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affecting the soil organic carbon pool
and the dynamics of decomposition
in hemiboreal coniferous forests



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ORIGINAL PUBLICATIONS

This thesis is based on the following publications which are referred by their Roman numerals in the thesis:

- I. Hernández, L., Lehtonen, A., Moreno-Fernandez, D., Marin, G., Alberdi, I., Cañellas, I., Ostonen, I., **Kriiska, K.**, Didion, M., Varik, M., Jandl, R., Adermann, V., Blujdea, V. (2017). Towards complete and harmonized assessment of soil carbon stocks and balance in forests: the ability of the Yasso07 model across a wide gradient of climatic and forest conditions in Europe. *Science of the Total Environment*, 599: 1171–1180.
- II. Djukic, I., Kepfer-Rojas, S., Schmidt, I.K., Larsen, K.S., Beier, C., Berg, B., Verheyen, K., **Kriiska, K.**, Ostonen, I., TeaComposition. (2018). Early stage litter decomposition across biomes. *Science of the Total Environment*, 628–629: 1369–1394.
- III. **Kriiska, K.**, Frey J., Asi, E., Kabral, N., Uri, V., Aosaar, J., Varik, M., Napa, Ü., Apuhtin, V., Timmusk, T., Ostonen, I. (2019). Variation in annual carbon fluxes affecting the SOC pool in hemiboreal coniferous forests in Estonia. *Forest Ecology and Management*, 433: 419–430.
- IV. **Kriiska, K.**, Lõhmus, K., Frey, J., Asi, E., Kabral, N., Napa, Ü., Ostonen, I. (201X). The dynamics of mass loss and nutrient release of fine roots, needle litter and standardised substrates in hemiboreal coniferous forests. Manuscript has been submitted for publication to the journal of *Plant and Soil*.

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Author's contribution:

- I. The author is partially responsible for the data processing, data analysis, and interpretation and writing of the manuscript.
- II. The author is partially responsible for the field data collection, data processing, and preparation of the manuscript.
- III. The author is primarily responsible for the data analysis and writing of the manuscript and contributed to the study design, the field data collection and data processing.
- IV. The author is primarily responsible for the data analysis and writing of the manuscript and contributed to the study design, the field data collection and data processing.

ABBREVIATIONS

FRB	fine root biomass (g m^{-2})
FRP	fine root production ($\text{g m}^{-2} \text{ yr}^{-1}$)
MAP	mean annual precipitation (mm)
MAT	mean annual temperature ($^{\circ}\text{C}$)
NEP	net ecosystem production, net primary production minus carbon losses in heterotrophic respiration ($\text{Mg C ha}^{-1} \text{ yr}^{-1}$)
NPP	net primary production, net production of organic matter by plants in an ecosystem ($\text{Mg C ha}^{-1} \text{ yr}^{-1}$)
Rs	soil respiration, the sum of heterotrophic (decomposition of dead organic matter by decomposers) and autotrophic (root and rhizosphere) respiration ($\text{Mg C ha}^{-1} \text{ yr}^{-1}$)
Rh	heterotrophic soil respiration ($\text{Mg C ha}^{-1} \text{ yr}^{-1}$)
Ra	autotrophic soil respiration ($\text{Mg C ha}^{-1} \text{ yr}^{-1}$)
SOC	soil organic carbon (Mg C ha^{-1})
Ts	soil temperature ($^{\circ}\text{C}$)
Ta	air temperature ($^{\circ}\text{C}$)
Q ₁₀	temperature sensitivity of respiration, the proportional increase in respiration when temperature increases by 10°C
TOC	total organic carbon (%)
TR	turnover rate (yr^{-1})

1. INTRODUCTION

1.1. Forest soil organic carbon pool, carbon fluxes and net ecosystem production

Forest soils are one of the largest and most important pools of terrestrial organic carbon (C) in the biosphere (Hartmann et al., 2013), containing more than 700 Gt C (Prentice et al., 2001). Hence, minor changes in the balance between the forest soil organic carbon (SOC) stocks and associated C fluxes could have a significant effect on the atmospheric CO₂ concentration and the global carbon budget (Johnston et al., 2004). Therefore, it is essential to understand and estimate the dynamics of both the stocks and fluxes of the SOC to improve our knowledge of forest ecosystem functioning and to develop climate change policies and adaptation and mitigation actions.

The SOC pool is determined by the balance of C inputs from organic matter and C outputs due to soil respiration (R_s) and the leaching of dissolved organic carbon (DOC) (Davidson and Janssens, 2006; Smith, 2008). More than 50% of net primary production is returned to the soil in the form of above- and below-ground litter (Wardle et al., 2004), whereas approximately 20% of carbon stored in the litter is annually emitted to the atmosphere via decomposition (Houghton, 2007). While the production of litter is primarily controlled by the physiology and functioning of plants (Epron et al., 2001), the decomposition of litter material is influenced by interacting biotic and abiotic factors, including litter quality, decomposer community, soil temperature, soil water content, pH, clay content and soil structure among several other soil properties (Prescott, 2010).

Foliar litterfall is the primary aboveground C input to the forest floor and soil (Vitousek et al., 1995). In coniferous forests, the needles are retained for many years, resulting in potentially high variability in annual needle litterfall (Bhatti and Jassal, 2014), which can be up to three-fold for both Scots pine (*Pinus sylvestris*) (Starr et al., 2005) and Norway spruce (*Picea abies*) stands (Saarsalmi et al., 2007) in the boreal region. Fine root (<2 mm) biomass (FRB) and production (FRP) are the primary contributors of belowground C inputs (Finér et al., 2011; Lukac, 2012), while studies in the last decade have suggested that fine roots may be dominating the accumulation and long-term sequestration of SOC (e.g., Rasse et al., 2005; Clemmensen et al., 2013). Although tree fine root biomass accounts for a relatively small amount of the total belowground biomass (on average 6% in the boreal forests; Vogt et al., 1996), it has been estimated that fine root production contributes up to 75% of the annual net primary production (NPP) in forest ecosystems (Finér et al., 2011). Estimating FRP is complicated and labour-intensive and is therefore one of the major uncertainties in C cycle studies (Lukac, 2012; Leppälammil-Kujansuu et al., 2014a). Understorey vegetation, comprising shrubs and herbs, is another component that is often underestimated or omitted from the forest C budget, although it makes a considerable contribution to NPP, particularly in the

northern latitudes, where understory could constitute up to one third of the total above- and belowground litter production (Kolari et al., 2006; Kleja et al., 2008; Hansson et al., 2013; Leppälammil-Kujansuu et al., 2014a).

Soil respiration, in particular microbial-mediated heterotrophic respiration (Rh), is the dominant pathway of SOC loss (Hanson et al., 2000; Bond-Lamberty and Thomson, 2010). Temporal variation in soil respiration is primarily explained by soil temperature and soil moisture (Raich and Schlesinger, 1992; Raich and Potter, 1995), whereas Janssens et al. (2001) hypothesised that differences in Rs between forests are more likely to depend on productivity than on temperature, through changes in C input into the soil. Among the coniferous forests, Norway spruce stands have been reported to have higher CO₂ efflux from the forest floor than Scots pine stands (Kanerva and Smolander, 2007). However, Boriken et al. (2002) found no significant difference in the rate of Rs between stands dominated by pine and spruce.

Quantifying heterotrophic losses allows the estimation of net ecosystem production (NEP), which enables the classification of forests as C sinks or sources. Boreal and hemiboreal forest ecosystems are often identified as potential C sinks (Luysaert et al., 2007; Krasnova et al., 2019), although the decrease in NEP in old boreal stands (Goulden et al., 2011) drives the forest C balance close to equilibrium and may switch from being a C sink one year to a C source the next (Valentini et al., 2000).

1.2. Decomposition in forest ecosystems: mass loss and nutrient release

Decomposition comprises the breakdown (biological and chemical processes) and leaching of soluble compounds (physical process) of detritus (i.e., dead plant, animal, and microbial material), as well as of soil organic matter, followed by mineralisation and humification of the organic compounds (Aerts, 1997; Chapin et al., 2002). Decomposition controls the ecosystem carbon and nutrient cycle and is a key driver in the formation of humic substances that contribute to soil fertility, as well as to the long-term storage of carbon (Berg and McLaugherty, 2008).

The decomposition of plant litter is controlled by three main drivers – climate, litter quality and microbial communities, and can be separated into at least two stages (Berg and McLaugherty 2008). The early stage decomposition process (mass loss approximately up to 40%) is characterised by the leaching of water soluble compounds and by the decomposition of solubles, cellulose and hemicellulose (Couteaux et al., 1995; Heim and Frey, 2004). The later stages of decomposition (approximately 40–100% mass loss) comprise the degradation of more recalcitrant compounds such as lignin. In general, climate is assumed to determine decomposition on a global scale, whereas litter chemical composition and decomposers dominate the process on regional or local scales (Aerts, 1997;

Berg, 2000; Bradford et al., 2016). Studies have found that increased temperature or precipitation accelerate litter decomposition by stimulating the activity of soil microbes (Bradford et al., 2016; Djukic et al., 2018; Prescott, 2005; Zhang et al., 2008). Litter quality that is mainly determined by the relative content of recalcitrant organic compounds (e.g. lignin or phenols) and macronutrients is of particular importance in controlling the mass loss and dynamics of litter nutrients during decay under similar climatic conditions (Berg and McCaughey, 2008; Prescott et al., 2000). Several studies have shown that high initial nitrogen (N), phosphorus (P) and potassium (K) concentrations in litter regulate the early stages of decomposition by stimulating the decay of celluloses and solubles (Berg and Matzner, 1997; Berg and Staaf, 1980; Chen et al., 2002; Cusak et al., 2009; Taylor et al. 1991); however high N inhibits the decay in the later stages by suppressing the activity of lignolytic enzymes (Carreiro et al., 2000) and shifting the composition of the decomposer community (Cousteaux et al., 1995).

Considering the decomposition of soil organic matter, two opposing N cycling processes can be distinguished: immobilisation as N accumulation in the substrate and mineralisation as N release from the substrate. The point at which this switch from net accumulation to net release occurs is called the “critical N concentration” (Ågren and Bosatta, 1996). The critical N concentration depends on the initial N concentration of the litter, N availability in the soil as well as on the temperature and moisture conditions.

Litterbags, in which specific litter material is retained for a certain period of time is the most commonly used approach to determine litter decomposition in all ecosystems (Berg et al., 1993; Johansson, 1994). The litterbag method can be applied by using site-specific litter or standardised substrates. Site-specific litter is commonly used to determine the specific decomposition rate of local litter since the decomposer communities are often adapted to the site-specific litter, while the use of cellulose or commercially available teabags provide process-driven information on soil functions at local, regional and global scales, and may therefore be used for assessing the relative decomposition potential of the soil and implemented in SOC modelling (Keuskamp et al., 2013).

1.3. Carbon accounting and the Yasso soil carbon model

All of the countries that have ratified the United Nations Framework Convention on Climate Change (UNFCCC), its Kyoto Protocol and the Paris Agreement are obliged to submit annual national greenhouse gas inventories (GHGI). The quantitative information in these GHGIs provide fundamental support for national or international climate policy (Andersson et al., 2009). Carbon accounting rules agreed under UNFCCC require countries to provide transparent, complete, consistent, accurate and comparable estimations of C stock changes in all sectors including the land use, land use change and forestry (LULUCF) sector that encompasses C pools of living biomass, soil and dead organic matter (UNFCCC, 2013).

