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Belowground carbon dynamics in Scots pine stands

Kira Ryhti

Institute for Atmospheric and Earth System Research (INAR) /
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University of Helsinki

Academic dissertation

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ABSTRACT

Boreal forest soils are globally one of the most extensive carbon storages, whereas soil respiration (CO_2 efflux) forms the largest carbon flux from the ecosystem to the atmosphere. Current changes in the world climate may have unpredictable effects on belowground carbon processes, and thereby, on the carbon balance of boreal forests.

To better understand the various processes in soil and to quantify the potential changes in the carbon cycle, forest-floor respiration (R_{FF}) was partitioned into five different components, and tree-root respiration (R_R) was estimated, using four different methods in a mature boreal Scots pine (*Pinus sylvestris* L.) stand in southern Finland. Non-structural carbohydrate (NSC) concentrations in tree roots were determined, and carbon allocation to belowground by trees was estimated with the whole-tree carbon model 'CASSIA'. In addition, R_R and heterotrophic soil respiration (R_H) were separated using root exclusion in seven coniferous forests along a latitudinal gradient in Northern and Central Europe.

The R_R comprised almost half of the R_{FF}, the R_H almost a third, and ground vegetation and respiration of mycorrhizal hyphae the remaining fifth in the boreal Scots pine stand. While the annual R_R decreased throughout the first three study years, the R_H increased when the mycorrhizal roots were excluded from the treatments. The R_R and most of the NSC concentrations were higher in the warmer years and lower in the cooler, as estimated with most of the methods. Three methods resulted in rather similar R_R estimations, while the R_R estimated with root incubation was significantly lower. The R_R was over 50% of the annual photosynthesis in the northernmost forest stand, whereas in the southernmost stand it was only up to 15%. Carbon allocation to the belowground, as modelled with CASSIA was a third of the annual photosynthesis on average and almost 5% for the symbiotic mycorrhizae.

Keywords: soil respiration, CO_2, roots, non-structural carbohydrate (NSC), *Pinus sylvestris*, boreal forest

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Jämsä, August 2022,
Kira Ryhti

LIST OF ORIGINAL ARTICLES

This dissertation is based on the following four original research articles published in peer-reviewed journals, which are referred to in the text by their Roman numerals.

I **Ryhti K**, Kulmala L, Pumpanen J, Isotalo J, Pihlatie M, Helmisaari H-S, Leppälammi-Kujansuu, J, Kieloaho A-J, Bäck J, Heinonsalo J (2021). Partitioning of forest floor CO_2 emissions reveals the belowground interactions between different plant groups in a Scots pine stand in southern Finland. Agricultural and Forest Meteorology 297: 108266. https://doi.org/10.1016/j.agrformet.2020.108266

II Mäki M, **Ryhti K**, Fer I, Ťupek B, Vestin P, Roland M, Lehner I, Köster E, 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 317: 108876. https://doi.org/10.1016/j.agrformet.2022.108876

III **Ryhti K**, Schiestl-Aalto P, Tang Y, Rinne-Garmston K, Ding Y, Pumpanen J, Biasi C, Saurer M, Bäck J, Kulmala L (2022). Effects of variable temperature and moisture conditions on respiration and nonstructural carbohydrate dynamics of tree roots. Agricultural and Forest Meteorology 323: 109040. https://doi.org/10.1016/j.agrformet.2022.109040

IV 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. Frontiers in Forests and Global Change 2(17). https://doi.org/10.3389/ffgc.2019.00017

AUTHOR'S CONTRIBUTION

Kira Ryhti (KR) was responsible for the summary of this thesis.

I. KR was responsible for conducting the measurements for one year, for the data analyses (except the linear mixed-effect model) and for leading the writing process.

II. KR was taking part in supervising the data analysis and participated in planning and writing of the manuscript as a co-author of the article.

III. KR was responsible for planning the setup, establishing the experiments, conducting part of the measurements, for the data and statistical analyses and for leading the writing process.

IV. KR participated in sample analysis and writing of the manuscript as a co-author of the article.

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LIST OF SYMBOLS AND ABBREVIATIONS

C	carbon
CASSIA	Carbon Allocation Sink-Source Interaction, dynamic tree growth model
CO_2	carbon dioxide
CON	intact control including tree roots
CUT	all ground vegetation cut in ground vegetation treatment
EC	eddy covariance
FC	field capacity
GPP	gross primary production
N	nitrogen
NEE	net ecosystem carbo-dioxide exchange
NOR	normal intact ground vegetation
NPP	net primary production
NSC	non-structural carbohydrates
P	phosphorus
Q_{10}	temperature-response coefficient
r_0	basal respiration rate at 0 °C temperature
R_{FF}	respiration of forest floor
R_{GMH}	respiration of ground vegetation species other than dwarf shrubs (e.g. grasses, mosses, herbs)
R_{GV}	respiration of ground vegetation
R_H	heterotrophic soil respiration
R_{MY}	respiration of mycorrhizal fungal hyphae
R_R	tree-root respiration
R_{RES}	residual respiration; the difference between predicted and measured values
R_{SHR}	respiration of dwarf shrubs
RWC	relative water content
SHR	only dwarf shrubs left in ground vegetation treatment
SMEAR	Station for Measuring Ecosystem-Atmosphere Relations
SOM	soil organic matter
SWC	soil-water content
T_A	air temperature
TER	total ecosystem respiration
TR	trenching (i.e. root exclusion)
TR1	trenching (i.e. root exclusion) using mesh fabric with 1-µm pore size
TR50	trenching (i.e. root exclusion) using mesh fabric with 50-µm pore size
T_S	soil temperature
VPD	vapour-pressure deficit
WP	wilting point

1 INTRODUCTION

1.1 Boreal forests and belowground dynamics

The boreal forest, or taiga, encircles the earth roughly between 48° and 70° N latitudes, covering North America, Northern Europe, Russia and Northeastern China. The boreal ecosystem is the second largest forested biome (Kasischke 2000) and is globally one of the most extensive reservoirs of carbon (C) (Bradshaw and Warkentin 2015). The boreal region is characterized by a cool, wet climate, with long winters and short summers, resulting in low decomposition rates and accumulation of C. However, the average temperature has continued to increase, being greatest in the high latitudes of Northern Europe, especially during winter (IPCC 2014). On the one hand, warming increases photosynthetic production (i.e. gross primary production; GPP) (McMahon et al. 2010; Keenan et al. 2014), which may even further enhance C sequestration in boreal ecosystems (Briceño-Elizondo et al. 2006; Jansson et al. 2008; Ueyama et al. 2013). On the other hand, it may increase the activity of autotrophic plants and decompositioning in soils, thus increasing carbon-dioxide (CO_2) emissions as soil respiration (Rustad et al. 2001; Bond-Lamberty et al. 2010, 2018; Wang et al. 2014). Warming may shorten the snow-cover period in spring and advance the start of the growing season in the Northern Hemisphere (Collins et al. 2013), while also postponing the start of autumn (McMahon et al. 2010), thereby increasing the length of the growing season. However, the delayed snowfall and weakened insulation by the snow cover can, in turn, decrease temperatures in the soil (T_S) (Halim and Thomas 2018). With increasing temperatures, vapour-pressure deficits (VPDs) of the air may increase leading to higher evapotranspiration rates from forests (Kirschbaum 2000), which may, in turn, enhance the drying of soils. Therefore, the soil-water content (SWC) may become a more important factor determining terrestrial C exchange in boreal forests than currently (Liu et al. 2019). Even though summers have rarely been extremely hot and dry in Northern European forests, some examples from recent years (such as 2018) are available (Lindroth et al. 2020; Peters et al. 2020).

Coniferous trees such as spruce (*Picea* A. Dietr.), larch (*Larix* Mill), pine (*Pinus* L.) and fir (*Abies* Mill), which are adapted to cold temperatures, snow and tolerate varying water availability during the year, e.g. due to frozen soil, predominate in boreal forests (Kasischke 2000). The forest floor is inhabited by many evergreen dwarf shrubs, such as heather (*Calluna vulgaris* (L.) Hull), lingonberry (*Vaccinium vitis-idaea* L.), crowberry (*Empetrum nigrum* L.), and deciduous bilberry (*Vaccinium myrtillus* L.), also in addition to grasses and herbs. The ground floor is often covered by mosses and lichens. The soil microbiota are dominated by saprotrophic microbes and fungi, which are primary decomposers of soil-organic matter (SOM) (Read 1991). Boreal forests have relatively cold, wet acidic soils in which decomposition and nutrient cycling rates are relatively low, and plant roots and microorganisms in the soil compete mostly for nutrients (Kuzyakov and Xu 2013). Many of the coniferous tree species form symbiotic associations with ectomycorrhizal fungi, whereas dwarf shrubs form symbioses with ericoid mycorrhizae (Read 1991). Host plants benefit from gaining nitrogen (N), phosphorus (P) and other nutrients from mycorrhizae that would otherwise be unavailable to them, while the mycorrhizae benefit from the host plant by obtaining photosynthates (i.e. C compounds) (Smith and Read 2008). Substantial amounts of C are allocated to the mycorrhizal fungi by the host plant (Leake et al. 2001); thus the

mycorrhizal hyphal necromass together with root litter forms a significant fraction of the SOM (Clemmensen et al. 2013).

Ecto- and ericoid mycorrhizal fungi also have saprotrophic capabilities by releasing degrading enzymes, mostly to scavenge nutrients from recalcitrant organic C resources in the soil (Read and Perez-Moreno 2003; Phillips et al. 2014). The presence of ecto- and ericoid mycorrhizal fungi may suppress the saprotrophic activity in a so-called 'Gadgil effect' (Gadgil and Gadgil 1971, 1975), which may result from multiple causes, e.g. from competition for resources between saprotrophic and ectomycorrhizal fungi, or from the chemical inhibition or parasitism of one by the other (Fernandez and Kennedy 2016). With a secure flow of organic C from the host plant, mycorrhizal fungi are likely in a favourable position to compete for nutrients with saprotrophs (Smith and Read 2008). Due to the Gadgil effect, the exclusion of mycorrhizal roots may enhance the activity of heterotrophic saprotrophs in the soil. Moreover, soil heterotrophic microbes also benefit from plant-derived C from roots and mycorrhizae, resulting in increase in decomposition in a so-called 'rhizosphere-priming effect' (Kuzyakov 2006; Bengtson et al. 2012). However, free exudation from plant roots to soil in forested ecosystems with ectomycorrhizal plants is considered negligible (Nehls 2008; Jones et al. 2009), and most of the photosynthates are allocated to fungal symbionts.

1.2 C cycling in boreal forest floor

Due to extensive C storage, boreal ecosystems play important roles in the global C budget; thus changes in their C balance may greatly impact the atmospheric CO_2 concentration. Most of the C resides in soils and peatlands in the boreal region (Raich and Schlesinger 1992; Bradshaw and Warkentin 2015), while as the largest C flux from the ecosystem to the atmosphere, soil respiration is a key component of CO_2 exchange (Janssens et al. 2001). Soil respiration consists of autotrophic respiration of tree roots (R_R), respiration of the external hyphae of symbiotic mycorrhizal fungi (R_{MY}) and nonsymbiotic heterotrophic microbes (R_H), such as saprotrophic bacteria and fungi, that decompose SOM (Figure 1) (Kuzyakov 2006; Kutsch et al. 2009). In addition to trees and soil microbiota, respiration of ericaceous dwarf shrubs (R_{SHR}) and other ground vegetation (e.g. grasses, mosses and herbs; R_{GMH}) forms a significant part of the total forest-floor respiration (R_{FF}).

