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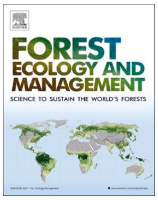

Different effects of continuous-cover and rotation forest management on soil organic carbon stabilization in a boreal Norway spruce forest

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ABSTRACT

Clear-cut-based rotation forest management (RFM) is the dominant silvicultural system in boreal forests. Continuous-cover forestry (CCF), an emerging alternative, operates without clear-cutting. How these silvicultural regimes affect long-term SOC storage and quality remains unclear. This field study examined the effects of CCF and RFM on SOC quantity and stabilization in spruce-dominated forests in central Finland. We sampled (1) recently clear-cut plots, (2) even-aged mature plots (both representing RFM stages), (3) uneven-aged CCF plots, and (4) uncut controls. We analysed SOC stocks, root biomass, condensed tannins (root metabolites) and soil fungal necromass. SOC recalcitrance and accessibility for decomposition were assessed through chemical and physical fractionation and laboratory incubation. ^{13}C and ^{15}N abundances indicated the decomposition stage of soil organic matter (SOM) and contribution of mycorrhizal residues. Uncut forests had marginally higher root biomass than clear-cut and even-aged forests, while uneven-aged forests fell in between. Tannin concentrations were decreased in clear-cut plots. Fungal necromass correlated strongly with SOC but was unaffected by forest management. Contrastingly, greater ^{15}N enrichment in CCF plots suggested higher impact of mycorrhizae in SOM formation. Although soil respiration rate in uncut plots was higher than in managed plots, chemical and physical fractionation analyses showed no treatment effects. While we did not find differences in total SOC stocks between treatments, our results revealed long-term management impacts on SOC quality and stabilization processes, as mycorrhizal fungi appeared to be more involved in SOM formation in uneven-aged plots. This may indicate a greater potential for long-term accumulation of stable SOM.

1. Introduction

Boreal forests account for one third of the global forest carbon (C) stock and thus play an important role in climate change mitigation (Pan et al., 2024, 2011). The majority of C is stored as soil organic carbon (SOC) in boreal forests (Pan et al., 2024) and contributes to the long-term storage of C (Liang et al., 2017). SOC at higher latitudes—where boreal forests are situated—is particularly vulnerable to climate change. This is due to a higher warming rate compared to the rest of the globe (Rantanen et al., 2022) and to an expected stronger response of the microbial communities in colder soils (Davidson and Janssens, 2006; Karhu et al., 2014). As boreal forests are chiefly managed for wood production (Gauthier et al., 2015), there is an urgent need to understand how their SOC stocks are affected by forest management practices. However, the impacts of forest management on C stabilization processes are still poorly understood (Mäkipää et al., 2023).

Plants take up atmospheric C and transport it belowground where it sustains a complex food web and turns into SOC (Prescott and Grayston, 2023). With the removal of trees during harvesting these processes are altered. The two predominant forest management options in boreal forests—rotation forest management (RFM) and continuous cover forestry (CCF)—operate with different harvesting methods and

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intensities and are thus hypothesized to affect the accumulation and stabilization of SOC differently (Roth et al., 2023). CCF comprises a group of silvicultural systems that maintain a continuous forest cover through the application of partial harvesting methods, such as selection cutting, instead of clear-cutting (Brunner et al., 2025). Selection cutting typically leads to multi-layered uneven-aged forest stands (Brunner et al., 2025; Pukkala et al., 2012). RFM commonly includes a final harvest via clear-cutting and several preceding thinnings and leads to even-aged forest stands (Cedergren et al., 2025). There are two different pathways for SOC formation that are likely impacted by the forest management: In the first pathway SOC is formed from chemically more recalcitrant plant litter (Prescott, 2024). Root litter is considered particularly recalcitrant as it is high in lignin and other recalcitrant compounds (Sun et al., 2018). The fragmented but relatively undecomposed plant tissue from root and leaf litter mainly contributes to the particulate organic carbon (POC) pool in the soil (Lavallee et al., 2020). In RFM, this pathway may be enhanced by massive but infrequent litter availability associated with clear-cuts while in CCF frequent cuttings provide smaller but more frequent litter additions. In the second pathway soil microorganisms transform labile C compounds exuded from roots and associated mycorrhizal fungi or labile plant litter to form SOC (Prescott, 2024). Microbial residues or metabolic products mainly contribute to mineral associated carbon (MAOC) (Prescott, 2024; Sokol et al., 2019). This pathway is likely more evenly fed in CCF than in RFM with clear-cuts.

Once entered the soil, C may stabilize through different mechanisms in boreal forests:

I. Soil microbiota take up plant residues and transform them, leaving behind their own necromass or metabolic products, which are not easily decomposable (Liang et al., 2017). The transformation increases the ability of the material to stabilize on mineral surfaces (Lehmann and Kleber, 2015; Liang et al., 2017). Continuous microbial C recycling leads to an accretion of the natural isotopes ^{13}C and ^{15}N in SOM (Clemmensen et al., 2013; Kyaschenko et al., 2019) as these isotopes are discriminated in chemical reactions due to their slightly higher molecular weight (Fry, 2006a).
II. Root-derived secondary metabolites such as condensed tannins inhibit the decomposition of fungal necromass as they form chemically resistant complexes with proteins and chitin from fungal cell walls (Adamczyk et al., 2019b, 2019a).
III. SOC is protected from decomposition by soil minerals, either through physical protection in soil aggregates or stabilization on mineral surfaces through organo-mineral interactions (Lehmann and Kleber, 2015). While organic matter generated through the microbial pathway stabilizes on mineral surfaces resulting in MAOC (Cotrufo et al., 2019, 2015; Lavallee et al., 2020), POC can be physically protected in larger soil aggregates (Lavallee et al., 2020).

The mechanisms are interconnected and stabilize chemically recalcitrant as well as labile SOC in the soil (Lehmann and Kleber, 2015). However, occlusion in aggregates slows decomposition less than mineral association (Lehmann and Kleber, 2015) and thus MAOC tends to persist longer in the soil, whereas POC cycles faster and is more vulnerable to disturbances (Poeplau et al., 2018).

Forest harvesting is an anthropogenic forest disturbance that induces losses from the soil C stock, which can be explained with reduced litter inputs after harvesting and accelerated decomposition processes caused by a warmer and wetter stand microclimate (Mayer et al., 2017, 2020; Roth et al., 2023; James and Harrison, 2016). SOC stocks need several decades to recover to pre-cutting levels after clear-cut harvesting (James and Harrison, 2016; Mayer et al., 2023, 2020). Immediately after harvesting, a high amount of fresh organic material is entering the SOC pool from logging residues and dead roots, which may stimulate mineralization processes and induce priming (James and Harrison, 2016; Vanguelova et al., 2010). At the same time rhizosphere C inputs through root exudates cease (Karhu et al., 2022) which will likely affect the replenishment of persistent MAOC through the microbial pathway (Prescott, 2024). In boreal forests about 50–70 % of C inputs to the soil derive from roots and root-associated microorganisms (Baldrian, 2017; Clemmensen et al., 2013). Clear-cut harvesting was found to disturb the belowground fungal and microbial communities (Kim et al., 2021; Kohout et al., 2018; Prescott and Grayston, 2023; Tomao et al., 2020). We found in an earlier study that clear-cutting altered the fungal community composition and decreased the abundance of ectomycorrhizal fungi on this study site (Roth et al., 2025). Accordingly, fungal necromass may decline through harvesting disturbance (Chen et al., 2025). Retaining a certain number of living tress and roots to sustain the belowground ecosystem may mitigate post-harvest SOC losses (Prescott and Grayston, 2023) and several studies found a reduced or shortened impact on SOC of partial harvesting (Mayer et al., 2020; Pötzelsberger and Hasenauer, 2015; Strukelj et al., 2015). CCF stands furthermore usually show a higher tree species diversity than mature even-aged stands (Pukkala et al., 2012) and a complementary root growth of different species (niche partitioning) may lead to higher root density (Liu et al., 2021). Hence, CCF has been suggested to protect the SOC storage. Yet, RFM is the prevailing silvicultural system in boreal forests, with CCF previously being legislatively discouraged in Nordic countries such as Finland and Sweden (Brunner et al., 2025; Eyvindson et al., 2021). Thus, empirical studies of CCF are still sparse.

