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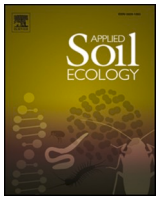

A mesocosm study on carbon transfer mechanisms from deadwood to litter through fungal hyphal growth

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ABSTRACT

Hyphae-forming fungi play a critical role in decomposing deadwood and plant litter, utilizing a variety of resources in forest ecosystems. While the redistribution of nitrogen and phosphorus by fungal hyphae between deadwood and soil has been established, the translocation of carbon (C) and its subsequent utilization remains unexplored. This study examines the fungal-mediated transfer of ^{13}C-cellulose from deadwood of European beech and Norway spruce to Norway spruce litter from an Oi/Oe horizon. We used a mesocosm double-chamber controlled system with a perforated intersection, including beech and spruce deadwoods (chamber I) and spruce litter (chamber II). After fungal hyphae growth in the intersection between the two chambers, mesocosms were incubated for 8–10 weeks at 20 °C in the dark. Following a pre-treatment phase, ^{13}C-cellulose was added to half of the deadwood chambers while the other half served as control without cellulose addition. The transfer of ^{13}C-cellulose from deadwood to spruce litter was assessed by measuring the abundance of ^{13}C in respiration and microbial biomass within the spruce litter. After incubation, the ^{13}C-cellulose recovered in spruce litter was higher for both respiration (7.75 ± 0.98 %) and microbial biomass (1.66 ± 1.01 %) for beech compared to the spruce deadwood (3.88 ± 1.07 % in respiration and 1.55 ± 1.37 % in microbial biomass). This indicates that, in both deadwood setups, more ^{13}C was recovered in respiration than in microbial biomass. Molecular analysis of the fungal hyphae at the intersection between the deadwood and spruce litter chambers identified *Clitopilus baronii* and *Kuehneromyces mutabilis* as the common and active deadwood-decaying fungi facilitating significant ^{13}C transfer (240–270 δ‰ in respiration, and 100–160 δ‰ in MBC), while the baseline without ^{13}C was −25 δ‰. This research provides new insights into the mechanisms of C transfer from deadwood to litter, suggesting an enhanced decomposition of litter by deadwood decaying fungi.

1. Introduction

Forests play a vital role in global C cycling, serving as significant reservoirs of C stored in living biomass, soil, litter, and deadwood (Meena et al., 2023; Pan et al., 2011). Among these components, litter and deadwood contribute substantially to global C stocks, holding 2831 Tg C and 36 to 72 Pg C, respectively, while annually respiring about 60 Tg C and 2.1 to 11 Pg C. These plant materials are integral to maintaining the C balance through C stocking and respiration in forest ecosystems (Bani et al., 2018). The turnover of C within forests is crucial to the long-term global C cycle, with litter decomposing more quickly than deadwood, leading to longer turnover times and higher C allocation in deadwood (Pugh et al., 2019, 2020). Microbial and fungal activity in deadwood plays a key role in these processes by increasing dissolved organic C (DOC) production and biological respiration (*i.e.*, mineralization of wood components to CO_2), which subsequently affects soil DOC levels and overall C cycling in the forest floor (Peršoh and Borken, 2017). In parallel, litter decomposition significantly contributes to forest C cycles by impacting respiration, soil C stocking, and plant nutrient availability (Strukelj et al., 2018; Prescott, 2010).

Deadwood decomposition, in particular, has been shown to increase microbial biomass in the soil, highlighting its crucial role in enhancing litter decomposition and promoting the incorporation of C compounds into the soil (Nazari et al., 2023). The composition of deadwood and

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litter, which varies between coniferous and deciduous species, also affects decomposition rates. Coniferous deadwood typically has higher cellulose and lignin content compared to deciduous species, which influences the speed of decay (Rowell et al., 2012; Vacek et al., 2015). While lignin has been traditionally considered resistant to decomposition, recent studies suggest it may decompose faster under certain conditions (Thevenot et al., 2010). These differences in substrate qualities between tree species and plant materials have a significant impact on the microbial community and decomposition dynamics, particularly the interactions between fungi, deadwood, and litter (Bani et al., 2018). Despite these findings, the specific mechanisms driving nutrient and C transfer from deadwood to litter, and their effects on respiration and microbial biomass, remain largely unexplored in natural settings.

Certain fungal groups, such as white-rot and brown-rot Basidiomycota, are known to degrade specific components of deadwood, such as lignin and cellulose (Lundell et al., 2014; Arantes et al., 2012), while Ascomycota play a significant role in early-stage litter decomposition, breaking down starch, amino acids, and sugar (Snajdr et al., 2011). Although the enzymatic processes of these fungi have been well characterized in laboratory settings (Floudas et al., 2012; Riley et al., 2014), much less is known about how naturally occurring fungal communities drive C transfer from deadwood to litter *in situ*. Active fungal hyphal networks may transport nutrients and C between these components, enhancing decomposition and microbial biomass (Minnich et al., 2021). This raises important questions about the role of fungi in nutrient transfer and the subsequent effects on C cycling in forest ecosystems.

In this context, early research by Chigineva et al. (2011) and Hughes and Boddy (1994) explored the efficiency of phosphorus (P) translocation through hyphal networks. Lindahl et al. (2001) demonstrated the bidirectional movement of P between interconnected wood pieces, revealing a relationship between resource size and decomposition rates. Boddy and Watkinson (1995) identified a source-to-sink effect in fungal networks, where ^{14}C nutrients flow directionally, and Wells et al. (1995) noted similar dynamics of C transfer within the fungus *Phanerochaete velutina*. Given the nitrogen (N) scarcity in deadwood, fungi use their networks to transport N, aiding decomposition (Boddy and Watkinson, 1995). Building on these insights, Frey et al. (2003) and Philpott et al. (2014) demonstrated that fungi facilitate a bidirectional exchange of N and C between litter-associated fungi and soil, enhancing soil N and C sequestration.

Peršoh and Borken (2017) observed that decomposing deadwood significantly boosts microbial activity in adjacent soils compared to less decomposable materials. In litter, fungal diversity increases from early to intermediate decomposition phases, though the community composition remains relatively stable across major taxonomic groups, indicating rapid turnover and potentially less time for significant C transfer processes (Purahong et al., 2016; Voříšková and Baldrian, 2013). By contrast, deadwood provides a more stable, long-lasting substrate for fungal colonization, offering a broader temporal window for C transfer. Studies show that species richness in decaying wood increases across decomposition stages (Hoppe et al., 2016; Kubartova et al., 2012), with different parts of the wood decaying at varied rates, reflecting a complex history of microbial colonization (Laiho and Prescott, 1999). Therefore, the slower, more varied decay process in deadwood presents fungi with more opportunities for C transfer compared to the quicker, more uniform decomposition observed in litter. However, the effects of nutrient and C transfer on respiration and microbial biomass from deadwood to litter remain poorly understood.

Addressing these knowledge gaps requires further investigation into how fungal communities facilitate C transfer in natural settings. In this study, we used a controlled mesocosm experiment to explore the dynamics of C transfer from deadwood to litter, focusing on fungal hyphal growth as a key mechanism. By adding ^{13}C-labeled cellulose (97 atom%) to deadwood, we aimed to trace C transfer to litter, minimizing external factors such as temperature, precipitation, and soil fauna. Our study offers new insights into the ecological mechanisms of C cycling, with the following hypotheses: (i) C transfer from deadwood increases respiration and microbial biomass in litter, (ii) fungal hyphae transfer more C from beech deadwood to spruce litter as compared to spruce deadwood, and (iii) deadwood-decaying fungi are primarily responsible for C transfer from deadwood to litter.