Forest-floor vegetation in boreal forests contributes significantly to GPP (Goulden and Crill 1997; Morén and Lindroth 2000; Kulmala et al. 2011, 2019). Mosses in the ground floor are known to affect soil moisture and temperature by controlling hydrological processes (Clymo and Hayward 1982; Beringer et al. 2001) and acting as insulators (Bonan, 1991; Beringer et al. 2001; O'Donnell et al. 2009; Soudzilovskaia et al. 2013). Ericaceous dwarf shrubs and their ericoid roots 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). Trees and ground vegetation species compete for recourses in the forest floor, yet they also have interconnections belowground. Studies have shown that trees and dwarf shrubs may be interconnected via common mycorrhizal networks (Villarreal-Ruiz et al. 2004; Sietiö et al. 2018), while trees exchange C assisted by common ectomycorrhizal networks (Pickles et al. 2017), even in substantial amounts among tall trees (Klein et al. 2016). The effects of different ground vegetation species on various ecosystem properties e.g. respiration can be determined, e.g. using vegetation removals (see Wardle and Zackrisson 2005; Hautala et al. 2008), while R_{MY} can be determined using mesh fabrics with various pore sizes (Moyano et

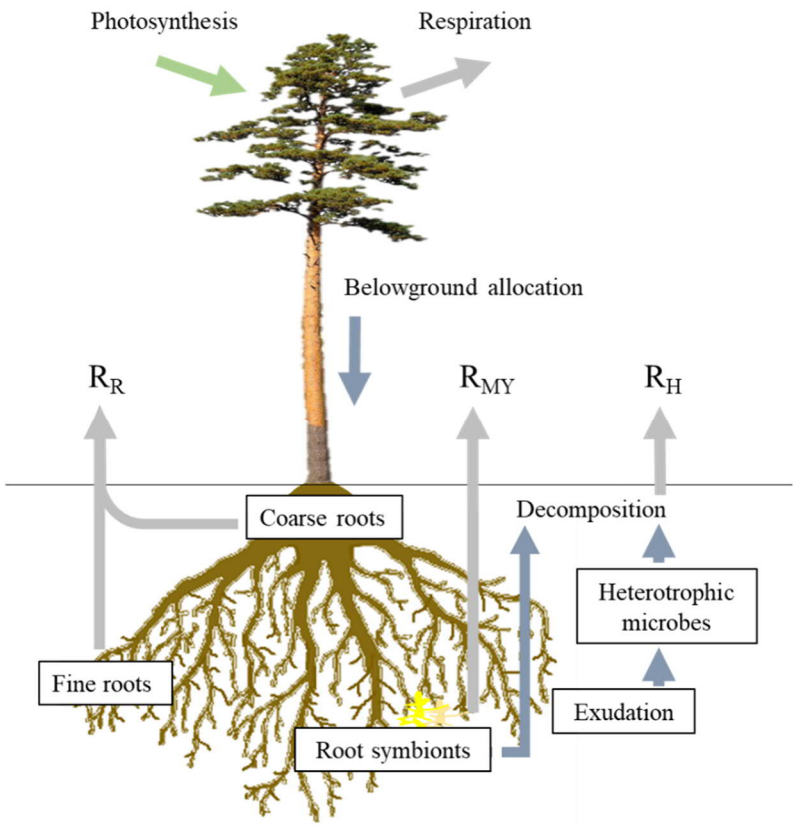


Figure 1. Schematic figure of aboveground carbon (C) exchange in photosynthesis and respiration, belowground C allocation to roots and root-associated mycorrhizal symbionts and to exudation, and various respiration sources of tree roots (R_R), symbiotic mycorrhizal fungi (R_{MY}), and heterotrophic microbes (R_H). Photo of Scots pine by Juho Aalto.

al. 2008; Fenn et al. 2010; Heinemeyer et al. 2012; Yan et al. 2019), such as 50 µm (Andrew et al. 2014; Hagenbo et al. 2019), enables ingrowth of external mycorrhizal fungal hyphae.

Tree roots, especially fine roots, are an important component of the belowground biogeochemical (Ostonen et al. 2017) and C cycles, since two-thirds of the net primary production (NPP) of trees in a Scots pine could be allocated to roots (Helmisaari et al. 2002). Trees allocate C compounds as nonstructural carbohydrates (NSCs, mostly sugars and starch) to different organs for growth, metabolic processes and C storage (Hartmann and Trumbore 2016). NSCs are also used for other purposes, such as cold tolerance in plants, and soluble sugars (mainly glucose, fructose and sucrose) to regulate water and osmotic potential in plant cells (Hartmann and Trumbore 2016). Soluble sugars in roots are used, e.g. for sustaining nutrients and water acquisition via osmoregulation, whereas starch plays a role as a reservoir for future use (Dietze et al. 2014; Martínez-Vilalta et al. 2016). Increased NSC concentration can be observed in stressed trees, e.g. under drought conditions (Körner 2003; Salmon et al. 2020), even though NSC depletion can be a sign of decline in plant vitality. Trees may increase belowground C allocation in early drought to produce root biomass to maintain water uptake and promote drought resistance and recovery (Hartmann et al. 2020).

The R_R is an important indicator for root C dynamics and overall tree metabolisms and is controlled by allocation of photosynthates to roots during the growing season (Pregitzer et al. 2000; Hopkins et al. 2013). T_S is one of the most important drivers for the R_R, and with global warming, increased temperatures may increase the activity of tree roots, and thereby their respiration (Pregitzer et al. 2000; Wang et al. 2014). However, since roots are in direct contact with the soil, it has been challenging to separate and measure only the R_R or R_H. Several ways for estimating the R_R have been used, such as various physical separation methods (e.g. root exclusion, girdling) and isotopic approaches (Hanson et al. 2000). In addition, the R_R can also be directly measured from living roots in the soil (Rakonczay et al. 1997) or excised roots (Burton and Pregitzer 2003; Makita et al. 2012, 2013). The root-exclusion method, or so-called 'trenching' (TR), has long been used to physically separate the R_H from the R_{FF} to obtain the contribution of the R_R (Hanson et al. 2000; Kuzyakov 2006). In the method, the roots are excluded from the soil by cutting them around the intact plot, and new ingrowth of roots is prevented by installing root-impermeable material (e.g. deep-reaching collar or mesh fabric). Root exclusion is reasonably simple and inexpensive in comparison to other methods (e.g. C isotopic analysis), although it is laborious when constructed. It is also problematic to label mature trees with C isotopes in the field, a method often forbidden at long-term experimental sites, since they induce disturbances in future studies using natural isotope abundances. In addition to the physical methods, the R_R has been estimated by modelling. Examples of these methods include separation of the R_R and R_H, using their different temperature sensitivities (e.g. Pumpanen et al. 2008, 2015), or modelling the R_R directly with a tree-level model such as in Schiestl-Aalto et al. (2015).

2 AIM AND OBJECTIVES OF THE STUDY

The aim of this dissertation was to determine the C dynamics of the forest floor, especially in boreal tree roots, and to analyse the effects of physical (e.g. climate) and biological (e.g. interaction between forest-floor organisms) factors on the seasonal and interannual variations in belowground C dynamics. The objectives were to determine: 1) the respiration rates of different forest-floor components and 2) the dynamics of tree-root NSC concentrations in comparison to environmental factors and other C fluxes of the tree.

Furthermore, four specific research questions were addressed:

1. What is the contribution of the different forest-floor components (e.g. heterotrophic microbes, ground vegetation species and mycorrhizal fungi) to the forest-floor respiration? (**I**)
2. What are the pros and cons of the various methods used to determine the respiration of different forest-floor components and tree roots? (**I**–**III**)
3. What drives the respiration and the NSC dynamics of tree roots? (**I**–**IV**)
4. How much NSC is allocated to tree roots and to belowground symbionts in the whole-tree C balance method? (**IV**)

For this purpose, various experiments were conducted in a Scots pine stand located at the Station for Measuring Ecosystem-Atmosphere Relations (SMEAR II) in Hyytiälä, southern Finland (**I**–**IV**) and in seven conifer stands along a latitudinal gradient from the boreal to the temperate climate zones in Northern and Central Europe (**II**). Measurements at the sites were conducted during several growing seasons under varying weather conditions.

3 MATERIALS AND METHODS

3.1 The study sites (I–IV)

Most of the field experiments (**I**–**IV**) were conducted between 2012 and 2018 at the SMEAR II station located in Hyytiälä (61°51’ N, 24°17’ E), southern Finland (Figure 2) (Hari and Kulmala 2005). The stand is dominated by mature Scots pine (*Pinus sylvestris* L.) and was established by sowing after prescribed burning in 1962. The stand is classified as *Vaccinium*-type with medium fertility (Cajander 1926). The stand has a scarce undergrowth of Norway spruce (*Picea abies* (L.) H. Karst.) and mature deciduous trees, such as silver birch (*Betula pubescens* Ehrh.), downy birch (*B. pendula* Roth) and European aspen (*Populus tremula* L.). The mean height and diameter of the dominant trees in 2016 was 18.6 m and 18.5 cm (at breast height), respectively, and the stand density was 683 stems ha^{-1} (with diameter > 15 cm) and 1177 stems ha^{-1}, when smaller trees (< 15 cm) were included. The vegetation on the forest floor is characterized by the presence of ericaceous dwarf shrubs, such as bilberry, lingonberry, and heather, mosses such as Schreber’s big red stem moss (*Pleurozium schreberi* (Brid.) Mitt.), splendid feather moss (*Hylocomium splendens* (Hedw.) Schimp.) and dicranum mosses (*Dicranum* Hedw. sp.), and herbs and grasses, such as wavy hairgrass (*Deschampsia flexuosa* (L.) Trin). The soil above the bedrock is a medium-fertility Haplic podzol with soil depth of 0.5–0.7 m. The site is characterized by a boreal climate with mild, humid summers and cold, snowy winters. The mean annual temperature is 3.5 °C, varying from −7.7 °C in February to 16.0 °C in July (years 1980−2009; Pirinen et al. 2012). The mean annual rainfall at the site is 711 mm, which is distributed rather evenly throughout the year (Pirinen et al. 2012). The growing season (i.e. daily mean temperatures constantly over 5 °C) length is approximately 165−175 days.

In addition to Hyytiälä, field experiments and measurements were conducted in seven conifer stands along a latitudinal gradient (in the boreal, hemiboreal and temperate climate zones) in Northern and Central Europe (Figure 2) (**II**). The northernmost boreal site, SMEAR I, is located in Värriö, northern Finland (67°46’ N, 29°35’ E). The stand was a 65-year-old naturally populated uneven Scots pine stand (Santalahti et al. 2018) with a basal area weighted mean tree height of 10 m and a density of 750 stems ha^{-1} (Kulmala et al. 2019). The forest-floor vegetation is characterized by the presence of ericaceous dwarf shrubs, such as lingonberry, heather and black crowberry, mosses such as Schreber’s big red stem moss and broom fork-moss (*Dicranum scoparium* Hedw.), and lichens, such as the grey-green reindeer lichen (*Cladonia rangiferina* (L.) F. H. Wigg.) (Matkala et al. 2021). The other boreal Scots pine and Norway spruce stands were located in Punkaharju (61°81’ N, 29°32’ E and 61°81’ N, 29°32’E, respectively) and Tammela (60°62’ N, 23°84’ E and 60°65’ N, 23°81’ E, respectively) in southern Finland. The sites in Punkaharju were a 90-year-old Scots pine stand and an 80-year-old Norway spruce stand with heights of 24 m and 28 m and densities of 741 and 370 stems ha^{-1}, respectively (Ťupek et al. 2019). The sites in Tammela were a 70-year-old Scots pine stand and a 70-year-old Norway spruce stand with a height of a 22 and 22 m and density of 619 and 633 stems ha^{-1}, respectively (Ťupek et al. 2019). Both of the sites are *Vaccinium vitis-idaea*-type according to Cajander site type classification (Salemaa et al. 2008). The hemiboreal site is located in Norunda, southern Sweden (60°05’N, 17°29’E) and the temperate site in Brasschaat, Belgium (51°18’N, 4°31’E). The site in Norunda was a 120-year-old stand with a mixture of Scots pine and Norway spruce with heights of 25 m–28 m and a density of 429 stems ha^{-1} in 2009 (Lindroth et al. 2018). The forest floor in Norunda is