Changes in the forest soil and litter C stocks are one of the most poorly reported pools across countries (Blujdea et al., 2016); however, efforts have been made to improve the estimations and provide cost-efficient means to assess the SOC stocks and changes, e.g. by applying simulation models such as the Yasso model. The Yasso07 model (Liski et al., 2005; Tuomi et al., 2009, 2011a, 2011b) is specifically intended to estimate C stocks and changes in both forest mineral soils and dead organic matter across a wide range of ecological and climatic conditions. The model predicts the soil C stock and stock change in the upper 1 m of the soil column and requires climate and the litter production of above- and belowground forest vegetation data along with litter quality information (Tuomi et al., 2009, 2011a, 2011b). The litter production of vegetation is calculated by multiplying stand biomass estimates (derived from forest inventories) by compartment-specific turnover rates. The Yasso model is parametrised based on a global database containing over 10 000 measurements of litter mass loss (Tuomi et al., 2009) that cover various litter types, dead wood decomposition measurements (Tuomi et al., 2011b) and soil chronosequences (Liski et al., 2005). C input in the Yasso model is partitioned into four species and litter-fraction dependent chemical fractions (AWEN) according to whether they are insoluble (N), soluble in ethanol (E), in water (W) or in acid (A) with specific mass loss rates affected by temperature and precipitation. Hence, at the core of the Yasso07 model is the decomposition of the chemically defined AWEN fractions of the litter and the fluxes between those fractions.

1.4. The aims of the study

The overall aim of this thesis was to estimate SOC-related annual carbon fluxes and the dynamics of the associated processes, such as above- and belowground litter production, decomposition, soil respiration and nutrient release along with environmental factors affecting them in hemiboreal coniferous forests. In addition, the applicability of the Yasso07 model in carbon balance accounting was evaluated.

The specific objectives were:

1. To estimate the variation of above- and belowground litter production along with soil respiration and determine which C fluxes represent the highest variability and thus most affect the SOC stocks in hemiboreal coniferous forests (III).
2. To examine decomposition and nutrient dynamics (N, P, K) of site-specific fine roots and needle litter and mass loss of standardised substrates (α -cellulose, green tea, rooibos tea) as well as to determine the key drivers controlling decomposition from local to global scale (II, IV).
3. To test the suitability and accuracy of the Yasso07 model for simulating SOC stocks and stock changes across a range of climatic conditions and forest types in six European countries (I).

The main hypotheses were:

1. Fine root production of trees is one of the key factors in determining the SOC pool in forest ecosystems.
2. Stand productivity and dominating tree species significantly affect soil respiration, whereas R_s is higher in the more fertile spruce stands.
3. Substrate type and initial chemistry, in particular the N content are the main drivers of substrate decomposition on the local scale, while temperature and precipitation control the mass loss on the global scale, respectively.
4. The SOC stock and stock change estimations provided by the Yasso07 model are sufficiently accurate across a broad range of ecological and climatic conditions to meet the carbon reporting criteria required under the UNFCCC.

2. MATERIAL AND METHODS

2.1. Study sites in Estonia

The hemiboreal forest study sites in Estonia (Publications II, III & IV) included four Scots pine (*Pinus sylvestris* L.) and four Norway spruce (*Picea abies* (L.) Karst) dominated stands (Fig. 1) with varying site productivity and soil fertility conditions (Table 1, Fig. 2). The age of the stands ranged from 48 to 132 years, and the stands were not subjected to forest management for at least the last 20 years. All the stands are classified as upland mineral soils, except for the drained *Polytrichum* stand that is growing on lowland mineral soil. Most of the stands belong to the long-term forest monitoring network of International Co-operative Programmes on Assessment and Monitoring of Air Pollution Effects on Forests (*ICP Forests*) and to the International Co-operative Programme on Integrated Monitoring of Air Pollution Effects on Ecosystems (*ICP IM*) that were established in the 1990s.

The average air temperature of the stands was 18.0 °C in July and –4.0 °C in January and mean annual precipitation ranged from 492 mm (*Fragaria* pine) to 648 mm (*Polytrichum* spruce) during the main study period from 2013–2015.

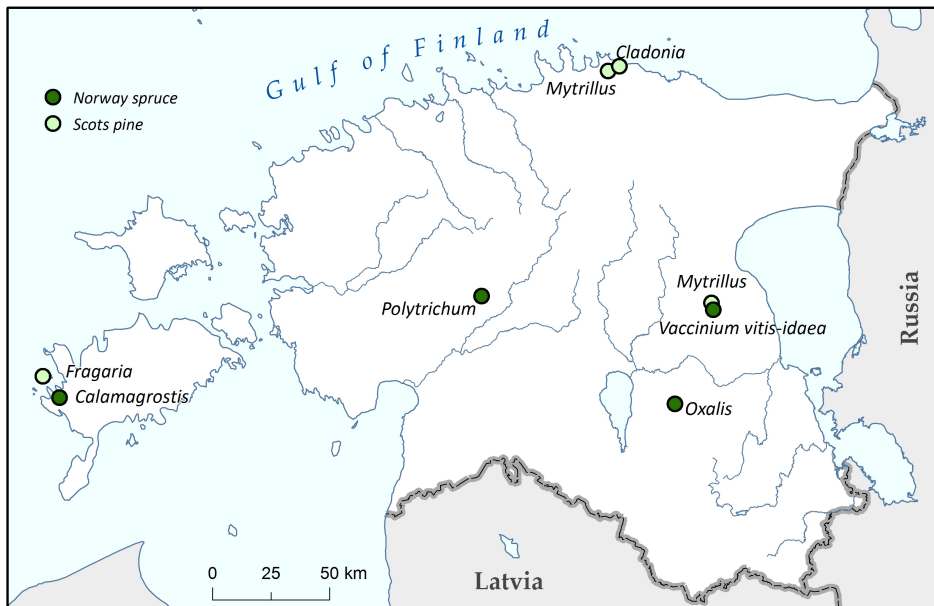


Fig. 1. Locations of the four Scots pine and four Norway spruce study sites in Estonia.

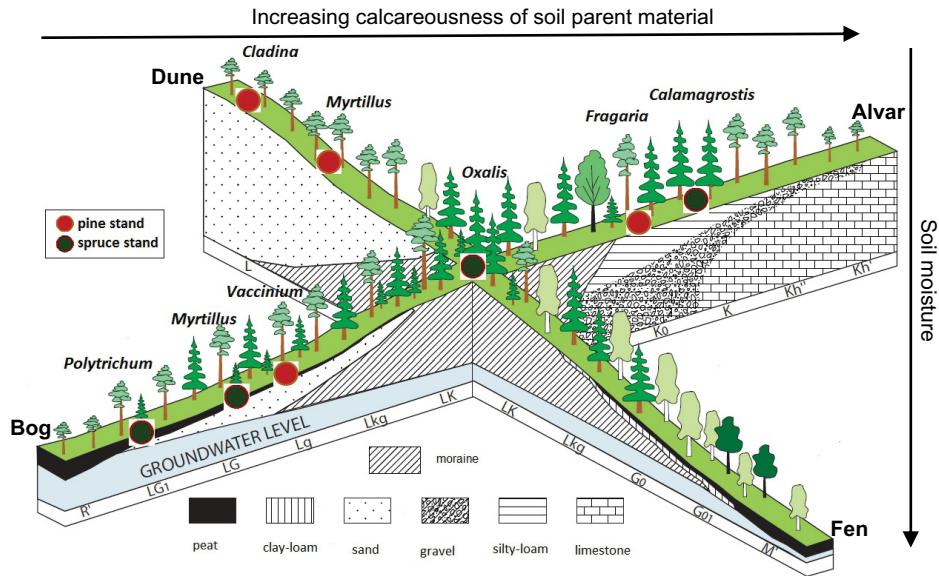


Fig. 2. Scots pine and Norway spruce study sites in Estonia according to the environmental gradients of soil moisture and soil parent material.

2.2. European and global study sites

In publication I, Yasso07 model was applied to the permanent sample plots of the national forest inventory in Austria, Estonia, Finland, Romania, Spain and Switzerland (Table 1, Fig. 3 in Publication I). Forest types included conifer, broadleaf and mixed forests from boreal, hemiboreal, temperate, Alpine mountain and Mediterranean zones.

In publication II, the decomposition of rooibos and green tea was investigated at 336 sites (including the eight Estonian study sites) ranging from -9 to $+26$ °C MAT and from 60 to 3113 mm MAP across different land use types in nine biomes ranging from arctic to semi-arid tropical climate (Table 1 and Fig. 2 in Publication II).

Table 1. Site characteristics and the chemical parameters of the soil organic layer of the studied Scots pine and Norway spruce stands in Estonia. DBH – diameter at breast height, SOC – soil organic carbon, N – total nitrogen, K – potassium, P – phosphorus, MAP – mean annual precipitation in 2013–2015, Ts – average soil temperature during the vegetation period (May–September) in 2013–2015.

Site type	Location	Stand age (yr)	Stand density (trees ha ⁻¹)	Tree height (m)	DBH (cm)	Soil type ¹	Soil moisture	SOC ² (Mg C ha ⁻¹)	N (g kg ⁻¹)	K (mg kg ⁻¹)	P (mg kg ⁻¹)	pH _{CaCl2}	MAP (mm)	Ts (°C)
Pine stands														
<i>Vaccinium vitis-idaea</i> **	58° 39'N 26° 45'E	132	263	29.7	32.0	<i>Albic Podzol</i>	dry	51.3	8.2	200	710	3.0	591	12.6
<i>Myrtillus</i> *	59° 34'N 26° 07'E	90	1130	19.2	20.3	<i>Gleyic Podzol</i>	mesic	61.2	10.7	622	627	3.3	552	12.5
<i>Fragaria</i> **	58° 23'N 21° 50'E	112	440	20.0	35.5	<i>Calcaric Arenosol</i>	mesic-dry	74.1	10.2	154	475	4.4	492	12.7
<i>Cladonia</i> *	59° 33'N 26° 02'E	82	1590	15.0	14.9	<i>Albic Podzol</i>	dry	57.8	7.0	744	694	3.4	552	13.0
Spruce stands														
<i>Oxalis</i> * ³	58° 16'N 26° 27'E	58	650	24.5	25.1	<i>Haplic Luvisol</i>	mesic	83.6	1.5	1333	450	5.2	620	12.5
<i>Polytrichum</i> *	58° 42'N 25° 03'E	48	1015	17.0	16.0	<i>Histic Podzol</i>	wet (drained)	108.9	15.5	955	925	3.5	648	11.1
<i>Myrtillus</i> **	58° 59'N 26° 45'E	97	422	23.5	28.0	<i>Albic Podzol</i>	mesic	77.6	14.0	144	610	2.9	591	12.1
<i>Calamagrostis alvar</i>	58° 18'N 21° 58'E	90	800	12.3	18.6	<i>Calcaric-gleyic Leptosol</i>	dry, occasionally flooded	69.5	8.8	1533	400	5.9	513	12.1

* – ICP Forests programme site, ** – ICP IM programme site. 1) According to the World Reference Base for Soil Resources 2015 classification. 2) Organic + top 40 cm mineral layer. 3) The soil chemical parameters of the A horizon (depth 0–5 cm) are given here because the soil organic layer is < 1 cm thick

2.3. Measurements and modelling of soil respiration

Total soil respiration (R_s) (Publication III) was measured at eight Estonian forest study sites (Fig.1, Table 1) from 16 randomly placed PVC collars per site on a monthly bases from June 2013 to December 2015 in a snow-free period using a portable infrared gas analyser (EGM-4; PP Systems International Inc., Amesbury, MA, USA) with an opaque closed dynamic soil respiration chamber (SRC-1; PP Systems International Inc., Amesbury, MA, USA). Heterotrophic soil respiration (R_h) measurements were conducted monthly from April to December in 2015 according to the trenching method. Five PVC cylinders (inner diameter 18.5 cm, height 50 cm) were randomly installed in the soil to a depth of 40 cm within each site in early spring, at least one month prior to the first soil CO_2 measurement cycle. All herbaceous vegetation was continuously clipped away from the R_s and R_h plots with minimal soil disturbance.

