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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 this is essential to better understand long-term dynamics of C stocks in soils. Using ^{13}C-labelled leaf (isotope ratio (δ^{13}C) = −40.8‰) and twig litter (δ^{13}C = −38.4‰), we tracked down the litter-derived C in the soil respiration, in the dissolved organic C (DOC) and in the soil organic matter of a beech forest in the Swiss Jura. After one year of decomposition, mass loss in the litter layer was almost twice as great for leaves as it was for twigs (75% vs. 40%). This difference was not the result of a slow mineralisation of the woody litter, but primarily of the only slight incorporation of twig-derived C into mineral soils. The C mineralisation rates of the twig litter were only slightly lower than those of the leaf litter (10–35%), in particular after the loss of the readily available litter fraction. However, the leaching of DOC from twigs amounted only to half of that from leaves. Tracing the litter-derived DOC showed that DOC from both litter types was mostly retained (88–96%) and stabilised in the top centimetres of the mineral soil. In the soil organic C at 0–2 cm depth, we recovered 8% of the initial leaf C, but only 4% of the twig C. Moreover, the ^{13}C mass balance suggested that a substantial fraction of the leaf material (~30%) was transported via soil fauna to soil depths below 2 cm, while the twig litter mainly decomposed in situ on the soil surface, probably due to its rigid structure and low nutritional value. In summary, our study shows that decaying twigs are rapidly mineralised, but seem to be clearly less important for the C storage in this beech forest soils than leaf litter.

1 Introduction

Litterfall represents the mayor 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

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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 Finland found that leaf and needle litter lost about twice as much C as twig litter (Guo et al., 2007; Vávřová et al., 2009). On the other hand, 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).

Regarding twig decomposition, 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

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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 could be retained in mineral soils than leaf-derived DOC since high-molecular, lignin-derived components of DOC, the so-called "hydrophobic" DOC have a higher affinity to mineral surfaces than the "hydrophilic" fraction with less 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 our present study was to compare the decomposition pathways of leaf and twig litter in a mixed beech forest in the Swiss Jura. Over the course of one year, we measured the CO_2 production, DOC leaching and translocation of C from ^{13}C-depleted leaves and twigs originating from four-year-old beech trees. The specific objectives of our study were: (1) to verify the general assumption that fine woody litter decomposes much slower 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 calcareous forest soils.

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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 the mean 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. The annual litterfall is larger on the Rendzina (330 g C m^{-2}) than on the Cambisol (230 g C m^{-2}), but consists of about 70% leaf litter and of 30% fine woody litter in both soils (N. Ruehr, personal communication).

2.2 Labelled litter experiment

The litter experiment started in November 2007, lasted for one year 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

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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 the final harvest of a four-year CO_2 enrichment experiment in Switzerland where ^{13}C-depleted CO_2 was used (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. To prevent litter loss due to wind and inputs of fresh litter, the litter plots were framed with acrylic glass (12 cm height) and covered with a polyethylene net (mesh size = 0.7 × 0.3 mm). We also minimized root respiration by digging a 30 cm deep trench around each plot to amplify the ^{13}C signal of litter-derived CO_2. A plastic foliar was inserted to prevent external root ingrowths. Vegetation growth on the plots was suppressed by periodically weeding.

2.3 Soil respiration and its $\delta^{13}C$

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 respiration ($\delta^{13}C_{resp}$) 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 closed for 8–40 min with a lid, allowing for a CO_2 increase of about 400 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 (12 ml), which had

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been previously evacuated and closed with an airtight rubber septum. 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 $\delta^{13}C$ using a Gasbench II, coupled with a isotope ratio mass spectrometer Delta Plus (both Thermo Finnigan Mat, Bremen, Germany). More details on the IRMS system employed in this study 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:

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

where $[CO_2]$ is the concentration and $\delta^{13}C$ the isotopic composition of CO_2 in the ambient air and in the soil chamber.

