Agricultural and Forest Meteorology 297 (2021) 108266

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Research paper

Partitioning of forest floor CO_2 emissions reveals the belowground interactions between different plant groups in a Scots pine stand in southern Finland

Kira Ryhti [1,2,*], Liisa Kulmala [1,2], Jukka Pumpanen [3], Jarkko Isotalo [4], Mari Pihlatie [1,5,6], Heljä-Sisko Helmisaari [7], Jaana Leppälammi-Kujansuu [7], Antti-Jussi Kieloaho [8], Jaana Bäck [1], Jussi Heinonsalo [1,2,6,9]

[1] Institute for Atmospheric and Earth System Research (INAR) / Forest Sciences, University of Helsinki, P.O. Box 27, FI-00014 University of Helsinki, Helsinki, Finland
[2] Finnish Meteorological Institute, P.O. Box 503, FI-00101 Helsinki, Finland
[3] Department of Environmental and Biological Sciences, University of Eastern Finland, P.O. Box 1627, FI-70211 Kuopio, Finland
[4] Tampere University, P.O. Box 1001, FI-33014 Tampere University, Tampere, Finland
[5] Department of Agricultural Sciences, University of Helsinki, P.O. Box 27, FI-00014 University of Helsinki, Helsinki, Finland
[6] Viikki Plant Science Centre (ViPS), University of Helsinki, P.O. Box 27, FI-00014 University of Helsinki, Helsinki, Finland
[7] Department of Forest Sciences, University of Helsinki, P.O. Box 27, FI-00014 University of Helsinki, Helsinki, Finland
[8] Natural Resources Institute Finland (Luke), P.O. Box 2, FI-00790 Helsinki, Finland
[9] Department of Microbiology, University of Helsinki, P.O. Box 56, FI-00014 University of Helsinki, Helsinki, Finland

ARTICLE INFO

Keywords:
boreal forest
Pinus sylvestris
root exclusion
mycorrhiza
soil respiration
ericaceous dwarf shrubs

ABSTRACT

Changes in the climate may have unpredictable effects on belowground carbon processes and thus, the carbon balance of boreal forests. To understand the interactions of these processes in soil and to quantify the potential changes in the carbon cycle, partitioning of forest floor respiration is crucial. For this purpose, we used nine different treatments to separate the sources of forest floor carbon dioxide (CO_2) emissions in a mature Scots pine (*Pinus sylvestris* L.) stand in southern Finland. To partition the belowground CO_2 emissions, we used two different trenching methods: 1) to exclude roots and mycorrhizal fungal mycelia (mesh with 1-μm pores) and 2) to exclude roots, but not mycorrhizal hyphae (mesh with 50-μm pores). Additionally, we used 3) a control treatment that included roots and fungal hyphae. To partition the CO_2 emissions from the forest floor vegetation, we 1) removed it, 2) left only the dwarf shrubs, or 3) left the vegetation intact. The forest floor CO_2 emissions were regularly measured with a flux chamber throughout the growing seasons in 2013–2015. The total forest floor respiration was partitioned into respiration of tree roots (contributing 48%), heterotrophic soil respiration (30%) and respiration of ground vegetation other than shrubs (10%), dwarf shrubs (8%), and hyphae of mycorrhizal fungi (4%). Heterotrophic respiration increased in the trenched treatments without ground vegetation over time, due to the so-called 'Gadgil effect'. In the absence of tree roots, but when hyphal access was allowed, respiration in the dwarf shrub treatment increased throughout the experiment. This indicated that dwarf shrubs had fungal connections to outside the experimental plots via their ericoid mycorrhiza. At the same time, other ground vegetation, such as mosses, suppressed the dwarf shrub respiration in trenched treatments. Our results show that competition on the forest floor is intense between plant roots and soil microbes.

1. Introduction

The soil in boreal forests constitutes one of the most extensive storages of carbon (C) globally, and changes in this storage may greatly impact the atmospheric carbon dioxide (CO_2) concentration (Raich & Schlesinger, 1992). In forested ecosystems, soil respiration is a key component of CO_2 exchange, since it forms the largest C flux from the ecosystem to the atmosphere (Janssens et al., 2001). Soil CO_2 emissions originate from soil respiration that consists of autotrophic respiration of tree roots (R_{TREE}), activity of the external hyphae of symbiotic

* Correspondence: Kira Ryhti, tel. +358 503149934
E-mail address: kira.ryhti@helsinki.fi (K. Ryhti).

https://doi.org/10.1016/j.agrformet.2020.108266
Received 30 April 2020; Received in revised form 13 November 2020; Accepted 25 November 2020
Available online 13 December 2020

mycorrhizal fungi (R_{MY}) and emissions from the activity of nonsymbiotic heterotrophic microbes (R_H), such as saprotrophic bacteria and fungi, all of which decompose soil organic matter (SOM) (Kutsch et al., 2010; Kuzyakov, 2006). In addition to the trees, the typical vegetation structure of northern forests consists of dense forest floor vegetation that contributes significantly to gross primary production (GPP) (Goulden & Crill, 1997; Kulmala et al., 2011; Kulmala et al., 2019; Morén & Lindroth, 2000). The respiration of woody ericaceous dwarf shrubs (R_{SHR}) and other ground vegetation (*e.g.* grasses, mosses, and herbs; R_{GMH}) contributes notably to total forest floor respiration (R_{TOT}). Accordingly, the forest floor comprises the organic topsoil and mineral soil, ground-level vascular plants and bryophytes that often cover the ground almost totally in boreal forests, and belowground plant parts with their associated microbiota.

The roots of different plant species and microorganisms in soil compete mostly for nutrients (Kuzyakov & Xu, 2013). In the boreal zone, many of the coniferous tree species form ectomycorrhizal symbioses, dwarf shrubs form ericoid mycorrhizal symbioses (Read, 1991) while other vascular plants, such as grasses, form arbuscular symbioses (Smith & Read, 2008). These symbiotic relationships enable mycorrhizal fungi to provide nitrogen (N), phosphorus (P) and other nutrients to the host plants from sources that would otherwise be unavailable, while the mycorrhizae benefit from the host plant by obtaining photosynthates for their growth (Smith & Read, 2008). Ecto- and ericoid mycorrhizal fungi release organic matter-degrading enzymes, mostly to scavenge nutrients from recalcitrant organic compounds (Read & Perez-Moreno, 2003), thus having saprotrophic capabilities. Furthermore, the mycorrhizal hyphal necromass forms a significant fraction of the SOM (Clemmensen et al., 2013), since substantial amounts of C are allocated to the mycorrhizal fungi by the host plant (Leake et al., 2001; Schiestl-Aalto et al., 2019). The presence of plant roots and their associated mycorrhizal fungi also directs soil chemistry towards more recalcitrant organic pathways (Adamczyk et al., 2016, 2019a, 2019b; Kallenbach et al., 2016), thus playing a significant role in soil chemistry and C sequestration (Treseder & Allen, 2000).

The soil microbiota are dominated by saprotrophic soil bacteria and fungi, which are primary decomposers of SOM (Read, 1991). Plant root exudation stimulates saprotrophs, and the resulting increase in decomposition caused by plant-released carbohydrates is known as the rhizosphere-priming effect (Kuzyakov, 2006). In contrast, the existence of plant root-associated microbes, such as mycorrhizal fungi in boreal forests, may suppress the saprotrophic activity in a so-called 'Gadgil effect' (Gadgil & Gadgil, 1971). The Gadgil effect has been hypothesized to result from multiple reasons, for example, from competition for resources such as nutrients and water between saprotrophic and ectomycorrhizal fungi and secondly from the chemical inhibition or parasitism of one by the other (Fernandez & Kennedy, 2015). In boreal forests, mycorrhizal fungi are thought to have an advantage over saprotrophs, because symbiotic relationships with plants provide a secure flow of energy for fungal growth. This allows mycorrhizae to allocate more resources for foraging nutrients such as N, which are often bound to energy-poor complex organic forms. Plant and mycorrhizal uptake of N increases the C:N ratio, making soil an even more unfavourable growth substrate for saprotrophs (Adamczyk et al., 2016; Fernandez & Kennedy, 2015). Additionally, ericaceous dwarf shrubs are known to alter their living conditions, not only by lowering the soil pH and degrading SOM, but also by forming recalcitrant compounds (Adamczyk et al., 2016).

There is an urgent need to find ways to separate these different sources of respiration of the forest floor to estimate how the soil C pool and root C dynamics will respond to potential changes in climate (Bond-Lamberty et al., 2004; Pregitzer et al., 2000). At the same time, quantifying the C released from the belowground parts of the plants would improve our understanding of whole-ecosystem C dynamics. Partitioning of the various C sources is challenging, because the processes responsible for different sources are tightly interconnected and affected by similar environmental drivers (Kuzyakov, 2006). To date, the sources of soil respiration are separated mainly by physical separation of the various forest floor components under field conditions or by using C isotopic methods (*e.g.* ^{13}C- or ^{14}C-labelling) (Hanson et al., 2000; Kuzyakov, 2006). It is, however, problematic to label mature trees or to analyse repeated labelling events for studying the seasonal dynamics of the various sources in respiration. The isotopic labelling methods are also quite expensive and, most importantly, are usually forbidden from conducting at long-term experimental sites, due to resulting disturbances in future studies using natural ^{13}C and ^{14}C abundances. Trenching (TR) methods have long been used for separating R_{TREE} from R_H by simply excluding ground vegetation and tree roots from the bulk soil and by subtracting these from undisturbed soil respiration to obtain the contribution of R_{TREE} (Bond-Lamberty et al., 2011; Hanson et al., 2000; Kutsch et al., 2010). Additionally, other CO_2 sources can be separated, for example, by using ground vegetation treatments and mesh fabrics with various pore sizes (Fenn et al., 2010; Heinemeyer et al., 2012; Moyano et al., 2008; Yan et al., 2019), such as 50 μm (Andrew et al., 2014; Hagenbo et al., 2019) which enables ingrowth of external mycorrhizal fungal hyphae.

The aim of this study was to partition the CO_2 emissions from the forest floor into the various sources of R_H, R_{TREE}, R_{MY}, R_{SHR} and R_{GMH}; excluding each one at the time, using TR treatment and various ground vegetation removals in combination. We were particularly interested in the interaction between the various CO_2 sources. We addressed four specific research questions: 1) how does the presence of tree roots affect forest floor CO_2 emissions, 2) how does the competition between plant groups change their contributions to forest floor CO_2 emissions, 3) what is the role of mycorrhizal fungi in forest floor CO_2 emissions, and 4) do the fungal connections between dwarf shrubs and trees increase forest floor CO_2 emissions due to their interaction?

2. Materials and methods

2.1. SMEAR II forest

The study site is a Scots pine (*Pinus sylvestris* L.) stand at the Station for Measuring Ecosystem-Atmosphere Relations (SMEAR II) in southern Finland (61.51° N, 24.17° E) (Hari & Kulmala, 2005). It was established by sowing in 1962 on a medium fertile site, classified as *Vaccinium* type (Cajander, 1926).The stand is dominated by Scots pine with a sparse undergrowth of Norway spruces (Picea abies (L.) Karst.) and scattered mature deciduous trees, mainly downy birch (*Betula pubescens* Ehrh.) and silver birch (*B. pendula* Roth). In 2012, the dominant height and mean stem diameter at breast height were 17.5 m and 19.6 cm, respectively (Bäck et al., 2012), and the density of trees with diameter >15 cm was 683 stems per hectare (Schiestl-Aalto et al., 2019). The understorey vegetation is formed by ericaceous dwarf shrubs such as lingonberry (mountain cranberry) (*Vaccinium vitis-idaea* L.), whortleberry (bilberry) (*Vaccinium myrtillus* L.) and heather (*Calluna vulgaris* (L.) Hull), feather mosses such as Schreber's big red stem moss (*Pleurozium schreberi* (Brid.) Mitt.), dicranum mosses (*Dicranum* Hedw. sp.) and splendid feather moss (*Hylocomium splendens* (Hedw.) Schimp.), with sparse occurrence of grasses and herbs such as wavy hairgrass (*Deschampsia flexuosa* (L.) Trin). The soil above the bedrock is a Haplic podzol and the soil depth is approximately 0.5–0.7 m.