R_s and R_h were calculated according to the ideal gas law, using the slope of the concentration change inside the chamber headspace over time corrected for changes in air temperature and air pressure. Soil CO_2 flux measurements with an R^2 value of the concentration evolution >0.90 only were included in the analyses in order to ensure high quality flux data. Autotrophic respiration (R_a) was calculated as the difference between R_s and R_h .

The annual soil respiration was modelled using a van't Hoff type exponential function (Davidson et al., 2006) to describe the temperature dependence of soil respiration (Eq. 1):

$$R_s = a \exp^{bT_s} \quad (1)$$

where R_s is the soil respiration rate measured in situ at soil temperature T_s ($^{\circ}C$), a is a fitted parameter, and b is a parameter describing the temperature sensitivity. The equation was fitted individually for every study year and for each stand and calculated on an hourly basis using site-specific soil temperatures.

Q_{10} , known as the temperature sensitivity of soil respiration, was calculated as follows (Eq. 2):

$$Q_{10} = \exp^{b10} \quad (2)$$

where b is a parameter describing the temperature sensitivity obtained from Eq. 1.

2.4. Fine root biomass and production

The fine root (<2 mm in diameter) biomass (FRB) of the Estonian study sites (Fig.1, Table 1) was estimated by soil cores (Publication III). In each stand, 15 soil cores were randomly collected from the 30 cm topsoil layer in the fall of 2011 or 2012. Fine roots of trees were washed free of soil and separated into living and dead roots based on colour, elasticity and toughness (Ostonen et al., 2005).

The fine root production of the trees (FRP_t) and the understory roots and rhizomes (FRP_u) were estimated according to the root mesh (root inclusion net) method (Hirano et al., 2009). During 2009–2012, 90–150 nylon nets (7×30 cm, 1 mm mesh size) were installed in every study site (Fig. 1, Table 1) to a depth of 30 cm. The root nets (7–30 per sampling and site, totally 320) were extracted from the soil as 10×10 cm soil blocks (Lukac and Godbold, 2010) annually from 2010 to 2014 at the end of the vegetation period. The first extraction took place one year after the installation. The extracted nets were stored at 4 °C until processing, subsequently washed free of soil and the fine roots grown through the mesh were separated into living and dead tree and understory fine roots under the microscope. All root samples were dried at 65°C and weighed.

Annual fine root production, which was assumed to be equal to annual belowground litter production, was calculated analogously using the combined method proposed by Löhmus and Ostonen (2006) and Ostonen et al. (2005). Since the relative measures of the fine root production measured by nets could be underestimated (Montagnoli et al., 2014), we first calculated the fine root turnover rate for the nets (TR) by using the estimate of fine root ingrowth for 24 months ($FRP_{net_{24\text{month}}}$) divided by the mean of that three-year biomass that grew into the nets ($FRB_{net_{\text{mean of 1-3 yr}}}$) (Eq.3):

$$TR = \frac{FRP_{net_{24\text{ months}}}}{FRB_{net_{\text{mean of 1-3 year}}}} \quad (3)$$

FRP_t was calculated by multiplying the turnover rate of the nets by the mean fine root biomass estimated by soil coring. For the FRP_u , the three year average production estimate obtained from the nets was applied in the subsequent analysis and fine root turnover rate for understory roots was assumed to be one yr^{-1} (Majdi and Andersson, 2005).

2.5. Woody biomass increment and tree litter production

The annual increment of stem volume (Publication III) was estimated for each Estonian study site (Fig.1, Table 1) by combining long-term forest measurement data and yield tables (Krigul, 1971). The branch biomass was assumed to be 5–10% of the aboveground biomass depending on the tree species (Helmisaari et al., 2002; Uri et al., 2007; unpublished National Forest Inventory database). The coarse root biomass was estimated to be 20% of the aboveground biomass (Küllä, 1997; Uri et al., 2017). The production of branches and coarse roots were calculated on the basis of the equal relative increments of the aboveground woody biomass, and the relative increments of the aboveground and belowground woody biomass fractions were assumed to be equal (Uri et al., 2017). Species-specific wood densities (Pikk and Kask, 2014; Laas, 2004) and an average C concentration of 50% was applied when calculating the woody biomass related carbon fluxes for estimating the net ecosystem production of the stands.

The aboveground tree litter was collected from the eight Estonian study sites according to the *ICP Forests* and *ICP IM* manuals (methodology available at the ICP Forests website: <http://icp-forests.net/>) from 10 systematically placed funnel-shaped litter traps per stand (Publication III). The traps were placed 1.5 m from the ground and had a surface area of 0.25 m². Litter samples were collected on a monthly bases from 2013–2015, except during the winter period from December to April due to snow cover. The litter was separated into needles and other miscellaneous fractions (twigs, cones and all the other material), air-dried samples were dried at 65°C for 48 hours, weighed and the total organic carbon (TOC) content was determined from the dry matter. The annual C flux of the litter was calculated by multiplying the amount of annual litter production with the respective TOC content of the litter.

2.6. Understory aboveground biomass and production

Five understory samples (Publication III), containing herbs and shrubs, were removed from each Estonian study site in 2016 by clipping all of the aboveground biomass from randomly selected 40 × 40 cm squares. The samples were collected before the beginning of the vegetation period (April) and during the peak plant growth (August). The biomass of the perennial woody parts of the shrubs was estimated by separating fresh leaves and stems from the rest of the plant. The annual aboveground production of the herbs was assumed to be equal to the maximum biomass collected. The shrub NPP was calculated as the difference between the total biomass in August and the perennial biomass in April. Estimating the belowground NPP (i.e. FRP) of understory is described in chapter 2.4.

2.7. Stand net ecosystem production

The net ecosystem production (NEP) (Publication III) was estimated for each Estonian study site by subtracting carbon losses via heterotrophic respiration from the total net primary production (Luyssaert et al., 2007) (Eq. 4):

$$\text{NEP} = \text{NPP} - \text{Rh} \quad (4)$$

where Rh here is the heterotrophic soil respiration; NEP > 0 denotes the forest ecosystem carbon uptake.

NPP was calculated by summing the annual increment of the aboveground components (stem and branches of trees, needles, and understory) and belowground production (tree and understory fine roots and rhizomes, and tree coarse roots).

2.8. Mass loss of needle litter, fine roots, α -cellulose, green tea and rooibos tea

The decomposition studies (Publication II and IV) were carried out using the *in situ* litterbag method. The decomposition of site-specific Scots pine and Norway spruce fine roots and needle litter and α -cellulose was examined over a 3-year period from 2012 to 2015 in Estonia (Publication IV). The global mass loss study of green tea viz. green leaves (*Camellia sinensis*; EAN no.: 8722700 055525) and rooibos tea (*Aspalanthus linearis*; EAN no.: 8722700 188438) (Publication II and IV) started in 2016 and is still ongoing. Before the start of the incubation all litter types were oven-dried at 65°C for 48 hours and the initial weight was recorded. 0.5 g of fine roots, 1 g of needle litter and 1 g of α -cellulose (1 mm thick, 30x50mm wide sheets) was put in nylon bags (40 litter bags of each litter type per each site; Fig.1) with the mesh size of 1 mm for the α -cellulose and needle litter and 0.1 mm for the fine roots. Needle litter bags were placed on the soil surface and lightly covered with surrounding litter, while the α -cellulose and fine root bags were inserted to a depth of 5 cm into the soil organic horizon or in the humus horizon (in case of the *Oxalis* site) during October and November 2012. Five to seven samples of each litter type were collected at all sites after a field incubation period of 1 month, 7–8 months, 1 year, 2 years and 3 years. A standardised protocol (Djukic et al., 2018) was applied for the decomposition of green and rooibos tea (Publication II). Tea bags were buried in June or July 2016 at the upper 5 cm of the soil and four samples of both tea types were retrieved after 3, 12 and 24 months. Soil and ingrown material (roots, mosses etc.) were removed from all the retrieved tea and litterbags, the decomposing material was dried to a constant weight at 65–70 °C for a minimum of 48 hours and the remaining mass was weighed to the nearest 0.1 mg. Mass loss was calculated for each litter sample as the relative difference between the initial and retrieved dry mass.

2.9. Decomposition rate and nutrient release of fine roots and needle litter

The decomposition rate (k) (Publication IV) (Eq. 5) was calculated from the percentage of dry mass remaining using an exponential decay model (Olson, 1963):

$$\frac{M_t}{M_0} = e^{-kt} \quad (5)$$

where M_t is the mass (g) at time t , M_0 is the initial mass of incubated litter (g), the constant k is the decomposition coefficient, and t is the elapsed time (year).

Nutrient release rate (Publication IV) (Eq. 6) was calculated from the percentage of nutrient mass remaining at time t (Lin et al., 2011):

$$R_t = \frac{(100 - N_t)}{t} \quad (6)$$

where R_t is the nutrient release rate (% year⁻¹) at time t , N_t is the percentage of nutrient remaining (as percent of original mass) at time t , and t is the elapsed time (year). R_t of nitrogen was calculated in the end of the experiment, i.e. from the litter retrieved after three years of decomposition. R_t of phosphorus and potassium were calculated from the litter retrieved after 1.7 years of decomposition.

2.10. Soil data, litter chemical analyses and meteorological parameters

The soil types, SOC stocks and soil chemical composition of the Estonian study sites (Publications III and IV) were determined during the BioSoil project in 2006–2008 according the *ICP Forests* and *ICP IM* manuals. SOC stocks were calculated from the organic C content, bulk density and coarse fragments of different soil horizons.

Composite samples of the collected, incubated and retrieved fine root and needle litter were used for the chemical analyses (Publications III and IV). Litter samples were analysed for TOC (IR-spectrometry), total N (modified Kjeldahl method), total P (inductively coupled plasma atomic emission spectrometry) and K (flame-emission spectrometry). The concentrations of cellulose and lignin were determined using the acid detergent lignin method. All soil and litter samples were analysed at the Estonian Environmental Research Centre laboratory that holds a certificate for chemical analysis for ICP Programmes. Chemical composition of green and rooibos tea was obtained from Keuskamp et al. (2013).

Data loggers (S0141; COMET System, s.r.o., Czech Republic) with 4 soil temperature (T_s , °C) sensors (T155A-M8E; COMET System, s.r.o) were installed in the centre of each study site in Estonia in 2013. Soil temperature sensors were installed at a depth of 5–7 cm. In 2015, additional data loggers (Em50; Decagon Devices, Pullman, WA, USA) with 4 soil temperature and moisture sensors (5TM; Decagon Devices) were installed at a depth of 5–7 cm at each study site. The soil parameters were recorded with both data loggers at hourly intervals.

Hourly air temperature and precipitation data were obtained from the nearest national meteorological station managed by the Estonian Weather Service. In publication II, climate data were measured at the site, taken from nearby weather station or extracted from WorldClim (Fick and Hijmans, 2017) in cases where no climate data were provided.