Our study aimed to assess the long-term effects of CCF and RFM on SOC stocks and stability in boreal forests. We sampled clear-cuts and even-aged mature stands (both representing RFM), uneven-aged CCF plots, and an uncut control. We expected the SOC dynamics in CCF forests would be more similar to uncut forest plots rather than RFM forests, given that harvesting disturbances are decreased in CCF and thus the stand microclimate is less affected. Specifically, we hypothesized that:

(1) Structural complexity in uneven-aged CCF plots and high stand density in uncut plots lead to higher amounts of living tree roots compared to RFM plots, especially in clear-cut plots. This would lead to higher amounts of root derived tannins and higher share of POC in uncut and CCF plots.
(2) The expected higher root biomass leads to a higher share of chemically recalcitrant SOC in CCF and uncut plots, which can be seen in the organic layer and POC fraction in the mineral soil.
(3) Higher stand density and less disturbance of the fungal community lead to increased fungal necromass in CCF and uncut forests compared to clear-cuts of RFM forests.
(4) A higher contribution of ectomycorrhizal residues to SOC pool in CCF and uncut plots would be shown as higher δ^{15}N values, as these fungi tend to enrich SOM with ^{15}N when they are contributing to the soil N cycle.

2. Material and methods

2.1. Research site

The forest site featured in this study is part of a long-term silvicultural experiment by Natural Resources Institute Finland (Luke) to study different harvesting methods and intensities (Lähde et al., 2001; Pukkala et al., 2016). It is located in Vessari, central Finland (62°2′9″N, 24°16′0″E) on an elevation of about 110 m above sea level (Geological Survey of Finland, 2023). The site is a mesic and comparatively fertile *Oxalis-Myrtillus* site type according to Cajander (1926) classification. We identified the soil type as a skeletic albic podzol (IUSS Working Group, 2022) formed on glacial till, soil texture is a sandy loam and humus type is a mor. Thus, the soil is characterized by organic material accumulating on the forest floor as a purely organic soil layer formed on top of the mineral soil. The annual mean temperature ranges between 4 and 5° C and annual mean precipitation between 600 and 650 mm (Finnish Meteorological Institute, 2023, reference period 1991–2020). The coldest month in this region is February with a mean temperature of −6 ° C and the warmest month is July with a mean of 17° C (Climate & Weather Averages in Orivesi, Finland, 2025).

The Norway spruce (*Picea abies* (L.) Karst.) dominated forests are admixed with Birch (*Betula spec*.), Scots pine (*Pinus sylvestris* L.), Rowan (*Sorbus aucuparia* L.) and Poplar (*Populus tremula* L.). The forests originated in the 1940s from natural regeneration after shelterwood cutting. In our study we included mature even-aged plots and post clear-cut plots (as the pre- and post-cutting stages in RFM respectively), uneven-aged plots (representing CCF), and uncut plots. The experimental site covers about 16 ha, the individual plots are 50 × 50 m in size, and we included 4 replicates of each treatment. The uneven-aged and even-aged structures were established in winter 1985/86 with single-tree selection cuts and low thinning, respectively. Thinning and selection cuts were repeated in 1994, 2002 and 2009 as described in Roth et al. (2025). Clear-cutting was conducted in 2009, plots were then partly replanted with Norway spruce saplings and naturally colonized by *Betula spp*. Clear-cuts where thus 11 years old when we sampled. For simplicity they will henceforth be referred to as clear-cuts to distinguish them from the plots that have not experienced clear-cutting. Uncut plots, even-aged plots and old trees in uneven-aged plots were about 85 years old.

2.2. *Soil sampling and stand inventory*

We sampled the soil every 4 m in a systematic sample grid of 16 × 16 m (n = 25) according to the sampling layout depicted in Fig. 1a. The organic layer was sampled with a stainless-steel soil auger with an inner diameter of 6 cm and the mineral soil was sampled with a slimmer auger with a diameter of 1.9 cm to depth of 10 cm, measured from the beginning of the mineral soil (Fig. 1b). Sampling deeper mineral soil layers was not possible due to the stoniness of the soil. We pooled the samples to one composite sample per plot for organic layer and mineral soil respectively. To assess the effects of the management system on the root biomass we additionally took three root core samples (at the northern and southern point of the sample grid and in the centre) in each treatment plot with a 6 cm diameter soil corer.

We measured the stand parameters stem density, diameter at breast height (DBH), dominant tree height (DTH), and basal area (BA) on each plot as described in Roth et al. (2025). We recorded tree species and identity (broadleaved or coniferous) for each tree. The structural complexity of the stand was assessed through the coefficient of variation of the DBH, and the Shannon index was calculated as an indicator for tree species diversity. We visually assessed the ground coverage of different functional groups (dwarf shrubs, herbs, grasses, bryophytes and lichen) on 4 squares covering 2 m^2 each, along a north-south oriented transect using a method modified after in Reinikainen and Nousiainen (1995).

2.3. *Soil analyses*

2.3.1. *Basic soil analyses*

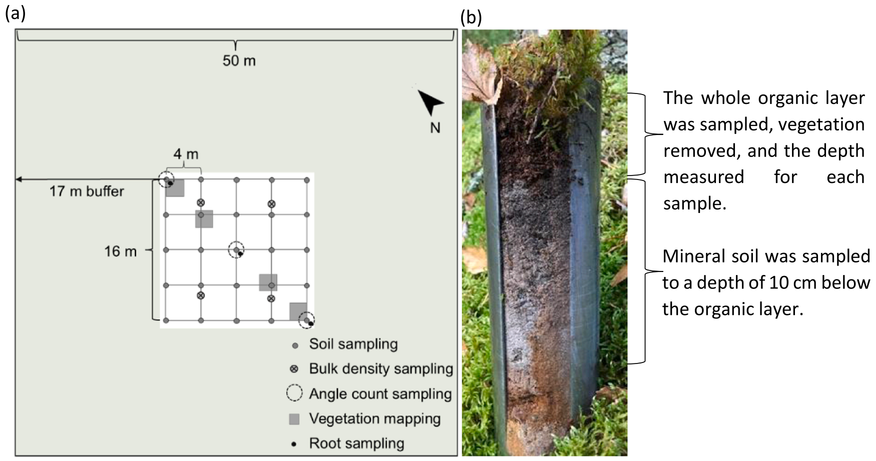
To characterize the site conditions, we analysed the bulk soil samples for soil texture and soil pH. The analyses were conducted as described in Roth et al. (2023). To estimate indirect effects of the forest management on decomposition and stabilization processes, we recorded soil moisture and temperature in the field (Wild et al., 2019). One logger was installed in the centre of each sampling grid (replicate plot) and data was recorded every 15 min. Soil temperature was measured in a depth of about 8 cm (from the soil surface) and soil moisture was recorded down to a depth of approximately 14 cm. To evaluate the management effects on SOC, we determined soil C content, organic soil layer thickness and bulk density for both organic and mineral soil layers (Supplementary table S1) and calculated soil C stocks based on these factors as described in Roth et al. (2023). Stoniness was not considered in the calculation of SOC stocks due to very high variability. We present the SOC stocks for the mineral soil calculated for the fine earth fraction of the soil.

2.3.2. *Roots*

Roots of two soil cores per plot were handpicked from the soil, washed with water and oven-dried at 65° C to constant weight and then weighed to determine root biomass. The roots of one core per plot were furthermore sorted prior to drying into four classes: tree fine roots (<2 mm), tree coarse roots (>2 mm), dead roots and understorey roots. Subsequently we measured the C content of the dried roots with Leco CN828 analyser (LECO Corporation, St. Joseph, MI, USA).

2.3.3. *Condensed tannins*

We analysed the concentration of condensed tannins with a modified acid-butanol assay as previously described by Smolander et al. (2005). We used about 150 mg of organic and 500 mg of mineral soil. After an HCL-catalyzed depolymerisation of condensed tannins in butanol (1-butanol:HCL, 95:5 v/v) for 2 h at 95 °C, the concentration of condensed tannins was determined with a spectrophotometer



The whole organic layer was sampled, vegetation removed, and the depth measured for each sample.

Mineral soil was sampled to a depth of 10 cm below the organic layer.

Fig. 1. a) Sampling layout in each treatment plot. Temperature loggers were positioned at the central point of the sampling grid. The green area indicates the buffer area around each sampling grid. The arrow on the plan indicates the direction of North. b) A freshly extracted soil sample showing the typical diagnostic horizons of a podzol. We sampled the organic topsoil layer and the underlaying mineral soil to a depth of 10 cm, measured from the surface of the mineral soil. The mineral soil was sampled with a thinner corer than shown in the figure.

(PerkinElmer Lambda 12, UV/VIS Spectrometer, Germany). The standard curves were determined from condensed tannins extracted and purified from Norway spruce needles (Adamczyk et al., 2013).

