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2022-04-15

pö M ä k i , M , Ryhti , K , Fer , I , dupek , B , Vestin , P , Roland , M , Lehtonen , A , Bäck , J , Heinonsalo , J , Pumpanen , J & Kulmala , L 2022 , ' Heterotrophic and rhizospheric respiration in coniferous forest soils along a latitudinal gradient ' , Agricultural and Forest Meteorology , vol. 317 , 108876 . <https://doi.org/10.1016/j.agrformet.2022.108876>

<http://hdl.handle.net/10138/341555>

<https://doi.org/10.1016/j.agrformet.2022.108876>

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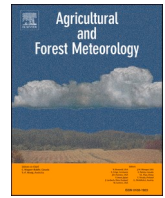
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Heterotrophic and rhizospheric respiration in coniferous forest soils along a latitudinal gradient

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ARTICLE INFO

Keywords:

Chamber measurements
Land-surface modelling
Soil carbon
Soil respiration
Trenching
CO₂ efflux
Scots pine
Norway spruce
Forest soil
Carbon cycle

ABSTRACT

Northern forest soils are a major carbon (C) reservoir of global importance. To estimate how the C balance in these soils will change, the roles of tree roots and soil microbes in C balance should first be decoupled. This study determined how the activity of heterotrophs and tree roots together with root-associated microbes in the rhizosphere varies in coniferous forest soils in boreal, hemiboreal, and temperate climates along a latitudinal gradient using a trenching approach. We created experimental plots without living tree roots, measured soil respiration (CO₂ efflux) from these and from unmanipulated plots using the chamber technique, and partitioned the efflux into root-rhizosphere (R_R) and heterotrophic (R_H) respiration. The share of R_R in ecosystem gross primary production (GPP) decreased from north to south in the Scots pine (*Pinus sylvestris* L.) and the Norway spruce (*Picea abies* (L.) Karst.) forests, with the exception of a mixed site, where the share of R_R in GPP varied strongly between the years. R_R per ground area and per root biomass were mainly independent of climate within the gradient. R_H per ground area increased from north to south with temperature, while R_H per soil C did not change with temperature. Soil moisture did not significantly affect the respiration components in the northernmost site, whereas soil moisture was positively connected with R_H and negatively with R_R in other Scots pine sites and positively connected with R_R in pure Norway spruce stands. The dynamic ecosystem model LPJ-GUESS was able to capture the seasonal dynamics of R_H and R_R at the sites, but overall accuracy varied markedly between the sites, as the model underestimated R_H in the southern site and R_R elsewhere. Our study provides knowledge about the nature of soil respiration components. The valuable insights can be used in more accurate land-ecosystem modelling of forest ecosystems.

1. Introduction

Northern forest ecosystems, and especially soils, are a major global carbon (C) sink and reservoir (Bradshaw and Warkentin, 2015). Photosynthesis (i.e. gross primary production; GPP) will likely be accelerated by increasing atmospheric CO₂ concentration and temperature, thus possibly also enhancing C sequestration in northern forest soils (Sakalli et al., 2017). However, it is not clear whether the increased

GPP will result in increased biomass growth due to nutrient limitation and increased soil carbon accumulation due to possible changes in plant belowground carbon allocation and microbial decomposition of the soil organic matter.

The carbon dioxide (CO₂) efflux released through belowground activities is called *soil respiration* (R_S). It consists of two main components: 1) autotrophic root and rhizosphere respiration (R_R) and 2) heterotrophic soil respiration (R_H) mainly by soil microbes decomposing litter and

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<https://doi.org/10.1016/j.agrformet.2022.108876>

Received 7 July 2021; Received in revised form 7 February 2022; Accepted 11 February 2022

Available online 26 February 2022

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SOM (Ryan and Law, 2005 Subke et al., 2006;). The seasonality of R_S is influenced by many biological and abiotic factors, e.g. soil temperature, soil water availability, plant phenology, root activity, and C availability as litter and root substrates (Lloyd and Taylor, 1994 Davidson et al., 1998; Subke et al., 2006; Savage et al., 2013; Han and Jin, 2018). R_R and R_H may, however, respond differently to environmental changes such as an increase in soil temperature (Boone et al., 1998 Lee et al., 2003; Wang et al., 2014;) and changes in soil water content. If soil temperature increases but soil water content (SWC) decreases simultaneously, microbial abundance and R_S may decline in drier boreal soils (Allison and Treseder, 2008). Indeed, decreasing SWC has already been observed to decrease R_S in temperate and boreal forests (Davidson et al., 1998 Pumpanen et al., 2003; Kolari et al., 2009;). With changes in weather patterns and higher occurrence of droughts, soil moisture may become a more important factor determining the C exchange in boreal forests during the growing seasons, as the transpirational demand of trees increases with temperature (Dai 2013; Liu et al., 2020).

Within a climate zone, forest ecosystems differ in many ways, including soil type, soil moisture conditions, and nutrient availability, reflecting not only to the ecosystem dynamics but also to main tree species. As R_S varies accordingly, it is important to determine how the different CO_2 sources in the forest floor respond to the increase in temperature and GPP in different forest types under different climate conditions. Trees are known to allocate more C to roots and their fungal symbionts on nutrient-poor soils compared to nutrient-rich soils to enhance nutrient availability in the rhizosphere (Baret et al., 2015). Thus, the ratio between R_R and GPP could increase with decreasing mean temperature, when the availability of nutrients in soil will decrease. Measurements for decoupling the various respiration components can be laborious and expensive (e.g. isotopic methods) and are not possible to conduct in field conditions in all ecosystems and study sites. Thus, assessing the overall feedback of changing climate in forested ecosystems requires dynamic models that simulate the activity and responses of a heterotrophic community, root-rhizosphere, and soil C reservoirs. Although the model formulations and results widely vary (Todd-Brown et al., 2013; Hashimoto et al., 2017), the largest uncertainties and disagreements between decomposition models and observations are reported at high temperatures and at high and low soil moisture (Sierra et al., 2015).

In this study, we aimed to quantify and describe the nature of R_R and R_H in Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) sites in different climates. We had two specific research questions:

- 1 How does the ratio between R_R and GPP as an indicator of below-ground C allocation currently vary with mean temperature in both tree species?
- 2 Do R_R and R_H follow changes in soil moisture similarly?

In practice, we measured GPP and soil CO_2 effluxes on plots with and without tree roots along a latitudinal gradient in Northern Europe. In addition, we compared these respiration components with simulations by LPJ-GUESS (Smith et al., 2001, 2014). We chose LPJ-GUESS because it is a widely used model that has been calibrated and tested using the Plant Functional Type (PFT) parameters for the species in this study (Hickler et al., 2012). However, Tang et al. (2014) found out that modelled R_H was much lower than the reported data for temperate forests and more comparisons with field measurements of R_S and its partitioning into R_R and R_H are needed for better understanding these discrepancies.

2. Materials and methods

2.1. Description of measurement sites

This study was carried out at eight measurement sites along a

latitudinal gradient (boreal, hemiboreal, and temperate conifer forest) in Northern Europe (Fig. 1, Table 1).

The northernmost site, the Station for Measuring Ecosystem-Atmosphere Relations (SMEAR I), is an unevenly aged Scots pine stand (*Pinus sylvestris* L.) in Värriö, northern Finland (67°46' N, 29°35' E) with 1025 stems ha^{-1} (Köster et al., 2014). This northern boreal forest floor is covered by lichens, mosses, and vascular plants such as *Vaccinium vitis-idaea* L., *Empetrum nigrum* L. and *Calluna vulgaris* L. (Santalahahti et al., 2018).

The sites in Punkaharju, Finland comprised a 90-year-old Scots pine stand (61°77' N, 29°33' E) and an 80-year-old Norway spruce (*Picea abies* (L.) Karst.) stand (61°81' N, 29°32' E) with 741 and 370 stems ha^{-1} , respectively (Tupek et al., 2019). The Scots pine forest belongs to the *Vaccinium vitis-idaea* site type and the Norway spruce forest to the *Oxalis acetocella*–*Vaccinium myrtillus* site type according to the Cajander site type classification (Salemaa et al., 2008).

The SMEAR II station in Hyytiälä, southern Finland (61°51' N, 24°17' E) is a 60-year-old Scots pine stand with 955 stems ha^{-1} (diameter >10 cm; Schiestl-Aalto et al., 2019) and it belongs to the *Vaccinium myrtillus* site type. The forest floor is covered by mosses, including *Pleurozium schreberi* (Brid.) Mitt., *Dicranum polysetum* Sw., *Dicranum scorparium* Hedw., and *Hylocomium splendens* (Hedw.) Schimp., and ericoid shrubs such as *V. myrtillus* L. and *V. vitis-idaea* L.

The sites in Tammela, Finland comprised a 70-year-old Scots pine stand (60°62' N, 23°84' E) and a 70-year-old Norway spruce stand (60°65' N, 23°81' E) with 619 and 663 stems ha^{-1} , respectively (Tupek et al., 2019). The Scots pine forest belongs to the *Vaccinium vitis-idaea* site type and the Norway spruce forest to the *Vaccinium myrtillus* site type (Salemaa et al., 2008).