2.11. Site productivity index

The site productivity index (B , Eq. 9) was calculated according to the Forest management and Planning Guidance of Estonia to obtain a continuous stand variable necessary for correlation analyses. The site productivity index expresses forest productivity, specifically the rate of height growth reflecting the economic value of a stand or the suitability of a forest site type for a given tree species. The site productivity index was calculated from the tree height index as follows:

$$H_{100} = \frac{H_{50}}{[1 + (\alpha + \beta \times H_{50}) \times (0.5^c - 1)]} \quad (7)$$

$$H_{50} = \frac{H \times \left\{ 1 + \alpha \times \left[\left(\frac{50}{A} \right)^c - 1 \right] \right\}}{\left\{ 1 - \beta \times H \times \left[\left(\frac{50}{A} \right)^c - 1 \right] \right\}} \quad (8)$$

where H_{100} and H_{50} are the height indices at the stand age of 50 years and 100 years, respectively; H is the height of the dominating tree species (m); A is the age of the dominating tree species; and α , β and c are the tree species-specific coefficients.

$$B = \frac{33.5 - H_{100}}{4} \quad (9)$$

Smaller B values denote higher site productivity.

2.12. Yasso07 input data and modelling

Annual SOC stocks and stock changes in Estonian forest mineral soils were modelled (Publication I) for the period 1990–2013 using the Yasso07 model (version 1.0.1) in the R environment (RStudio, Inc version 0.99.473). Annual growing stock, separated into different tree species (Norway spruce, Scots pine, birch and other tree species), and coarse woody debris data were obtained from the national forest inventory database. Growing stock was converted into biomass by applying biomass expansion factors (IPCC, 2006) and further into litter sub-compartments by applying species-specific fractional distribution of tree foliage, branches, stem, stump, coarse and fine roots (Küllä, 1997; Ostonen et al., 2005; Uri et al., 2012; Varik et al., 2013). The Scandinavian parameter set with species-dependent turnover rates per tree biomass fractions and litter quality (AWEN) estimates of Southern-Finland from Rantakari et al. (2012) were implemented for the Yasso07 simulations. Understorey litter production

was not included in the model due to lack of data. Annual weather data (temperature, precipitation) corresponding to the modelling period were obtained from the Estonian Weather Service. Previously measured and estimated SOC stocks in Estonian forest soils published by Kõlli et al. (2004) were used to validate the applicability of the Yasso07 model.

2.13. Statistical analyses

Statistical analyses were carried out using the STATISTICA 7.1 software (StatSoft, Inc., 2005) and SigmaPlot 12.5 (Systat Software Inc., 2011), level of significance was set at $p < 0.05$. The normality of the variable distribution was verified using the Kolmogorov-Smirnov test. The *t*-test for independent samples by groups was applied to compare stand and soil characteristics, litter mass loss and chemical composition, biomass pools and carbon fluxes between the pine and spruce stands in Estonia. A one-way analysis of variance (ANOVA), followed by Tukey's HSD, was performed to test the differences in soil respiration rates and mass loss within and between the different substrate types and the studied stands. The coefficient of variation (CV) was used to describe the variability of the measured stocks and carbon fluxes. Pearson's correlations were applied to estimate the correlations between soil and stand characteristics and to evaluate the relationships between the nutrient release and the initial fine root and needle litter quality.

Redundancy analysis (RDA) (CANOCO program; ter Braak & Šmilauer, 2002) was applied to examine the relationships between the mean mass loss per site across all substrate types and the site productivity, chemical parameters of the soil organic layer at the Estonian study sites. Analysis of covariance (Fixed Effect Test, Type III) was used to determine the relationships between the mass loss of site-specific litter (i.e. fine root and needle litter) and the combined effect of initial litter and the soil chemical parameters, using tree species and litter type as the grouping variables.

Stepwise multiple linear regression analyses were performed to evaluate relationships between soil respiration and the environmental parameters (T_s , T_a , precipitation, soil moisture) and to determine the effect of the site productivity, environmental (MAP, soil moisture and T_s during the vegetation period) and soil chemical parameters on the mass loss of each litter type.

A type III generalised linear model (GLM) analysis was used to assess the impact of soil carbon input and output fluxes along with the stand age on the SOC pool at the Estonian study sites. Soil C input fluxes were comprised of tree aboveground litterfall (needles and other fractions), fine root production of the tree and understory roots and rhizomes and the production of understory aboveground compartments. The soil C output fluxes included heterotrophic soil respiration. Tree species and stand age were included in the analysis as a categorical predictor and a continuous covariable, respectively. GLM analysis

was also performed to test the significance of stand age and site productivity on the NEP of the stands.

In the global tea bag study, linear mixed models were used to quantify the differences in the remaining litter mass between biomes and to investigate the effect of climate variables on the remaining tea mass.

3. RESULTS AND DISCUSSION

3.1. Biomass of the aboveground understory vegetation and tree fine roots (III)

The aboveground biomass of the understory was significantly higher in Scots pine compared to Norway spruce stands in Estonia, being 209 ± 38 and 49 ± 24 g m⁻², respectively (Table 2 in publication III). Higher ground flora at the pine stands is explained by its relatively open canopy that results in the high availability of solar radiation to the understory vegetation (Baldocchi et al., 2000). FRB of Scots pine ranged from 196 to 366 g m⁻² that is in the same range previously reported for Scots pine in boreal forests (Helmisaari et al., 2007). FRB values of 284–825 g m⁻² of Norway spruce in Estonia were higher than observed for spruce in Finland 148–370 g m⁻² by Helmisaari et al. (2007), yet comparable with the range reported in Sweden (145–656 g m⁻²) by Persson et al. (1995) and Majdi and Persson (1995). The highest FRB values of spruce were estimated at the most extreme sites in Estonia – the drained *Polytrichum* and the calcareous *Calamagrostis* sites (see Fig. 2). The first site has a deep organic layer and an extensive root system similar to that of peatlands; however, it is classified as a lowland mineral soil (histic podzol) because the thickness of the organic layer is less than 30 cm. *Calamagrostis* site represents the poorest site productivity and is prone to occasional flooding in the spring and drought in the summer. We assume that high FRB (as well as FRP as discussed further below) at the *Calamagrostis* site is caused by nutrient and environmental stress conditions, since the stand is growing on a shallow calcareous soil with a high level of pH due to which the uptake of phosphorus is limited (Frey and Frey, 1995), and additionally the seasonal drying of the soil has been shown to accelerate fine root growth as an adaptive response (Brunner et al., 2015).

3.2. Site productivity index and N concentration of fine roots (III)

The site productivity index (B) ranged from 0.6 to 5.1, being lowest (i.e. most productive) in the fertile *Oxalis* spruce stand and highest (i.e. least productive) in the *Calamarostis* spruce site (Table 2 in publication III). B revealed a significant relationship with the total N content in the tree fine roots ($R^2=0.58$, $p=0.03$) indicating higher N in the fine roots growing in more fertile sites. The fine root N concentration in Estonian coniferous forests varied from 0.8% to 1.2%. This result compares well with respective values from boreal forests in Finland, varying from 0.6% to 1.1% (Helmisaari et al., 2007) and along European coniferous forest gradient, where the fine root N% varied from 0.6% to 1.6% (being higher in temperate coniferous forests; Ostonen et al., 2011; 2017). The latter affirms that the fine root N is strongly related to the fertility and N availability of the site and that the hemiboreal forests represent the ecological conditions of both boreal and temperate forests.

3.3. Above- and belowground litter production and fine root turnover (III)

The total annual above- and belowground litter production of the studied stands was in the same magnitude and varied from 381 to 613 g m⁻² and from 211 to 1040 g m⁻², respectively (Table 3 in publication III). Needle litter production, which was the least variable C flux among the studied soil input and output fluxes, ranged from 190 to 340 g m⁻² yr⁻¹ and did not differ significantly between the pine and spruce stands. The measured annual aboveground litterfall rates found in Estonia cover the range of observed mean litterfall in European coniferous forests, moreover, the average C content of needle litter in our studied stands (52.8%) coincides exactly with the mean C content of 52.9% for the northern Europe conifers reported by Neumann et al. (2018).

The annual litter production of the aboveground parts of the understory was significantly higher in the pine (mean 119±10 g m⁻² yr⁻¹) than in the spruce (mean 25±9 g m⁻² yr⁻¹) sites, however there was no difference in the production of understory fine roots that ranged from 6 to 68 g m⁻² yr⁻¹ across the coniferous stands studied. FRP_u comprised up to 28% of the total fine root production (*Vaccinium vitis-idaea* stand), supporting the conclusions of several studies (e.g., Kleja et al., 2008; Finér et al., 2011) that understory vegetation can contribute substantially to belowground C allocation especially in boreal and hemiboreal forests, thus it is essential to incorporate understory C fluxes when estimating and modelling forest ecosystem C cycle.

The fine root production of trees that expressed one of the highest variability among the measured soil input and output fluxes ranged from 152 to 1034 g m⁻² yr⁻¹. The average FRP_t per tree was significantly higher in the spruce (7.5±0.9) than in the pine stands (3.8±0.8 kg yr⁻¹) revealing the importance of the tree species on the belowground litter production. The mean total (FRP_t+FRP_u) fine root production of the stands growing on upland mineral soils (N=7) was estimated to be 359±46 g m⁻² yr⁻¹, which is strongly consistent with the results of Finér et al. (2011) who found that the mean total FRP for boreal forests is 311±259 g m⁻² yr⁻¹. However, our *Polytrichum* spruce site had approximately 3 times higher FRP than the rest of the stands. The drained *Polytrichum* stand is growing on histic podzol and is similar to the boreal peatlands as discussed above. Yet, the FRP of the *Polytrichum* stand was higher than reported by Bhuiyan et al. (2017) for drained peatland forests in Finland which may result from several factors, e.g., better soil aeration and nutrient status and higher site productivity of the Estonian site.

Several studies have suggested that the FRB and FRP are higher at poorer sites (Helmisaari et al., 2007; Lehtonen et al., 2016), because more fine roots are needed in order to ensure sufficient water and nutrient uptake (Keyes and Grier, 1981) and to maintain a threshold aboveground biomass when nutrient availability is low. In our study no significant relationship was found between the FRP and site productivity. However, a strong relationship appeared between the site productivity index and the FRP_t to the stand total NPP ratio in the pine stands (R²=0.91, p=0.048) and similar trend emerged in the spruce stands.

FRP_t:NPP_{total} ratio increased from 21 to 33% and from 22 to 62% in the studied pine and spruce stands, respectively, on the gradient from the highest to the lowest site productivity. The lower share of FRP_t to total stand NPP in both fertile spruce and pine dominated stands coincides with the assessment for temperate pine dominated forests in north-eastern China, where the FRP_t:NPP_{total} ratio of mixed and pine forests was 17% and 18%, the respectively (Cai et al., 2016). This indicates that the fertile coniferous forests in the hemiboreal zone might be more similar to the temperate forests, justifying the large variability of tree fine root production in our study sites.

The fine root turnover rate (TR) of trees, which ranged from 0.66 to 1.26 yr⁻¹ among the eight studied coniferous stands, expressed a strong negative correlation with the site productivity index in the Norway spruce stands ($R^2=0.93$, $p=0.04$) demonstrating that the turnover of FR is faster in more productive sites. The same trend occurred in the pine stands. The fine root TR also showed a significant positive correlation with the forest SOC pool ($R^2=0.69$, $p=0.01$) (Fig. 3) indicating that higher fine root turnover contributes to a larger forest SOC pool through greater C input from continually renewing the fine roots. The challenge in understanding species effects, as well as the impact of other biotic and abiotic factors on the development of SOC, is disentangling the mechanisms behind the observed SOC stock differences (Vesterdal et al., 2013). Our results may suggest that fine root turnover could be one of the key processes controlling the differences in SOC pools of different forest sites, which is supported by the recent results by Solly et al. (2018), who indicated the underestimation of carbon inputs from fine roots to soils.

