Eesti Maaülikool
Estonian University of Life Sciences

SHORT-TERM EFFECT OF FELLING ON CARBON FLUXES AND STORAGES IN DIFFERENT ESTONIAN FOREST ECOSYSTEMS

RAIETE LÜHIAJALINE MÕJU SÜSINIKU VOOGUDELE JA VARUDELE ERINEVATES EESTI METSAÖKOSÜSTEEMIDES

KRISTIINA AUN

A Thesis
for applying for the degree of Doctor of Philosophy
in Forestry

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filosoofiadoktori kraadi taotlemiseks
metsanduse erialal

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Opponent:	**Professor Jukka Pumpanen**, PhD Department of Environmental Sciences University of Eastern Finland
Supervisor:	**Professor Veiko Uri**, PhD Institute of Forestry and Rural Engineering Estonian University of Life Sciences

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following three original publications (**I-III**). The articles are referred to in the text by their Roman numerals.

I Uri, V.; Kukumägi, M.; Aosaar, J.; Varik, M.; Becker, H.; **Aun, K.**; Krasnova, A.; Morozov, G.; Ostonen, I.; Mander, Ü.; Lõhmus, K.; Rosenvald, K.; Kriiska, K.; Soosaar, K. (2019). The carbon balance of a six-year-old Scots pine (*Pinus sylvestris* L.) ecosystem estimated by different methods. Forest Ecology and Management, 433, 248−262

II **Aun, K.**; Kukumägi, M.; Varik, M.; Becker, H.; Aosaar, J.; Uri, M.; Buht, M.; Uri, V. (2021). Short-term effect of thinning on the carbon budget of young and middle-aged silver birch (*Betula pendula* Roth) stands. Forest Ecology and Management, 480

III **Aun, K.**; Kukumägi, M.; Varik, M.; Becker, H.; Aosaar, J.; Uri, M.; Buht, M.; Uri, V. (2021). Short-term effect of thinning on the carbon budget of young and middle-aged Scots pine (*Pinus sylvestris* L.) stands. Forest Ecology and Management, 492

The contributions of the authors to the papers were as follows:

Paper	Original idea and study design	Data collection	Data analysis	Manuscript preparation
I	VU	VU, **KA**, KS, MK, MV	VU, KL, AK, **KA**, MK, KK	VU, KL, IO, **KA**, KS, ÜM
II	VU	HB, VU, **KA**, MB, MV, MK	VU, MK, **KA**	HB, VU, JA, MV, **KA**, MK
III	VU	VU, GM, MV, **KA**, MU	VU, **KA**, MK	VU, MK, JA, MV, HB, **KA**

AK – Alisa Krasnova, HB – Hardo Becker, GM – Gunnar Morozov, IO – Ivika Ostonen-Märtin, JA – Jürgen Aosaar, **KA – Kristiina Aun**, KK – Kaie Kriiska, KL – Krista Lõhmus, KS – Kaido Soosaar, MB – Mikko Buht, MK – Mai Kukumägi, MU – Marek Uri, MV – Mats Varik, VU – Veiko Uri, ÜM – Ülo Mander.

ABBREVIATIONS

C	Carbon
Ca	Calcium
$D_{1.3}$	Breast height diameter of the stand
d	Diameter
EC	Eddy covariance
FRB	Fine root biomass
FRP	Fine root production
K	Potassium
L	Leaching
Mg	Magnesium
N	Nitrogen
n.e	Not estimated
NEE	Net ecosystem exchange
NEP	Net ecosystem production
NPP	Net primary production
P	Phosphorus
Rh	Heterotrophic respiration
Rs	Soil respiration
Ts	Soil temperature
TOC	Total organic carbon

1. INTRODUCTION

Global climate change and increased CO_2 concentration in the atmosphere has become an important issue all over the world. Europe attempts to become the first climate-neutral continent by 2050 and sustainable forest management plays a substantial role in fighting with the climate crisis. Forest ecosystems cover around 40% of the European Union´s (EU) land area and are especially important carbon (C) sinks for achieving the EU´s C neutrality targets, as they absorb around 10% of total EU greenhouse gas emissions every year (Mauser, 2021). Boreal and hemiboreal forests have been recognized as ecosystems with high C sequestration capacity (Dixon et al., 1994; Valentini et al., 2000; Gough et al., 2008), accumulating C both in biomass and in soil (Cannell, 1999; Mund et al., 2002; Hartmann et al., 2013; Körner, 2017). However, C storages and fluxes can be highly variable due to the heterogeneity of different forest ecosystems. C accumulation capacity is affected by tree species composition, stand age and site fertility, as well as management regimes (Usi and Lal, 2017). For providing relevant suggestions to foresters and policymakers for sustainable forest management, the effect of fellings on the forest ecosystem´s C cycling deserves more attention and requires in-depth studies. Both clear-cuttings and thinnings are the main conventional silvicultural practises that have been widely used by foresters for centuries, however, their effect on the stand´s C cycling is still poorly studied.

Although forests generally act as C sink ecosystems, clear-cutting changes the situation a great deal (Paul-Limoges et al., 2015) and the site turns into a C source due to removed photosynthetically active biomass and intensified heterotrophic soil respiration (Rh). Moreover, higher Rh may be evoked by altered environmental conditions, as well as by a larger amount of decomposable organic matter (Pumpanen et al., 2004). After harvesting a new forest generation emerges and C cycling will recover and achieve again C neutrality or the C sink status. The age of the stand at which the ecosystem will turn from a C source to a C sink is defined as the ecosystem´s C compensation point (Kowalski et al., 2004), which is a relevant indicator for characterizing post harvesting C dynamics of managed forest. Balancing the C fluxes after harvesting may take 10-15 years (Kolari et al., 2004; Amiro et al., 2010, Goulden et al., 2011), or even longer (Noormets et al., 2012).

Also, thinning changes the functioning of a forest ecosystem considerably, decreasing the production of a stand for a short period due to the reduced growing stock. At the same time, thinning can produce considerable environmental changes that potentially affect heterotrophic respiration, litter input and the soil microbial community and its activities (Ma et al., 2004; Tang et al., 2005; Peng and Thomas, 2006; Olajuyigbe et al., 2012). The current thesis analyses the short-term effect of fellings in Scots pine and silver birch stands in Estonia. Scots pine (*Pinus sylvestris* L.) is the most widespread species of the *Pinus* genus in the world (Eckenwalder, 2009), having huge ecological and economic importance globally and being one of the commercially most important species, particularly in the Nordic countries (Houston et al., 2016). Also, in Estonia Scots pine is the most widespread tree species, covering over 31% of the total area of Estonian forest (Yearbook Forest 2019). Birch species have a wide natural distribution area in Eurasia, Northern Europe and also in the Baltic countries, where they are the most important commercial broadleaved tree species (Hynynen et al., 2010). Although silver birch (*Betula pendula* Roth) occurs almost throughout the whole Europe, the most abundant birch resources are located in the boreal and temperate forests of Northern Europe and North America as well, it is the most common deciduous tree species in Estonia, covering 29% of total forest land (Yearbook Forest 2019).

Estimation of the post-harvesting C cycling is essential for understanding the recovery process of the forest ecosystem as well as the response to thinning. The C budgeting method serves as a relevant tool for estimating the C accumulation dynamics and for demonstrating how the forest ecosystem is functioning after a disturbance like clear-cutting or thinning. The essential advantage of the C budgeting method is the complex and detailed consideration of all main C fluxes of the ecosystem, including trees, understorey, fine roots, soil respiration etc. At the same time, the main disadvantages of this method is the need for extensive empirical estimation of all C fluxes separately in situ, making it labour intensive. Yet estimation of each C flux involves error, which reduces the accuracy of the method. An alternative method for studying forest C cycling is the eddy covariance (EC) technique, which is based on direct and continuous measurements of C fluxes during a certain period, allowing more precise estimation of C exchange between the ecosystem and the atmosphere (Baldocchi, 2014). This method provides quantification of the input and output fluxes, but without detailed specification of the sources or sinks. The direct EC method is considered to be a more reliable tool, in view of the cumulated uncertainties involved with the indirect method (Meyer et al., 2013).

Combining the two mentioned methods could yield a result of higher quality; similar or coincidental results of the C output and input fluxes, obtained by different methods for the same site, would improve the reliability of a study. Cross-validation of individual methods is imperative to vertify C budget estimates of ecosystems on the regional to the global scale (Peich et al., 2010). We applied this validation approach in a post-clear-cut study in a young pine stand, combining C budgeting and the EC method (**I**).

The present thesis is a synthesis of three research papers. The short-term effect of thinning on the ecosystem´s C budget was studied in young- and middle-aged Scots pine (**III**) and silver birch stands (**II**). The recovery of the ecosystem's C balance after clear-cutting was evaluated in a 6-year-old Scots pine stand (**I**).

The current thesis addresses two novel aspects in forest carbon studies:

a) Estimation of main C fluxes to compile a C budget was carried out simultaneously with eddy covariance measurements, which allowed to validate the C budgeting method and to enhance the relevance of the study. There are few similar studies involving parallel measurement methods, however, in the current study all fluxes for C budget were empirically estimated, ensuring good accordance between annual NEP and NEE values.
b) The effect of thinning on the ecosystem´s C cycling is a quite new issue in forest C studies. Although the effect of thinning on particular traits, like stand production or soil respiration has been studied in several papers, then the complex approach which takes account of all C fluxes, including the production of fine roots and ground vegetation has not been published earlier.

2. REVIEW OF THE LITERATURE

2.1. Estimation of different C fluxes and storages of forest ecosystems

C budgeting is based on the estimation of net ecosystem production (NEP), which is a widely used and informative parameter indicating if the forest ecosystem is acting as a C sink or as a C source (Chapin et al., 2006; Waring and Running, 2007). In the present study C budgeting was applied to estimate the effect of thinning on ecosystem´s C cycling and to study the recovery of C accumulation in the post harvesting period. C budgeting provides information about the partitioning of the ecosystem´s C storages, as well as characterizes the role of each particular C flux in shaping NEP. Annual NEP depends, on the one hand, on the different C input fluxes and, on the other hand, on the C output fluxes. Plants´ annual production serves as the ecosystem´s C input and heterotrophic soil respiration (Rh) as the main C output flux from the forest ecosystem. Belowground plant respiration and Rh are the components of total soil respiration (Rs) which can account for two thirds of ecosystem respiration in Scots pine forest (Kolari et al., 2009). Rh comprises a large part of the forest ecosystem's C fluxes, accounting for up to 80% of total ecosystem respiration (Raich and Schlesinger, 1992; Janssens et al., 2001; Davidson et al., 2006). Leaching as another C output flux is rarely estimated, as it is usually very low in Estonian forest ecosystems (Uri et al., 2017b) and due to its negligible role is often ignored in C budgeting (Varik et al., 2015).

Fine root production (FRP) is an important belowground C input flux to the soil (Finér et al., 2011; Lukac, 2012) and when fine root biomass (FRB) forms a relatively small share of the ecosystem´s C pool, then FRP can make up to 75% of annual NPP (Finér et al., 2011). However, despite the important role of FRP as the main belowground C flux, both FRP and FRB are often underestimated, modelled or even excluded from forest C research, because fine root studies are highly complicated and labor intensive. Hence, obtaining fine root data is the main bottleneck in forest C cycling studies (Leppälammi-Kujansuu et al., 2014). Peichl et al. (2010) brings out that use of inadequate allometric equations and uncertainty in fine root litter production estimates can potentially introduce significant error into biometric NPP estimates.

An alternative forest C cycling investigation method is the eddy covariance (EC) technique, which provides accurate estimation of C exchange between the ecosystem and the atmosphere and is based on direct and continuous measurements during a certain period (Baldocchi, 2014). Although EC is a direct measurement method, unaccounted C losses due to uncertainty associated with gap-filling procedures might considerably affect the accuracy of EC based C flux estimates (Peichl et al., 2010).

As pointed out above, combining the two mentioned methods could yield a result of higher quality; similar or coincidental results of the C output and input fluxes, obtained by different methods for the same site, would improve the reliability of a study. When accumulated uncertainties remain to be resolved by using the indirect method, then the direct method is considered to be a more reliable tool for obtaining precise C budget estimates (Meyer et al., 2013). C accumulation in a mixed stand in Estonia was studied using the EC method supported by biometric and chamber measurements (Krasnova et al., 2019). It was also a good example of comparable results obtained by applying different methods: the NEE value of the studied forest was 5.9 t C ha^{-1} yr^{-1} and the results of forest stand biometric, litter and soil chamber measurements for NEP estimation gave the mean annual value of 6.3 t C ha^{-1} yr^{-1}(Krasnova et al., 2019).

2.2. C cycling in the post clear-cutting ecosystem

Clear-cutting is a conventional and most frequently used regeneration cutting method in boreal and hemiboreal forests. However, its effect on C cycling at the site level and the further post harvesting recovery of the ecosystem is still poorly studied. Clear-cut changes the C cycling of the ecosystem to a large extent for many years, turning the site from a C sink to a C source (Paul-Limoges et al., 2015), due to the biomass of removed trees and increased Rh. Intensified Rh resulted from elevated soil temperature and decomposition of soil organic matter (Pumpanen et al., 2004). After harvesting the ecosystem starts to recover and turns again into a C sink after a certain period of time, which depends largely on site fertility, tree species, understorey and regeneration. In managed forest, the recovery time of the C fluxes to a pre-harvest level can take around 10-15 years (Amiro et. al., 2010) or longer (Noormets et al., 2004). Also the harvesting method (whole tree or stems only) plays a role; clear-cut areas with logging residues have been found to have larger soil respiration fluxes than sites without logging residues (Pumpanen et al., 2004; Moroni et al., 2009). However, according to Kolari et al. (2004) cumulative annual total ecosystem respiration was of the same magnitude in the clear-cut area and in forest stand. The clear-cut area remained a C source mostly because of low biomass production rather than because of intensified soil respiration fluxes.

From the perspective of climate change mitigation, it is essential to clarify when a clear-cut site will attain a neutral or positive C budget, which is considered to be the C compensation point (Kowalski et al., 2004; Aguilos et al., 2014). In Finland, a Scots pine stand reached the C compensation point at the age of 12 (Kolari et al., 2004). However, some authors have reported that 5- and 13-years old pine stands have still acted as C sources (Schulze et al., 1999; Rannik et al., 2002). Also a 5-6-year-old spruce dominating stand in the hemiboreal part of Canada was a C source (Fredeen at al., 2007). According to a long-term EC study in northern Japan, supported by biometric measurements, a planted hybrid larch stand reached C neutrality at the age of 7 years (Aguilos et al., 2014). Similar results were found in a 5-year-old jack pine stand, which was a small net source, but at the age of 10-years maintained a weak C sink status (Howard et al., 2004). An EC study in Estonia showed that after clear-cutting a 6-year-old forest ecosystem was a weak C-sink, while an 8-year-old stand demonstrated a stronger C sink status during the measurement period (Rebane et al., 2020). Several studies in boreal and hemiboreal forests indicate that stands usually reach the C compensation point between 10 and 20 years (Aguilos et al., 2014; Amiro et al., 2010; Grant et al., 2010). After that it usually takes around 8–34 years for the ecosystem to pay back lost CO_2, in case the off-site C storage in forest products is not taken into account (Aguilos et al., 2014).

2.3 The effect of thinning on ecosystem´s C cycling

Thinning is the main forest management tool for shaping stand composition, productivity and quality, as well as growth conditions (Tullus, 2002). Although thinning has been a well-known and widely used silvicultural method in conventional forest management for a long time, its environmental impacts, especially the effect on C cycling, is still poorly investigated.

Thinning changes the functioning of a forest ecosystem a great deal in various ways. On the one hand, it decreases the production of stand for a short period due to the reduced growing stock. On the other hand, thinning can induce considerable changes in the environment, as well as the factors that potentially affect soil heterotrophic respiration, such as microclimate, litter fall input, fine root biomass and necromass, soil microbial community and its activity (Ma et al., 2004; Tang et al., 2005; Peng and Thomas 2006; Olajuyigbe et al., 2012). Tree removal reduces the leaf litter input, thereby decreasing Rh (Sullivan et al., 2008). However, root necromass and harvest residues provide a labile substrate for microbes, which, in the presence of higher soil temperature and moisture, stimulates microbial activities and potentially increases decomposition rates and hence Rh (Misson et al., 2005; Sullivan et al., 2008; Olajuyigbe et al., 2012). Thinning intensity is crucial both from the silvicultural and C cycling aspects: Mäkinen and Isomäki (2004) reported an increase in diameter increment with moderate to heavy thinning, but a loss of volume increment with increasing thinning intensity. Also, an extensive study by del Río et al. (2017) concludes that thinning intensity and regime have a huge impact on the post-harvesting conditions in the forest ecosystem. Tullus (2002) pointed out that moderate thinning intensity can induce development of a valuable conifer stand.

Several studies report minor effects of thinning on C sequestration in forest and the recovery time from thinning within a couple of years (Misson et al., 2005; Vesala et al., 2005; Dore et al., 2010, 2012; Saunders et al., 2012, Trant, 2013). For example, thinning reduced markedly NEE in a ponderosa pine stand, but its productivity recovered during four post-treatment years; the net C uptake in the thinned stand was slightly higher compared to the unthinned stand (Dore et al., 2012). Also, studies conducted in boreal forest demonstrated that reduction in the basal area of stand by 26% did not result in significant differences in NEE between the unthinned and thinned sectors, as increased C uptake by the ground vegetation compensated for reduced canopy photosynthesis (Vesala et al., 2005). Some studies report a reallocation of C sinks after thinning and emphasize the importance of understorey growth (Campbell et al., 2009; Moreaux et al., 2011; Trant, 2013). Others claim that thinning can greatly affect the C storages and fluxes of the forest ecosystem (Jandl et al., 2007; Pang et al., 2013; Bravo-Oviedo et al., 2015; Çömez et al., 2019; etc.) and stands need longer time to recover from the loss of C uptake caused by thinning (Scott et al., 2004; Lindroth et al., 2018).

3. AIMS OF THE STUDY

The present thesis focuses on clarifying the effect of the two main forest management methods, clear-cut and thinning, on the C fluxes and storages in pine and birch stands. The aims of the study are the following:

1. to estimate net annual production (NEP) of a Scots pine stand 6 years after the clear-cut and evaluate the role of different ecosystem components in recovery of C budget (**I**);

2. to validate the C budgeting method by using eddy covariance (EC) measurements in a young pine stand simultaneously with C budgeting (**I**);

3. to estimate the short-term effect of thinning on the ecosystem´s C budget in young- and middle-aged:
a) silver birch stands (**II**);
b) Scots pine stands (**III**).

Hypotheses:

1. We hypothesize that a 6-year-old Scots pine stand acts as a C source, due to its low annual biomass production and intensive soil heterotrophic respiration (Rh) during the post harvesting period (**I**).
2. The values of NEP estimated by the C budgeting method, and the values of NEE estimated by the EC method will be of the same magnitude, confirming the relevance of the C budgeting method for forest C studies (**I**).
3. After thinning heterotrophic respiration (Rh) intensifies significantly in both silver birch and Scots pine stands due to elevated soil temperature. However, despite the decreased annual production and increased C loss, the whole ecosystem will still act as a C sink (**II; III**).

4. MATERIALS AND METHODS

4.1. Study sites (I, II, III)

The data presented in the current thesis and in the original scientific publications are based on the different study sites of Scots pine and silver birch.

4.1.1. Scots pine (I, III)

Three Scots pine stands growing on mesotrophic sandy soils in the southeastern part of Estonia were included in the studies (**I, III**). All stands were growing in a *Myrtillus* site type according to a local classification (Lõhmus, 1984). The recovery of C accumulation in the post harvesting period was studied in a 6-year-old pine stand (Kõnnu site). The clear-cut of the previous forest generation (100-year-old pine stand) was carried out in early 2009 and the soil was scarified with a disc trencher in the late autumn of the same year. In spring 2010, the area was regenerated by sowing. Also natural generation contributed markedly to sowing, since the seed trees of pine had been left in the clear-cut and the area borders with mature pine stands (**I**).

Thinnings were carried out in 25- and 45-year-old stands, Veriora and Ahja, respectively. In both stands, two sample plots were established and thinning was carried out in one plot and the other remained the control plot (**III**). Also, the area adjacent to the treated plot was thinned in a similar mode to avoid the edge effect. This buffer zone allowed to further harvest model trees without disturbing the intact sample plots. The intensity of thinning was 31% and 24% of the basal area for the Veriora stand and for the Ahja stand, respectively which can be considered as moderate thinning rate. The C budgets for the Veriora and Ahja stands were compiled two years after thinning.

Table 1. Main characteristics of the studied Scots pine stands. $D_{1.3}$ – breast height diameter of the stand, n.e-not estimated.

Stand	Age,	Treatment	Average $D_{1.3}$,	Average height,	Stand density,	Basal area,
	yr		cm	m	trees ha^{-1}	m^2 ha^{-1}
Kõnnu	6	Clear-cut	n.e	0.94	15,000	n.e
Veriora	27	Thinning	14.2	13.7	1178	18.8
		Control	11.3	14.2	2722	27.2
Ahja	47	Thinning	19.5	18.9	813	24.2
		Control	17.2	18.1	1373	31.8

4.1.2. Silver birch (II)

Two silver birch stands in southeastern Estonia, Kambja and Kiidjarve were included in the study (**II**). Both stands were naturally regenerated and were growing in a fertile *Oxalis* site type (Lõhmus, 1984). Like in the Scots pine study, two sample plots in either stand were established in 2015; thinning was carried out in one plot and the other plot remained the control. Thinning was done with the below method, following common management practice, i.e. stems were removed and the residues (tops, branches) were left on site. The intensity of thinning was 17% and 21% of the basal area for the Kambja stand and for the Kiidjarve stand, respectively. The Kambja stand has a longer research history and has been thoroughly studied earlier (Uri et al., 2007ab, 2012; Varik et al., 2015; Aosaar et al., 2016; Morozov et al., 2019). The existing sample plot within this stand was considered the control (Morozov et al., 2019) and the thinned plot was established next to the existing plot.

Table 2. Main characteristics of the studied silver birch stands two years after thinning. $D_{1.3}$ – breast height diameter of the stand.

Stand	Age, yr	Treatment	Average $D_{1.3}$, cm	Average height, m	Stand density, trees ha^{-1}	Basal area, $m^2\ ha^{-1}$
Kambja	21	Thinning	12.1	20.3	1840	21.3
		Control	11.1	18.2	2500	24.2
Kiidjarve	30	Thinning	18.3	22.6	667	17.5
		Control	15.2	19.8	1233	22.4

4.2. Soil

At all study sites, seven soil pits (depth 1.0 m) were dug; the soil profile was described and the soil type was determined according to the IUSS Working Group WRB (2006). From every soil pit, bulk density samples were taken from different soil depth layers (0 - 50 cm) using a stainless steel cylinder (Ø 40 mm; V=50 cm^3), to avoid compression of the soil and to preserve soil structure. The soil samples were dried to constant weight at 105 °C and weighed in the laboratory. For estimation of soil nutrient and C content as well as pH, samples from twelve random points over the study plot were taken from different depths (0-10 cm and 10-20 cm) with a soil corer (Uri et al., 2017ab) to form a composite sample for chemical analyses. In the silver birch stands, the decomposition of organic matter was favourable due to high soil fertility and readily degradable litter (Morozov et al., 2019), owing to which no soil organic layer was formed.

For estimation of the C storage in the organic soil layer (forest floor) in the Scots pine stand, samples from 10 random points over the plot were taken with a soil corer (Ø 108 mm). The cutting edge of the soil corer was sharpened and the internal diameter of the upper part of the auger was 2 mm larger than the diameter of the cutting edge to avoid compression of the organic layer. The formed monolith of the organic layer was divided into the O1 and O2 horizons according to decomposition rate. The thickness of the layers was measured in forest and all samples were packed in plastic bags and transported to the laboratory where they were dried to constant weight at 70 °C and weighed. The content of C, nutrients and ash was analysed from composite samples separately in the O1 and O2 layers. For calculating the mass of the forest floor and C storage for the whole horizon, the dry weight of the soil was corrected by taking ash content into account.

For analysing N (Kjeldahl) in the soil samples, a Tecator ASN 3313 was employed. Available ammonium lactate extractable phosphorus in the soil was determined by flow injection analysis using a Tecator ASTN 9/84. Available potassium was determined from the same solution using the flame photometric method. Soil magnesium was determined by flow injection analysis employing a Tecator ASTN 90/92. Soil pH in 1M KCl suspensions was measured at a ratio of 10 g:25 ml. The carbon content of oven-dried samples was determined by the dry combustion method using a varioMAX CNS elemental analyser (ELEMENTAR, Germany). Chemical analyses were carried out at the Biochemistry Laboratory of the Estonian University of Life Sciences.

Table 3. Soil characteristics of the studied stands; N – Kjeldahl nitrogen, P – available phosphorus, K – available potassium, Ca – calcium, Mg – magnesium, organic C – organic carbon content. All characteristics are presented as average for the 0-20 cm topsoil layer.