The hemiboreal site in Norunda, Sweden (60°05' N, 17°29' E) is a 120-year-old stand with a mixture of Scots pine and Norway spruce with 429 stems ha^{-1} (Lindroth et al., 2018). The soil is covered by a mixture of *V. myrtillus* L., sphagnum mosses (*Sphagnum* spp.), and bracken (*Pteridium aquilinum* L.) (Acosta et al., 2013).

The temperate site in Brasschaat, in the Campine ecoregion of Belgium (51°18' N, 4°31' E), is a 90-year-old Scots pine forest with 360 stems ha^{-1} (Gielen et al., 2013 Horemans et al., 2020;). The forest floor is covered by mosses (*Hypnum cupressiforme* Hedw), grasses (*Molinia caerulea* (L.) Moench), and seedlings of *Betula pendula* Roth, *Quercus*

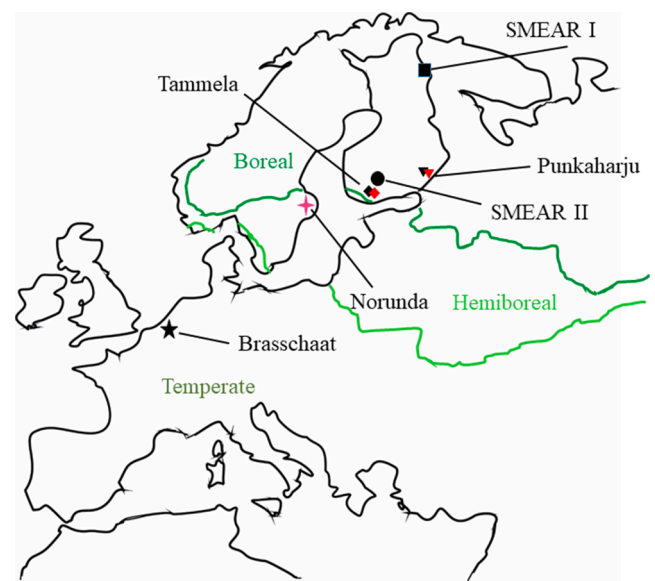


Fig. 1. Eight study sites along a latitudinal gradient in boreal, hemiboreal, and temperate climate zones. Norway spruce stands are indicated in red, Scots pine in black, and a mixture of Scots pine and Norway spruce in pink. SMEAR I and II, Norunda and Brasschaat are ICOS Ecosystem sites.

Table 1

Main tree species, mean annual air temperature (T), mean annual precipitation (P), tree root biomass (M_R), soil type, and soil organic C pool (SOC) at the study sites. SP indicates Scots pine and NS Norway spruce.

Site	Tree species	T (°C)	P (mm)	M_R (kg m ⁻²)	Soil type	SOC (kg m ⁻²)
SMEAR I	SP	-0.5 ^a	601 ^a	0.68 ^b	Haplic Podzol ^b	2.08 ^b
Punkaharju	SP	3.6 ^c	593 ^c	0.67 ^d	Rustic Podzol ^c	4.50 ^c
Punkaharju	NS	3.6 ^c	594 ^c	0.94 ^d	Haplic Regosol ^c	8.87 ^c
SMEAR II	SP	3.5 ^a	711 ^a	0.73 ^f	Haplic Podzol ^e	6.56 ^g
Tammela	SP	4.4 ^c	627 ^c	0.50 ^d	Albic Arenosol ^f	8.32 ^c
Tammela	NS	4.3 ^c	625 ^c	1.05 ^d	Haplic Arenosol ^c	8.40 ^c
Norunda	SP and NS	5.5 ^h	527 ^h	0.62 ⁱ	Dystric Regosol ^h	9.70 ⁱ
Brasschaat	SP	10.9 ^j	1 011 ^j	0.52 ^k	Haplic Podzol ^k	11.47 ^l

^a Pirinen et al. (2012), for the years 1971–2000

^b Köster et al. (2014) Santalahti et al. (2018); no size info

^c Tupek et al. (2019), total soil SOC to a depth of 50 cm

^d Merilä et al. (2014), fine roots (< 2 mm) + small roots 2–5 mm

^e Ilvesniemi et al. (2010)

^f Ding et al. (2021), fine roots (< 2 mm) + small roots 2–5 mm

^g Ilvesniemi et al. (2009), total soil C to a depth of 50 cm

^h Lundin et al. (1999)

ⁱ Widén and Majdi (2001), small roots (< 5 mm), total soil C to a depth of 40 cm.

^j Horemans et al. (2020).

^k Janssens et al. (2002), small roots (< 5 mm).

^l Janssens et al. (1999), total soil C to a depth of 1 m.

robur L., and *Pinus sylvestris* L. (Janssens et al., 1999 Gond et al., 1999; Curiel et al., 2005). The measurement sites are described in more detail in Table 1.

2.2. Experimental setup

The experiments were established in 2012 at the SMEAR II station, in 2014 in Punkaharju and Tammela, and in 2015 at all other measurement sites. Measurements were started in May 2013 at the SMEAR II station, and in May 2015 at all other sites. We used the trenching method to separate and measure heterotrophic respiration (R_H), with which we estimated root-rhizosphere respiration (R_R) by subtracting the R_H from total forest floor respiration (i.e. soil respiration; R_S). In practice, a trench was dug to a minimum depth of 40 cm around the intact plot. Roots around the plot were cut and the plot was isolated from the surrounding soil using a mesh with 1 μ m pore size. The mesh prevents the ingrowth of roots and mycorrhizal fungi, while allowing the flow of water and nutrients. Exceptions were Tammela and Punkaharju, where the ingrowth of new tree roots was prevented by installing a root impenetrable fabric with 50 μ m pore size, which also allowed the possible ingrowth of long-distance exploration type mycorrhizal fungi. After fabric installation, the soil excavated from the trench was returned to the trench, whereas control plots were left intact. Understorey vegetation was kept intact on all plots. Detailed descriptions of experimental setups at all sites are provided in Supplementary Section 1. Number of replicate plots was 2–36, depending on the site (Table 2).

2.3. Soil chamber measurements

Forest floor CO₂ effluxes were measured at study sites (Table 2) using a static (non-steady-state) chamber technique, where CO₂ concentration in the chamber headspace was monitored and the CO₂ efflux was estimated based on linear or exponential fitting against time. The chamber

Table 2

Setup of soil chamber measurements at the study sites.

Site	Chamber type	Control plots (#)	Trenching plots (#)	Frequency	Years
SMEAR I	Manual	20	8	2–3/month	2015–2018
Punkaharju	Manual	36	13	2–3/month	2015–2016
Punkaharju	Manual	36	13	2–3/month	2015–2016
SMEAR II	Manual	12	6	2–3/month	2013–2015
Tammela	Manual	36	13	2–3/month	2015–2016
Tammela	Manual	36	13	2–3/month	2015–2016
Norunda	Automatic	3–4	2–3	Two/hour	2015–2018
Brasschaat	Automatic	6	4	Two/hour	2015–2018

was darkened, except in Norunda, where CO₂ fluxes were measured using automated transparent chambers without darkening. In the analysis, we used only night-time measurements without photosynthesis from Norunda based on Pumpanen et al. (2015). Detailed descriptions of chamber measurements at all sites are presented in Supplementary Section 1.

2.4. Ancillary data

The net ecosystem CO₂ exchange (NEE) was measured using the eddy covariance (EC) technique and partitioned into gross primary production (GPP) and ecosystem respiration (R_E) at SMEAR I, SMEAR II, Norunda, and Brasschaat. The semi-empirical model PRELES (Peltoniemi et al., 2015a; Minunno et al., 2016) was used to estimate GPP in Tammela and Punkaharju. Instrumentation, processing, and flux calculation are described in detail in Supplementary Section 1.

Soil temperature and water content (SWC) were measured from each site between 2015 and 2018, and between 2013 and 2015 at SMEAR II. In addition, soil temperature and SWC were measured manually at each experimental plot at SMEAR I and II stations during the CO₂ efflux measurements. Instrumentation and measurements are described in Supplementary Section 1.

The effective temperature sum (degree-day, °Cd) was calculated as the sum of the daily mean air temperatures over 5 °C.

Litterbags with 1 mm mesh size were placed between the organic layer and the mineral soil surface in the control and trenching plots at SMEAR I, SMEAR II, Norunda, and Brasschaat (Supplementary Section 1) in order to estimate residual dead root and needle litter decomposition (described in Supplementary Section 2).