2.3.4. Particulate organic carbon and Mineral associated organic carbon

To draw conclusions regarding the stabilization of SOC we separated the organic matter stored in the mineral soil into particulate organic carbon (POC) and mineral associated organic carbon (MAOC), separating first by size and then by density (Cotrufo et al., 2019; Lavallee et al., 2020). Dried and sieved fine earth fractions of the soil were first shaken with water and glass beads overnight to disperse larger aggregates and then wet-sieved through a 0.63 μm sieve as MAOC is associated with silt and clay minerals. To separate the DOC dissolved in the fractionation process from the MAOC, the dispersion was filtered through 0.45 μm membrane disc filters (Pall Corporation, Supor® PES), and MAOC was collected from top of the filter and dried at 40° C for 48 h. The coarser fraction remaining on top of the 0.63 μm sieve, was separated by density fractionation into a light fraction floating on top of sodium polytungstate solution with a density of 1.85 g cm^{-3} and the heavy fraction sinking to the bottom of the liquid (Plante et al., 2006). After rinsing the fractions free of SPT they were dried at 40° C for 48 h. Hereafter we call the light fraction POC, and the heavy fraction "heavy POC" according to Lavallee et al. (2020). After drying, the different fractions were milled with a mortar grinder and analysed for C content with LECO CN828 analyser (LECO Corporation, St. Joseph, MI, USA).

2.3.5. SOC quality and degradability

To determine the quality of the SOC we separated fractions of different recalcitrance from organic soil layer samples and from the POC fraction with sequential chemical fractionation, first extracting nonpolar extractives with dichloromethane, followed by a hot water extraction to dissolve polar extractives and followed by acid hydrolysis with sulphuric acid (Hilasvuori et al., 2013; Roth et al., 2023; Wieder and Starr, 1998). The remaining acid-insoluble residue is considered biochemically recalcitrant. To assess the degradability of SOC we measured the soil respiration from the bulk soil under standardized conditions in a lab-experiment as described in Roth et al. (2023). To determine microbial biomass carbon (MBC) as a driver of C turnover we performed chloroform ($CHCl_3$) fumigation extraction following the method by Vance et al. (1987) as modified by Blagodatskaya et al. (2014).

2.3.6. Isotopes

As indicators for the degree of decomposition of SOM we determined the natural abundance of the isotopes ^{13}C and ^{15}N. Our samples were analysed at the Centre for Stable Isotope Research and Analysis, Georg August University Göttingen, Germany. Organic and mineral bulk soil samples and POC samples were freeze-dried, finely ground, and homogenized prior to the analysis with an isotope ratio mass spectrometer (Delta XP Thermo-Electron, Bremen Germany) alongside an elemental analyser (Flash EA 1112, Thermo-Electron, Rodano, Milano, Italy) as described by Werner et al. (1999). Acetanilide was used as standard. Delta values $\delta^{13}C$ and $\delta^{15}N$ values (in ‰) were calculated as the ratio of the relative abundance against international standard reference values for Belemnite from the PeeDee formation (V-PDB)($\delta^{13}C$) and atmospheric nitrogen (for $\delta^{15}N$) as described in Fry (2006b).

2.3.7. Amino sugars

To quantify the contribution of fungal and bacterial necromass to SOC we analysed the amino sugars in the soil following a protocol by Zhang and Amelung (1996). A detailed method description can be found from Meyer et al., (2023). We considered glucosamine (GlcN) (corrected for the contribution of bacterial glucosamine) as an indicator for fungal necromass and muramic acid (MurN) as indicator for bacterial necromass (Joergensen, 2018). We calculated fungal necromass C with Eq. (1) (Appuhn and Joergensen, 2006; Faust et al., 2017), subtracting bacterial GlcN from total GlcN based on the assumption that MurN and GlcN occur at a 1:2 molar ratio in bacteria (Engelking et al., 2007). In the formula 179.17 equals the molar mass of GlcN, whereas 251.23 is the molar mass of MurN and 9 is a conversion factor from fungal GlcN to fungal necromass C.

$$\mu g \text{ fungal C g}^{-1}\text{soil} = (((\mu g \text{ GlcN g}^{-1}\text{soil}/179.17) - (2 \times \mu g \text{ MurN g}^{-1}\text{soil}/251.23)) \times 179.17) \times 9 \tag{1}$$

2.4. Data analysis

We conducted all statistical analyses in R version 4.2.0 (R Core Team, 2022). The effects of the forest management treatments on different SOC stability pools or stand parameters were determined with parametric one-way analysis of variance (ANOVA) after checking the data for normal distribution with Shapiro-Wilk test and checking the homogeneity of variances with Levene's test. After ANOVA we compared the treatments pairwise with Tukey's post-hoc test. If the data did not fulfil requirement of normality or equality of variances for parametric testing, we used non-parametric Kruskal-Wallis ANOVA followed by Mann-Whitney U post-hoc test with Bonferroni correction. Comparisons between chemical fractions in organic layer and POC were made with paired samples T-test (when the differences between grouped values were normally distributed) and with Wilcoxon signed rank test on paired samples (in case the differences were not normally distributed).

We tested for Pearson's correlation between the variables in our dataset with the rcorr function of the Hmisc package (Harrell, 2024). We visualized the correlation matrix by means of the corrplot package (Wei and Simko, 2021). Selected correlations were furthermore explored with simple linear regression analysis.

We assessed the impact of the forest management treatment on soil temperature and soil moisture throughout one year separately for each month with linear mixed effect models based on calculated daily means with treatment set as fixed effect and plot and date set as random effect. Furthermore, we used linear mixed effect models to assess the treatment effect on the ground coverage of understorey plants, with treatment set as fixed effect and plot as random effect. Proportional response variables were logit transformed before the analyses (Warton and Hui, 2011). Residuals of linear models were visually assessed for normal distribution with diagnostic plots.

3. Results

3.1. Microclimate

The forest management treatment affected the soil temperature (Supplementary Fig. S1, Fig. S2). From May until September the soil temperature was higher in clear-cut plots, whereas from October till January, it was lower, due to missing protective canopy cover (Table S2). However, soil temperature was not related to SOC stability variables in the organic layer (Fig. S5). The soil moisture was mainly unaffected by the treatment, only in October the uncut treatment showed lower soil moisture content than the clear-cut treatment (Fig. S3, Table S3).

3.2. Roots, root-derived tannins, SOC, POC and MAOC

We found more total root biomass per m^2 in uncut plots (1389 ± SD 684 g m^{-2}) than in clear-cut and even-aged mature plots (839 ± SD 450 g m^{-2} and 815 ± SD 170 g m^{-2} respectively), with a significance of $p < 0.1$. Uneven-aged plots were intermediate between uncut plots and the other two treatments (Fig. 2a). Uncut plots featured higher amounts of dead roots compared to even-aged mature plots and higher amounts of coarse tree roots compared to clear-cut plots. Uneven-aged plots also showed higher amounts of coarse roots compared to clear-cuts (Fig. 2a).

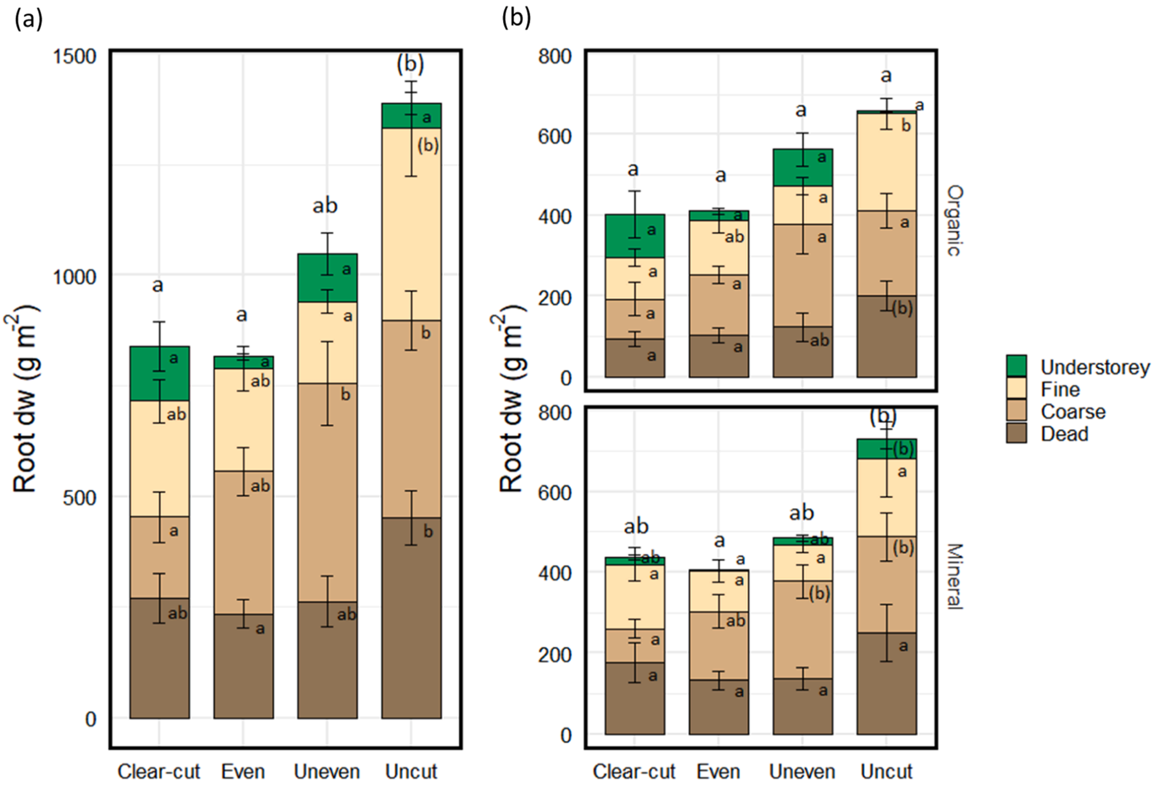


Fig. 2. (a) Root biomass in g dry weight m^{-2} of the different root types: understorey roots, fine tree roots, coarse tree roots and dead roots for all the data and (b) listed separately for organic and mineral soil for the four treatments: clear-cut, even-aged, uneven-aged and uncut. Note: Error bars depict the standard error of the mean. Statistical differences between treatments are indicated by different letters ($p < 0.05$). Letters displayed inside the bars indicate differences between the proportions of different root types. Letters on top of error bars indicate differences in the total root biomass. Letters in brackets indicate marginal differences with $p < 0.1$. We determined statistical differences with ANOVA followed by Tukey's post-hoc test.