2.4 Water, litter and soil sampling

Water was sampled 1.5 m above the forest floor (throughfall) with PE funnels (Ø 11 cm), below the litter with zero-tension lysimeters (13 × 17 cm PVC boxes) and at a soil depth of 5 cm with suction plates (Ø 5.5 cm) made of borosilicate glass (pore size P5; Schmizo, Zofingen, Switzerland). Four openings (Ø 1 cm) on the bottom of the zero-tension lysimeters allowed soil animals to feed on the litter. The soil solution in the suction plates was evacuated by applying a constant low pressure of −400 hPa with a vacuum pump (EcoTech, Bonn, Germany). Both the lysimeters and the suction plates were installed on the lower 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 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 one year, the bags were collected from the forest floor and the litter

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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 and 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 molar 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 $\delta^{13}C$ 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 concentrations and the isotope ratios of C and N 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). 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).

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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 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, assuming extraction efficiencies of 0.45 (K_{EC}) and 0.54 (K_{EN}) (Jensen et al., 1997).

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. The precipitation was measured at the eddy covariance flux tower 80 m away.

2.7 Calculations and statistics

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:

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

where $\delta^{13}C_{soil+litter}$ is the $\delta^{13}C$ measured in the "soil + litter" treatment, $\delta^{13}C_{control}$ is the ^{13}C signature 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 −38.4‰) and the soil organic C (SOC; −26.7 to −27.8‰). This approach is based on the assumption that isotopic fractionation of ^{13}C

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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).

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 with water fluxes simulated with the COUP model (Jansson and Karlberg, 2001). 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.

Modeling CO_2 *effluxes:* The temperature dependency of the soil-respired CO_2 was fitted with the following equation (see 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).

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:

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

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

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fluxes, which were calculated with Eq. (4) for all sampling days. This ratio (factor P) was used as a correction factor:

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

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.

Statistics: Analyses of variance (ANOVA) were performed with *R* (v 2.8.1) to test for litter and soil-type effects on the C fluxes and C pools. A nested split-unit design was applied with the soil type (Rendzina or Cambisol) as the main unit and the litter layer ("bare soil"; "soil + leaves", "soil + twigs") as the sub-unit. The sample time was an additional sub-unit.

3 Results

3.1 Changes in the mass and quality of the litter

The amount of litter C that remained in litterbags (mesh size 1 mm) after one year of decomposition ranged from 66 to 73% (Fig. 6). It was larger on the Rendzina than on the Cambisol ($p < 0.01$), and was slightly but not significantly larger for twig than for leaf litter (69.5% vs. 67.5%; $p = 0.19$). In contrast, the proportion of the ^{13}C-depleted litter recovered in the litter layer (not 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. 6).

The C/N ratio of both the bulk litter and the microbial biomass on the litter decreased over the course of the experiment and was clearly wider in the twig than in the leaf litter (Table 2). After one year, concentrations of hot water-soluble substances were equally small in both litter types, whereas this fraction was twice as small in the twig as in the leaf litter at the beginning. The lignin concentrations (Klason lignin + soluble lignin) increased by a factor of 1.5 during decomposition, and, surprisingly, were about

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20% lower in the twig than in the leaf litter (Table 2). Only a slight (+0.1–0.4‰) and not significant increase in the $\delta^{13}C$ of the litter material was observed.

3.2 Contribution of litter C to SOC

At the end of the experiment, slight shifts (0.2–0.5‰; $p < 0.001$) in the $\delta^{13}C$ 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. 6). However, no significant litter effect on the $\delta^{13}C$ 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 ($p < 0.001$; Fig. 1). Moreover, the CO_2 release was significantly more pronounced in plots with twig litter than in those with leaf litter (+25%; $p < 0.001$). Using the strong dependency of the soil respiration 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 1040 g m^{-2} yr^{-1} in the Rendzina with a twig layer (Table 3).

The ^{13}C signature of CO_2 respired from the bare soils varied between −23 and −28‰ (Fig. 2) in both the Rendzina and the slightly acidic Cambisol. Small differences in the $\delta^{13}C$ between the two soils indicate 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 (Fig. 2).

The fraction of litter-derived C in the soil CO_2 effluxes (f_{litter}) peaked at 45–60% in January shortly after a cold period during which no litter decomposition was observed at air temperatures clearly below 0 °C (Fig. 3). 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

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from February to November ($p = 0.39$). As a consequence, f_{litter} was not dependent on the litter type in winter ($p = 0.88$), but was considerably larger for twigs than for leaves over the warm season independent of the soil type ($p_{litter} < 0.001$). In agreement with this temporal pattern, twig-derived C was mineralised 40% slower than leaf-derived C in winter, but only 15% slower over the warm season. These small differences in the second part of the experiment were only significant in the Rendzina ($p < 0.05$). By modelling CO_2 effluxes from litter between measurements (Eq. 5), we estimated that, after one year, the twig litter had lost 22–26% of its initial C through CO_2 and the leaf litter 29–34% (Fig. 4).