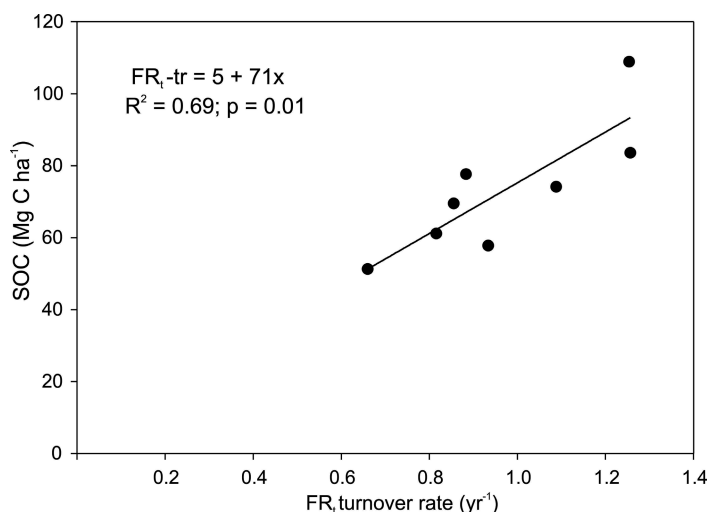


Fig. 3. Soil organic carbon pool (SOC) and fine root turnover rate of trees (FR_t).

3.4. Soil respiration (III)

Soil temperature was the driving environmental factor that explained 63–86% of the temporal variation in the total soil respiration (Rs). The absence of a relationship between soil moisture and Rs at our hemiboreal study sites suggests that soil moisture was not a limiting factor. Rs rates ranged between 4.4 and 8.4 Mg C ha yr⁻¹ (Table 4 in publication III), which is consistent with the Rs values of mature Norway spruce and Scots pine stands reported in the literature (Borken et al., 2002; Kolari et al., 2009; Kukumägi et al., 2017). Although several studies have demonstrated the impact of tree species on soil respiration through various mechanisms, primarily by controlling the quality and quantity of the above- and belowground litter input (Vesterdal et al., 2012; Makita and Fujii, 2015), our results showed no significant difference between the Scots pine

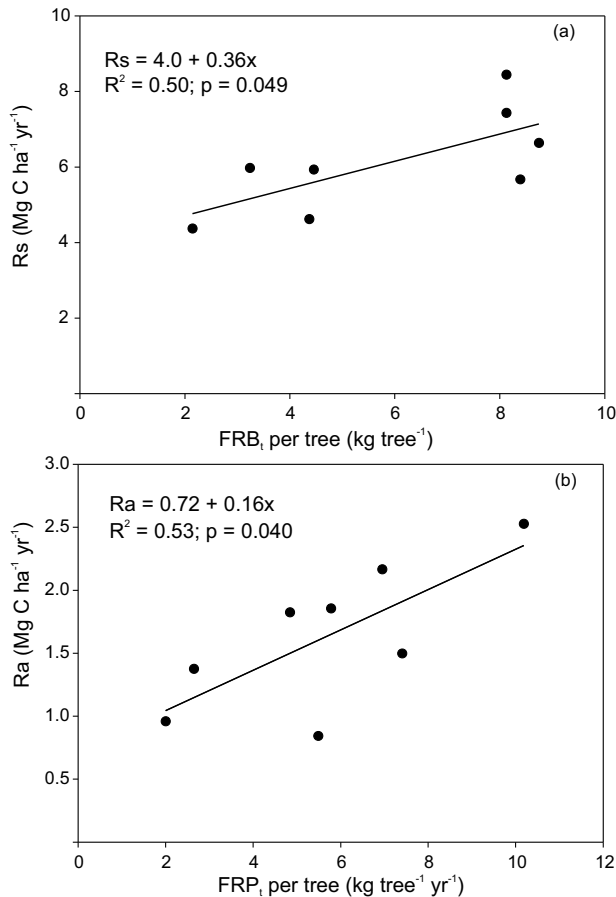


Fig. 4. Relationship between annual soil respiration (Rs) and fine root biomass per tree (FRB_t) (a) and autotrophic soil respiration (Ra) in relation to fine root production per tree (FRP_t) (b) in Scots pine and Norway spruce stands.

and Norway spruce dominated stands or between the study years from 2013–2015, while R_s was also the least variable SOC-related carbon flux. We suggest that R_s in the current study is determined by the combination of environmental conditions (e.g. forest site type) and weather factors rather than by the dominating tree species alone.

Significant relationships were found between R_s and FRB per tree ($R^2=0.50$, $p=0.049$) and between the R_a and FRP per tree ($R^2=0.53$, $p=0.04$) (Fig. 4a and 4b, respectively). These relationships occurred at the tree level but not on the stand level, which indicates the high variation within and between the studied stands derived from the differences in stand density, dominating tree species and soil conditions.

3.5. The effect of C input and output fluxes on SOC stocks (III)

GLM analysis performed with the sum of soil C input (tree and understory above- and belowground litter production) and output (R_h) flux showed that only the soil C input flux had a significant effect on the SOC stocks ($F=16.0$, $p=0.03$), while R_h , the stand age and tree species were statistically non-significant ($p>0.05$). When soil C input fluxes were tested separately, our analysis revealed that only the tree-derived carbon fluxes resulted in a significant impact on the SOC stocks (tree needle and other fractions $F=57.2$, $p=0.02$; FRP_t $F=33.3$, $p=0.03$), while understory above- and belowground litter production did not significantly affect SOC stocks ($p>0.05$).

SOC pool is influenced by fresh carbon inputs via above- and belowground litter (Lukac, 2012; Leppälammil-Kujansuu et al., 2014a) and decomposition-derived respiratory processes (Hanson et al., 2000), whereas C input to the soil from the belowground plant structures often equals or exceeds the aboveground C litterfall (Keyes and Grier, 1981; Kleja et al., 2008; Leppälammil-Kujansuu et al., 2014b). In addition, the root litter is considered to be major source for long-term soil C storage due to its recalcitrance and soil organic matter protection mechanisms (Rasse et al., 2005). Therefore, we hypothesised that the SOC pool could be most influenced by the production of tree fine root litter. However, in our study the above- and belowground litter production were of the same magnitude (see chapter 3.3) and both showed a significant impact on the SOC pool. FRP demonstrated the largest variability, while needle litter production and R_h were the most stable SOC related fluxes, hence we suggest that the SOC pool is more sensitive to the changes in the most dynamic C fluxes.

3.6. Net ecosystem production (III)

The total net primary production of the aboveground tree and understory (NPP_{AG}) components ranged from 1.4 to 4.8 Mg C ha⁻¹ yr⁻¹ in the studied stands in Estonia (Appendix B in publication III). The highest NPP_{AG} was estimated in the most productive *Oxalis* spruce stand, and the lowest NPP_{AG} was estimated in the least productive *Calamagrostis* spruce site. The total belowground net primary production (NPP_{BG}) of the tree fine and coarse roots and understory root and rhizome production varied from 1.1 to 5.8 Mg C ha⁻¹ yr⁻¹, while the maximum production was observed at the drained *Polytrichum* spruce site. The total fine root production ($FRP_t + FRP_u$) was the largest C sink in the stands, accounting for an average of $42 \pm 5\%$ of the total annual NPP among the study sites, followed by needle production (an average of $26 \pm 3\%$ of the total stand NPP).

The net ecosystem production ranged from -1.8 to 4.2 Mg C ha⁻¹ yr⁻¹. The highest net C sequestration was observed at the *Polytrichum* stand, while the *Vaccinium vitis-idaea* and *Fragaria* pine stands and the *Calamagrostis* spruce site acted as net C sources. NEP decreased significantly along with the increasing stand age ($R^2=0.76$, $p=0.005$) (Fig. 5).

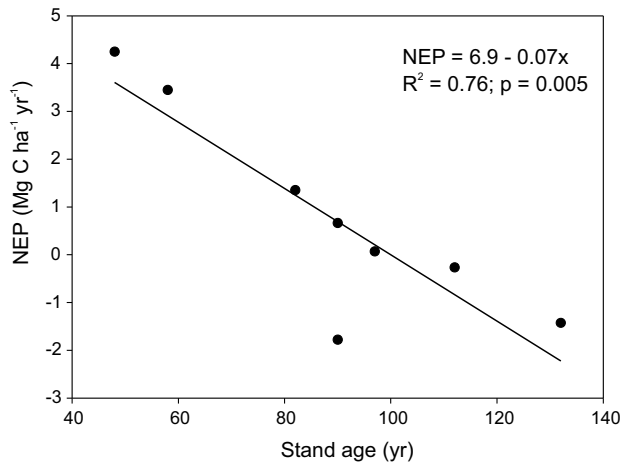


Fig. 5. Relationship between net ecosystem production (NEP) and stand age.

The magnitude of a forest C sink or source has been reported to depend on forest age (Law et al., 2003). In our study, the NEP decreased significantly with increasing stand age, shifting towards a moderate carbon source in stands over 100 years old. Mature and old-growth forests approach a steady state or can become sources of carbon due to their decline in forest productivity and accelerated mortality (Ryan et al., 1997; Goulden et al., 2011), although the opposite results have been reported in the literature. For example, Kolari et al. (2004) found no reduction in the carbon sink with stand age in Scots pine stands in Finland. A decrease in the NEP may also be the result of increased soil

respiration in older forests due to the larger soil carbon stocks (Goulden et al., 1996). However, in the current study, R_h depended on the stand age. Thus, the decline of NEP can be attributed to the decreased productivity in the old-growth stands. However, the NEP calculation in our study did not include fluxes related to coarse woody debris, although the detrital pool in the mature stands builds up over time and may result in an extended period of carbon accumulation and a positive NEP, while the net increment of the living biomass ceases (Luysaert et al., 2008; Goulden et al., 2011). Therefore, the results of this study should be considered more as a sensitivity analysis of the most dynamic C fluxes affecting the NEP and SOC pools rather than an estimation of the effect of age on the forest ecosystem C balance.

3.7. Mass loss of fine roots, needle litter, α -cellulose, green tea and rooibos tea (II and IV)

The decomposition of standardised substrates (α -cellulose, green and rooibos tea) and site-specific fine roots and needle litter was studied during two and three years, respectively, in coniferous forest in Estonia (Fig. 1; publication IV), while the early stage (three months) decomposition experiment of green and rooibos tea was conducted across nine biomes globally (Fig. 2 and Table 1 in publication II). In Estonia, the pattern of mass loss varied substantially among the different substrate types (Fig. 6). The highest mass loss was recorded for the α -cellulose that was nearly completely decomposed by the end of the second year ($98\pm 1\%$) (Table 3 in publication IV). Although the mass loss of fine roots was higher compared to the α -cellulose one month after the start of the incubation ($8\pm 2\%$ and $2\pm 1\%$, respectively), the mass loss of fine roots remained the lowest among the substrate types throughout the study period, reaching $23\pm 2\%$ (i.e. three times less than the mass loss of needle litter) by the end of the third year. These findings are in agreement with the results found in the literature, showing that roots decompose up to 10 times more slowly than leaf litter due to their higher concentrations of lignin and suberin (Silver and Miya, 2001; Rasse et al., 2005; Kvaschenko et al., 2019). An earlier study conducted in Estonia by Lõhmus and Ivask (1995) reported that the fine roots of Norway spruce lost 21 to 33% of their dry weight after one year of incubation, which is higher than the average mass loss of spruce fine roots ($17\pm 2\%$) in our study. However, the average site productivity of the stands in Lõhmus and Ivask (1995) was higher compared to the stands in the current study. Furthermore, the difference in the decomposition rate could be related to different initial concentration of lignin in the fine roots and also to differences in the structure of root colonising ectomycorrhizal communities.