2. Materials and methods

2.1. Experimental setup

Our study used a double-chamber controlled system (Fig. 1) to investigate C transfer from deadwood to spruce litter *via* fungal hyphae. Both chambers (1.8 L each) were separated by a perforated intersection that allowed fungal hyphal growth from one into the other chamber. The intersection consisted of two stainless steel plates (90 cm^2) with a partial perforation area (30 cm^2) covered by a gauze (160 µm mesh size). The distance between the two plates was 2 mm resulting in a volume of 18 mL. Both chambers and the intersection were equipped with connections for gas flushing, gas sampling and CO_2 measurements. Further details on the double-chamber system are given in Guhr et al. (2015). The system featured chambers for European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*) deadwood, and Norway spruce litter. Deadwood and spruce litter (Oi/Oe horizon) were sampled from a spruce forest at the Fichtel Mountains, Germany. Spruce litter was sorted, mixed and adjusted to 60 % of the maximum water holding capacity, yielding a gravimetric water content of 2.86 g water per g dry matter. Beech and spruce deadwood each originated from the same tree and were placed on the forest floor of the spruce forest three years before sampling. Freshly collected beech and spruce deadwood were cut into 3 cm thick discs, weighing 18.1–63.5 g (dry weight), and placed in Chamber I, while 25.9 g (dry weight) of spruce litter was placed in Chamber II. Deadwood and spruce litter filled about 10 % of the chamber volume.

A total of 20 chambers containing beech and spruce deadwood (10 chambers for each deadwood type) were pre-incubated at 20 °C in a climate chamber in darkness for 8–10 weeks. The pre-incubation time was required for fungal hyphal growth into the intersection. For technical reasons, pre-incubation and incubation with spruce and beech deadwood were carried out one after the other. While the overall incubation times were similar, with 42 days for spruce and 38 days for beech, there was a notable difference in the duration prior to cellulose addition. Specifically, the period before cellulose addition was extended for beech deadwood (32 days) due to a slower rate of visual hyphal growth compared to spruce. Prior to pre-incubation, deadwood and litter were adjusted to 60 % of the maximum water holding capacity. After pre-incubation, 40–50 mg of ^{13}C-labeled cellulose (97 atom% ^{13}C, IsoLife, Wageningen, Netherlands) was inserted into a drill hole (1 cm in diameter, 1.5 cm in depth) in deadwoods to trace ^{13}C transfer by fungal hyphae from deadwood to spruce litter. The four treatments included (i) beech deadwood with ^{13}C cellulose, (ii) beech deadwood without cellulose, (iii) spruce deadwood with ^{13}C cellulose, and (iv) spruce

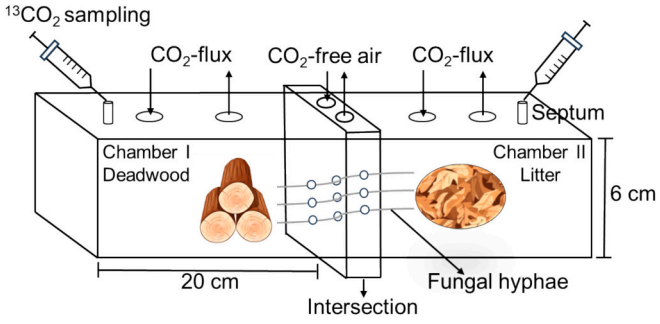

Fig. 1. Schematic representation of a mesocosm double-chamber controlled system with intersection, adapted from Guhr et al. (2015).

deadwood without cellulose, with each treatment having $n = 5$. In the litter chamber, only spruce litter without cellulose was used. Only a single experimental cycle for each deadwood setup was conducted, without repetitions due to time constraints and high costs. The residual ^{13}C-cellulose was removed from the drill holes of deadwoods, dried and weighed to quantify decomposition of cellulose.

2.2. Respiration and ^{13}C signature of CO_2

Before each respiration measurement, the chamber system including interspace was flushed with CO_2-free air for 30 min. Thereafter, chamber systems were incubated for 3 h, and gas samples were taken at 0, 30, 60 and 120 min using a 1 mL syringe. The intersection was continuously flushed with CO_2-free air at a flow rate of 12 mL min^{-1} to prevent CO_2 exchange between chamber I and chamber II *via* the perforated intersection plates during the incubation period. However, a complete gas exchange prevention between the intersection and the deadwood or litter chambers could not be achieved. We believe that this exchange was minimal, as only a small portion of the intersection plate was perforated, with most of the openings occupied by fungal hyphae. Consequently, any residual gas exchange from the intersection may have slightly contributed to an underestimation of CO_2 production in both chambers. Nevertheless, our primary goal was to inhibit CO_2 and $^{13}CO_2$ transfer between the deadwood and litter chambers, which was effectively managed by flushing the intersection. Pre-tests, where 5 mL ^{13}C-labeled CO_2 (98 atom%) was injected either in chamber I or in chamber II, revealed no exchange of $^{13}CO_2$ between the chambers within 2 h. For CO_2 analysis, a 0.3 mL gas sample was injected directly into a gas chromatograph (SRI Instruments Model 8610C, Torrance, USA) equipped with a Flame Ionization Detector (FID). Three CO_2 standards (380, 600, and 1000 ppmv) were used for the calibration of the GC. Respiration rate (μg CO_2-C g^{-1} h^{-1}) was calculated from linear increase in CO_2 concentration over time, considering the gas volume of each chamber, air pressure, molar volume of CO_2, atomic mass of C, incubation temperature, universal gas constant, and the dry weight of deadwood and spruce litter. The cumulative respiration (mg CO_2-C g^{-1}) was calculated by linear interpolation between sampling events over the total incubation period.

The ^{13}C signature (δ‰) of CO_2 in chamber I and II was determined in both the with and without cellulose addition treatments at five to six occasions over the entire incubation period. For ^{13}C signature of CO_2 in the with and without cellulose chambers we used N_2-flushed 12 mL glass vials (Labco Exetainer, Lampeter, UK). The ^{13}C signatures were measured with isotope mass spectrometer (Delta plus XP, Thermo Fisher Scientific, Germany), and results were reported in δ‰, based on the $^{13}C/^{12}C$ isotope ratio. In addition, we determined the ^{13}C signature of CO_2 from spruce litter, which was separately incubated after the removal of the deadwood chamber and intersection following the chamber experiment (42 days after for spruce, and 38 days after for beech), to test whether $^{13}CO_2$ was released from the spruce litter without a hyphal connection to the deadwood. The total transfer of ^{13}C from ^{13}C cellulose (chamber I) to spruce litter and its use for respiration (chamber II) was calculated as follows:

$$^{13}C_R\ (mg) = \frac{(atom\%_{with\ cellulose} - atom\%_{without\ cellulose}) \times R_{Cum}\ (mg)}{100}$$

where $^{13}C_R$ is the recovery of ^{13}C in respiration (chamber II) over the incubation period after addition of ^{13}C cellulose to deadwood, atom $\%_{with\ cellulose}$ and atom% $_{without\ cellulose}$ are the mean ^{13}C fractions (converted from ^{13}C(δ‰)) in respiration (chamber II) of the with and without cellulose deadwood setups, and R_{Cum} is the cumulative respiration (mg CO_2-C) of spruce litter in the 'with cellulose' deadwood setups after addition of ^{13}C cellulose. Here, ^{13}C recovery in respiration refers to the amount of added ^{13}C-cellulose. The relative proportion ^{13}C cellulose transferred to spruce litter and used for respiration ($^{13}C_R$, %) was calculated as follows:

$$^{13}C_R\ (\%) = \frac{^{13}CR\ (mg)}{(\text{initial cellulose } ^{13}C\ (mg) - \text{residual cellulose } ^{13}C\ (mg)} \times 100$$

where initial cellulose ^{13}C is the amount of ^{13}C added to beech and spruce deadwood, and residual cellulose ^{13}C is the amount of non-used ^{13}C after the incubation period.