2.5. Daily CO₂ effluxes

To obtain daily R_S , R_H , and R_R for the whole year, we used an empirical equation describing the effects of soil temperature (T, °C) and soil water content (SWC, m³ m⁻³) on daily respiration R_i of chamber i at moment t according to Mäkelä et al., (2008) and Ryhti et al. (2021) as follows:

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

In the equation, α , r_0 , v , and Q_{10} are parameters, i is a chamber, and RWC_i is the relative water content estimated using Eq. (2):

$$RWC_i(t) = \frac{SWC_i(t) - WP}{FC - WP} \quad (2)$$

In the equation, SWC_i is measured soil water content, FC is field capacity, and WP is wilting point. We used 0.25 m³ m⁻³ as FC and 0.06 m³ m⁻³ as WP in SMEAR I, SMEAR II, Brasschaat, and the Scots pine sites

in Tammela and Punkaharju. These were determined for the SMEAR II stand by [Ilvesniemi et al. \(2010\)](#). For Norunda and the Norway spruce sites in Tammela and Punkaharju, we used $0.27 \text{ m}^3 \text{ m}^{-3}$ as FC and $0.053 \text{ m}^3 \text{ m}^{-3}$ as WP, which were determined for the Norunda stand based on [Stähli et al. \(1995\)](#). The parameter estimation for each chamber in [Eq. \(1\)](#) was performed in two stages. First, we used constant ν and α to estimate parameters r_0 and Q_{10} . We used values $\nu = 11$ and $\alpha = 1.062$ for SMEAR II, Tammela pine site, Punkaharju pine site, and Norunda according to [Mäkelä et al. \(2008\)](#), who determined these for Norunda. We used $\nu = 11$ and $\alpha = 0.30$ for Tammela spruce site, $\nu = 11$ and $\alpha = 0.48$ for Punkaharju spruce site, $\nu = 3$ and $\alpha = 0.843$ for Brasschaat, and $\nu = 27$ and $\alpha = 0.23$ for SMEAR I, as these parameter values estimated R_H and R_R accurately compared to measured R_H and R_R . Next, the estimated parameters r_0 and Q_{10} were used to estimate the parameter α . Finally, we used the fitted, chamber-specific parameters (α , r_0 and Q_{10}) and measured soil moisture and temperature to determine daily R_i for each chamber or measurement location. Data processing and flux calculation are described in detail in [Fig. 2](#).

SWC was generally higher in trenching plots without roots than in control plots. For this reason, R_H of each trenched plot was modelled using the daily mean of SWC in the control plots to dismiss the potentially altered CO_2 emissions due to higher SWC in the trenching plots. Daily R_R was determined as a mean of the differences between mean R_S over the intact plots and individual R_H of trenched plots. For SMEAR II, we used the daily R_H and R_R available in [Ryhti et al. \(2021\)](#), who used the same equations and followed the same principles.

2.6. Annual CO_2 fluxes

We summed the daily means for each intact and trenched plot to obtain R_S and R_H , respectively, for each site and year. However, the construction of trenching treatment increases the amount of dead root biomass inside the plots when the ingoing roots are cut. Therefore, the annual R_H ($\text{g C m}^{-2} \text{ y}^{-1}$) was corrected by reducing the estimated annual mass loss of additional root litter in the trenching plots, f_{tr} ($\text{g C m}^{-2} \text{ y}^{-1}$), estimated as follows:

$$f_{tr} = (M_R (D_R/100) C_R) \quad (3)$$

In the equation, M_R is fine root biomass (g m^{-2} , [Table 1](#)), D_R ($\% \text{ y}^{-1}$) the annual mass loss of root litter, and C_R the C content in fine roots, assumed to be 50%. D_R was measured at SMEAR I, SMEAR II, Norunda, and Brasschaat ([Fig. S1](#)). For Tammela and Punkaharju, we used the

annual mass loss of root litter at SMEAR II and site-specific fine root biomass (g m^{-2} , [Table 1](#)). The annual R_R for each site and year was then estimated as the difference between annual R_S and R_H . For SMEAR II, we used the annual R_R and R_H from [Ryhti et al. \(2021\)](#).

2.7. Statistical analyses

Data analyses were carried out using MATLAB software (version 2018a, MathWorks, Natick, MA, USA). As the data of mass loss of root and needle litter were non-normally distributed, the non-parametric Kruskal-Wallis test (degree of freedom 1 and significance level of $P < 0.05^*$) was used to determine whether the mass losses at the different sites were statistically different ([Supplementary Fig. S1](#)). Linear regression of the ratio of R_R to GPP and the annual effective temperature sum was calculated for all sites and also for the Scots pine sites with eddy covariance (*i.e.* sites where GPP was derived from net ecosystem exchange on site). The annual R_H and R_R for each measurement site were analysed as such and derived per soil C content and fine root biomass, respectively, to see if these are related to the effective temperature sums on the latitudinal gradient. To compare the seasonal dynamics of R_H and R_R , monthly mean values were normalized by dividing these with the annual maximum of daily values of R_H and R_R , respectively.

To determine the effect of different environmental drivers on the measured R_H and R_R , we used linear mixed-effects models that were estimated based on the maximum likelihood (ML) method, and the best model was chosen based on the Bayesian information criterion (BIC) and the Akaike information criterion (AIC). We tested the effect of a fixed intercept parameter (B_0), soil temperature (B_T), RWC (B_{RWC}), and interaction of all these parameters on R_H and R_R . Only the variables and parameters with a statistically significant effect on R_H and R_R were included in the model. The linear mixed-effects models were carried out separately for the northern boreal Scots pine site (SMEAR I), for the southern boreal Scots pine sites (SMEAR II, Punkaharju pine, Tammela pine), for the temperate Scots pine site (Brasschaat), for the Norway spruce sites (Punkaharju spruce, Tammela spruce), and for the mixed site (Norunda).

R_H and R_R were estimated based on [Eq. \(4\)](#):

$$R_H = B_0 + B_T + B_{RWC} + \epsilon \quad (4)$$

We assumed that the error term ϵ in [Eq. \(4\)](#) takes the following form:

$$\epsilon = \alpha_{CY} + \alpha_T + u \quad (5)$$

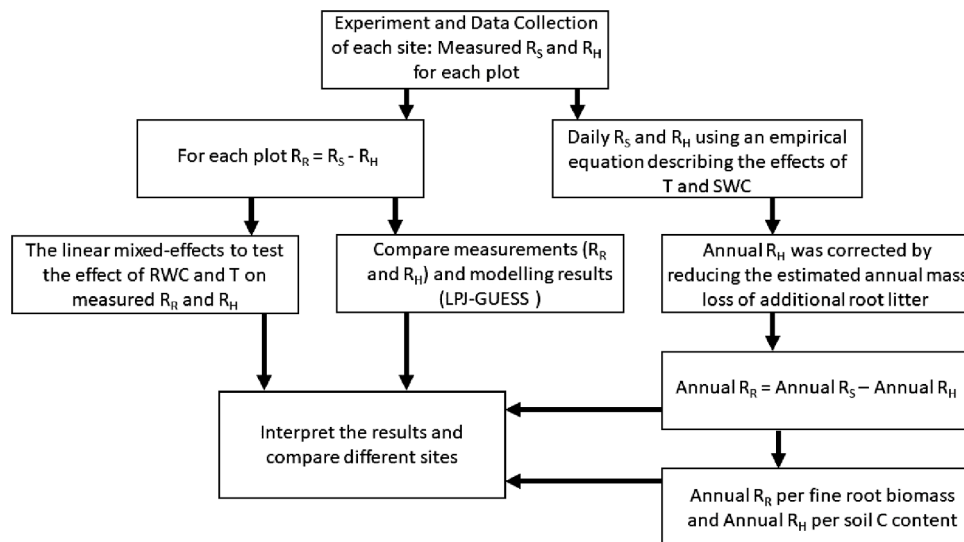


Fig. 2. The workflow map of the data analyzing protocol. The trenching method was used to separate and measure heterotrophic respiration (R_H), with which we estimated root-rhizosphere respiration (R_R) by subtracting the R_H from total forest floor respiration (*i.e.* soil respiration; R_S).

where α_{CY} denotes a random parameter related to the interaction measurement location of chambers and measurement years, α_T denotes a random parameter related to measurement time, and u is an unmeasurable random error term.

2.8. Modelling R_R and R_H with LPJ-GUESS

The dynamic ecosystem model LPJ-GUESS (version 4.0.1, Smith et al., 2001, 2014) was used to estimate the daily R_H and daily autotrophic root respiration (R_A), which is equivalent to R_R but without root-associated microbes, for the different sites. We chose LPJ-GUESS because it is a widely used process-based dynamic global vegetation model (Hickler et al., 2012). While full details of the model are available in Smith et al. (2014) and the references therein, relevant R_A and R_H schemes of the model follow in most part the LPJ-GUESS SOM dynamics, mainly adopting the CENTURY model with updates and modifications (Parton et al., 1993, 2010). Daily R_H is computed by temperature, soil moisture, and soil texture, taking C:N stoichiometry into account. Daily R_A computation is driven by plant species, phenological stage, daily net assimilation, and air and soil temperatures taking into account tissue C:N ratios. Modelled R_A is later referred to as modelled R_R .

In order to run the model at the flux sites (SMEAR I, SMEAR II, Norunda, Brasschaat) for the study years (Table 2), we used daily averages of meteorological drivers (e.g. temperature, precipitation, radiation) from the Drought-2018 ecosystem eddy covariance flux product (Drought 2018 Team and ICOS Atmosphere Thematic Centre, 2020). LPJ-GUESS also requires a spin-up period to start from bare-ground to build up vegetation and soil C and N pools to a near steady-state. Therefore, we initialized the simulations with a 500-year spin-up period that recycles 1901–1930 CRUNCEP data (Viovy, 2018). In practice, the model ran a historical period with CRUNCEP drivers from 1901

to the first available year of the site-level data, then used Drought-2018 ecosystem eddy covariance flux product drivers that were gap-filled and consolidated with downscaled ERA-Interim reanalysis data product for the remaining simulation period (Table S1). The model's spin-up was able to capture the initial conditions at the sites. More details on the modelling protocol and PFT parameters used in this study can be found in Supplementary Section 3.