The mass loss of needles varied from 25–35% in the first year at the Estonian sites, which falls in the mass loss range of 11–44% reported for pine and spruce needles in boreal coniferous forests (Berg and Staaf, 1980; Taylor et al., 1991;

Johansson, 1994; Prescott et al., 2004). In three years, the needle litter had lost more than half of its original mass ($66\pm 2\%$).

The mass loss of green and rooibos tea after three months of field incubation was $66\pm 2\%$ and $27\pm 2\%$ in the hemiboreal coniferous forests and $62\pm 1\%$ and $22\pm 1\%$ across all biomes, respectively. Faster initial decomposition of green tea is expected due to its higher fraction of water-soluble compounds in contrast to the low content of soluble or hydrolysable compounds in rooibos tea (Didion et al., 2016).

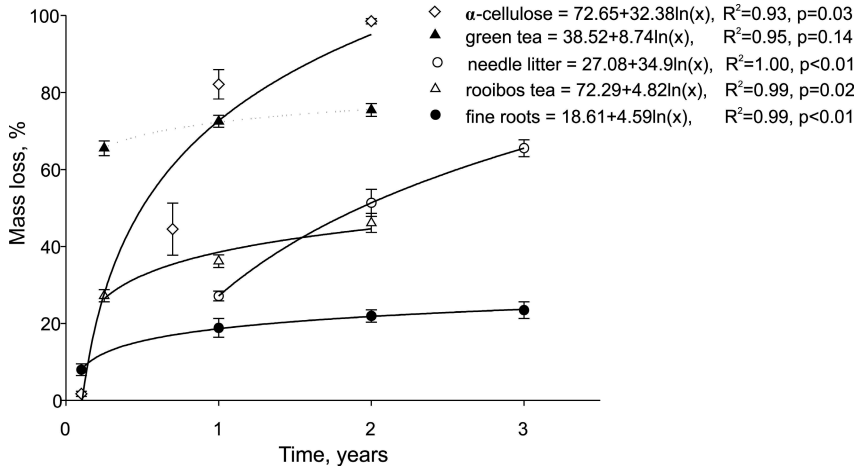


Fig. 6. Mass loss (%) of α -cellulose, needle litter, fine roots, green tea and rooibos tea in hemiboreal coniferous forests in Estonia. Error bars represent the standard error of means.

3.8. Factors controlling decomposition (II and IV)

In Estonia, the potassium content of the soil organic layer was the only soil chemical characteristic that related significantly to the one- and two-year mass loss across all the substrate types (RDA, $p < 0.05$). However, K in the soil described only about 1.5% of the variability of the mass loss, while the substrate type was the primary driver describing about 92.6% of the variability. Similar results were found at the global scale, where the tea type was the predominant controlling factor, which explained 65% of the variability in decomposition. The latter in turn implies that potential shifts in the relative abundance of vegetation types in the future caused by climatic changes could have large effects on global carbon budgets alone due to the differences in litter quality and consequently decomposition rates (Cornwell et al., 2008; Cornelissen et al., 2007).

At the local scale in Estonia, multiple regression analysis with environmental parameters such as soil moisture, soil temperature and precipitation did not reveal any significant relationships with substrate mass loss. Similarly, climate (air temperature and precipitation) had little effect on the early stage mass loss

of tea on a global scale; however, it was of significance only under unfavourable decomposition conditions (i.e. xeric versus mesic environments). At the aggregated biome scale, climate expressed significant role on the decomposition of tea, mass loss increasing with increasing MAP (Table 3 in publication II) which is in agreement with several studies showing a positive relationship between moisture availability and decomposition rates (e.g. Prescott, 2010). Mean annual temperatures below 10°C and moisture contents below 30% or over 80% have been suggested as inhibiting thresholds for litter decay (Prescott, 2010). The absence of any significant effect of temperature on the mass loss of different substrates in our studies may be due to the fact that the sites had relatively favourable decomposition conditions where temperature values were generally within the “optimal” decay range. Additionally, local-scale factors (e.g. soil properties, disturbances) other than climate may have strong controls on regional litter mass loss dynamics (Cornwell et al., 2008).

According to the regression analysis with mass loss and soil and site characteristics carried out for each substrate type separately in Estonia, the one-year mass loss of α -cellulose depended on the site productivity ($p=0.03$, $R^2=0.58$), the mass loss being higher in the more fertile and productive sites (Appendix A.1 in publication IV). The latter has also been observed by Johansson (1994) who found a positive linear correlation with site productivity indices. The two-year mass loss of the needle litter ($p=0.02$, $R^2=0.67$) and green tea ($p=0.01$, $R^2=0.68$) related negatively to the soil K content (Appendix A.2 in publication IV). Published literature on the role of soil K on decay processes is scarce. However, Ochoa-Hueso et al. (2019) who studied the importance of litter quality and nutrient addition on decomposition in forests and grasslands found that K addition significantly affected the ability of microbes to degrade organic matter, suggesting the potential key role for soil K in controlling litter decomposition. In our study, soil K correlated with soil pH which in turn strongly influences the biomass, composition (fungi:bacteria ratio) and activity of soil microorganisms (e.g., Matthies et al., 1997; Högberg et al., 2007). Hence, soil K could control litter decomposition indirectly via affecting the functioning of soil microbial communities.

Correlation analysis with initial substrate chemistry revealed that the one-year mass loss of Scots pine fine roots ($p=0.01$, $R^2=0.98$) and one- and three-year mass loss of pine needle litter ($p=0.04$, $R^2=0.93$ and $p=0.047$, $R^2=0.91$, respectively) was significantly and positively related to the initial N content in the incubated substrate. For spruce litter, the same trends, although non-significant, emerged. Additionally, the one-year mass loss of pine needles showed a strong positive correlation with the initial P and K concentration ($p<0.01$, $R^2=0.99$ for both nutrients) and one-year mass loss of pine fine roots expressed a positive relationship ($p=0.03$, $R^2=0.94$) with initial K in the litter. The positive effect of macronutrients (N, P) on the degradation of plant litter has been presented in a wide range of studies (e.g., Berg and Staaf, 1980; Aerts, 1997; Berg, 2000). K in conifers needle litter has been shown to have a positive impact on

mass loss both in the early (Prescott et al., 2004) and late stages (Berg et al., 2000) of decomposition.

Covariance analysis with site-specific fine roots and needle litter taking into account the combined effects of initial substrate quality and soil properties showed that substrate type was the dominating factor that affected mass loss throughout the three-year study period (Table 2), while the later stage (3-year) mass loss was significantly related to the N, P and K concentration of the initial substrate and to the TOC, P and K content of the soil organic layer. The fact that we could not clearly determine single environmental and soil or substrate chemical factors controlling mass loss across all the five different incubated substrates may suggest that analysing single factors is not sufficient; instead, the combination of environmental parameters, litter quality and soil chemistry drive the rate of decomposition. The latter assumption is also supported by Prescott (2010) and Zhang et al. (2008) who argue that single factors, e.g., lignin and nutrient concentrations are useful for predicting mass loss rate; however, they do not determine the decay rate of litter on their own.

Table 2. Analysis of covariance of the pooled fine roots and needle litter mass loss (N=15) after 1, 2 and 3 years, initial substrate and soil chemistry. Subscripts sub and soil denote the chemistry of the initial fine roots and needle litter and the soil organic layer, respectively. ns denotes non-significant relationship ($p>0.05$)

	1-year mass loss		2-year mass loss		3-year mass loss	
	F	p	F	p	F	p
N _{sub}	–	ns	–	ns	12.5	0.04
TOC _{sub}	–	ns	–	ns	–	ns
P _{sub}	–	ns	–	ns	47.1	0.01
K _{sub}	–	ns	–	ns	14.6	0.03
N _{soil}	–	ns	–	ns	–	ns
TOC _{soil}	–	ns	–	ns	45.1	0.01
P _{soil}	–	ns	–	ns	39.2	0.01
K _{soil}	–	ns	–	ns	53.3	0.01
Substrate type	9.7	0.05	99.8	<0.01	1776.7	<0.01
Tree species	–	ns	–	ns	–	ns
Tree species*substrate type	–	ns	–	ns	48.8	0.01

3.9. Nutrient dynamics of the decomposing fine root and needle litter (IV)

N concentration increased significantly in the retrieved fine roots ($p < 0.01$, $N=56$) and in the needle litter ($p < 0.01$, $N=42$) during the three-year decay period. Simultaneously, the C:N ratio of the decomposing needles ($p < 0.01$, $N=38$) and fine roots ($p=0.02$, $N=56$) decreased with time.

The release rate of N correlated significantly with the initial C:N ratio in the fine roots (Table 3), indicating higher N release from roots where the initial relative N content is higher. Similarly, the net release of P from the fine roots and needle litter both related negatively to the initial N:P ratio, while the R_tP of fine roots also correlated with the initial litter P content. The release rate of K revealed a strong positive relationship with the initial N and K concentration in the needle litter.

Table 3. Significant Pearson correlations ($p < 0.05$) between the fine roots and needle litter initial chemistry, respectively, and nutrient release rates (R_t). R_tN calculated from litter retrieved after 3 years, R_tP and R_tK from litter retrieved after 1.7 years of decomposition.

Initial chemistry	Fine roots (N=8)		Needles (N=7)	
	R_tN	R_tP	R_tP	R_tK
N	–	–	–	0.84
P	–	0.83	–	–
K	–	–	–	0.85
C:N	–0.71	–	–	–
N:P	–	–0.71	–0.93	–

A well-observed dynamic of N mobilisation-immobilisation occurred in the incubated fine roots but the pattern was of a smaller magnitude and less clear in the needle litter (Fig. 7), even though the initial N concentrations were similar in both substrate types (Table 2 in publication IV). Hence, the differences in N release pattern is determined not only by the initial N concentration, but might also be caused by the different physicochemical environments or microbial composition in relation to the position where roots and needles decompose (Fujii and Takeda, 2010). N accumulation in the decomposing fine roots displayed a two-peaked pattern, as described by Melillo et al. (1984). The first stage of net N accumulation occurred at around 0.7 years (8 months) that is in agreement with other studies reporting peak N immobilisation in decomposing fine roots between 6 and 10 months after incubation (Löhmus and Ivask, 1995; Chen et al., 2002). The later stage N accumulation peak of fine roots appeared at around two years after the start of the incubation, which falls in the time range of 1.4 and 2.3 years reported for the Norway spruce fine and finest roots

(<1mm), respectively, in the decomposition study carried out in Estonia by Lõhmus and Ivask (1995).

The decomposing fine roots immobilised up to 1.5 times (*Myrtilus* pine) and needle litter up to 1.1 times (*Myrtilus* spruce) of the initial N amount. Fine roots also retained relatively more N compared to the initial amount than the needles at the end of the three-year decomposition period in all the studied stands, indicating a longer retention of N in the fine roots. The delay of N release in fine roots as compared to foliar decomposition is in line with the results of previous studies (Ostertag and Hobbie, 1999; Fujii and Takeda, 2010; Luo et al., 2017), emphasising that fine roots have a significant role in nitrogen retention in forest ecosystems.

Our results showed a lower critical N value for the fine roots and needle litter of Scots pine (0.9–1.3% N) compared to Norway spruce (1.5–1.9% N); however, this was in good accordance with the critical N concept by Ågren and Bosatta (1996), who predicted the N release to start in the range from 1.4% to 1.7% N.