Stand	Treatment	Soil type	pH_{Cl}	N,	P	K	Ca	Mg	Bulk density,	Organic C,
				%	mg kg^{-1}				g cm^{-3}	%
Kõnnu	Clear-cut	*Gleyic Folic Podzol*	3.0	0.70	26.3	83.9	208.3	50.5	0.70	17.40
Veriora	Thinned	*Endogleyic Podzol*	3.9	0.10	34.2	31.2	104.0	9.6	1.05	4.15
	Control		4.0	0.11	31.4	38.8	87.7	8.2	1.05	3.85
Ahja	Thinned	*Endogleyic Albic Podzol*	3.5	0.02	9.5	13.2	45.9	7.9	1.01	5.01
	Control		3.7	0.03	13.4	16.4	49.5	10.8	1.02	5.12
Kambja	Thinned	*Albeluvisol*	5.5	0.10	58.0	134.9	581.8	97.4	1.22	1.28
	Control		5.4	0.09	76.9	118.5	656.9	108.2	1.24	1.43
Kiidjarve	Thinned	*Umbric-Endogleyic Arenosol*	3.9	0.11	25.9	45.0	126.7	15.5	1.21	1.64
	Control		3.8	0.11	33.9	47.6	120.2	20.7	1.23	1.85

4.3. Estimation of biomass and production

4.3.1. Aboveground biomass and production of the trees

Aboveground biomass in the studied stands was estimated using the model tree method (Bormann and Gordon, 1984; Uri et al., 2017ab). At all sites 5-9 model trees were felled per treatment (outside the sample plots) in August 2017, according to the diameter (**II**, **III**) or height (**I**) distribution of the trees. The stems of the model trees were divided into 5 sections: 0-1.3 m, 1.3 m until the beginning of the living crown and the crown was divided into 3 sections with equal length (Uri et al., 2017ab) exept for the Kõnnu stand where whole stems were fractioned because of the trees´ small dimensions A stem disc from each section was taken for determining the proportion of the stemwood and stembark and dry matter content, as well as for measuring radial increment. The stems and the branches were weighed in forest and one model branch was chosen from each crown section and fractionated in the laboratory. For the pine trees, current year needles, current year shoots, older needles and older branches were separated. For the birches, model branches were fractionated into current year shoots, leaves and older branches. Subsamples from every fraction were taken for determining dry matter content. In the laboratory the subsamples were weighed, dried at 70 °C and reweighed to 0.01 g. Dry mass for each fraction was calculated by multiplying fresh mass by dry matter content.

To estimate annual production in the Kõnnu stand, the trees were measured and model trees were felled in three consecutive years. The difference in the trees´ biomass between the studied years was taken as annual production.

Allometric equation (1) was compiled for estimation of the aboveground biomass and stemwood production of the sample plot (Uri et al., 2017ab)

$$y=ax^b \tag{1}$$

where y is the aboveground biomass, or stem mass, or annual stemwood production of tree, x is diameter at breast height (**II**, **III**) or tree height (**I**) (cm), a and b are parameters of the regression model. The biomass of the needles, current shoots and branches, as well as the proportion of the stemwood and bark were calculated on the basis of the percentage distribution of the fractions of the model trees.

Stemwood production in older stands was estimated on the basis of radial increment which was measured from the cross section discs, that were cut from each stem section. The discs were dried, polished and the widths of the annual rings were measured to 0.001 mm using the software WINDENDRO (Regent Instruments Inc.). Annual stemwood production for the different sections of the model trees was calculated with the Whittaker and Woodwell (1968) equation (2)

$$W_i = W_0 \left(r^2 - (r - i)^2\right) / r^2 \qquad (2)$$

where, W_i is the annual dry mass increment of stemwood (g), W_0 is the dry mass of the stemwood (g), r is the radius of the analysed disc (mm), i is the thickness of annual ring (mm). The production of the sections was summed up for calculation of the stemwood production of model tree. The relative increments of the wood and bark fractions were assumed to be equal and the production of the branches was calculated using the relative increment of the stemwood (Uri et al., 2012).

4.3.2. Aboveground biomass and production of the understorey plants

For estimation of the aboveground biomass of the understorey plants in all studied stands, ten random samples over the whole plot were taken in July, when aboveground biomass was assumed to be at a maximum. The aboveground biomass of all ground vegetation was collected from a 0.5 m^2 quadrat (cut as close to the ground surface as possible), dried at 70 °C to constant weight and weighed in the laboratory. The quadrat was placed on the ground randomly along the diagonal traversing the sample plot (five samplings per one diagonal and five per the other diagonal).

In the Scots pine stands, for estimation of the biomass of mosses, a metal frame (25×25 cm) was placed randomly in the quadrat and all mosses within the frame were collected and the dry mass of moss samples was estimated. The annual production of the herbaceous plants was assumed to be equal to their biomass, since the biomass of herbs is annual (Uri et al., 2017ab). For estimation of the production of the dwarf shrubs, subsamples were taken and the current-year growth (shoots, leaves) was separated and considered as annual production. The annual production of moss biomass at the ecosystem level was calculated by using the average share (%) of annual increment in the total biomass of the mosses (**I, III**).

4.3.3. Stump and coarse root production of the trees

At the Kõnnu study site the root system of nine model trees was excavated for estimation of coarse root biomass. All excavated root systems were washed free of soil, placed in plastic bags and separated in the laboratory into two fractions: the roots (d>2 mm) and the stump core. Considering that the share of fine roots (d<2 mm) was small and excavation is not a reliable method for fine root estimation (Lõhmus and Oja, 1983; Lõhmus et al., 1991), this fraction was excluded from further calculations. The fractions were dried at 70 °C until constant weight and weighed to 0.1 g. The biomass of the coarse root fraction of the young pine trees for all studied years (2015–2017) was estimated using an allometric relationship (1). Annual coarse root production of the Kõnnu stand was calculated as the difference in the biomasses between the studied and the preceding year.

The biomass of the stump and coarse roots of the Veriora and Ahja pine trees was assumed to be 19.9% of aboveground woody biomass according to a regional study (Külla, 1997) and the representative proportion used for the silver birch stands was 21% (Varik et al., 2013). Annual coarse root production was calculated on the basis of the equal relative increments of wooden aboveground biomass; the relative increments of the aboveground and belowground woody biomass fractions were assumed to be equal (**II, III**).

4.3.4. Fine root biomass and production of the trees and understorey plants

The fine root (d<2mm) biomass (FRB) of the trees, dwarf shrubs and the belowground biomass of the herbaceous plants were estimated using the soil coring method in all studied stands (Vogt and Persson, 1991; Stober et al., 2000; Ostonen et al., 2005). In Scots pine stands, sampling was carried out once, in autumn, when 15-20 soil monoliths were taken randomly along the diagonal traversing the sample plot from all treatment plots to a soil depth of 40 cm. The monoliths were divided into depth layers (0-10; 10-20; 20-30 and 30-40 cm) and were packed, labelled and transported to the laboratory, where the samples were stored in the freezer at -5 °C until further processing. Further, all samples were defrosted and washed carefully for extracting roots from the soil. The samples were sorted under the binoculars into the different fractions:

the living and dead fine roots of the trees and dwarf shrubs, and the roots and rhizomes of the herbaceous plants. The sorted samples were dried at 70 °C to constant weight and weighed to 0.001 g for calculating FRB.

Fine root production (FRP) in the Kõnnu stand was estimated using the root mesh (root inclusion net) method (Hirano et al., 2009; Lukac and Godbold, 2010; Uri et al., 2017ab). Vertical nylon meshes (mesh size 1.5 mm, width 7 cm and length 20 cm) were inserted in the soil in autumn 2015. The first 25 samples were taken one year after installation, i.e. in October 2016. Using a spade, a soil block with a height of 20 cm and with edges at about 10 cm from either side of the net was carefully extracted from the soil, placed in a plastic box, packed in a polyethylene bag and transported to the laboratory. To extract the nets, the soil was cut at 1 cm beyond a net with a long-blade sharp knife. The fine roots and rhizomes penetrating the net were washed out and carefully removed. The roots were placed in Petri dishes in water and were sorted into the living roots of the trees and into the roots and rhizomes of the dwarf shrubs and herbaceous plants. The separated roots were dried at 70 °C and weighed. Fine root turnover rate (yr^{-1}) was calculated by dividing FRP ($g\ m^{-2}\ yr^{-1}$) by mean FRB ($g\ m^{-2}$) according to McClaugherty et al. (1982). Fine root longevity (yr) was calculated as the reciprocal of root turnover rate. Since the root mesh method enables to estimate FRP only for the upper 0–20 cm soil layer, we calculated FRP for the deeper (20–40 cm) soil layer by multiplying FRB by topsoil fine root turnover rate.

For estimation of fine root production (FRP) in the Veriora and Ahja stands, an average turnover rate of 0.84 yr^{-1} was used (Brunner et al., 2009) and 0.20 yr^{-1} was used for dwarf shrubs (**I**).

The sequential coring method (Vogt and Persson, 1991; Stober et al., 2000; Ostonen et al., 2005) was used for estimation of FRP in the silver birch stands. Sampling was carried out in October 2016 and in May, August and October 2017. At each sampling, fifteen soil monoliths were taken randomly across both plots to a soil depth of 40 cm. Mean FRB was calculated as the mean biomass across of all four samplings to avoid its seasonal variations (Brunner et al., 2013). FRP was calculated by balancing fine root bio- and necromass according to the decision matrix (Fairley and Alexander, 1985). FRP was assumed to be equal to the input of annual belowground litter, i. e. the C flux, to the soil (Kleja et al., 2008; Varik et al., 2015; Ding et al., 2019). For estimation of the belowground biomass of the herbaceous plants, the samples for August were used.

4.4. Aboveground litter flux of the trees

At the thinning study sites, seven litter traps with a collecting area of 0.36 m^2 each were placed randomly in the plots of the studied stands in early spring 2016 to estimate the annual litter flux of the trees. Litter samples were collected once a month during the three-year study period (2016–2018). The samples were dried at 70 °C to constant weight, divided into three fractions, i.e. the needles/leaves, branches and other material (e.g. seeds, pieces of bark, buds etc.), and every fraction was weighed.

4.5. Soil respiration and microclimate

The rates of total soil respiration (Rs) and heterotrophic respiration (Rh) (µmol CO_2 m^{-2} s^{-1}) were measured monthly from April to October 2016 at all studied sites and additionally from May to November 2017 at the thinning study sites, using the closed dynamic chamber method (PP Systems SRC-1 chamber (volume 1.170 cm^3, enclosed soil surface 78 cm^2), with a gas analyser CIRAS-2 (Differential CO_2/H_2O Infrared Gas Analyzers)). To distinguish Rh from Rs, the trenching method was applied with insertion of 12 deep PVC cylinders (Ø20 cm, height 50 cm) to a depth of 40-45 cm in each plot in October-November 2015. To avoid any CO_2 leakage from the soil respiration chamber, PVC collars (Ø 10 cm, height 5 cm) were inserted at a depth of 3 cm for Rs measurements and inside the trenched plots for Rh measurements. The herbaceous vegetation was carefully removed from the deep cylinder and the collar with minimum soil disturbance, and both were kept free of the live vegetation throughout the study.

Soil temperature (°C) was measured simultaneously with soil respiration in the untrenched and trenched plots, using an attached soil temperature probe STP-1 (PP Systems International, Inc., USA) inserted at a depth of 5 cm. Volumetric soil moisture (%) was also measured at a depth of 5 cm, using a HH2 Moisture Meter Version 2 (Delta-T Devices Ltd, UK). In addition, soil temperature (model 1425, Spectrum Technologies, Inc, USA) and volumetric soil moisture (Water Scout sensor model SM 100, Spectrum Technologies, Inc, USA) were measured continuously every hour during the study period. Data was stored with a data logger (WatchDog 1425, Spectrum Technologies, Inc, USA).

4.6. Carbon leaching

Leaching of total organic carbon (TOC) was estimated using stainless steel plate lysimeters (Roots and Voll, 2011; Uri et al., 2011; Becker et al., 2015; Morozov et al., 2019). In all studied stands, 6-7 stainless steel plate lysimeters were installed per plot in the soil at a depth of 40 cm at random points across the plot. The collecting area of a lysimeter was 627 cm^2. The lysimeters were connected to water collectors (6000 ml polyethylene canisters disposed at a depth of 1 m) by means of polyethylene tubes. Water from the canisters was sampled monthly from early spring to late autumn (up to the freezing of the soil), using a peristaltic vacuum pump, through a plastic pipe. The annual cumulative leaching flux was calculated by adding up the amounts of leached C for the different months (Uri et al., 2017b; Morozov et al., 2019).

4.7. Carbon budgeting

The C budget for the studied stands was compiled by balancing the data of the input and output fluxes of C. It is a relevant approach for estimating net ecosystem production (NEP), which is the difference between net primary production (NPP) and loss of C through heterotrophic respiration (Rh) and leaching (L) (Clark et al., 2001; Lovett et al., 2006; Meyer et al., 2013):

$$NEP=NPP-(Rh+L), \tag{3}$$

where NEP represents the amount of C accumulated in the ecosystem. In the current thesis a positive value of NEP implies a net transfer of C into the forest ecosystem (C sink) and a negative NEP indicates a net C loss from the forest ecosystem to the atmosphere (C source). Exceptionally, article **I** considers NEP values inversely due to the eddy covariance method used for estimating annual NEE. NPP was calculated by summing up the annual increments of the aboveground and belowground biomass fractions of the trees and the understorey plants (Varik et al., 2015; Uri et al., 2017ab, 2019).

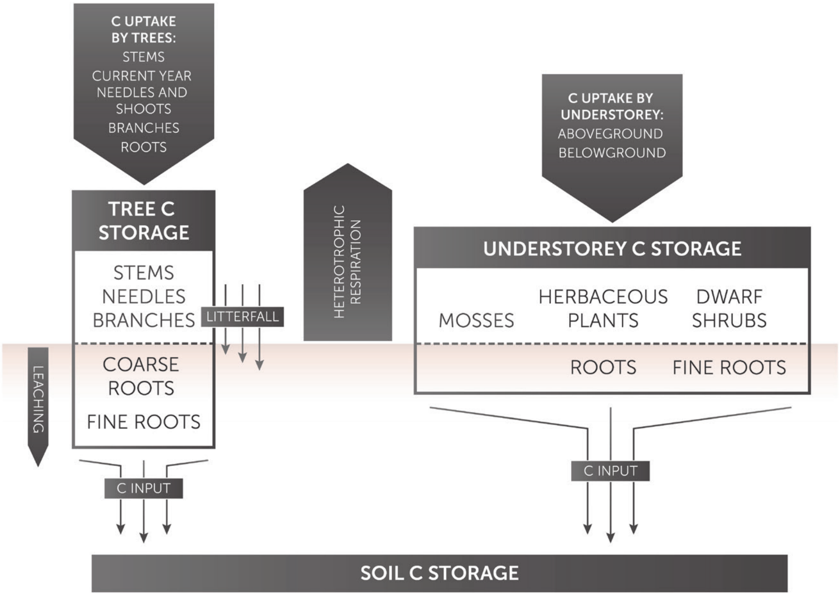

Figure 1. Estimated carbon storages and fluxes in the studied forest ecosystems.

4.8. Eddy covariance measurements (I)

Continuous measurements of net ecosystem exchange (NEE) were carried out in the Kõnnu stand from April 2016 to April 2017 using the eddy covariance (EC) technique simultaneously with the C budgeting method (**I**). The measurement system was installed in a tower at 4.35 m from the ground, 2 m above the ecosystem canopy (maximum tree height 2.4 m). The tower was established in the middle of the clear-cut and the footprint covered most of the studied area. CO_2 and H_2O concentrations were measured from surrounding air with an enclosed path infrared gas analyser LI-7200 (LI-COR Biosciences, Lincoln, NE, USA). Three wind speed components and sonic temperature were measured with a Gill HS-50 sonic anemometer (Gill Instruments, Lymington, UK). The measurements were performed at a frequency of 10 Hz. The half-average fluxes of CO_2 were calculated using the EddyPro v6 software (LI-COR Biosciences, Lincoln, NE, USA) as the covariance between CO_2 concentration and vertical wind speed. The data processing steps included raw data filtering and despiking (Vickers and Mahrt, 1997), 2D coordinate rotation, block-averaging, time lag optimisation, and low and high-frequency spectral corrections (Moncrieff et al., 1997, 2005). NEE was estimated for every half-hour period as the sum of the CO_2 flux and the CO_2 storage calculated with the discrete approach (**I**).

Partitioning of NEE into two oppositely directed components gross primary production and ecosystem respiration was performed in the Reddy ProcWeb online tool with a nighttime based fluxpartitioning algorithm (Reichstein et al., 2005).

4.9. Statistical analysis

Throughout the studies, the normality of variables was checked with the Lilliefors-test and the Shapiro-Wilk test. Statistical differences of the means were analysed by the t-test. The Mann Whitney U test was used for analysing the data that did not follow a normal distribution. Allometric regression models were employed for estimating relationships between model tree biomass fractions or stemwood production with tree diameter. The quality of the fit of the models was evaluated by the coefficient of determination (R^2) and the significance level (p).

Soil respiration data were normalised by log-transformation. The effects of treatment (thinning), time (month) and their coeffect on Rs, Rh, soil temperature and soil moisture were tested using repeated measures ANOVA followed by Tukey´s post-hoc test. The t-test was used to estimate significant differences in soil temperature and soil moisture between the trenched and untrenched plots. An exponential model (4) was used to describe the relationship between Rs (or Rh) and soil temperature at a depth of 5 cm:

$$Rs\ (\text{or } Rh) = ae^{bTs} \tag{4}$$

where a and b are fitted parameters, and Ts is soil temperature (°C). Pearson correlation coefficient between Rs (or Rh) and soil moisture was calculated; to eliminate the confounding effect of temperature, partial correlation analysis was further used. In case the correlation with soil moisture was significant ($p<0.05$), a multiple linear regression, with temperature and moisture being the two independent variables, was conducted. The cumulative Rs and Rh fluxes for the studied periods and for the annual fluxes were modelled using the values of daily mean soil temperature and soil moisture from the data loggers.

5. RESULTS

5.1. Post-harvest carbon storages and fluxes of the young pine forest ecosystem

Ecosystem C storages

The soil C stock formed the main share of the ecosystem C storages and the aboveground C storage in the understorey vegetation exceeded slightly the corresponding storage of the trees in the six-year-old Scots pine stand (Table 4). The belowground C storage of the pine trees was larger than the corresponding C storage of the understorey.

Table 4. Average carbon concentrations of the biomass fractions and carbon storages in the studied 6-year-old Scots pine stand, C – carbon concentration.

	Component	C	Kõnnu
			C storage
		%	t C ha^{-1}
Trees	*Aboveground*		
	Stems	47.5	0.62
	Current year needles	49.9	0.39
	Current year shoots	49.7	0.10
	Old needles	49.9	0.05
	Old branches	49.3	0.26
	Belowground		
	Stump and roots	47.5	1.09
Understorey	*Aboveground*		
	Herbaceous	43.4	0.09
	Mosses	42.7	0.90
	Dwarf shrubs	46.4	2.04
	Belowground		
	Herbaceous roots	46.4	0.07
	Dwarf shrubs		0.59
Soil	Forest floor		44.8
	Mineral soil to a depth 50 cm		60.9
Total			111.9

Ecosystem C fluxes

The studied six-year-old Scots pine stand acted as a moderate C source, NEP=-1.37. The C accumulation by the understorey vegetation made up 56% of the total ecosystem NPP, being slightly larger than C accumulation by the trees. The main C efflux was heterotrophic respiration, C leaching was negligible (Table 5).

Table 5. The carbon budget of the studied 6-year-old Scots pine stand, NPP – net primary production, NEP – net ecosystem production.

			Kõnnu
		Fluxes	t C ha^{-1} yr^{-1}
		Plants aboveground	
C inputs	1	Stems	0.30
	2	Current year needles	0.39
	3	Current year shoots	0.10
	4	Old branches	0.09
	5	Moss production	0.32
	6	Herbaceous plants	0.09
	7	Dwarf shrub production	0.97
		Plants belowground	
	8	Coarse roots	0.10
	9	Tree fine root production	0.24
	10	Herbaceous plants´ roots	0.08
	11	Dwarf shrub fine root production	0.13
		Soil	
C outputs	12	Heterotrophic respiration	4.2
	13	Leaching	0.015
		Productivity	
	14	NPP = (1+2+3+4+6+7+8+9+10+11)	2.85
	15	NEP = (14-(12+13))	-1.37

The annual gross primary production (GPP) measured with the EC technique was 9.87 t C ha^{-1} and the total ecosystem respiration was 11.05 t C ha^{-1}, hence NEE calculated from the EC measurements was 1.19 t C ha^{-1}.

5.2. The effect of thinning on the ecosystem carbon storages and fluxes

5.2.1. Silver birch stands

Ecosystem C storages

The C storage in tree aboveground biomass was higher in the unthinned plots and the trees made up to 99% of the total aboveground C storage. 42-50% of total ecosystem C was stored in mineral soil and 53-58%, in plant biomass. Thinning reduced the C storage of the trees by 11-16% (Table 6) but increased the biomass of the herbaceous ground vegetation: the aboveground C storage of the herbaceous plants was larger in the thinned plot compared to the control plot in both studied silver birch stands (Table 6).

Table 6. Carbon storages of the studied silver birch stands two years after thinning; C % – carbon concentration.

	Component	C	Kambja		Kiidjarve	
			Thinned	Control	Thinned	Control
			C storage			
		%	t C ha^{-1}			
Trees	*Aboveground*					
	Stemwood	49.3	46.9	51.0	47.1	56.5
	Stembark	54.0	8.0	9.9	6.2	6.4
	Leaves	51.0	1.4	1.6	1.1	1.4
	Current year shoots	51.8	0.2	0.2	0.3	0.2
	Old branches	50.8	3.2	4.5	4.1	5.6
	Belowground					
	Stumps and roots	49.7	18.1	20.3	17.8	21.0
Understorey	*Aboveground*					
	Herbaceous plants´	43.4	0.5	0.3	0.9	0.6
	Belowground					
	Herbaceous plants´ roots	46.4	0.1	0.1	0.7	0.7
Soil	Mineral soil to a depth of 50 cm		77.8	77.7	64.9	67.0
Total			156.2	165.7	143.0	159.3

Ecosystem C fluxes

All plots acted as C sinks in the studied silver birch stands irrespective of treatment. The main C efflux was soil heterotrophic respiration (Rh), which was in both cases slightly higher in the thinned plots, however, the difference from the unthinned plots was not significant ($p>0.05$). Thinning decreased NEP by 21% in the Kambja stand and 30% in the older Kiidjarve stand; annual NPP was 0.9 t C ha^{-1} yr^{-1} lower in the thinned plot compared to the control plot in both silver birch stands. The largest amount of C was accumulated in the stems of the trees. Thinning did not significantly affect the aboveground litter flux of the trees, but the belowground litter input, (FRP of the trees) was larger in the thinned plot of the younger stand (Kambja), compared to control plot; however, an opposite trend was seen in older Kiidjarve stand.

Regarding soil C exchange, the output and input fluxes were roughly balanced for the middle-aged control plot. For the other treatment plots, soil C loss by Rh exceeded the C input into the soil by organic litter (Table 7).

Table 7. Carbon budgets of the studied silver birch stands two years after thinning, NPP – net primary production, NEP – net ecosystem production.

			Kambja		Kiidjarve	
			Thinned	Control	Thinned	Control
		Fluxes	t C ha^{-1} yr^{-1}			
		Plants aboveground				
C inputs	1	Stem increment	4.69	5.31	3.96	4.36
	2	Current year shoots	0.18	0.19	0.25	0.18
	3	Branch increment	0.27	0.39	0.31	0.38
	4	Leaf litter	1.36	1.58	1.05	1.36
	5	Branch litter	0.14	0.12	0.14	0.34
	6	Other litter	0.10	0.14	0.13	0.12
	7	Production of herbaceous plants	0.52	0.30	0.91	0.56
		Plants belowground				
	8	Coarse root biomass increment	1.03	1.18	0.88	0.99
	9	Tree fine root production	0.71	0.66	0.57	0.94
	10	Herbaceous plants´roots	0.12	0.12	0.66	0.73
		Soil				
C outputs	11	Heterotrophic respiration	4.46	4.13	4.84	4.16
	12	Leaching	0.01	0.01	0.01	0.01
	13	C input to the soil (4+5+6+7+9+10)	2.95	2.92	3.46	4.05
	14	Soil C exchange (13-(11+12))	-1.51	-1.21	-1.39	-0.11
		Productivity				
	15	NPP = (1+2+3+4+7+8+9+10)	8.89	9.74	8.59	9.50
	16	NEP = 15-(11+12)	4.43	5.60	3.75	5.34

5.2.2. Scots pine stands

Ecosystem C storages

The relative share of the above- and belowground C storages of the trees formed 51-64% of the total ecosystem C stocks across the studied Scots pine stands, being slightly higher in the control plots. Thinning reduced the C storage in tree biomass by 24% and 21% in the Veriora stand and in the older, Ahja, stand, respectively. Stemwood accounted for 63-68% of tree biomass allocation across the treatment plots. The soil C storage accounted for 22-31% of the total ecosystem C storages across the studied plots (Table 8).