3. Results

3.1. Prevailing conditions

The monthly mean air temperature was highest during the study years in the temperate Scots pine forest (Brasschaat) and lowest in the northernmost boreal Scots pine forest (SMEAR I) (Fig. 3a). The monthly mean SWCs showed remarkable site-to-site variation but were somewhat similar between the Scots pine sites and lower than in the Norway spruce sites (Fig. 3c). The annual GPP was highest in the temperate forest (1 610–1 720 g C m⁻² y⁻¹) and lowest in the northern boreal forest (420–550 g C m⁻² y⁻¹). The annual effective temperature sum was the highest in the temperate forest (2 610–3 010°Cd) and lowest in the northern boreal forest (560–790°Cd).

The annual mass loss of pine roots in the litterbags was 29.9–49.0% and the mass loss of needles was 27.9–53.5% after the first year of the experiment (Fig. S1). The mass loss of needles and roots was highest in the temperate forest and lowest in the northern boreal forest.

3.2. Autotrophic and heterotrophic respiration along the temperature gradient

The annual R_S and R_H increased with the annual effective temperature sum, while annual R_R was not clearly connected to the effective

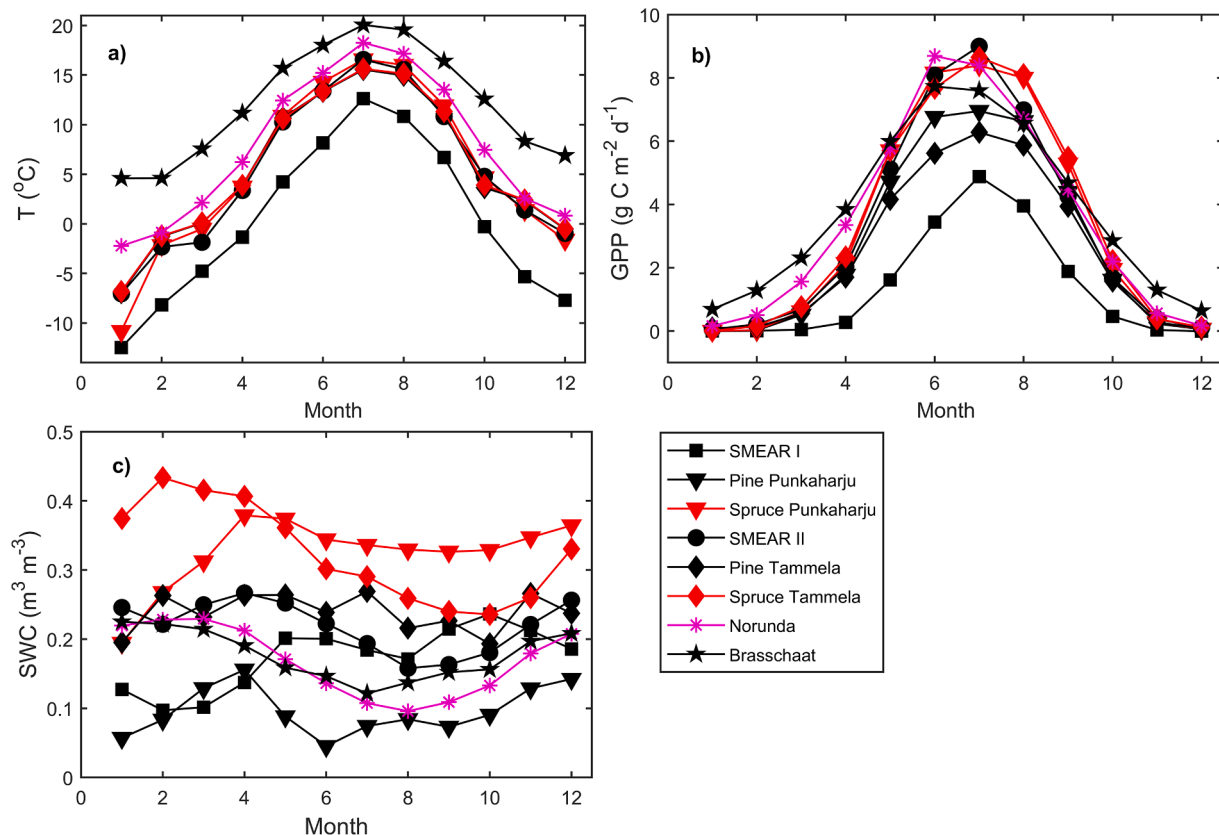


Fig. 3. Monthly mean (a) air temperature (T), (b) gross primary production (GPP), and (c) soil water content (SWC) in the Scots pine forests (in black), Norway spruce forests (in red), and the mixed forest (in pink) over the campaign. The exact study years are shown in Table 2.

temperature sum (Fig. 4a–c). The annual R_H varied between 112 and 1362 $\text{g C m}^{-2} \text{y}^{-1}$, R_R between 135 and 1230 $\text{g C m}^{-2} \text{y}^{-1}$, and R_S between 327 and 1937 $\text{g C m}^{-2} \text{y}^{-1}$ amongst all sites. The annual R_H , R_R , and R_S were highest in the hemiboreal forest (Norunda) with a mixed canopy of Norway spruce and Scots pine (Fig. 4). The annual R_H was clearly lowest in the northern boreal forest (SMEAR I) (Fig. 4a). The annual R_R was lowest in the Scots pine forests in Brasschaat and Tammela (Fig. 4b).

The annual ratio of R_R to GPP varied between 0.15 and 0.55 in the Scots pine forests and between 0.20 and 0.25 in the Norway spruce forests (Fig. 5a). The ratio of R_R to GPP was 0.53 in the mixed forest (Norunda) (Fig. 5a). The ratio between annual R_R and GPP showed a slight but non-significant decreasing trend when all sites were included ($R^2 = 0.341$, $P > 0.1$) (Fig. 5a). When we considered only the Scots pine stands (SMEAR I, SMEAR II and Brasschaat) with eddy covariance (*i.e.* sites where GPP was derived from net ecosystem exchange on site), the ratio decreased with the effective temperature sum ($R^2 = 0.997$, $P < 0.05^*$) (Fig. 5a). The ratio between R_H and R_R increased together with the annual effective temperature sum amongst all sites ($R^2 = 0.73$, $P < 0.01^{**}$) (Fig. 5b).

R_R per fine root biomass varied between 0.39 and 0.60 $\text{g C g}_{\text{roots}} \text{y}^{-1}$ in Scots pine forests (Fig. 6a) and between 0.26 and 1.19 $\text{g C g}_{\text{roots}} \text{y}^{-1}$ in Norway spruce forests (Fig. 6b). No trend emerged with the effective temperature sum (Fig. 6a). Mean R_R per fine root biomass was highest in the mixed forest (Norunda) and lowest in Norway spruce forests in the boreal climate (Fig. 6b). R_H per soil C was quite similar (0.03–0.09 $\text{g C g}_{\text{soil C}} \text{y}^{-1}$) between the Scots pine forests, missing a clear trend along the air temperature sum gradient (Fig. 6c). Mean R_H per soil C was the highest in the mixed forest (0.10 $\text{g C g}_{\text{soil C}} \text{y}^{-1}$) and lowest in Norway spruce forests (0.03–0.04 $\text{g C g}_{\text{soil C}} \text{y}^{-1}$) in the boreal climate (Fig. 6d) and the Tammela Scots pine forest (Fig. 6c).

3.3. Seasonal dynamics of autotrophic and heterotrophic respiration

When the CO_2 effluxes were normalized with the daily maximum CO_2 efflux of each year, the monthly mean R_R and R_H had rather similar seasonal dynamics in northern (SMEAR I) and southern boreal (SMEAR II) and temperate (Brasschaat) climates (Fig. 7abd). In the hemiboreal mixed site (Norunda), R_R peaked before R_H (Fig. 7c).

3.4. Moisture dependency of autotrophic and heterotrophic respiration

RWC had a significant effect on R_R in all stands, except the northern boreal Scots pine stand (SMEAR I) (Table 3). In other Scots pine stands, the connection between RWC and R_R was negative (*i.e.* decreasing RWC increased R_R), while the slope between RWC and R_H was positive

(Table 3). However, the situation was not clear in the southern temperate Scots pine stand (Brasschaat), where RWC and soil temperature had joint effects on both respiration components R_H and R_R . Nevertheless, RWC alone had a higher slope with R_H and R_R than soil temperature alone (Table 3). In contrast to the Scots pine sites, both R_H and R_R increased with increasing RWC in the southern boreal Norway spruce stands (Tammela and Punkaharju). In the hemiboreal mixed stand (Norunda), RWC and R_R again had a negative connection (Table 3).