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. 2 and 3). 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. 4). 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 one year, 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. Thus, the DOC leaching corresponded to about 8% and 13% of the C respired as CO_2 from the twig and leaf litter, respectively.

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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%; $p = 0.19$; Fig. 4). Consequently, less DOC leached from twigs was retained when it passed through the uppermost mineral soil than DOC leached from leaves. Furthermore, clearly less litter-derived DOC was recovered in the mineral soils of the Cambisol than in those of the Rendzina (−40%; $p < 0.01$).

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 $l\,mol^{-1}\,cm^{-1}$), and contributed large amounts to the DOC leached from the litter layer especially after the green up of trees in spring (Fig. 3). This is indicated by the $\delta^{13}C$ of the DOC (Fig. 2). 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. 5). The twig-derived DOC also had a lower UV absorptivity (−15%) than the leaf-derived DOC throughout the experiment ($p < 0.001$).

4 Discussion

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

Fine woody litter is commonly thought to decompose much slower 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. 6).

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 one year, the twigs lost only 10–35% less C through CO_2 than the

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leaves (Fig. 4). 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. 6). Our findings are supported by a study with litterbags (mesh-sizes of 0.02–2 mm) on a Rendzina soil near Basel (Switzerland), where the mass losses after one year 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. 6), 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 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 phenomena 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 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).

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Surprisingly, the determination of the Klason lignin indicated a smaller proportion of lignin in the twig than in the leaf litter (Table 2), which seems to be in conflict with the woody tissue of the twigs. 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 comprised a significant fraction of these interfering substances. The evidence that both litter types were rich in refractory components fits our finding of similar C mineralisation rates. This agreement, in turn, 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 mm) 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).

One aim of this ^{13}C-tracer study was to assess whether litter decomposition is a significant source of soil CO_2 effluxes at the Lägern research site. Our results show that litter-derived CO_2 can indeed be a major component of the soil respiration, particularly on warm winter days when the leaf litter is still fresh (Fig. 3). But on an annual scale, respiration of C from freshly fallen tree litter (< 1 yr) probably contributes less than 20% to the heterotrophic soil respiration and less than 10% to the total soil respiration, given that the root respiration accounts for about 50% of the total soil CO_2 effluxes in this beech forest soils (Ruehr, 2009). By combining the C mineralisation rates (22–34%) with the amounts of litterfall at our site, we estimated that the decomposition of recent leaf litter contributed to 10–12% of the annual C losses from soils and recent twig litter 4–6%. The fraction of leaf litter is clearly smaller than that found in a ^{13}C-tracer study in a French beech forest, where decomposing beech leaves contributed about 20% to the heterotrophic soil respiration (Ngao et al., 2005). In contrast to our study, they estimated twice as large C losses through CO_2 from leaf litter (62% of initial C during

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one year), possibly because they interpolated between the litter-derived CO_2 effluxes and did not account for the temperature dependency of litter decomposition.

4.2 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 beech forests. Leaching of DOC from twig litter amounted only to half of that from leaf litter throughout the experiment, which contrasts with the small differences in the C mineralisation rates (Fig. 4). 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 molar UV absorbance of the twig litter DOC (Fig. 5), 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 (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

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coarse woody debris contained a slightly larger hydrophilic fraction 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 degrading 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 small 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 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, 2009; Müller et al., 2009).

Our results suggest that the sorption of DOC to mineral surfaces was the key mechanism for the retention of litter DOC: (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 stronger for twigs than for leaves (Fig. 4). The most likely reason for this is that twig-derived DOC had a lower specific UV absorbance (Fig. 5), and thus contained less "hydrophobic" DOC, which has a higher affinity to mineral surfaces than "hydrophilic" DOC (Kaiser and Guggenberger, 2000).

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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 is less important for twig than for leaf litter. 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 at the end of the experiment in contrast with only 4% of the twig C (Fig. 6). A substantial source of this "new" SOC was probably DOC leached from the litter layer.