There was no significant difference in the retention of P in the fine root and needle litter after 1.7 years of incubation ($70\pm 4\%$ and $75\pm 8\%$, respectively). However, pine needles that also had low initial P concentrations ($<400 \text{ mg kg}^{-1}$, Table 2 in publication IV) displayed a net P accumulation, while spruce needles that had a high initial P concentration ($>800 \text{ mg kg}^{-1}$) were constantly losing P from the beginning of the decomposition study. These results are consistent with previous studies (Johansson, 1993; Berg and Cortina, 1995) that reported initial P leaching from P-rich litters, and net uptake of P in pine needles, confirming that if carbon is relatively available, the immobilisation of a limiting nutrient is common during litter decomposition (Prescott, 2005).

K is not a structural component of plant litter or bound into any known organic compounds (Aber and Melillo, 2001), thus it was most rapidly lost from the incubated fine root and needle litter as found in many studies (e.g., Berg and Cortina, 1995; Lin et al., 2011). After about one month of decomposition approximately 80% of K was lost from the fine roots irrespective of the initial concentration. Needle litter, however, expressed a slower K release, probably because the sampling interval was less frequent compared to that in fine roots, especially in the beginning of the incubation study.

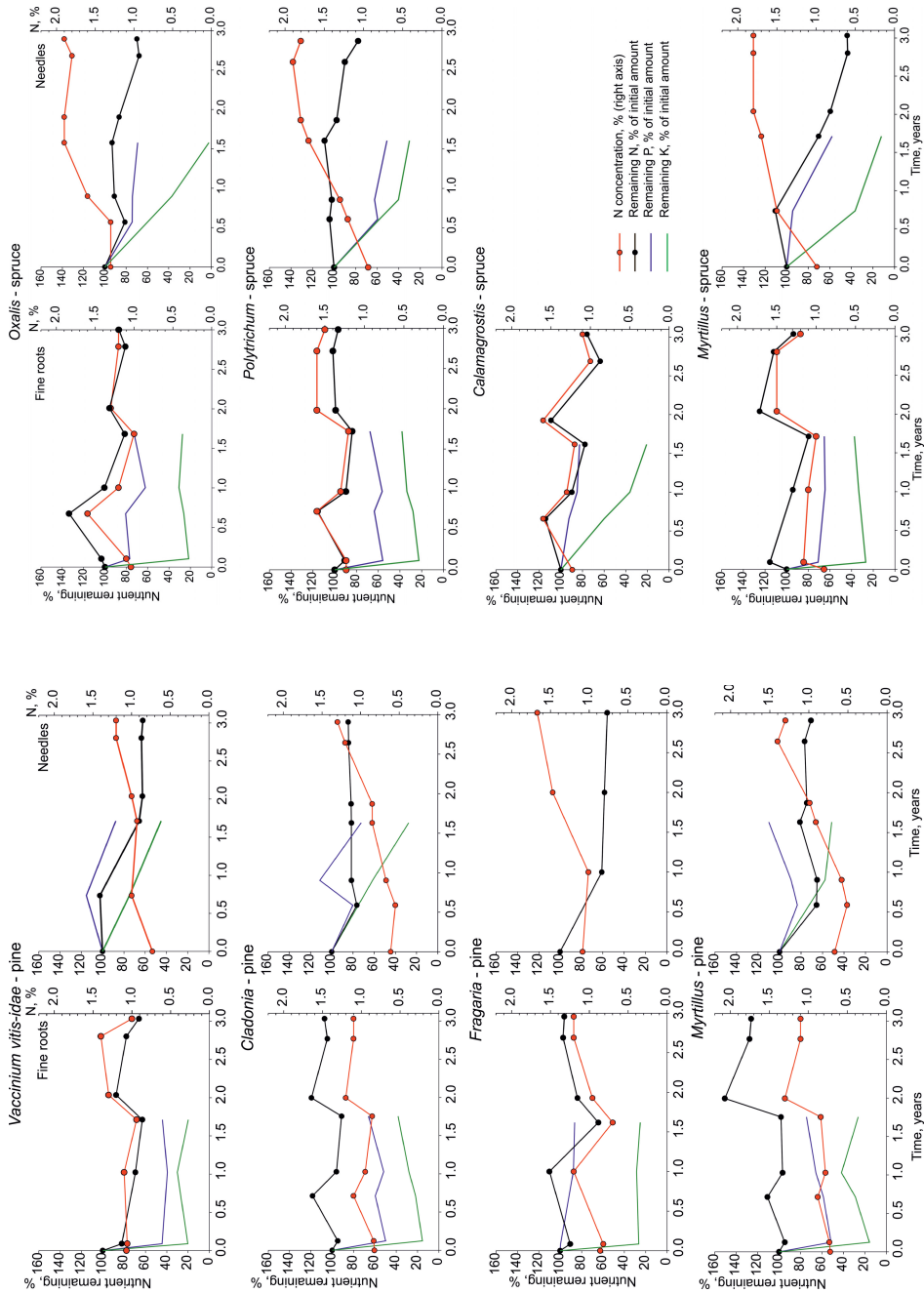


Fig. 7. Changes in mass remaining (percentage of initial amount) of nitrogen (N), phosphorus (P) and potassium (K) in the incubated pine and spruce fine roots and needle litter.

3.10. Yasso07 simulations in European and Estonian forests (I)

The suitability of Yasso07 was tested in six European (Austria, Estonia, Finland, Romania, Spain and Switzerland) forests growing on mineral soils for simulating SOC stocks and stock changes and for reporting purposes under the UNFCCC. The modelled SOC stock values remained within the 95% confidence limits of the observed values for the same forest types and locations (Table 2 in Publication I). In the case of Estonia, the simulated SOC stock was $79.4 \pm 3.10 \text{ Mg C ha}^{-1}$, which is comparable with the average observed value of 68 Mg C ha^{-1} published by Kõlli et al. (2004) and the reported value of 74 Mg C ha^{-1} (Greenhouse Gas Emissions in Estonia 1990–2012, 2014) for Estonian forest mineral soils. According to Kõlli et al. (2004), the thickness of Estonian forest soil cover mostly varies between 40 and 90 cm, whereas Yasso07 predicts soil C stock by default in the upper 100cm of the soil column. Thus, the Yasso model is somewhat overestimating the thickness of soil cover and the SOC pool in the case of Estonia. The simulated SOC values overestimated the national stocks also in the case of Switzerland and Spain up to 30% and 55%, respectively. An inter-annual sink effect with regard to SOC change was found for most of the forest types, which is in line with the soil C pool trends that were previously projected for European forests (Yigini and Panagos, 2016). In Estonia, the model predicted an average annual SOC increase of $0.10 \pm 0.02 \text{ Mg C ha}^{-1}$, which falls in the range of $0.10\text{--}0.16 \text{ Mg C ha}^{-1}$ simulated for the boreal forest mineral soils in Finland.

Due to the lack of consistent empirical data on soil from field studies, models such as Yasso07 provide realistic and plausible SOC estimates and the possibility to fulfil international obligations regarding the C balance in associated soil pools (Didion et al., 2016). Nevertheless, certain divergences between the Yasso07 model and field estimations were found that might have been due to the difference in the field sampling protocols and model assumptions. In the case of Spain, soil samples used for model validation did not consider the topmost organic layer included in the Yasso model, while differences in the assumed depth of the soil column lead to the overestimation of forest SOC pool in Estonia. Furthermore, the Yasso model requires data inputs for forest litter production in accordance with different litter sub-compartments and both from trees and understory vegetation. Empirical data and functions with regional validity for the estimation of different biomass compartments and species-dependent turnover rates, especially regarding fine roots and understory, are scarce. Therefore fixed biomass expansion factors and global turnover rates are often used that, in turn, involve substantial uncertainty and may lead to biased SOC estimates. The accuracy of the estimations of forest SOC pool and soil C balance in Estonia could be substantially improved by implementing the local species-specific fine root turnover rates and above- and belowground litter production values of the understory published in paper III.

4. CONCLUSIONS

This thesis presents empirical estimates of the SOC-related carbon fluxes and the dynamics of the main associated processes (litter production, decomposition, nutrient release) in hemiboreal coniferous forests; provides estimates of the litter mass loss in the hemiboreal region in the frame of a global decomposition study, and evaluates the applicability of the Yasso model for simulating SOC stocks and stock changes in a variety of European forests.

Research into the forest ecosystem carbon budget has mainly been focused on the final assessment of forests as a net C sink or source, while less attention has been paid to analysing variations in annual fluxes that determine the net result of the carbon balance. Special emphasis should be paid to the SOC pool since in boreal and temperate forest ecosystems the amount of carbon stored in soils is often greater than the amount stored aboveground in living and dead plant biomass.

The fine root production of trees and understory along with the production of understory aboveground parts expressed the highest variability, while needle litter production and soil respiration showed the lowest variability of the measured C fluxes in hemiboreal Scots pine and Norway spruce stands. Our results suggest that the forest SOC pool is most sensitive to changes in the above- and belowground tree-derived litter at the stand level, while heterotrophic soil respiration is not a determining factor. Thus, respiration and needle litter production rates obtained in this research can be implemented as proxy values when quantifying C budget for the hemiboreal coniferous forests. One of key findings was that the fine root turnover rate related significantly to the size of the SOC pool across the eight hemiboreal stands, indicating that higher fine root turnover contributes to a larger forest SOC pool through greater C input from continually renewing the fine roots. Hence, fine root production and turnover could be one of the controlling factors that determine the size (confirming hypothesis 1) and the C dynamics of forest soil organic carbon pool.

Annual soil respiration varied from 4 to 8 Mg C ha⁻¹ across the eight study sites in Estonia. Contrary to our hypothesis, the mean annual rate of Rs did not differ significantly among the stands dominated by Norway spruce and Scots pine nor between the years within the same forest sites. Hence, hypothesis 2 was not confirmed, and we conclude that Rs is driven by a combination of site and weather conditions rather than by tree species or stand productivity alone.

Both, the global teabag experiment as well as the regional decomposition study with site-specific fine roots and needle litter showed that substrate type has the strongest influence on the substrate mass loss, supporting partly hypothesis 3, while the effect of temperature and precipitation is only important under less favourable climatic conditions. When comparing the decay rate and nutrient release of different substrates in the course of three years, the decomposition of fine roots was three-fold slower and FR retained relatively more nitrogen compared to the needle litter suggesting that fine roots have a

substantial role in the carbon and nitrogen accumulation in boreal and hemiboreal forest ecosystems. We also identified that the critical N concentration for N release was clearly lower for Scots pine fine roots and needle litter than for the Norway spruce.

Despite the effect of higher mass loss with higher initial nitrogen concentration in the pine litter, substrate chemistry alone did not predict the rate of decomposition. Interestingly, potassium concentration in the soil organic layer expressed a significant effect on the mass loss of all the studied substrate types which has rarely been reported in the literature. Furthermore, soil and incubated substrate macronutrients in combination became increasingly important in the later stage of litter decomposition. These findings are relevant for general understanding of litter decay and carbon dynamics in relation to biosphere-atmosphere feedback and confirm the inherent complexity of the decomposition process while affirming the need for further research in this field.

In light of the recent developments in the global climate change policy and more rigorous reporting requirements under the Paris agreement, cost-effective, yet consistent and accurate carbon-balance accounting due to the application of simulation models is supported. The Yasso07 model, which has been developed for simulating the C dynamics in forest mineral soils, predicted regionally credible values for the SOC stocks and annual stock changes in Estonia, yet not in the case of Mediterranean forest soils. In general, the hypothesis 4 was proved, because difficulties encountered when applying the Yasso07 model were not conceptual shortcomings of the model but rather reflected a lack of available input data. The greenhouse gas reporting and accuracy of the estimates could be further improved in Estonia by applying the country- and species-specific fine root turnover rates and the above- and belowground production of the understory outlined in publication III.