The site is characterized by a boreal climate with long cool days in summer and short cold days in winter. The mean annual air temperature is 3.5 °C, whereas the mean monthly temperature varies from −7.7 °C in February to 16.0 °C in July (mean for 1980–2009) (Pirinen et al., 2012). The monthly average temperatures vary from 8.8–16.0 °C in the growing season (May – September). The mean annual rainfall of 711 mm is distributed quite evenly throughout the year and varies from 35 mm in February to 92 mm in July, and from 45–92 mm in the growing season.

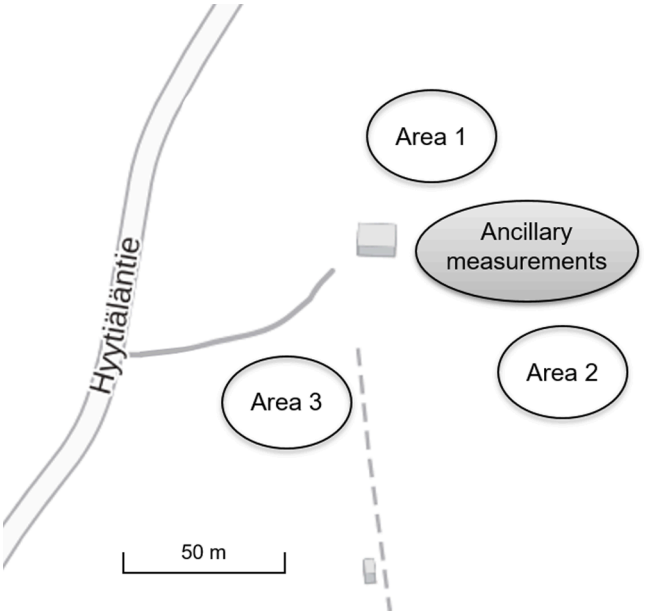

Fig. 1. Map of the Station for Measuring Ecosystem-Atmosphere Relations (SMEAR II) forest. The trenching experiment was performed in areas 1–3, each containing 20 experimental plots with all 9 different treatments (*Table 1*). Ancillary measurements included forest floor respiration in 14 intact plots and soil-moisture and -temperature measurements from 6 soil pits (base map (C) Maanmittauslaitos, National Land Survey of Finland, 2019).

2.2. Ancillary measurements in the SMEAR II forest

The soil temperature was measured with thermocouples (Philips AG, Horgen, Switzerland) continuously in the eluvial layer (A-horizon) (2–5-cm depths) at 1-min intervals, and volumetric soil-water content (SWC, $m^3\ m^{-3}$) at 15-min intervals (Ilvesniemi et al., 2010) by time-domain reflectometry (TDR100; Campbell Scientific Inc., Logan, UT, USA) located in the soil in the A and B horizons at 2–6-cm and 14–25-cm depths, respectively. The air temperature was measured with a Pt100 sensor at a height of 4.2 m. The thermal time (W), i.e. the effective temperature sum (degree-day, °Cd), was calculated as the sum of the daily average temperatures (T_d) above 5.0 °C from days when the average temperature was more than 5.0 °C:

$$W = \Sigma(T_d - 5), when\ T_d > 5.0°C. \quad (1)$$

The forest floor respiration (CO_2 emissions) at the SMEAR II station as measured at 14 permanent collars at 2–4-week intervals during snow-free periods with manual chambers, using a standard closed-chamber technique (Pumpanen et al., 2015). The cylindrical chamber was 19.7 cm in diameter and 23.9 cm in height, equipped with a small fan and covered with aluminium foil to exclude sunlight, enclosing all the natural ground vegetation (mosses, dwarf shrubs *etc.*) at the specific location. The CO_2 concentration in the chamber headspace was measured with a GMP343 infrared sensor CO_2 probe (Vaisala Oyj, Vantaa, Finland). During the measurements, the chamber was attached to the collar for 5 min. The CO_2 emission was calculated by linear fitting against time and the CO_2 concentration inside the chamber headspace. Only measurements between 45 sec and 4 min were used.

For background information, we used net ecosystem CO_2 exchange (NEE). It was measured with a closed-path eddy-covariance measuring system installed above the stand at a height of 23 m. The instrumentation is documented in detail in Vesala et al. (2005), and the post-processing of the data in Kolari et al. (2009). In principle, NEE is the difference between total ecosystem respiration (TER) and GPP. TER was modelled from accepted night-time turbulent fluxes, using an exponential equation with temperature of the organic layer of the soil as the explanatory factor (Kolari et al., 2009).

Table 1
The various sources of respiration in the treatments, including the manipulations aboveground: all ground vegetation removed (CUT), only dwarf shrubs left (SHR), normal intact vegetation (NOR) and belowground: trenching (TR) treatments 1 μm (TR1) and 50 μm (TR50), and non-trenched controls (CON) on the forest floor. R_H stands for heterotrophic respiration, R_{MY} for respiration by mycorrhizal fungal hyphae, R_{TREE} for tree roots, R_{SHR} for dwarf shrubs and R_{GMH} for other forest floor grass, moss and herb vegetation. R_{SHR} and R_{GMH} included corresponding root-associated microbial respiration and their potential priming effects.

Treatment	Areas	Plots per area	Total number of plots	Sources
TR1 - CUT	3	2	6	R_H
TR1 - SHR	3	2	6	$R_H + R_{SHR}$
TR1 - NOR	3	2	6	$R_H + R_{SHR} + R_{GMH}$
TR50 - CUT	3	2	6	$R_H + R_{MY}$
TR50 - SHR	3	2	6	$R_H + R_{SHR} + R_{MY}$
TR50 - NOR	3	2	6	$R_H + R_{SHR} + R_{GMH} + R_{MY}$
CON - CUT	3	2	6	$R_H + R_{MY} + R_{TREE}$
CON - SHR	3	2	6	$R_H + R_{SHR} + R_{MY} + R_{TREE}$
CON - NOR	3	4	12	$R_H + R_{SHR} + R_{GMH} + R_{MY} + R_{TREE}$
Total	3	20	60	

2.3. Experimental setup

2.3.1. Soil and ground vegetation treatments

The experiment was established close to the ancillary measurements in three replicate experimental areas approximately 50 m apart in July–October 2012 (*Fig. 1*). In each area, we installed nine different treatments in plots that modified the belowground C allocation to the soil. The treatments consisted of three plots with aboveground (CUT, SHR, NOR) and three with belowground (TR1, TR50, CON) manipulations and all their combinations (*Table 1*). The plots with aboveground treatments included manipulation of forest floor vegetation by removing all ground vegetation by cutting (CUT), removing other plants except ericaceous dwarf shrubs (SHR), and leaving the normal ground vegetation intact (NOR). Growth on the forest floor is low in this region and did not require high cutting intensity. Thus, all regrown ground vegetation was removed a few times per year from the entire CUT plot, whereas all other plants except dwarf shrubs were removed in the SHR treatment plots. However, all possible unwanted regrowth in the CUT and SHR treatments was removed from inside the collars when the measurements were conducted. The plots with belowground treatments consisted of TR, in which the connection to the standing trees was excluded, using a mesh fabric with either 1-μm (TR1) or 50-μm (TR50) pore size. TR1 allowed water and nutrients to flow through, but inhibited the ingrowth of both plant roots and plant-associated mycorrhizal fungi, whereas TR50 allowed the ingrowth of mycorrhizal fungi, but no plant roots. The non-trenched plots included controls with undisturbed roots and microbes (CON). In practice, the TR1 and TR50 plots were constructed by digging a minimum 40-cm-deep ditch around a 90 × 90 cm plot and installing root isolating permeable mesh fabric (pore size 1 μm or 50 μm) into the ditch before refilling. Both permeable meshes allowed water and nutrient exchange. The CON plots contained no mesh or any other disturbance to the soil. Treatments were established in 20 plots in each three replicate area, area with two replicate plots of each treatment (four replicates of the CON-NOR treatments), resulting in six (and 12 of CON-NOR) replicates altogether (*Table 1*). The total forest floor CO_2 emissions (R_{TOT}) were separated into different sources (*Table 1*), in which R_H stands for heterotrophic respiration, R_{MY} for respiration by ericoid and ectomycorrhizal fungal hyphae, R_{TREE} for tree roots, R_{SHR} for ericaceous dwarf shrubs, and R_{GMH} for other forest

floor vegetation, such as grasses, mosses, and herbs. R_{SHR} and R_{GMH} included corresponding root-associated microbial respiration and their potential priming effects.

2.3.2. Litter decomposition

Litterbags of 1-mm mesh size filled with 1.0 g (dry weight) mixture of dried Scots pine and dwarf shrub root litter (diameter 2–5 mm) were placed between the organic layer and mineral-soil surface in each plot in early October 2012 and collected annually in late September 2013, 2014 and 2015. The fresh weight of the remaining litter in the bags was measured, and a subsample of the litter was dried (60.0 °C) for the dry weight, and later burned to determine the ash content and finally the mass loss. The ash content of the litter was analysed to correct the error in mass loss data caused by possible mineral soil particles attached to the litter.

2.3.3. Soil respiration, temperature and moisture

The CO_2 emissions were measured at each experimental plot with the same type of manual chamber as described above (see 2.2. Ancillary measurements in the SMEAR II forest), on permanently installed collars in each plot at 2-week or 1-month intervals during the snow-free seasons in 2013–2015. The data from one CON-NOR plot were later discarded from the analysis, due to its thin soil layer, which was less than 6 cm on average on top of the bedrock. Otherwise the soil depth of the experimental plots was at least 10 cm, and in most of the plots it was more than 25 cm.

The soil temperature was measured in each plot, using temperature sensors (iButton®; Maxim Integrated Inc., San Jose, CA, USA) at 4-h intervals, the sensors being installed between the organic and mineral horizons. We interpolated the hourly values and calculated a daily morning hour (09:00–12:00 a.m.) mean from these, since the CO_2 emission measurements were measured during the same hours. The sensors were used during the growing season, in practice over the nonfrozen period from approximately May until October/November. The daily soil temperatures ($\overline{T}_i$) for each plot i were derived for the winter period, using the linear relationships between the daily means of the thermocouples in SMEAR II and the plot-specific morning hour means of CO_2 emissions during the measurement days.

The soil moisture (*i.e.* SWC) at each plot (see the following) was measured, using a PR2 soil moisture profile probe (Delta-T Devices, Cambridge, UK) and recorded with an HH2 moisture meter (Delta-T Devices). Two of the plots were too thin for moisture profile tube installation and measurements of the plots in the same treatment were used for these instead. The measurements were conducted biweekly or monthly, always at the time when the soil CO_2 emission was measured. We selected measurements that were taken between 5- and 15-cm depths from the soil surface. The overall level of the soil moisture values measured showed striking variation among plots, even at times when the continuous measurements showed values of field capacity (FC) (0.25 m^3 m^{-3} for soil in 5–9-cm depths at SMEAR II) (Ilvesniemi et al., 2010). We assumed that the offset resulted from the microtopography, heterogeneous structure of the glacial till and variation in SOM content. Thus, we looked annually for periods when the soil was in FC according to the continuous measurements at SMEAR II and derived the difference between the FC and the actual value measured at each plot. Then, this difference was added to all the measured values, which were further used in the analysis. We found linear relationships between the daily means of the continuous SMEAR II measurements and the plot-specific soil moisture values, which were used to estimate the daily moisture ($\overline{M}_i$) for each plot i.