Table 8. Carbon storages of the studied Scots pine stands two years after thinning; C % – carbon concentration.

			Veriora		Ahja	
			Thinned	Control	Thinned	Control
		C	C storage			
	Component	%	t C ha^{-1}			
Trees	*Aboveground*					
	Stemwood	47.5	27.96	39.30	46.49	57.61
	Stembark	47.5	3.26	4.59	4.39	5.44
	Current year needles	47.9	1.29	1.04	0.92	1.17
	Current year shoots	49.7	0.51	0.36	0.30	0.35
	Old needles	50.5	0.80	0.73	0.85	1.16
	Old branches	49.3	3.89	3.10	4.52	6.99
	Belowground					
	Stump and roots	47.5	8.09	11.13	11.28	14.09
Understorey	*Aboveground*					
	Herbaceous	43.4	0.24	0.07	0.03	0.04
	Mosses	44.5	0.20	0.31	0.81	0.85
	Dwarf shrubs	46.4	0.01	0.02	0.32	0.21
	Belowground					
	Herbaceous roots	46.4	0.58	0.27	0.03	0.06
	Dwarf shrubs		n.e	n.e	0.11	0.26
Soil	Forest floor		8.70	8.30	35.30	34.70
	Mineral soil to a depth of 20 cm		23.40	25.40	28.90	30.10
Total			78.94	94.62	134.25	153.02

Ecosystem C fluxes

Although thinning reduced NEP by 22-37% in the Scots pine stands, still both thinned plots acted as C sinks during the study period. Average post-thinning decrease of NPP was 9-11%, being more marked in the younger stand (Table 9). The main C efflux was Rh, which was higher in the Veriora stand. Still, thinning did not significantly affect Rh in either studied stand. The annual leaching of organic C was very small in both stands and did not affect the balance of C budgets. The production of the herbaceous understorey and needles increased after thinning, while the, production of the mosses and dwarf shrubs did not change. Thinning slightly reduced litterfall in the studied stands, but differences between the thinned and the control plots were statistically not significant ($p>0.05$) for either studied stand. Needles formed the largest share of tree litterfall (68-77%), being 5-7% larger in the thinned than in the control plot. Annual fine root production at the stand level was higher in the control plots of both studied stands.

Table 9. Carbon (C) budgets of the studied Scots pine stands two years after thinning; NPP – net primary production, NEP – net ecosystem production.

			Veriora		Ahja	
			Thinned	Control	Thinned	Control
		Fluxes	t C ha^{-1} yr^{-1}			
		Plants aboveground				
C inputs	1	Stems	2.14	2.81	2.68	3.07
	2	Current year needles	1.29	1.04	0.92	1.17
	3	Current year shoots	0.51	0.36	0.30	0.38
	4	Old branches	0.26	0.20	0.85	0.34
	5	Litterfall (needles, branches, other)	1.47	1.87	1.11	1.52
	6	Moss production	0.07	0.11	0.30	0.31
	7	Herbaceous plants	0.24	0.07	0.03	0.04
	8	Dwarf shrub production	0.004	0.007	0.13	0.08
		Plants belowground				
	9	Coarse roots	0.75	0.78	0.70	0.88
	10	Tree fine root production	1.14	1.97	0.85	1.26
	11	Herbaceous plants´ roots	0.56	0.27	0.03	0.06
	12	Dwarf shrub fine root production	n.e	n.e	0.02	0.05
		Soil				
C outputs	13	Heterotrophic respiration	5.5	5.3	4.3	4.4
	14	Leaching	<0.01	<0.01	0.02	0.02
	15	C input to the soil=(5+6+7+8+10+11+12)	3.49	4.30	2.46	3.32
	16	Soil C exchange=(15-(13+14))	-2.02	-1.01	-1.86	-1.10
		Productivity				
	17	NPP=(1+2+3+4+6+7+8+9+10+11+12)	6.96	7.62	6.80	7.64
	18	NEP=(17-(13+14))	1.45	2.31	2.48	3.22

6. DISCUSSION

6.1. C storages and fluxes of the post-harvest young pine forest ecosystem

Clear-cutting represents considerable disturbance to the forest ecosystem after which a site will turn from a C sink to a C source (Paul-Limoges et al., 2015). Six years after clear-cut the soil C storage exceeded the C storage in biomass, as the aboveground tree layer had been removed and the new tree generation was in the early development stage. The understorey vegetation responded to changed environmental conditions by increasing its biomass after disturbance: in the studied Scots pine stand the understorey vegetation accounted for 56% of NPP, exceeding the production of the trees. Dwarf shrubs formed the main share of the ground vegetation production, while the contribution of the mosses to NPP made up 24%.

Total C uptake by the trees and understorey vegetation could not compensate for the annual C loss through Rh (4.2 t C ha^{-1} yr^{-1}), as a result of which the studied 6-year-old pine stand was a moderate C source with a NEP of -1.37 t C ha^{-1} yr^{-1}. However, although the Rh efflux after clear-cut was expected to be high, estimated Rh was still of the same magnitude as reported for mature Scots pine or spruce stands in Estonia (Kriiska et al., 2019; Kukumägi et al., 2017). Thus, clear-cut strongly affects the annual production of the young post-harvest stand, but not so much Rh. Similar results have been reported from a jack pine chronosequence study where soil respiration and the Rh flux were lower in a 5-year-old stand than in older stands (Howard et al., 2004). However, the interval from disturbance is a crucial factor affecting the soil respiration flux. In France a C loss of 2-3.5 t C ha^{-1} was estimated for a clear-cut of maritime pine (Kowalski et al., 2003) and in northern Japan annual C loss in the first years amounted to 5-5.7 t C ha^{-1} yr^{-1} after the clear-cut of a mixed forest (Aguilos et al., 2014).

C exchange between the atmosphere and the ecosystem was simultaneously measured by using the EC technique, to check the results of the input and output fluxes of the C budgeting method, as EC measurements are considered to be a more reliable tool for estimating C exchange between the ecosystem and the atmosphere (Meyer et al., 2013; Baldocchi, 2014;

Howard et al., 2004). The main advantage of EC is high accuracy, but this method does not provide information about the contribution of the particular ecosystem components to C uptake. Combining these two methods improves the quality of research and allows to validate the result of NEP obtained with the C budgeting method. In the present study, the NEE measured with the EC method was consistent with the NEP estimated by C budgeting, -1.19 and -1.37 t C ha^{-1} yr^{-1}, respectively. Usually, such close results are not very typical in research where similar approaches have been used; in a peatland forest the average annual NEE determined by the two methods differed by almost 2 t C ha^{-1} yr^{-1} (Meyer et al., 2013). However, in the mentioned study annual biomass production was modelled, which may be one reason for the differences between the results. Another good example of the comparable results obtained by different methods can also be drawn from Estonia where the NEE value of a mixed forest was 5.9 t C ha^{-1} yr^{-1} and the NEP value, calculated on the basis of forest stand biometric and soil chamber measurements, was 6.3 t C ha^{-1} yr^{-1} (Krasnova et al., 2019).

Although the trees made a modest contribution to ecosystem C uptake (43% of NPP), due to their small dimensions, the situation changed rapidly: when the amount of C accumulated in tree biomass was roughly 1 t C ha^{-1} yr^{-1} in 2016, then in the following year it was more than doubled, amounting to 2.4 t C ha^{-1} yr^{-1}. Assuming that the annual R_h flux remains stable and is of the same magnitude in the subsequent year, the ecosystem will become a C sink already at the age of 7 years, which is in accordance with a EC study in Estonia, where after clear-cutting a 6-year-old forest ecosystem was a weak C-sink, but a 8-year-old stand demonstrated already a stronger C-sink status during the measurement period (Rebane et al., 2020). In Finland, the C budget of Scots pine forest reached a balance in a 12-year-old stand (Kolari et al., 2004). Yet, Schulze et al. (1999) and Rannik et al. (2002) found that both 5- and 13-year-old Scots pine stands were still C sources. In boreal and sub-boreal forests, the C compensation point is usually reached when stands are 10-20 years old (Amiro et al., 2010; Grant et al., 2010; Aguilos et al., 2014).

6.2. The effect of thinning on the ecosystem C storages and fluxes

Thinning is the main forest management practice used for shaping the stand´s species composition, as well as for increasing the productivity and quality of future trees and hence the value of the whole stand. Thinnings can also have a considerable effect on the stand C fluxes and storages, as a consequence of removed biomass and changed environmental conditions. The reduced growing stock of stand leads to a temporary decrease of the stand C storage and thus its C sequestration ability. Thinning alters environmental factors, which in turn has an impact on particular components of the forest ecosystem, resulting in the changed functioning of the whole forest C cycle. In the current study thinnings were carried out in line with conventional forest management practice in Estonia, where thinning intensity is moderate to avoid possible windfall and snow damage.

Silver birch stands

In both silver birch stands, thinnings led to a slight decrease of C storages at the stand level, at 6% and 10% in the Kambja and Kiidjarve stands, respectively. This modest decrease can be explained by the below method and moderate thinning intensity used, while the effect of thinning was slightly stronger in the older stand.

Thinning decreased annual net ecosystem production (NEP) in the second post-thinning year; NEP was 20-30% lower in the thinned silver birch stands compared to the unthinned plots, but all stands still remained C sinks. The lower NEP of the thinned plots resulted from the reduced NPP of the trees, which was 8-10% lower in the thinned plots. However, this decrease is probably short-term because, according to several earlier studies, silver birch is a highly productive tree species, especially at a young age (Hynynen et al. 2010; Hytönen et al. 2014; Varik et al. 2015), and the removed biomass of the trees will recover quickly. Also, thinning increased the growth of herbaceous understorey plants. Still, the increased biomass of the herbaceous plants compensated for only a modest share of the reduced C sink of the tree layer. In the Kambja stand the total production of the trees decreased 1.1 t C ha^{-1} yr^{-1}, while the production of the herbaceous plants increased only 0.2 t C ha^{-1} yr^{-1}; in the Kiidjarve stand the respective values were 1.3 and

0.3 t C ha yr^{-1}. Of course, the biomass and species composition of the herbaceous understorey depends on many factors among which soil fertility and light conditions play a major role.

The C balance of an ecosystem depends on the C input fluxes and on the C output fluxes, of which Rh represents the main C efflux. The annual Rh flux was of the same magnitude across the treatments, being only slightly higher in the thinned plots, and thus contributed moderately to the decrease of NEP. In general, thinning did not significantly influence the soil CO_2 effluxes at the early post-thinning stage: modelled mean Rs and Rh were similar in all studied plots. The effect of thinning on Rs is a combined result of changes in the microclimate, caused by both thinning and inter-annual climate variability, and changes in the substrate supply, i.e. litterfall and fine root biomass and production (Tang et al., 2005), which are all expected to change by forest thinning (Peng and Thomas, 2006; Zhang et al., 2018). Since there was no significant difference in litterfall or fine root production between the thinned and control plots, this may be a possible reason for the non-response of Rs and Rh to thinning.

The annual leaf litter flux across both stands and treatments varied from 1.7 to 3.1 t ha^{-1} yr^{-1}, which fits well in the range of the annual leaf litter flux of silver birch and downy birch stands of different ages in Estonia (Uri et al., 2012, 2017b). The similar leaf litterfall fluxes between the studied plots can be explained by low thinning intensity, but mainly by the removal of suppressed trees with short crowns and small leaf mass, as is typical for the below method. The main belowground C input to the soil is fine root production (FRP) (Finér et al., 2011; Lukac, 2012), which was of the same magnitude in both plots of the Kambja stand and slightly lower in the thinned plot compared to the control plot of the Kiidjarve stand, indicating that thinning did not intensify FRP during the short two-year period. In the silver birch stands, FRB varied between 2.4 and 2.7 t ha^{-1} across the studied plots, being of the same magnitude as reported for silver birch boreal forests (Ding et al., 2019), and similar to the general average value of FRB (2.3 t ha^{-1}) as reported for boreal forests (Jackson et al., 1997). These results are also in good accordance with earlier estimations for young and middle-aged Estonian birch stands (Varik et al., 2013).

Soil C exchange was slightly negative across all studied plots; a similar result was also found in an earlier silver birch chronosequence study (Varik et al., 2015). This phenomenon could be explained by the production and turnover of mycorrhizal mycelia (Wallander et al., 2013), which is commonly not taken into account in C budgets. Yet the C inputs from fine roots and mycorrhizal hyphae might be of the same magnitude (Wallander et al., 2004). Clark et al. (2001) notes that rhizodeposition and root losses to consumers may account for a large proportion of total NPP in forests, but these traits have not been quantified at the forest level.

Scots pine stands

Trees acted as the main C stock in the studied forest ecosystem, making up 51-64% of the total ecosystem C storage. Thinning clearly reduced the ecosystem C storages, at 17% and 12% in the younger Veriora stand and in the older Ahja stand, respectively, due to the removal of trees. The C storage of the understorey vegetation remained of the same magnitude in both stands. However, the biomass of the herbaceous plants increased in the thinned plot, but the biomass of the mosses and dwarf shrubs remained unaffected in the second post-thinning year. As the aboveground biomass of herbaceous plants is annual, their response is faster, while the dwarf shrubs and mosses grow slower and need more time to adapt to changed environmental conditions.

Thinning reduced annual NEP by 22-37% in the studied Scots pine stands, but the thinned plots still acted as C sinks. The lower NEP of the thinned stands (decrease 9-11% compared to the unthinned plots) was largely caused by the lower NPP of the trees, which is the consequence of lower stand density and biomass production. However, the difference between the plots was not drastic and will probably level out in the nearest future, as tree growth is expected to increase in thinned plots (Zhang et al., 2019). At the same time, self-thinning reduces stand density in naturally developing control plots (Brunet-Navarro et al., 2016). Dore et al. (2012) reported that although thinning reduced markedly NEE in a ponderosa pine stand, its productivity recovered during four post-treatment years when the net C uptake in the thinned stand was slightly higher compared to the unthinned stand.

Annual litterfall decreased 21-26% in the thinned plots in the second post-thinning year, but the difference between the treatment plots was not significant. The relatively moderate decrease can be explained by the thinning method (thinning from below) used and by the increased needle production of the thinned plots. A similar result was also found in a Turkish study, where thinnings decreased litterfall by 22% in a mature Scots pine stand (Çömez et al., 2019).

Thinning significantly reduced FRB in both studied stands and the decrease was more marked in the younger Veriora stand than in the Ahja stand, being 42% and 33%, respectively. FRP varied between 1.7 and 3.9 t ha^{-1} yr^{-1} across the studied stands, which was lower than the values reported for middle-aged Scots pine stands in Finland (Makkonen and Helmisaari, 1999; Helmisaari et al., 2002), but still of the same magnitude as the corresponding values for older Scots pine stands in Estonia (Kriiska et al., 2019). Several studies have highlighted the reallocation of C sinks after thinning and have emphasized the importance of understorey growth (Vesala et al., 2005; Campbell et al., 2009; Moreaux et al., 2011; Trant, 2013). However, in the studied Scots pine stands, the production of the understorey plants made up a moderate share (4-13%) of NPP across all study plots and thinning significantly increased the production of the herbaceous plants only in the Veriora stand, as herbaceous plants were almost absent from the Ahja stand.

The main C efflux from the pine forest was Rh, which remained in the range found for coniferous forests in the boreal and hemiboreal zones (Kolari et al., 2009; Kukumägi et al., 2017; Kriiska et al., 2019). Thinning had no significant effect on Rh and Rs, which is in accordance with earlier individual studies (Ma et al., 2004; Campbell et al., 2009; Pang et al., 2013) as well as with a meta-analysis by Zhang et al. (2018). Estimation of the differences between the parameters of the exponential model showed that thinning did not significantly change the response of Rs and Rh to soil temperature, which was the driving factor of the variation in both soil respiration fluxes. Besides Rh, soil C loss through leaching is another output flux that should be considered. However, C leaching was negligible in the Veriora stand and very low in the Ahja stand.

7. CONCLUSIONS

1. The first hypothesis was proved: the 6-year-old Scots pine stand acted as a moderate C source, with a NEP of -1.37 t C ha^{-1} yr^{-1}. The negative C budget was caused by the low annual production of the young forest generation, while the soil heterotrophic respiration flux was still of the same magnitude as estimated for mature pine or spruce stands in Estonia. However, on the basis of the stand growth dynamics, it can be expected that the ecosystem will become a C sink already in the nearest future, at the age of 7 years.

2. The results of NEP, estimated by using the C budgeting method, and the results of NEE, obtained by using EC measurements, for the studied 6-year-old Scots pine stand were in good accordance, -1.37 and -1.19 t C ha^{-1} yr^{-1}, respectively. This confirms that C budgeting is a reliable method for estimating C uptake by forest ecosystems, assuming empirical *in situ* estimation of all main C fluxes.

3. The third hypothesis was proved partly: C accumulation by the trees at the stand level decreased in all thinned plots due to removed biomass, however, all thinned ecosystems still maintained their C sink status. Thinnings did not significantly affect soil heterotrophic respiration in the studied young and middle-aged silver birch or Scots pine stands.

4. Thinning affected the annual production of the understorey herbaceous plants, but the effect on the production of the dwarf shrubs and mosses was not revealed due to the too short post-thinning period. However, increased C accumulation by the herbaceous plants did not compensate for the decrease of C accumulation by the trees.

5. Thinning did not significantly affect aboveground litterfall in the studied Scots pine and silver birch stands on the second post-thinning year.

Suggestions for forestry practice

The present thesis provides new knowledge about the effects of forest management on the C storages and fluxes of silver birch and Scots pine stands, confirming the standpoint that after clear-cut the young pine ecosystem still acts as a C source. Since the magnitude of C loss via soil heterotrophic respiration was similar to that seen in matured stands, then reaching the C neutral or C sink status for the new ecosystem depends mostly on stand production capacity, and hence timely and vigorous regeneration after clear-cut plays a critical role from the aspect of C accumulation. Forest managers should apply effective forest regeneration methods and make efforts to attain the new forest generation as fast as possible.

Our results demonstrated the modest impact of thinning from below on stand C cycling in young and middle-aged birch and pine stands. Thinnings caused a temporary decrease in annual production of the trees at the stand level due to removed tree biomass and therefore reduced the stand C storages and C uptake. At the same time, thinnings did not induce a significantly higher C efflux from the soil in the studied stands (**II, III**). Thus, we can suggest that moderate thinning rate with the below method is an appropriate approach to avoid turning the ecosystem temporarily into a C source in post-thinning period. This is in accordance with existing silvicultural recommendations for thinning in order to avoid storm or snow damage in the nearest post-thinning period. We can speculate that too extensive thinning leads to temporary C loss from pine or birch stands.

Although it was not an issue of the present study, then additional impact upon the effect of thinning on forest C cycling and mitigation of climate changes should also take account of two important aspects. Firstly, for managed stands, the proportion of high-quality timber in final felling is larger, which allows to produce products with a longer lifetime and to ensure C capture for a longer period. Secondly, the timber collected from thinnings can also be used in the wood industry or in the energy sector, replacing fossil fuels or materials with larger carbon footprint.

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SUMMARY IN ESTONIAN

RAIETE LÜHIEALINE MÕJU SÜSINIKU VOOGUDELE JA VARUDELE ERINEVATES EESTI METSAÖKOSÜSTEEMIDES

Suurenevast CO_2 kontsentratsioonist atmosfääris ja sellest tulenevatest kliimamuutustest on tänapäeval kujunenud üks aktuaalsemaid globaalseid keskkonnaprobleeme. Seetõttu on Euroopa seadnud eesmärgiks saada 2050. aastaks esimeseks kliimaneutraalseks maailmajaoks ning jätkusuutlikul metsamajandusel nähakse olulist rolli selle eesmärgi täitmisel ning kliimakriisi leevendamisel. Metsaökosüsteemid katavad ligikaudu 40% Euroopa maismaast, olles tähtsad süsiniku sidujad, sidudes igal aastal 10% Euroopa kasvuhoonegaaside emissioonist (Mauser, 2021). Boreaalsed ja hemiboreaalsed metsad on efektiivselt süsinikku siduvad ökosüsteemid, talletades seda nii biomassi kui ka mulda (Canell, 1999; Mund et al., 2002; Hartmann et al., 2013; Körner, 2017). Samas erinevate metsade süsiniku vood ja varud varieeruvad suurtes piirides, sõltuvalt kliimast, kasvukoha viljakusest, puuliikidest, puistu vanusest, aga ka metsade majandamisest. Eespool toodust tulenevalt on metsaökosüsteemide süsinikuringe uuringud aktuaalsed nii globaalsel kui ka regionaalsel tasandil.

Tänapäeva metsateaduse üheks olulisemaks väljakutseks on selgitada, kuidas erinevad metsamajandusmeetodid mõjutavad nende ökosüsteemide süsinikuringet, olles aluseks teaduspõhisele metsamajandusele. Erinevatest majandamisvõtetest on harvendus- ja lageraie ühed enam levinud ja neid rakendatakse laialdaselt, samas on nende mõju metsade süsinikuringele seni suhteliselt vähe uuritud ning vastavad teadmised seetõttu üsna tagasihoidlikud.

Raietest suurim mõju metsaökosüsteemidele on lageraietel, mis toovad endaga kaasa kasvukoha muutumise süsinikku siduvast kooslusest C allikaks (Paul-Limoges et al., 2015). Raiejärgse metsaökosüsteemi arengu ning sellega kaasneva süsinikuringe dünaamika uurimine võimaldab hinnata ökosüsteemi taastumise ulatust ja kiirust ning seeläbi hinnata lageraiete mõju ka regionaalsel tasandil.

Lisaks uuendusraietele on ka harvendusraietel oluline mõju kogu metsaökosüsteemi arengule ja funktsioneerimisele. On ilmne, et produtseeriva biomassi vähendamine puurindes viib ka süsinikusidumise vähenemiseni teatud ajaperioodiks. Edasine süsiniku sidumise taastumine raie-eelsele tasemele sõltub aga paljudest teguritest, millest puuliik, kasvukoha viljakus ja raiekraad omavad suurimat mõju. Harvendamisega kaasnevad ka keskkonnatingimuste muutused puistus, sealhulgas mullatemperatuuri tõus, mis aga on peamine heterotroofset mullahingamist ja ühtlasi peamist C väljundvoogu mõjutav keskkonnategur puistus (Raich ja Schlesinger 1992; Peng ja Thomas 2006; Cheng et al., 2014; Kukumägi et al., 2017). Ka suureneb raiejärgselt surnud peenjuurte mass, selle lagunemine panustab veelgi heterotroofse mullahingamise intensiivistumisele. Seetõttu ongi hooldusraiete mõju selgitamisel puistute C sidumisele üheks oluliseks võtmeküsimuseks raiejärgse mullahingamise voo hindamine. Vähenenud C sidumine puude poolt ning samal ajal oluliselt suurenev C kadu läbi mullahingamise võivad viia kogu ökosüsteemi C bilansi ajutiselt negatiivseks, st raiejärgselt võib mets muutuda C allikaks.

Käesolev töö põhineb erinevates männikutes ja arukaasikutes läbi viidud süsinikuringe uuringutel:

Metsaökosüsteemi lageraiejärgset süsinikubilansi taastumist hinnati kuueaastase männinoorendiku põhjal (**I**),

Harvendusraiete lühiajalist mõju süsinikuringele hinnati lati- ja keskealistes arukaasikutes (**II**) ning männikutes (**III**).

Töö põhieesmärgid:

1. hinnata männinoorendiku netoproduktsiooni ja teiste ökosüsteemi komponentide rolli puistu süsinikubilansis 6 aastat peale lageraiet (**I**);

2. valideerida töös kasutatud süsinikubilansi meetodit samaaegsete mõõtmistega turbulentsete kovariatsioonide meetodil (**I**);

3. hinnata harvendusraie lühiealist mõju lati- ja keskealiste arukaasikute ning männikute süsinikubilansile (**II, III**).

Töös püstitati järgmised hüpoteesid:

1. Madala biomassi produktsiooni ja samaaegse intensiivse heterotroofse mullahingamise tõttu on kuueaastane männikultuur süsinikku emiteeriv ökosüsteem (**I**).

2. Ökosüsteemi süsinikuvoogude samaaegne hindamine bilansimeetodil ja turbulentsete kovariatsioonide meetodil annab sarnased tulemused, kinnitades bilansimeetodi sobivust metsa süsinikuringe uuringutes (**I**).

3. Harvendusraie järgne mullatemperatuuri tõus ja mulda jõudva surnud orgaanilise aine hulga suurenemine intensiivistavad mulla heterotroofse hingamise voogu, kuid vaatamata langenud primaarproduktsioonile ja suurenenud süsiniku emissioonile jäävad harvendatud puistud siiski süsinikku siduvateks ökosüsteemideks (**II; III**).