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SUMMARY IN ESTONIAN

Mulla orgaanilist süsinikuvaru mõjutavate süsinikuvoogude varieeruvus ja lagunemise dünaamika hemiboreaalsetes okasmetsades

Maailma muldades on salvestunud rohkem süsinikku kui atmosfääris ja taimesdes kokku, kusjuures metsamullad on ühed suurimad orgaanilise süsiniku reservuaaridest, mis sisaldavad üle 700 Gt süsinikku (Prentice, 2001). Seega võivad juba väikesed muutused mullasüsinikuvoogudes oluliselt mõjutada nii regionaalset kui globaalset süsinikuringet. Kliimamuutuste seisukohalt on erilise tähtsusega suurima süsinikuvaruga põhjapoolkera boreaalsed ja hemiboreaalsed metsad, kuhu kuuluvad ka Eesti metsad. Metsa süsinikuringe uuringud on tänapäeval suuresti keskendunud eelkõige maa-aluste süsinikuvoogude uurimisele, sest näiteks boreaalsetes metsades on mullas ja kõdus hinnanguliselt 85% kogu metsaökosüsteemi süsinikust ning vaid umbes 15% on seotud maapealse biomassis.

Rahvusvahelise kliimapoliitika ja Pariisi kliimakokkuleppe raames on riigid kohustatud vähendama kasvuhoonegaaside heidet ning raporteerima süsinikuvaru muutuseid erinevates sektorites, sealhulgas metsas. Metsamulla süsinikuvarude muutus on riikideüleselt, sealhulgas Eestis, üks kõige puudulikumalt raporteeritavaid valdkondi (Blujdea et al., 2016), sest muutused mulla orgaanilise süsiniku (MOS) varudes toimuvad aeglaselt ning nende empiirilise hindamine on väga aja- ja ressursimahukas. MOS varu ja selle dünaamika suureksaalaliseks ja kuluefektiivseks hindamiseks on arendatud erinevaid simulatsioonimudeleid, millest üks kõige laialdasemalt testitud ja tunnustatumaid on Soomes arendatud Yasso mudel.

Mulla süsinikuvaru on dünaamiline ning sõltub sisend- ja väljundvoogudest. Mullasüsiniku sisendvoo moodustavad valdavalt maapealne lehe- ja okkavaris ning maa-alune juurte produktsioon, kusjuures peenjuurte (läbimõõt <2mm) juurdekasv võib hõlmata kuni 75% kogu metsaökosüsteemi aastasest netoprimaarproduktsioonist (Finér et al., 2011). Orgaanilise aine lagunemine ning sellega kaasnev mullahingamine on väljundvoona teine oluline süsinikuringet mõjutav protsess, mille käigus vabaneb süsinik mullast tagasi atmosfääri ning toitained uuesti mulda.

Käesolevas doktoritöös hinnati Eesti hemiboreaalsete okasmetsade kõige dünaamilisemaid maapealseid ja maa-aluseid mulla süsinikuvoogusid, täpsemalt puude ning alustaimestiku maapealsete osade (okkad ja muu varis) ning peenjuurte produktsiooni, hariliku kuuse (*Picea abies* (L.) Karst) ning hariliku männi (*Pinus sylvestris* L.) okaste ja peenjuurte ning standardmaterjalide (α -tselluloos, roheline ja roobos tee) lagunemist, mullahingamist ning okka- ja peenjuurte varisest makrotoitainete (lämmastik, fosfor, kaalium) vabanemist kolmeaastase lagunemise käigus. Eesti katsealad hõlmasid nelja kuuse- ja nelja männi- enamusega mineraalmullal kasvavaid puistusi vanuses 48–132 a. Globaalse

„teekoti“ (*TeaComposition*) uuringu käigus hinnati rohelse ja punase tee kui standardmaterjalide kolme kuu massikadu ning analüüsi orgaanilise aine varajast lagunemisstaadiumit mõjutavaid keskkonnategureid, peamiselt temperatuuri ja sademete mõju. Käesoleva doktoritöö praktilise väljundina analüüsi Yasso07 mudeli kasutatavust, simulatsioonitulemusel usaldusväärsust ja vastavust rahvusvaheliste süsinikuraporteerimise tingimustele ning modelleeriti MOS varu ja varu muutused erinevates Euroopa metsades, sealhulgas Eestis, mille tulemusena on võimalik täpsustada ja parendada ka Eesti kasvuhoonegaaside inventuuraruande hinnanguid metsasektoris.

Eesti hemiboreaalsete okaspuumetsade aastane maapealne ja maa-alune variseproduktioon olid samas suurusjärgus, vastavalt 381–613 g m⁻² ja 211–1040 g m⁻². Okkavarise produktioon (keskmiselt 250±20 g m⁻² a⁻¹) oli kõige stabiilsem mulla süsiniku sisendvoog, mis ei erinenud oluliselt vaadeldud kuusikute ning männikute ega ka erinevate uuringuaastate vahel. Alustaimestiku aastane maapealne produktioon oli männikutes (119±10 g m⁻² a⁻¹) oluliselt kõrgem kui kuusikutes (25±9 g m⁻² a⁻¹) eelkõige paremate valgustingimuste tõttu. Samas ei erinenud uuritud okaspuupuistute alustaimestiku maa-alune peenjuurte produktioon, mis varieerus vahemikus 6 kuni 68 g m⁻² a⁻¹. Alustaimestiku peenjuurte produktioon moodustas kuni 28% kogu maa-alusest produktioonist, mis viitab alustaimestiku tähtsusele boreaalsete ja hemiboreaalsete metsade süsinikuringes.

Puude peenjuurte produktioon oli kõige varieeruvam uuritud mulla süsinikuvoog, mis varieerus vahemikus 152–1034 g m⁻² a⁻¹, kusjuures keskmise kuuse peenjuurte produktioon ühe puu kohta (7,5±0,9 kg a⁻¹) oli kaks korda kõrgem kui männil (3,8±0,8 kg a⁻¹), mis näitab, et puu liigil on oluline mõju mulla süsinikuvaru moodustumisel. Lisaks leiti, et puistu produktiivsuse vähenedes peenjuurte osakaal kogu puistu primaarproduktioonist suureneb, seega on puud kohastunud raskemates kasvukohatingimustes investeerima rohkem maa-alustesse organitesse, sest just peenjuurte kaudu toimub vee ja toitainete liikumine puu maapealsetesse osadesse.

Käesoleva töös hinnati puude peenjuurte käibekiirust, mis näitab, kui suur osa kõikidest peenjuurtest aasta jooksul välja vahetub ning iseloomustab selle kaudu maa-aluse süsinikuringe intensiivsust. Peenjuurte käibekiirus varieerus vahemikus 0,7 kuni 1,3 a⁻¹, kusjuures peenjuurte käive oli kiirem produktiivsemates okaspuu puistutes. Ühe põhitulemusena leiti, et peenjuurte käibekiirus korreleerub oluliselt puistu MOS varuga ehk puistutes, kus on kiirem peenjuurte käive on ka suurem mullasüsiniku varu. See omakorda viitab, et peenjuurte produktioon ja käive on ühed olulisemad tegurid, mis määravad mullasüsiniku varu suuruse.

Aastane mullahingamine oli üks kõige stabiilsemaid uuritud süsinikuvoogusid, mis varieerus Eesti okaspuumetsades vahemikus 4 kuni 8 t C ha⁻¹. Erinevad teadustööd on näidanud, et mullahingamine on suurem produktiivsemates puistutes ning sõltub domineerivast puu liigist, mistõttu eeldati ka antud töös, et viljakamate kuusikute mullahingamisvoog ületab vähemviljakate männikute oma. Olulist erinevust siiski kuuse ja männi puistute vahel ei leitud, seega võib

väita, et antud puistutes sõltus mullahingamine pigem erinevatest keskkonningimustest (näiteks puistu kasvukoha omadustest ja ilmastikust), mitte ainult puu liigist või puistu produktiivsusest.

Erinevate varise ja standardmaterjalidega läbiviidud lagunduskatsed nii globaalsel kui regionaalsel tasandil jõudsid samale tulemusele, et substraadi tüüp on kõige olulisem lagunemise kiirust määrav tegur, kusjuures temperatuuri ning sademete mõju avaldus ainult ebasoodsates (näiteks väga kuivades) tingimustes. Eestis läbiviidud lagunduskatsed näitasid, et lisaks substraadi tüübile mõjutab massikadu oluliselt ka laguneva materjali ning mulla makrotoitainete (N, P, K) sisaldus. Üldiselt kõrgem toitainete sisaldus soodustab lagunemist, kuid kõrgem kaaliumi kontsentratsioon mullas hoopis vähendas substraadi massikadu Eesti puistutes, mis võib olla tingitud K varu seosest mulla pHga. Peenjuured lagunesid kolm korda aeglasemalt kui okkad ja ka lämmastiku vabanemine toimus peenjuurtest aeglasemalt, mis näitab, et peenjuurteil on oluline roll nii süsiniku kui lämmastiku mulda akumulatsioonil ning vastavalt nende varude moodustumisel. Käesoleva doktoritöö lagunemiskatsete raames määrati männi ja kuuse okkavarise ja peenjuurte kriitilised lämmastiku kontsentratsioonid, mis näitavad, millise N taseme juures hakkab lämmastik lagunevast substraadist tagasi mulda vabanema. Kriitiline N tase mõjutab puistu produktiooni omavahel tugevalt seotud süsiniku- ja lämmastikuringe kaudu, sest mulla lämmastiku vähene kättesaadavus piirab metsaökosüsteemis süsiniku sidumist biomassi (Warland et al., 2014).

Yasso07 dünaamilise mullamudeli rakendamisel saadud Eesti mineraalmuldadel kasvavate metsade süsinikuvaru suurus ($79 \pm 3 \text{ t C ha}^{-1}$) oli sarnane varasemalt empiiriliste andmete baasil hinnatud MOS varuga (68 t C ha^{-1} ; Kölli et al., 2004). Yasso07 mudel andis usaldusväärseid MOS varu ja aastase MOS varu muutuse hinnangu tulemusi ka teiste Euroopa riikide, väljaarvatud Vahe-mere piirkonna metsamuldade kohta. Viimane oli aga tingitud puudulikest sisendandmetest. Käesolevas doktoritöös avaldatud maapealse ja maa-aluse produktiooni ning peenjuurte käibekiiruse empiiriliste väärtuste kasutamine Yasso mudeli sisendparameetritena võimaldab veelgi täpsemalt hinnata Eesti metsamuldade süsinikuvaru muutuseid ning seeläbi oluliselt parandada ka Eesti kasvuhoonegaaside inventuuraruande kvaliteeti ja usaldusväärsust.

Käesoleva doktoritöö raames saadud empiirilised metsamulla süsinikuvoogude hinnangud on olulised hemiboreaalsete okasmetsade süsinikubilansi ja sellega seotud protsesside iseloomustamisel, sest kogu metsa süsinikubilansi on Eesti okasmetsades tänaseni väga vähe määratud just suure tömahukuse tõttu. Kõige stabiilsemate süsinikuvoogude (okkavarise ja mullahingamise) hinnanguid saab kasutada modelleerimisel koefitsiendina sarnaste metsade jaoks ilma kogubilansi mõõtemääramatust oluliselt suurendamata. Töö käigus mõõdetud ja modelleeritud mulla süsinikuvoogude ja varude hinnangud on oluline sisend maakasutuse, maakasutuse muutuse ja metsandussektori (LULUCF) andmete täpsustamisel Eesti kasvuhoonegaaside raportis, toetades seeläbi teaduspõhist kliimapoliitika arengut.

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