2.4. Estimating the daily CO_2 emissions

We assumed that the CO_2 efflux ($f_i(t)$) at plot i was driven by the T_i and M_i as follows,

$$f_i(t) = \left(1 + \left(\frac{1 - RWC_i}{\alpha_i}\right)^{v}\right)^{-1} r_{0_i} Q_{10,i}^{\frac{T_i}{10}} \quad (2)$$

where α, r_0, v, and Q_{10} are parameters, T the soil temperature, and RWC the relative water content, calculated as follows,

$$RWC_i = \frac{M_i - WP}{FC - WP} \quad (3)$$

In the equation, FC is the field capacity (0.25 m^3 m^{-3}) and WP the wilting point (0.06 m^3 m^{-3}), both set according to Ilvesniemi et al. (2010). We used $v = 11$ (in accordance with Mäkelä et al., 2008) first to estimate the parameters α, r_0 and Q_{10} and used these as starting values to simultaneously estimate the parameters α, r_0, and Q_{10} with the nls-function (non-linear regression) in R (R Core Team, 2019), using the 'port' algorithm. Then, we used these plot-specific parameters in *Eq. 2* to estimate the daily CO_2 emissions at each plot, using the mean M and T values in the experiment intact CON plots to overcome the possible effect of altered M and T on the CO_2 emissions in the trenched plots, since decrease in living root biomass and therefore lower transpiration from trenched plots may cause potential changes in soil moisture and temperature.

The CO_2 emissions in the trenched plots were also corrected by taking into account additional CO_2 emissions from decomposing residual roots in the TR1, TR50, SHR and CUT treatments, due to cutting of tree roots or ground vegetation shoot removal. The corrections needed to adjust the CO_2 emissions measured due to decomposing residual roots are described in detail in the Appendix.

The daily CO_2 emissions ($f_i(t)$) at each plot i (*Eq. 4*) were summed to obtain the annual CO_2 emissions (R_i^y) in year y, as follows:

$$R_i^y = \sum_{t=1}^{t=365} f_i(t) \quad (4)$$

2.5. Partitioning of total CO_2 emissions into different sources

The yearly cumulative CO_2 emissions (R_i^y) were divided into different sources, assuming R_H as the mean soil respiration in TR1-CUT and the others according to *Table 1*, as follows:

$$R_{TREE} = \mathbf{CON} - \mathbf{TR50} \quad (5)$$

$$R_{MY} = \mathbf{TR50} - \mathbf{TR1} \quad (6)$$

$$R_{GMH} = \mathbf{NOR} - \mathbf{SHR} \quad (7)$$

$$R_{SHR} = \mathbf{SHR} - \mathbf{CUT} \quad (8)$$

Having several vegetation and TR treatments allowed three different calculation procedures for each component. For example, R_{TREE} can be calculated as the difference between CON and TR50 in the CUT, SHR and NOR treatments, and R_{GMH} as the difference between treatments NOR and SHR in the TR1, TR50 and CON treatments (*Eqs. 5–8*). The mean emissions arising from these sources were calculated as the mean of these three differences in the various treatments and further used to calculate the mean contribution in R_{TOT}.

2.6. Normalization of the total CO_2 emissions

The CO_2 emissions of the individual plots were normalized for years 2014 and 2015 to reduce the yearly variation caused by differences in the weather and to show the effects of treatments more pronounced. In practice, we normalized the CO_2 emission R of individual plot i in year y, using the relationship between the emissions of CON-NOR in year y and in 2013 (*Eq. 9*), as follows:

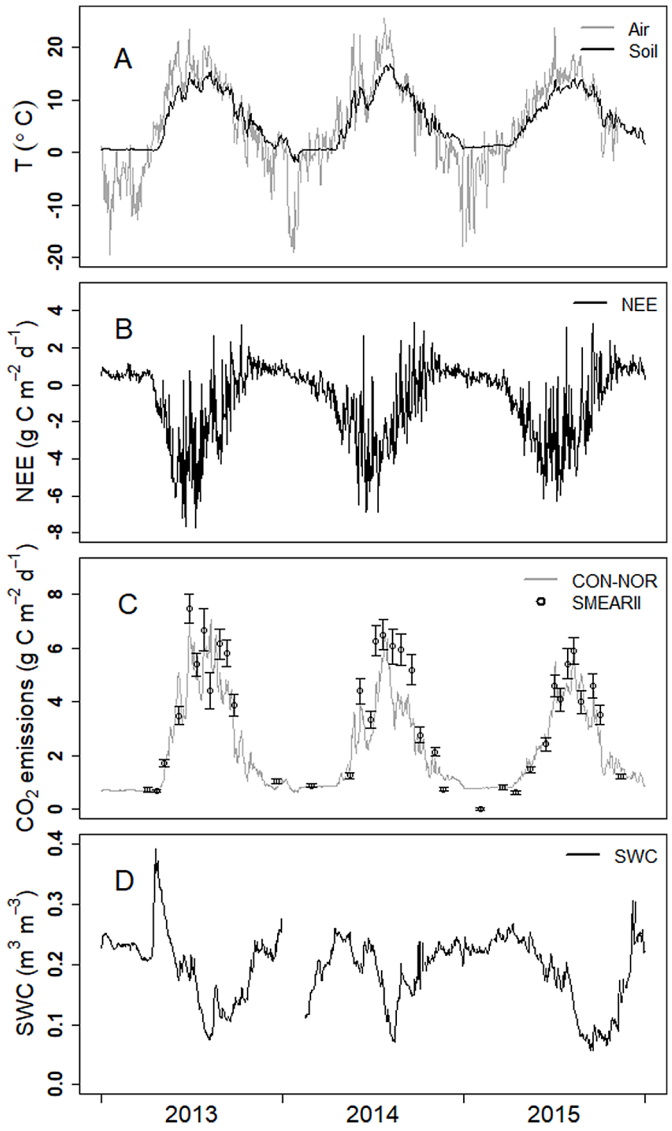

Fig. 2. Daily mean temperature (T) in the air (grey) and soil A-horizon (black) (A), measured net ecosystem CO_2 exchange (NEE) (B), mean forest floor CO_2 emissions at the Station for Measuring Ecosystem-Atmosphere Relations (SMEAR II) ± standard error (SE) in black (C), and soil-water content (SWC) in the A-horizon (D) during the study years at the SMEAR II station. In addition, panel C shows the modelled mean total CO_2 emissions of the forest floor (R_{TOT}) for the non-trenched control-normal intact ground vegetation (CON-NOR) treatment in grey.

$$N_i^y = R_i^y \frac{R_i^{2013}(CON - NOR)}{R_i^y(CON - NOR)} \tag{9}$$

2.7. Statistical analyses

Statistical testing between years and treatments was performed using the cumulative sum of the CO_2 produced (g C m^{-2} yr^{-1}) over a year in 2013, 2014, and 2015 (see Supplementary *Fig. S4*). For testing the effects of vegetation, TR treatment and period, we used the linear mixed-effect model:

$$y_{ijhkt} = \beta_0 + \beta_1 t + \alpha_j + \gamma_h + \beta_{2j} t + \beta_{3h} t + \psi_{i0} + \psi_{i1} t + \delta_k + \varepsilon_{ijhkt} \tag{10}$$

where α_j, γ_h are fixed parameters related to the categories of the vegetation and TR treatment, respectively, and $\beta_0, \beta_1, \beta_{2j}, \beta_{3h}$ are fixed parameters associated with the linear main and interaction effects with vegetation and TR treatment of year t. In the model, each sampling unit (i) has its own linear structure with respect to year t by the random effects $\psi_{i0} \sim N(0, \sigma^2_{\psi_0}), \psi_{i1} \sim N(0, \sigma^2_{\psi_1})$. The effect of area is included in the model by the random effects $\delta_k \sim N(0, \sigma^2_\delta)$. Furthermore, the random error terms are assumed to follow the normal distribution $\varepsilon_{ijht} \sim N(0, \sigma^2_\varepsilon)$. The effects of vegetation and TR treatment within each year were tested with the general linear-hypothesis test (Hothorn et al., 2008) at significance levels of $P < 0.001$ and $P < 0.01$. The normalized yearly CO_2 emissions of the treatments were compared in year 2013 to years 2014 and 2015 with the Wilcoxon signed-rank test at a significance level of $P < 0.05$. R (R Core Team, 2019) and SPSS statistics software (IBM SPSS, Armonk, NY, USA) was used in the statistical analysis.

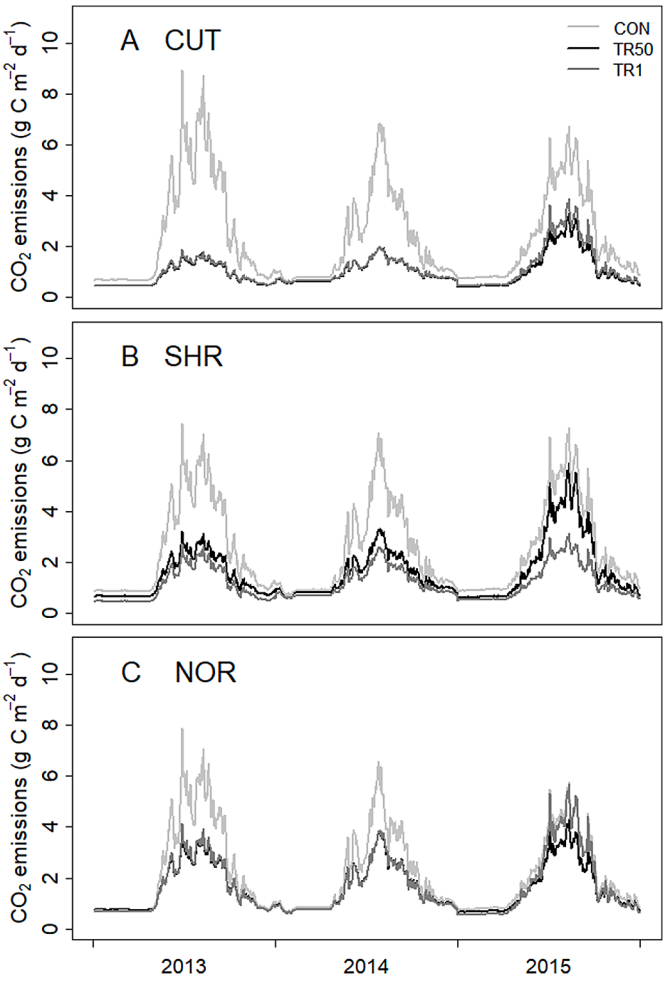

Fig. 3. Average daily CO_2 emissions in the various treatments in years 2013–2015 (n = 6, in CON-NOR n = 11). Trenching (TR) treatments 1 μm and 50 μm in grey (TR1) and black (TR50), and nontrenched controls (CON) in light grey line divided by different vegetation treatments: (A) all vegetation removed (CUT), (B) only dwarf shrubs left (SHR) and (C) normal intact ground vegetation (NOR).