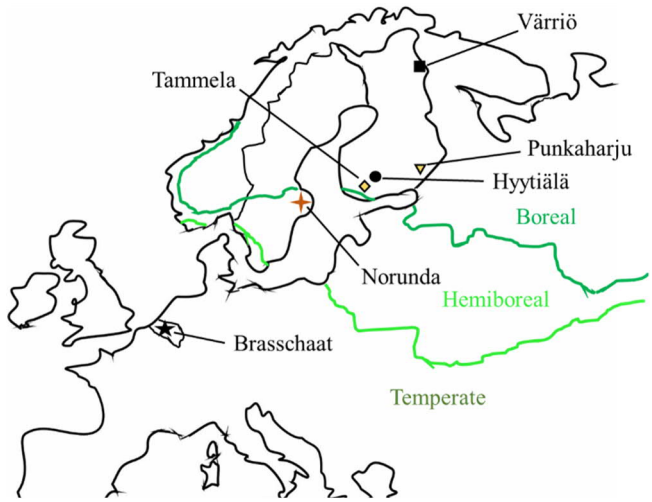


Figure 2. Six study sites along a latitudinal gradient in the boreal, hemiboreal, and temperate climate zones in Northern Europe (**II**) (original drawing by Mari Mäki). Scots pine stands in Värriö (SMEAR I station) and Hyytiälä (SMEAR II station) in black, Scots pine and Norway spruce stands Punkaharju and Tammela in yellow, a mixed Scots pine/ Norway spruce stand in Norunda in orange, and a Scots pine stand in Brasschaat in black.

covered by bilberry, sphagnum mosses (*Sphagnum* spp.), and bracken (*Pteridium aquilinum* (L.) Kuhn) (Morén and Lindroth 2000). The site in Brasschaat was a 90-year-old Scots pine stand with patches of deciduous tree species, such as the pedunculate oak (*Quercus robur* L.), with an average dominant tree height of 21.3 m in 2012 (Bequet et al. 2012) and a density of 384 stems ha^{-1} in 2014 (Horemans et al. 2020). The forest floor in Brasschaat is covered by mosses, such as the cypress-leaved plait-moss (*Hypnum cupressiforme* Hedw.) and grasses, such as Purple moor-grass (*Molinia caerulea* (L.) Moench) (Janssens et al. 1999; Curiel et al. 2005).

3.2 Ancillary environmental measurements (I–IV)

T_S, soil moisture and SWC were measured automatically at the SMEAR II station in Hyytiälä. The T_S was measured with thermocouples (NXP Semiconductors, Eindhoven, the Netherlands) at 2–5-cm and 9–14-cm depths, respectively. SWC was measured using time-domain reflectometry (Campbell Scientific Inc., Logan, UT, USA) and with a Delta-T Theta probe soil-moisture sensor (Delta-T Devices Ltd., Cambridge, UK) at 14–25-cm and 10-cm depths, respectively. The air temperature (T_A) was measured with a Pt100 sensor at a height of 16.8 m at the SMEAR II station in Hyytiälä. The thermal time (i.e. the effective temperature sum; T_{SUM}; degree-day, °Cd) (Trudgill et al. 2005), was calculated as the sum of the daily average temperatures above 5 °C from days when the average temperature was permanently more than 5 °C.

The net ecosystem CO_2 exchange (NEE) was measured using the eddy covariance (EC) technique, with a closed-path CO_2/H_2O gas analyser (LI-COR Inc., Lincoln, NE, USA) and an ultrasonic 3D anemometer (Gill Instruments Ltd. Lymington, Hampshire, UK) above the

stand at a height of 24 m until 2017 (and 2.5 m higher in 2018) in Hyytiälä (**I**–**IV**). In Värriö, Norunda and Brasschaat, the NEE was measured using the EC technique with a closed-path CO_2/H2O gas analyser (LI-COR Inc.) and with an ultrasonic 3D anemometer (METEK Ltd., Elmshorn, Germany or Gill Instruments Ltd.) above the stand at a height of 16.6 m, 36 m and 41 m, respectively (**II**). The instrumentations are described in detail for Hyytiälä in Vesala et al. (2005), for Värriö in Kulmala et al. (2019), for Norunda in Lindroth et al. (2018) and for Brasschaat in Carrara et al. (2004). The total ecosystem respiration (TER) was modelled from the night-time turbulent fluxes, using an exponential function with T_A or T_S as the explanatory factor (e.g. Reichstein et al. 2005; Kolari et al. 2009). The GPP was derived from the NEE and TER, as follows:

$$GPP = -NEE + TER. \quad (1)$$

The GPP in Punkaharju and Tammela (**II**) was estimated using a semi-empirical ecosystem model PRESLES (PREdict Light-use efficiency, Evapotranspiration and Soil water) using daily mean T_A, VPD, precipitation and photosynthetic photon flux density data measured at the sites as model inputs according to Peltoniemi et al. (2015) and Minunno et al. (2016).

3.3 Partitioning of forest-floor respiration with trenching (I–III)

3.3.1 Root exclusion and ground vegetation treatments

Various belowground forest floor components were partitioned using TR. The TR experiments were established in 2012 (**I**) and in 2017 (**III**) in Hyytiälä, in 2014 in Tammela and Punkaharju, and in 2015 in Värriö, Norunda and Brasschaat (**II**). Trenching plots were constructed by excavating a minimum 40-cm-deep ditch (when possible) around a 90 × 90 cm square plot in 2012 (**I**) (Figure 3A) and a circular plot with a diameter of 60–70 cm in 2017 (**III**) (Figure 3B) in Hyytiälä, a 100 × 100 cm square plot Tammela and Punkaharju (for further details see Ťupek et al. (2019)), a 120 × 120 cm square plot in Norunda and a circular plot with a diameter of 60–70 cm in Värriö and Brasschaat (**II**).

All roots around the TR plots were cut, and the plots were isolated from the surrounding soil using a mesh fabric (Figure 3B) with either 1-µm (TR1) or 50-µm (TR50) pore size (LK-Suodatin Oy, Tampere, Finland) (**I**), and with TR1 (**III**) in Hyytiälä, with TR1 in Värriö, Norunda and Brasschaat, and with TR50 in Tammela and Punkaharju (**II**). Both TR1 and TR50 allowed water and nutrients to flow through, but TR1 prevented the ingrowth of both plant roots and plant-associated mycorrhizal fungi, whereas TR50 allowed the ingrowth of mycorrhizal fungi, but not of plant roots. After installation of the mesh fabric, the ditch around the plot was refilled with excavated soil. The non-trenched controls (CON) included undisturbed roots and soil microbes (**I**–**III**).

Alongside the belowground treatments, the ground vegetation treatments were applied to partitioning of forest-floor components aboveground in Hyytiälä (**I**). The aboveground parts of the ground vegetation was either totally removed by cutting (CUT), all aboveground parts of other than ericaceous dwarf shrubs were removed (SHR), or all plants were left intact as would be normally (NOR) on the plots, resulting in nine different treatment combinations (Figure 5) (**I**). All regrown ground vegetation was removed several times per year from CUT and SHR, and more often from the measured area (i.e. the collar). The ground vegetation on the plots was left intact (NOR) at all other sites (**II**), except for Hyytiälä (**III**), when all ground



Figure 3. A square root-exclusion (trenching) plot with normal ground vegetation in 2015 (**I**) (photo by Jussi Heinonsalo) (A), and a round trenching plot under construction after trench excavation and mesh fabric installation around the intact soil in 2017 (**III**) (photo by Kira Ryhti) (B) in Hyytiälä.

vegetation was cut from the plots (CUT). The combinations of below- and aboveground treatments and the number of plots for each site are presented in Table 1.

After construction of the plots and ground vegetation treatments, the collars for the manual chamber measurements, tubes for soil-moisture profile probe (Delta-T Devices Ltd.) in Hyytiälä (**I**, **III**) and collars for the manual chamber measurements in Värriö, Punkaharju and Tammela (**II**) were installed.

3.3.2 Chamber- and plot-specific measurements

The CO_2 effluxes were measured with manual and automated chambers, using a standard closed-chamber technique (e.g. Pumpanen et al. 2015) at each experimental plot on permanently installed collars during the snow-free seasons (**I**–**III**). The chambers enclosed all the intact ground vegetation (mosses, dwarf shrubs etc.), if there were any left in the treatment (i.e. CUT, SHR) (Table 1), and were ventilated with ambient air between the measurements. All the chambers were darkened and ventilated, except for Norunda where they were transparent (Table 1) (**I**–**III**).

The manual cylindrical chamber in Hyytiälä (Figure 4A) was 19.7 cm in diameter and 23.9 cm (**I**) or 19.9 cm (**III**) in height. The CO_2 concentration in the headspace of a chamber was measured with a GMP343 infrared sensor (Vaisala Oyj, Vantaa, Finland) at 5-sec intervals for 5 min (**I**) and 5, 15 or 30 min (**III**). The same data measured in **I** were also used for Hyytiälä in **II** (Table 1, 2), and the same measurement protocol as described previously for Hyytiälä were used in Värriö (**II**), but the chamber was 20 cm in diameter and 25 cm in height. The CO_2 effluxes in Tammela and Punkaharju were manually measured using a cylindrical chamber with a diameter of 30 cm and a height of 21 cm (**II**). The CO_2 concentration was measured in the chamber headspace with a portable infrared CO_2 analyser

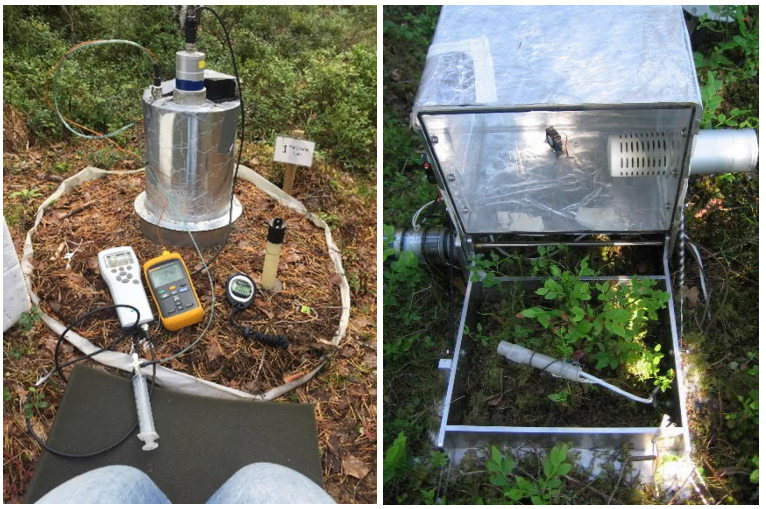


Figure 4. Manual chamber measurement on root-exclusion (trenching; TR) plot without ground vegetation (**I**, **III**) (A), and automated chamber (B) at the Hyytiälä field site (**III**). Photos A and B were taken by Kira Ryhti and Liisa Kulmala, respectively.

(PP Systems Inc., Amesbury, MA, USA) at 4.8-sec intervals for 2 min. The measurements in Tammela and Punkaharju are described in detail in Ťupek et al. (2019).

The automated chamber in Hyytiälä was an acrylic box (20 × 20 cm in area and 25 cm in height) covered with aluminium foil to exclude the light (Figure 4B) (**III**). The CO_2 concentration in the chamber was measured with a GMP343 infrared sensor (Vaisala Oyj) at 5-sec intervals for a total of 3.5 min. The CO_2 effluxes in Norunda were measured with rectangular chambers (48 cm × 48 cm × 40 cm) placed on collars installed in the mineral soil (**II**). The CO_2 concentration was measured inside the chamber headspace using an infrared gas analyser (LI-COR Inc.) at 10-s intervals for a total of 3 min. The chamber measurements in Norunda are described in detail in Lindroth et al. (2018). The CO_2 effluxes in Brasschaat were measured with an automated soil CO_2 flux system equipped with a dark chamber bowl (LI-COR Inc.) (**II**).