Metoodika

Katsealad

Käesolev töö põhineb viiel erineval katsealal, mis asuvad Tartu- ja Põlvamaal. Hariliku männi ökosüsteemi taastumist lageraie järgselt uuriti kuueaastases mustika kasvukohatüübi männinoorendikus. Kultuur rajati vahetult peale lageraiet külvi teel ja sellele eelnes maapinna ettevalmistamine ketasadraga. Lisaks tekkis rohkelt looduslikku männi uuendust, tagades puistu suure tiheduse (**I**, Tabel 1).

Harvendusraiete mõju metsa süsinikuringele uuriti männikutes (**III**, Tabel 1) ja arukaasikutes (**II**, Tabel 2). Mõlemal juhul oli uuringus üks latiealine ja üks keskealine puistu. Igasse puistusse rajati kaks proovitükki, millest ühel tehti harvendusraie alameetodil ning teine jäi kontrollalaks. Raied tehti keskmise raiekraadiga, väljaraie jäi vahemikku 17-31% puistu rinnaspindalast.

Puude maapealse biomassi ja produktsiooni hindamine

Puistu maapealset biomassi hinnati mudelpuude meetodil (**I**, **II**, **III**, Bormann and Gordon, 1984). Selleks langetati vegetatsioooniperioodi lõpus harvendusraie katsealadelt 5-7 ja männinoorendikust 7-9 mudelpuud, mis fraktsioneeriti. Suuremate puude tüved jagati sektsioonideks, mis kaaluti kohapeal ja igast sektsioonist lõigati analüüsiketas radiaaljuurdekasvude mõõtmiseks ning puidu ja koore osakaalu hindamaiseks. Erinevad fraktsioonid kaaluti, leiti nende kuivainesisaldus ning arvutati biomassid kuivaines (**I**, **II**, **III**).

Hooldusraiealadel leiti tüvepuidu aastased produktsioonid mõõdetud aastarõngaste põhjal, kasutades (Whittaker ja Woodwell, 1968) valemit (2)

$$W_i = W_0 (r^2 - (r - i)^2) / r^2 \qquad (2)$$

kus, W_i on aastane tüvepuidu kuivmassi juurdekasv (g), W_0 on tüvepuidu kuivmass (g), r on analüüsiketta raadius (mm), i on aastarõnga laius (mm).

Männinoorendikus mõõdeti puid kolmel järjestikusel aastal ning tüvemassi produktsioon arvutati järjestikuste aastate biomassi hinnangute vahena.

Alustaimestiku maapealse biomassi ja produktsiooni hindamine

Alustaimestiku maapealse biomassi ja selles seotud süsinikukoguse hindamiseks koguti uuritud puistutest proove kümnest juhuslikust punktist 0,5 m^2 suuruselt alalt. Juhuslikult maha asetatud raamis lõigati võimalikult maapinna lähedalt kõik rohttaimed ning puhmad. Proovid kuivatati, määrati nende kuivmass ja arvutati süsinikuvaru. Männikutes hinnati ka samblarinde biomass, selleks võeti proovid 25x25 cm suuruse metallraamiga taimeraami (0,5 m^2) seest.

Puhmaste ja sammalde maapealse osa produktsiooni hindamiseks eraldati neist osa taimi alamprooviks ja nendelt lõigati jooksva aasta juurdekasvud, mustikataimedelt ka lehed. Et rohttaimede maapealne biomass on üheaastane, siis loeti see ühtlasi aastaseks produktsiooniks.

Maa-aluse biomassi ja produktsiooni hindamine

Männinoorendikus kaevati puude maa-aluse biomassi hindamiseks välja 9 mudelpuu juurestikud, mis fraktsioneeriti (**I**). Vanemates puistutes kasutati jämejuurte ja kändude biomassi arvutatamiseks varasemate uuringute põhjal saadud maapealse ja maa-aluse osa suhtearvusid (Külla, 1997; Varik et al., 2015) (**II**, **III**). Jämedate juurefraktsioonide produktsioon leiti maapealse puitunud biomassi ja produktsiooni suhtena, st. eeldades, et puude maapealne ja maa-alune puitunud osa areneb proportsionaalselt.

Puude ja alustaimestiku peenjuurte biomassi hinnati mullamonoliitide meetodil *(soil coring method)* (**I**, **II**, **III**, Vogt et al., 1981; Persson, 1983; Ostonen et al., 2005). Puude peenjuurte produktsiooni hindamiseks kasutati männinoorendikus juurevõrkude meetodit *(nn. root mesh method)* (**I**, Hirano et al., 2009; Lukac and Godbold, 2010), kaasikutes aga järjestikuste mullamonoliitide meetodit (**II**, Vogt and Persson, 1991; Stober et al., 2000; Ostonen et al., 2005). Harvendusraie männi katsealadel leiti peenjuurte aastane produktsioon publitseeritud keskmise käibekiiruse (Brunner et al., 2013) ja empiiriliselt hinnatud peenjuurte biomassi põhjal (**III**).

Mullahingamine

Mullahingamise mõõtmiseks kasutati suletud dünaamilise kambri meetodit (SRC-1 kamber koos gaasianalüsaatoriga CIRAS-2 (Differential CO_2/H_2O Infrared Gas Analyzers)). Heterotroofse hingamise (Rh) ja kogu mullahingamise eraldi mõõtmiseks paigaldati igale katsealale 12 PVC toru läbimõõduga 20 cm ja pikkusega 50 cm. Süsiniku emissiooni mullast mõõdeti uuritavatel aladel igakuiselt kevadest-talveni, so. lumevabal perioodil.

Paralleelselt mullahingamise mõõtmisega mõõdeti samadest kohtadest ka mullatemperatuuri ja -niiskust. Mullatemperatuuri mõõdeti *ca* 5 cm sügavuselt CIRAS-2 juurde kuuluva sondiga STP-1 (PP Systems International, Inc., USA), ning mullaniiskust mõõdeti vahetult peale kambri eemaldamist, samuti *ca* 5 cm sügavuselt analüsaatoriga HH2 Moisture Meter 2 (Delta-T Devices Ltd, UK). Lisaks paigaldati igale alale mullatemperatuuri ja -niiskuse andurid koos andmelugejatega, mis salvestasid nimetatud mullaparameetrid iga tunni järel.

Süsinikubilanss

Süsinikubilansi koostamiseks hinnati uuritud puistutes peamised süsiniku sisend- ja väljundvood. Ökosüsteemi süsinikubilanss ehk aastane netoproduktsioon (3) (NEP) arvutati taimestiku primaarproduktsiooni

(NPP) ja heterotroofse hingamise (Rh) ning leostumise (L) vahena (Clark et al., 2001; Lovett et al., 2006; Meyer et al., 2013):

$$NEP=NPP-(Rh+L) \quad (3).$$

Käesolevas töös näitab positiivse väärtusega NEP süsiniku sidumist ökosüsteemi ning negatiivse väärtusega NEP näitab süsiniku kadu puistust, st süsinikku emiteerivat ökosüsteemi.

Statistilised meetodid

Analüüsitavate valimite normaaljaotust kontrolliti Lillieforsi ja Shapiro-Wilki testidega. Statistiliselt usaldusväärset erinevust uuritavate tunnuste keskmiste väärtuste vahel hinnati t-testi ja Mann Whitney U-testiga. Mudelpuude diameetri või kõrguse ja biomassi vaheliste seoste kirjeldamiseks kasutati allomeetrilisi mudeleid. Mudelite sobivust hinnati korrigeeritud determinatsioonikordaja (R^2) ja olulisuse tõenäosuse (p) alusel. Kõigil juhtudel kasutati olulisuse nivood 0,05. Statistiliste arvutuste tegemisel kasutati programme MS Excel, Minitab ja Statistica 7.0.

Harvenduse, mõõtmisaja (kuu) ja nende koosmõju mulla CO_2 voogudele, mullatemperatuurile ja -niiskusele hinnati korduvmõõtmistega dispersioonanalüüsil. Mullahingamise ja –temperatuuri vahelise seose iseloomustamiseks kasutati eksponentsiaalset võrrandit (4)

$$Rs \text{ (või Rh)} = ae^{bTs} \quad (4)$$

kus, Rs on kogu mullahingamine (µmol CO_2 m^{-2} s^{-1}), Rh on heterotroofne mullahingamine, a ja b on võrrandi koefitsiendid ja Ts on mulla temperatuur (°C) 5 cm sügavusel.

Keskkonnategurite ja mullahingamise vahelisi seoseid hinnati Pearsoni korrelatsioonanalüüsil ja osakorrelatsioonil. Juhul kui mullaniiskuse ja mullahingamise vaheline seos oli oluline, kasutati mitmest regressioonanalüüsi. Kumulatiivsete ja aastaste mullahingamise voogude arvutamiseks rakendati regressioonanalüüsi võrrandeid, milles kasutati ööpäeva keskmisi mullatemperatuuri ja -niiskuse väärtusi.

Tulemused ja arutelu

Metsaökosüsteemi süsiniku varud ja vood lageraiejärgses männinoorendikus

Lageraietel on ulatuslik mõju metsaökosüsteemi süsinikuvarudele ja voogudele, muutes kasvukoha lühiajaliselt süsinikku siduvast ökosüsteemist süsinikku emiteerivaks (Paul-Limoges et al., 2015). Käesolevas töös ületas kuueaastases männinoorendikus mulla süsiniku varu oluliselt taimede biomassis salvestatud C varu. Samas moodustas alustaimestiku aastane produktsioon suurema osa (57%) ökosüsteemi primaarproduktsioonist, kuna puude biomass selles vanuses on veel väike. Uuritud kuueaastane männik osutus süsiniku allikaks (NEP -1.37 t C ha^{-1} a^{-1}), seda peamiselt puurinde madala süsiniku sidumisvõime tõttu. Samas jäi heterotroofse mullahingamise voog samasse suurusjärku Eestis küpsetes männikutes ja kuusikutes hinnatuga (Kriiska et al., 2019; Kukumägi et al., 2017). Tulemused on kooskõlas Howard et al. (2004) poolt leituga, kus viieaastases halli männi noorendikus oli aastane mullahingamise voog väiksem, võrreldes vanuserea keskealise või küpse puistuga.

Lisaks bilansimeetodile mõõdeti uuritud noorendikus ökosüsteemi süsiniku sisend- ning väljundvooge ka turbulentsete kovariatsioonide meetodiga (EC), mis võimaldas valideerida bilansimeetodi tulemusi ning selle sobivust taoliste uuringute läbi viimiseks, kuna EC on kõrge täpsusega meetod atmosfääri ja ökosüsteemi vaheliste ainevoogude hindamiseks (Meyer et al., 2013; Baldocchi, 2014). Kahe erineva meetodiga saadud süsinikuvoogude hinnangud olid väga sarnased, EC meetodiga vastavalt -1.19 t C ha^{-1} a^{-1} ja bilansi meetodiga -1.37 t C ha^{-1} a^{-1}, mis kinnitab bilansimeetodi sobivust metsaökosüsteemide süsinikuringe uuringuteks.

Harvendusraie mõju metsaökosüsteemi süsiniku voogudele ja varudele

Harvendusraied mõjutavad lisaks puistu koosseisule ja kasvutingimustele ka selle süsinikuvoogusid ja -varusid. Peale harvendamist langeb puude biomassi vähenemise tulemusena ajutiselt puurinde ja ühtlasi ka kogu ökosüsteemi süsinikuvaru. Aga harvendamine muudab ka keskkonnatingimusi, eelkõige valgust ja temperatuurirežiimi puistus, mis toob endaga kaasa muutusi ökosüsteemi funktsioneerimisel ja süsiniku sidumisel.

Arukaasikud

Teisel harvendusraie järgsel aastal oli uuritud arukaasikutes süsiniku varu 6% - 10% väiksem kui harvendamata aladel. Latiealine ja keskealine harvendatud puistu sidusid teisel raiejärgsel aastal 3,8 ja 4,4 t C ha^{-1} a^{-1}, samal ajal kui harvendamata alad sidusid vastavalt 5,3 ja 5,6 t C ha^{-1} a^{-1}. Ökosüsteemi netoproduktsioon (NEP) oli harvendatud proovitükkidel 20-30% madalam kui kontrollaladel, samas jäid kõik uuritud puistud siiski süsinikku siduvateks ökosüsteemideks. Harvendusraie järgselt langes puistute primaarproduktsioon 8-10%, vähendades ökosüsteemi süsiniku sidumist. Harvendusraied ei intensiivistanud peamist süsiniku väljundvoogu, so mulla heterotroofset hingamist. Puistu produktsiooni vähenemist leevendas vähesel määral alustaimestiku suurem biomass harvendatud aladel: teisel raiejärgsel aastal oli uuritud arukaasikutes rohttaimede produktsioon usaldusväärselt suurem kui harvendamata aladel. Samas ei katnud rohttaimede produktiivsuse tõus väljaraiest tingitud puistu C sidumise vähenemist, mis latiealises kaasikus vähenes 1,1 t C ha a^{-1}, samas kui rohttaimede produktsioon oli vaid 0,2 t C ha a^{-1} suurem kui harvendatud alal. Keskealises kaasikus oli vastav suhe 1,3 ja 0,3 t C ha a^{-1}.

Männikud

Männikutes oli kaks aastat peale harvendamist süsiniku varu 12-17% väiksem kui kontrollaladel. Harvendatud puistud sidusid 1,5 ja 2,5 t C ha^{-1} a^{-1}, samal ajal kui süsiniku sidumine kontrollaladel oli vastavalt 2,3 ja 3,2 t C ha^{-1} a^{-1}. Männikutes vähenes süsiniku sidumine raiejärgselt 22-37%, kuid sarnaselt arukaasikutega, jäid ka männikud peale harvendamist süsinikku siduvateks ökosüsteemideks. Samuti oli ka männikute puhul süsiniku sidumise langus tingitud madalamast primaarproduktsioonist, aga mitte süsiniku emissiooni suurenemisest. Puistu primaarproduktsiooni langus oli omakorda tingitud väiksemast puistu tagavarast ja sellest, et allesjäänud puud ei ole teisel raiejärgsel aastal veel jõudnud reageerida harvendamisega muudetud kasvutingimustele ja vähenenud konkurentsile. Sarnaselt arukaasikutega suurenes raiejärgselt rohttaimede produktsioon ka männikutes, kuid alustaimestikus domineerivad samblad ja puhmad polnud teiseks raiejärgseks aastaks veel jõudnud reageerida muutunud kasvutingimustele.

Kokkuvõte

Doktoritöös hinnati konventsionaalse metsamajandamise mõju erinevatele süsiniku (C) voogudele ja varudele arukase ja hariliku männi metsaökosüsteemides. Kuueaastane männinoorendik osutus mõõdukaks süsiniku emiteerijaks (NEP -1.37 t C ha^{-1} a^{-1}), seda peamiselt puurinde madala biomassi ja produktsiooni tõttu. Atmosfääri ja metsaökosüsteemi vahelist süsinikuvahetust iseloomustevad tulemused (NEP ja NEE) olid mõlema kasutatud meetodi puhul lähedased: vastavalt -1.37 ja -1.19 t C ha^{-1} a^{-1} süsiniku bilansi ja turbulentsete kovariatsioonide meetodi puhul, mis kinnitab süsinikubilansi meetodi usaldusväärsust metsade süsinikuringe uuringutes.

Harvendusraied ei suurendanud mulla heterotroofse hingamise voogu teisel raiejärgsel aastal arukaasikutes ega männikutes. Ootuspäraselt vähenes peale harvendusraiet puistu maapealne süsiniku varu ja puurinde süsiniku sidumise võime, samas jäid kõik uuritud puistud süsinikku siduvateks ökosüsteemideks.

Metsanduslikud hinnangud ja soovitused

Käesolevas doktoritöös selgitati olulisemate raieviiside lühiajalist mõju metsaökosüsteemide süsinikuringele. Selgus, et lageraie järgselt ei olnud uuritud männinoorendikus mulla heterotroofne hingamine oluliselt suurem vanemates puistutes mõõdetust, mis näitab, et ökosüsteemi negatiivne bilanss oli tingitud puistu madalast produktiivsusest. Puude tagasihoidlik juurdekasv aga omakorda puude väikestest mõõtmetest. Seega sõltub metsaökosüsteemi lageraie järgne süsiniku sidumise taastumine otseselt õigeaegsest ja kvaliteetsest metsauuendamisest. Mida kiiremini ala taasmetsastub, seda varem muutub noor metsapõlvkond süsinikku siduvaks.

Käesolevas töös uuritud puistuid harvendati alameetodil ja mõõduka raiekraadiga, mistõttu vähenes lühiajaliselt küll puistute süsiniku tagavara ja puurinde süsiniku sidumise võime, kuid raied ei intensiivistanud mulla heterotroofset hingamist ega muutnud ökosüsteemi süsinikubilanssi negatiivseks. Seetõttu on süsinikuringe seisukohast soovitatav teostada hooldusraieid alameetodil ja mõõduka raiekraadiga, et raiejärgselt ei muutuks puistud ajutiselt süsinikku emiteerivateks ökosüsteemideks.

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The carbon balance of a six-year-old Scots pine (*Pinus sylvestris* L.) ecosystem estimated by different methods

Veiko Uri[a,*], Mai Kukumägi[b], Jürgen Aosaar[a], Mats Varik[a], Hardo Becker[a], Kristiina Aun[a], Alisa Krasnova[a,b], Gunnar Morozov[a], Ivika Ostonen[b], Ülo Mander[b], Krista Lõhmus[b], Katrin Rosenvald[b], Kaie Kriiska[b], Kaido Soosaar[b]

[a] *Estonian University of Life Sciences, Institute of Forestry and Rural Engineering, Kreutzwaldi 5, 51014 Tartu, Estonia*
[b] *University of Tartu, Institute of Ecology and Earth Sciences, Vanemuise 46, 51014 Tartu, Estonia*

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ABSTRACT

Clear-cutting is a conventional method of forest management which significantly changes carbon (C) cycling at the ecosystem level for a long time. Estimation of the interim period during which the ecosystem turns from a C source to a C sink is crucial for clarifying the environmental effects of management on forest C cycling. The current study provided new knowledge of C cycling in young pine stand and demonstrated the recovery of C sequestration of the forest ecosystem during the post harvesting period.

We estimated the C balance in a 6-year-old Scots pine stand by using two different methods: carbon budgeting, for estimating annual net ecosystem production (NEP), and eddy covariance (EC), for estimating net ecosystem exchange (NEE). For C budgeting, the above- and belowground biomass production of the ecosystem, as well as the soil heterotrophic respiration efflux at the studied site was estimated.

Annual NEE at the studied young forest ecosystem was 1.19 ± 0.36 t C ha^{-1}, gross primary ecosystem production was 9.87 and total ecosystem respiration was 11.06 t C ha^{-1}. Estimated NEE was in good accordance with the results of NEP (1.37 t C ha^{-1}), which confirms the relevance of the C budgeting method.

Increased annual woody biomass production is the main factor which induced the young Scots pine ecosystem to act as a C sink: annual C accumulation in tree biomass in a 6-year-old stand was 1.0 t C ha^{-1} but reached already 2.4 t C ha^{-1} in the following year. Assuming that the annual R_h flux is of the same magnitude in the subsequent years, the ecosystem will become a C sink already during a short period after clear-cut. Annual soil respiration (R_s) and heterotrophic soil respiration (R_h) were 6.0 and 4.2 t C ha^{-1}, respectively and the R_h/R_s ratio was 0.70. However, at this stage also the understorey vegetation contributed essentially to NEP, making up 56% of the annual C uptake accumulated in the plants. The methane flux and the leached C flux were negligible, 0.004 and 0.015 t C ha^{-1} yr^{-1}, respectively. Our results demonstrate that well regenerated young Scots pine stand on a former clear-cut area will be able to turn into a C sequestering ecosystem already before ten years after cutting.

1. Introduction

During recent decades, the concentration of atmospheric carbon dioxide (CO_2) has rapidly increased inducing climate change. According to the Paris Agreement (2015), governments should significantly reduce carbon (C) emission and increase the share of bioenergy in the nearest future (UNFCCC eHandbook). In this aspect, it is essential to focus on forest ecosystems at the global and regional scales since forests mitigate climate change (Schimel et al., 2001) by accumulating carbon (C) in plant biomass as well as in soil (Cannell, 1999; Mund et al., 2002; Pussinen et al., 2002; Ågren and Hyvonen, 2003; Laiho et al., 2003). In general, boreal and hemiboreal forests have been reported as ecosystems with high C sink capacity (Dixon et al., 1994; Valentini et al., 2000; Liski et al., 2002, 2003; Gough et al., 2008).

As changes in the C stocks may affect the balance between terrestrial and atmospheric C (Keith et al., 2009), clarification of C budgets at the ecosystem level is essential for understanding the driving forces behind the C cycle and sequestration capacity (Fang et al., 2007) which is very variable due to the high heterogeneity of different forest ecosystems.

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[*] Corresponding author.
E-mail address: veiko.uri@emu.ee (V. Uri).

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Forest management has a great impact on the functioning of forest ecosystems, as well as on their C sequestration capacity. To provide foresters and policymakers with adequate information, the efficiency of forest management should be improved in order to attain more effective C sequestration. Among the different management activities, it is important to clarify the effect of forest harvesting on C dynamics. Clear-cut is a widely used conventional forest management method, which changes C cycling at the ecosystem level to a great extent for a long period. Although forest ecosystems act mainly as C sinks, the situation changes drastically after harvesting; clear-cuts turn a site to a C emitting system due to removed photosynthetically active biomass as well as intensified heterotrophic soil respiration (R_h). Higher R_h may be evoked by altered environmental conditions such as increased soil temperature and moisture, which in turn may favour decomposition of logging residues (Pumpanen et al., 2004).

Estimation of C cycling during the post-harvest period is crucial for understanding the recovery dynamics of the forest ecosystem, which can be highly variable depending on many factors (climate, site fertility, tree species etc). In managed forests, balancing of the C fluxes after harvest to preharvest level may take 10(15) years (Amiro et al., 2010; Goulden et al., 2011), or even longer (Noormets et al., 2012).

To study C cycling in forest ecosystems, the C budgeting method is often used. However, also eddy covariance (EC) is becoming a widely used approach in forest science to directly measure net ecosystem exchange (NEE), as well as to examine changes in the C fluxes and stocks in several forest ecosystems (Kolari et al., 2004; Meyer et al., 2013; Aguilos et al., 2014). The EC method has emerged as one of the most reliable measurement techniques for quantifying NEE in terrestrial ecosystems (Peichl et al., 2010). Both methods have specific advantages and disadvantages, but their combination has given more sophisticated and reliable results (Kolari et al., 2004; Peichl et al., 2010; Goulden et al., 2011; Meyer et al., 2013; Aguilos et al., 2014).

The current case study was carried out in a 6-year-old Scots pine (*Pinus sylvestris*) stand growing on poor sandy soil, which is a very typical site for pine stands in the Nordic and Baltic regions. Scots pine has a wide natural distribution area on the Eurasian continent. In Estonia, it is one of the most important species in terms of forest management, accounting for approximately 32% of the total area of Estonian forests (Yearbook Forest, 2016).

We hypothesised that the studied 6-year-old Scots pine forest is a C emitting ecosystem because of its still low annual biomass production and intensive soil heterotrophic respiration.

To test this hypothesis, we estimated the annual net ecosystem production (NEP) of the young Scots pine stand by using C budgeting and simultaneously estimated NEE by using the EC method. To compile the C budget, we estimated the above- and belowground biomass and production of the ecosystem, as well as the soil heterotrophic respiration efflux at the studied site. The specific aim was to estimate the post-harvest C compensation point, i.e. the age of the stand when the studied ecosystem will turn from a C source to a C sink.

2. Material and methods

2.1. Site description

The study site is located in the southeastern part of Estonia, Tartu county (58°17′01.0″ N 27°09′43.0″ E). The total area of the regenerated clear-cut was 2.1 ha. The clear-cut of the previous forest generation (100-year-old pine stand) was carried out in early 2009; in the late autumn of the same year, the soil was scarified with a disc trencher. In spring 2010, the area was regenerated by sowing. Also natural generation contributed markedly to sowing since the seed trees of pine were left in the clear-cut and the area borders on mature pine stands. Regeneration was very successful as the stand's density was roughly as high as 15,000 trees per ha, the average height (± st. deviation) of the trees was 0.94 ± 0.34 m at the beginning of the vegetation period of 2016. There were no other tree species in the stand because in 2011 and 2014 this area was tended and all individuals of the other tree species were removed, which is common forestry management practice in Estonia. All field works at the study site were carried out from spring 2015 to late autumn 2017.

2.2. Soil

In the studied area, six soil pits (depth 1.0 m) were dug in 2016; the soil profile was described and the soil type was determined according to the IUSS Working Group WRB (2006). Soil texture was sand and soil type was *Gleyic Folic Podzol*. According to the Estonian classification, the area belonged to the ***Myrtillus*** site type (Lõhmus, 1984). The thickness of the E-horizon and of the organic soil horizon varied across the study area.