3. Results

3.1. Overview of the weather and emissions in the various treatments

Air temperature and the NEE showed clear seasonal cycles in the measurement years (*Fig. 2A, B*). The year 2013 was the warmest and 2015 the coolest; the *W* level in years 2013–2015 was 1421, 1341, and 1231°Cd, respectively. Nevertheless, the photosynthetic uptake was similar during the study years, being 1268, 1250 and 1283 g C m^{-2} yr^{-1} in 2013, 2014 and 2015, respectively. The site was an overall C sink,

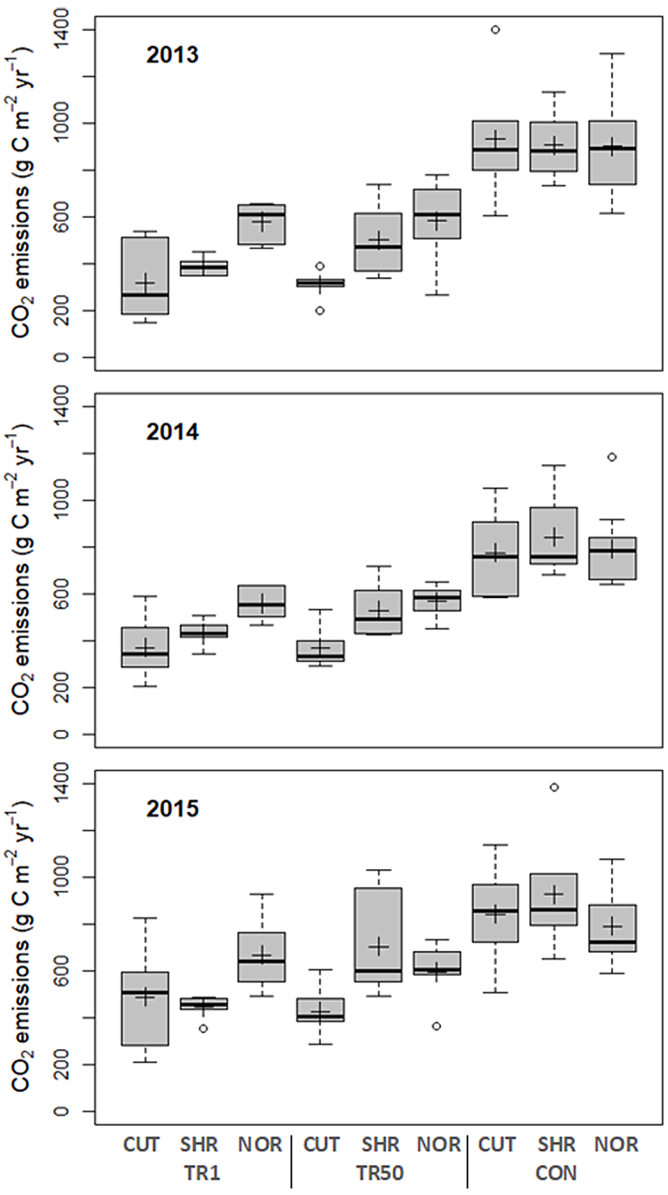

Fig. 4. Annual cumulative CO_2 emission medians (thick black line), means (crosses), minimum and maximum (lowest and highest lines), quartiles (lower edge of the box 25th percentile; upper edge of the box 75th percentile) and outliers (circles) from the various treatments in the study years (n = 6, in CON-NOR n = 11). The P-values and significant differences are shown in *Table 2*. For abbreviations, see caption for *Table 2*.

since the annual NEE for the same years was −301, −304 and −321 g C m^{-2} yr^{-1}. The seasonal forest floor respiration patterns were comparable between the CON-NOR treatment and the SMEAR II station, with somewhat higher midsummer values in 2013 than in 2015 (*Fig. 2C*). In general, the SWC was high early and late in the season, decreasing between every year. The number of days with low soil moisture (below 0.10 m^3 m^{-3}) were 18, 13 and 68 in 2013–2015, respectively. Yet, the dry period in 2015 occurred late in the season, whereas in the other years, soil moisture was lowest in early August (*Fig. 2D*).

The CO_2 emissions in the forest floor showed distinct differences between the treatments (*Fig. 3*). The daily average CO_2 emissions across the years 2013–2015 in TR1 were 1.07, 1.15, 1.65 g C m^{-2} d^{-1} in CUT, SHR and NOR treatments, respectively. In TR50, the daily average CO_2 emissions were 1.00, 1.58, 1.59 g C m^{-2} d^{-1} in CUT, SHR and NOR, respectively. The CON treatment had the highest daily average CO_2 emission over the years 2013–2015: 2.32, 2.44, 2.17 g C m^{-2} d^{-1} in

Table 2
Resulting P-values in the comparison of cumulative CO_2 emissions in the various belowground and aboveground treatments in different years (see *Fig. 4*). The asterisks mark significant differences between treatments. Trenching (TR) treatments: 1 μm and 50 μm (TR1) and (TR50), and non-trenched controls (CON). Vegetation treatments: all vegetation removed (CUT), only dwarf shrubs left (SHR) and normal intact ground vegetation (NOR).

Treatment		2013	2014	2015
TR1	TR50	0.77	0.73	0.78
TR1	CON	<0.001 ***	<0.001 ***	<0.001 ***
TR50	CON	<0.001 ***	<0.001 ***	<0.001 ***
CUT	SHR	0.27	0.15	0.17
CUT	NOR	<0.01 **	<0.05 *	0.34
SHR	NOR	0.32	0.90	0.88

* $P < 0.05$,
** $P < 0.01$,
*** $P < 0.001$

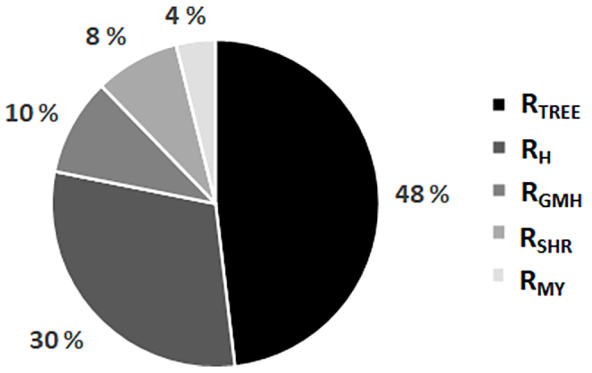

Fig. 5. Mean contributions of respiration of tree root (R_{TREE}), heterotrophic respiration (R_H), ericaceous dwarf shrubs (R_{SHR}), ground vegetation other than shrubs (*e.g.* grasses, mosses and herbs) (R_{GMH}) and ericoid and ectomycorrhizal fungal hyphae (R_{MY}) in total forest floor CO_2 emissions (R_{TOT}) in year 2013.

CUT, SHR and NOR treatments, respectively. TR1 showed in general the lowest CO_2 emissions, with some increase in 2015 (*Fig. 3*). At the same time, the emissions in the TR50 plots increased more than in TR1 with the SHR treatment (*Fig. 3B*). In general, the CO_2 emissions in most of the TR plots tended to increase towards year 2015 and to decrease in the CON plots (*Fig. 3*).

3.2. Cumulative CO_2 emissions from the various treatments

The annual CO_2 emissions were highest in the CON treatments (*Fig. 4*), differing significantly from the TR treatments (TR1 and TR50) in all years ($P < 0.001$) (*Table 2*). Overall, the CO_2 emissions in TR1 and TR50 were not statistically different (*Table 2*). The emissions tended to increase with increasing ground vegetation, especially in TR1 and TR50 in 2013 and 2014 (*Fig. 4*), but only CUT and NOR differed significantly in 2013 and 2014 ($P < 0.01$ and $P < 0.05$) (*Table 2*). In 2015, there were no significant differences between the vegetation treatments, even though the emissions from TR50-SHR plots increased over the emissions from the TR treatments with NOR vegetation, whereas the emissions in TR1-SHR remained similar (*Fig. 4*). In addition, the emissions from TR1-CUT without any ground vegetation exceeded the emissions from TR1-SHR with dwarf shrubs (*Fig. 4*).

3.3. Partitioning of forest floor CO_2 emissions into different sources and temporal changes

The CO_2 emissions of the forest floor were partitioned into mean contributions of R_{TREE}, R_H, R_{SHR}, R_{GMH} and R_{MY} in 2013–2015. The data from year 2013 that were collected 9 months after TR, were used to

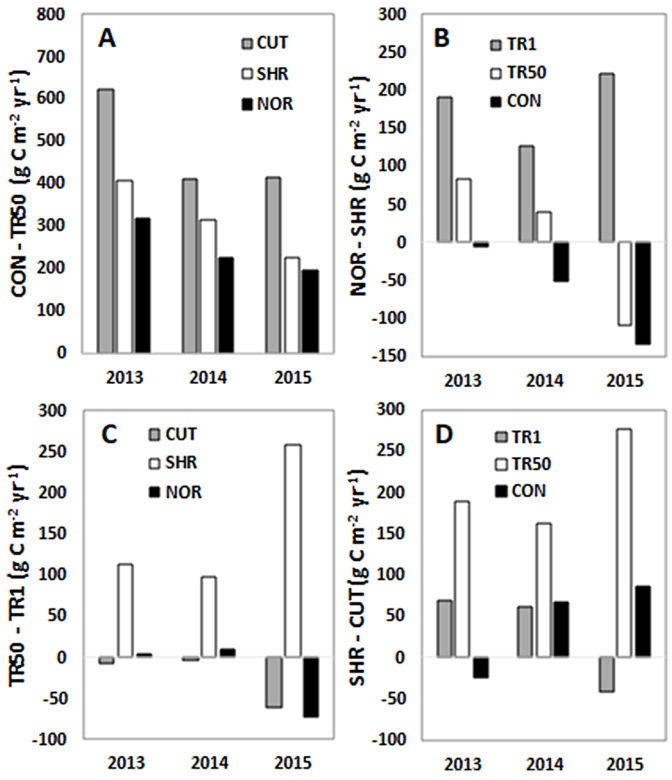

Fig. 6. Differences in CO_2 emissions between A) non-trenched control (CON) and 50-µm trenching (TR50) treatments, B) normal intact ground vegetation (NOR) and dwarf shrubs only (SHR) treatments, C) TR50 and 1-µm trenching (TR1) and D) SHR and all vegetation removed (CUT) in various years. Vegetation treatments: CUT in grey, SHR in white and NOR in black. Trenching (TR) treatments: TR1 in grey, TR50 in white and CON in black.

show the overall contribution of the various CO_2 sources (*Fig. 5*), since they showed the least time for development of treatment-related changes in the system (*e.g.* Gadgil effect). The mean contributions of R_{TREE} and R_H were 48% and 30%, respectively (*Fig. 5*). The other sources played smaller roles in the CO_2 emissions and comprised about 22% in total (*Fig. 5*).

R_{TREE}, calculated as the difference in CO_2 emissions between the CON and TR50 plots (*Eq. 5*), was lower in the NOR and SHR than in the CUT treatments in all study years (*Fig. 6A*). R_{GMH}, defined as the difference between NOR and SHR (*Eq. 7*), decreased in the CON and TR50 treatments and was notable only in TR1 (*Fig. 6B*). R_{MY}, defined as the difference in CO_2 emissions between TR1 and TR50 (*Eq. 6*), was small or negative in the CUT and NOR treatments, but was always positive in the SHR treatment (*Fig. 6C*). R_{SHR}, calculated as the difference between SHR and CUT (*Eq. 8*), was clearly highest in the TR50 treatment (*Fig. 6D*).

The normalized cumulative yearly CO_2 emissions increased with time in all treatments in which tree roots were excluded (all vegetation treatments in TR1 and TR50), the increase being statistically significant ($P < 0.05$) for TR1-CUT, TR1-SHR, TR50-CUT and TR50-SHR in both years 2014 and 2015 (*Fig. 7*). In CON, this trend was not seen ($P > 0.05$). The increases in average CO_2 emissions were largest in TR1-CUT and TR50-SHR, in which the emissions increased to 1.8- and 1.6-fold, from 317 to 564 g C m^{-2} yr^{-1} and from 499 to 814 g C m^{-2} yr^{-1}, respectively.