Soil-moisture profiles were measured manually with a PR2 profile probe soil-moisture sensor and recorded with an HH2 moisture meter (Delta-T Devices Ltd.) at each plot in Hyytiälä at the same time as the manual chamber measurements at 2–4-week intervals (**I**, **III**). The daily soil moisture for each plot and day of the year in Hyytiälä were derived, using the linear relationship between plot-specific soil-moisture profile measurements, which were chosen between 5- and 15-cm depths from the soil surface, and continuous measurements conducted at SMEAR II station in Hyytiälä (**I**, **III**). In Värriö, SWC was manually measured at each plot at the same time with the manual chamber measurements with a ML3 soil moisture sensor (Delta-T Devices Ltd.), and with a ThetaProbe (Delta-T Devices Ltd.) in Punkaharju and Tammela (**II**). The SWC was also measured continuously at each plot with soil moisture sensors (Delta-T Devices Ltd. and Soil Scout Oy, Helsinki, Finland) in Punkaharju and Tammela, and measured continuously with ThetaProbe ML2x sensors (Delta-T Devices Ltd.) in both Norunda and Brasschaat (**II**). The T_S was manually measured at each plot with a portable thermometer at the time of the manual chamber measurements in Värriö, Punkaharju and Tammela (**II**). The T_S was measured continuously at each plot using

iButton temperature sensors (Maxim Integrated, San Jose, CA, USA) in Hyytiälä (**I**, **III**), Värriö, Punkaharju and Tammela, using type T thermocouples in Norunda and a T_S probe (LI-COR Inc.) in Brasschaat (**II**).

Table 1. Chamber method, site, included in article, ground vegetation treatments: ground vegetation removed (CUT), only dwarf shrubs left (SHR), normal intact vegetation (NOR) and trenching treatments: trenching (TR) using 1-µm (TR1) and 50-µm (TR50) mesh fabric, and non-trenched controls (CON), number of the plots at each site (**I**–**III**).

Chamber	Site	Article	Trenching	Plots	Control	Plots
Manual	Hyytiälä	**I**	TR1/50-CUT	6	CON-CUT	6
			TR1/50-SHR	6	CON-SHR	6
			TR1/50-NOR	6	CON-NOR	12
	Hyytiälä	**II**	TR1-NOR	6	CON-NOR	12
	Värriö	**II**	TR1-NOR	8	CON-NOR	20
	Punkaharju	**II**	TR50-NOR	12	CON-NOR	24 (+12)
	Tammela	**II**	TR50-NOR	12	CON-NOR	24 (+12)
	Hyytiälä	**III**	TR1-CUT	6	CON-NOR	12
Automatic	Norunda	**II**	TR1-NOR	2–3	CON-NOR	3–4
	Brasschaat	**II**	TR1-NOR	4	CON-NOR	6
	Hyytiälä	**III**	–		CON-NOR	2–3

Table 2. Chamber method, site, included in article, transparency of the chamber, measurement period and interval at each site (**I**–**III**).

Chamber	Site	Article	Transparency	Years	Interval
Manual	Hyytiälä	**I / II**	Darkened	2013–2015	2–4 weeks
	Värriö	**II**	Darkened	2015–2018	2–4 weeks
	Punkaharju	**II**	Darkened	2015–2016	1 week
	Tammela	**II**	Darkened	2015–2016	1 week
	Hyytiälä	**III**	Darkened	2017–2018	2–4 weeks
Automatic	Norunda	**II**	Transparent	2015–2018	30 min
	Brasschaat	**II**	Darkened	2015–2018	30 min
	Hyytiälä	**III**	Darkened	2013–2015	30 min
			Darkened	2017–2018	30 min

3.3.3 Litter decomposition

To determine decomposition in the experimental plots, nylon litterbags of 1-mm mesh size (LK-Suodatin Oy, Tampere, Finland) filled with 1.0–2.0 g (dry weight) of a mixture of dried Scots pine and dwarf shrub root litter (diameter 2–5 mm) or dried Scots pine needles were placed between the organic layer and mineral-soil surface at each plot in Hyytiälä in 2012 (**I**), in Värriö, Norunda and Brasschaat in 2015 (**II**), and in Hyytiälä in 2017 (**III**) and collected annually as long as measurements were made at each site. First, the fresh weight of the remaining litter in the bags was measured, then 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 for the error in mass loss data caused by possible mineral-soil particles attached to the litter. The annually decomposed root masses were calculated in different size classes (**I**) or for fine roots (**II**).

3.3.4 Estimating daily carbon dioxide emissions

The CO_2 emissions were calculated by linear fitting against time and the CO_2 concentration inside the chamber headspace (**I**–**III**). For Hyytiälä, measurements between 45 sec and 4 min (**I**, **III**) or between 1 min and 4 min (**III**) were used in the analysis. However, in a few cases when the early measurement seemed unstable (**III**), we used later measurements keeping the time the same in fitting (3 min), and checked that the level of the flux was comparable to that of the others. All the other chambers were darkened, containing only respiration, except for Norunda, where only measurements during night-time without photosynthesis were used in calculations according to Pumpanen et al. (2015) (**II**).

All the roots in the plots were assumed to die in cutting during construction of the TR plots and ground vegetation removals, and begin slowly to decompose, producing additional CO_2 emissions. The additional CO_2 emissions from dead residual roots were determined for trenched (TR1, TR50) (**I**–**III**) or ground vegetation removal (SHR, CUT) (**I**, **III**) treatments, and estimated using the total root biomasses and the annually decomposed root masses at each site (see 3.3.3 Litter decomposition). The same mass-loss rate of root litter measured in Hyytiälä was used for Punkaharju and Tammela (**II**). The CO_2 emissions for each TR and SHR or CUT plot were corrected by reducing the estimated additional CO_2 emissions from the measured CO_2 emissions in Hyytiälä (**I**, **III**), and from annual CO_2 emissions at other sites (**II**).

The CO_2 efflux ($f_i(t)$) at plot i was assumed to be driven by the T_S and the SWC as follows,

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

where α and v are empirical parameters determining the response of the CO_2 efflux to soil moisture, r_0 the basal respiration rate at 0 °C temperature, Q_{10} the temperature-response coefficient, $T_{S_i}(t)$ the T_S in soil horizon B, and RWC the relative water content at moment t. The RWC at plot i was calculated according to Mäkelä et al. (2008) as follows,

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

where $M_i(t)$ is the SWC in soil horizon B at plot i, FC the field capacity and WP the wilting point. A field capacity (FC) and wilting point (WP) were set for Hyytiälä (**I**, **III**) in

accordance with Ilvesniemi et al. (2010). The same FC and WP values were used for Värriö, Punkaharju, Tammela and Brasschaat, and for Norunda FC and WP were set according to Ståhli et al. (1995) (**II**). First, the starting values of parameters r_0 and Q_{10} (and α in **I**) were estimated (**I**–**III**) in accordance with Mäkelä et al. (2008). Parametrization was conducted with the nls-function in R (R Core Team 2019), using the 'port' algorithm. Secondly, these estimated parameters were set as starting values during estimation of the parameters r_0 and Q_{10} (and α in the article **I**), which were then used to estimate the daily CO_2 emissions at each plot with Equation 2.

After the tree roots in the TR plots were cut and died, the lack of water uptake by the roots caused changes in soil moisture and T_S, which were clearly visible, especially in the warm, dry year 2018 in Hyytiälä (**III**) (Figure 7D). Therefore, the mean T_S and moisture of the intact CON were used in parameter estimation to overcome the possible effects on the CO_2 emissions of altered T_S and moisture in the TR plots.

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

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

3.3.5 Partitioning of total carbon dioxide emissions into different sources

The yearly cumulative CO_2 emissions (R_i^y) were divided into different sources in Hyytiälä (**I**) (Figure 5), assuming that respiration of TR1-CUT contained only heterotrophic microbes and their respiration (i.e. R_H) and the others as follows,

$$R_R = CON - TR50, \quad (5)$$

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

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

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

where R_R stands for respiration of tree roots, R_{MY} for mycorrhizal fungal hyphae, R_{SHR} for ericoid dwarf shrubs, and R_{GMH} for ground vegetation other than dwarf shrubs (e.g. grasses, mosses and herbs).

In Punkaharju and Tammela R_R was partitioned with TR50 as in Equation 5 and in Värriö, Norunda and Brasschaat (**II**), and Hyytiälä (**III**) with TR1 as follows:

$$R_R = CON - TR1. \quad (9)$$

Both the TR and CON plots contained intact ground vegetation (NOR) in Värriö, Hyytiälä, Norunda and Brasschaat (**II**), and the TR plots (TR50) also mycorrhizal fungal hyphae in Punkaharju and Tammela (**II**). All ground vegetation was cut (CUT) from the TR plots in Hyytiälä (**III**), while it was left intact in the CON plots. Therefore, the parameters estimated (**I**) were used to estimate respiration of ground vegetation (R_{GV}) (**III**), which was then reduced from the R_{FF} at the same time as the R_H (Equation 9).

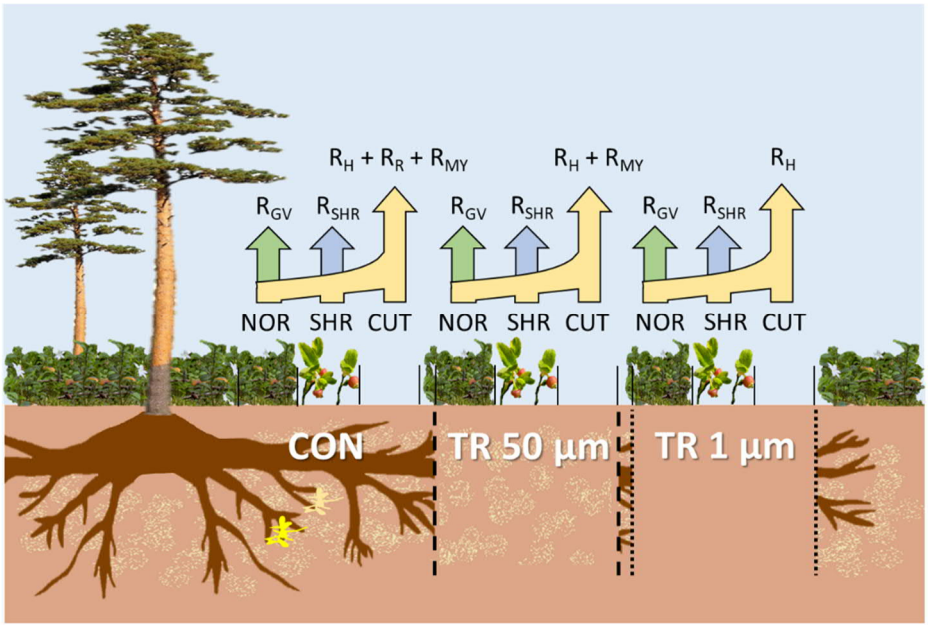


Figure 5. Schematic illustration of various treatments, including the three manipulations aboveground: 1) all ground vegetation removed (CUT), 2) only dwarf shrubs left (SHR), 3) normal intact vegetation (NOR) and three belowground: 1) trenching (TR) treatments 1 µm (TR1) and 2) 50 µm (TR50), and 3) non-trenched controls (CON) on the forest floor of the Scots pine stand in Hyytiälä (drawing by Kira Ryhti, photos of Scots pine and ground vegetation by Juho Aalto). All CON plots comprise respiration of heterotrophic microbes (R_H), tree roots (R_R) and mycorrhizal fungi hyphae (R_{MY}), TR50 R_H and R_{MY}, and TR1 R_H. In addition, plots with NOR and SHR contain respiration of ground vegetation (R_{GV}) and dwarf shrubs (R_{SHR}), respectively (**I**).