For estimation of the C storage in the organic soil horizon (forest floor), samples from 10 random points over the area were taken with a soil corer (Ø 108 mm). The cutting edge of the soil corer was sharpened and the internal diameter of the upper part of the auger was 2 mm larger than the diameter of the cutting edge to avoid compression of the organic layer. The formed monolith of the organic layer was divided into the O_1 and O_2 horizons according to degree of decomposition. The thickness of all layers was measured in forest and all samples were packed into plastic bags and transported to the laboratory where they were dried to constant weight at 70 °C and weighed. The content of C, nutrients and ash in the O_1 and O_2 layers was analysed from composite samples (Table 1). For calculating the mass of the forest floor and nutrient storage for the whole horizon, the dry weight of the soil was

Table 1
Main soil characteristics of the study area: C% – organic carbon content, N – Kjeldahl nitrogen, P – available (AL) phosphorus, K – available (AL) potassium, Ca – available calcium and Mg – available magnesium. Average ± standard errors are presented.

	Organic layer	Mineral layers			
	Soil depth layer, cm				
	0–10	10–20	20–30	30–40	40–50
N, %	1.27 ± 0.02	0.08 ± 0.02	0.04 ± 0.01	0.04 ± 0.01	0.03 ± 0.005
N storage, t ha^{-1}	2.41	0.92	0.52	0.49	0.37
P, mg kg^{-1}	41.4 ± 7.33	11.1 ± 1.91	4.8 ± 1.63	3.7 ± 1.42	1.0 ± 0.33
K, mg kg^{-1}	152.1 ± 24.59	15.7 ± 2.46	6.0 ± 0.33	7.7 ± 0.38	6.5 ± 0.42
Mg, mg kg^{-1}	89.5 ± 10.31	11.5 ± 2.56	2.8 ± 0.69	1.6 ± 0.34	1.3 ± 0.24
Ca, mg kg^{-1}	326.8 ± 22.38	89.8 ± 4.27	55.2 ± 5.40	56.2 ± 6.04	50.9 ± 5.55
C, %	32.40 ± 0.13	2.37 ± 0.38	0.90 ± 0.14	0.92 ± 0.12	0.64 ± 0.09
C storage, t ha^{-1}	44.79	27.04	11.84	12.99	8.99
pH	2.72 ± 0.12	3.18 ± 0.22	3.60 ± 0.27	4.09 ± 0.23	4.22 ± 0.19
Bulk density, g cm^{-3}	0.18 ± 0.04	1.14 ± 0.08	1.31 ± 0.06	1.41 ± 0.06	1.12 ± 0.05

corrected by taking ash content into account.

For estimation of the soil C and nutrient pools in the mineral layer, samples from twelve random points over the study area were taken from different depths with a soil corer to form a composite sample for chemical analyses (Table 1). The content of C and nutrients was analysed in three replicates for each depth layer. For calculation of the C and N storages in the soil, its bulk density was also determined. From every soil pit, bulk density samples were taken from different soil mineral layers (0–50 cm) using a stainless steel cylinder (Ø 40 mm; $V = 50\,cm^3$), to avoid compression of the soil and to preserve soil structure (Uri et al., 2014). In the laboratory, the samples were dried to constant weight at 105 °C and weighed.

2.3. Estimation of biomass and production

2.3.1. Aboveground biomass and production of the trees

The aboveground biomass and the annual production of the trees were estimated in October 2015, 2016 and 2017 when the process of biomass formation was completed; the method of model trees (Uri et al., 2012, 2017b) was used. For this, four randomly situated round sample plots ($25\,m^2$) were established in the study area and tree height as well as annual height increment of all trees were measured.

The measured trees were divided into five classes by height, and a model tree was selected randomly from each class. Seven model trees were felled in 2015 and 9 model trees were felled in 2016. In 2017, all trees in the sample plots were measured and the different biomass fractions were calculated by using elaborated models (Table 2).

The model trees were divided into the following fractions: stems, branches, current-year shoots and needles. The needles, in turn, were divided into the current-year needles (from current-year shoots) and the needles from the older branches. From every fraction, a subsample was taken for determination of dry matter and C content. The subsamples of the fractions were dried at 70 °C until constant weight and weighed to 0.01 g. The dry mass of the different fractions was calculated for each model tree by multiplying corresponding fresh mass by the dry matter ratio (Uri et al., 2012, 2017a,b).

For estimating the total aboveground biomass of the stand as well as the biomass of different biomass fractions the allometric Eq. (1) provided the best fit:

$$y = aH^b \quad (1)$$

where y is the total aboveground biomass and the biomass of the separate compartments of a model tree (stem, branches, needles; (g)), H is tree height (m), a and b are parameters (Table 2).

For reducing estimation error, which caused by variability of the trees, as well as to attain a better regression model of the total aboveground biomass and of the stem mass of the trees, the data of the model trees for 2015 and 2016 were pooled. On the basis of the allometric models, total aboveground tree biomass, as well as the mass of the different fractions for 2015–2017 were calculated.

The annual production of stem mass (wood and bark) and branch mass was calculated as the difference between the masses of the respective fractions for the two consecutive years. The production of the current year shoots was equal with their biomass. The biomass of the current year needles was considered as the annual production of the needles. The current year production of shoots and needles was calculated by using the data of the model trees for 2016.

Table 2
Parameter estimates (a, b) of regression Eq. (1) for estimation of total aboveground tree biomass and of the mass of the different biomass fractions of the young pine stand. R^2-coefficient of determination; $P < 0.001$ in all cases.

Fraction	a	b	R^2
Total aboveground	88.15	3.12	0.90
Stems	33.19	3.20	0.95
Branches	10.77	3.80	0.82
Current year shoots[a]	3.89	4.05	0.94
Current year needles[a]	11.06	3.92	0.85
Needles	20.10	3.43	0.83
Coarse roots	14.22	2.73	0.94

[a] 2016 model trees data.

2.3.2. Coarse root biomass and production of the trees

Excavation of the root system of the model trees was used for estimation of coarse root biomass. In 2016, nine model trees were felled according to diameter distribution and the root systems of all model trees were manually excavated as described in our earlier studies (Uri et al., 2002; Varik et al., 2013). All excavated root systems were washed free of soil, placed in plastic bags and separated in the laboratory into two fractions: the roots ($d > 2$ mm) and the stump core. As the share of fine roots ($d < 2$ mm) was small, the excavation data were not used for fine root biomass estimation. From both coarse root fractions, a subsample was taken for determination of C%. The fractions were dried at 70 °C until constant weight and weighed to 0.1 g. The biomass of the coarse root fraction of the young pine trees for all studied years (2015–2017) was estimated using allometric relationship (1) (Table 2). Annual coarse root production was calculated as the difference in biomasses in the studied and the preceding year.

2.3.3. Biomass and production of the understorey plants

For estimation of the aboveground biomass of the understorey (herbaceous plants and dwarf shrubs), ten random samples over the whole study area were taken at the end of July 2016 when plant growth was assumed to be at a maximum. The aboveground part of all ground vegetation was harvested and collected from a $0.5\,m^2$ quadrat. Additionally, for estimation of the biomass of mosses, a metal frame (25 × 25 cm) was placed randomly in the quadrat and all mosses within the frame were collected. All samples were transported to the laboratory and weighed to 0.1 g. For estimation of dry matter content and C%, subsamples were taken, dried in the laboratory at 70 °C to constant weight and weighed to 0.01 g. For estimation of the production of the dwarf shrubs (*Calluna*, *Myrtillus*, etc.), subsamples were taken and the current-year growth (shoots, leaves) was separated and considered as annual production. As the aboveground part of the herbs is annual, aboveground production was assumed to be equal to biomass. The annual biomass production of the mosses was determined by separating the shoot increment of the current-year for different moss species (mainly the most abundant *Hylocomium splendens* and *Pleurozium schreberi*) under a binocular microscope. The annual production of moss biomass at the ecosystem level was calculated by using the average share (%) of annual increment in the total biomass of the mosses.

2.3.4. Fine root biomass and production of the trees and understorey plants

The fine root ($d < 2$ mm) biomass (FRB) of the trees and dwarf shrubs was estimated by using the soil coring method. Twenty soil cores were taken randomly all over the study site with a cylindrical soil auger in autumn 2016. To avoid compression of the soil layers, the internal diameter of the upper part of the auger was 1.6 mm larger than the diameter of the cutting edge (Ø 38 mm) (Uri et al., 2002, 2017a,b). The soil cores were divided into four depth layers (0–10, 10–20, 20–30 and 30–40 cm), placed in polyethylene bags and stored in a refrigerator at −5 °C until processing. The fine roots of the pines, as well as the roots of the understorey plants, were separated from the washed-out samples under a binocular microscope. The samples were dried up to 70 °C and weighed to 0.001 g. The soil core data were used for estimation of FRB per hectare, summing up the average values for the successive soil core layers.

Fine root production (FRP) was estimated by using the root mesh (root inclusion net) method (Hirano et al., 2009; Lukac and Godbold, 2010; Uri et al., 2017a,b). In the studied stand, vertical nylon meshes (mesh size 1.5 mm, width 7 cm and length 20 cm) were inserted in the soil in autumn 2015. The first 25 samples were taken one year after installation, i.e. in October 2016. Using a spade, a soil block with a height of 20 cm and with its edges at about 10 cm from both sides of the net was carefully extracted from the soil, placed in a plastic box, packed in a polyethylene bag and transported to the laboratory. To extract the nets, the soil was cut at 1 cm beyond a net with a long-blade sharp knife. The fine roots and rhizomes penetrating the net were washed out and carefully removed. The roots were placed in Petri dishes in water and were sorted into the living roots of the trees and into the roots and rhizomes of the dwarf shrubs and herbaceous plants. The separated roots were dried at 70 °C and weighed.

Fine root turnover rate (yr^{-1}) was calculated by dividing FRP ($g\,m^{-2}\,yr^{-1}$) by mean FRB ($g\,m^{-2}$) according to McClaugherty et al. (1982). Fine root longevity (yr) was calculated as the reciprocal of root turnover rate. Since the root mesh method enables to estimate FRP only for the upper 0–20 cm soil layer, we calculated FRP for the deeper (20–40 cm) soil layer multiplying FRB by topsoil fine root turnover rate.

2.4. Soil respiration measurements

Total soil respiration (R_s) and heterotrophic respiration (R_h) rates (μmol CO_2 $m^{-2}\,s^{-1}$) were measured once a month from April to December 2016, using the manual closed dynamic chamber method (PP *Systems* SRC-1 chamber (volume 1170 cm^3, enclosed soil surface area 78 cm^2), with a gas analyser CIRAS-2 (Differential CO_2/H_2O Infrared Gas Analyzers)). To distinguish R_h from R_s, the trenching method with insertion of deep PVC cylinders (Ø 20 cm, height 50 cm) to a depth of 40–45 cm was applied in October 2015. The deep PVC cylinders were installed randomly across the study plot. The herbaceous vegetation was carefully removed from the inside of the trench with minimum soil disturbance and the trenched plots were kept free of the living vegetation throughout the measurement period. Close (~40 cm) to each deep PVC cylinder (trenched), PVC collars (Ø 10 cm, height 5 cm) for R_s measurement were installed at a depth of 3 cm. Ten R_s and R_h measurements were made during each visit to the study site.

Soil temperature (T_s, °C) and soil moisture (%) were measured both discretely and continuously. Discrete T_s measurements at a depth of 5 cm were made simultaneously with R_s and R_h measurements using a soil temperature probe STP-1 (PP Systems International, Inc., USA) attached to a manual chamber system. Discrete volumetric water content (%) was measured after each soil respiration measurement at a depth of 5 cm using a HH2 Moisture Meter Version 2 (Delta-T Devices Ltd, UK). Soil temperature (soil external temperature sensor, WatchDog Technologies, Inc, USA) and volumetric water content (%) (Water Scout sensor model SM 100, Technologies, Inc, USA) were measured continuously every hour from April 2016 to March 2017 and the data was stored with a data logger (WatchDog 1425, Spectrum Technologies, Inc, USA).

To characterize the diurnal dynamics of R_s during the growing season (May-October) two automated soil respiration stations were placed ~ 10 m away from the EC tower. An automatic CO_2 exchange system ACE (Automated CO_2 exchange station, ADC BioScientific Ltd., UK) was equipped with a soil chamber, an infra-red gas analyser (IRGA), a sensor for detecting photosynthetic active radiation and a soil temperature sensor. The soil chamber with a volume of 2.6 L was equipped a small fan for mixing the air. Also a stainless steel collar for the soil chamber was inserted into the soil at a depth of 3–4 cm. The ACE station was operated in a closed mode with zero option. The time between the start of measurements was 60 min. The end of each log record had an eight-character label which contained information about the assay. Measurements with errors in their log record were excluded from data analysis.

2.5. Methane measurements

The in situ measurements of the methane (CH_4) efflux from the soil were carried out twice a month from May 2016 to April 2017 using the manual static chamber method (Hutchinson and Livingston, 1993). Gas chambers (65 L opaque static chambers with a truncated conical shape, height 40 cm, Ø 50 cm, volume 65 L, sealed with a water-filled ring on soil surface, painted white to avoid heating during application) were used in five replicates (Mander et al., 2012). Gas samples were drawn in pre-evacuated (0.3 mbar) 100 ml bottles from the chamber headspace. Four samples from each chamber were collected within one hour at 20-minute intervals. The air samples were analysed in the laboratory of the Institute of Technology at the University of Tartu using the Shimadzu GC-2014 gas chromatography system (Soosaar et al., 2011; Hansen et al., 2013). Gas concentration in collected air was determined by ECD and FID detectors modified according to Loftfield et al. (1997). The emission rate of trace gas was calculated, using the slope of linear regression between gas concentration and time, and corrected for the area and volume of the chamber.

2.6. Carbon leaching

The C leaching was estimated by using 6 plate lysimeters (stainless steel; collecting area 627 cm^2) which were randomly installed in the soil at a depth of 40 cm in the studied stand in April 2016. Polyethylene tubes connected the lysimeters to water collectors (6000 ml polyethylene canisters disposed at a depth of 1 m). Water from the canisters was sampled monthly from June 2016 to December 2017, through a plastic pipe, using a peristaltic vacuum pump. The annual leaching of C was calculated by summing the leached fluxes of the different months, taking account of the corresponding C concentrations from percolated water (Becker et al., 2016; Uri et al., 2017b).

2.7. Carbon budgeting

The C budget for the studied site was compiled by balancing the data of the input and output fluxes of C for the 6-year-old stand (2016). We used a well-known approach for defining net ecosystem production (NEP), which is the difference between net primary production (NPP) and loss of C through heterotrophic respiration (R_h) and leaching (L) (Clark et al., 2001; Lovett et al., 2006; Meyer et al., 2013):

$$NEP = NPP - (Rh + L) \tag{2}$$

NEP represents the rate at which C is accumulated in the ecosystem, and is the main parameter characterizing forest as a C sink or as a C source (Chapin et al., 2006; Waring and Running, 2007). NPP was calculated by summing the annual increments of the aboveground ecosystem compartments (trees, understorey plants) and the annual increments of the belowground ecosystem compartments (tree coarse root system, fine roots, roots and rhizomes of the understorey). Further, in the C budget we considered the fluxes from and into the atmosphere. Thus, in present study a positive value of NEP indicates the net transfer of C from forest to the atmosphere when the ecosystem is a C source. A negative value of NEP indicates the net transfer of C from the atmosphere to forest when the ecosystem acts as a C sink.

2.8. Eddy covariance measurements

Continuous measurements of net ecosystem exchange (NEE) were carried out from April 2016 to April 2017 using the eddy covariance (EC) technique. The measurement system was installed in the tower at 4.35 m from ground, 2 m above the ecosystem canopy (maximum tree height 2.4 m). The tower was established in the middle of the clear-cut and the footprint covered most of the studied area (Fig. 1). CO_2 and H_2O concentrations were measured from surrounding air by an enclosed path infrared gas analyser LI-7200 (LI-COR Biosciences, Lincoln, NE, USA). Three wind velocity components and sonic temperature were measured with a Gill HS-50 sonic anemometer (Gill Instruments, Lymington, UK). The measurements were performed at a frequency of

Fig. 1. Footprint area of the study site (using the model by Kljun et al., 2004). Thinner lines and corresponding numbers represent the distances from the tower in metres and direction in degrees from the north. Thick solid lines are the cumulative footprint (1%, 10%, 30%, 50%, 70%, 90%) distances. Dashed line denotes the peak contributing distance. The road in the footprint area has a low traffic load.

10 Hz.

The half-average fluxes of CO_2 were calculated using the EddyPro v6 software (LI-COR Biosciences, Lincoln, NE, USA) as the covariance between CO_2 concentration and vertical wind speed. The data processing steps included raw data filtering and despiking (Vickers and Mahrt, 1997), 2D coordinate rotation, block-averaging, time lag optimisation, and low and high-frequency spectral corrections (Moncrieff et al., 1997, 2005). NEE was estimated for every half-hour period as the sum of the CO_2 flux and the CO_2 storage calculated with the discrete approach. The storage term was calculated using the half-hourly change of CO_2 concentration measured with the eddy system assuming the uniform distribution of CO_2 in the air column under the measurement point (Hollinger et al., 1994).

Single outstanding physically impossible NEE values ($> 80\ \mu mol\ m^{-2}\ s^{-1}$) were removed from analysis. Friction velocity filtering was applied to the night-time ($Rg < 5\ W\ m^{-2}$) data. The threshold value ($0.05–0.07\ ms^{-1}$) was determined following the method of Reichstein et al. (2005). Data coverage for the measurement period after the filtering procedures was 74%. Following the convention, negative NEE values were considered as CO_2 uptake and positive values represented CO_2 release for the ecosystem.

To estimate the budget sums for the measurement period, gap-filling was performed with the lookup tables method (Reichstein et al., 2005) using the Reddy ProcWeb online tool (http://www.bgc-jena.mpg.de/bgi/index.php/Services/REddyProcWeb). Total uncertainty ($u_{t.y}$) was calculated following Jensen et al. (2017):

$$u_{t.y} = \sqrt{\sum_{i=1}^{N-G} (u_{r.hh})^2 + \sum_{i=1}^{G} (u_{g.hh})^2} \tag{3}$$

where $u_{r.hh}$ is the random uncertainty related to sampling error, estimated for every half an hour as the variance of covariance between CO_2 concentration and vertical wind speed (Finkelstein and Sims, 2001); $u_{g.hh}$ is random uncertainty due to gap-filling, estimated for every half-hour as the standard deviation of the data points used for gap-filling; N is the total number of half-hourly flux values during the summation period; G is the number of gap-filled half-hourly flux values for the same period.

Partitioning of NEE into two oppositely directed components (gross primary production (GPP), and ecosystem respiration (R_{eco})) was performed in the Reddy ProcWeb online tool with a nighttime based flux-partitioning algorithm (Reichstein et al., 2005). The regression model (Lloyd and Taylor, 1994) was fitted to the relationship between the data of nighttime NEE (assumed to be equal to nighttime R_{eco} as there is no photosynthesis in absence of solar radiation) and air temperature. The obtained parameters were used to estimate daytime R_{eco}. Daytime GPP was calculated as the difference between NEE and R_{eco}.

In order to assess the possible influence of forested parts of the footprint area on the estimation of clear-cut carbon balance, we split daytime NEE into two sectors according to the direction of the wind: the data for 230 to 310° from the north and for 40 to 130° from the north was attributed to the "Forest" sector; the data for 310 to 40° from the north and 130 and 230° from the north was considered the "Clear-cut" sector. Each of the two sectors were then split further into four 2 °C air temperature classes, 14 °C to 22 °C (based on data availability and assuming the air temperatures to be most favourable for plant carbon assimilation). For each class, light response curves were obtained using the Michaelis-Menten model (4):

$$NEE = \frac{\alpha \cdot GPP_{max} \cdot PAR}{\alpha \cdot PAR \cdot GPP_{max}} + RE \tag{4}$$

where the fitted parameters are light use efficiency (α), light-saturated gross C uptake (GPP_{max}) and daytime respiration (RE). NEE is daytime net ecosystem exchange and PAR is photosynthetically active radiation.

2.9. Chemical analysis

From every biomass fraction (needles, current-year shoots, older branches, stem wood and stem bark) of the model trees, as well as from the understorey plants, subsamples were taken for estimation of C concentration. To analyse the plant material for C content (%) and for soil C_{org} in the oven-dried samples, the dry combustion method was used with a varioMAX CNS elemental analyser (ELEMENTAR, Germany). For analysing N (Kjeldahl) in the soil samples, the Tecator ASN 3313 was employed. Available phosphorus was determined by flow injection analysis with the use of the Tecator ASTN 9/84 and the content of available potassium was determined from the same solution by the flame photometric method. Soil magnesium content was determined by flow injection analysis with the Tecator ASTN 90/92 and calcium content was determined from the same solution by the flame photometric method. The analyses were carried out at the Biochemistry Laboratory of the Estonian University of Life Sciences. Water samples were analysed for total organic carbon (TOC) at the Laboratory of the Estonian Environmental Research Ltd using standard methods for water research (APHA 1989).

2.10. Statistical methods

The normality of variables was checked by the Lilliefors and Shapiro-Wilk tests. The Tukey HSD test was employed to perform multiple post hoc comparisons between mean C concentrations for different tree compartments. Allometric regression models were employed for estimating relationships between model tree biomass fractions and height. The quality of the fit of the models was evaluated by the coefficient of determination (R^2) and the level of probability (P). For estimation of the confidence limits for aboveground biomass values, the bootstrapping procedure (Aho, 2014) was used for the measured trees. To test the effect of soil moisture on R_s (or R_h), a multiplelinear regression, where temperature and moisture were the two independent variables, was conducted. Soil moisture had no significant effect on soil respiration rates. Thus, an exponential model (5) was used to describe the relationship between R_s (or R_h) and soil temperature at a depth of 5 cm:

$$R_S(or\ R_h) = ae^{bTs} \tag{5}$$

where a and b are fitted parameters, and T_s is soil temperature (°C).

First, model (5) was applied for discrete measurements (April-December 2016) and the annual R_s and R_h fluxes (April 2016-March 2017) were then modelled using the daily mean T_s values from the data loggers. Finally, the soil respiration fluxes were converted from μmol CO_2 $m^{-2} s^{-1}$ to t C $ha^{-1} yr^{-1}$.

The *t*-test was used to identify significant differences in T_s and soil moisture between the control and the trenched plots. Trenching did not affect T_s ($P > 0.05$). Although it affected soil moisture ($P < 0.05$), the difference was small: mean soil moisture on the control plots was 22.5 ± 0.72% and mean soil moisture on the trenched plots was 27.0 ± 0.83%.

In all cases, the level of significance $\alpha = 0.05$ was accepted. The programs STATISTICA 13.0 and R (Crawley, 2007) were employed.

3. Results

3.1. Carbon accumulation in biomass

3.1.1. Trees

The allometric model (1) described well both the aboveground biomass and the stem mass of the young pine trees on the basis of tree height (Fig. 2).

The growth of the young trees at this age stage was very rapid and biomass increment accelerated annually, which resulted in higher C accumulation in the trees from year to year. In 2017 the total biomass of the trees was roughly four times as large as it was at the time of first measurement in 2015 (Table 3). The main share of C was accumulated in the stems and branches while the contribution of the coarse roots was modest. The leafless root-shoot ratio demonstrated a decrease from 0.24 to 0.18 during the three study years.

As C% in the stem wood and stem bark of the pine trees was similar (47.45% and 47.48%, respectively), the average value (47.46 ± 0.25%) was used for calculation of C accumulated in the stems (Table 3).

3.1.2. Aboveground part of the understorey

The main share of the biomass of the understorey plants was formed of dwarf shrubs (Table 4). The dominating species were cowberry (*Vaccinium vitis-idaea* L), heather (*Calluna vulgaris* (L.) Hull) and blueberry (*Vaccinium myrtillus* L). The dominating moss species were red-stemmed feathermoss (*Pleurozium schreberi* (Brid.) Mitt.) and glittering woodmoss (*Hylocomium splendens* (Hedw.) B., S & G.). The share of herbaceous plants, represented mainly by graminaceous Korean feather reed grass (*Calamagrostis arundinacea* (L.) Roth) and fireweed (*Epilobium angustifolium* (L.) Scop.), was smaller. The C accumulation in the aboveground biomass of the understorey (1.38 t $ha^{-1} yr^{-1}$) in the six-year-old stand exceeded C accumulation in the trees (0.98 t $ha^{-1} yr^{-1}$) (Tables 3 and 4).

3.1.3. Fine roots

The total fine root biomass (FRB) of the stand was estimated at 3.35 t ha^{-1}, with the fine roots of the trees accounting for 57% of this value (Table 5). Annual fine root production (FRP) of the trees, estimated by using the root mesh method, was 0.47 t ha^{-1} (Table 5). On the basis of FRP, calculated turnover rate (0.25) was low and indicated an average fine root longevity of 4 years.

The total FRP of the stand was estimated at 0.88 t ha^{-1} yr^{-1}. The fine roots of the trees made up the main share in total annual FRP, the share of the herbaceous plants was negligible (Table 5). The average C% of the fine roots of the pine trees was 50.07 ± 0.14%, which was used for calculation of C accumulation (Table 5).