4.3 Biologically mediated transport of litter

We have strong evidence that the export of litter via soil fauna played an important role primarily for the leaf litter, even though this pathway of C loss was not explicitly measured. 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% of the added twig litter C, but only to 70% of the initial leaf litter C (Fig. 6). We assume that the missing C in this mass balance can be attributed to a biologically mediated transport of litter-derived C to the deeper soil, where it was no longer detectable as the ^{13}C label vanished in the large SOC pool.

Our estimation that 30% of the leaf-derived C were translocated via faunal activity is similar to findings from a recent tracer experiment in an Italian poplar forest (Rubino et al., 2010) and a microcosm experiment in calcareous soils (Scheu, 1997), where soil fauna removed 30–60% of the leaf litter during one year. The ^{13}C-mass balance in our study additionally indicates that the proportion of twig litter that was incorporated into mineral soils by bioturbation was about 10%, and thus only one third of the leaf litter. These estimates are confirmed by the mass losses from the litterbags with a mesh size of 1 mm, which excludes macro fauna. After one year, about twice as much leaf litter remained in the litterbags as in the unconfined litter on the forest floor (Fig. 6). In contrast, litterbags only slightly affected the mass loss from the twig litter. This finding is in accordance with that of Hättenschwiler et al. (1999) that restricting access of

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soil fauna to decomposing litter affected mass losses from beech leaves but not from spruce branchlets.

4.4 Implications for C storage in forest soils

One of the uncertainties in predicting future C stocks in forest soils is the relative contribution of different types of litter to SOM (Crow et al., 2009). Our ^{13}C-tracer experiment in a temperate beech forest suggests that decomposing twigs are clearly less important for the C storage in these soils than leaves because: (1) The C mineralisation rates of the two litter types differed little (10–35%), in particular after the loss of the readily available litter fraction. By multiplying the rates of C loss through CO_2 with the annual litterfall, to which leaves contribute 70% and twigs "only" 30%, we estimated that the net input of C to the soil after one year of decomposition is approximately twice as large for leaf as for twig litter. (2) The twig litter also appears to have a considerably 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 than of the leaf-derived C through DOC leaching or through bioturbation. Moreover, the DOC leached from twigs probably had a lower affinity to mineral surfaces than leaf DOC as it contained less "hydrophobic" components. More twig litter will probably not be transported downwards before twigs lose their rigid structure and break down into smaller pieces. At this stage of decomposition, however, a large proportion of the twig-derived C might have already been mineralised to CO_2, and thus cannot contribute to C storage in mineral soils.

Our findings go against the assumption of most soil C models (e.g. YASSO), which basically assume that fine woody litter mineralises much slower 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), we propose that the ratio of mineralisation and incorporation into mineral soil C is distinctly larger for twig litter than for leaf litter in

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most forest ecosystems of the temperate zone. More tracer studies, however, are needed to confirm this conclusion.

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

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Table 2. Selected parameters of leaf and twig litter at the beginning and after 1 yr of decomposition. The values are means ± standard errors.

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)	11 (0.3)
Twig	”	95 (2)	127 (5)	10 (0)	280 (2)	−38.4 (0.1)	14 (0.3)
Leaf	1 yr	20 (1)	66 (4)	10 (1)	530 (8)	−40.4 (0.2)	6.5 (0.4)
Twig	”	51 (6)	72 (8)	6 (1)	420 (20)	−38.3 (0.5)	12 (0.5)

* Klason lignin + soluble lignin.

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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)