3.5. Forest floor CO_2 effluxes in LPJ-GUESS

The LPJ-GUESS estimates were close to observed daily R_H at the SMEAR I and II sites (Fig. 8ab). However, LPJ-GUESS strongly underestimated R_H in Norunda and Brasschaat, with the exception of the first measurement year in Norunda (Fig. 8cd; Table S3). The seasonal dynamics of simulated R_H and R_R were close to observed ones at the different measurement sites (Supplementary Fig. S2). LPJ-GUESS strongly underestimated R_R at SMEAR I and Norunda throughout the experiment and slightly underestimated at SMEAR II during the first year (Fig. 9, Table S3). The modelled and measured R_R were quite similar in Brasschaat (Fig. 9d).

4. Discussion

4.1. Effect of climate and tree species on belowground C allocation

Soil respiration (R_S) is tightly connected to carbon (C) allocation of plant photosynthates to roots and their mycorrhizal fungi (Högberg et al., 2001). Trees are known to allocate more C to roots and their fungal symbionts on nutrient-poor soils (Baret et al., 2015) which is seen as increased share of gross primary production (GPP) in the total ecosystem respiration in nutrient-poor soils compared to nutrient-rich soils (Fernández-Martínez et al., 2014). In boreal forests the decomposition is slow and therefore, nitrogen bound in soil organic matter (SOM) is not easily available for plants (Schulden and Schnitzer, 1998; Adamczyk et al., 2018) Falge et al. (2002). found that a larger proportion of assimilated C was allocated to the total ecosystem respiration in boreal forests than in temperate forests. Our discoveries are in line with these findings: As a result to our first research question, we found that the activity of root-rhizosphere was relatively higher in the northern boreal forest than in the southern boreal forests, as the share between root-rhizosphere respiration (R_R) and GPP decreased along a north-to-south gradient (Fig. 5a). In our study, R_R was more than 50% of GPP in the northernmost and most probably also poorest site, in terms of productivity and nutrients, whereas in the southernmost site the share

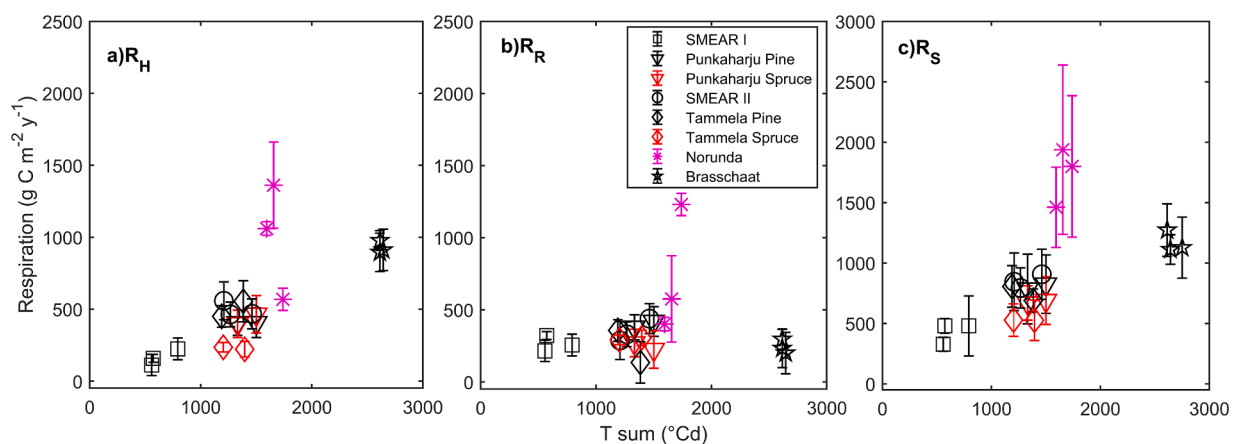


Fig. 4. Relationship of the modelled heterotrophic respiration (R_H), root-rhizosphere respiration (R_R), and total soil respiration (R_S) with the annual effective temperature sum in the Scots pine forests (black), Norway spruce (red), and mixed forests (pink). Error bars are the standard error of the different chambers.

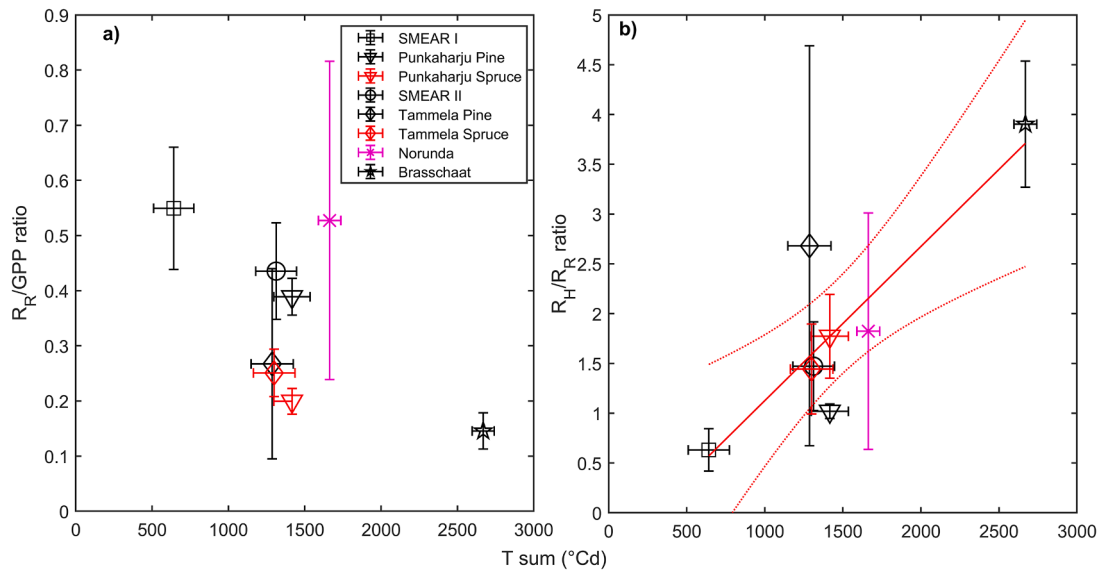


Fig. 5. The ratios (a) between root-rhizosphere respiration (R_R) and gross primary production (GPP) and (b) between heterotrophic respiration (R_H) and R_R during the different study years in Scots pine forests (in black), Norway spruce forests (in red), and a mixed forest (in pink) against the mean of effective temperature sums within the sites. The symbols represent the mean and error bars the standard deviation of the different years. Linear regression was used to describe a statistically significant trend within all data points.

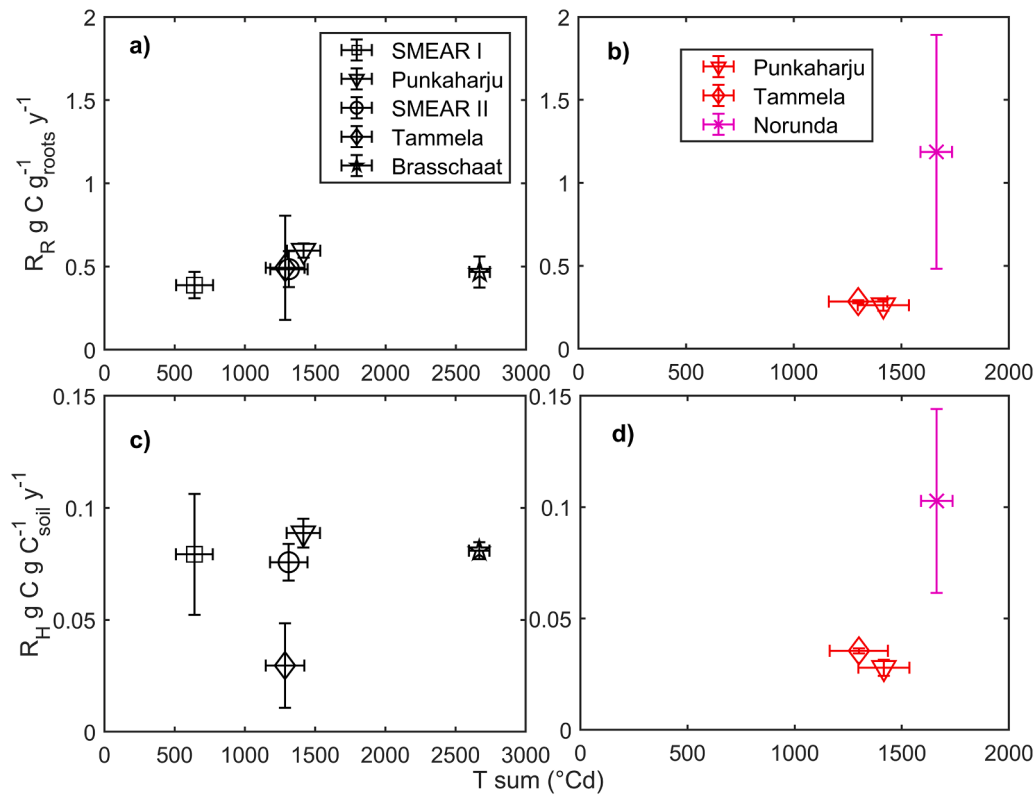


Fig. 6. Annual effective temperature sum with root-rhizosphere respiration (R_R) per fine root biomass (a, b) and heterotrophic respiration (R_H) per soil C content (c, d) in Scots pine (a and c), Norway spruce, and mixed (b and d) forests. Error bars are the standard deviation of the different years.

was only approximately 15%. These ratios are somewhat lower than earlier estimates for belowground allocation, which often include not only respiration of fine and coarse roots, root exudates, and C transfer to root symbionts, as in this study, but also root growth, which was not studied here. For example, Grayston et al. (1997) reported that trees in general allocate 40–73% of the photosynthesized C into the rhizosphere, whereas Höglberg et al. (2002) estimated that trees allocated 63% of

photosynthesized C belowground for growth and respiration of roots in a boreal Scots pine forest. In the temperate Scots pine forest in Belgium, the belowground C allocation was estimated to be 28–49% of the annual GPP in an earlier study (Janssens et al., 2002).

