and the Cambisol (dashed line). Means and standard errors of five replicates.

4 Discussion

4.1 Almost equal mineralisation of ^{13}C-labelled leaf and twig litter

Fine woody litter is commonly thought to decompose much more slowly than leaf litter (Liski et al., 2005). The recovery of the ^{13}C-labelled litter on the soil surface (not confined in litterbags) appears to confirm this assumption. One year after litter addition, about 60 % of the twig litter C remained in the litter layer, more than twice as much as that of the leaf litter (Fig. 1). Our results show, however, that microbial decomposition was not the main reason for the different mass losses from leaves and twigs in the forest floor. Contrary to our expectations, the mineralisation rates of the two litter types differed surprisingly little. Cumulated over 1 yr and averaged for both soils, the twigs lost only 1.2 times less C through CO_2 than the leaves (Fig. 5). In the Cambisol, the rates at which the two litter types mineralised even became equal after the loss of the most labile C pool at the end of winter. In agreement with the C mineralisation rates of the ^{13}C-labelled litter, the twigs in the litterbags lost only slightly, but not significantly, less C than the confined leaves (Fig. 1). Our findings are supported by a study with litterbags (mesh-sizes of 0.02–2 cm) on a Rendzina soil near Basel (Switzerland), where the mass losses after 1 yr of decomposition were very similar for beech leaves and spruce branchlets (Hättenschwiler et al., 1999). Almost identical mineralisation rates for both litter types were also found in a lab experiment using a mixture of beech and oak litter (Park et al., 2002). In our study, the differences between the litter types were less pronounced in litterbags than in the unconfined ^{13}C-labelled litter (Fig. 1), possibly because the mesh bags inhibited the fragmentation of the leaf litter through soil macrofauna, and thus suppressed litter decay (Cotrufo et al., 2010). In contrast to the leaf litter, twig litter was not fragmented either inside or outside the litterbags.

The small differences we found between the leaf and twig litter mineralisation rates can probably be attributed to both a relatively fast decomposition of beech twigs and a relatively slow decomposition of beech leaves because: (1) the annual C losses from twigs through CO_2 and DOC observed in our study (24–33 %) were at the upper end of weight losses (15–31 %) found across several forest ecosystems and tree species of the temperate zone (Boddy and Swift, 1984); (2) C losses from beech leaves determined in litterbags and laboratory experiments are commonly among the lowest of various leaf litter types (Moore et al., 1999; Hoorens et al., 2003; Hagedorn and Machwitz, 2007) possibly because they are tough, have a comparatively small proportion of water solubles and are rich in lignin and polyphenols (Schaefer et al., 2009). Therefore, we assume that similar decay rates for fine-woody and non-woody litter is a specific phenomenon for beech, while in forest ecosystems dominated by other tree species, the decomposition of the two litter types might differ much more. Large differences between the mass losses of leaves and twigs have recently been observed, for instance, for litter from *Tilia*, *Betula*, *Picea*, and *Pinus* (Guo et al., 2007; Vávřová et al., 2009).

In our experiment, the similar mineralisation rates of the leaf and twig litter might be related to a smaller difference in litter quality as we expected. While the leaves contained more hot-water solubles and more N, the twigs surprisingly had smaller contents of Klason lignin (Table 2). However, it is known that the Klason procedure can overestimate lignin in plant tissues that contain other high-molecular-weight components, such as proteins and tannins (Hammel, 1997). We assume that the beech leaves contained a significant fraction of these interfering substances. The evidence that both litter types were rich in refractory components suggests that the decomposability of these two litter types was controlled primarily by the fraction of high-molecular-weight substances, and less importantly by the initial N concentration, which was four times lower in the twig litter (Table 2). Finally, it should be noted that the diameters of the twigs used in this experiment were relatively small (0.1–0.8 cm) and hence, the bark-to-wood ratio was high. This ratio might be positively correlated with the decomposability of twigs and branches as the bark is more enriched in nutrients than the wood, and larger diameters impede the access of the microbes to the inner parts of woody litter (Swift, 1977; Miller, 1983).