The tree fine root biomass differed between treatments in the organic layer: more fine roots were found in uncut plots than in clear-cut and uneven-aged plots and marginally more than in even-aged mature plots (Fig. 2b). Differences between understorey root biomass found in the different treatments were not significant (Fig. 2a), and not related to stand structural variables (Fig. S5 and S6), even though the ground coverage of understorey vegetation was significantly less in dense uncut plots (Supplementary tables S4 and S5).

Stand structural variables had a significant effect on root biomass. We found a positive relationship between tree density and total root biomass and dead roots biomass (Fig. 3a and b). Tree fine root biomass increased with increasing tree density (Fig. 3c.) and with increasing stand basal area (Fig. 3e) in the organic layer. Total root biomass in both layers combined also increased with increasing stand basal area (Fig. 3d). Increasing tree species Shannon diversity led to an increase in coarse root biomass (Fig. 3f). We did not find a significant relationship between the coefficient of variation of the DBH (as a measure of stand complexity) with root biomass (data not shown).

We found an effect of the treatments on condensed tannins in the soil. There were significantly less condensed tannins in the organic layer of clear-cut plots than the other treatments (Fig. 4a). In the mineral soil the occurrence of tannins showed a similar pattern to the total root biomass, however without statistical differences between treatments (Fig. 4b). The amount of condensed tannins in the soil correlated positively with the stand variables basal area, dominant tree height and diameter at breast height in the organic soil layer (Fig. S5) and with fungal necromass and total root biomass in the mineral soil (Fig. S6).

The SOC contents were similar in all treatments, ranging between 34.5 % (uneven-aged) and 39.9 % (uncut) in the organic layer and between 2.26 % (clear-cut) and 3.15 % (even-aged) in the mineral soil. Similarly to SOC content, C stocks did not differ between treatments (Table 1).

The forest soils under the different management treatments stored about 56 % of their total SOC (in mineral soil) in MAOC, about 36 % as POC, and about 8 % as heavy POC (Fig. 5a). In clear-cuts a lower share of SOC was allocated to POC compared to the other treatments, and highest share of POC was found in the uncut treatments, however, these differences were not statistically significant. Accordingly, the percentage of MAOC was highest in clear-cuts and lowest in uncut plots (without statistical significance) with the two other treatments ranging in between (Fig. 5a). A similar pattern was displayed in absolute amounts in g C kg^{-1} dry soil (Fig. 5b, Table 1). MAOC correlated with the clay and silt content of the soil, and with soil moisture (Fig. S6). POC showed a positive correlation with fungal necromass in the soil (Fig. S6).

3.3. *Chemical recalcitrance and degradability of SOC*

3.3.1. *Chemical fractionation*

The organic layer showed higher amounts of the non-extractable fraction than POC samples ($p = 0.0039$, T-test, $n = 15$) and less of the polar fraction ($p = 5.191e\text{-}07$, T-test, $n = 15$). The differences in the chemical fractionation results between the treatments were neither significant in the organic layer, nor in the POC (Fig. 6a and b). There was a positive correlation between fraction A of POC and soil temperature (Fig. S6).

3.3.2. *Respiration during laboratory incubation*

The cumulative respiration from the organic soil samples in standard laboratory conditions (normalised per soil C content) was higher from uncut sites than the other treatments (Fig. 7). Mineral soil samples from the clear-cut samples appeared to have respired less than the mineral soils from other treatments, though the difference was not statistically

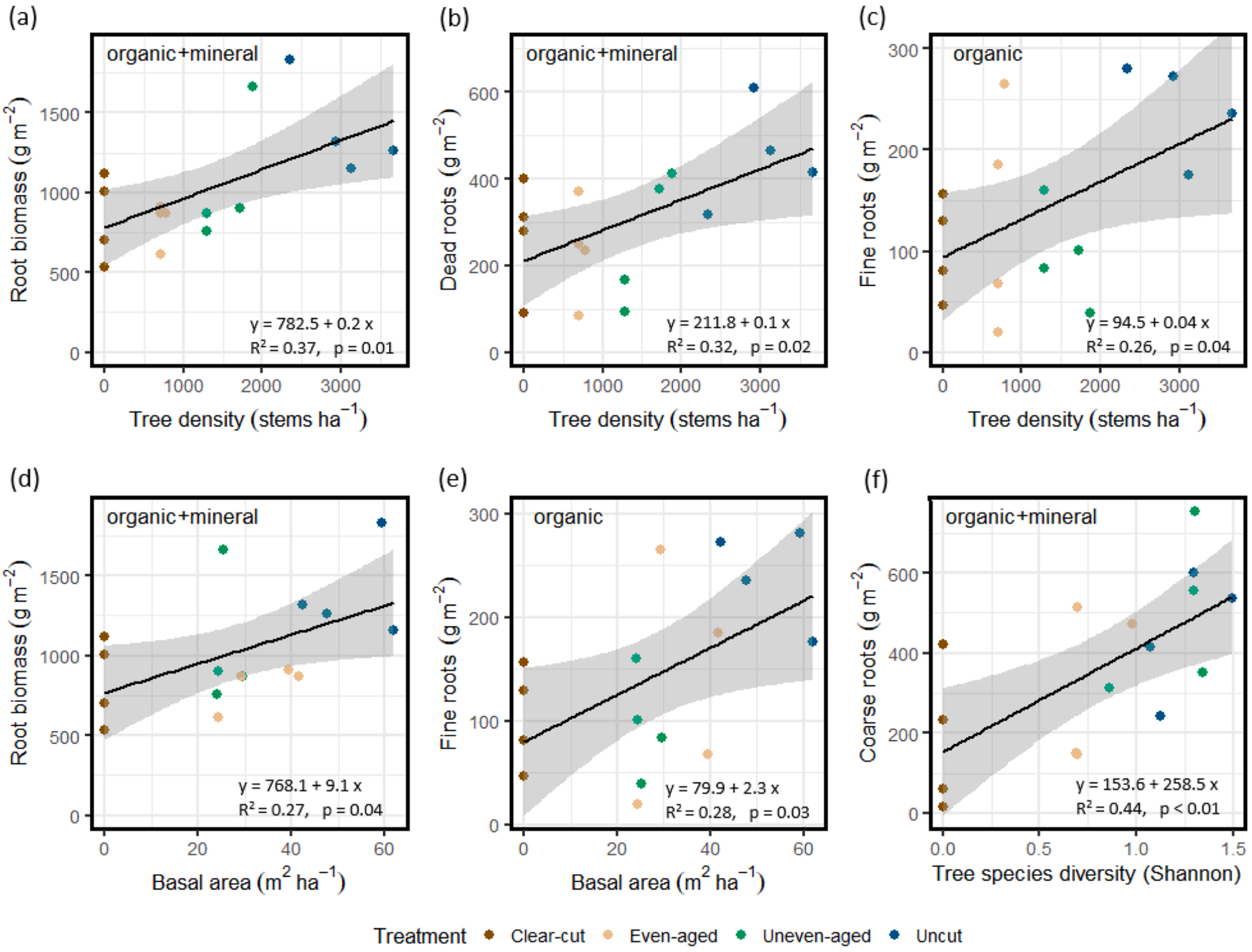


Fig. 3. Linear relationships between stand structural variables and root biomass given for tree density and sum of all roots (a), tree density and dead roots (b) and tree density and fine roots in the O-layer (c) and for basal area and all roots (d), basal area and fine roots in the organic layer (e) and for coarse roots and Shannon diversity of tree species.