Even though the allocation to R_R decreases with increasing temperature, we found that R_R per ground area or per root mass is rather independent of the effective temperature sum, unlike R_H , which is driven

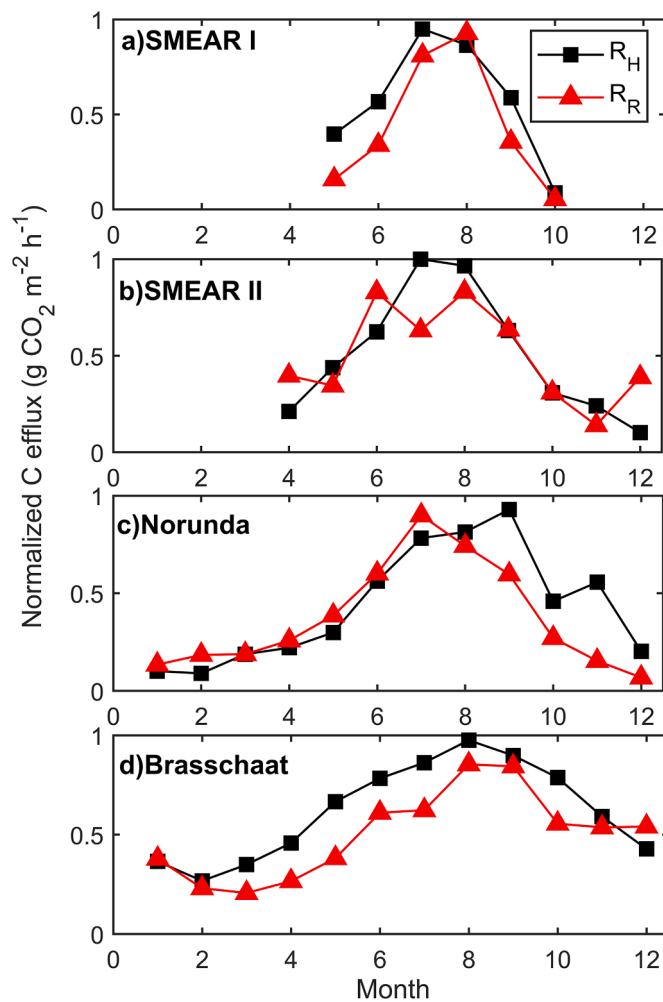


Fig. 7. Normalized monthly mean heterotrophic respiration (R_H) in black and root-rhizosphere (R_R) respiration in red at different sites with increasing mean annual temperature from a to d (see Table 1).

by microbial activity that increases with temperature along a climate gradient (Fang et al., 2014). The exception was the mixed forest in Norunda, where R_S was generally high and R_R was notably higher than at other sites. This might arise from the methodological shortcomings as discussed later. On the other hand, higher ratio between R_R and GPP at the site compared with the pure spruce forests might be explained by shorter root longevity and faster root turnover of Norway spruce at higher soil temperatures compared with lower temperatures (Kilpeläinen et al., 2019). However, it is important to note that the temperature gradient in this study was much broader in Scots pine forests than in Norway spruce forests. In addition to the overall trend, R_R :GPP ratio varies within boreal Scots pine sites subjected to rather similar temperature conditions, probably due to altered C allocation between rhizosphere, stem, and shoots, for example, due to nitrogen availability and photosynthetic activity, as suggested by Vogt et al., (1995) and Högberg et al., (2010).

Fine root biomass is reported to decrease in the organic soil from north to south along a latitudinal gradient (Finér et al., 2019) and to increase with precipitation and temperature (Yuan and Chen, 2010). On the other hand, nutrient-poor soils in the north are reported to have five times more fine roots per tree basal area than fertile soils in southern boreal forests (Lehtonen et al., 2016). In our study, root biomass was one of the highest in the northern boreal Scots pine forest compared with other Scots pine sites but in practise, the differences were rather small between the sites (Table 1). Sampling design, depth, and sorting

decisions, when separating the roots from soil, cause variation in the observed root mass. Therefore, future studies would benefit from a standardized determination of root biomass.

Major and Mosseler (2019) found that the ratio of root biomass to total tree biomass of spruces (*Picea glauca*, *P. rubens*, *P. mariana*, and *P. abies*) was higher than that of pines (*Pinus rigida*, *P. resinosa*, *P. strobus*, and *P. banksiana*) in a greenhouse experiment with seedlings. As the annual R_R per ground area was somewhat similar between the species (Fig. 5), the higher root mass (Table 1) leads to lower R_R per root mass in pure Norway spruce sites than in Scots pine (Fig. 6). Apart from Norunda, our results are partly in conflict with an earlier study by Bläsko et al. (2020) who observed on average 32% lower CO_2 effluxes in boreal Scots pine and mixed stands than in Norway spruce stands. Nevertheless, that might arise from generally higher soil C content in Norway spruce sites (Table 1) and overall site-to-site variation. For example, the difference in maturities of ecosystems will likely influence R_R per root mass and R_H per soil C content, as Huang et al. (2016) showed that both R_R and R_H decreased with the increased maturity of forests.

4.2. Seasonal dynamics and connections to soil moisture

R_S is reported to increase in the late growing season (Hansen et al., 1997) and in August (Högberg et al., 2001) due to increased below-ground C allocation and root activity. Our study is consistent with this, as R_R was highest in July and August in the northern and southern boreal forests and a little later in the temperate Scots pine forest, where the growing season is also longer. In our study, the two respiration components followed rather similar seasonal dynamics in boreal and temperate climates on monthly time steps, which is not surprising as in these regions, temperature drives both microbial (Lee et al. 2003; Baldrian et al., 2017) and vegetation dynamics such as phenology (Kramer et al., 2000). Also, the increased biomass and abundance of mycorrhizal fungi are shown to be highest in August in the boreal Norway spruce forest (Haas et al., 2018).

Our second research question was to determine if R_R and R_H follow changes in soil moisture similarly. The effect of soil moisture on R_R and R_H was statistically insignificant in the northern boreal Scots pine stand but in the southern ones, the relationship between RWC and respiration was positive with R_H and negative with R_R , indicating that a decrease in soil moisture decreases also heterotrophic activities, whereas R_R was proportionally increased in lower soil moisture conditions. On pure spruce sites, the effect of soil moisture was positive to with both respiration components, which probably arises from the more superficial location of spruce roots (Helmisaari et al., 2007). In general, Scots pine is also known to tolerate drier growing conditions than Norway spruce (Lagergren & Lindroth, 2002). The different response to soil moisture between R_H and R_R in Scots pine stands might arise of the dependency of heterotrophic activity on microscale conditions, whereas trees are able to maintain living root biomass through stressful periods by providing water from lower soil horizons. Therefore, R_R may not respond as quickly to a short-term decrease in soil moisture as R_H . For example, seedlings of Scots pine were observed to increase C allocation to roots in increased drought stress in order to maintain sufficient water uptake (Aaltonen et al., 2016). Moreover, plants may benefit from mycorrhiza with an extensive network of hyphae by extending their reach in the soil for water and nutrient uptake, although maintaining efficient nutrient uptake during drought might be more important to the plants than direct water uptake by mycorrhiza (Lehto and Zwiazek, 2011). Increasing precipitation due to a warming climate may have a positive effect on decomposition in boreal forest soils by increasing soil water content (Allison and Treseder, 2011). The global warming may also cause quicker and more intense droughts in areas where drought periods already occur (Trenberth et al., 2014). Our results indicate that drought periods might increase root respiration by Scots pines, possibly due to enhanced life processes to attract water and nutrients from the drying soil.

Table 3

Results of the linear mixed-effects models for heterotrophic respiration (R_H) and root-rhizosphere respiration (R_R). R-squared was used to show the estimation accuracy of the model. The asterisks indicate a significant fixed effect: ***, **, and * denote $P < 0.001$, $P < 0.01$, and $P < 0.05$, respectively. The modelling was carried out separately for the northern boreal Scots pine site, for the southern boreal Scots pine sites, for the Norway spruce sites, and for the mixed forest site. RWC stands for relative water content.