2.3. Chemical properties of deadwood and litter

To understand microbial activity on each litter type, initially we investigated chemical properties of deadwood and litter separately. Deadwood and litter were milled and then analyzed by measuring elemental contents. C and N contents were determined using a CN elemental analyzer (vario MAX, Elementar, Germany). Contents of Al, Ca, Fe, Mg, Mn and P were assessed by digestion in a microwave with nitric acid and hydrochloric acid, and then analysis using an ICP-OES spectrometer (3800XL, Perkin Elmer, USA).

2.4. Microbial biomass C and ^{13}C abundance

Microbial biomass C (MBC) in spruce litter was determined using the chloroform-fumigation extraction method (Vance et al., 1987). Immediately after the chamber experiment, 9 g of spruce litter (fresh weight) from the 'with cellulose' and 'without cellulose' chambers was fumigated with chloroform for 24 h. Fumigated and non-fumigated samples were extracted using a 0.05 M K_2SO_4 solution which was 10 times lower than suggested by Vance et al. (1987) to enable isotopic analysis of extracts and avoid high salt content (Dijkstra et al., 2006). Extracts were filtered (cellulose fold filters) and then freeze-dried for isotopic analysis (Delta plus XP, Thermo Fisher Scientific, Germany) or frozen at −22 °C for analysis of organic C concentration (Analytik Jena GmbH - multiN/C 2100, Germany). Microbial biomass C was calculated using a correction factor kEC is 0.45 (Vance et al., 1987). By comparing the ^{13}C signature of spruce litter from the 'with cellulose' and 'without cellulose' treatments, we assessed the incorporation of ^{13}C from cellulose degradation into microbial biomass. The ^{13}C signature of the microbial biomass was calculated using a mass balance approach as outlined by Dijkstra et al. (2006).

$$\delta^{13}C_{MB} = \left[\delta^{13}C_F \times C_F - \delta^{13}C_E \times C_E\right] / C_{MB}$$

MB, F and E represent the microbial biomass (chloroform-labile), fumigated and extractable (unfumigated) fractions, respectively. The total transfer of ^{13}C from ^{13}C cellulose (chamber I) to spruce litter (chamber II), and its use for microbial biomass (chamber II) was calculated as follows:

$$^{13}C_{MB}\ (mg) = \frac{(atom\%_{with\ cellulose} - atom\%_{without\ cellulose}) \times MB\ (mg)}{100}$$

where $^{13}C_{MB}$ is the recovery of ^{13}C in microbial biomass (chamber II) at the end of the incubation period, atom$\%_{with\ cellulose}$ and atom$\%_{without\ cellulose}$ are the mean ^{13}C fractions (converted from ^{13}C(δ‰)) in microbial biomass (chamber II) of the with and without cellulose deadwood setups, respectively, and MB is the total amount of microbial biomass C (mg) in spruce litter of the with cellulose setups. The relative proportion ^{13}C cellulose transferred to spruce litter and used for microbial biomass ($^{13}C_{MB}$, %) was calculated as follows:

$$^{13}C_{MB}\ (\%) = \frac{^{13}CMB\ (mg)}{(\text{initial cellulose } ^{13}C\ (mg) - \text{residual cellulose } ^{13}C\ (mg)} \times 100$$

where initial cellulose ^{13}C is the amount of ^{13}C added to beech and spruce deadwood, and residual cellulose ^{13}C is the amount of non-used ^{13}C after the incubation period.

2.5. Fungal community analysis

Fungal community composition was assessed for both beech and spruce deadwoods, as well as spruce litter after incubation. Samples of approximately 500 μL in volume were stored at −80 °C until DNA was extracted using the NucleoSpin® Soil Kit (Macherrey-Nagel, Düren, Germany) according to the manufacturer protocol. Fungal community composition was assessed by metabarcoding as detailed by Peršoh and Borken (2017). Briefly, a library of the fungal barcoding region (ITS rRNA gene region) was prepared in two consecutive PCR amplifications. Following purification and quality assessment, sequencing was performed by the sequencing service of the Faculty of Biology at LMU Munich on an Illumina MiSeq® sequencer (Illumina, Inc., San Diego, CA, USA) with 2 × 250 bp paired end sequencing (MiSeq Reagent Kit v3 Chemistry, Illumina, Inc., San Diego, CA, USA). Sequencing reads were processed using QIIME version 1.9.0 (Caporaso et al., 2010), FastX toolkit (http://hannonlab.cshl.edu/fastx_toolkit/), and CD-HIT-OTU (Li et al., 2012). The resulting OTU table (Table S1) was used for statistical analysis. For both with and without cellulose addition treatments, based on Pearson correlation, R^2 and *P* values, we identified which OTUs were associated with specific microbial functional attributes and therefore for the C transfer from deadwood to spruce litter (into respiration and MBC). The Unite database (*v8*, Kõljalg et al., 2005) served as reference for taxonomic assignment, and responding significant taxa were cross-checked using NCBI nr. Fungal OTUs were named using the unique OTU number prepended by the highest taxonomic level assignable. OTUs were assigned to functional groups based on their taxonomic affiliation, as detailed by Peršoh et al. (2018).

2.6. Extracellular enzyme activity

We examined the activities of eight extracellular lignocellulolytic enzymes in deadwood and litter, focusing on enzymes breaking down labile (endoglucanase, endoxylanase, cellobiohydrolase, xylosidase, glucosidase) and recalcitrant (laccase, general peroxidase, manganese peroxidase) organic matter compounds, following the protocol by Noll et al. (2016). Frozen samples were ground, homogenized in distilled water, agitated, and centrifuged to obtain aqueous extracts. Ligninolytic enzymes were quantified using ABTS oxidation (Eggert et al., 1996; Madhavi and Lele, 2009). Peroxidase activities, differentiated by Mn^{2+} ion dependency, were initiated with H_2O_2 (Arnstadt et al., 2016; Liers et al., 2011; Hahn et al., 2013). Cellulolytic and hemicellulolytic activities were measured photometrically using AZO substrates (Větrovský et al., 2011) and *via* HPLC with 4-MU derivatives (Freemann, 1997; Stemmer, 2004).