4.2 Litter-derived CO_2 effluxes and experimental limitations

In the investigated beech forest ecosystem, litter-derived CO_2 appears to be a major component ($\sim$50 %) of soil CO_2 effluxes mainly on warm winter days when the leaf litter is still fresh (Fig. 4). On an annual scale, however, the contribution

of litter decomposition to soil CO_2 effluxes seems to be much smaller. Taking the natural litterfall at our site (Rendzina: 330 g litter C^{-1} yr^{-1}; Cambisol: 230 g litter C^{-1} yr^{-1}; 30 % fine woody litter; N. Ruehr, personal communication, 2009) and assuming that the measured mineralisation rates of litter C (22–34 % of added litter C) apply for the decomposition of the natural litter, annual C losses from recent litter (<1 yr) through CO_2 amount to 47–77 g C m^{-2} yr^{-1} for leaf litter and to 18–22 g C m^{-2} yr^{-1} for twig litter. These amounts of CO_2 from leaf and twig litter account for 10–12 % and 4–6 % of the heterotrophic component of annual soil respiration. The estimated contribution of leaf litter is roughly half of that found in a ^{13}C-tracer study in a French beech forest, where decomposing leaves contributed to 20 % of annual heterotrophic respiration (Ngao et al., 2005). In their study, leaf litter also mineralised much more rapidly over the first year (62 % of initial C) than did ours (31 %). It must be noted, however, that they linearly interpolated between litter-derived CO_2 effluxes measured during the day and did not account for the temperature dependency of litter decomposition.

In our study, we might have underestimated the contribution of litter decomposition to soil CO_2 effluxes, because the CO_2 effluxes from mineral soils were probably increased after the trenching of soils due to mineralisation of dead roots. Moreover, the mineralisation rates of the ^{13}C-depleted litter might have differed from those of native beech litter. For instance, the amount of added litter exceeded the annual litter fall by a factor of 1.7 for leaf litter and by a factor of 11 for twig litter. The larger litter amounts possibly affected the moisture conditions in the litter layer. Furthermore, we isolated woody and non-woody litter, which excluded any potential interaction between the two litter types associated with altered nutrient availability and decomposer community (Hättenschwiler et al., 2005). However, it is very difficult to predict whether a mixture of leaf and twig litter would have enhanced, decreased or not affected the litter decomposition as compared to the isolated litter (Hättenschwiler et al., 2005; Ball et al., 2008; Jonsson and Wardle, 2008). Finally, it is also uncertain how the difference in litter quality due to the previous exposure of trees to elevated CO_2 for four years affected the litter decomposition (see Hättenschwiler and Bretscher, 2001). The litter had 14 % smaller N contents as compared to that from plants grown under ambient CO_2, but reported CO_2-effects reach from small decreases in mass loss (e.g. Hättenschwiler et al., 1999; Parsons et al., 2008), negligible changes in the decay of woody litter (Hättenschwiler et al., 1999; Cotrufo and Ineson, 2000) to a 5 % increase in litter C mineralisation (Hagedorn and Machwitz, 2007).

4.3 Twig litter is a small source of DOC

Several studies of coarse woody debris have suggested that DOC leached from decaying wood is a significant transport pathway of C from forest floors to mineral soils (Zalamea et al., 2007; Kahl, 2008). Our results, however, provide little evidence that this applies also to decaying twigs in this beech forest. Leaching of DOC from twig litter amounted to only half of that from leaf litter throughout the experiment, which contrasts with the similar C mineralisation rates of the two litter types (Fig. 5). These findings are supported by an incubation experiment with forest floor material from a German beech forest, where the net release of DOC differed much more between leaf and fine woody litter than the CO_2 production (Park et al., 2002). We think that the reduced leaching of twig-derived DOC resulted in part from the limited contact of the inner parts of the twigs with the percolating water and hence from the spatial segregation of a substantial proportion of the woody material from the leaching.