3.2. Ecosystem carbon storages

The main share of the total ecosystem C stock (106 t C ha^{-1}) was stored in the upper 50 cm soil layer, the share of C accumulated in the trees was smaller. The average thickness of the organic soil layer (forest floor) was 10 cm and the amount of C accumulated in this layer was 45 t C ha^{-1} (Table 6). Also, C% was more than an order higher in the organic soil layer than in the mineral soil (Table 1).

In the studied stand the C stock in plant biomass accounted roughly for 6% of the total ecosystem C pool.

3.3. Soil respiration and the microclimate

Air and soil temperature had a distinct seasonal dynamics with a maximum in summer (July) and a minimum in winter (for air temperature in January and for soil temperature in February) (Appendix A). Short very cold periods occurred in the first third of January and February when air temperature dropped lower than −20 °C while soil temperature fluctuated very little, daily means ranging from −2.0 to 0.2 °C (Fig. 3). The seasonal dynamics of soil moisture was less distinct than that of temperature. The lowest soil volumetric moisture content was recorded in June (monthly mean 20.6%) and the highest value was recorded in December (monthly mean 34.7%) (Appendix A).

The diurnal dynamics of R_s for the growing season, measured by using automatic chambers, as well as the annual seasonal dynamics of R_s and R_h, based on manual chamber measurements, followed changes in Ts (Figs. 4 and 5). Seasonally R_s ranged from 0.42 ± 0.01 in February to 3.91 ± 0.01 μmol CO_2 m^{-2} s^{-1} in July and R_h ranged from 0.39 ± 0.01 in February to 2.46 ± 0.06 μmol CO_2 m^{-2} s^{-1} in July, coinciding with the minimum and maximum values of T_s (Appendix A). Total cumulative annual R_s was 6.0 t C ha^{-1} and R_h was 4.2 t C ha^{-1}, R_h/R_s ratio was 0.70.

Soil temperature was the main driver of seasonal variation in the soil CO_2 effluxes describing 72% of the variation in R_s and 66% of the

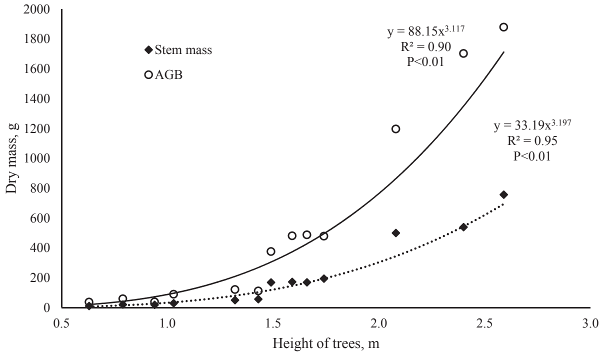

Fig. 2. The regression model of the aboveground biomass (AGB) and stem mass on the basis of the Scots pine model trees (n = 13).

Table 3
The biomass dynamics of the different fractions of the trees and annual carbon accumulation in the tree biomass of the young Scots pine stand, C% - average carbon content of the fractions (± standard error).

Fraction	Biomass, $t\ ha^{-1}$			Annual production, $t\ ha^{-1}\ yr^{-1}$		C, %	Carbon accumulation, $t\ C\ ha^{-1}\ yr^{-1}$	
	2015	2016	2017	2016	2017		2016	2017
Stem	0.66	1.30	2.74	0.64	1.44	47.46 ± 0.25	0.30	0.68
Old branches	0.34	0.52	1.59	0.18	1.07	49.27 ± 1.27	0.09	0.53
Shoots	0.09	0.21	0.54	0.21	0.54	49.69 ± 0.26	0.10	0.27
Needles	0.42	0.88	1.92	0.78	1.45	49.87 ± 0.57	0.39	0.72
Coarse roots	0.26	0.47	0.89	0.21	0.42	45.84 ± 0.34	0.10	0.19
Total	1.77	3.38	7.68	2.02	4.92		0.98	2.39
Lower/upper 95%[a]	1.17/2.23	2.61/4.15	5.23/8.38					

[a] Estimated by bootstrapping procedure.

Table 4
The biomass, production and annual carbon accumulation in the aboveground part of the understorey plants of the six-year-old Scots pine stand, C, % - average carbon concentration of the fractions (± standard error).

	Biomass, $t\ ha^{-1}$	C, %	Production, $t\ ha^{-1}\ yr^{-1}$	C accumulation, $t\ ha^{-1}\ yr^{-1}$
Herbaceous plants	0.21 ± 0.11	43.41 ± 0.57	0.21	0.09
Dwarf shrubs	4.44 ± 0.69	46.38 ± 0.32	2.09	0.97
Mosses	2.1 ± 0.37	42.69 ± 0.62	0.74	0.32
Total	**6.84**		**3.04**	**1.38**

Table 5
The biomass and production of the fine roots of the trees, dwarf shrubs and herbaceous plants. Fine root biomass (FRB) and annual fine root production are presented for the 0–40 cm upper soil layer.

Soil depth layer, cm	FRB, $t\ ha^{-1}$			Total	C stock/accumulation, $t\ ha^{-1}$
	Tree roots, $t\ ha^{-1}$	Herbaceous plants	Dwarf shrubs		
0–10[a]	1.37 ± 0.45	0.01	1.23 ± 0.27	2.61	1.31
10–20	0.24 ± 0.04	0.09	0.04 ± 0.02	0.37	0.19
20–30	0.24 ± 0.08	0.05	0.01 ± 0.01	0.30	0.15
30–40	0.07 ± 0.02	0.00	0.00	0.07	0.03
Total biomass	**1.92 ± 0.43**	**0.15**	**1.28**	**3.35**	**1.68**
Annual production	0.47 ± 0.07	0.15	0.26 ± 0.10	0.88	0.44
Turnover rate	0.25	1	0.20		
Longevity, yr	4.0	1.0	5.0		

[a] Organic (O) layer.

Table 6
Carbon storages in the studied 6-year-old Scots pine stand.

Component	Carbon stock, t ha^{-1}	Share in total ecosystem C stock, %
Organic layer	44.8	40.01
Mineral soil to a depth of 50 cm	60.9	54.39
Soil total	*105.7*	*94.40*
Trees (aboveground)	1.89	1.69
Trees (belowground)	1.09	0.97
Trees, total	*2.98*	*2.66*
Herbaceous plants (aboveground + belowground)	0.16	0.14
Dwarf shrubs[a]	2.19	1.96
Mosses	0.94	0.84
Plants, total	*6.27*	*5.60*
Total	**111.97**	**100**

[a] The biomass of the belowground coarse root systems of the shrubs is not included.

variation in R_h (Fig. 6). The effect of soil moisture on the soil respiration fluxes was not significant.

3.4. Methane flux and carbon leaching

The flux of methane showed a clear seasonal trend with soil assimilation being higher during the vegetation period and decreasing thereafter during the winter period (Fig. 7). CH_4 was assimilated by the soil during the whole measurement period, varying from −8.14 to −76.83 µg C m^{-2} h^{-1}. Its average annual input was −44.60 µg C m^{-2} h^{-1} (−0.004 t C ha^{-1} yr^{-1}).

The annual leaching of total organic carbon (TOC) at the studied site for the two study years (2016 and 2017) was low, 15.4 and 10.2 kg ha^{-1} yr^{-1}, respectively.

3.5. Eddy covariance and NEE

Eddy covariance (EC) measurements of the CO_2 fluxes were carried out from April 2016 to April 2017 and the calculated net ecosystem exchange (NEE) for this period was 1.19 ± 0.36 t C ha^{-1}. The annual gross primary production (GPP) of the ecosystem was 9.87 and total ecosystem respiration (R_{eco}) was 11.05 t C ha^{-1}.

During most of the measurement period South was a prevailing wind direction (Fig. 8). Night-time periods had more wind coming from West, otherwise being quite similar.

The peak average signal distance from the tower was 30.08 m and was as long as 40 m during some nights. Of the cumulative signal 90% arrived from an average of 82 m during the measurement period (Fig. 1). The cumulative footprint of the periods corresponding to the quality controlled (filtered) NEE values showed no difference between day and night.

The fluxes originating from the forested and non-forested parts of the footprint differed only at moderate temperatures and were quite similar in the warmer periods (Fig. 9). Considering that southern winds were prevailing (Fig. 8), we can assume that the influence of the forested areas in the footprint area during the study period was negligible.

During the growing season, NEE ranged on average between −2 and 2 g C m^{-2} d^{-1}. The highest net CO_2 uptake (−3.1 g C m^{-2} d^{-1}), as well as the highest CO_2 release (4.6 g C m^{-2} d^{-1}), occurred in July. Starting from mid-August, NEE was more positive, i.e. the ecosystem acted as a C source (Fig. 10).

From the end of September, with the exception of single days, the ecosystem turned into a CO_2 source. The days with positive NEE values (source days) during the growing season were related to low GPP values rather than increased R_{eco}. These days were characterized by lower radiation while air temperature did not differ notably from that of the adjacent days.

R_{eco} had three distinctive peaks during the measurement period: the highest values were recorded in July and the two other peaks occurred at the end of August and in the second part of September – beginning of October. Similar peaks, although less pronounced, were noted in soil respiration. GPP also reached maximum values in July with a subsequent decline.

3.6. Carbon budgeting on the basis of the estimated input and output fluxes

The studied Scots pine acted as a C source at the age of six years and there was good accordance between NEP, which was calculated on the basis of the C fluxes, and NEE which was estimated by the eddy covariance technique (Table 7). At that stage, C accumulation in the

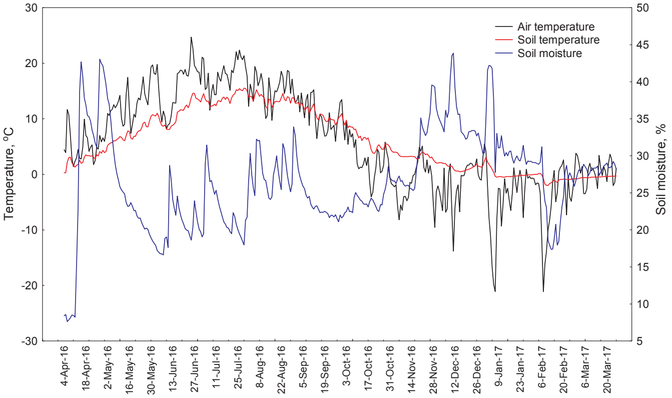

Fig. 3. Seasonal dynamics of daily air temperature, soil temperature and soil moisture from April 2016 to March 2017.

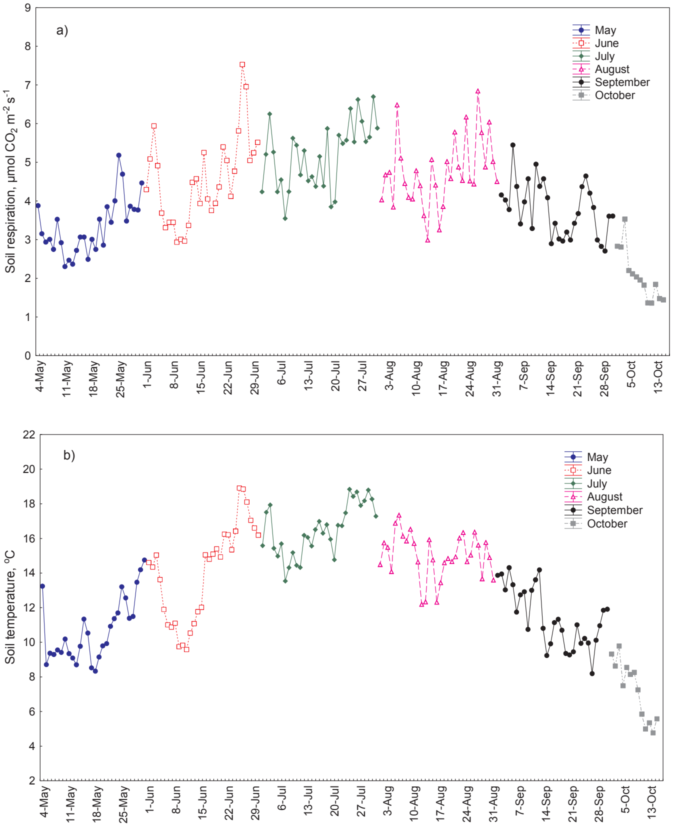

Fig. 4. Seasonal dynamics of daily (a) total soil respiration and (b) soil temperature for the growing season (from May 2016 to October 2016) at automated soil respiration stations.

understorey plants exceeded C accumulation in the trees. The main C emission source was R_h, and the share of C leaching as well as the share of the methane flux were negligible. However, the ecosystem was a methane sink (Fig. 7). Total annual ecosystem respiration was 11.06 t C ha^{-1} yr^{-1} and R_s was 6 t C ha^{-1} yr^{-1}. Thus the C flux into the atmosphere through the respiration of the aboveground parts of the plants was 5.1C ha^{-1} yr^{-1}. Since in EC studies the C sink is usually denoted by negative values (decrease in the atmosphere), we used a similar approach for compiling the C budget for the studied stand (Table 7).

4. Discussion

Forest harvesting by clear-cut is a considerable disturbance which alters the C cycle of the whole ecosystem for long time; after clear-cut a site turns from a C sink into a net C source (Paul-Limoges et al., 2015). In this study, we estimated the C balance in a 6-year-old Scots pine stand by using simultaneously two different methods. A similar approach has also been adopted in several earlier studies (Peichl et al., 2010; Meyer et al., 2013; Aguilos et al., 2014). However, in the earlier studies general models were used for estimation of biomass production and C accumulation of trees; even fine root production was sometimes estimated by indirect methods. In the present study the contribution of all components of the young pine stand (incl. fine roots, mosses, dwarf shrubs, etc.) to C accumulation in the forest ecosystem were estimated directly and simultaneously, which guaranteed good accordance between the results obtained with the two methods used.

After harvest, C sequestration into forest biomass decreases drastically, followed thereafter by an increase owing to the recovery of the understorey vegetation as well as to the growth of a new tree

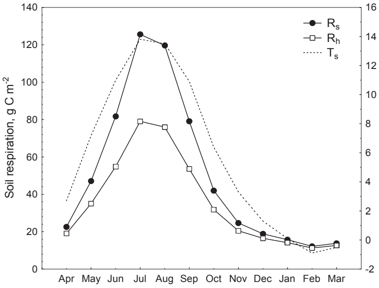

Fig. 5. Annual seasonal dynamics of total soil (R_s) and heterotrophic respiration (R_h) (g C m^{-2}) and soil temperature (T_s, °C) from April 2016 to March 2017. Each respiration point represents a monthly cumulative flux.

generation. At the studied 6-year-old stand the understorey vegetation contributed essentially (57%) to NPP, i.e. the production of the understorey vegetation exceeded that of the trees, which is typical successional development of a young forest. Among other understorey species, also mosses can contribute much to the ecosystem NPP at the early stage of stand development at poor sites. However, the productivity of mosses may also vary to a large extent in different forest ecosystems, depending mainly on light conditions and species composition; in a black spruce forest the annual production of mosses varied between 0.1 and 3 t C ha^{-1} yr^{-1} (Bona et al., 2013). In the present study, the annual production of mosses was estimated at 0.74 t C ha^{-1} yr^{-1} which accounted for 11% of total ecosystem NPP (Table 6). The average C content of mosses was 42.7 ± 0.6%, which is consistent with the results of an earlier study (Campioli et al., 2009) reporting an average moss C content of 41–43%.

The uptake of C by the plants (both the understorey and the trees) could not compensate for respiration loss from the sapling-stage stand. The estimated annual R_h in the studied 6-year-old stand was 4.2 t C ha^{-1}, exceeding NPP roughly by 1.4 t C ha^{-1}. Although photosynthetic uptake decreases after clear-cut and loss of respiring roots causes a reduction in soil autotrophic respiration, R_h losses continue at his stage. At the study site, R_s comprised mainly R_h; the R_h/R_s ratio was 0.70. Often R_h can be favoured by post-harvest because of increased soil temperature, amount of harvest residues and dead root biomass. Soil temperature is usually the dominating environmental factor influencing soil respiration fluxes under optimum soil moisture conditions in boreal forests (Hibbard et al., 2005; Moroni et al., 2009; Kukumägi et al., 2014, 2017; Uri et al., 2017a,b). Clear-cut areas with logging residues have been found to have higher soil respiration fluxes than clear-cuts without residues (Pumpanen et al., 2004; Moroni et al., 2009). Although the results concerning the effect of clear-cut on soil respiration fluxes are contradictory (Luo and Zhou, 2006; Peng et al., 2008), variation in the results can be related to the length of the post-harvest recovery time (Peng and Thomas, 2006), i.e. at what time point (immediately after clear-cut or several years later) the study has been conducted. For example, Peng and Thomas (2006) found that R_s increased immediately after harvest, but recovered its preharvest level 5–6 years later. Due to intensive R_h during the early stages of stand development, the soil C stock may temporarily decrease. However, a large review showed that, with all harvesting intensities combined, the C stock of both the forest floor and mineral soil was not affected by harvesting (Hume et al., 2018). In our study, of the ecosystem C stock 94% was located in the soil, and the total soil C pool was estimated at 106 t C ha^{-1} (Table 6). Henceforth the C stock of the trees will increase and in a middle-age stand the relative share of the C stock in biomass and soil will usually be balanced (Uri et al., 2012). We expected to see an intensive R_h flux in the studied clear-cut area, however, the estimated R_h flux was of the magnitude inherent in pine stands. We measured the annual R_h flux in chronosequent pine stands in Estonia at the age of 10–109 years (unpublished data) and it was between 4 and 6 t C ha^{-1} yr^{-1}. Thus the level of the annual R_h flux at a regenerated post-harvest site is comparable to that of older pine stands. Also Kolari et al. (2004) pointed out that the soil respiration of clear-cut was similar to that of forest stand while its primary production showed lower values.

From the point of view of climate change and the mitigation effect of forests, the crucial issue is the length of the post-harvest period during which the C budget of the ecosystem will again attain a balance, which is considered the C compensation point (Kowalski et al., 2004; Aguilos et al., 2014). Based on the measurements of aboveground tree biomass production (2015–2017) and on the assumption that the R_h flux will be relatively stable over the subsequent few years, we can expect that already in a seven-year-old stand the annual C budget will be balanced, or the site will turn into a C sink. It is obvious that there can occur some fluctuations in the R_h flux which are mainly related to weather conditions (temperature and moisture) in different years (Kukumägi et al., 2017; Uri et al., 2017a,b). However, in the present case, the production capacity of the trees is more crucial than R_h in terms of the C balance since the studied stand is at the developmental stage where tree biomass increases significantly from year to year. Although the trees contributed a modest share to ecosystem C uptake (43% of NPP) due to their small dimensions (Tables 3 and 7), this

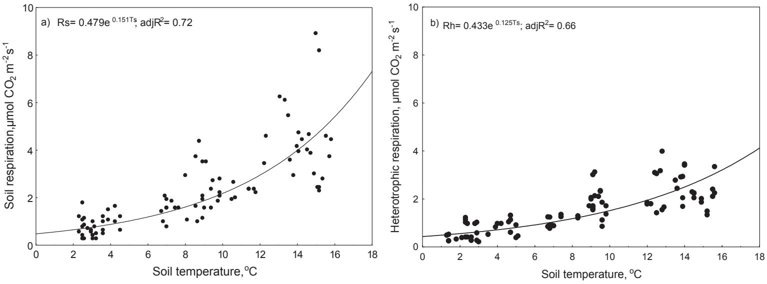

Fig. 6. Relationships between (a) total soil respiration, (b) heterotrophic respiration and soil temperature. The exponential equation and the adjusted determination coefficients are presented, $P < 0.001$ in both cases, $n = 90$.

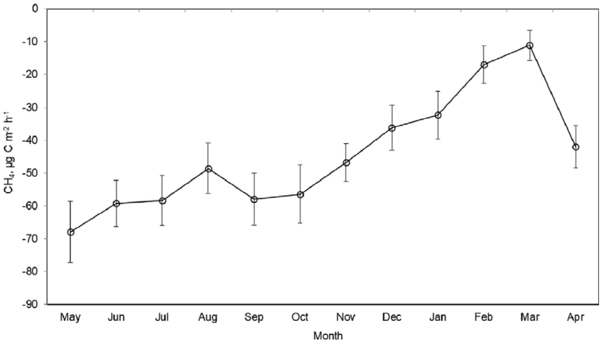

Fig. 7. Seasonal dynamics of the methane flux in the young Scots pine ecosystem from May 2016 to April 2017. Points denote the average values across all collars and bars indicate standard error values.

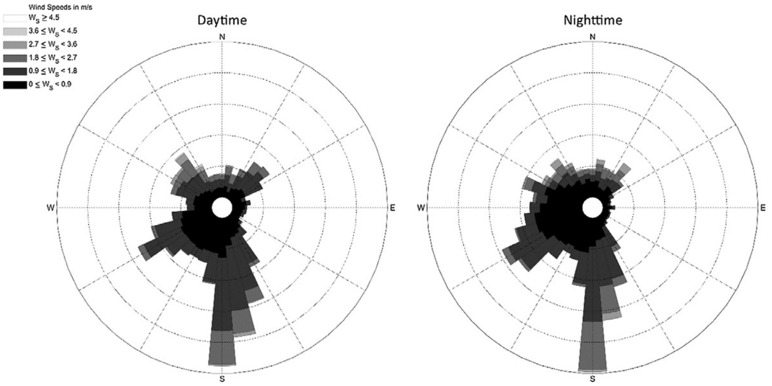

Fig. 8. Wind rose of daytime and nighttime winds of the measurement period.

situation changed rapidly: when the amount of C accumulated in tree biomass in 2016 was roughly 1 t C ha^{-1}, then in 2017 it was more than doubled, amounting to 2.4 t C ha^{-1} yr^{-1}. Assuming that the annual R_h flux is of the same magnitude in the subsequent year, the ecosystem will become a C sink already in a 7-year-old stand. In Finland, the C budget of Scots pine forest reached a balance in a 12-year-old stand (Kolari et al., 2004). However, Schulze et al. (1999) and Rannik et al. (2002) found that both 5- and 13-year-old Scots pine stands were still C sources. A clear-cut was an obvious source of CO_2 5–6 years after harvesting a spruce-dominated stand in the hemiboreal part of Canada (Fredeen et al., 2007). According to a 10-year EC study in Japan, the C compensation point was estimated to be seven years in a hybrid larch ecosystem (Aguilos et al., 2014), which is in good accordance with the present study.

It should be taken into account that not only the high production of individual trees but also stand density affects total C accumulation in young stands. Our study the area was successfully regenerated and the number of growing trees (15,000 per ha) was high, which ensured intensive biomass production. Fast and effective forest regeneration after clear-cut is a very important forest management operation ensuring that the ecosystem will soon turn into a C sink.

The EC method, based on continuous measurements during a certain period, allows a quite accurate estimation of C exchange between the ecosystem and the atmosphere and is the most direct method for C cycling studies (Baldocchi, 2014). However, this method only provides estimation of the quantity of input and output fluxes without detailed specification of the sources or sinks of the flux, which is its major shortcoming. The carbon budgeting method gives a good picture of the contribution of the various ecosystem components, such as the trees, understorey plants, aboveground biomass, roots etc., to C uptake. Yet the estimate of each single C flux involves error, which makes this method less accurate than EC is. The direct method (EC) is considered a more reliable tool, in view of cumulated uncertainties involved in the indirect method (Meyer et al., 2013). The EC method also allows to measure C fluxes in different periods; it is possible to visualize daily or monthly dynamics of C exchange between the atmosphere and the

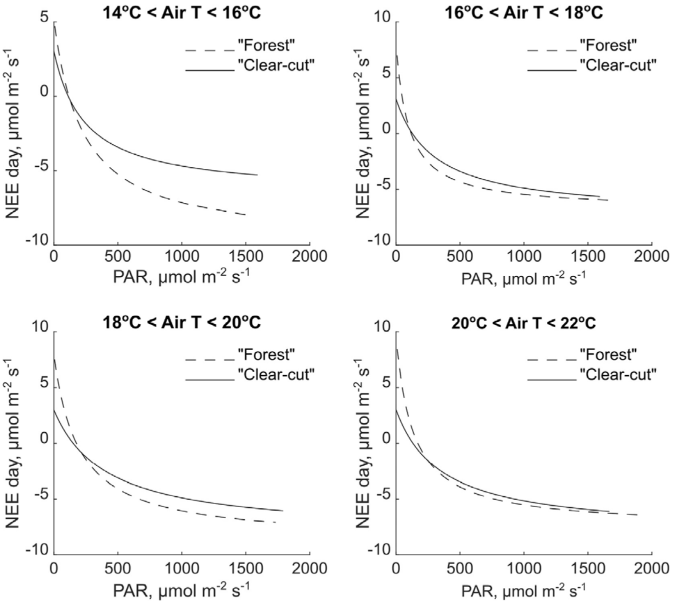

Fig. 9. Light response curves of daytime NEE data for different air temperature classes. “Forest” represent easterly and westerly winds directions with forest in the footprint area. “Clear-cut” represents northern and southern parts of the footprint that are free of trees.

ecosystem (Fig. 10) Hence, combining of the two methods could yield a result of higher quality; similar or coincidental results of the C output and input fluxes, obtained by different methods for same site, would improve the reliability of a study. Exact estimation of different C fluxes allows to quantify and assess their share in the whole C budget. In the present study, the results of one-year EC measurement and a simultaneous indirect estimation of the C fluxes gave very similar results (Table 7): NEE and NEP were 1.19 and 1.37 t C ha^{-1} yr^{-1}, respectively. Such good accordance is not very typical; in a peatland forest the average annual NEE determined by the two methods differed by almost 2 t C ha^{-1} (Meyer et al., 2013). However, in that study annual biomass production (including the fine roots) was modelled by using the biomass functions, which may be a reason for the difference between their results. Relevant C budgeting assumes empirical data collection, i.e. a thorough estimate of all C fluxes in situ as well as the use of relevant biomass models.