3.4 Partitioning of respiration in components based on temperature responses (III)

The R_R was separated from the R_{FF} using the temperature responses of the CO_2 effluxes in the automated chambers on different temporal timescales in Hyytiälä (**III**) according to Pumpanen et al. (2015). The short-term temperature responses fitted over the 7-day periods were assumed to represent the CO_2 efflux of heterotrophic microbes decomposing SOM (R_H) and long-term temperature response fitted over the growing season CO_2 efflux of the forest floor (R_{FF}), i.e. both autotrophs and heterotrophs (Pumpanen et al. 2015). The R_H in each chamber *i* was calculated with an exponential function as follows:

$$R_{H_i}(t) = r_{0_i} Q_{10h_i}^{\frac{T_i(t)}{10}}, \quad (10)$$

where R_H is the heterotrophic respiration, r_0 the average 7-day temperature response fitting in the second week of May in 2013–2015, Q_{10h} the mean Q_{10} value over the 7-day periods and $T_i(t)$ the T_S at moment *t*. An average of r_0 fitted over the 7-day period beginning the second week of May 2013–2015 was used for both study years because the measurements were begun later in the study years 2017–2018. The R_{FF} for each chamber was calculated in

the same way as in Equation 2, but using parameters Q_{10} and r_0 of the long-term fitting over the growing season. The R_R in each chamber i was separated by removing the calculated R_H from the R_{FF} as follows:

$$R_{R_i}(t) = R_{FF_i}(t) - R_{H_i}(t). \quad (11)$$

3.5 Root incubations (III)

The tree roots were excavated from the soil of the Scots pine stand (**III**) approximately 100 m from the main experimental area at the SMEAR II station in Hyytiälä to prevent disturbance of the study site. Three root samples were excavated from depths of approximately 5–15 cm from the ground level at 2–4-week intervals from April to November in 2017–2018. The root samples were cut from coarse roots or root systems as a whole with root tips, with only one cutting surface to minimize additional respiration from the extra cuts, although Makita et al. (2013) concluded that the respiration rate was significantly higher only when root samples were cut more than 10 times. The root samples were cleaned by hand of the excess soil, while the microbial respiration from adhering soil was expected to have minimal impact on respiration (Makita et al. 2013). The diameter of the root samples at the thickest point was approximately 1–2 mm and full length of the sample root was approximately 15–20 cm (Figure 6B).

The root samples were incubated with the self-built incubation system (Figure 6A) at the field site. The samples were put in multilayer 1-l gas-sampling bag within 5 min after cutting to prevent a major decrease in CO_2 emissions. The bag was sealed, emptied of air and refilled with 500 ml ambient air. The CO_2 concentration in the bag was measured at ambient temperature with a nondispersive GMP343 infrared sensor (Vaisala Oyj) every 5-sec for a total of 15 min in each measurement. The air in the chamber bag was circulated (0.5 l min^{-1}) during the measurement with a small pump (KNF Neuberger Inc., Freiburg, Germany).

The CO_2 efflux was calculated from the increase in CO_2 concentration inside the bag by linear fitting with time. Only measurements between 1 min and 5 min were used in the analysis. Since the size of the samples varied, mass-based respiration rates were derived, using the dry weight of the individual root sample. The dry-mass-based respiration of excised roots was upscaled to the ground area, using an estimate for daily living pine root biomass at the study site in Hyytiälä (SMEAR II station). The daily living root biomass per ground area was calculated for each day of the year, using the total pine root (diameter < 5 mm) biomass of 221 g m^{-2} at the site (Ding et al. 2021) and daily growth measured at the site in 2018 (Ding et al. 2020), whereas the turnover rate of the roots was assumed to be 1 yr.

The residual respiration (R_{RES}) was calculated, reducing the predicted values ($R_i(t)$) from the measured CO_2 fluxes ($f_i(t)$) within treatment i as follows,

$$R_{RES_i}(t) = f_i(t) - r_0 Q_{10}^{\frac{T(t)}{10}}, \quad (12)$$

where r_0 is the basal respiration rate, Q_{10} the temperature coefficient and $T(t)$ the T_A or T_S at measurement time t. First, the Q_{10} and r_0 were fitted to the measured CO_2 fluxes, and then the Q_{10} and r_0 values obtained were used for predicting the respiration with T_A or T_S measured at SMEAR II in Hyytiälä (**III**).

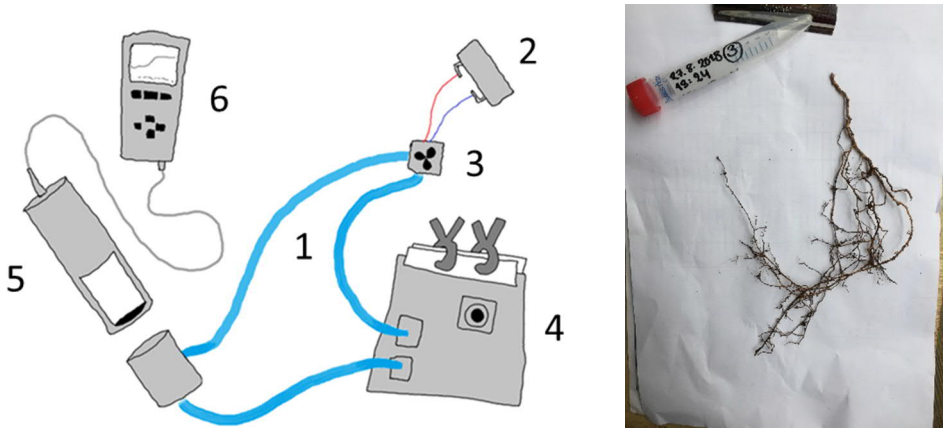


Figure 6. Illustration of an incubation system including: 1) tubing (in blue), 2) battery, 3) pump and 4) chamber bag on the right and 5) Vaisala infra-red CO_2 probe with 6) logger on the left (A), and an example of excised root sample in the field site in Hyytiälä (B) (**III**). Drawing A by Sini Salko and photo B by Kira Ryhti.

3.6 Whole-tree carbon-balance modelling (III, IV)

The process based model 'Carbon Allocation Sink-Source Interaction' (CASSIA) (Schiestl-Aalto et al. 2015) was used to analyse the seasonal dynamics of whole tree C balance and allocation to different functional pools at SMEAR II in Hyytiälä (**III**, **IV**), with a time-step of 1 day. In the model, photosynthesized C (photosynthesis; *P*) is allocated to the tree organs (e.g. foliage xylem, fine roots), and used for structural growth (*G*), released as respiration (*R*) or allocated to mycorrhizal symbionts belowground (*B*). The change in total NSC storage (*W*; kg C tree^{-1}) is as follows:

$$\frac{dW}{dt} = P - R - G - B. \quad (13)$$

The NSC storage was further divided into soluble sugars and starch. The photosynthesis was modelled (**IV**), using SPP (Stand Photosynthesis Program) model (Mäkelä et al. 2006), which was calibrated to our study site at SMEAR II (Kolari et al. 2007; Duursma et al. 2009) and provides photosynthesis of different size classes of trees in a stand. The GPP derived from the EC measurements conducted at SMEAR II was used as photosynthesis in the modelling (**III**). Continuous measurements of T_A, T_S and SWC measured at SMEAR II were used as the other inputs (**III**, **IV**).

Belowground C allocation to mycorrhizal fungi was added to the model (**IV**). NSCs were allocated to the belowground after the T_S in the B-horizon increased to above 10 °C, simultaneously with cessation of shoot growth. A proportion (a_B; 0.0–0.3) of daily photosynthesis was allocated to belowground symbionts if the total NSC storage exceeded a threshold (W_B; kg C tree^{-1}). The threshold was determined as the sum of total NSC storage, in which growth decreases in the original model version (W_{crit}), and the average C pool was used for autotrophic respiration late season (October–December) in 1997–2012, according to Schiestl-Aalto et al. (2015). Allocation to belowground symbionts (B_i) on day *i*, after shoot

growth cessation was as follows,

$$B_i = \begin{cases} a_B P_i, & if\ W_i \geq W_B \\ 0, & if\ W_i < W_B \end{cases}, \quad (14)$$

where P_i is the photosynthesis (kg C tree^{-1} day^{-1}), W_i the total NSC storage, and W_B the threshold for C allocation to belowground symbionts.

Root growth in the CASSIA model was updated (**III**) according to the daily root elongation rate determined from flat-bed scanner images at SMEAR II in 2018 by Ding et al. (2020). Responses of the daily growth rate of pioneer and fibrous roots to T_S and SWC presented by Ding et al. (2020) were added to the CASSIA model. The R_R was calculated as the sum of growth and maintenance respiration of roots modelled with CASSIA, in which the maintenance respiration is dependent on the T_S and moisture, and growth respiration is proportional to the growth rate.

3.7 Non-structural carbohydrates (III, IV)

The same roots as for incubation were used in the NSC analysis in Hyytiälä (**III**). The sampling and incubation of the roots is described in section 3.5 Root incubations. After incubation, the root samples were put into 15-ml plastic tubes and kept in the cold in a cooler for approximately 1 hr before heating in a microwave oven (1 min, 600 W) to stop the enzymatic activity. The root samples incubated were stored in a freezer (–18 °C) until they were dried (**III**). Fine root samples were collected from nearby the sample trees or other tree-organ sampling (**IV**) at the SMEAR II station in Hyytiälä. The fine root samples were collected every 3 weeks during the snow-free period and less frequently outside the growing season for a total of nine times during year 2015. The samples were taken with soil cores (with a diameter of 5 cm) from the humus and A-horizon layers in the soil. The fine roots were identified and divided into two size classes (< 1 mm and 1–2 mm) and later pooled together for each sampling day, since the NSC concentrations did not vary significantly between these size classes. The root samples were frozen in liquid N after being washed from the soil and stored in an ultra-low freezer (–80 °C) (**IV**). Thereafter, all the root samples (**III**, **IV**) were freeze-dried (SciQuip Ltd. Merrington, Shropshire, UK) for 3 days (72 hr) and milled into fine powder (Spex SamplePred, Metuchen, NJ, USA) before the laboratory analysis.

The concentrations of NSCs, soluble sugars (alpha and beta glucose, fructose, sucrose and raffinose) and starch in the incubated roots (**III**), and the fine-root samples (**IV**) were analysed at the Natural Resources Institute, Helsinki, Finland (LUKE). In practice, the soluble sugars were extracted from approximately 50 mg of finely ground samples and the concentrations were analysed with a gas chromatograph (Agilent Technologies Inc., Santa Clara, CA, USA) equipped with a mass spectrometer (Agilent Technologies Inc.). After extraction of the soluble sugars, the starch was enzymatically degraded to glucose and the concentration was analysed with a spectrophotometer (Shimadzu Co., Kyoto, Japan). The NSC concentrations were determined per dry weight.

3.8 Statistical analyses

The effects of the vegetation and TR treatments on the CO_2 emissions within each year in 2013–2015 in Hyytiälä (**I**) were tested, using the linear mixed-effect model and with the

general linear-hypothesis test (Hothorn et al. 2008) at significance levels of $P < 0.01$ and $P < 0.001$. The normalized yearly CO_2 emissions of the treatments in Hyytiälä were compared in year 2013 to years 2014 and 2015 with the Wilcoxon signed-rank test at a significance level of $P < 0.05$ (**I**).

The effects of the various environmental drivers (i.e. T_S and SWC) on the R_H and R_R measured at each site (**II**) were tested, using linear mixed-effect 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). The effect of a fixed-intercept parameter (B_0), T_S (B_T) and RWC (B_{RWC}), and interaction of all these parameters was tested and only statistically significant parameters were included in the model. In addition, linear-regression analysis was conducted between the R_R and GPP, and between the R_R and the annual temperature sum at a significance level of $P < 0.05$ (**II**).

The associations between the various environmental variables (i.e. temperature, SWC), NSC concentrations and variables of the R_R and R_{RES} of incubated roots in Hyytiälä in 2017–2018 were tested with Pearson's correlation analysis and linear regression analysis at a significance level of $P < 0.05$ (**III**). In addition, the correlations between the four methods of determining the R_R in Hyytiälä were tested with Pearson's correlation analysis (**III**).