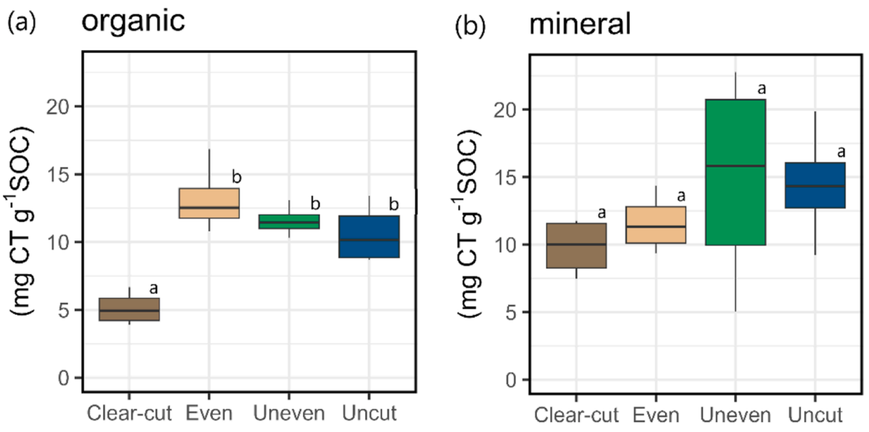


Fig. 4. Amount of condensed tannins (CT) in mg g^{-1} SOC for (a) organic and (b) mineral soil layer. Different lowercase letters indicate statistical differences between treatments. The central line of the boxplots shows the median of the data, the box depicts the values within the 25 % and 75 % quantile. The whiskers represent the 1.5 interquartile range (1.5 IQR) value.

significant. The cumulative respiration measured in the organic layer correlated positively with the amount of tree fine roots and with the fungal necromass in the organic soil (Pearsonś correlation coefficient r = 0.68 and 0.53 respectively, $p < 0.05$, n = 16) and the stand variables tree density and basal area (Fig S.5). In the mineral soil it correlated strongly with the proportion of POC, the concentration of condensed tannins and with the amount of fungal necromass (Corr.Coef. = 0.95, 0.76 and 0.9 respectively, $p < 0.05$, n = 16, Fig. S6).

Table 1

Soil organic carbon (SOC) content in percent of soil dry weight (± standard deviation), soil C stocks (in g m^{-2}) and Carbon-to-Nitrogen ration (C:N) in organic soil layer and mineral soil and combined C stocks for both layers. For mineral soil the SOC was furthermore separated into particulate organic carbon (POC, light and heavy) and mineral associated organic carbon (MAOC) (both given as percentage of soil dry weight). Differences between SOC and the sum of POC and MAOC are caused by the inaccuracy of the method of separating POC and MAOC in the laboratory. Statistical differences between treatments are indicated with different lowercase letters.

	Clear-cut		SD		Even-aged		SD		Uneven-aged		SD		Uncut		SD	
Organic layer																
SOC (% of soil dw)	37.59	±	4.33	a	39.74	±	3.94	a	34.50	±	5.96	a	39.9	±	1.82	a
C:N-ratio	28.69	±	1.08	a	32.58	±	1.91	b	29.49	±	2.23	ab	29.23	±	1.15	ab
SOC stock (g m^{-2})	1 693.63	±	486.11	a	2 071.15	±	655.40	a	1 669.72	±	594.20	a	1 644.67	±	212.30	a
Mineral soil																
SOC (% of soil dw)	2.26	±	1.17	a	3.15	±	1.69	a	2.63	±	1.26	a	2.54	±	0.34	a
C:N-ratio	27.86	±	1.86	a	29.00	±	1.19	a	26.66	±	2.02	a	28.35	±	1.35	a
SOC stock (g m^{-2})	2 227.20	±	986.73	a	2 425.79	±	892.40	a	2 228.41	±	985.80	a	2 055.23	±	371.30	a
POC (% of soil dw)	0.79	±	0.33	a	1.15	±	0.33	a	1.44	±	1.01	a	1.34	±	0.62	a
MAOC (% of soil dw)	1.72	±	0.87	a	1.44	±	0.51	a	1.32	±	0.22	a	1.15	±	0.39	a
Combined C stock (g m^{-2})	3 920.83	±	1428.81	a	4 496.93	±	823.30	a	3 898.13	±	1158.00	a	3 699.90	±	296.30	a

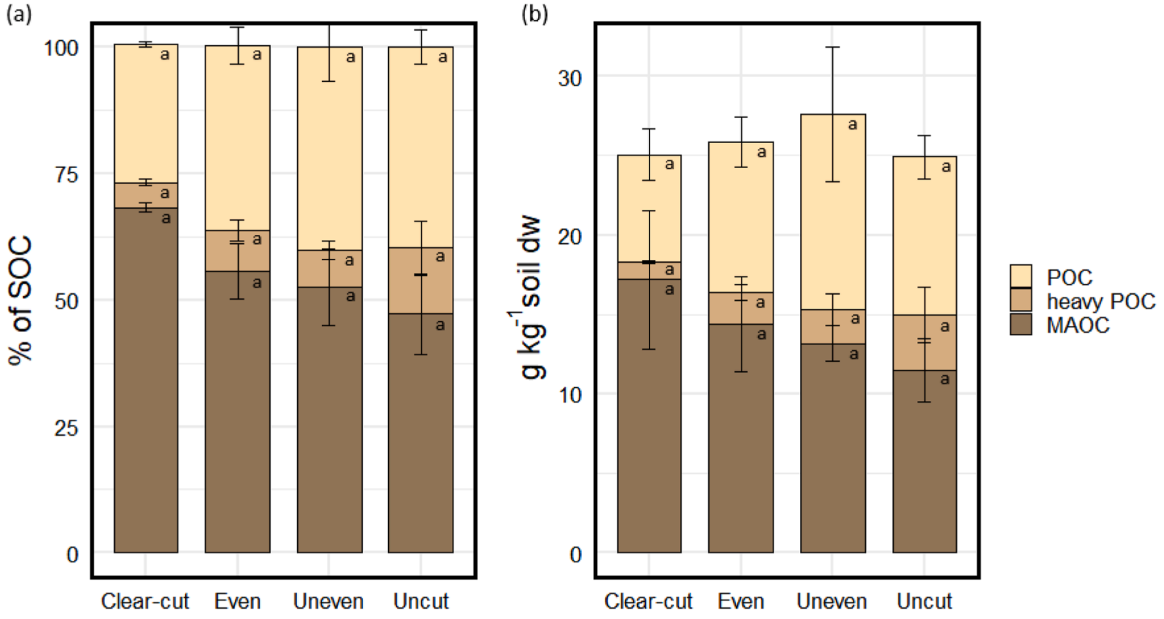


Fig. 5. (a) Percentage of SOC in mineral soil stored in light particulate organic matter (POC), heavy POC and mineral associated organic matter (MAOC) in the four different treatments. Dissolved organic carbon (DOC) was not evaluated and is not included in any of the fractions. (b) POC, heavy POC and MAOC in g kg^{-1} bulk soil (dry weight). Note: Error bars show the standard error of the mean. Different lowercase letters indicate statistical differences between treatments.

3.4. Fungal necromass pool and isotopic composition of the different SOC pools

The fungal necromass C ranged between 51 and 91 g kg^{-1} dry soil in the organic layer and between 1.8 and 7.5 g kg^{-1} in the mineral soil (Fig. 8a and b), i.e. that the fungal necromass accounted for about 18.2 % (±2.6 % SD) of the SOC in the organic soil layer and for about 13.8 % (±2.5 % SD) in the mineral soil (Fig. 8c and d). The amounts of amino sugars in the soil showed a significant positive linear relationship with the total SOC also in the organic layer, but particularly in the mineral soil (Fig. 8e and f, $R^2 = 0.31$ and 0.87 respectively). Furthermore, we observed a close positive linear relationship between POC and fungal necromass in the soil (Fig. 8g, $R^2 = 0.8$). We could not detect a significant impact of the forest management treatment on the amount of fungal necromass or the contribution of fungal necromass to total SOC (Fig. 8a-d). In the organic layer it correlated positively with the soil moisture and in the mineral soil it correlated negatively with the soil pH (Fig. S5 and S6). Living microbial biomass C was also not affected by the management treatment (Fig. S4).

The ^{13}C and ^{15}N signature were significantly different between the different SOC pools (organic topsoil, POC and MAOC), and significantly affected by the forest management treatment. The natural abundance of ^{15}N and ^{13}C increased with soil depth from organic layer to mineral soil, where the isotopes accumulate in POC and MAOC (Fig. 9a and b). The more stabilized MAOC furthermore shows higher δ^{15}N and δ^{13}C values than the more labile POC.

The organic layer material was depleted in ^{15}N by about 2.4 ‰ compared to the POC, and POC has an about 1.8 ‰ lower δ^{15}N value than the MAOC. The organic layer in the uneven-aged plots was significantly (1.32–1.55 ‰) enriched in δ^{15}N compared to the organic layer of other treatments (Fig. 9b). In the POC the ^{15}N signature was 0.86 ‰ higher in uneven-aged plots than clear-cuts but did not differ from the other treatments. There was no significant correlation between fungal necromass and δ^{15}N in the organic layer. However, δ^{15}N in the MAOC correlated with the abundance of ectomycorrhizal fungi, with basal area and with diameter at breast height (Fig. S6). The δ^{15}N value in POC correlated strongly with fungal necromass in the soil and relative abundance of ectomycorrhizal fungi, and with the stand variables dominant tree height and diameter at breast height (Fig. S6).