Fine root production (FRP) is the basic contributor to belowground C inputs (Finer et al., 2011); on the other hand, FRP is the most sophisticated issue in forest C budgeting. The belowground part is the main bottleneck in studying forest ecosystem’s C cycling (Leppälammi-Kujansuu et al., 2014) as well as in compiling C budgets. Peichl et al. (2010) pointed out that uncertainty in fine root litter production estimates may potentially introduce significant error into primary production estimates. Lack of empirical data of belowground tree biomass has often hampered relevant estimation of forest C pools and a better understanding of forest C dynamics (Russell et al., 2015). In the present study, we assumed that the FRP of the trees can be underestimated because of the short incubation time of the root mesh used (Lukac and Godbold, 2010), as well as because of possibly too small mesh size (Montagnoli et al., 2014). The turnover rate, calculated by us, indicating a replacement of about 25% of fine roots per year, was lower than the values typically reported for Scots pine (Brunner et al., 2013). The longevity of the fine roots of pine (4 yr) prognosticated by us, is clearly the highest among earlier data (Makkonen & Helmisaari, 1999; Janssens et al., 2002). On the other hand, the share of thin woody roots (diameter 1–2 mm) might be larger in young trees, increasing the total longevity of fine roots. Thus we can assume that actual annual C accumulation is probably larger due to larger actual FRP, which is one factor which can partly explain the difference between estimated NEE and NEP. Although the root mesh method probably gives good results in the case of fertile mineral-organic soils already in the first study year (Uri et al., 2017a,b), first-year sampling in poor sandy soils with an organic forest floor layer may result in underestimation.

Only scanty data is available about TOC leaching in different forest ecosystems. In the current study TOC leaching made up a minor share in the C budget. The estimated annual TOC flux (10–15 kg C ha^{-1} yr^{-1}) is consistent with the results from a clear-cut area in a similar *Myrtillus* site type where annual TOC leaching varied between 7 and 14 kg C ha^{-1} yr^{-1} (Becker et al., 2016). Since TOC leaching as well as methane oxidation are negligible in mineral soils, these fluxes are often ignored in C budgeting studies.

5. Conclusions

Our hypothesis was confirmed: the six-year-old young Scots pine stand on a poor sandy soil was a modest carbon source (NEE 1.19 and

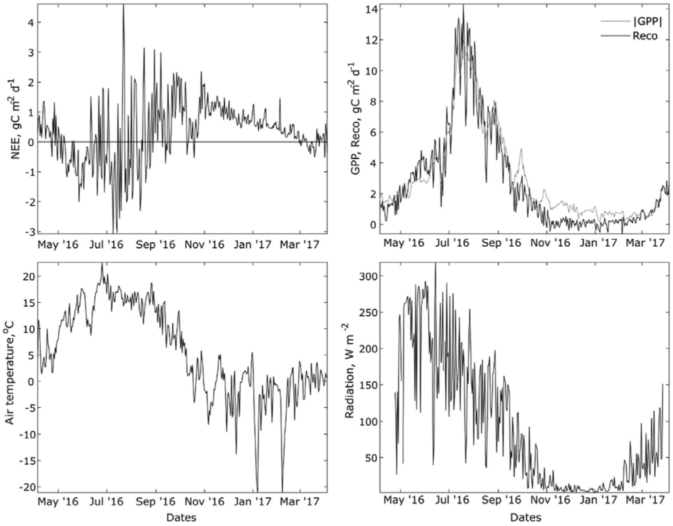

Fig. 10. Annual dynamics of NEE, GPP, air temperature and radiation for the studied Scots pine stand.

Table 7
The carbon budget and the data of eddy covariance for the studied 6-year-old Scots pine stand in 2016. The input C fluxes are presented by negative values and the output emissions are presented by positive values.

Flux, t C ha^{-1} yr^{-1}		
C inputs		
1	*Plants, aboveground*	
	Trees	−0.89
	Understorey plants	−1.39
2	*Plants, belowground*	
	Trees, coarse roots	−0.10
	Trees, fine roots	−0.24
	Understorey, roots and rhizomes	−0.21
3	Methane oxidation	−0.004
C outputs		
4	Heterotrophic respiration	4.20
5	TOC leaching	0.015
Productivity		
6	NPP = (1) + (2) + (3)	−2.85
7	NEP = (6) − (4 + 5)	1.37
Eddy covariance		
	GPP	−9.87
	R_{eco}	11.06
	NEE	1.19 ± 0.36

NEP 1.37 t C ha^{-1} yr^{-1}). However, because of the high biomass production of young trees, C uptake will most probably exceed C loss already after one year, assuming that the R_h flux will be of same magnitude. Thus, a well regenerated young Scots pine stand in a *Myrtillus* site type acts as a C source during short time after clear-cut and will turn into a C sequestering ecosystem already before ten years. Although we expected to see an intensified R_h flux in the studied post-harvest area, the estimated flux (4.2 t C ha^{-1} yr^{-1}) was comparable to that recorded for older pine stands. Both methods (EC and C budgeting) gave similar results about the annual C balance in the studied ecosystem, which confirms the relevance of the C budgeting method. However, reliable C budgeting assumes collection of empirical data, i.e. accurate estimation of all C fluxes in situ, as well as the use of relevant biomass models.

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Appendix A

Mean air temperature (T_{air}, °C), soil temperature (T_s, °C) and soil moisture (SWC, %) from April 2016 to March 2017 from data loggers.

	Period	T_{air}	T_s	SWC
2016	April	5.2	2.7	27.8

	May	12.7	7.2	25.3
	June	15.9	11.0	20.6
	July	18.0	13.8	22.3
	August	15.5	13.5	28.3
	September	10.8	10.9	23.5
	October	3.0	6.4	23.9
	November	−1.6	3.3	30.0
	December	−1.4	1.3	34.7
2017	January	−4.5	0.1	32.0
	February	−4.2	−0.9	24.4
	March	0.4	−0.5	28.3

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II

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Short-term effect of thinning on the carbon budget of young and middle-aged silver birch (*Betula pendula* Roth) stands

K. Aun[a,*], M. Kukumägi[b], M. Varik[a], H. Becker[a], J. Aosaar[a], M. Uri[a], M. Buht[a], V. Uri[a]

[a] *Estonian University of Life Sciences, Institute of Forestry and Rural Engineering, F. R. Kreutzwaldi 5, 51006 Tartu, Estonia*
[b] *University of Tartu, Institute of Ecology and Earth Sciences, Vanemuise 46, 51014 Tartu, Estonia*

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Carbon budget

ABSTRACT

Although thinning is a widely used silvicultural method, its effect on stand carbon (C) cycling is still poorly studied at the ecosystem level. The present case study estimated the two-year post-thinning effect on the C balance of a pole and a middle-aged silver birch stand. The results demonstrate the multifaceted impact of thinning on the different C fluxes of deciduous forest ecosystems.

The effect of thinning on the C budget of the studied stands was modest: net ecosystem production (NEP) decreased by 1.2 and 1.6 t C ha^{-1} yr^{-1} in the pole and the middle- aged stand, respectively; still, both stands remained C sinks. Lower annual production in the thinned stands as a result of the decreased standing biomass of the trees was the main factor for reduced C sequestration capacity. Thinning increased the C accumulation of the herbaceous plants in both stands, however, it did not compensate for the lower C accumulation by the trees. In general, thinning did not affect significantly the soil respiration fluxes; the small post-thinning increase of the annual soil heterotrophic flux, 0.33–0.68 t C ha $^{-1}$, was most probably related to elevated soil temperature during the active growing season. The annual aboveground litter flux, i.e. the labile C source of Rh, was not significantly changed by thinning. Fine root production and the belowground C input to the soil remained at the same level in the pole stand and decreased slightly in the middle-aged stand. We conclude that the high production ability and fast C accumulation recovery of silver birch stands growing on fertile soils leads to a balanced C budget already during the short post-thinning period.

1. Introduction

Birches are the most important commercial broad-leaved tree species in various forests in Northern Europe (Hynynen et al., 2010) and silver birch *(Betula pendula)* among them is known as a fast-growing pioneer tree species with high biomass productivity (Oikarinen, 1983; Hynynen et al., 2010; Uri et al., 2012; Aosaar et al., 2016). Naturally regenerated silver birch stands on abandoned agricultural land are a common type of novel forest ecosystems in Northern and Eastern Europe. In the last half-century two waves of natural extensive forestation of farmland took place in the Baltic region: one after World War II and the other after the collapse of the Soviet Union (Daugaviete, 2003; Urbaitis, 2003; Wall and Hytönen, 2005). Consequently, the importance of silver birch in the forestry of these regions increased even more. The total growing stock of birch stands increased by 78 mil m^3 between 1975 and 2018 and birch stands cover around 30% of the Estonian forest area (Yearbook Forest, 2018). Moreover, intensive natural regeneration of silver birch is very common also in clear-cut areas of the Nordic and Baltic regions, creating preconditions for forming birch or mixed stands in the nearest future. On the other hand, in recent decades intensive development has taken place in wood processing industry. New veneer and plywood enterprises were established in the Baltic countries, considering the increasing demand for high quality birch timber at the local level. However, in order to increase the quality and thereby the economic value of birch forests, the management of such stands became more relevant.

Thinning is the main "silvicultural tool" for improving stand quality and the effect of thinnings on stand development and growth has therefore attracted the interest of forest managers and scientists for a long time. Usually, the main aim of this kind of studies has been to find optimum thinning practices for ensuring the maximum use of the site potential for high quality timber production (Skovsgaard, 2009). Even though it is known that standing biomass in unmanaged stands is higher than in thinned stands (Rice et al., 2001; Simard et al., 2004; Repola et al., 2006), timely thinnings are crucial for harvesting quality timber at

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* Corresponding author.
E-mail address: kristiina.aun@emu.ee (K. Aun).

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the final felling. For directing stand development, thinnings are especially important in naturally regenerated dense stands, where the stem properties of trees are highly variable (Rytter and Werner, 2007). Removal of low quality trees reduces competition between remaining trees, leading to the increased growing area and expanded foliage and larger root biomass.

This results in favourable diameter increment of future trees and in redistribution of available resources for the production of best quality trees. Earlier studies have highlighted the importance of timely pre-commercial thinnings, since the height growth of birches is most intensive in stands aged around 20 years (Eriksson et al., 1997). For light demanding tree species, crown development and stem growth are hindered in the case of high stand density (Hynynen et al., 2010).

In addition to silvicultural and economic issues, sustainable modern forestry should take into account all environmental impacts related to forest management, among them the effect on the carbon (C) sink capacity of stands. Increasing CO_2 content in the atmosphere, resulting in climate changes, is one of the key environmental problems nowadays. The importance of both boreal and hemiboreal forests in mitigating climate changes has been emphasized because of their ability to accumulate a large amount of C (Dixon et al., 1994; Goodale et al., 2002; Gough et al., 2008; Pan et al., 2011). Among the various factors affecting forest C accumulation, management has a strong impact on C sequestration capacity (Usi and Lal, 2017). Although thinning is a widespread silvicultural method, its effect on ecosystem nutrient and C cycling is still poorly studied (Morozov et al., 2019).

Thinning changes the functioning of a forest ecosystem a great deal and in different ways. Usually, the production of a stand decreases for a short period due to the decreased number of trees and stand volume. At the same time, thinning can produce considerable changes in factors that potentially affect heterotrophic respiration (Rh) (resulting from decomposition of litter and soil organic matter), as well as microclimate, litter fall input, fine root biomass and necromass, and soil microbial community and its activity (Ma et al., 2004; Tang et al., 2005; Peng and Thomas, 2006; Olajuyigbe et al., 2012). Tree removal reduces the leaf litter input, thereby decreasing Rh (Sullivan et al., 2008). However, at the same time, increased root necromass and harvest residues, providing a labile substrate for microbes, through interaction with higher soil temperature, potentially increase Rh, i.e. the main output flux of C budget (Misson et al., 2005; Sullivan et al., 2008; Olajuyigbe et al., 2012).

Hence, it is obvious that the outcome of thinning is multifaceted and is affected not only by soil processes and Rh but also by the aboveground litter of trees and by the production of fine roots and herbaceous plants, which serve as an input of organic C to soil. As all these components were taken into account in analysing the effect of thinning at the ecosystem level. The main aim of the current case study was to evaluate the short-term effect of thinning on C budget in young and middle-aged silver birch stands. For this, all main C fluxes of the ecosystem were estimated and C budgets were compiled simultaneously for thinned and unthinned stands. We hypothesised that although Rh intensifies after thinning due to increased soil temperature and C accumulation by trees at the stand level decreased, the whole ecosystem will still act as a C sink.

2. Materials and methods

2.1. Study sites

Two silver birch stands in Southeastern Estonia, a 20-year-old (pole) stand and a 30-year-old (middle-aged) stand, were selected for the study (Table 1). In both stands two sample plots were established in 2015; thinning was carried out in one plot (TP) in September 2015 and the other remained the control plot (CP) (Table 1). Also, the area adjacent to the treated plot was thinned in a similar way to avoid the edge effect. This buffer zone allowed to further harvest model trees without disturbing the intact sample plots. Thinning was performed following common management practice, i.e. stems were removed and residues (tops, branches) were left on site.

Table 1
Characteristics of the study sites in autumn 2017; $D_{1,3}$ – average stand diameter at breast height, H – average stand height, BA– basal area of stand, V- volume of stand.

Stand	Treatment	Stand density, trees ha^{-1}	$D_{1.3,}$ cm	H, m	BA, $m^2\ ha^{-1}$	V, $m^3\ ha^{-1}$
Pole	TP	1840	12.1 ± 0.3^a	20.3 ± 0.6^a	21.3	285.1
	CP	2500	11.1 ± 0.4^b	18.2 ± 0.6^b	24.2	320.5
Middle-aged	TP	667	18.3 ± 0.6^a	22.6 ± 0.6^a	17.5	282.3
	CP	1233	15.2 ± 0.4^b	19.8 ± 0.7^b	22.4	336.4

Statistically significant difference between the treatments is denoted with letters ^{a} and ^{b}.

The pole stand had a longer research history and had been thoroughly studied (Uri et al., 2007a, 2007b, 2008, 2012; Varik et al., 2015; Aosaar et al., 2016) and the existing sample plot within this stand was considered CP; TP was established next to the existing plot (Morozov et al., 2019). In the middle-aged stand both CP and TP were established simultaneously.

Both stands were naturally regenerated and were growing in a fertile *Oxalis* site type, according to a local classification (Lõhmus, 1984). The intensity of thinning was 17% and 21% of the basal area for the pole stand and the middle-aged stand, respectively. The area of the established sample plots was 0.03 ha and 0.09 ha in the pole stand and in the middle-aged stand, respectively. The main stand characteristics of the study sites were measured after thinning (Table 1).

2.2. Soil

At both study sites, seven soil pits (depth 1.0 m) were dug in 2016; the soil profile was described and the soil type was determined according to the IUSS Working Group WRB (2006). From every soil pit, bulk density samples were taken from different soil depth layers (0–50 cm) using a stainless steel cylinder (Ø 40 mm; V = 50 cm^3), to avoid compression of the soil and to preserve soil structure. The soil samples were dried to constant weight at 105 °C and weighed in the laboratory. For estimation of soil nutrient and C content as well as pH, samples from twelve random points over the sample plot were taken from different depths (0–10 cm and 10–20 cm) with a soil corer to form a composite sample for chemical analyses (Table 2) (Uri et al., 2017a,b). In both stands the decomposition of organic matter was favourable due to high soil fertility and readily degradable leaf litter (Morozov et al., 2019). The soil organic layer (forest floor) was not formed.

For analysing N (Kjeldahl) in the soil samples, a Tecator ASN 3313 was employed. Available ammonium lactate extractable phosphorus in the soil was determined by flow injection analysis using a Tecator ASTN 9/84. Available potassium was determined from the same solution using the flame photometric method. Soil magnesium was determined by flow injection analysis employing a Tecator ASTN 90/92. Soil pH in 1 M KCl suspensions was measured at a ratio of 10 g:25 ml. The carbon content of oven-dried samples was determined by the dry combustion method using a varioMAX CNS elemental analyser (ELEMENTAR, Germany). Chemical analyses were carried out at the Biochemistry Laboratory of the Estonian University of Life Sciences (Table 2).

2.3. Estimation of biomass and production

2.3.1. Aboveground biomass and production of the trees

Aboveground biomass was estimated using the model tree method (Bormann and Gordon, 1984; Uri et al., 2012, 2017a,b). In both stands 5–7 model trees were felled in both treatments (outside of the sample plots) in August 2017, according to the diameter distribution of the trees. The stems of the model trees were divided into 5 sections: 0–1.3 m,

Table 2
Soil characteristics in the studied silver birch stands; N – Kjeldahl nitrogen (%), P – available phosphorus (mg kg^{-1}), K – available potassium (mg kg^{-1}), Ca- calcium (mg kg^{-1}), Mg- magnesium (mg kg^{-1}), bulk density (g cm^{-3}), C storage- carbon storage (t ha^{-1}), TP – thinned plot, CP – control plot. All characteristics are presented for the 0–20 cm topsoil layer.

Stand	Treatment	Soil type	pH$_{Cl}$	N	P	K	Ca	Mg	Bulk density,	C storage,
				%			mg kg^{-1}		g cm^{-3}	t ha^{-1}
Pole	TP	*Albeluvisol*	5.51	0.10	58.0	134.9	581.8	97.4	1.22	40.1
	CP		5.39	0.09	76.9	118.5	656.9	108.2	1.24	39.2
Middle-aged	TP	*Umbric-Endogleyic Arenosol*	3.98	0.11	25.9	45.0	126.7	15.5	1.21	39.0
	CP		3.77	0.11	33.9	47.6	120.2	20.7	1.23	42.4

All values, except for C storage, from Morozov et al. (2019).

1.3 m until the beginning of the living crown and the crown was divided into 3 sections of equal length (Uri et al., 2017a,b). A stem disc from each section was taken for determining stemwood and stembark proportions and dry matter content, as well as for measuring annual rings. One model branch was chosen from each crown section and fractionated in the laboratory into the leaves, twigs (i.e current-year shoots) and older branches. The stems and the branches were weighed in the field and subsamples were taken from every fraction for determining dry matter content. In the laboratory the subsamples were weighed, dried at 70 °C and reweighed to 0.01 g. Dry mass for each fraction was calculated by multiplying fresh mass by dry matter content.

Allometric equation (1) was compiled for estimation of the aboveground biomass and stemwood production of the plot (Uri et al., 2002, 2007a, 2007b, 2012)

$$y = ax^b \tag{1}$$

where y is the aboveground biomass, or stem mass, or stemwood annual production of tree, x is diameter at breast height (cm), a and b are the parameters of the regression model (Table 3). For better biomass models, the data of the model trees from TP and CP were pooled, assuming that for the short post-thinning period, the allometric relationship between tree dimensions and biomasses was similar for TP and CP.

The biomass of the leaves, current shoots and branches, as well as the proportion of the stemwood and bark were calculated on the basis of the percentage distribution of the fractions of the model trees.

Stemwood production was estimated on the basis of radial increment which was measured from the cross section discs cut from each stem section and crown section in 2017. The discs were dried, polished and the widths of the annual rings were measured to 0.001 mm using the software WINDENDRO (Regent Instruments Inc.). Annual stemwood production for the different sections of the model trees was calculated with Whittaker and Woodwell (1968) equation (2)

$$W_i = W_0\left(r^2 - (r-i)^2\right)/r^2 \tag{2}$$

where W_i is the annual dry mass increment of stemwood (g), W_0 is the dry mass of the stemwood (g), r is the radius of the analysed disc (mm), i is the thickness of annual ring (mm). The production of the sections was summed up for calculation of the stemwood production of the model tree. Allometric equation (1) was used for estimation of the annual stemwood production, where y is the annual stem mass production of tree, x is diameter at breast height (cm), a and b are the parameters of the regression model (Table 3).

Table 3
Parameters of regression model (1) for estimation of aboveground biomass and annual stemwood production. R^2 denotes the coefficient of determination, p-value indicates the level of significance.

Stand	a	b	R^2	p-value
		Aboveground biomass		
Pole	162.75	2.3778	0.99	<0.0001
Middle-aged	125.59	2.4885	0.97	<0.0005
		Annual stemwood production		
Pole	17.497	2.1934	0.92	<0.0001
Middle-aged	2.8383	2.8125	0.90	<0.0002

The relative increments of the fractions of the wood and bark were assumed to be equal (Uri et al., 2012). The production of the branches was calculated using the relative increment of the stemwood (Uri et al., 2012). The C pools for the different fractions of the stand were calculated using the biomass and C concentration of the different fractions of the middle-aged silver birch stand (Uri et al., 2012).

2.3.2. *Aboveground biomass and production of the herbaceous plants*

For estimation of the aboveground biomass of the herbaceous plants, ten random samples over the whole plot were taken in mid-July 2017 when aboveground biomass was assumed to be at a maximum. The aboveground biomass of all ground vegetation was collected from a 0.5 m^2 quadrat (cut as close to the ground surface as possible) and weighed in the laboratory (Uri et al., 2017a,b). The quadrat was placed on the ground randomly along the diagonal traversing the sample plot (five samplings per one diagonal and five per the other diagonal). From every sample subsamples were taken for estimation of dry matter content. The subsamples were dried at 70 °C to constant weight and reweighed to 0.01 g.

The annual production of the herbaceous plants was assumed to be equal to their biomass, since the biomass of herbs is annual (Uri et al., 2012). A C concentration of 43.4% was used to calculate the C storage of the herbaceous plants (Uri et al., 2017b). The share of the mosses was negligible and their biomass was ignored.

2.3.3. *Stump and coarse root biomass and production of the trees*

For estimation of stump and coarse root biomass, an average proportion of 21% for belowground biomass was used (Varik et al., 2013). Annual coarse root production was calculated on the basis of the equal relative increments of wooden aboveground biomass; the relative increments of the aboveground and belowground woody biomass fractions were assumed to be equal (Uri et al., 2012). The C concentrations for different belowground biomass fractions of silver birch stands (Varik et al., 2013) were employed to estimate the belowground C storages and accumulation.

2.3.4. *Fine root biomass and production of the trees, and root and rhizome biomass of the herbaceous plants*

Fine root ($d < 2$ mm) biomass (FRB) and fine root production (FRP) were estimated using the sequential soil coring method (Vogt and Persson, 1991; Stober et al., 2000; Ostonen et al., 2005), which is labour consuming, but has provided the most reliable results for European forests (Brunner et al., 2013). Sampling was carried out in October 2016 and in May, August and October 2017. At each sampling, fifteen soil monoliths were taken randomly across both plots to a soil depth of 40 cm. The monoliths were divided into depth layers (0–10; 10–20; 20–30 and 30–40 cm), then packed, labelled and transported to the laboratory, where the samples were stored in the freezer at −5 °C until further processing. Further, the samples were defrosted and washed carefully for extracting roots from the soil and sorted under the binoculars into the different fractions: the living and dead fine roots of birch and the roots and rhizomes of the herbaceous plants (Varik et al., 2013; Uri et al., 2017a,b). The sorted samples were dried at 70 °C to constant weight and weighed to 0.001 g for calculating FRB. Mean FRB was calculated as mean biomass across of all four samplings to avoid its seasonal variations (Brunner et al., 2013). FRP was calculated by balancing fine root bio- and necromass according to the decision matrix (Fairley and Alexander, 1985). Fine root turnover rate was calculated by dividing FRP by mean FRB (McClaugherty et al., 1982; Gill and Jackson, 2000) and fine root longevity was calculated as its reciprocal value of turnover. FRP was assumed to be equal to the input of annual belowground litter as well as the C flux to the soil (Kleja et al., 2008; Varik et al., 2015; Ding et al., 2019). The ratio of above- to belowground litter was calculated by dividing the mean annual aboveground leaf litter flux by annual FRP. For estimation of the belowground biomass of the herbaceous plants, the samples for August were used. An average C concentration of 51.4% (Varik et al., 2013) was used for calculation of the C storage in the fine roots of the trees. For calculation of the C storage in the roots of the herbaceous plants, a C concertation of 46.4%, established by the dry combustion method with a varioMAX CNS elemental analyser (ELEMENTAR, Germany), was used.