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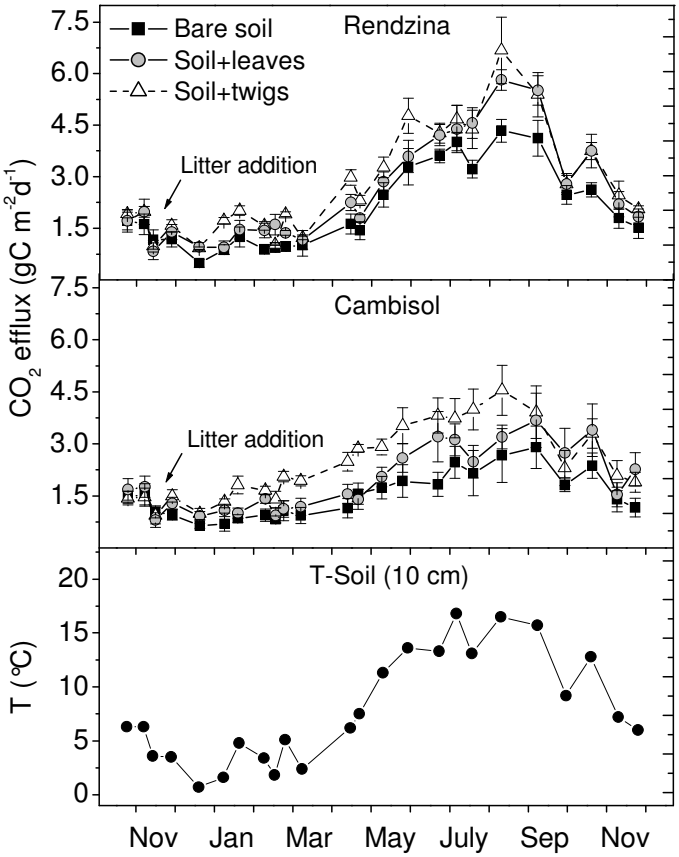

Fig. 1. Seasonal course of the heterotrophic soil respiration in the Rendzina and the Cambisol and of the soil temperature at a depth of 10 cm. The CO_2 effluxes are the means of five replicates (± standard error).

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Decomposition of ^{13}C-labelled leaf and twig litter

A. Kammer and F. Hagedorn

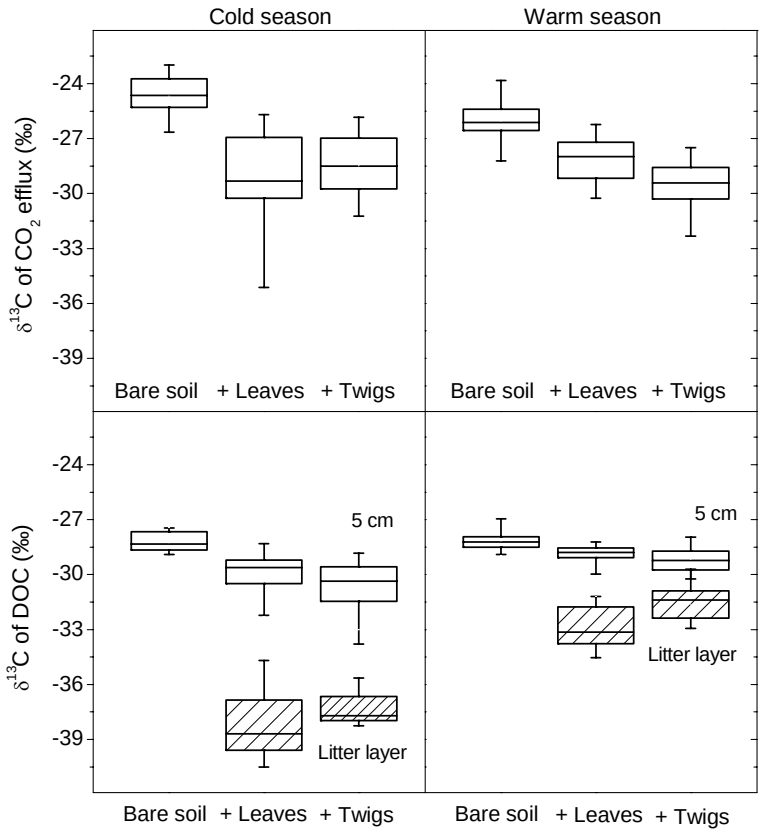

Fig. 2. Variability in the $\delta^{13}C$ of the soil CO_2 efflux (upper figures) and of the DOC leached from both the litter layer and the mineral soil at a depth of 5 cm. The values of the Rendzina and the Cambisol are combined. Each box shows the median value, the quartiles and the 2.5%- and 97.5%-quantiles of 50 single measurements for the CO_2 and of 30 measurements for the DOC in the cold (November 2007–April 2008) and in the warm season (April 2008–November 2008).