2.7. Statistical analysis

Statistical analysis was performed using R *v.* 4.3.1 (R Core Development Team, Austria, 2023). Microbial activity such as respiration, MBC, and ^{13}C in respiration and MBC were checked for normality using the Shapiro–Wilk test. Where data did not meet the normality assumption, log transformations were applied to ensure compliance with parametric test requirements. However, we opted to present the original (non-transformed) data for clarity in our results. For microbial and enzyme activities in spruce and beech plant materials under different treatments (incubation day, without cellulose *vs.* with cellulose, deadwood *vs.* litter), descriptive statistics were calculated, and two-way ANOVA was performed using the 'aov()' function, with significance set at $P < 0.05$. For analyses focusing on the two treatments (without and with cellulose) as the independent variable, we separately assessed the dependent variables: ^{13}C in respiration, MBC, and ^{13}C in MBC using one-way ANOVA, also performed with the 'aov()' function. The R packages ggplot2, ggpubr, gridExtra, dplyr, and tidyverse were used for data visualization. To analyze the fungal community, Pearson correlation analysis, conducted with the 'cor.test' function from R's 'stats' package, determined significant correlations ($P < 0.001$) between microbial activities (*e.g.*, respiration, MBC, and enzyme activity) and fungal Operational Taxonomic Units (OTUs). Additionally, Principal Component Analysis (PCA), using the 'FactoMineR' and 'factoextra' packages, was utilized to further explore relationships between these variables, providing insights through data preprocessing and visualization.

2.8. Data availability

Accession numbers: Sequence reads were deposited in the European Nucleotide Archive (http://www.ebi.ac.uk/ena) under accession PRJEB81881.

3. Results

3.1. Respiration and ^{13}C transfer to respiration in spruce litter

Respiration rates of deadwood were consistently higher than of spruce litter in both deadwood setups (spruce and beech) and treatments (without and with cellulose addition) during the entire incubation period (Fig. 2). For spruce litter, the 'with cellulose' treatment exhibited mean respiration rates of 14 and 13 μg CO_2-C g^{-1} h^{-1} for spruce and beech setup, respectively, surpassing those of the 'without cellulose' treatment, which showed rates of 9 for spruce and 7 μg CO_2-C g^{-1} h^{-1} for beech setup (treatment effect, $P < 0.001$). Observations from both setups and treatments indicate that the incubation day significantly influenced respiration in spruce litter (incubation day effect, $P < 0.05$). In the 'with cellulose' treatment, peak respiration was observed in mid-incubation, with a subsequent decline towards the end of the incubation period in both setups. Higher respiration in spruce deadwood observed in around day 20 (20–22 μg CO_2-C g^{-1} h^{-1}, Fig. 2B) corresponds with a closely similar respiration rate in spruce litter throughout the mid-incubation days (around 14 μg CO_2 g^{-1} h^{-1}). Contrastingly, in the beech setup (Fig. 2D), we observed a concurrent rise in respiration for both beech deadwood and spruce litter until day 35, indicating a synchronized activity in both substrates within this period. The cumulative respiration in spruce litter for the spruce setup was 13 ± 0.64 mg CO_2-C g^{-1} d.w. over 54 days, while for the beech setup, it was 14 ± 0.65 mg CO_2-C g^{-1} d.w. over 70 days.

Investigation into the dynamics of ^{13}C in respiration revealed significant influences of incubation day and ^{13}C abundance across the two setups (Fig. 3). After adding ^{13}C-cellulose to deadwood (day 0), spruce litter in both setups exhibited negative ^{13}C values, approximately −15 δ‰. As the incubation progressed, ^{13}C in spruce litter increased to around 150 δ‰ by day 42 in the spruce setup (Fig. 3A). In the beech setup, the ^{13}C in spruce litter showed a more substantial rise, reaching ~400 δ‰ by day 28 (Fig. 3B). The highest ^{13}C values recorded were 839 δ‰ in spruce deadwood by day 42 and 742 δ‰ in beech deadwood by day 28. The spruce litter associated with spruce setup displayed lower ^{13}C values (70–150 δ‰), in contrast to the spruce litter in the beech setup, which exhibited higher ^{13}C values (200–400 δ‰). After day 28, a reduction in ^{13}C was noted in beech deadwood and its corresponding spruce litter (Fig. 3B).

The separately incubated spruce litter immediately following the chamber experiment displayed considerable variability in the ^{13}C abundance in respiration between 'without cellulose' and 'with cellulose' treatments ($P < 0.05$, Fig. 4A and B). In both deadwood setups, ^{13}C in respiration was around −25 δ‰ in 'without cellulose' treatment and substantially higher in 'with cellulose' treatment, exceeding 200 δ‰ in the spruce setup compared to only 40 δ‰ in the beech setup. Overall, the ^{13}C recovery in spruce litter respiration was significantly higher (Welch two sample *t*-test, $P = 0.03$) in the beech setup (7.75 ± 0.98 %) than in the spruce setup (3.88 ± 1.07 %) (Table 1).