4. Discussion

4.1. Partitioning of forest floor CO_2 emissions

To study the soil-vegetation interactions, the forest floor respiration was first partitioned into five different CO_2 sources. Tree root respiration (R_{TREE}) comprised on average 48% of the total forest floor CO_2 emissions (R_{TOT}), which is in accordance with Hanson et al. (2000), who estimated from 37 published field-based studies that root respiration contributes 49% of total soil respiration for sites with forest vegetation. Both girdling and trenching (TR) experiments in boreal coniferous forests support our findings (*e.g.* Comstedt et al., 2011; Högberg et al., 2001; Lavigne et al., 2003; Vogel et al., 2005). Using only TR (*i.e.* root exclusion) methods allowed us to separate the rhizosphere respiration so that the R_{TREE} estimated here may have contained a fraction of microbially derived respiration, in particular part of R_{MY}.

Respiration of external mycorrhizal hyphae (R_{MY}) amounted to 4% of R_{TOT} on average in our study in 2013, which was considerably less than in most published studies. However, estimates of R_{MY} from the boreal

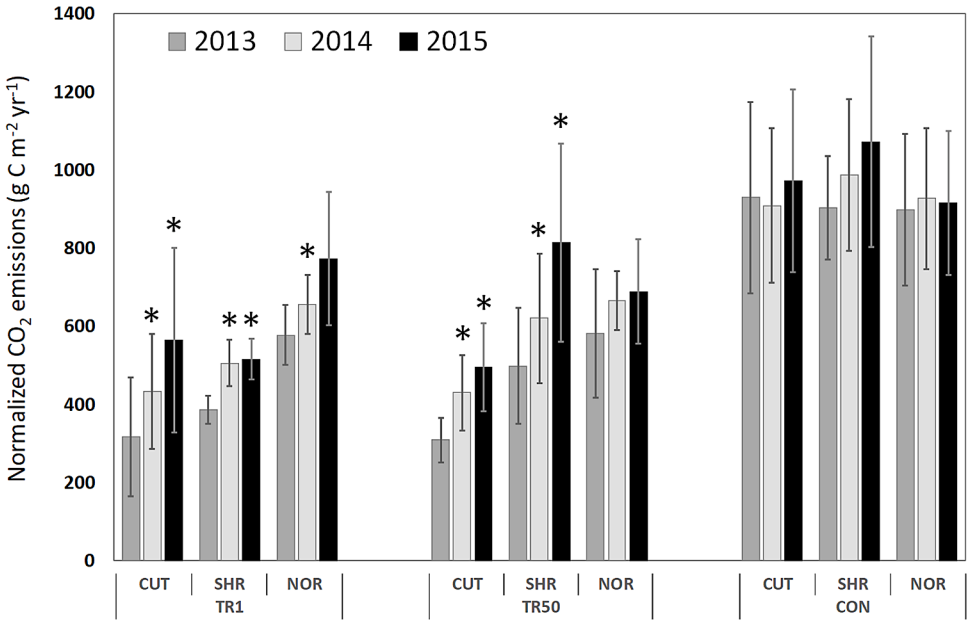

Fig. 7. Means of annual CO_2 emissions from the various treatments normalized for 2014 and 2015 by the CO_2 emissions from CON-NOR in 2013. The error bars show standard deviation, and the asterisks above the series indicate significant differences compared with year 2013 (Wilcoxon signed-rank test, $P < 0.05$). For abbreviations, see caption for *Fig. 5*.

zone are still sparse and can vary, due to different separation methods and vegetation types. A recent study conducted by incubating ingrowth mesh bags in Scots pine stands in central Sweden showed that R_{MY} in the growing season contributed 17% of R_{TOT} on average (Hagenbo et al., 2019). In other studies conducted in various temperate and boreal ecosystems, the authors estimated that R_{MY} may contribute 3%–31% of R_{TOT} (Andrew et al., 2014; Fenn et al., 2010; Heinemeyer et al., 2007, 2012; Moyano et al., 2008; Yan et al., 2019). Other potential reasons for our low R_{MY} values are discussed later.

In our experiment, respiration of dwarf shrubs (R_{SHR}) comprised 8% and ground vegetation other than shrubs (*e.g.* grasses, mosses and herbs) (R_{GMH}) comprised 10% of R_{TOT}. R_{GMH} was not partitioned further in our study, but other studies have found that the contribution of mosses can be substantial. For example, the average feather moss (*e.g.* splendid feather moss and Schreber's big red stem moss) respiration contributed 5–10% of the forest floor CO_2 efflux in three black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) forests in Alaska at different elevations (Vogel et al., 2005). Similarly, in a black spruce forest in Canada, the respiration of feather mosses (*e.g.* Schreber's big red stem moss) accounted for 7% of the R_{TOT} of the forest floor (Swanson & Flanagan, 2001). The roles played by ground vegetation species in forest floor CO_2 emissions have rarely been quantified, and thus new estimates are needed in the field. Nevertheless, the CO_2 emissions in our experiment also included the respiration of the aboveground parts of the ground vegetation, which was higher than the root respiration with young common dwarf shrub species in a laboratory experiment (Kulmala et al., 2017). The partitioning of ground vegetation above- and belowground respiratory sources is challenging under field conditions and thus remains to be investigated in further studies.

4.2. Effects of trenching

In the first research question, we were interested in determining how the presence of tree roots affects the forest floor CO_2 emissions. The results showed that heterotrophic respiration (R_H) increased over time in trenched plots without tree roots, presumably due to exclusion of tree roots and ectomycorrhizal fungi. This so-called 'Gadgil effect' was seen in both TR treatments throughout the years when the ground vegetation was also removed. When the yearly variation was normalized, the CO_2 emissions increased almost two-fold in the TR treatments without ground vegetation 3 yr after root removal, indicating a strong increase in soil heterotrophic microbial activities. The CO_2 emissions also increased significantly with dwarf shrubs in the TR treatments, but not with normal intact ground vegetation (NOR). The ground vegetation species seemed to suppress the heterotrophic activity, and since many of them support mycorrhizal fungi, this would be expected.

Gadgil & Gadgil (1971) observed that removing or leaving the cut roots or mixing the soil in trenched plots did not result in significant differences in the dry weight of the litter layer after 12 months. Later, Gadgil & Gadgil (1975) concluded that the effect was not caused by experimental artefacts, but was because of the increase in saprotrophic activity due to removal of mycorrhizae. Sterkenburg et al. (2018) concluded that roots and mycorrhizae reduced litter decomposition by limiting the N available for saprotrophs, and thus their results supported the Gadgil effect. In contrast, removal of tree roots in a field experiment in northern Sweden demonstrated a significant effect by reducing soil microbial respiration and litter decomposition while increasing the amount of available mineral N (Wardle & Zackrisson, 2005). Furthermore, removal of bilberry, lingonberry or three dwarf shrub species (bilberry, lingonberry and black crowberry (*Empetrum nigrum* L. ssp. *hermaphroditum* (Lange ex Hagerup) Böcher)), showed similar effects (Wardle & Zackrisson, 2005), suggesting that ericaceous dwarf shrubs, especially bilberry and lingonberry, also showed strong positive effects on microbial activity and reduction of mineral N in soil (Nilsson & Wardle, 2005).

In our study, the CO_2 emissions in some individual trenched plots increased in 2015 unexpectedly, indicating potential changes in the competitive situation. Theoretically, the tree roots could have grown inside the plots from under the mesh fabric (below 40 cm) and caused the increase in soil emissions measured. However, since the majority of pine roots grow in the top 10 cm at this forest site (Helmisaari et al., 2007), and since the distance between the trench and the collar is more than 30 cm and pioneering pine roots grow in this forest 2–5 cm yr^{-1} (Ding et al., 2021), it is highly unlikely that root ingrowth would have affected our results.

TR methods have been criticised because they may cause changes in soil moisture and nutrient mineralization, as well as additional CO_2 emissions, due to decomposition of residual roots (Epron et al., 1999). Trenched plots may be moister, due to lack of root water up-take compared with undisturbed soil, which may impact soil respiration. The moisture impact is limited (*e.g.* Lee et al., 2003; Wang et al., 2008) except under extremely high or low soil moistures (Comstedt et al., 2011; Hanson et al., 2000). Usage of permeable sheeting, such as mesh fabric that allows water and nutrients to flow in, but prevents tree root growth into the plots, may moderate moisture differences compared with isolation with impermeable plastic sheeting (Bond-Lamberty et al., 2011). Using the modelling approach, Comstedt et al. (2011) estimated that 29% of the CO_2 emissions was produced due to altered soil moisture and 16% from decomposing roots and mycelia in the first 5 months after TR in a Norway spruce forest. In a review by Subke et al. (2006), additional CO_2 emissions from decaying residual roots in TR studies contributed 12% of total emissions on average. However, the impacts of soil moisture and additional CO_2 emissions from dead root material in trenched plots were taken into account in our data analysis and, thus, are not likely to have caused the increased emissions in some individual plots in 2015.

4.3. Competition between plant groups

Regarding the second research question, our study showed a tendency for CO_2 emissions to increase with increasing ground vegetation in trenched plots, whereas such tendencies were not as pronounced when tree roots were present in the control (CON) plots. This would indicate that either the ground vegetation is adjusting to the presence of tree roots, or that heterotrophic activity is higher in plots with less ground vegetation or when all vegetation has been removed. Based on the comparison of normalized data, the latter may be the most probable outcome, because heterotrophic activity increased almost two-fold when tree roots were excluded from the plots. The level of CO_2 emissions in the CON treatments in which tree roots were present varied widely, suggesting that the emissions from tree roots were spatially very heterogeneous, even inside a homogeneous closed stand. Since aboveground tree physiology (*e.g.* photosynthesis) partly determines the activity of the roots (Heinemeyer et al., 2012; Högberg et al., 2001; Moyano et al., 2008), weather and soil conditions (*i.e.* effective temperature sum, soil moisture) may explain the slight decrease in CO_2 emissions in the CON plots containing tree roots. In contrast, variation in the emissions of trenched plots was generally low, even though it increased with time.

The activity of dwarf shrubs and their mycorrhizae may have decreased when accompanied by other ground vegetation, such as mosses or tree roots, in the same plot. Forest floor mosses affect soil moisture and temperature by controlling hydrological processes in the ground floor (Beringer et al., 2001; Clymo & Hayward, 1982) and acting as an insulator (Beringer et al., 2001; Bonan, 1991; O'Donnell et al., 2009; Soudzilovskaia et al., 2013). Removal of mosses and lichens also leads to increased growth of dwarf shrubs (Hautala et al., 2008). Suppressed growth by mosses may have been due to retention of N in ground-floor vegetation, as shown in the case of dwarf shrubs and Scots pine seedlings (Zackrisson et al., 1997, 1999). Gornall et al. (2007) discovered that the soil under thin or removed moss layers showed higher microbial biomass and activity due to warmer soil conditions,

which led to increased N availability to plants. The dominant feather mosses in our experimental plots, such as Schreber's big red stem moss, may have suppressed the activity of dwarf shrubs in the NOR plots, since the same increase in CO_2 emissions in 2015 was not detected in TR50 (mesh with 50 μm-pores) with NOR treatment as treatment with only dwarf shrubs (SHR). However, the interactions between bryophytes and ericaceous plants, and their impact on the forest floor CO_2 emissions are not well known and need to be resolved in future studies.