The δ^{13}C value increased about 0.6 ‰ between organic layer

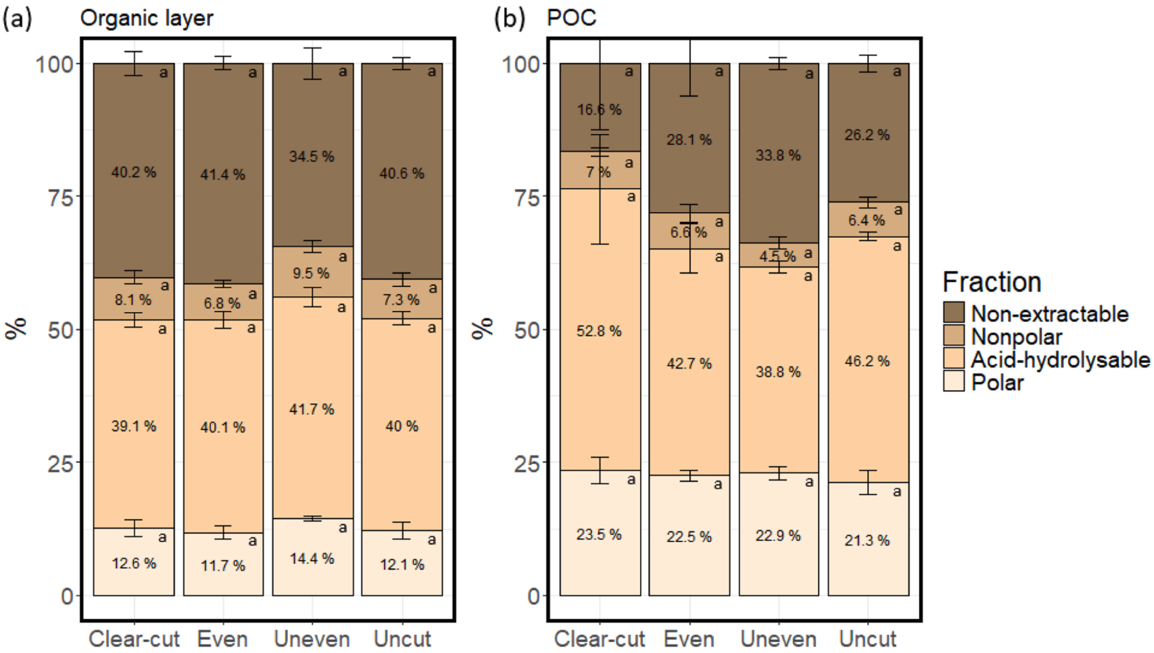


Fig. 6. Fractions of different biochemical recalcitrance in (a) organic layer and (b) POC, inspected by sequential chemical fractionation. Polar extractives were extracted with hot H_2O, acid-hydrolysable extractives with sulphuric acid, nonploar extractives with dichloromethane. The remaining fraction is considered non-extractable. Recalcitrance of fractions increases with the darkness of the brown color: the darker the color, the more recalcitrant the fraction. Note: Error bars show the standard error of the mean. Different lowercase letters indicate statistical differences between treatments.

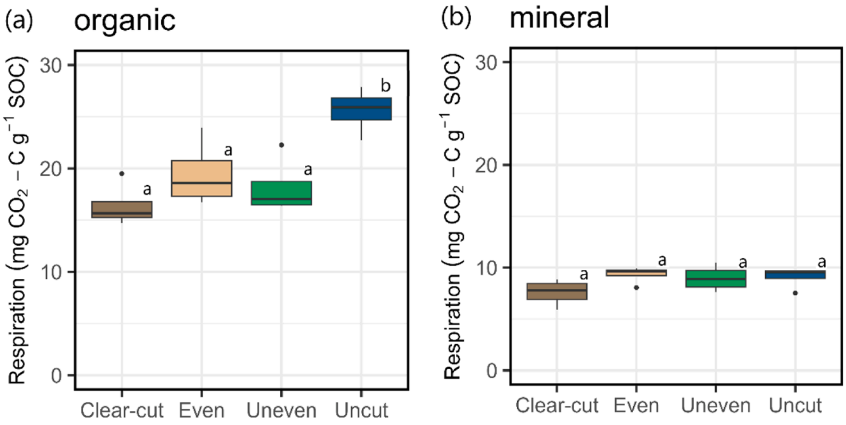


Fig. 7. Cumulative respiration during laboratory incubation in mg CO_2-C g^{-1} SOC for (a) organic layer samples and (b) mineral soil samples.

material and POC. The value furthermore increases about 0.5 ‰ when transformed from POC to MAOC (Fig. 9a). In organic layer there were no differences between management treatments. In POC the isotopic $\delta^{13}C$ signature in clear-cuts was significantly 0.68 ‰ lower than in even-aged plots and in MAOC it was significantly lower than uncut and even-aged plots (0.64 ‰ and 0.68 ‰ respectively). The $\delta^{13}C$ in the organic layer correlated positively with the amount of condensed tannins, with abundance of ectomycorrhizal fungi and with stand variables (basal area, dominant tree height and diameter at breast height) (Supplementary Fig. S5). In the MAOC $\delta^{13}C$ showed a positive correlation with the relative abundance of ectomycorrhizal fungi and with stand related variables and a negative correlation with the amount of MAOC in the mineral soil (Fig. S6).

4. Discussion

To advance our understanding of forest management effects on soil C dynamics, we studied long-term experimental plots with uneven-aged CCF, even-aged RFM and uncut plots and explored biological, physiochemical and isotopic indicators of SOC stability as affected by these management practices. We expected that the forest management treatment would alter stabilization processes through the presence or absence of roots and the resulting effect on root-associated fungi. Our results showed that the choice of silvicultural practice affects C stabilization processes in the soil. Our study revealed that uneven-aged CCF and even-aged RFM affect SOC stabilization processes in the soil as shown by isotopic indicators and soil respiration. However, not all the studied C pools showed a response to the forest management practice.

4.1. Forest management effects on roots, root-derived tannins and SOC stabilization in POC and MAOC

First, we hypothesised that the structural complexity in uneven-aged CCF plots and high stand density in uncut plots would lead to higher amounts of living tree roots compared to RFM plots, especially clear-cut plots. This would result in higher amounts of root derived tannins and