R (R Core Team 2019), MATLAB (version 2018a, MathWorks, Natick, MA, USA) and SPSS Statistics (IBM SPSS, Armonk, NY, USA) softwares was used in the statistical analyses.

4 RESULTS AND DISCUSSION

4.1 Overview of environmental conditions and fluxes (I–IV)

The T_A levels in spring and summer were lowest in 2017 than in other years within the period 2013–2018 in Hyytiälä (Figure 7A). This resulted in wide differences in the T_{SUM} (i.e. thermal time; the sum of the daily average temperatures above 5 °C), which were 1463, 1417, 1213, 1347, 1040 and 1669 °Cd in 2013–2018, respectively, 2018 being the warmest year. The T_S fluctuation lagged behind that of T_A, being lower than in the T_A in summer and higher during winter (Figure 7A). The monthly mean T_A and annual T_{SUM} were highest in the southernmost temperate Scots pine forest (Brasschaat) and lowest in the northernmost boreal Scots pine forest (Värriö) (**II**).

The annual GPPs (1307, 1266, 1289, 1309, 1204, and 1249 g C m^{-2} yr^{-1} in 2013–2018, respectively; Figure 7B) and annual NEEs (–293, –299, –323, –295, –299, and –324 g C m^{-2} yr^{-1} in 2013–2018, respectively; Figure 7B) in Hyytiälä were comparable in different years, despite larger interannual changes in T_{SUM} values. The annual GPP was highest at the southernmost site in Brasschaat and lowest at the northernmost site in Värriö (**II**)

The mean R_{FF} measured with manual chambers in Hyytiälä was highest in summer 2018, while the mean respiration in the TR plots by heterotrophic microbes (i.e. R_H) was highest in 2015 (Figure 7C). Similarly, the R_{FF} in mature Scots pine and mixed Norway spruce stands in Sweden was higher in the warmer, dryer year 2018 than in the cooler, wetter year 2017 (Chi et al. 2021). The mean R_{FF} decreased from 2013 to 2015, probably following the changes in the T_S and SWC, whereas R_H in the TR plots increased due to the 'Gadgil effect' (Gadgil and Gadgil 1971, 1975) (**I**). The annual R_{FF} increased with the T_{SUM} in both Scots pine and Norway spruce stands along the latitudinal gradient, with exception of the mixed Scots pine/ Norway spruce forest in Norunda, where R_{FF} was highest in all of the study years (**II**). Norunda is known to be a long-term net source of CO_2, potentially due to high levels of decomposition of old SOM and thereby high R_H (Lagergren et al. 2019; Shahbaz et al. 2022). Janssens et al. (2001) found that neither soil respiration nor the TER of 18 forested sites throughout Europe was associated with the mean annual temperature, but that both were significantly associated with the GPP, and thus with the productivity of the site. However, the T_{SUM} is probably a better measure of growing season temperature than is the annual mean temperature, since it only accounts for daily average temperatures above 5 °C.

The mean SWC in the TR plots was higher in most years than in the continuously measured SWCs in the intact soil of Hyytiälä (Figure 7D). The driest year was also the warmest year, i.e. 2018, when the continuously measured SWC in the soil of the upper B horizon was lowest (< 0.2 m^3 m^{-3}) from June to September, whereas in 2013 and 2014, the SWC was lowest in early August and during September to October in 2015 (Figure 7D). The years 2016 and 2017 were moist, and the SWC was above 0.2 m^3 m^{-3} throughout the year. The monthly mean SWCs varied between the sites along the latitudinal gradient, but were usually higher at the boreal Norway spruce sites than at the Scots pine sites (**II**).

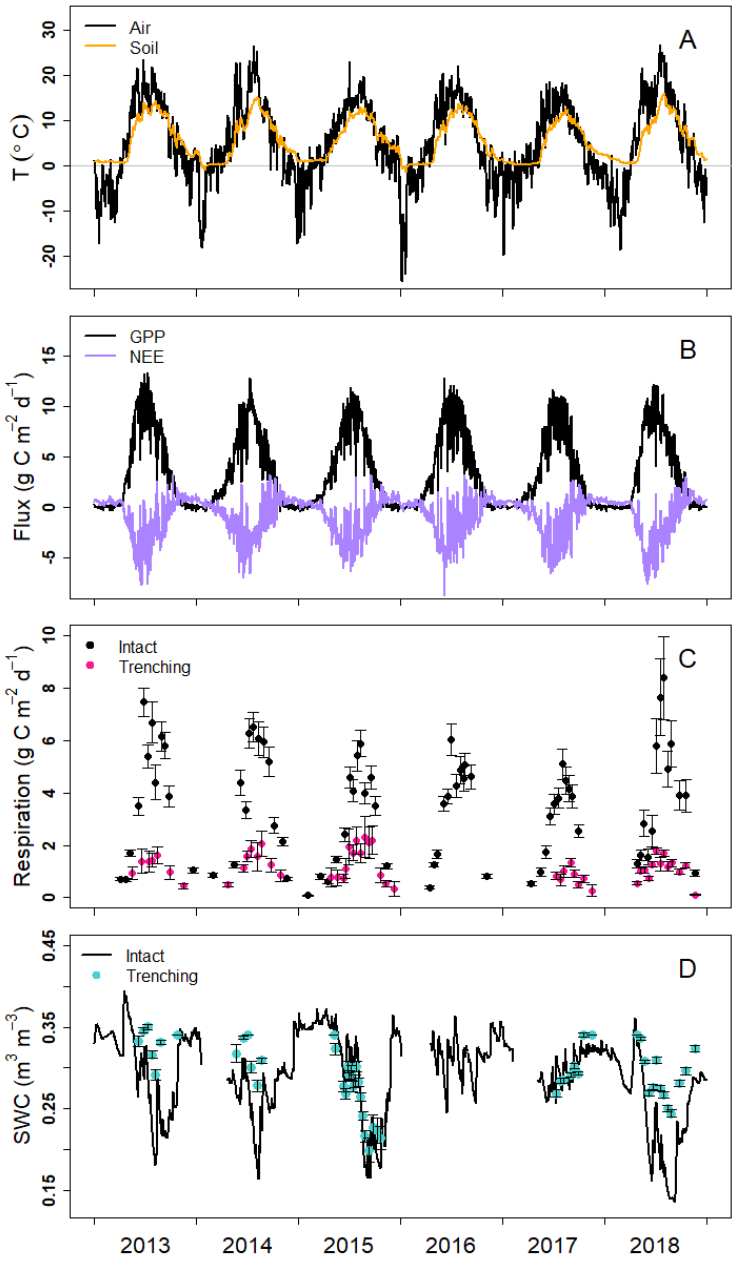


Figure 7. Daily mean air temperature (T) in black and soil T at 9–14-cm depths in orange (A), gross primary production (GPP) and measured net ecosystem carbon dioxide (CO_2) exchange (NEE) (B), mean forest floor respiration at intact plots ± standard error (SE) in black and mean respiration of root-exclusion (trenching; TR) plots without ground vegetation (TR1-CUT) ± SE in pink (C), soil-water content (SWC) in the soil at 10-cm depth at intact plots in black and in TR plots ± SE in blue (D) at the Hyytiälä field site in 2013–2018 (**I**–**IV**).

4.2 Forest floor respiration components (I, II)

The annual R_{FF} was partitioned into mean R_R, R_H, R_{SHR}, R_{GMH} and R_{MY} in 2013–2015 in Hyytiälä (**I**). The data collected 9 months after TR in 2013 were used to show the overall contribution of the various CO_2 sources, before treatment-related changes were established in the system (e.g. the Gadgil effect). The mean contributions of R_R and R_H were 48% and 30%, respectively, while R_{GMH}, R_{SHR}, and R_{MY} were 10%, 8%, and 4%, respectively, of the total R_{FF} (Figure 5 in **I**). The annual R_{FF} was partitioned into R_H and R_R at seven conifer sites along a latitudinal gradient (Figure 2) (**II**).

The R_H in the TR plots increased over time, presumably due to exclusion of tree roots and mycorrhizal fungi (**I**). This so-called 'Gadgil effect' (Gadgil and Gadgil 1971, 1975; Fernandez and Kennedy 2016) was seen in both TR treatments (TR1 and TR50) throughout the years, especially when the ground vegetation was removed (CUT) (Figure 7C) or everything other than dwarf shrubs was removed (SHR) (**I**). The CO_2 emissions in the TR treatments without ground vegetation increased almost two-fold when the yearly variation was normalized (**I**), indicating a strong increase in soil heterotrophic microbial activities. Similar enhancement was not seen in the CON treatments (**I**), in R_{FF} measured in Hyytiälä (Figure 7C) or in **III**. The annual R_H increased with the T_{SUM} in both Scots pine and Norway spruce stands, being exceptionally high in most of the study years in the mixed Scots pine/ Norway spruce forest in Norunda (**II**). However, when the R_H was normalized with soil C at each site, the R_H per soil C was seemingly independent of the annual T_{SUM} (**II**). The T_S and soil moisture showed a statistically significant association with the R_H at all sites, except soil moisture in the northernmost stand in Värriö (**II**).

The R_R comprised on average 48% of the R_{FF} (**I**), which is in accordance with Hanson et al. (2000), who estimated from 37 published field-based studies that the R_R contributes 49% of the total soil respiration for sites with forest vegetation. Similar results found with both girdling and TR experiments in boreal coniferous forests support the finding (e.g. Högberg et al. 2001; Lavigne et al. 2003; Vogel et al. 2005; Comstedt et al. 2011). In contrast to the R_{FF} and R_H, the annual R_R of the stands did not show as clear an association with the T_{SUM} along a latitudinal gradient, and even normalizing the R_R with fine-root biomass at each site did not differ in outcome (**II**). The T_S showed a statistically significant association with the R_R at all sites, with the exception of the southernmost stand in Brasschaat (**II**). Soil moisture also showed a statistically significant association with the R_R at all sites, except in the northernmost stand in Värriö (**II**).

The R_{MY} comprised up to 4% of the R_{FF} in Hyytiälä (**I**), which was considerably less than in most published studies varying from 3% to 31% of the R_{FF} in various temperate and boreal ecosystems (Heinemeyer et al. 2007, 2012; Moyano et al. 2008; Fenn et al. 2010; Andrew et al. 2014; Yan et al. 2019). A recent study conducted in Scots pine stands in central Sweden, in which incubating ingrowth mesh bags were used, showed that the R_{MY} in the growing season contributed up to 17% of the R_{FF} on average (Hagenbo et al. 2019). The CO_2 emissions were expected to be higher in TR50 than in TR1 (Equation 6), since mycorrhizal fungi could enter the plot through a pore size of 50 µm, but not through 1 µm (**I**). However, the annual CO_2 emissions within the TR50 and TR1 treatments were similar, indicating that the distance between the collar for chamber measurements and the intact soil with roots and their mycorrhizae around the plot may have been too long to detect the main R_{MY}, especially in the first years (**I**). Nevertheless, in the TR50 treatments where dwarf shrubs were left intact (SHR), the R_{MY} was higher than on average or with CUT or normal intact ground vegetation (NOR), and increased throughout the study years in 2013–2015 (**I**). The ericaceous dwarf

shrubs roots and their mycorrhizae more probably passed through the 50-µm mesh from inside to outside the plot, rather than the other way around (**I**). Dwarf shrubs have been suspected of having fungal interconnections with boreal trees via ericoid, endophytic, or ectomycorrhizal fungi (see Vrålstad 2004). Klein et al. (2016) showed belowground C trade-offs among the trees in a temperate forest via overlapping rhizospheres assisted by common ectomycorrhizal networks, while Pickles et al. (2017) studied the fungal networks between Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) seedlings.

The R_{GMH} comprised 10% of the R_{FF} in Hyytiälä and was not partitioned further in our study (**I**), but other studies have found that the contribution of mosses can be substantial, accounting for 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) and 7% in a black spruce forest in Canada (Swanson and Flanagan 2001).