Interestingly, DOC leached from the twigs was lower in refractory components, and hence probably more biodegradable than leaf-derived DOC. This was indicated by the smaller specific UV absorbance of the twig litter DOC (Fig. 7), which suggests smaller proportions of aromatic compounds and a higher biodegradability of the DOC (Dilling and Kaiser, 2002; Hagedorn and Machwitz, 2007). The UV absorbance of litter-derived DOC was lower for twigs than for leaves not only during the initial DOC flush, which probably consisted largely of water-soluble substances in the litter itself (Fröberg et al., 2007), but also thereafter, when DOC is assumed to be generated during the degradation of lignin (Kalbitz et al., 2006). This finding corresponds with analyses of DOC leached from eight different types of leaf litter, which showed that the biodegradability of DOC was negatively correlated to the decomposability of the litter material itself (Hagedorn and Machwitz, 2007). Moreover, our results are in agreement with the litter manipulation experiment at the DIRT study site in Oregon, in which DOC derived from recent coarse woody debris contained a slightly larger fraction in "hydrophilic", and thus, carbohydrate-rich, low-molecular-weight compounds than DOC leached from the litter layer (Yano et al., 2005).

The reason for the leaching of more biodegradable DOC from the woody litter could be a different microbial community on the two litter types. The C/N ratio of the microbial biomass was clearly higher for twigs than for leaves (Table 2), which suggests that fungi are more dominant on the woody litter (Ross and Sparling, 1993). Fungi are better adapted to degrade lignin-derived C (Hammel, 1997). Thus, aromatic compounds in the twig litter might be mineralised more completely than in the leaf litter. This could also have contributed to the smaller net release of DOC from the twigs as compared to the C mineralisation.

By tracking the ^{13}C-signal of litter-derived DOC in the mineral soil, we found that less than 10 % of the DOC leached from the litter layer was recovered at a depth of 5 cm, and the greatest fraction of litter DOC was thus retained in the uppermost mineral soil. This strong immobilisation of forest floor DOC confirms results from the long-term litter

manipulation at the Oregon DIRT site, where the DOC mass balance indicated that DOC from coarse woody litter was largely removed with its passage across the organic layers and mineral soils (Yano et al., 2005). Similar retentions of DOC have recently been observed for ^{13}C- and ^{14}C-labelled leaf and needle litter (Fröberg et al., 2007 and 2009; Müller et al., 2009).

On the basis of our results, we may hypothesise that sorption of DOC to mineral surfaces was the key mechanism for the retention of litter DOC because: (1) DOC was strongly immobilised in winter and thus at low microbial activities. (2) Litter-derived DOC was retained more effectively in the more acidic Cambisol than in the Rendzina, possibly due to a stronger sorption to soil minerals at lower pH values (Tipping, 2002). (3) Moreover, the retention of litter-derived DOC in the mineral soil was smaller for twigs than for leaves (Fig. 5). The twig-derived DOC had a lower specific UV absorbance (Fig. 7), and thus contained less "hydrophobic" DOC which is less biodegradable but has a higher affinity to mineral surface than "hydrophilic" DOC (Kaiser and Guggenberger, 2000; Hagedorn and Machwitz, 2007).

In summary, the tracing of litter-derived DOC showed that less DOC was leached from twigs than from leaves and that the twig DOC was less strongly retained in the mineral soil. Both findings suggest that the sorptive stabilisation of litter-derived C via leaching was less important for twig than for leaf litter in our experiment in a beech forest ecosystem. This is further confirmed by the recovery of labelled litter C in the SOC at 0–2 cm depth, where 8 % of the initial leaf C was stored 1 yr after litter addition in contrast with only 4 % of the twig C (Fig. 1). A substantial source of this "new" SOC might have been DOC leached from the litter layer.