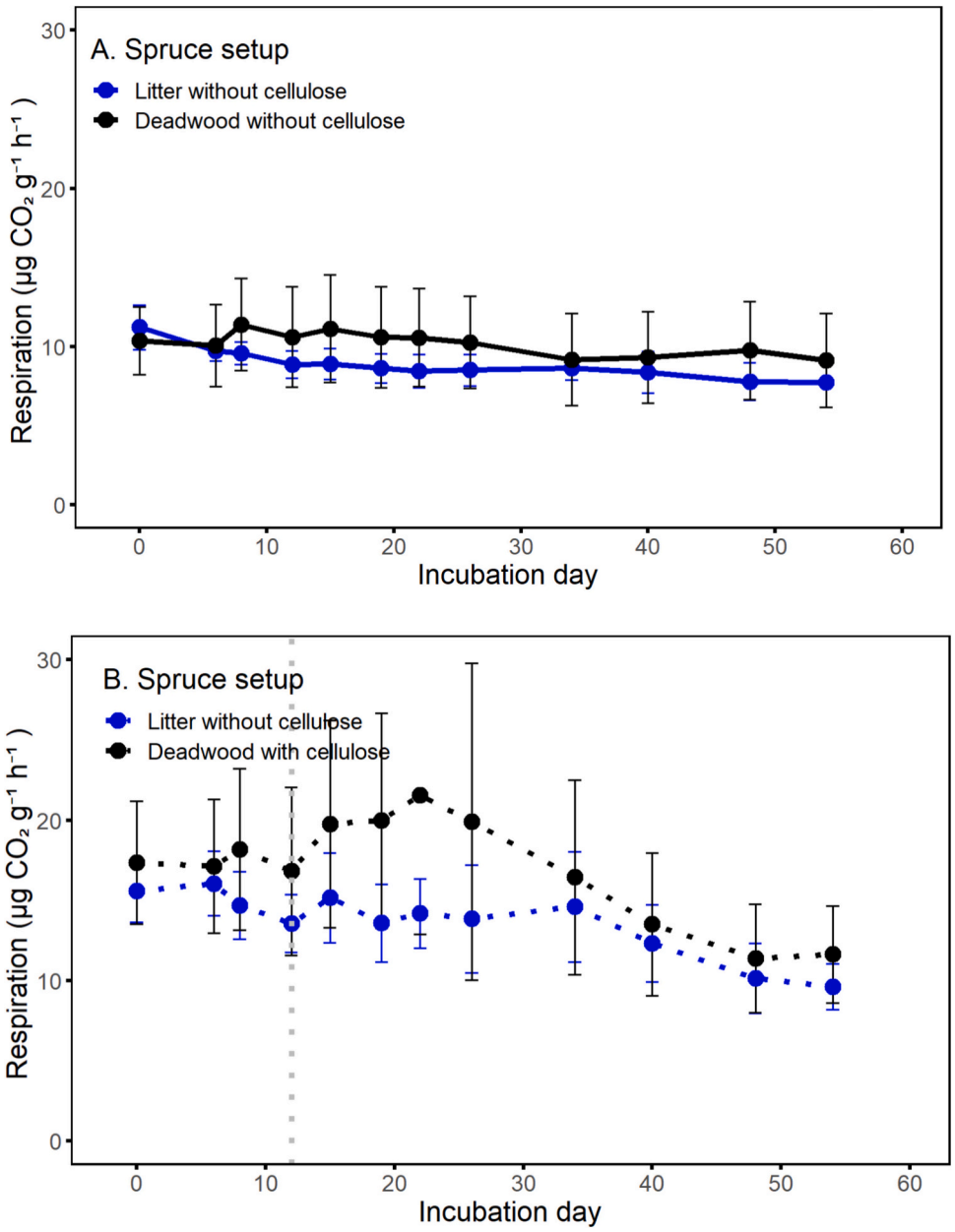

Fig. 2. Respiration in deadwood and litter over incubation days for both treatments of without and with ^{13}C-cellulose addition in deadwoods. Panels A and B represent spruce setup *i.e.*, spruce deadwood and spruce litter, and panels C and D represent beech setup *i.e.*, beech deadwood and spruce litter. The vertical gray dotted lines in panels B and D indicate the addition of ^{13}C-cellulose in both spruce and beech deadwoods under the cellulose treatment.

3.2. ^{13}C transfer to microbial biomass in spruce litter

The average MBC in spruce litter was 5.1 ± 1.2 mg C g^{-1} in the 'without cellulose' and 5.6 ± 0.8 mg C g^{-1} in the 'with cellulose' treatment within the spruce setup (Fig. 4C). In the beech setup, MBC in spruce litter were 2.5 ± 0.2 mg C g^{-1} and 3.6 ± 0.4 mg C g^{-1} for without and with cellulose addition treatments, respectively (treatment effect on litter, $P < 0.05$, Fig. 4D). Moreover, in both setups, the ^{13}C in MBC in the spruce litter differed between without and with cellulose addition treatments (treatment effect, $P < 0.05$), with 'without cellulose' deadwood showing a ^{13}C abundance was of −25 δ‰ (for both setups) whereas 'with cellulose' deadwood ranged from 200 to 400 δ‰ for spruce and beech setups (Fig. 4E and F). The spruce litter revealed similar and non-significant mean ^{13}C recoveries in microbial biomass for the beech (1.66 ± 1.01 %) and spruce setup (1.55 ± 1.37 %) (Table 1). Thus, more ^{13}C was recovered in respiration than in microbial biomass of both deadwood setups. The mass balance revealed a total ^{13}C-cellulose transfer of 5.44 ± 2.40 % and 9.41 ± 0.89 % for spruce and beech deadwood to spruce litter, respectively (Table 1).

3.3. Fungal community and ^{13}C transfer via fungal hyphae

We found a total of 376 fungal Operational Taxonomic Units (OTUs) in spruce and beech setups (*i.e.*, both deadwoods and spruce litter) showed in Table S1. The PCA revealed distinct associations between OTUs and key functional attributes within the microbial community (Fig. 5A), delineating the roles of various fungal OTUs in MBC, ^{13}C in MBC, respiration, ^{13}C in respiration, and enzymatic activities, including cellulolytic and ligninolytic enzymes (Table S2). The PCA biplot explained 47 % of the total variance, with 27 % attributed to PC1 and 20

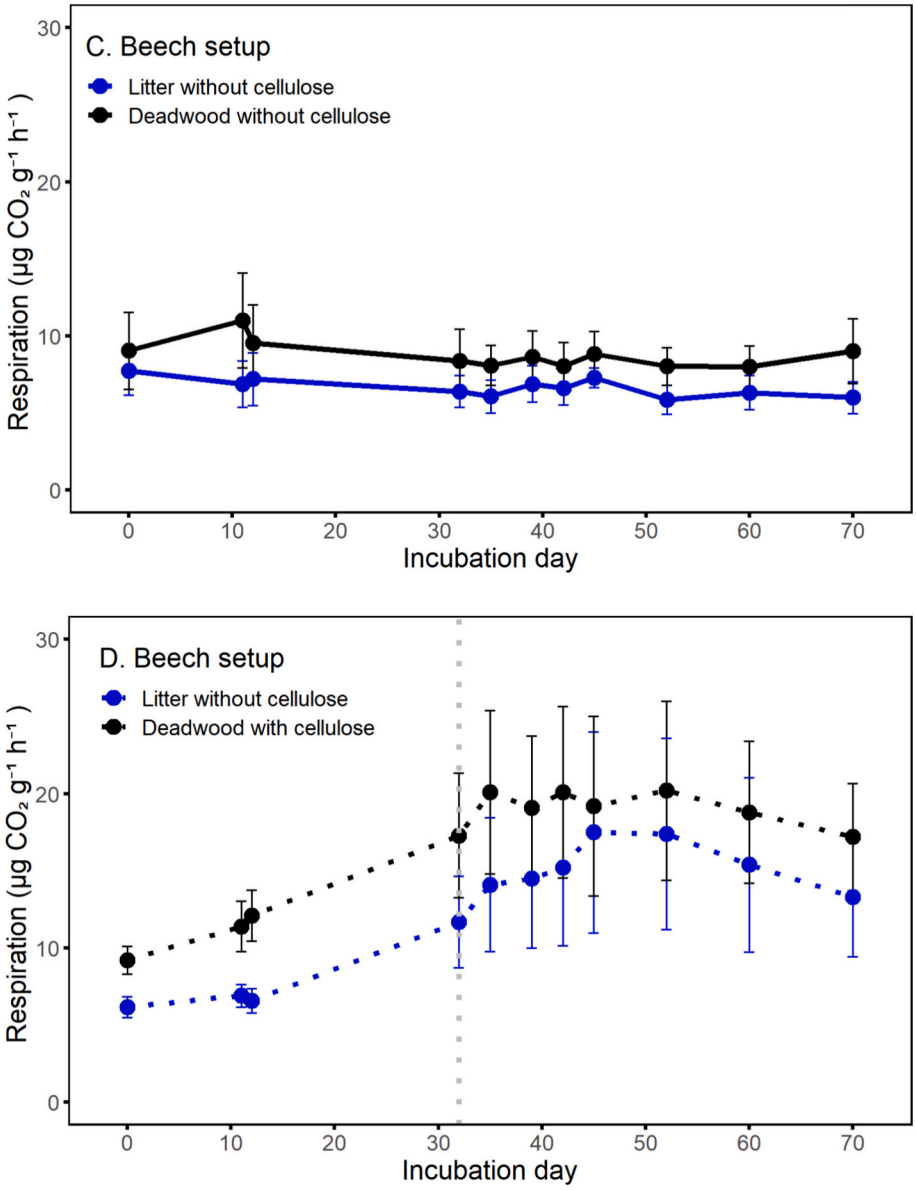

Fig. 2. (*continued*).