R_H				R_R			
Fixed effects coefficients	Slope	Std. error	R^2	Fixed effects coefficients	Slope	Std. error	R^2
Northern boreal Scots pine site (SMEAR I)							
Intercept	0.021	0.038	0.70	Intercept	-0.087	0.050	0.66
Soil temperature	0.025***	0.006		Soil temperature	0.028***	0.004	
RWC	0.025	0.018		RWC	-0.006	0.046	
Southern boreal Scots pine sites (SMEAR II, Tammela, and Punkaharju)							
Intercept	0.292***	0.044	0.75	Intercept	-0.120***	0.030	0.49
Soil temperature	0.008*	0.004		Soil temperature	0.027***	0.002	
RWC	0.108***	0.020		RWC	-0.262***	0.033	
Temperate Scots pine site (Brasschaat)							
Intercept	0.236***	0.025	0.88	Intercept	0.086***	0.022	0.61
Soil temperature	0.015***	0.001		Soil temperature	0.001	0.001	
RWC	-0.050***	0.007		RWC	-0.027**	0.009	
RWC + Soil temperature	0.006***	0.001		RWC + Soil temperature	0.003**	0.001	
Southern boreal Norway spruce sites (Tammela and Punkaharju)							
Intercept	-0.017	0.031	0.85	Intercept	-0.330***	0.033	0.71
Soil temperature	0.042***	0.003		Soil temperature	0.027***	0.002	
RWC	0.078***	0.009		RWC	0.384***	0.028	
Mixed forest site (Norunda)							
Intercept	0.284***	0.073	0.83	Intercept	0.576***	0.110	0.82
Soil temperature	0.061***	0.001		Soil temperature	0.006***	0.001	
RWC	-0.090***	0.011		RWC	-0.191***	0.015	

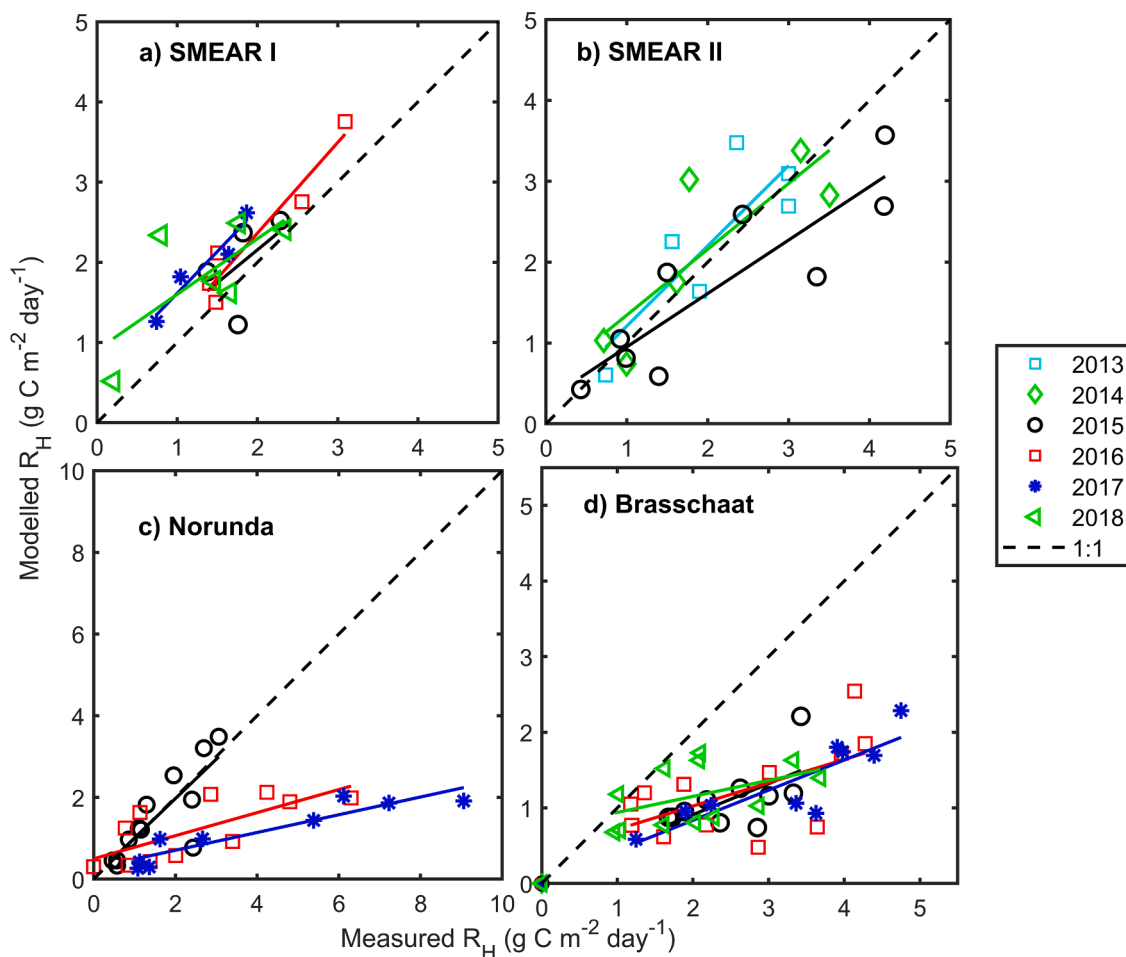


Fig. 8. Measured mean of the plots and LPJ-GUESS estimates of heterotrophic respiration (R_H) at SMEAR I (a), SMEAR II (b), Norunda (c), and Brasschaat (d). Linear regression was used to compare measurements and modelling results. Colours represent different measurement years.

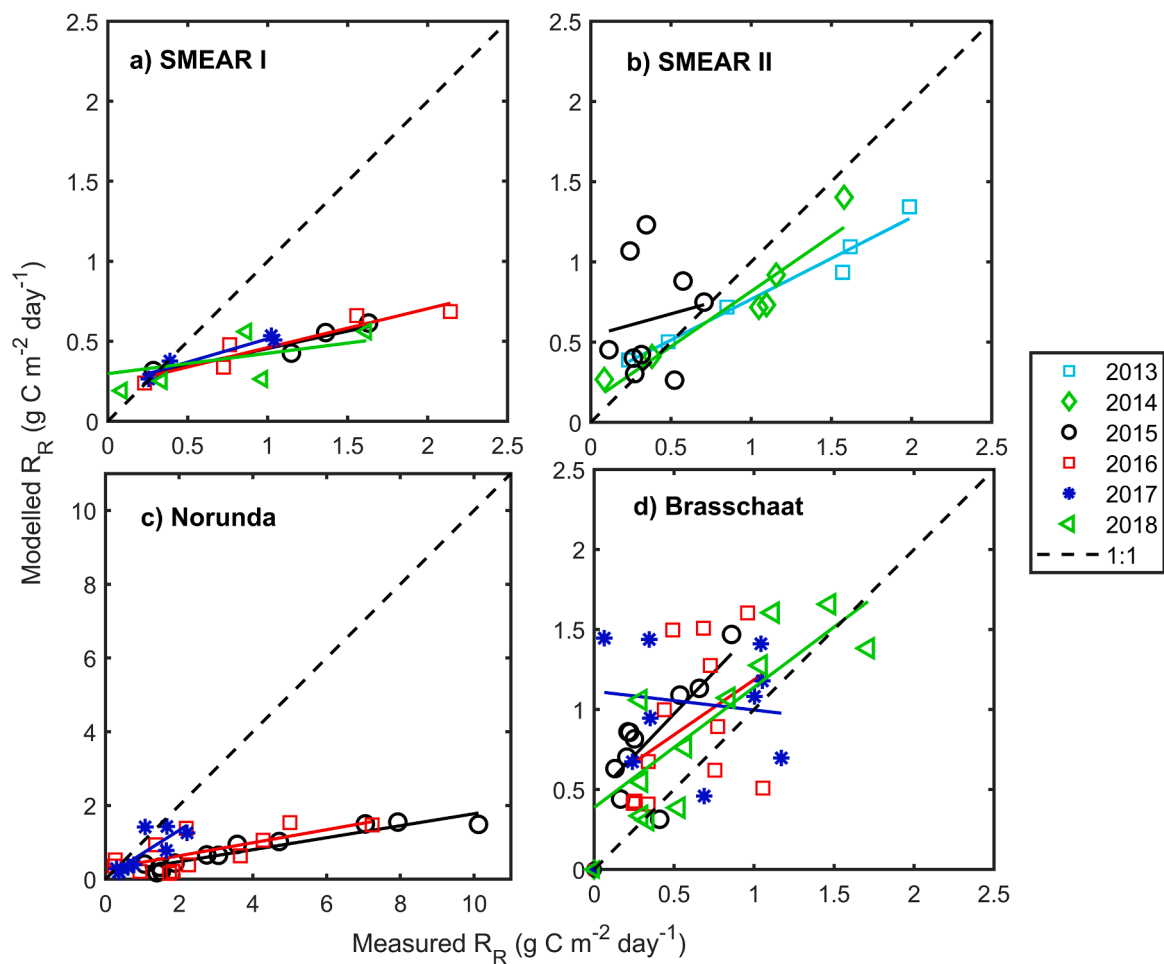


Fig. 9. Measurement-based means of plots and modelled root-rhizosphere respiration (R_R) at SMEAR I (a), SMEAR II (b), Norunda (c), and Brasschaat (d). R_R was modelled using LPJ-GUESS. Linear regression was used to compare measurements and modelling results. Colours represent different measurement years.