The R_{SHR} comprised 8% of the R_{FF} in Hyytiälä and increased throughout the study years 2013–2015 in the absence of tree roots, but only when hyphal access was allowed (TR50) (**I**). The R_{SHR} and TR50 increased throughout the study years in 2013–2015 (**I**). This could indicate dwarf shrubs having fungal associations outside the plots via their ericoid mycorrhizae. In turn, the R_{SHR} in our study may have become reduced when accompanied by other ground vegetation, such as mosses, or tree roots, in the same plot (**I**). 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 than did soil with deeper moss layers, which led to increased N availability to plants. Mosses (e.g. *Pleurozium schreberi*) may suppress growth in Scots pine seedlings and dwarf shrubs due to retention of N in ground-floor vegetation (Zackrisson et al. 1997, 1999), while removal of mosses and lichens leads to increased growth of dwarf shrubs (Hautala et al. 2008).

4.3 Respiration of tree roots (I–III)

The R_R calculated by the root exclusion method in Hyytiälä (**I**, **III**) agreed well with that determined with the temperature response method and the CASSIA model, except in 2015 (Figure 8). Exclusion of tree roots and their mycorrhizae from the soil imparts competitive advantage to heterotrophs (i.e. the 'Gadgil effect'), resulting in overestimation of the R_H over time (**I**, **II**), which would, in turn, result in underestimation of the R_R. Partitioning in 2013–2015 was conducted using TR50, which allows ingrowth of mycorrhizal hyphae into the plot. However, ingrowth of mycorrhizal fungi seemed negligible, which was not enough to suppress the heterotrophic activity (**I**). The R_R derived with the temperature-response method was similar to that modelled with CASSIA, although somewhat lower also in 2015 (Figure 8). The R_R was higher in the warmer years, such as 2013, 2016 and 2018, than in the cooler years 2015 and 2017 (Figure 8).

The R_R derived from the excised root-incubation method was notably lower during the summer months than those from the other three methods in 2017–2018 (Figure 8) (**III**). This may indicate that the method was not successful, because it considered only the respiration and biomass of smaller roots (diameter < 5 mm), while upscaling of the dry-mass-based respiration was conducted, using an estimate of the daily living biomass of roots (**III**). For example, standardizing the sample size is difficult, which again may have resulted in differences in respiration between samples. Thus, weighting the incubated R_R only with the dry weight of the samples may not have been sufficient, since most of the variation in respira-

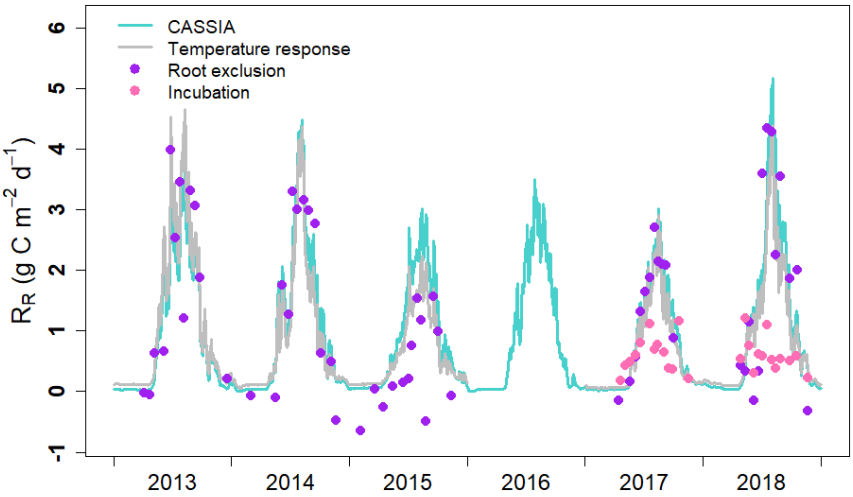


Figure 8. Mean tree root respiration (R_R), using excised root incubation in pink, mean R_R partitioned from total forest floor respiration in the field using the root exclusion method in purple, mean R_R between chambers partitioned with a temperature response approach from total forest floor respiration in grey and R_R simulated with the whole-tree carbon (C) balance model 'CASSIA' in blue in 2013–2018 in Hyytiälä (I–IV).

tion of fine roots can be explained by diameter, root tissue density, N content or total root length per unit root mass, which also accounts for branching of the roots (Burton et al. 2002; Makita et al. 2009, 2012, 2016). Moreover, the root samples were excavated from topsoil, which may be significantly drier than the deeper soil layers, which may not represent the status of the entire root system, including the deeper soil layers, varying root types and symbiotic microbes.

The R_R showed a statistically significant association with soil moisture at all sites, except in the northernmost stand in Värriö (**II**). Besides, Matkala et al. (2021) found no effect of extreme weather events (e.g. extremely warm, dry years; including year 2018) on the TER, respiration potential or water exchange of a Scots pine stand in Värriö located in eastern Finnish Lapland (Figure 1). In contrast, the TER and respiration potential decreased, due to warm, dry summers in a Norway spruce forest in western Finnish Lapland (Matkala et al. 2021). The significant associations between the R_R and soil moisture (**II**) were mostly negative at the Scots pine sites, while in the pure Norway spruce stands, the associations were positive. This indicates that a decrease in soil moisture also decreases the activity of tree roots (i.e. R_R), as shown by Norway spruce, which are less resilient to warm, dry periods than are Scots pine (Lagergren and Lindroth 2002; Baumgarten et al. 2019; Matkala et al. 2021), which may be seen (**II**) as a decrease in the R_R with soil moisture in the Norway spruce stands. Various tree species also have different types of root systems and strategies for responding to drought stress by modifying their water uptake dynamics (Grossiord et al. 2017). Plants can, for example, grow roots deeper to reach deeper water sources (Mackay et al. 2020). Furthermore, a decrease in soil moisture decreased the R_R of the incubated roots when the temperature effect was removed (i.e. R_{RES}; Equation 12) in Hyytiälä (**III**). Likewise, Burton and Pregitzer (2003) found that dry conditions significantly reduced the respiration rates of the excised roots of sugar maple (*Acer saccharum* Marshall) and red pine (*Pinus*

resinosa Alton) in Michigan, USA. However, as noted previously, the root samples for incubation were excavated from the topsoil, which may be significantly drier than the deeper soil layers (**III**), whilst the CO_2 efflux measured in the TR experiments (**I–III**) also arose from the deeper soil layers.

4.4 Non-structural carbohydrate dynamics of tree roots (III, IV)

The raffinose concentration in the incubated roots in Hyytiälä (**III**) was clearly higher in spring and autumn than in summer, and rather similar in 2017–2018 (Figure 9A), while the results for 2015 were lacking (**IV**). The fructose and glucose concentrations were on average higher in warm year 2018 than in 2015 or 2017 (Figure 9B). The annual pattern of the fructose and glucose concentrations varied between the study years, decreasing during the summers in 2015 and 2017, and increasing during summer 2018. The sucrose + glucose + fructose (SGF) sum and the sucrose concentrations tended to increase towards the end of the study years (Figure 9C). The starch content showed no clear interannual differences between the study years (Figure 9D). The total NSC (i.e. soluble sugars and starch) concentration, upscaled for the whole tree in 2015, increased in spring, peaked in June and decreased again towards autumn, mainly due to changes in starch concentration (**IV**).

The sucrose, glucose and fructose concentrations were higher in the drier, warmer year 2018 than in the moister, cooler year 2017, indicating osmoregulation in the roots (**III**). Under dry conditions, the concentration of solutes (i.e. sugars) increases in tree tissues, such as roots, to increase the osmotic pressure in response to water stress and to maintain water balance in the cells. The glucose and fructose concentrations especially were correlated negatively with the SWC, but also sucrose, SGF and soluble sugars were also negatively associated with the SWC (**III**). The soil moisture also decreased in late summer 2015, while the glucose concentration seemingly increased along with it (Figure 9B). Similarly, Koppenaal et al. (1991) found higher glucose and fructose concentrations in the roots of water-stressed jack pine (*Pinus banksiana* Lambert) and white spruce (*Picea glauca* (Moench) Voss) seedlings after exposure to 7 days of water stress. Zang et al. (2014) observed a significant negative correlation between the root fructose concentrations and reduced soil moisture in European beech (*Fagus sylvatica* L.) saplings. Furthermore, the soluble sugar concentrations correlated negatively with the SWC, which is in line with previous findings of increased soluble sugar concentrations in roots under water stress (Kim et al. 2000; Rogiers et al. 2011; Galiano et al. 2017). The raffinose concentrations in the incubated roots correlated positively with the SWC; however, the correlation was likely due to coincidence between the higher SWC and lower T_S, and a strong negative correlation between the T_S and raffinose concentrations in the roots (**III**). Likewise, Niederer et al. (1992) found higher raffinose concentrations in Norway spruce roots during winter and lower concentrations in summer. Decreasing temperatures and a change from long to short days in autumn stimulate cold and frost adaptation and induce raffinose synthesis. However, Wiemken and Ineichen (1993) noticed that raffinose accumulated in Norway spruce roots when they were cooled, even if the shoots, which primarily perceive the photoperiod and temperature changes were kept in a warm environment or removed. The starch concentration in the incubated roots was insensitive to changes in the SWC, but correlated positively with the T_S (**III**). After removing the effect of temperature on the R_R of the incubated roots, the

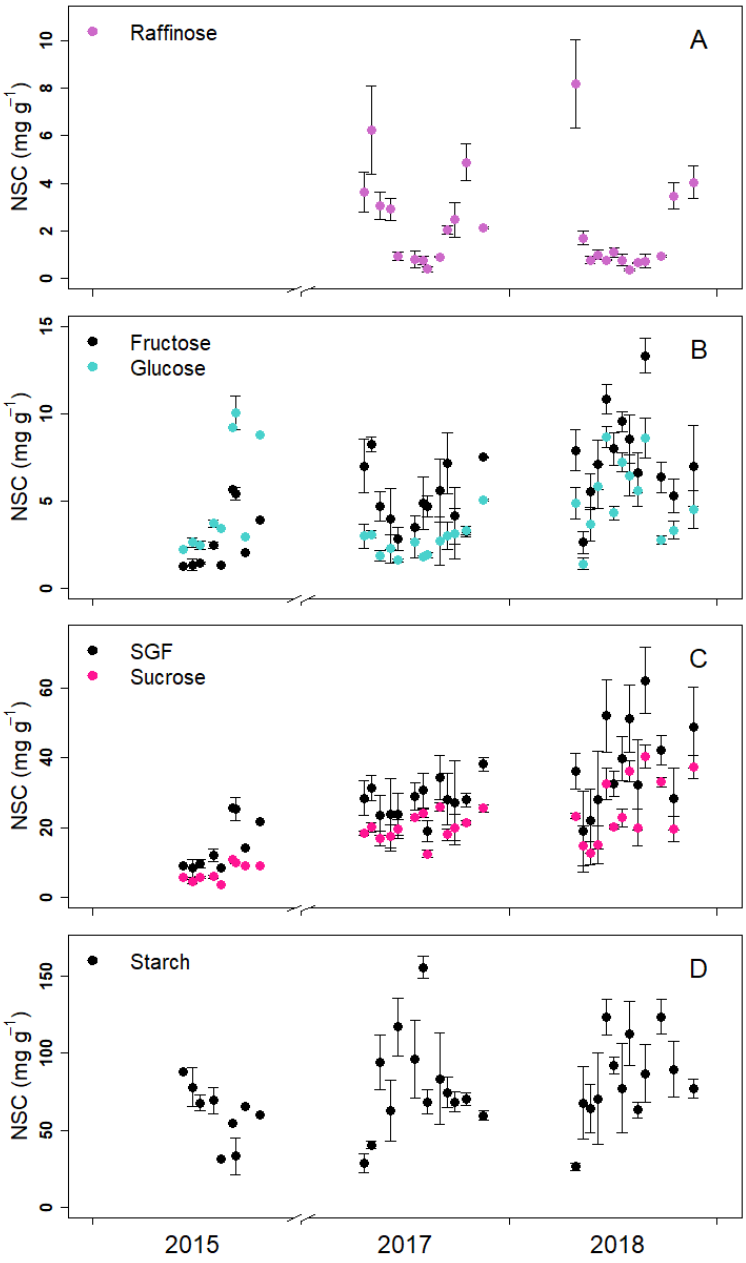


Figure 9. Mean concentrations ± standard error (SE) of raffinose in purple (A), fructose and glucose in black and light blue, respectively (B), sucrose, glucose and fructose (SGF) combined and sucrose in black and pink, respectively (C) and starch in black (D) in fine roots obtained with a soil corer in 2015 (**IV**) and incubated root samples in 2017 and 2018 (**III**) in Hyytiälä.