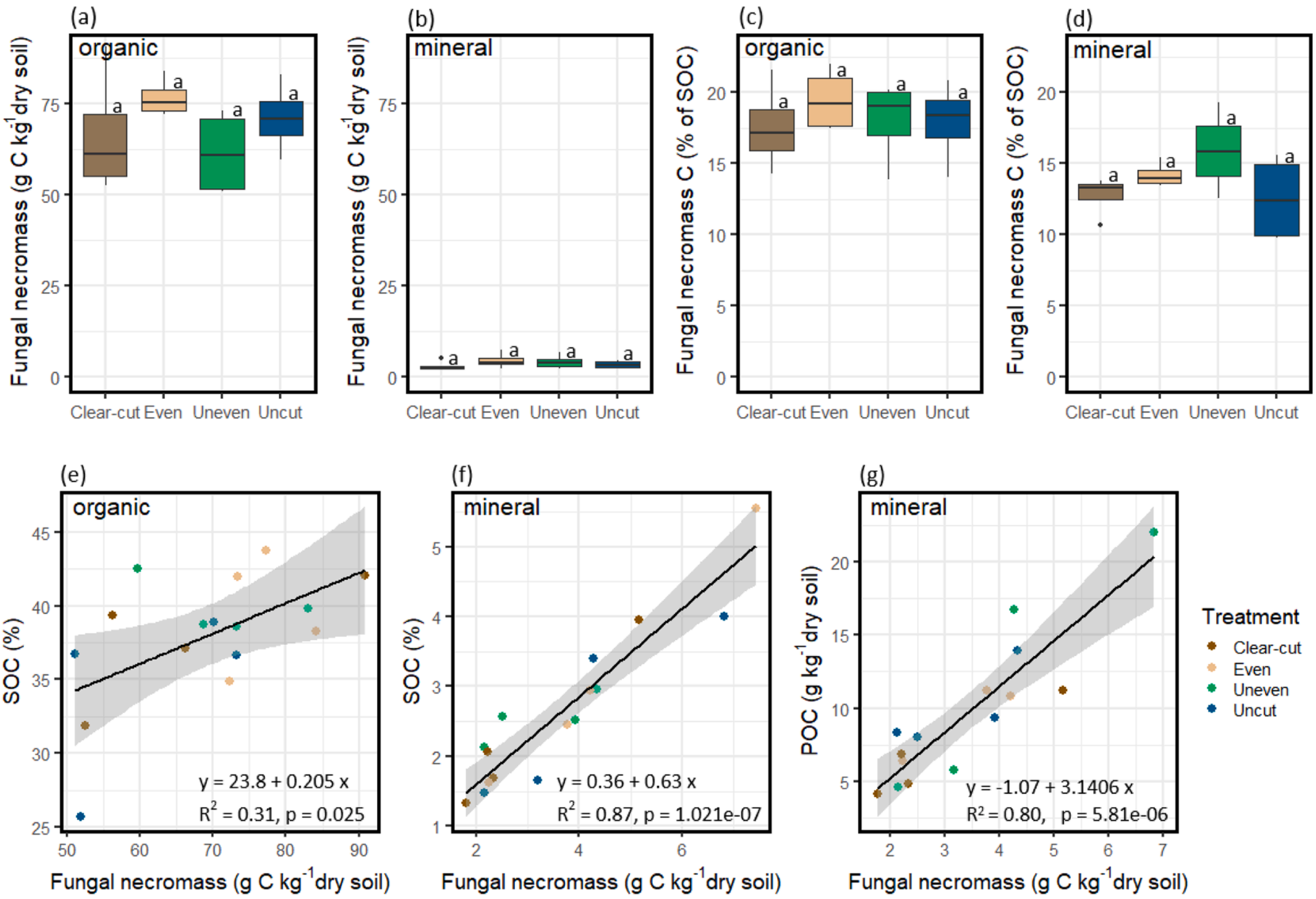


Fig. 8. Fungal necromass C in g kg^{-1} dry soil in (a) organic and (b) mineral soil layer and as proportion of the total SOC in (c) organic and (d) mineral soil. Different lowercase letters indicate statistical differences. The central line shows the median of the data, the box depicts the values within the 25 % and 75 % quantile. The whiskers represent the 1.5 interquartile range (1.5 IQR) value. Linear regression of fungal necromass C and SOC content in the organic (e) and mineral (f) soil. Linear regression between fungal necromass C and POC in the soil (g). Note the different axis scales in the three figures (e-g).

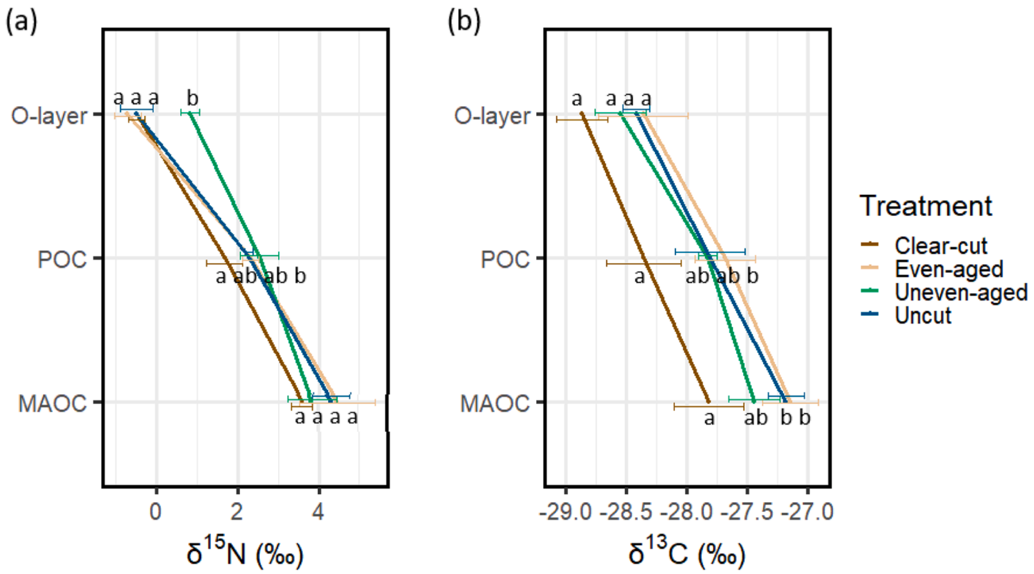


Fig. 9. Mean (a) δ^{15}N and (b) δ^{13}C values ± standard deviation (SD) shown for organic layer, POC and MAOC. Different lowercase letters indicate statistical differences between treatments, tested with ANOVA and Tukey's post-hoc test.

higher shares of POC in uncut and CCF plots.

Our results partly supported our first hypothesis with higher coarse living tree roots in uneven-aged and uncut plots than clear-cuts (and even-aged plots being intermediate). As expected, the tree fine root biomass was highest in uncut plots and was linked to stand density and basal area. However, against our hypothesis it was lowest in uneven-aged plots. Fine roots are particularly important to the SOC cycle due to their high turnover (Ding et al., 2021). We found total and fine root biomass to increase with increasing tree density and basal area but not with variation in the tree diameter and only coarse root biomass increased with tree species diversity. Thus, structural complexity did not clearly increase root biomass, contrary to our hypothesis. This resonates with the results of similar studies which also could not find that tree species diversity increased fine root biomass (Domisch et al., 2015; Finér et al., 2017). As hypothesised, we found less condensed tannins in the organic layer of clear-cut sites than other treatments, even though root biomass in clear-cut, even- and uneven-aged stands was similar to each other.

It was surprising that the tree fine root biomass was not lower in clear-cut plots, as there were no mature trees on these plots and considering that the fine root biomass has been shown to increase with stand basal area in boreal forests (Finér et al., 2007; Helmisaari et al., 2007; Lehtonen et al., 2016a). Thus, the young re-growing trees seem to have a vigorous fine root growth. However, until today a large part of the variation in fine root biomass remains unexplained (Lehtonen et al., 2016b). Fine roots are very laborious to extract from the soil, which limited our sample size. Hence, it might be that we could not capture the effects of the forest management on the fine root density. It was also unexpected that there were no differences between the understorey root biomass as uncut stands were so much denser and had thus little understorey on the forest floor.

The higher root density in uncut plots could be assumed to lead to an accumulation in soil C through an increased allocation of C to the roots and root-associated fungi (Clemmensen et al., 2013). However, we could neither observe this in organic nor mineral soil layer.

While the ratios of POC and MAOC changed according to our first hypothesis, as there appeared to be less of the labile POC in clear-cuts and more in the other treatments, the differences between treatments were not statistically significant due to large spatial variability in the data. As POC is considered a main precursor of MAOC (Angst et al., 2023; Witzgall et al., 2021), POC accumulation could indicate future trends in the SOC accumulation and stabilization. MAOC was correlated with the amount of silt and clay in the soil, which has been frequently observed (Begill et al., 2023; Matus, 2021). We did not find an influence of stand variables such as tree density or basal area on POC and MAOC fractions. MAOC was also not correlated with the root density or fungal necromass in the soil, opposing the idea of living root inputs as a major contributor to the MAOC formation as found in earlier studies (Rossi et al., 2020; Sokol et al., 2019; Teixeira, 2024).

4.2. Forest management effects on chemical recalcitrance and degradability of SOC

Our second hypothesis stated that through the impact of roots, forest management practice would alter the chemical recalcitrance of SOM. We expected higher amounts of chemically recalcitrant SOM in CCF and uncut plots from root litter inputs and less recalcitrant SOM in even-aged and clear-cut plots.

We did not find clear support for this hypothesis. Only in the POC fraction of uneven-aged plots there was a higher share of non-extractable recalcitrant compounds, but differences between treatments were not statistically significant. The chemical fractions in the O-layer did not differ between treatments. There were slightly higher shares and amounts of POC in uneven and uncut treatments that could indicate higher input of recalcitrant root C into POC in mineral soil, but again these differences were not statistically significant.

We found that POC contains more labile fractions and less of the non-extractable fraction than material from the organic layer, even though root litter that is considered the main source of POC, is known to contain higher fractions of lignin and chemically recalcitrant compounds than leaf litter (Sun et al., 2018).

Contrary to our hypothesis, we found a higher cumulative soil respiration in uncut plots than clear-cuts and the other treatments in the organic layer. Short-term incubation is dominated by respiration from the labile SOC pool, and therefore the higher respiration from organic soil of uncut treatments could indicate a higher labile C pool size (Fissore et al., 2008; Karhu, 2010). Higher respiration in soils with higher amounts of tree fine root biomass indicates that roots contributed to the labile SOM pool with root exudates even though they may be simultaneously contributing their necromass to the recalcitrant SOM pool. Similarly Adamczyk et al. (2019b) found roots to increase decomposition in a boreal forest soil. We did not directly measure root exudates but assume fine root biomass to determine root exudates (Hari et al., 2017; Heinzle et al., 2023). In the clear-cut plots the sampled labile pools may already have been efficiently depleted, due to more favourable conditions for decomposition. These results correspond to our earlier finding of a higher cumulative respiration in uncut pine (*Pinus sylvestris*) forests compared to clear-cuts (Roth et al., 2023).