4.3. Capability of LPJ-GUESS to simulate forest floor C effluxes

LPJ-GUESS is optimized for a regional scale, and it includes vegetation dynamics of different tree species and understorey vegetation, while soil dynamics are estimated using the SOM scheme from the CENTURY model (Smith et al., 2014) McGuire et al. (2012). estimated that process-based models, including LPJ-GUESS, can capture the seasonal cycle of R_H . Nevertheless, Tang et al. (2014) concluded that more comparisons between field measurements and modelling studies are needed to estimate total R_S , as the model often underestimated R_H compared with field studies. In this study, R_H estimated by LPJ-GUESS was close to observed values at the boreal sites (SMEAR I and II), but was underestimated in the temperate Scots pine site (Brasschaat) and in the hemiboreal mixed site (Norunda), especially in the later phase of the campaign years. Climate and soil temperature cannot solely explain the marked difference, as in LPJ-GUESS these were used as drivers for R_H . The overall high respiration in Norunda (Lindroth et al., 2018) and to high C content in Brasschaat (Janssens et al., 1999) likely are part of the underestimation. On the other hand, the visibly increasing trend in R_H , especially in Norunda, over the campaign years (Fig. S2) is a clear indication of the ‘Gadgil effect’ (Gadgil and Gadgil, 1971, 1975). The effect arises from competition changes in trenched plots, as the lack of roots leads to a death of ectomycorrhizal fungi, decreasing the competition and allowing increased activity of saprotrophic microbes. LPJ-GUESS seems to be unable to predict the high activity of R_H when it is driven by factors other than soil temperature. R_H and R_R showed variations between sites, such as a spring lag of R_R in southern sites and

an autumn lag of R_H in northern sites (Fig. 7) Āupek et al. (2019). suggested that the period of high R_H in north is in autumn longer than expected by models which may lead to this kind of discrepancies between field measurements and model estimates.

Our study demonstrates that especially the accuracy of modelled R_R varies strongly between the sites. We found that LPJ-GUESS markedly underestimates R_R at the northern boreal site (SMEAR I) and the hemiboreal mixed site (Norunda) throughout the experiment, whereas the estimate was within the range of observations at the southern boreal (SMEAR II) and temperate (Brasschaat) sites. The modelled total tree biomass estimate by LPJ-GUESS was approximately 2.0 kg C m^{-2} at the northernmost site, which is rather close to the observed total tree biomass, 1.9 kg C m^{-2} (Köster et al., 2014). Therefore, the underestimation must arise from miscalculated allocation to tree root activity at the northern boreal site. In Brasschaat, the modelled tree biomass (6.0 kg C m^{-2}) was considerably lower than observations (10.4 kg C m^{-2} , Janssens et al., 1999), which, however, did not lead to underestimation in annual R_R ; the model estimate was in fact a slight overestimate. Based on these findings and the non-existent relationship between annual R_R and temperature found here, it seems evident that the role of soil temperature as a driver for root respiration in LPJ-GUESS is overemphasized on an annual scale.

4.4. Experimental uncertainties of R_S , R_R , and R_H

The canopy in a boreal forest might be sparse, and therefore, the photosynthetic production of the dense forest floor vegetation is

notable, especially in the north (Kulmala et al., 2019, 2011). The respiration of understorey vegetation contributes to R_S and R_H , as the understorey vegetation was kept intact in this study. Nevertheless, Kolari et al. (2009) estimated that the forest floor vegetation had only a minor role in forest floor CO_2 effluxes in a boreal forest in a study conducted at SMEAR II, but in practice, the R_H values presented in this study include the respiration of belowground and aboveground parts of forest floor vegetation in addition to the CO_2 arising from heterotrophic activities in soil.

Our results show the high heterogeneity of boreal forests and their forest floor CO_2 effluxes. The variation in R_S cannot be explained only by climatic conditions, as forest ecosystems differ in many ways within a climatic gradient, reflecting the adaptation of tree species to site characteristics such as soil type, soil moisture conditions, and nutrient availability. Varying measurement time (measurement years and frequency) between the sites is a significant source of uncertainty in forest floor CO_2 effluxes. Spatial variation of individual sites is challenging to capture due to high heterogeneity of such forest floor properties as understorey vegetation cover, soil depth, stoniness, root depth of different tree species and root biomass. The respiration rates in Norunda differed from the other sites. That might arise from relatively small number of chambers there compared with other sites, which might have caused inaccuracy if the trenched plots were by coincidence located on spots with lower heterotrophic respiration than elsewhere. In addition, other stands were mainly on well-aerated soils, but Norunda features some waterlogged spots (Acosta et al., 2013), which might increase the spatial variation in R_S inside the stand.

As microbial and root activities are mostly affected by the same factors and tightly connected, studying their separate responses is challenging. Here, R_H was physically separated by the trenching method, where tree roots and their respiration are excluded from the bulk soil. The trenching method is rather inexpensive compared with, for example, isotopic methods, but the limitations of trenching include a potential increase in soil moisture due to lack of water uptake by roots (Comstedt et al., 2011; Savage et al., 2018). However, we took this into account and removed the possible increase in heterotrophic activity by modelling the daily fluxes using soil moisture measured in intact plots. In addition, it is well-known that decomposition of residual roots, mycorrhizal hyphae and associated microbes causes additional CO_2 emissions (Comstedt et al., 2011; Savage et al., 2018), but this was also taken into account in our study. Moreover, the Gadgil effect obscures the situation, as the death of tree roots and associated microbes changes the competition situation in the soil and increases the heterotrophic activity (Gadgil and Gadgil, 1971, 1975). Thus, it is proposed that most accountable results from the trenching experiment are measured during the first experiment year considering the emissions arising from deceased roots (Ryhti et al., 2021).

The semi-empirical model PRELES was used to estimate GPP in Tammela and Punkaharju, which may cause some uncertainty to GPP and therefore also to the ratio between R_R and GPP. However, PRELES is shown to produce comparable GPP estimates with measured GPP data in Finland (Peltoniemi et al., 2015a, 2015b).

5. Conclusions

We found that activity of the root-rhizosphere was relatively higher in northern forests than in southern forests. Soil respiration and especially its heterotrophic component increased with increasing temperature, but heterotrophic respiration (R_H) per soil carbon seemed to be independent of temperature, at least in Scots pine stands in the current climate. Soil moisture decreased heterotrophic activity, whereas in Scots pine stands autotrophic root activity and associated microbes were favoured by decreased soil moisture in the measured conditions. The only exception was the strongly temperature-limited, northern boreal site where soil moisture did not significantly affect either of the soil respiration components. Root-rhizosphere respiration (R_R) normalized

with fine root biomass was mainly independent of climate, with a couple of exceptions, which can be attributed to special features of sampling or the site. Dynamic land surface models are required to study the feedbacks of the C cycle, for instance, R_R and R_H in the warming climate. Modelled respiration components by LPJ-GUESS followed similar seasonal dynamics as the measured components but underestimated the overall level in half of the cases. According to our results, connecting the R_R and R_H to root biomass and soil carbon content, respectively, might provide more accurate estimates over the latitudinal gradient.

Disclaimer

The authors affirm that this work is original and the manuscript is not under consideration by another journal. The research was carried out without any competing financial interests.

Data availability statement

The CO_2 effluxes of the different study sites are provided in the Supplementary Data.

CRediT authorship contribution statement

Mari Mäki: Formal analysis, Data curation, Writing – review & editing, Writing – original draft. **Kira Ryhti:** Formal analysis, Data curation, Writing – original draft. **Istem Fer:** Methodology, Writing – original draft. **Boris Tůpek:** Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft. **Patrik Vestin:** Formal analysis, Data curation, Writing – original draft. **Marilyn Roland:** Data curation, Writing – original draft. **Irene Lehner:** Data curation, Writing – original draft. **Egle Köster:** Data curation, Writing – original draft. **Aleksi Lehtonen:** Conceptualization, Methodology, Data curation, Writing – original draft. **Jaana Bäck:** Data curation, Writing – original draft. **Jussi Heinonsalo:** Conceptualization, Methodology, Data curation, Writing – original draft. **Jukka Pumpanen:** Data curation, Writing – original draft. **Liisa Kulmala:** Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft.

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 work was supported by the Helsinki University Funds, the Jane and Aatos Erkko Foundation, Kone Foundation, the Academy of Finland (Grant No. 277623), and the Academy of Finland Flagship funding (Grant Nos. 337549 and 337552). The study was also partially funded by the Strategic Research Council at the Academy of Finland (SOMPA, Grant no. 312912). We acknowledge ICOS Sweden, Norunda station, for providing the measurement facilities and experimental support, and Irene Lehner and Anders Båth are thanked for assistance with the experiment. ICOS Sweden is funded through the Swedish Research Council (Grant no. 2015-06020).

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2022.108876.

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