Riegel et al. (1992) showed in a ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) forest in Oregon that reduced competition of tree roots with the TR method increased the aboveground biomass of understorey vegetation by 53% in the first year and 94% in the second year. This was most likely driven by the increased water and nutrient availability for understorey use. In our study, increases in the CO_2 emissions of the ground vegetation could be partly explained by the similar increase in biomass due to reduced competition by tree roots, especially in TR50-SHR. However, ground vegetation biomasses were not measured in our study. Ground vegetation probably has its own effect on tree roots, especially in the long term, but this experimental design (*i.e.* small plots, mature trees) was not ideal for examining these phenomena.

4.4. Effect of mycorrhizal fungal mycelia on soil respiration

Based on the third research question, we expected to see higher CO_2 emissions in TR50 than TR1, since the mycorrhizal fungi could enter the plot through a pore size of 50 μm (TR50), but not through 1 μm (TR1). However, the annual emissions within these treatments were similar, especially in 2013–2014, indicating that no mycorrhizal hyphae or not enough to be detected were growing from the host roots outside the plot into the TR50 plots. When TR was conducted, the soil had to be excavated and mixed at least 20 cm around the plot to reach a suitable plot depth and to ensure that all tree roots were cut around the plot, and the plot itself was left untouched. It therefore required time for tree roots and tree root-associated mycorrhizal fungi first to grow back from outside into the plot through the fabric and then up to the collar inserted in the middle of the plot (the distance was in all approximately 50 cm). This distance decreased the errors caused by the lateral CO_2 flow through the soil column, but may have been too long to detect the main R_{MY}, especially in the first years. However, in the TR50 treatments in which dwarf shrubs (SHR) were left intact, their root systems were only cut around the plots and already supported ericoid mycorrhizal fungi inside the plot. Therefore, a faster and more probable scenario would have been the interaction of the ericaceous roots and their mycorrhizae through the 50-μm mesh from inside the plot to outside the plot.

The various ectomycorrhizal fungi form very distinctive external hyphal networks in soil (Agerer, 2001). Some mycorrhizal species form only very short-distance exploration types, whereas others form medium- or long-distance types that extend tens of centimetres from the mycorrhizal root tips (Agerer, 2001). The soil fungal community structure at our study site was described in detail by Santalahti et al. (2016), and the most common ectomycorrhizal fungal genus in the site (*Lactarius* Pers.), with more than 23% of all obtained quality-controlled DNA sequence reads analysed with pyrosequencing, commonly forms a so-called 'smooth' hyphal exploration type and does not grow more than a few millimetres away from the colonized root tip. The genera Piloderma Jülich and *Cortinarius* (Pers.) Gray (5.5% and 2.3% of all DNA sequence reads) form medium-distance, and the genus *Suillus* Gray (3.2% of all DNA sequence reads) forms long-distance exploration types (Agerer, 2001). Medium- and long-distance external hyphal structures seemingly were in the minority at our study site (Santalahti et al., 2016), which may explain the low values of R_{MY}. Since Scots pine root tips are highly mycorrhizal in boreal soils (Smith & Read, 2006), it suggests that R_{TREE} includes significant contributions from R_{MY}.

Experimental setups and practices for measuring R_{MY} vary among studies, and thus the results are not necessarily comparable. Although the pore size of the mesh was similar in most of the studies, varying 35–50 μm (Andrew et al., 2014; Fenn et al., 2010; Hagenbo et al., 2019; Heinemeyer et al., 2012; Moyano et al., 2008; Yan et al., 2019), there could have been differences in growth of the hyphae through the mesh fabric, due to the experimental setup (*e.g.* mixing of the soil, sand-filling, plot size, width of the trench) or the ingrowth time. Most of the higher estimates for R_{MY} were measured in broad-leaved forests; however, on average almost a six-fold higher R_{MY} was measured in Scots pine stands in central Sweden by Hagenbo et al. (2019), where they incubated harvested mesh bags. In temperate forest ecosystems, where the role of medium- and long-distance-type ectomycorrhizal fungi is greater (Ostonen et al., 2011), the R_{MY} may have been larger than in our study.

4.5. Fungal connections of dwarf shrubs

Regarding the fourth research question, we expected to see that the fungal mycelial connections increased the R_{SHR}, seen as a higher increase in CO_2 emissions from TR50 than from TR1. Indeed, R_{SHR} was higher when these fungal connections were allowed than it was without them. Interestingly, studies have shown that trees and dwarf shrubs may be interconnected via common mycorrhizal fungi (Sietiö et al., 2018; Villarreal-Ruiz et al., 2004). Villarreal-Ruiz et al. (2004) showed that a fungal isolate from a *Rhizoscyphus ericae* (D.J. Read) W.Y. Zhuang & Korf (formerly *Hymenoscyphus ericae* (D.J. Read) Korf & Kernan) species aggregate simultaneously formed both ectomycorrhizae with Scots pine and ericoid mycorrhizae with bilberry. Bilberry benefitted from a fungal isolate of a *Rhizoscyphus ericae* aggregate (Villarreal-Ruiz et al., 2004), which may have been due to improved nutrition by mycorrhizae, as demonstrated in heathland ecosystems (Read, 1991). The *R. ericae* aggregate enhanced root growth and the number of root tips in bilberry, and although the effect was similar, it was not as pronounced as when the fungus also formed ectomycorrhizal interconnections simultaneously with Scots pine (Villarreal-Ruiz et al., 2004). Sietiö et al. (2018) found that the same fungal species received labelled ^{13}C from both ericaceous dwarf shrubs and Scots pine seedlings, indicating a potential for ericaceous-pine connections in the same forest soil in which our study was performed. Our results support the findings that dwarf shrubs may have fungal interconnections with boreal trees via ericoid, endophytic, or ectomycorrhizal fungi (see Vrålstad, 2004), but further determination would require tracing (*e.g.* with the labelled ^{13}C). The functional benefits of simultaneous formation of ecto- and ericoid mycorrhizal symbioses and quantitative importance in soil C dynamics are still unknown.

5. Conclusion

Our results show that differentiating the CO_2 sources of soil and ground level vegetation gives a deeper understanding of the soil-vegetation feedbacks. The presence of tree roots reduced the differences in respiration rates between the various ground vegetation treatments presuming intense competition between roots in the soil. Meanwhile, heterotrophic respiration increased in trenched treatments without tree roots and ground vegetation over time, due to so-called the 'Gadgil effect'. In the absence of tree roots, but when hyphal access was allowed, the respiration in the dwarf shrub treatment increased throughout the study years. This could indicate the presence of fungal connections of dwarf shrubs to outside the plots via their ericoid mycorrhizae, potentially with other plants. A similar increase in respiration was not seen when dwarf shrubs were accompanied by other ground-floor plants, suggesting that other plants, such as mosses, suppressed the dwarf shrub activity.

Better understanding of soil C dynamics and its consequences for soil C balance are needed, especially regarding soil C stock modelling in a changing climate. Since mycorrhizal fungi influence the quality of C residues and therefore greatly affect C cycling in these forests, further research on fungal connections would improve our understanding of

competitive traits in boreal forest soil between plants and microbes. Combining our experimental setup with ^{13}C-labelling would make it possible to further study the connections between plants via mycorrhizae under field conditions.

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.

Acknowledgements

This study was supported by the Academy of Finland (grant no. 263858, 277623, 2884941, 292669, 296116, and 307192), the Academy of Finland: Finnish Centre of Excellence Programme (grant no. 272041), the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement no. 757695), the University of Helsinki Funds, and Kone Foundation. We thank Matti Loponen and Sirpa Rantanen for help with the soil CO_2 flux and moisture measurements and Teppo Mattson for help with the statistics of normalized CO_2 data.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2020.108266.

Appendix

The soil was sampled to determine the biomasses of living pine, dwarf shrub, grass, and herb roots smaller than 5 mm in diameter in June 2011 (see *Table A.1*). In all, 15 soil cores, diameter 40 mm, five from each of the three sample areas, were taken from the site down to a maximum depth of 30 cm. The roots were washed free of soil and divided into living and dead tissue, diameter (< 1, 1–2 and > 2 mm), Scots pine roots and understorey (dwarf shrubs, grasses, and herbs) roots and rhizomes. The samples sorted were dried at 70.0°C for 48 h and weighed. The procedure is described in detail in Helmisaari et al. (2007). For larger roots, we used the estimations by Ilvesniemi et al. (2009), who studied the root biomass and size fractions and showed that the annual total root mass (m_{tot}) at the experimental site rose from 1.92 to 2.58 kg m^{-2} during 2001–2008. Extrapolation from these values resulted in an m_{tot} value of 3.07 kg m^{-2} in 2013. Roots smaller than 5 mm in diameter were subtracted from m_{tot} and the rest were divided into size classes (diameter 5–10, 10–20, >20 mm) according to the proportions presented in Ilvesniemi & Liu (2001). The root masses in the various size classes and functional groups are presented in *Table A.1*.

There were no significant differences between the treatments (trenching (TR) or vegetation) in their root litter mass loss rates (*Fig. S1*). Thus, the same mass loss values were used for all treatments: 18.6% in 1 yr, 32.1% in 2 yr and 41.2% in 3 yr, resulting in 18.6%, 16.6% and 13.4% annual decrease in the root mass in the first, second and third year, respectively. Note that the latter values were calculated from the actual available root litter mass early in the year. These values were used for the decomposition (d) of roots in the 2–5-mm size class, whereas the d in the smallest size class (< 2 mm) was assumed to be twice as fast for all 3 years. Palviainen & Finér (2015) showed that the k-value (mean annual decrease) for 5–10-cm-diameter roots was 3.4%, which we used for the largest size class (mean diameter 7.5 cm) for all 3 years. Then, we estimated the d for the first year for the missing size classes (5–10 mm and 10–20 mm) with a fitted power equation, using the three size classes (*Fig. S2*).

For these two size classes (s), the annual decomposition rates for years 2 and 3 were estimated, using the decomposition rate of the first years and the ratio between the two rates in the 2–5-mm size class:

$$d_s^{y+1} = \frac{d_{2-5}^{y+1}}{d_{2-5}^{y}} d_s^{y} \tag{A.1}$$

Note that the year was considered as beginning on 1 October and ending 30 September in the following year.

The annually decomposed root mass D_{tr}^{y} (kg C m^{-2} yr^{-1}) in year y for the various vegetation and trenching treatments (*Fig. S3*) (tr), was determined for every treatment as a sum of the decomposed root mass in different size classes (s), as follows:

$$D_{tr}^{y} = a \sum_{s=1}^{5} m_s^{y-1} d_s^{y} \tag{A.2}$$

where a is the percentage of C in the root biomass (0.5 g C g^{-1}), m_s^{y-1} is the dead root mass of size class s late in the previous year, and d_s^{y} the decomposition rate of size class s in year y.

We assumed that during the construction of the plots in July 2012, all roots died in the root exclusion (trenched) plots, whereas in the control (CON) plots with the ground vegetation removed (CUT) or all the other ground vegetation cut except the dwarf shrubs (SHR) treatments, only grass roots, or dwarf shrub and grass roots died and began slowly to decompose. The d between 1 July and 30 September in 2012 was assumed to follow temperature as estimated in 2013.

Table A.1
Root biomasses (kg m^{-2}) (m_s^0) used in different size classes at the beginning of the experiment.

Size class (mm)	s	Pine	Shrubs	Grasses
<2	1	0.142*	0.293*	0.059*
2–5	2	0.079*	0.154*	–
5–10	3	0.167 Derived	–	–
10–20	4	0.241 Derived	–	–
>20	5	2.438 Derived	–	–

* Ding et al., 2021 in prep.