% to PC2 (Fig. 5A). Fungal OTUs such as *Mycota-315*, *Sarea difformis-265*, *Nectriaceae-84*, *Mycota-168*, *Mycota-254*, *Mycota-281*, and *Mycota-44* were situated along the MBC vector on PC1. Short vectors indicate a weak contribution of OTUs such as *Mycena cinerella-270*, *Apodus deciduus-16*, *Clitopilus baronii-5* for ^{13}C in respiration; *Trechispora-240*, *Hygrophoropsis aurantiaca-262*, *Apodus deciduus-16*, *Mycota-58*, and *Clitopilus baronii-5* for respiration; and *Ascocorticium anomalum-149*, *Mycena-96*, *Phacidiaceae-244*, and *Mycena metata-130* for ^{13}C in MBC. Unidentified OTUs (*Mycota-252*, *-326*, *-48*, and *-157*) positioned with 'Enzyme activity' along PC2 were related cellulolytic enzyme activity, whereas the abundance of *Mycota-166* was associated with ligninolytic enzymes (Table S2). Furthermore, we identified 15 and 59 OTUs with a maximum abundance >1 % occurring only in deadwood and litter, respectively (Fig. 5B). Four OTUs contributed to the intersection between the chambers for >1 % of the community. Five OTUs (*Clitopilus baronii-5*, *Trichoderma-8*, *Apodus deciduus-16*, *Kuehneromyces mutabilis-17*, and *Mariannaea-47*) were common to litter, deadwood, and the intersection (Table S3). The chambers common with *Clitopilus* and *Kuehneromyces* deadwood decay fungi had higher MBC, and ^{13}C abundance in MBC and respiration than other fungi. *Clitopilus* associated chambers had an MBC of 12 mg C g^{-1} with ^{13}C values of 101 δ‰ in MBC and 243 δ‰ in respiration, while *Kuehneromyces* associated chambers had an MBC of 15 mg C g^{-1} with 153 δ‰ in MBC and 264 δ‰ in respiration. In the absence of ^{13}C-cellulose, these parameters for the same fungi were around 8 mg C g^{-1} and -25 δ‰.

4. Discussion

4.1. C transfer from deadwood to litter

We examined the C transfer from deadwood to spruce litter, focusing on how the addition of ^{13}C-cellulose affects respiration and microbial biomass. In the 'with cellulose' treatment, we observed a higher ^{13}C abundance in both respiration and MBC in spruce litter compared to the 'without cellulose' treatment over the total incubation periods. This pattern confirms our hypothesis that C transfer from deadwood *via* fungal hyphae enhances microbial processes in spruce litter (Figs. 2, 3, and 4). The significant ^{13}C recovery in spruce litter (Table 1) indicates that a portion of the added ^{13}C-cellulose was successfully transferred from deadwood to litter, facilitating microbial activities.

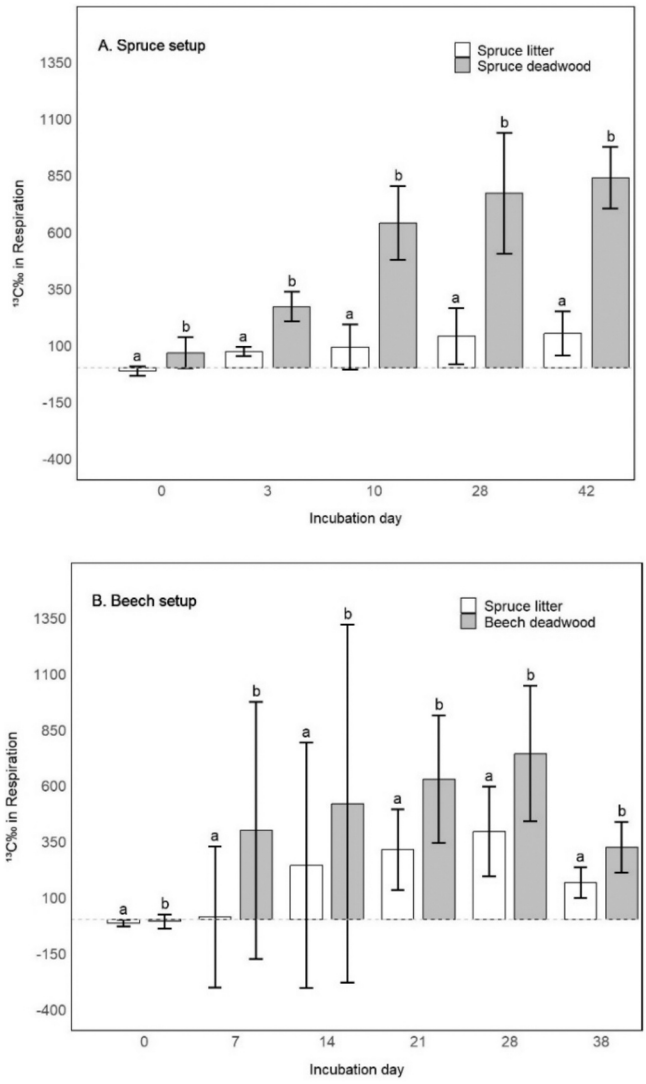

Fig. 3. Abundance of ^{13}C‰ in respiration over incubation days for spruce (A) and beech (B) setups.

Deadwood consistently showed higher respiration rates in both with and without cellulose addition treatments. This trend aligns with findings from other studies, which suggest that deadwood is a more accessible C source for microorganisms than spruce litter (Peršoh and Borken, 2017), likely due to its lower lignin content (50 %, see Table S4) which resists breakdown more than (hemi)cellulose (Lombardi et al., 2013; Fravolini et al., 2018). The decomposition resistance in spruce litter can be attributed to inhibitory compounds like monoterpenes and polyphenols, which limit microbial activity (Maurer et al., 2008; Hättenschwiler and Vitousek, 2000). Despite its slow degradability, spruce litter has a relatively higher nutrient content compared to deadwood, which likely encourages the ingrowth of decomposers from deadwood, aiding the transfer of C from deadwood to litter.

Studies have indicated that low nutrient availability in deadwood might drive the growth of fungal hyphal networks in search of nutrients within the forest floor, leading to C transfer along a source-to-sink gradient (Hughes and Boddy, 1994). Such nutrient transfer, while generally unidirectional from deadwood to litter, plays a significant role in the ecosystem's nutrient cycling. The impact of substrate quality, both in deadwood and litter, and the resulting dynamics of C transfer are further elaborated in Section 4.2.

4.2. Tree species effect on ^{13}C transfer

The second hypothesis explored whether fungal hyphae transferred more C from beech deadwood to spruce litter compared to spruce deadwood due to its distinct chemical characteristics. This hypothesis was partially validated. While ^{13}C recovery in microbial biomass varied between mesocosms, the ^{13}C recovery in respiration demonstrated consistent differences between the two tree species, suggesting a higher potential for C transfer from beech deadwood to spruce litter. The total ^{13}C transfer of 9.4 % in beech mesocosms (Table 1) indicates efficient cellulose degradation, likely driven by beech's lower phenolic content and favorable elemental stoichiometry, which are conducive to fungal colonization and activity (Kahl et al., 2017; Edelmann et al., 2023).