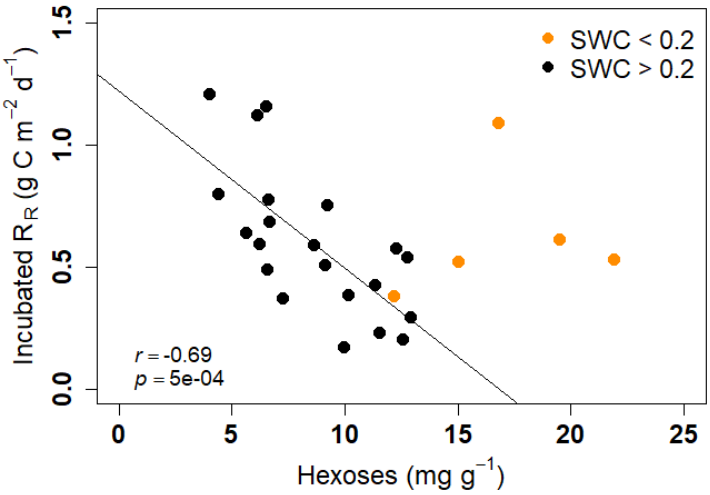


Figure 10. Root respiration rate (R_R) and the concentration of hexoses (i.e. glucose and fructose) of incubated roots at the SMEAR II Scots pine stand in 2017–2018 (**III**). The measurements during the drought in 2018 (soil-water content (SWC) < 0.2 m^3 m^{-3}) are indicated in orange. The line represents linear regression (P < 0.05), where the association between the means of the R_R and the concentration of hexoses with sufficient soil moisture (points in black) was calculated, using Pearson's correlation.

R_{RES} was negatively associated with the root fructose and glucose concentrations (**III**). NSCs are used as energy sources in plant metabolism, and therefore, the negative correlation between the root NSC concentrations and the R_{RES} could indicate consumption of C compounds by the roots. However, despite a clearly negative association (Figure 10) between the incubated R_R and concentration of hexoses (i.e. fructose and glucose) with sufficient soil moisture (SWC > 0.2 m^3 m^{-3}), it was lost when the soil moisture became too low (SWC < 0.2 m^3 m^{-3}) (r = –0.31, P > 0.05). Thereby, the low SWC was most probably driving the increase in these NSC compounds, while the respiration of the incubated roots did not directly follow the changes in NSCs in our study (**III**).

4.5 Belowground carbon allocation of trees (III, IV)

The belowground C allocation of trees was estimated with the whole-tree C balance model CASSIA in Hyytiälä (**III, IV**). Maximum photosynthesis, indicated by GPP, was rather similar in years 2013–2018 in Hyytiälä (Figure 7B). The estimated aboveground (i.e. foliage, shoot, stem) growth and respiration began in late March 2014 and 2015, in early April 2016 and 2017, and later in April in 2013 and 2018 according to modelling with CASSIA (Figure 11). The R_R and root growth modelled were highest shortly after the aboveground growth began to decrease throughout the period 2013–2018 (Figure 11). The growing period for the root growth modelled was very similar in all the years, but ended slightly earlier in 2016 (Figure 11).

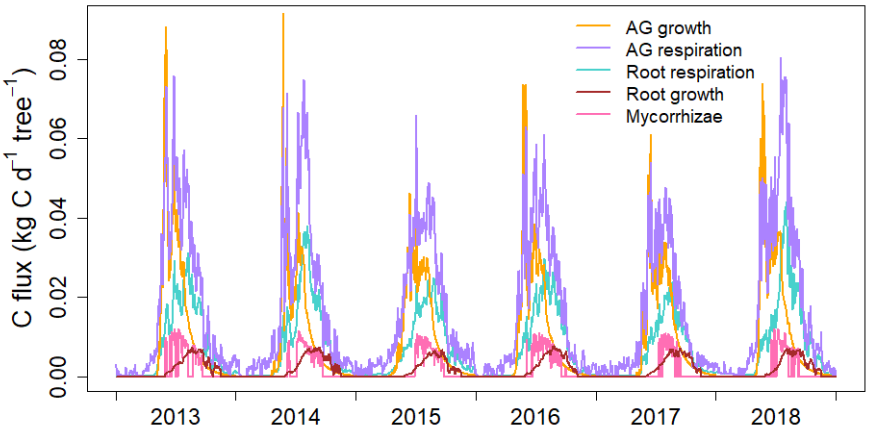


Figure 11. Aboveground (AG) respiration, AG growth, root respiration (R_R), fine-root growth and allocation to mycorrhizal fungi simulated with the whole-tree carbon (C) balance model 'CASSIA' in Hyytiälä (**III**, **IV**) 2013–2018.

The annual C allocation to root growth modelled with CASSIA was 0.64 kg C yr^{-1} $tree^{-1}$ on average in 2013–2018, being lowest in 2015 and highest in 2014 (Table 3). The annual R_R modelled was 2.7 kg C yr^{-1} $tree^{-1}$ on average in 2013–2018, being lowest in 2017 and highest in 2018 (Table 3). The annual root growth was 5.4% and annual R_R 23% of the annual photosynthesis estimated with CASSIA modelling. Janssens et al. (2002) estimated that fine-root growth in temperate Scots pine forest in Belgium accounted for 7–8% and R_R ~16–25% of the GPP. The annual C allocation to belowground symbionts (i.e. mycorrhizae) was 0.57 kg C yr^{-1} $tree^{-1}$ on average in 2013–2018, being lowest in 2017 and highest in 2016 (Table 3). This was 4.7% of the annual photosynthesis (i.e. GPP), and 14.7% of the NPP on average in 2013–2018, 14.7–17.3% in 2013–2016, but only 11.3% and 11.5% in 2017 and 2018, respectively. Similar results were found by Finlay and Söderström (1992), in which allocation to ectomycorrhizal fungi was estimated to be 15% of the NPP in a Scots pine stand in Sweden, and by Vogt et al. (1982) who estimated that 14% and 15% of the NPP was allocated to ectomycorrhizae in young and old Pacific silver fir (*Abies amabilis* Douglas ex J. Forbes) stands, respectively. In a ^{14}C labelling study with Scots pine saplings, Leake et al. (2001) estimated that ~16% of the NPP was allocated to ectomycorrhizal fungi. In contrast, C allocation to belowground symbionts and exudation was estimated by Janssens et al. (2002) to account for 5–15% in a temperate Scots pine stand in Belgium.

The belowground C allocation for root growth, respiration and mycorrhizae modelled with CASSIA resulted annually in 3.9 kg C yr^{-1} $tree^{-1}$ on average in 2013–2018, which was 33% of the annual photosynthesis. For comparison, the R_R was more than 50% of the GPP at the northernmost site in Värriö and approximately 15% at the southernmost site in Brasschaat (**II**). This is in line with other studies conducted across a latitudinal gradient in Europe, stating that trees allocate more C to fine roots and their associated mycorrhizae in N-poor subarctic soils than in soils in temperate forests with higher N-availability (Ostonen et al. 2017). Högberg et al. (2002) estimated that trees allocated 63% of the net photosynthetic production (GPP – respiration in foliage) for root growth and respiration in a boreal Scots pine forest in Sweden. In the temperate Scots pine forest in Belgium, the belowground C allocation accounted for 28–49% of the annual GPP (Janssens et al. 2002). On the one hand, trees grow

more absorptive fine roots under N-deficiency (Ostonen et al. 2017), but on the other may invest comparatively more resources in roots to obtain soil water under arid conditions (Ledo et al. 2018).

Table 3. Carbon (C) allocated for root growth, root respiration (R_R), mycorrhizae and as a sum of all in total belowground yearly value per tree modelled with CASSIA in Hyytiälä 2013–2018.

Year	Growth (kg C yr^{-1} $tree^{-1}$)	Respiration (kg C yr^{-1} $tree^{-1}$)	Mycorrhiza (kg C yr^{-1} $tree^{-1}$)	Total (kg C yr^{-1} $tree^{-1}$)
2013	0.65	2.8	0.62	4.08
2014	0.68	3.0	0.61	4.27
2015	0.56	2.6	0.62	3.75
2016	0.64	2.7	0.66	4.01
2017	0.65	2.1	0.41	3.20
2018	0.63	3.1	0.48	4.26

5 CONCLUSIONS

In the cool, wet climate of the boreal region, temperature and soil fertility are important factors determining soil C dynamics in forests. However, with global warming upon us, drying of the soils may increase, and thus, soil-water availability may also become a more important factor in boreal forests. Although extremely hot, dry summers have been rare in the boreal region, severe heat waves and droughts have occurred in recent years. Forests with mature trees and large root systems, different ground vegetation species, and their belowground interconnections via mycorrhizal networks are complex systems and rather difficult to study. While many studies about the effects of water-availability on trees and ground vegetation species have been conducted under controlled laboratory conditions, C dynamics in the field may act differently. Therefore, several experiments were conducted in a boreal Scots pine stand located in Hyytiälä, southern Finland and in seven conifer stands along a latitudinal gradient from boreal to temperate climate zones in Northern and central Europe over several growing seasons under varying weather conditions.

The results of this thesis show that competition for resources in the forest floor is intense. The roots of mature trees are strong competitors with wide reach in soil and with their root associated mycorrhizal fungi. When mycorrhizal tree roots are excluded from the soil and competition decreases, the activity of saprotrophic microbes usually increases, sometimes even with intact ground vegetation. Dwarf shrubs also benefit from their ericoid mycorrhizae, but when accompanied by other plants, such as mosses, their activity suppressed.

Trees allocated more photosynthetised C to belowground in the north than in the south. Trees need to grow their root systems larger to scavenge nutrients, because decomposition is slower and forest soil more N-limited in the north than in the south. In the northern boreal zone, trees did not experience a shortage of water, but rather of warmth, while trees in the temperature zone experienced contrasting shortages. With a warming climate, trees in the temperate zone may have even less water available for use during summer, while northern trees probably benefit from increased temperatures, at least with sufficient soil moisture.

Trees from a mature boreal Scots pine stand that were allocated more C belowground in the warmer study years showed less of it in the roots during the colder study years. Respiration and most of the NSC concentrations in the tree roots were also higher in the warmer, drier years than in the cooler, moister study years. The concentrations, especially, of sucrose, glucose and fructose increased with decreasing soil moisture, indicating osmoregulation in the tree roots. R_R was also positively associated with soil moisture. However, these roots were excavated from the topsoil, which was drier than the deeper soil layers, where part of the roots are located. Although summer 2018 was also hot in Northern Europe, the soil may also have to be drier to affect roots in the deeper soil layers and to visibly affect R_R in the total soil column.

The method used to study belowground C dynamics should be selected carefully and adjusted or calibrated to suit specific locations. Studying the forest floor is difficult enough to do without causing a disturbance, because all its components are tightly interconnected. Usually some empirical methods for determining belowground C dynamics are needed at least initially, while other non-destructive methods, such as isotopic analysis or modelling, may be possible after other required empirical information is collected.

The results of this dissertation also highlight the need for taking varying weather events into account in estimating the impacts of climate change on soil C dynamics.

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