In the decayed carbon pool (D^y_{tr},), the C was distributed to correspond to the CO_2 emissions throughout the season, assuming that the daily decomposition rate in year y and treatment tr $d^y_{tr}(t)$, was related to the mean temperature (T) in soil horizon A (T_A (t)) by a Q_{10}-type of exponential equation:

$$d^y_{tr}(t) = r^y_{tr} Q_{10}^{\frac{T_A(t)}{10}} \quad (A.3)$$

where Q_{10} is set to 2.5 and r^y_{tr} estimated by Excel Solver so that the sum of the daily rates of d^y_{tr} results in D^y_{tr}.

The corrected CO_2 emissions $F_i(t)$ at moment t in year y in treatment tr (kg C m^{-2} d^{-1}) were determined as the difference between the measured flux ($f_i(t)$), at plot i and the flux originating from the d of dead root litter at that treatment, $d^y_{tr}(t)$:

$$F_i(t) = f_i(t) - d^y_{tr}(t) \quad (A.4)$$

References

Adamczyk, B., Ahvenainen, A., Sietiö, O.-M., Kanerva, S., Kieloaho, A.-J., Smolander, A., Kitunen, V., Saranpää, P., Laakso, T., Straková, P., Heinonsalo, J., 2016. The contribution of ericoid plants to soil nitrogen chemistry and organic matter decomposition in boreal forest soil. Soil Biol. Biochem. 103, 394–404. https://doi.org/10.1016/j.soilbio.2016.09.016.

Adamczyk, B., Sietiö, O.-M., Biasi, C., Heinonsalo, J., 2019a. Interaction between tannins and fungal necromass stabilizes fungal residues in boreal forest soils. New Phytol 223 (1), 16–21. https://doi.org/10.1111/nph.15729.

Adamczyk, B., Sietiö, O.-M., Straková, P., Prommer, J., Wild, B., Hagner, M., Pihlatie, M., Fritze, H., Richter, A., Heinonsalo, J., 2019b. Plant roots increase both decomposition and stable organic matter formation in boreal forest soil. Nature commun 10, 3982. https://doi.org/10.1038/s41467-019-11993-1.

Agerer, R., 2001. Exploration types of ectomycorrhizae. Mycorrhiza 11 (2), 107–114. https://doi.org/10.1007/s005720100108.

Andrew, C.J., Van Diepen, L.T., Miller, R.M., Lilleskov, E.A., 2014. Aspen-associated mycorrhizal fungal production and respiration as a function of changing CO_2, O_3 and climatic variables. Fungal Ecol 10, 70–80. https://doi.org/10.1016/j.funeco.2013.10.005.

Bäck, J., Aalto, J., Henriksson, M., Hakola, H., He, Q., Boy, M., 2012. Chemodiversity of a Scots pine stand and implications for terpene air concentrations. Biogeosciences 9 (2), 689–702. https://doi.org/10.5194/bg-9-689-2012.

Beringer, J., Lynch, A.H., Chapin, F.S., Mack, M., Bonan, G.B., 2001. The representation of arctic soils in the land surface model: The importance of mosses. J. Clim. 14 (15), 3324–3335. https://doi.org/10.1175/1520-0442(2001)014<3324:TROASI>2.0.CO;2.

Bonan, G.B., 1991. A biophysical surface energy budget analysis of soil temperature in the Boreal forests of interior Alaska. Water Resour. Res. 27 (5), 767–781. https://doi.org/10.1029/91WR00143.

Bond-Lamberty, B., Wang, C., Gower, S.T., 2004. A global relationship between the heterotrophic and autotrophic components of soil respiration. Global Change Biol 10 (10), 1756–1766. https://doi.org/10.1111/j.1365-2486.2004.00816.x.

Bond-Lamberty, B., Bronson, D., Bladyka, E., Gower, S.T., 2011. A comparison of trenched plot techniques for partitioning soil respiration. Soil Biol. Biochem. 43 (10), 2108–2114. https://doi.org/10.1016/j.soilbio.2011.06.011.

Cajander, A.K., 1926. The theory of forest types. Acta For. Fenn. 29, 1–108. https://doi.org/10.14214/aff.7193.

Clemmensen, K.E., Bahr, A., Ovaskainen, O., Dahlberg, A., Ekblad, A., Wallander, H., Stenlid, J., Finlay, R.D., Wardle, D.A., Lindahl, B.D., 2013. Roots and associated fungi drive long-term carbon sequestration in boreal forest. Science 339 (6127), 1615–1618. https://doi.org/10.1126/science.1231923.

Clymo, R., Hayward, P., 1982. The Ecology of *Sphagnum*. In: Smith, A.J.E. (Ed.), Bryophyte Ecology. Springer, Dordrecht, pp. 229–289. https://doi.org/10.1007/978-94-009-5891-3_8.

Comstedt, D., Boström, B., Ekblad, A., 2011. Autotrophic and heterotrophic soil respiration in a Norway spruce forest: Estimating the root decomposition and soil moisture effects in a trenching experiment. Biogeochemistry 104, 121–132. https://doi.org/10.1007/s10533-010-9491-9.

Ding, Y., Schiestl-Aalto, P., Helmisaari, H.S., Makita, N., Ryhti, K., Kulmala, L., 2021. Temperature and moisture dependence of daily growth of Scots pine (*Pinus sylvestris* L.) roots in southern Finland. Tree Physiol 40 (2), 272–283. https://doi.org/10.1093/treephys/tpz131.

Epron, D., Farque, L., Lucot, E., Badot, P., 1999. Soil CO_2 efflux in a beech forest: The contribution of root respiration. Ann. For. Sci. 56 (4), 289–295. https://doi.org/10.1051/forest:19990403.

Fenn, K.M., Malhi, Y., Morecroft, M.D., 2010. Soil CO_2 efflux in a temperate deciduous forest: Environmental drivers and component contributions. Soil Biol. Biochem. 42 (10), 1685–1693. https://doi.org/10.1016/j.soilbio.2010.05.028.

Fernandez, C.W., Kennedy, P.G., 2015. Revisiting the 'Gadgil effect': do interguild fungal interactions control carbon cycling in forest soils? New Phytol. 209 (4), 1382–1394. https://doi.org/10.1111/nph.13648.

Gadgil, P.D., Gadgil, R.L., 1975. Suppression of litter decomposition by mycorrhizal roots of *Pinus radiata*. N. Z. J. For. Sci 5 (1), 33–41.

Gadgil, R.L., Gadgil, P.D., 1971. Mycorrhiza and litter decomposition. Nature 233, 133. https://doi.org/10.1038/233133a0.

Gornall, J., Jónsdóttir, I., Woodin, S., Van der Wal, R., 2007. Arctic mosses govern below-ground environment and ecosystem processes. Oecologia, 153 931–941. https://doi.org/10.1007/s00442-007-0785-0.

Goulden, M.L., Crill, P.M., 1997. Automated measurements of CO_2 exchange at the moss surface of a black spruce forest. Tree Physiol. 17 (8-9), 537–542. https://doi.org/10.1093/treephys/17.8-9.537.

Hagenbo, A., Hadden, D., Clemmensen, K.E., Grelle, A., Manzoni, S., Mölder, M., Ekblad, A., Fransson, P., 2019. Carbon use efficiency of mycorrhizal fungal mycelium increases during the growing season but decreases with forest age across a *Pinus sylvestris* chronosequence. J. Ecol. 107 (6), 2808–2822. https://doi.org/10.1111/1365-2745.13209.

Hanson, P.J., Edwards, N.T., Garten, C.T., Andrews, J.A., 2000. Separating root and soil microbial contributions to soil respiration: A review of methods and observations. Biogeochemistry 48, 115–146. https://doi.org/10.1023/A:1006244819642.

Hari, P., Kulmala, M., 2005. Station for measuring Ecosystem–Atmosphere relations (SMEAR II). Bor. Environ. Res. 10, 315–322.

Hautala, H., Tolvanen, A., Nuortila, C., 2008. Recovery of pristine boreal forest floor community after selective removal of understorey, ground and humus layers. Plant Ecol. 194, 273–282. https://doi.org/10.1007/s11258-007-9290-0.

Heinemeyer, A., Hartley, I.P., Evans, S.P., Carreira de La Fuente, J.A., Ineson, P., 2007. Forest soil CO_2 flux: uncovering the contribution and environmental responses of ectomycorrhizas. Global Change Biol 13 (8), 1786–1797. https://doi.org/10.1111/j.1365-2486.2007.01383.x.

Heinemeyer, A., Wilkinson, M., Vargas, R., Subke, J.-A., Casella, E., Morison, J.I.L., Ineson, P., 2012. Exploring the "overflow tap" theory: Linking forest soil CO_2 fluxes and individual mycorrhizosphere components to photosynthesis. Biogeosciences 9, 79–95. https://doi.org/10.5194/bg-9-79-2012.

Helmisaari, H., Derome, J., Nöjd, P., Kukkola, M., 2007. Fine root biomass in relation to site and stand characteristics in Norway spruce and Scots pine stands. Tree Physiol 27 (10), 1493–1504. https://doi.org/10.1093/treephys/27.10.1493.

Högberg, P., Nordgren, A., Buchmann, N., Taylor, A.F.S., Ekblad, A., Högberg, M.N., Nyberg, G., Ottosson-Löfvenius, M., Read, D.J., 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411, 789–792. https://doi.org/10.1038/35081058.

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biom. J. 50 (3), 346–363. https://doi.org/10.1002/bimj.200810425.

Ilvesniemi, H., Liu, C., 2001. Biomass distribution in a young Scots pine stand. Bor. Environ. Res. 6, 3–8.

Ilvesniemi, H., Levula, J., Ojansuu, R., Kolari, P., Kulmala, L., Pumpanen, J., Launiainen, S., Vesala, T., Nikinmaa, E., 2009. Long-term measurements of the carbon balance of a boreal Scots pine dominated forest ecosystem. Bor. Environ. Res. 14, 731–753.

Ilvesniemi, H., Pumpanen, J., Duursma, R., Hari, P., Keronen, P., Kolari, P., Kulmala, M., Mammarella, I., Nikinmaa, E., Rannik, Ü., Pohja, T., Siivola, E., Vesala, T., 2010. Water balance of a boreal Scots pine forest. Bor. Environ. Res. 15, 375–396.

Janssens, I.A., Lankreijer, H., Matteucci, G., Kowalski, A.S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grünwald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E.J., Grelle, A., Rannik, Ü., Morgenstern, K., Oltchev, S., Clement, R., Guðmundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, C., Jensen, N.O., Vesala, T., Granier, A., Schulze, E.-D., Lindroth, A., Dolman, A.J., Jarvis, P.G., Ceulemans, R., Valentini, R., 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. Global Change Biol. 7 (3), 269–278. https://doi.org/10.1046/j.1365-2486.2001.00412.x.

Kallenbach, C.M., Frey, S.D., Grandy, A.S., 2016. Direct evidence for microbial-derived soil organic matter formation and its ecophysiological controls. Nat. Commun. 7, 13630. https://doi.org/10.1038/ncomms13630.

Kolari, P., Kulmala, L., Pumpanen, J., Launiainen, S., Ilvesniemi, H., Hari, P., Nikinmaa, E., 2009. CO_2 exchange and component CO_2 fluxes of a boreal Scots pine forest. Bor. Environ. Res. 14, 761–783.

Kulmala, L., Pumpanen, J., Kolari, P., Muukkonen, P., Hari, P., Vesala, T., 2011. Photosynthetic production of ground vegetation in different-aged Scots pine (*Pinus sylvestris*) forests. Can. J. For. Res. 41 (10), 2020–2030. https://doi.org/10.1139/x11-121.