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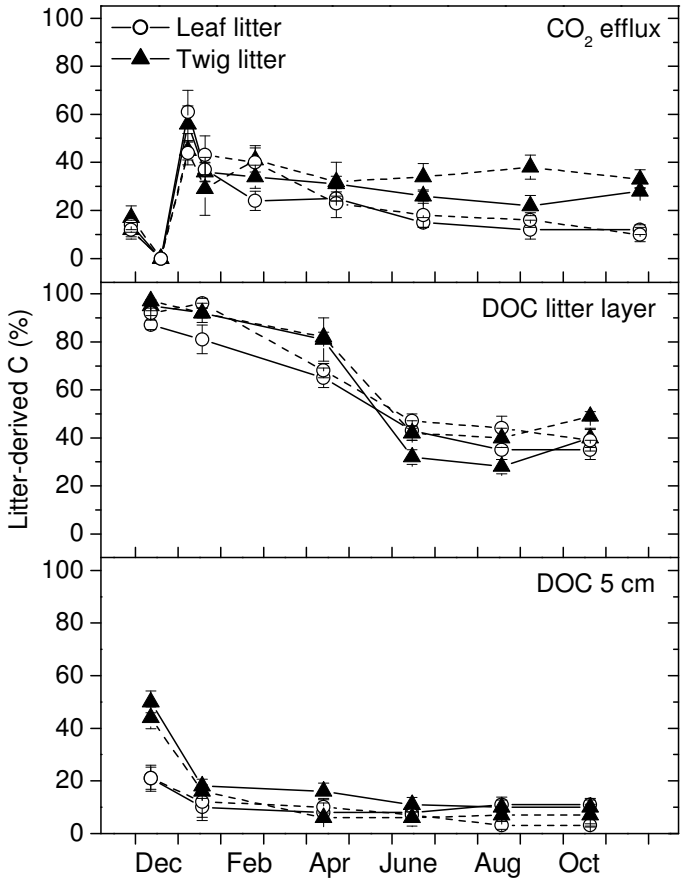

Fig. 3. Contribution of litter-derived C to the heterotrophic soil respiration and to the DOC leached from the litter layer and from the mineral soil at a depth of 5 cm. Means and standard errors of five replicates in the Rendzina (solid line) and the Cambisol (dashed line).

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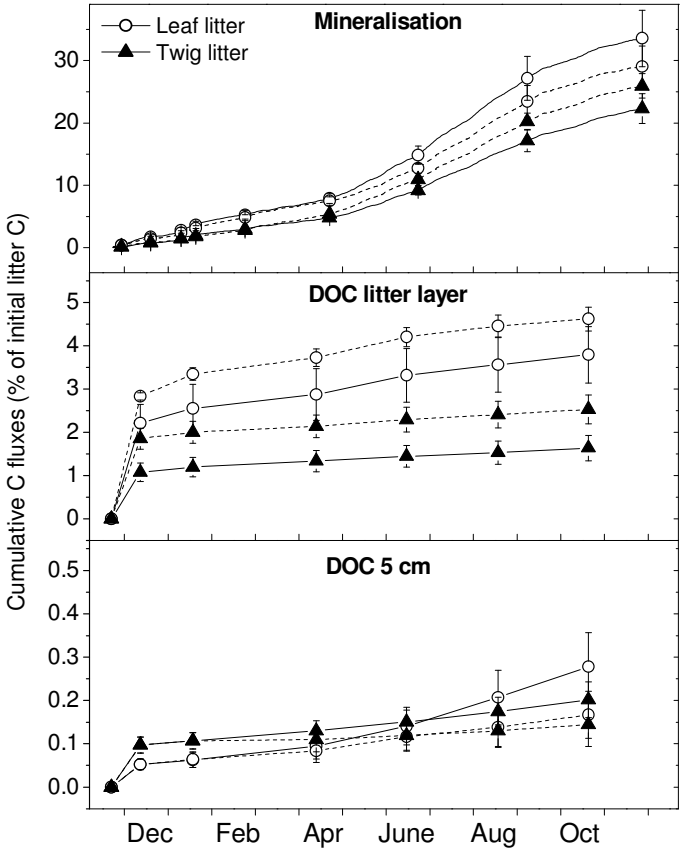

Fig. 4. Seasonal dynamics of litter-derived C respired as CO_2, leached as DOC from the litter layer and recovered in the DOC at a depth of 5 cm. The solid line represents the Rendzina and the dashed line the Cambisol. All values are the means of five replicates (± standard error).