4.3. Forest management effects on SOC stabilization as indicated by fungal necromass and natural abundance of isotopes

According to our third hypothesis, we expected that higher stand density and less disturbance of the fungal community would lead to increased fungal necromass in CCF and uncut forests compared to clear-cuts. Hence, we assumed in hypothesis four that a higher contribution of ectomycorrhizal residues to SOC pool in CCF and uncut plots would be shown as higher δ^{15}N values.

We could not confirm our third hypothesis as the fungal necromass in the soil did not significantly differ between management treatments and as there was no correlation between fungal necromass and stand density. This is contrary to the results of Zhang et al. (2024) who found that fungal necromass increased with increasing intensity of management in a bamboo forest. The mass of fungal necromass kg^{-1} dry soil in our site was much higher in the organic layer than the mineral soil and corresponded with earlier studies in boreal forests (Chen et al., 2020; Meyer et al., 2023; Xu et al., 2024). Also, the share of SOC constituted by fungal necromass was similar to earlier findings in boreal forests (Clemmensen et al., 2013; Xu et al., 2024) which are low compared to other forest biomes. The found close relationship of fungal necromass and POC suggests that the POC on our sites was largely constituted by fungal necromass. Particularly in the mineral soil the SOC formation appeared to be closely linked to fungal necromass, which supports the suggestion that microbial necromass drives the SOC formation (Liang et al., 2019). Our results challenge the view that POC is rather plant-derived (Golchin et al., 1994), whereas MAOC is rather formed from fungal necromass (Cotrufo et al., 2013; Lavallee et al., 2020). Our results agree with these of Klink et al. (2022), who found a high contribution of fungal necromass to POM fractions. However, as we did not directly measure the fungal necromass contributions to POC and MAOC we cannot conclude the exact contributions.

Contrary to the notion that stable SOC is mostly comprised of microbial compounds, a review-study found that > 50 % of MAOC might be formed by plant materials (Angst et al., 2021). Further, the contribution of plant compounds is higher in forests compared to grasslands, where conditions for microbial proliferation are more favourable. Whereas a different meta-study comes to the result that amino sugars are preferentially stored in MAOC rather than POC, particularly in forests (Xuan et al., 2024). They found that the amino sugar concentrations in MAOC (and to a lesser degree in POC) decreased with cooler climate. Zhang et al. (1998) reported an accumulation of microbially derived compounds with decreasing particle-size and a shift of amino sugars to smaller sized fractions with increasing mean annual temperature. Chen et al. (2024) reported that amino sugars can constitute more than 50 % of the POC in subtropical forests and that the contribution of amino sugars to POC increases with time after a forest disturbance. Another study from tropical forests found much lower contribution of amino sugars to POC (< 10 %) and identified plant compounds as the main driver in the formation of POC (Li et al., 2023). They identified soil nutrients and stoichiometries as the main impacts on amino sugar accumulation rather than forest management.

The increased ^{15}N values in the organic layer and POC of uneven-aged plots support our hypothesis of an increased contribution of mycorrhizae in N cycling. The ^{15}N signatures in our study resonate with earlier studies in boreal forest soils (Clemmensen et al., 2013; Pumpanen et al., 2017; Sah and Ilvesniemi, 2007). Sah and Ilvesniemi (2007) compared in their study the isotopic signature of ^{15}N between clear-cuts and closed forests and found differences between forest management treatments in the organic layer, but not the mineral soil. Similarly, we also found clearer differences in the organic layer and no differences between treatments in the MAOC fraction of the mineral soil. Our findings however are contrary to the ones of Sah and Ilvesniemi (2007), who found the organic soil in clear-cut forest had higher δ^{15}N values, compared to closed forest, whereas we did not find any differences between clear-cut and uncut forests, but higher δ^{15}N values in uneven-aged stands compared to other treatments in the organic layer. An increase in ^{15}N usually indicates an advanced level of decomposition of the organic material and an important role of mycorrhiza in N cycling (Clemmensen et al., 2013; Lindahl et al., 2007) because mycorrhizal fungi transfer mostly ^{15}N depleted N to their plant hosts (Högberg et al., 1996, 1999). Hence the increase of ^{15}N from organic layer to POC and further to MAOC shows an advancing level of decomposition. The increase of δ^{15}N with soil depth is typical for conditions of N-limitation (Högberg et al., 1996), which we observed on our plot as a wide CN-ratio. The topsoil usually has lower ^{15}N abundance as trees take up ^{15}N-depleted N and redeposition it onto the soil surface through litter-fall (Högberg et al., 1996). The impact of mycorrhizal fungi was further confirmed as we found correlations between δ^{15}N and fungal necromass and relative abundance of ectomycorrhizal fungi.

We observed an increase in ^{13}C with soil depth. This is commonly observed and can be explained by several mechanisms: (I) a depletion in ^{13}C in atmospheric CO_2 due to fossil fuel-derived CO_2 since 1850 (Suess effect), (II) increasing atmospheric CO_2 concentrations leading to a ^{13}C depletion in plant biomass and (III) isotopic fractionation during microbial C cycling and accumulation of necromass (Krüger et al., 2024). The observed enrichment in ^{13}C from POC to MAOC reflects this third mechanism, which is supported by the correlation we found between δ^{13}C in MAOC and the relative abundance of ECM in the soil. The higher natural abundance of ^{13}C in MAOC indicates more microbial-derived compounds and fewer plant-derived compounds (Lavallee et al., 2020). Whereas the forest treatment did not have a significant impact on the ^{13}C signature in the organic layer, an effect appeared in the mineral soil in POC and MAOC, where clear-cuts were depleted in ^{13}C compared to uncut plots or to uncut plots and even-aged mature plots respectively. This could reflect the high amounts of relatively recently added fresh litter on clear-cuts plots through harvesting residues. The abundance of ^{13}C in uneven-aged plots was more similar to the one of clear-cuts than to the other treatments in organic layer, POC and MAOC. This might be due to the different stand-structure and resulting different litter-quality, namely the higher share of broadleaf trees that we observed in uneven-aged plots. Broadleaf trees are known for having lower natural abundance of ^{13}C than coniferous trees (Brooks et al., 1997). The positive correlation between δ^{13}C and amounts of condensed tannins in the organic layer may reflect the impact of roots in the decomposition processes in the organic layer. The different isotopic signatures we found in POC and MAOC and the positive correlation with POC and respiration rate support the notion that these two fractions have distinct biogeochemical properties and turnover rates (Yu et al., 2022).

5. Conclusion

We found that some indicators for SOC stability were more sensitive to changes in forest management practice than others and overall, the effects of CCF and RFM on SOC stabilization differed less than hypothesized. We observed a marginally higher density of roots in uncut plots compared to clear-cuts, and accordingly a significantly lower content of condensed tannins in clear-cut plots. The fractionation into POC and MAOC as well as the chemical fractionation did not show significant differences for the different management treatments. However, cumulative respiration in the lab indicated more easily decomposable SOC in uncut plots. While fungal necromass, which contributed on average 16 % to the SOC, was not significantly affected by the management treatment, higher ^{15}N values indicated a higher contribution of mycorrhizal fungi to the SOM formation in uneven-aged plots and ^{13}C measurements indicate less decomposed material in POC and MAOC of clear-cuts. The accumulation of mycorrhizal remnants may indicate a higher potential for the build-up of stable SOC over time in continuous-cover plots. However, the development over a longer time needs to be further studied to prove this assumption.

35 years after the conversion of the stands to uneven-aged and even-aged structures, we did not find differences in the overall SOC stocks, but we found some differences between the stabilisation mechanisms of SOC. Not only did clear-cutting compared to uncut stands affect the SOC stabilization, by decreasing the amount of easily decomposable SOC, but also the different age-structures (even-aged vs uneven-aged) affected the stabilization processes as mycorrhizal fungi appeared to be more involved in SOM formation in uneven-aged plots.

CRediT authorship contribution statement

Eva-Maria Roth: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Outi-Maaria Sietiö:** Writing – review & editing, Validation. **Bartosz Adamczyk:** Writing – review & editing, Investigation, Conceptualization. **Pingping Xu:** Writing – review & editing, Investigation. **Sauli Valkonen:** Writing – review & editing, Resources. **Eeva-Stiina Tuittila:** Writing – review & editing, Supervision, Funding acquisition. **Heljä-Sisko Helmisaari:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Kristiina Karhu:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Eva-Maria Roth reports financial support was provided by Kone foundation. Eva-Maria Roth reports financial support was provided by Finnish Natural Resources Research Foundation. Eva-Maria Roth reports financial support was provided by Finnish Society of Forest Science. If there are other authors, they 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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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123347.

Data Availability

The data supporting the findings of this study are openly available in Dryad publishing platform at https://doi.org/10.5061/dryad.6m905qgdm.

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