Research consistently shows that broadleaf woods, like beech, decompose faster than coniferous woods such as spruce, due to differences in chemical properties. Beech deadwood, characterized by lower lignin content and higher concentrations of easily degradable cellulose, fosters stronger fungal biomass and enzyme activity compared to spruce (Noll et al., 2016; Peršoh and Borken, 2017). Our findings align with the literature, where cellulose-rich substrates facilitate faster fungal colonization and degradation processes, resulting in more rapid decomposition (Kögel-Knabner, 2002; Zhou et al., 2007). This accelerated decomposition can lead to more efficient C transfer from deadwood to spruce litter, as observed in the 'with cellulose' treatment.

In our experiment, the addition of ^{13}C-cellulose to deadwood enhanced both cellulolytic and ligninolytic enzyme activities, particularly in beech, which suggests a higher microbial efficiency in degrading added substrates (Table S5). The differential enzyme activity between beech and spruce deadwood underscores the impact of C ratios and other chemical properties on decomposition rates and nutrient dynamics (Tian et al., 2010; Fazhu et al., 2015). These findings emphasize that substrate quality, particularly the balance of lignin, cellulose, and nutrients, is a key driver in the C transfer processes from deadwood to litter.

Additionally, the observed source-to-sink effect, with spruce litter serving as a sink for C from beech deadwood, highlights the interplay between substrate composition and fungal activity. The presence of more recalcitrant compounds in spruce litter likely facilitates this effect, as fungi strive to balance nutrient demands by exploiting the more labile carbon sources in deadwood. For a deeper analysis of the chemical properties influencing these processes, please refer back to Section 4.1.

4.3. ^{13}C transferring fungi

Our third hypothesis proposed that deadwood-decaying fungi would play a key role in C transfer due to their high cellulolytic enzyme activity and the nutrient-poor nature of deadwood. We identified five fungi in the intersection between deadwood and litter (Table S3), with *Clitopilus*, *Kuehneromyces* (Basidiomycota), and *Trichoderma* (Ascomycota) primarily associated with deadwood decay (Jian et al., 2020a; Błaszczyk et al., 2016; Ute and Fritsche, 1997). *Apodus* was found in litter (Xi et al., 2023), and *Mariannaea* was present in both deadwood and litter (Kwaśna et al., 2017; Osono et al., 2004). Among these, *Clitopilus* and *Kuehneromyces*, both belonging to Basidiomycota, were common and likely contributed to the ^{13}C transfer from deadwood to litter. The significant increase in ^{13}C abundance in respiration and microbial biomass further suggests their involvement in C transfer, although there is limited literature explicitly linking these fungi to this process. Basidiomycota demonstrated a higher transfer of ^{13}C-cellulose from deadwood to litter compared to Ascomycota, likely due to their thick hyphae, extensive rhizomorph networks (Caesar-Tonthat et al., 2010), high enzyme activity, and ability to form microaggregates, which enhance nutrient regulation and release into the soil (Caesar-Tonthat, 2002). Hyphal widths for *Clitopilus* ranged from 10 to 30 μm (Jian et al., 2020b), and *Trichoderma* from 2 to 10 μm (Harman and Kubicek, 1998). Additionally, Basidiomycetes prefer lignin degradation in deadwood, while

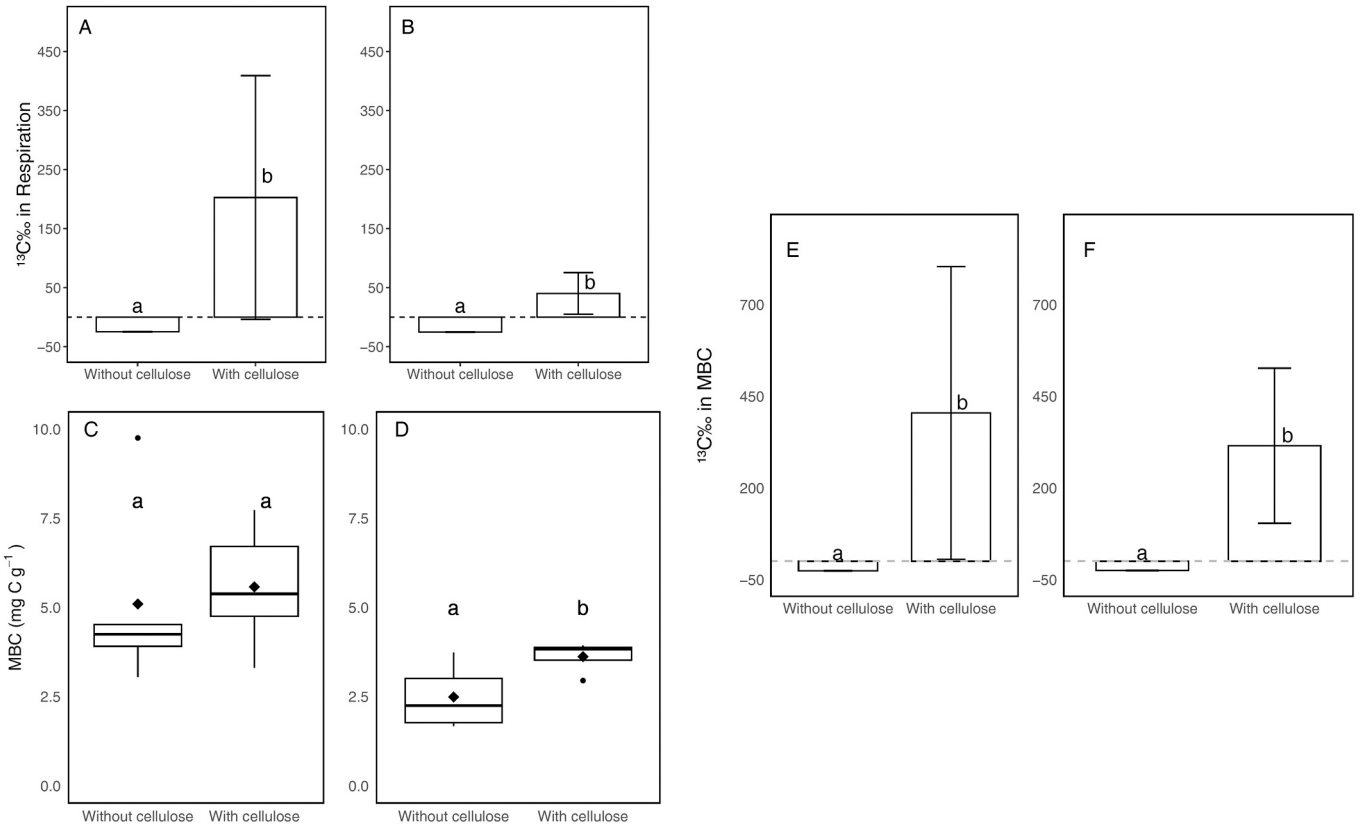

Fig. 4. Without and with cellulose addition treatments for spruce litter under both spruce (panels A, C, and E) and beech (panels B, D, and F) setups. Panels A and B represent ^{13}C‰ in respiration, panels C and D microbial biomass carbon (MBC), and panels E and F ^{13}C‰ abundance in MBC.