Kulmala, L., Dominguez Carrasco, M., Heinonsalo, J., 2017. The differences in carbon dynamics between boreal dwarf shrubs and Scots pine seedlings in a microcosm study. J. Plant Ecol. 11 (5), 709–716. https://doi.org/10.1093/jpe/rtx051.

Kulmala, L., Pumpanen, J., Kolari, P., Dengel, S., Berninger, F., Köster, K., Matkala, L., Vanhatalo, A., Vesala, T., Bäck, J., 2019. Inter- and intra-annual dynamics of photosynthesis differ between forest floor vegetation and tree canopy in a subarctic Scots pine stand. Agric. For. Meteorol. 271, 1–11. https://doi.org/10.1016/j.agrformet.2019.02.029.

Kutsch, W.L., Bahn, M., Heinemeyer, A. (Eds.), 2010. Soil Carbon Dynamics: An Integrated Methodology. Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9780511711794.

Kuzyakov, Y., 2006. Sources of CO_2 efflux from soil and review of partitioning methods. Soil Biol. Biochem. 38 (3), 425–448. https://doi.org/10.1016/j.soilbio.2005.08.020.

Kuzyakov, Y., Xu, X., 2013. Competition between roots and microorganisms for nitrogen: Mechanisms and ecological relevance. New Phytol. 198 (3), 656–669. https://doi.org/10.1111/nph.12235.

Lee, M.S., Nakane, K., Nakatsubo, T., Koizumi, H., 2003. Seasonal changes in the contribution of root respiration to total soil respiration in a cool-temperate deciduous forest. In: Abe, J. (Ed.), Roots: The Dynamic Interface between Plants and the Earth. Springer, Dordrecht, pp. 311–318. https://doi.org/10.1007/978-94-017-2923-9_30.

Lavigne, M.B., Boutin, R., Foster, R.J., Goodine, G., Bernier, P.Y., Robitaille, G., 2003. Soil respiration responses to temperature are controlled more by roots than by decomposition in balsam fir ecosystems. Can. J. For. Res. 33 (9), 1744–1753. https://doi.org/10.1139/x03-090.

Leake, J.R., Donnelly, D.P., Saunders, E.M., Boddy, L., Read, D.J., 2001. Rates and quantities of carbon flux to ectomycorrhizal mycelium following ^{14}C pulse labeling of *Pinus sylvestris* seedlings: effects of litter patches and interaction with a wood-decomposer fungus. Tree Physiol 21 (2-3), 71–82. https://doi.org/10.1093/treephys/21.2-3.71.

Morén, A., Lindroth, A., 2000. CO_2 exchange at the floor of a boreal forest. Agric. For. Meteorol. 101 (1), 1–14. https://doi.org/10.1016/S0168-1923(99)00160-4.

Moyano, F.E., Kutsch, W.L., Rebmann, C., 2008. Soil respiration fluxes in relation to photosynthetic activity in broad-leaf and needle-leaf forest stands. Agric. For. Meteorol. 148 (1), 135–143. https://doi.org/10.1016/j.agrformet.2007.09.006.

Mäkelä, A., Pulkkinen, M., Kolari, P., Lagergren, F., Berbigier, P., Lindroth, A., Loustau, D., Nikinmaa, E., Vesala, T., Hari, P., 2008. Developing an empirical model of stand GPP with the LUE approach: analysis of eddy covariance data at five contrasting conifer sites in Europe. Global change biol 14, 92–108. https://doi.org/10.1111/j.1365-2486.2007.01463.x.

Nilsson, M.-C., Wardle, D.A., 2005. Understory vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. Front. Ecol. Environ. 3 (8), 421–428. https://doi.org/10.1890/1540-9295(2005)003[0421:UVAAFE]2.0.CO;2.

O'Donnell, J.A., Romanovsky, V.E., Harden, J.W., McGuire, A.D., 2009. The effect of moisture content on the thermal conductivity of moss and organic soil horizons from black spruce ecosystems in interior Alaska. Soil Sci. 174 (12), 646–651. https://doi.org/10.1097/ss.0b013e3181c4a7f8.

Ostonen, I., Helmisaari, H.-S., Borken, W., Tedersoo, L., Kukumägi, M., Bahram, M., Lindroos, A.-J., Nõjd, P., Uri, P., Merilä, P., Asi, E., Lõhmus, K., 2011. Fine root foraging strategies in Norway spruce forests across a European climate gradient. Global Change Biol. 17 (12), 3620–3632. https://doi.org/10.1111/j.1365-2486.2011.02501.x.

Palviainen, M., Finér, L., 2015. Decomposition and nutrient release from Norway spruce coarse roots and stumps–a 40-year chronosequence study. For. Ecol. Manage. 358, 1–11. https://doi.org/10.1016/j.foreco.2015.08.036.

Pirinen, P., Simola, H., Aalto, J., Kaukoranta, J., Karlsson, P., Ruuhela, R., 2012. Tilastoja Suomen ilmastosta 1981 - 2010 – Climatological statistics of Finland 1981–2010. Ilmatieteen laitos – Finnish Meteorological Institute.

Pregitzer, K.S., King, J.S., Burton, A.J., Brown, S.E., 2000. Responses of tree fine roots to temperature. New Phytol 147 (1), 105–115. https://doi.org/10.1046/j.1469-8137.2000.00689.x.

Pumpanen, J.S., Kulmala, L., Linden, A.S., Kolari, P.P., Nikinmaa, E.H., Hari, P.K.J., 2015. Seasonal dynamics of autotrophic respiration in boreal forest soil estimated by continuous chamber measurements. Bor. Environ. Res., 20 637–650.

R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Raich, J., Schlesinger, W.H., 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus B: Chem. Phys. Meteorol. 44 (2), 81–99. https://doi.org/10.3402/tellusb.v44i2.15428.

Read, D., 1991. Mycorrhizas in ecosystems. Experientia 47, 376–391. https://doi.org/10.1007/BF01972080.

Read, D.J., Perez-Moreno, J., 2003. Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance. New Phytol. 157 (3), 475–492. https://doi.org/10.1046/j.1469-8137.2003.00704.x.

Riegel, G.M., Miller, R.F., Krueger, W.C., 1992. Competition for resources between understory vegetation and overstory *Pinus ponderosa* in northeastern Oregon. Ecol. Appl. 2 (1), 71–85. https://doi.org/10.2307/1941890.

Santalahti, M., Sun, H., Jumpponen, A., Pennanen, T., Heinonsalo, J., 2016. Vertical and seasonal dynamics of fungal communities in boreal Scots pine forest soil. FEMS Microbiol. Ecol. 92 (11) fiw170. https://doi.org/10.1093/femsec/fiw170.

Schiestl-Aalto, P., Ryhti, K., Mäkelä, A., Peltoniemi, M., Bäck, J., Kulmala, L., 2019. Analysis of the NSC storage dynamics in tree organs reveals the allocation to belowground symbionts in the framework of whole tree carbon balance. Front. For. Global Change 2, 17. https://doi.org/10.3389/ffgc.2019.00017.

Sietiö, O.-M, Tuomivirta, T., Santalahti, M., Kiheri, H., Timonen, S., Sun, H., Fritze, H., Heinonsalo, J., 2018. Ericoid plant species and *Pinus sylvestris* shape fungal communities in their roots and surrounding soil. New Phytol. 218 (2), 738–751. https://doi.org/10.1111/nph.15040.

Smith, S.E., Read, D.J., 2008. Mycorrhizal Symbiosis, (3rd ed.). Academic Press, Amsterdam.

Soudzilovskaia, N.A., Bodegom, P.M., Cornelissen, J.H., 2013. Dominant bryophyte control over high-latitude soil temperature fluctuations predicted by heat transfer traits, field moisture regime and laws of thermal insulation. Funct. Ecol. 27 (6), 1442–1454. https://doi.org/10.1111/1365-2435.12127.

Sterkenburg, E., Clemmensen, K.E., Ekblad, A., Finlay, R.D., Lindahl, B.D., 2018. Contrasting effects of ectomycorrhizal fungi on early and late stage decomposition in a boreal forest. ISME J 12, 2187–2197. https://doi.org/10.1038/s41396-018-0181-2.

Subke, J.A., Inglima, I., Francesca Cotrufo, M., 2006. Trends and methodological impacts in soil CO_2 efflux partitioning: a meta-analytical review. Global Change Biol 12 (6), 921–943. https://doi.org/10.1111/j.1365-2486.2006.01117.x.

Swanson, R.V., Flanagan, L.B., 2001. Environmental regulation of carbon dioxide exchange at the forest floor in a boreal black spruce ecosystem. Agric. For. Meteorol. 108 (3), 165–181. https://doi.org/10.1016/S0168-1923(01)00243-X.

Treseder, K., Allen, M., 2000. Mycorrhizal fungi have a potential role in soil carbon storage under elevated CO_2 and nitrogen deposition. New Phytol 147 (1), 189–200. https://doi.org/10.1046/j.1469-8137.2000.00690.x.

Vesala, T., Suni, T., Rannik, Ü, Keronen, P., Markkanen, T., Sevanto, S., Grönholm, T., Smolander, A., Kulmala, M., Ilvesniemi, H., Ojansuu, R., Uotila, A., Levula, J., Mäkelä, A., Pumpanen, J., Kolari, P., Kulmala, L., Altimir, N., Berninger, F., Nikinmaa, E., Hari, P., 2005. Effect of thinning on surface fluxes in a boreal forest. Global Biogeochem. Cycles 19 (2). https://doi.org/10.1029/2004GB002316.

Villarreal-Ruiz, L., Anderson, I.C., Alexander, I.J., 2004. Interaction between an isolate from the *Hymenoscyphus ericae* aggregate and roots of *Pinus* and *Vaccinium*. New Phytol 164 (1), 183–192. https://doi.org/10.1111/j.1469-8137.2004.01167.x.

Vogel, J.G., Valentine, D.W., Ruess, R.W., 2005. Soil and root respiration in mature Alaskan black spruce forests that vary in soil organic matter decomposition rates. Can. J. For. Res. 35 (1), 161–174. https://doi.org/10.1139/x04-159.

Vrålstad, T., 2004. Are ericoid and ectomycorrhizal fungi part of a common guild? New Phytol. 164 (1), 7–10. https://doi.org/10.1111/j.1469-8137.2004.01180.x.

Wang, X., Zhu, B., Wang, Y., Zheng, X., 2008. Field measures of the contribution of root respiration to soil respiration in an alder and cypress mixed plantation by two methods: trenching method and root biomass regression method. Eur. J. For. Res. 127, 285. https://doi.org/10.1007/s10342-008-0204-z.

Wardle, D.A., Zackrisson, O., 2005. Effects of species and functional group loss on island ecosystem properties. Nature, 435 806–810. https://doi.org/10.1038/nature03611.

Yan, T., Qu, T., Song, H., Sun, Z., Zeng, H., Peng, S., 2019. Ectomycorrhizal fungi respiration quantification and drivers in three differently-aged larch plantations. Agric. For. Meteorol. 265, 245–251. https://doi.org/10.1016/j.agrformet.2018.11.024.

Zackrisson, O., Nilsson, M., Dahlberg, A., Jäderlund, A., 1997. Interference mechanisms in conifer-Ericaceae-feathermoss communities. Oikos 78 (2), 209–220. https://doi.org/10.2307/3546287.

Zackrisson, O., Nilsson, M., Jäderlund, A., Wardle, D.A., 1999. Nutritional effects of seed fall during mast years in boreal forest. Oikos 84 (1), 17–26. https://doi.org/10.2307/3546862.