4.4 Biologically mediated transport of litter

To date, very few studies have made attempts to quantify downward transports of litter C via soil fauna which is a key process for the transfer of litter C into minerals soils particularly in base-rich forest soils (Scheu, 1997) where litter may become stabilised in faecal pellets from earthworms (Ziegler and Zech, 1992). In our study, this pathway of C loss could not explicitly be measured as the isotopic label of the added litter was too small for a recovery of litter C in the deeper mineral soil. Nevertheless, by the mass balance of the measured fluxes of litter-derived C, we can infer the biologically mediated transport of woody and non-woody litter.

In both soils, the sum of C fluxes from the ^{13}C-depleted litter and the litter recovered on the soil surface and at a depth of 0–2 cm amounted to about 90 ± 3 % of the added twig litter C, but only to 70 ± 9 % of the initial leaf litter C (Fig. 1). We attribute the gap in the ^{13}C-mass balance to the export via soil fauna although we cannot rule out that it may partly result from uncertainties in the measurement and modelling of litter-derived C fluxes. However, the fact that much more of the twig-derived C was recovered than of the leaf-derived C, despite identical methods used, provides evidence that the export of litter via soil fauna to the mineral soil was much larger for leaf litter (∼30 % of initial C) than for twig litter (∼10 %). This assumption is supported by the mass losses from the litterbags with a mesh size of 1 mm, which excludes macro fauna. While in the case of leaves, about twice as much litter remained in the litterbags as in the unconfined litter on the forest floor after 1 yr, litterbags only slightly affected the mass loss from the twig litter (Fig. 1). The preference for litter from leaves as compared to those from twigs is in accordance with the findings of Hättenschwiler et al. (1999) that demonstrated that restricting access of soil fauna to decomposing litter affected mass losses from beech leaves but not from spruce branchlets.

We assume that the macro fauna was even more important under natural conditions as the soil fauna's activity might not have increased linearly with the larger amounts of litter material. While about 25 % of the added leaf C was recovered on the soil surface within the screened plots after 1 yr of decomposition (Fig. 1), there was no leaf layer left on soils next to the plots.

4.5 Implications for C storage in forest soils

Although in our ^{13}C-tracer experiment we added litter in different amounts and qualities than under natural conditions, our results provide some evidence that decomposing twigs could be less important for the C storage in these base-rich soils than leaves for at least two reasons. First, the net input of litter C to the soil after 1 yr of decomposition is probably larger for leaf as for twig litter as the slightly faster mineralisation (factor of 1.2) of the leaf litter found in our experiment may not compensate for the clearly different contributions of leaf (70 %) and twig litter (30 %) to the annual litter fall. Second, the twig litter also appears to have a lower potential to be transferred and stabilised in the mineral soils via organo-mineral interactions than the leaf litter. Much less of the twig-derived C was transported to mineral soils over 1 yr than of the leaf-derived C through DOC leaching or through bioturbation. Moreover, the DOC leached from twigs had a lower affinity to mineral surfaces than leaf DOC as it contained fewer "hydrophobic" components and less twig than leaf C was recovered in the mineral soil. We might expect that twig litter will not be transported to the deeper mineral soil via soil fauna until twigs lose their rigid structure and break down into smaller pieces. By that stage of decomposition, a large proportion of twig C might have already been mineralised to CO_2, and thus would not contribute to C storage in mineral soils.

Our findings contradict the assumption of most soil C models (e.g. YASSO), which basically assume that fine woody litter mineralises much more slowly than leaf litter, but that similar proportions of the decomposed litter are transferred into more stable humus pools (Liski et al., 2005;

Carrasco et al., 2006; Scott et al., 2006). While the first assumption may possibly apply to litter from many tree species other than beech (Guo et al., 2007; Vávřová et al., 2009), the ratio of mineralisation versus faunal export into mineral soil could be distinctly larger for twig than for leaf litter in many forest ecosystems of the temperate zone. More tracer studies, however, are needed to confirm this assumption.

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