Table 1
Mass balance of ^{13}C-cellulose transfer from spruce and beech deadwood to spruce litter was assessed for respiration throughout the incubation period and for microbial biomass (MB) at the end of incubation. Mean (±SE) ^{13}C recovery represents the percentage of used ^{13}C cellulose for respiration and microbial biomass (MB) in spruce litter. Significant differences in ^{13}C recovery between spruce and beech setups are indicated by $P < 0.05$.

^{13}C transfer	Spruce setup	Beech setup	*P* value
Initial ^{13}C-cellulose added (mg ^{13}C)	40.5 ± 0.09	47.3 ± 8.46	
Recovery of ^{13}C-cellulose in respiration (%)	3.88 ± 1.07	7.75 ± 0.98	0.03
Recovery of ^{13}C-cellulose in MB (%)	1.55 ± 1.37	1.66 ± 1.01	n.s.
Total recovery of ^{13}C-cellulose (%)	5.44 ± 2.40	9.41 ± 0.89	n.s.

Ascomycetes mainly degrade on cellulose and holocellulose (Moore et al., 2020). This distinction may offer foundational insights into the ecological roles of deadwood-decaying fungi in C cycling within forest ecosystems.

Certain fungal OTUs have been found in both deadwood and litter habitats, raising the question of their ecological roles and interactions within these environments. The co-existence of fungi known for decaying deadwood and litter may indicate either a natural occurrence across these habitats or a behavior where litter-decaying fungi explore deadwood for nutrients or *vice-versa*. *Apodus deciduus*, a fungus typically associated with litter decay, was identified in conjunction with deadwood-decaying fungi in the intersection, suggesting a potential nutrient exploration in deadwood enriched with ^{13}C-cellulose. This aligns with field observations where straw mass loss correlated with the abundance of a saprotrophic fungus related to *Apodus deciduus*, alongside a network of C-degrading bacteria and other saprotrophic fungi, highlighting intricate ecological inter-kingdom co-occurrence interactions (Xi et al., 2023). Additionally, *Clitopilus baronii*, described from *Quercus cerris* wood, shows a preference for wood decay, although literature on this fungus is limited (Consiglio and Setti, 2019). *Trichoderma spp.*, many of which occur on decaying wood (Schuster and Schmoll, 2010), and *Kuehneromyces mutabilis*, known for its ability to mineralize polycyclic aromatic hydrocarbons in soil, underscore the diverse functional roles fungi play in these ecosystems (Kwaśna et al., 2017). *Mariannaea*, identified in both deadwood and litter, was found in different decay classes of deadwood in a Scots pine stand (Kwaśna et al., 2017) and in decomposing leaves of *Swida controversa* (Osono et al., 2004), further supporting the versatility and adaptive strategies of fungi in exploiting various substrates. These observations suggest a complex interplay between fungal species and their environments, where fungi may naturally occur across both deadwood and litter habitats or exhibit adaptive strategies to explore new nutrient sources. Our experimental setup may have altered and limited the fungal community in the intersection, by not allowing direct contact between the two substrates. In nature, there is often direct contact between deadwood and litter. It can be assumed that a larger number of hyphae-forming fungi can colonize and simultaneously use these distinct resources. However, the higher representation of deadwood-decaying fungi in this intersection reinforces the concept of more prevalent C transfer from deadwood to litter facilitated by fungal hyphae.

5. Conclusions and outlook

In conclusion, our research advances the understanding of the mechanisms behind cellulose-derived C transfer from deadwood to litter through fungal hyphae. This study emphasizes the substantial C transfer facilitated by fungal hyphae from beech and spruce deadwood to spruce litter. In our experiment, we connected deadwood and litter using fungal hyphae that bridged the gap at the intersection between two chambers.

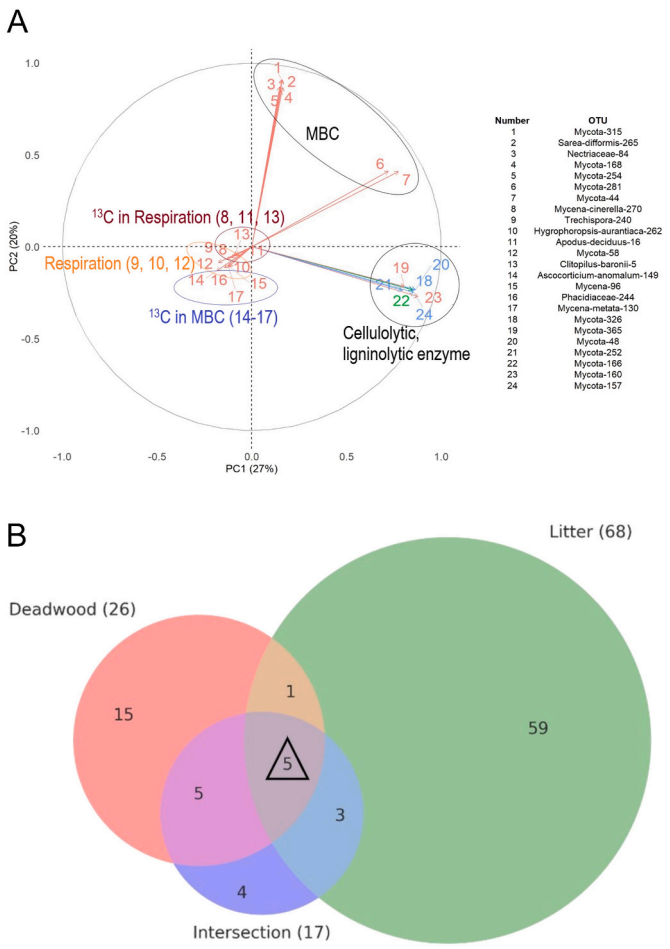

Fig. 5. A: Principal component analysis (PCA) illustrating the relationships between various operational taxonomic units (OTUs) based on microbial biomass carbon (MBC), ^{13}C in MBC, respiration, ^{13}C in respiration, and enzyme activity. Blue color OTUs denote cellulolytic, and green color OTU denote ligninolytic enzyme activities.
B: Venn diagram illustrating the distribution and overlap of Operational Taxonomic Units (OTUs) among 'Deadwood' and 'Litter' for both spruce and beech setups, and 'Intersection' between chamber I and II. Numbers within each section represent the count of unique or shared OTUs between the categories. The triangle highlights the number of OTUs that occur in all three compartments (see Table S3).

Under natural field conditions, the direct contact between these resources could potentially intensify fungal C transfer and enhance the decomposition of both deadwood and litter. Notably, deadwood appears to induce positive priming in the litter layer to acquire nutrients by mineralization of litter.

Looking ahead, it is crucial to explore the impact of different litter types, including those that decompose more quickly like deciduous litter, and various stages of deadwood decomposition for a comprehensive understanding of these processes. Implementing long-term studies that cover the entire spectrum of deadwood decomposition and employing labeled substrates for C transfer rates are essential for deciphering the complex dynamics within hyphal networks. Therefore, this research lays the groundwork for further enhancing our knowledge of C cycling in forest soils.

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CRediT authorship contribution statement

Mohammad Rahmat Ullah: Writing – original draft, Software, Data curation. **Katrin Wegend:** Resources, Investigation, Data curation. **Harald Kellner:** Writing – review & editing, Investigation. **Derek Peršoh:** Writing – review & editing, Investigation. **Werner Borken:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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