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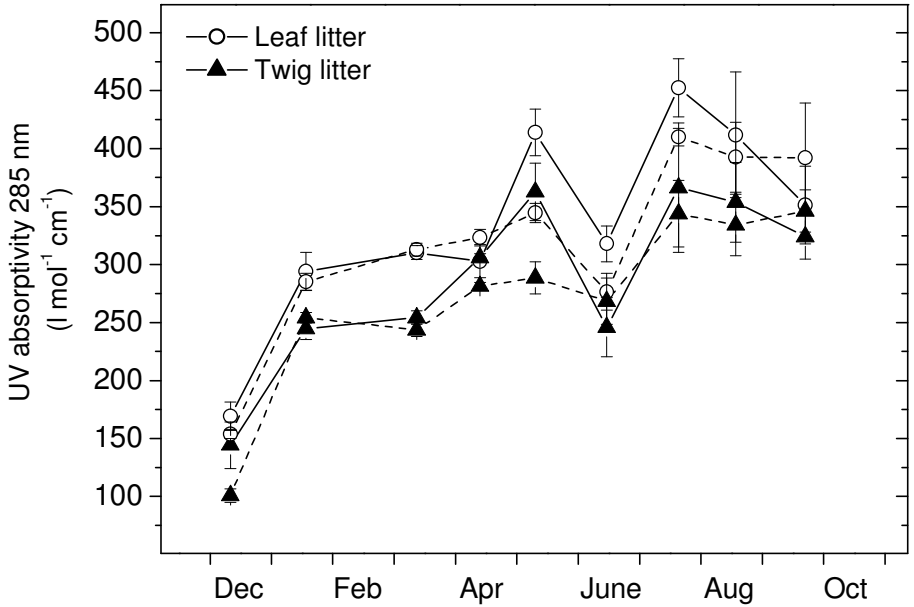

Fig. 5. Molar UV absorptivity of litter-derived C leached from the forest floor in the Rendzina (solid line) and the Cambisol (dashed line). Means and standard errors of five replicates.

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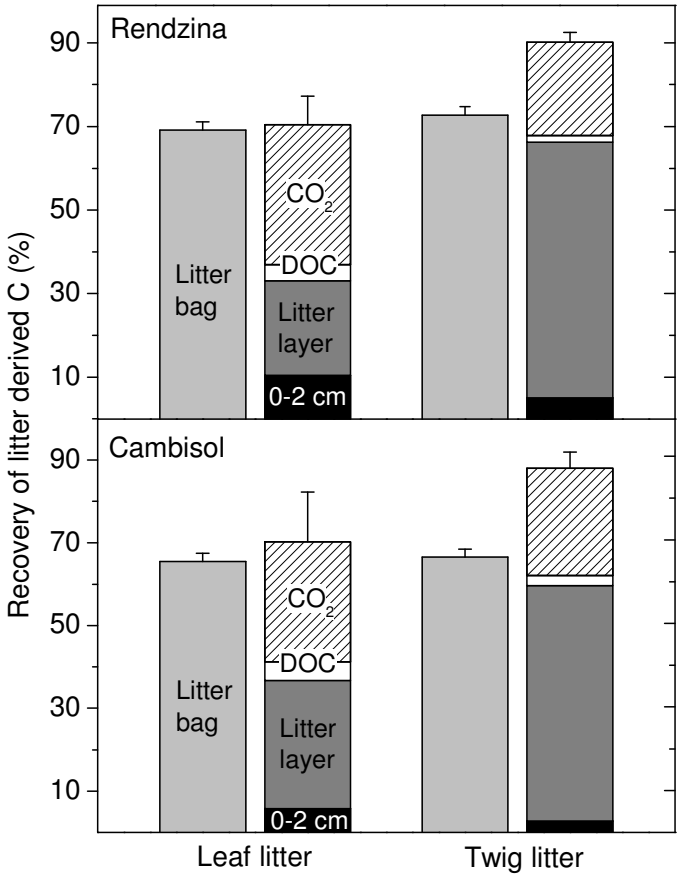

Fig. 6. Total recovery of the ^{13}C-labelled litter C in litterbags and in different C fluxes and C pools after 1 yr of decomposition. Means and standard errors of five replicates.

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