2.4. *Litter flux of the trees*

For estimation of the aboveground litter flux of the trees, seven litter traps with a collecting area of 0.36 m^2 each were placed randomly in the TP and CP of the both studied stands in early spring 2016. Litter samples were collected once a month during the three-year study period (2016–2018). The samples were dried at 70 °C to constant weight, divided into three fractions, i.e. the leaves, branches and other material (e.g. seeds, pieces of bark, buds etc.), and every fraction was weighed.

2.5. *Soil respiration and microclimate*

The rates of total soil respiration (Rs) and heterotrophic respiration (Rh) (μmol CO_2 m^{-2} s^{-1}) were measured once a month from April to October 2016 and from May to November 2017, using the closed dynamic chamber method (PP *Systems* SRC-1 chamber (volume 1170 cm^3, enclosed soil surface 78 cm^2), with the gas analyser CIRAS-2 (Differential CO_2/H_2O Infrared Gas Analyzers)). To distinguish Rh from Rs, the trenching method with insertion of 12 deep PVC cylinders (Ø20 cm, height 50 cm) to a depth of 40–45 cm was applied in each treatment plot in November 2015. Trenching up to this depth can be considered sufficient, since the bulk of the fine root biomass of silver birch is located in the upper 0–30 cm soil layer (Varik et al., 2013). Three subplots were established across the main study plot, i.e four Rs and Rh measurement points per each subplot. To avoid any CO_2 leakage from the soil respiration chamber, PVC collars (Ø 10 cm, height 5 cm) were inserted at a depth of 3 cm for Rs measurements, and inside of the trenched plots for Rh measurements. The herbaceous vegetation was carefully removed from the inside the deep cylinders and collars with minimum soil disturbance, and both were kept free of the live vegetation throughout the study.

Soil temperature (Ts, °C) was measured simultaneously with soil respiration in the untrenched and trenched plots using the attached soil temperature probe STP-1 (PP Systems International, Inc., USA) inserted to a depth of 5 cm. Volumetric soil moisture (%) was also measured at a depth of 5 cm using the HH2 Moisture Meter Version 2 (Delta-T Devices Ltd, UK). In addition, soil temperature (model 1425, Spectrum Technologies, Inc, USA) and volumetric soil moisture (Water Scout sensor model SM 100, Spectrum Technologies, Inc, USA) were measured continuously at every hour from April to December in both study years, 2016–2017, in the TP and CP the both study sites. The data was stored with a data logger (WatchDog 1425, Spectrum Technologies, Inc, USA).

2.6. *Carbon leaching*

Leaching of C was estimated using stainless steel plate lysimeters (Roots and Voll, 2011; Uri et al., 2012; Becker et al., 2015; Morozov et al., 2019). In all study stands, 14 stainless steel plate lysimeters were installed (7 for TP + 7 for CP) in the soil at a depth of 40 cm at random points across the plot. The collecting area of a lysimeter was 627 cm^2. The lysimeters were connected to water collectors (6000 ml polyethylene canisters disposed at a depth of 1 m) by means of polyethylene tubes. Water from the canisters was sampled monthly from early spring to late autumn 2017 (up to the freezing of the soil), using a peristaltic vacuum pump, through a plastic pipe. The annual cumulative leaching flux was calculated by adding up the amounts of leached C for the different months (Uri et al., 2017b; Morozov et al., 2019).

2.7. *Carbon budgeting*

A C budget for the studied stands was compiled by balancing the input and output C fluxes for the studied plots for 2017, i.e. for the second post-thinning year. For defining net ecosystem production (NEP) (3), a well-known approach was employed: we calculated the difference between net primary production (NPP) and C loss through heterotrophic respiration (Rh) and leaching (L) (Clark et al., 2001; Lovett et al., 2006; Meyer et al., 2013), which we have used also in our recent studies (Uri et al., 2017a,b, 2019):

$$\mathrm{NEP} = \mathrm{NPP} - (\mathrm{Rh} + \mathrm{L}) \tag{3}$$

where NEP represents the rate at which C is accumulated in the ecosystem and is the main parameter characterizing forest as a C sink or as a C source (Chapin et al., 2006; Waring and Running, 2007). In the current study a positive value of NEP implies a net transfer of C from the atmosphere into the forest ecosystem (C sink) and a negative NEP implies a net transfer of C from the forest ecosystem to the atmosphere (C source). NPP was calculated by summing up the annual increments of the aboveground and belowground biomass fractions of the trees and herbaceous plants (Varik et al., 2015; Uri et al., 2019).

2.8. *Statistics*

The normality of variables was checked with the Lilliefors-test and the Shapiro-Wilk test. Statistical differences of the means were analysed by the *t*-test. The Mann Whitney U (M−W) test was used for analysing the data that did not follow a normal distribution. Allometric regression models were employed for estimating relationships between model tree biomass fractions or stemwood production with tree diameter. The quality of the fit of the models was evaluated by the coefficient of determination (R^2) and the level of probability (p).

Soil respiration data were normalised by log-transformation. The effects of treatment (thinning), time (month) and their interaction with Rs (or Rh) were tested using repeated measures ANOVA. In the case of significant effects ($p < 0.05$), the means were compared using Tukeýs HSD test. The *t*-test was used to estimate significant differences in soil temperature and soil moisture between the trenched and control plots, and between the treatments. Multiple linear regression, where Rs (or Rh) was the dependent variable and temperature and moisture were the two independent variables, was carried out for CP and TP of the stands in both study years. Pearson correlation coefficient between Rs (or Rh) and soil moisture was calculated; to eliminate the confounding effect of Ts, partial correlation analysis was further used. Overall, soil moisture had no significant effect on soil respiration rates. Hence an exponential model (4) was used to describe the relationship between Rs (or Rh) and soil temperature at a depth of 5 cm:

$$\mathrm{Rs(or\ Rh)} = a e^{b\mathrm{Ts}} \tag{4}$$

where a and b are the fitted parameters and Ts is soil temperature (°C).

Cumulative Rs and Rh fluxes for the period April-December were modelled using the daily mean soil temperature values from the data loggers. The annual Rh flux for the C budget was modelled using the data of soil temperature (March 2017 and January- February 2018) from the data loggers (data not shown).

The fitness of the models was based on the coefficient of determination (R^2) and the level of probability (p). In all cases, the level of significance $\alpha = 0.05$ was accepted. The programs STATISTICA 13.0 and R (R Development Core Team, 2008) were employed.

3. Results

3.1. Biomass and production of the trees

The aboveground biomass and the annual production of the trees were higher in the unthinned control plot (CP) than in thinned plot (TP) of both studied stands (Table 4). Stems (wood + bark) formed the largest share (76–77%) of the allocation of tree woody biomass. The stem mass of an average tree was 11 and 48 kg tree^{-1} higher in TP than in CP in the pole stand and the middle-aged stand, respectively. After thinning, annual woody biomass production decreased by 9% in both stands.

3.2. Litter flux of the trees

There was no short-term effect of thinning on the annual litter flux (Table 5). Leaf litter accounted for the largest share (69–85%) of the annual litter flux (Table 5), fluctuating slightly over the study years, but without a significant difference between the treatments (M−W, $p > 0.05$).

3.3. Fine root biomass and production

The dynamics of FRB for the pole stand followed a clear seasonal trend in both treatments: it was the highest in autumn (October) and the lowest in spring (May) (Table 6). In the middle-aged stand FRB peaked in August irrespective of the treatment. Fine root necromass did not differ between the treatments, except for the middle-aged stand in the first year after thinning where it was higher in TP than in CP (Table 6).

Two years after thinning (2017) there was no significant effect of harvesting on birch fine root bio- or necromass in the pole stand: mean annual FRB in TP and CP were similar (M−W, $p > 0.05$), 1.84 ± 0.04 and 2.12 ± 0.05 t ha^{-1}, respectively. Also fine root production (FRP) and turnover rates were similar between the treatments (TP versus CP) in the pole stand (Table 7). However, in the middle-aged stand mean FRB was significantly higher in TP than in CP and both FRP and turnover rate were lower in TP than in CP. Fine root longevity across all stands varied from 1.1 to 2.3 years (Table 7).

Thinning did not affect the vertical distribution of FRB, which was similar in all studied stands; 70–90% of the fine roots were located in the upper 0–20 cm layers and less than 10% were located in the deeper 30–40 cm layer (Fig. 1).

3.4. Above- and belowground production of the herbaceous plants

Thinning had a strong effect on the production of the aboveground herbaceous plants, being 40% larger in TP than in CP for both stands (Table 8). The biomass of the herbaceous plants' roots and rhizomes was similar in TP and CP for both stands. Comparison of the treatments showed that the biomass of the herbaceous plants was higher in the middle-aged stand than in the pole stand. In the pole stand, the aboveground part of the herbaceous plants was 3–5 times as large as the belowground part. In the middle-aged stand belowground production exceeded aboveground production, but only in CP (Table 8).

Table 5
Annual aboveground tree litter fluxes of the studied silver birch stands in 2016–2018 (n = 56 per treatment per year), TP- thinned plot, CP-control plot, average ± standard error (SE).

Stand	Year	Treatment	Leaves,	Branches,	Other,	All litterfall,
			t ha^{-1}			
Pole	2016	TP	2.4 ± 0.10	0.2 ± 0.01	0.4 ± 0.02	2.9 ± 0.10
		CP	2.3 ± 0.10	0.4 ± 0.02	0.5 ± 0.02	3.3 ± 0.09
	2017	TP	2.7 ± 0.06	0.2 ± 0.02	0.2 ± 0.01	3.1 ± 0.05
		CP	3.1 ± 0.07	0.2 ± 0.01	0.3 ± 0.01	3.6 ± 0.07
	2018	TP	2.1 ± 0.14	0.5 ± 0.03	0.4 ± 0.04	3.0 ± 0.11
		CP	2.7 ± 0.13	0.6 ± 0.02	0.5 ± 0.03	3.8 ± 0.11
Middle-aged	2016	TP	1.7 ± 0.15	0.3 ± 0.03	0.5 ± 0.05	2.5 ± 0.12
		CP	2.3 ± 0.18	0.4 ± 0.05	0.5 ± 0.05	3.2 ± 0.12
	2017	TP	2.1 ± 0.12	0.3 ± 0.02	0.3 ± 0.02	2.6 ± 0.10
		CP	2.7 ± 0.13	0.7 ± 0.03	0.3 ± 0.02	3.6 ± 0.11
	2018	TP	2.2 ± 0.10	0.2 ± 0.02	0.4 ± 0.04	2.7 ± 0.09
		CP	2.3 ± 0.15	0.5 ± 0.03	0.2 ± 0.03	3.1 ± 0.11

Table 6
Seasonal dynamics of the fine root biomass and necromass (t ha^{-1}) of the trees in the 0–40 cm soil layer in the studied stands, TP - thinned plot, CP - control plot, mean ± SE is presented.

Sampling time	Fine root biomass, t ha^{-1}			
	Pole		Middle-aged	
	TP	CP	TP	CP
Oct 2016	2.06 ± 0.07^a	2.32 ± 0.18^a	2.70 ± 0.12^a	1.40 ± 0.10^b
May 2017	1.33 ± 0.06^a	1.66 ± 0.07^a	1.85 ± 0.09^a	1.43 ± 0.07^a
Aug 2017	1.49 ± 0.07^a	1.78 ± 0.07^a	2.95 ± 0.11^a	2.93 ± 0.13^a
Oct 2017	2.49 ± 0.09^a	2.73 ± 0.10^a	2.41 ± 0.09^a	2.53 ± 0.11^a
	Fine root necromass, t ha^{-1}			
	Pole		Middle-aged	
	TP	CP	TP	CP
Oct 2016	0.27 ± 0.01^a	0.27 ± 0.02^a	0.32 ± 0.01^a	0.18 ± 0.01^b
May 2017	0.42 ± 0.03^a	0.34 ± 0.03^a	0.53 ± 0.03^a	0.45 ± 0.02^a
Aug 2017	0.65 ± 0.04^a	0.56 ± 0.04^a	0.52 ± 0.02^a	0.47 ± 0.02^a
Oct 2017	0.36 ± 0.02^a	0.53 ± 0.02^a	0.46 ± 0.03^a	0.56 ± 0.02^a

Statistically significant difference between the treatments is denoted with letters ^{a} and ^{b}.

Table 4
Fractional distribution of the woody biomass and production in the studied silver birch stands two years after thinning (2017), TP-thinned plot, CP-control plot.

Fraction	Biomass, t ha^{-1}				Annual production, t ha^{-1} a^{-1}			
	Pole		Middle-aged		Pole		Middle-aged	
	TP	CP	TP	CP	TP	CP	TP	CP
Stemwood	95.16	103.5	95.54	114.6	8.13	9.01	7.1	7.95
Stembark	14.78	18.40	11.41	11.77	1.26	1.6	0.85	0.82
Current year shoots	0.35	0.37	0.49	0.34	0.35	0.37	0.49	0.34
Old branches	6.34	8.90	8.16	10.93	0.56	0.78	0.61	0.76
Stump and coarse roots	25.05	28.19	24.71	29.48	2.15	2.46	1.84	2.05
Total	*141.7*	*159.3*	*140.3*	*167.2*	*12.5*	*14.2*	*10.9*	*11.9*

Table 7
Mean fine root biomass (FRB), fine root production (FRP), fine root turnover rate and longevity for the studied stands two years after thinning (2017), TP - thinned plot, CP - control plot, mean ± SE is presented.

Stand	Treatment	Mean FRB, t ha^{-1}	FRP, t ha^{-1} yr^{-1}	Turnover rate, y^{-1}	Longevity, y
Pole	TP	1.84 ± 0.27^{a}	1.39	0.75	1.33
	CP	2.12 ± 0.25^{a}	1.29	0.61	1.65
Middle-aged	TP	2.48 ± 0.24^{a}	1.10	0.44	2.25
	CP	2.07 ± 0.40^{b}	1.82	0.88	1.14

Statistically significant difference between the treatments within stand are denoted with letters ^{a} and ^{b}.

Table 8
The above- and belowground biomass and production of the herbaceous plants in the studied stands in 2017 (n = 10 per treatment), TP - thinned plot, CP - control plot.

Biomass/production of the herbaceous plants	Pole		Middle aged	
	TP	CP	TP	CP
	t ha^{-1} yr^{-1}			
Aboveground	1.20 ± 0.20^{a}	0.70 ± 0.10^{b}	2.10 ± 0.20^{a}	1.30 ± 0.20^{b}
Belowground	0.26 ± 0.01^{a}	0.25 ± 0.01^{a}	1.43 ± 0.10^{a}	1.58 ± 0.11^{a}

Statistically significant difference between the treatments is denoted with letters ^{a} and ^{b}.

Table 9
Carbon storages of the studied stands, TP- thinned plot, CP-control plot.

	Pole		Middle-aged	
	TP	CP	TP	CP
Component	C storage, t C ha^{-1}			
Aboveground				
Trees (including leaves)	59.7	67.2	58.7	70.0
Herbaceous plants	0.5	0.3	0.9	0.6
Total	***60.2***	***67.5***	***59.6***	***70.5***
Belowground				
Trees	18.1	20.3	17.8	21.0
Herbaceous plants	0.1	0.1	0.7	0.7
Total	***18.2***	***20.4***	***18.4***	***21.8***
Aboveground + belowground	**78.4**	**88.0**	**78.1**	**92.3**
Soil	***77.8***	***77.7***	***64.9***	***67.0***
Biomass + soil	**156.2**	**165.7**	**143.0**	**159.3**

3.5. Ecosystem carbon storages

Overall, stand total C pools were of the same magnitude across all studied treatment plots (Table 9). However, the aboveground C storage was higher in the CPs in all cases and the trees made up to 99% of the total aboveground C storage. In the middle-aged stand, 55–57% of the total ecosystem C was stored in biomass and 43–45% in the mineral soil; in the pole stand its share was 50–53% and 47–50%, respectively.

3.6. Soil respiration and microclimate

The seasonal dynamics of soil temperature was very similar in CP and TP for both the pole and the middle-aged stand, with a peak in the summer months (S2); trenching did not affect soil temperature ($p > 0.05$). In the first post-thinning year (2016) overall mean soil temperature (April-Dec) was not significantly different between CP and TP in the pole stand ($p > 0.05$), but it was higher in TP than in CP for the middle-aged stand (S1; $p < 0.05$). Mean soil temperature (April-Dec) was not significantly different between CP and TP in the following year ($p > 0.05$), however, a trend for higher temperature during the growing season (May-September) was evident in TP vs CP (S1). The seasonal dynamics of soil moisture was also similar in CP and TP (S3). Trenching did not affect soil moisture in the middle-aged stand ($p > 0.05$) but increased it by 21% in CP and by 17% in TP of the pole stand over the measurement period ($p < 0.05$). In the pole stand TP was drier than CP; in the middle-aged stand TP was drier than CP only in the second post-thinning year (S1, S3; $p < 0.05$).

The seasonal dynamics of Rs and Rh showed a similar pattern for CP and TP in both studied stands (Fig. 2), following the dynamics of soil temperature. In general, thinning did not affect significantly Rs. Only in the middle-aged stand in 2017 did thinning increase Rs by 21% ($p < 0.05$). In the pole stand thinning increased Rh by 13% in the first post-thinning year ($p < 0.05$), but did not affect it in the following year; nor did thinning affect Rh in either year for the middle-aged stand ($p > 0.05$).

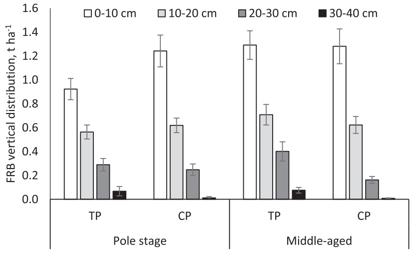

Fig. 1. Vertical distribution of fine root biomass (FRB), TP-thinned plot, CP-control plot; data was calculated across the four sampling sessions (Oct 2016-Oct 2017), bars indicate standard error.

The cumulative Rs fluxes for April-December across the studied stands varied between 5.3 and 6.7 t C ha^{-1}, except in TP of the middle-aged stand, where they amounted to 8.1 t C ha^{-1} (Table 10). The cumulative Rh fluxes varied between 3.6 and 5.1 t C ha^{-1}. Although cumulative Rh for both stands and cumulative Rs for the middle-aged stand increased after thinning (Table 10), the mean modelled soil C effluxes were not significantly different between TP and CP (*t*-test, $p > 0.05$). Thinning increased the average contribution of Rh to Rs in the pole stand, but decreased the corresponding ratio for the middle-aged stand (Table 10).

Overall, soil temperature was the main driver of seasonal variation in the soil CO_2 effluxes, describing 64–87% of the variation in Rs and 50–78% of the variation in Rh (S4). Weak relationship between Rh and soil temperature was found for the pole stand in two cases: in CP in 2016 (adjusted determination coefficient $R^2 = 28\%$) and in TP in 2017 (adjusted $R^2 = 20\%$). There was no significant difference in parameters a and b of Eq. (2) between CP and TP. The effect of soil moisture on the soil CO_2 effluxes was nonsignificant. A weak significant positive effect of soil moisture on Rh was only found for TP in the pole stand in 2016 (partial correlation $r = 0.47$, $p = 0.037$).

3.7. Leaching

The annual flux of C leaching in both stands was small, however, in the pole stand it was larger in CP than in TP, 9.7 versus 4.2 kg C ha^{-1} yr^{-1}, respectively. The amount of leached C in the middle-aged stand was 12.1 kg C ha^{-1} yr^{-1} in CP and 9.1 kg C ha^{-1} yr^{-1} in TP.

3.8. Ecosystem carbon budgets

Both TPs and CPs acted as C sinks in the studied stands (Table 11). The main C efflux was heterotrophic respiration, which was slightly higher in TP, but the difference was not significant ($p > 0.05$). Net primary production (NPP) of the pole and middle-aged stands were of

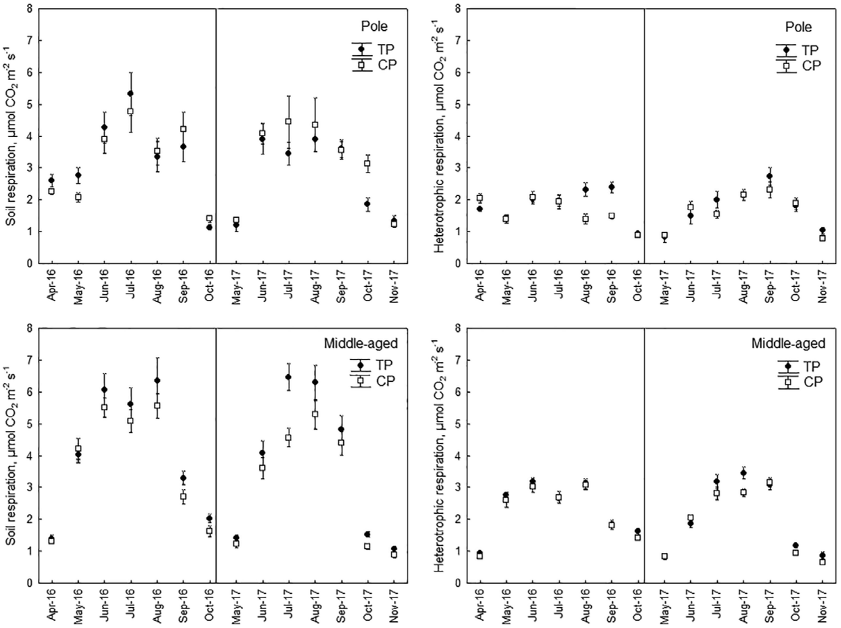

Fig. 2. Seasonal dynamics of total soil respiration (Rs) and heterotrophic soil respiration (Rh) of the studied stands in 2016 and 2017 (n = 168 per treatment), TP- thinned plot, CP- control plot; data represent mean (±SE).

Table 10
Cumulative total soil (Rs) and heterotrophic respiration (Rh) fluxes (t C ha^{-1}) and the Rh to Rs ratio for the studied stands in April-December 2016 and 2017, TP- thinned plot, CP- control plot.

Stand	Treatment	2016			2017		
		Rs	Rh	Rh/Rs	Rs	Rh	Rh/Rs
Pole	TP	6.4	4.1	0.63	5.3	3.8	0.70
	CP	6.7	3.8	0.56	6.4	3.6	0.56
Middle-aged	TP	8.1	5.1	0.63	7.3	4.3	0.60
	CP	6.5	4.5	0.69	5.5	3.7	0.67

the same magnitude. The largest share of C was accumulated in the stems of the trees. The leaf litter C input to the soil was larger than the fine root litter C input. The production of the herbaceous plants was higher in TP compared to CP for both studied stands.

4. Discussion

Thinning changes the functioning of a forest ecosystem in several ways, as the outcome is multifaceted and affected by many factors, of which tree species, stand age, site type and thinning intensity have the largest impact. Although thinning is a widespread silvicultural method, its influence on ecosystem C cycling is still poorly studied. Present case study examined the effect of thinning on silver birch stands C budget in pole- and middle-aged stand, for improving existing knowledge in this field of research. However, the lack of replications in the current study limits broader generalization of the results, as well as estimates of variability of C storages and fluxes.

Thinning usually leads to a temporary decrease of both the C storage and C accumulation of stands. However, results of the current case study demonstrate only a moderate decrease of NEP after thinning in both studied birch stands (Table 11); two years after thinning NEP was 1.2 t C ha^{-1} yr^{-1} smaller in TP of the pole and 1.6 t C ha^{-1} yr^{-1} smaller in TP of the middle-aged birch stand. However, their C budgets still remained strongly positive in both cases (Table 11). The decrease of NEP (Table 11) was the consequence of the reduced annual biomass production of the ecosystem, while its decline was less evident in the pole stand (23%) than in the middle-aged stand (30%). Thinning intensity was quite low, accounting for 17% and 21% of the basal area for the pole and the middle-aged stand, respectively, which is typical practice in Estonian traditional forest management, as forest owners tend to leave stands slightly denser to avoid wind and snow damage. Because of moderate thinning, decrease of the annual production of stand (trees) was only 9–12% (Table 4). It can be expected that the reduction is short-term, according to earlier studies. Silver birch is a highly productive tree species, especially at young age (Hynynen et al., 2010; Hytönen et al., 2014; Varik et al., 2015), and the removed biomass of the trees will recover quickly. Intensive biomass production after thinning is also inherent to other tree species; Dore et al., (2012) reported that although thinning reduced the NEE markedly in a ponderosa pine stand, its productivity recovered during four post-treatment years and the net C

Table 11
Carbon (C) budgets of the studied silver birch stands two years after thinning, NPP- net primary production, NEP- net ecosystem production, TP- thinned plot, CP-control plot.

			Pole		Middle-aged	
			TP	CP	TP	CP
		Fluxes		t C ha^{-1} yr^{-1}		
C inputs		*Plant aboveground*				
	1	Stem increment	4.69	5.31	3.96	4.36
	2	Current year shoots	0.18	0.19	0.25	0.18
	3	Branch increment	0.27	0.39	0.31	0.38
	4	Leaf litter	1.36	1.58	1.05	1.36
	5	Branch litter	0.14	0.12	0.14	0.34
	6	Other litter	0.10	0.14	0.13	0.12
	7	Production of herbaceous plants	0.52	0.30	0.91	0.56
		Plant belowground				
	8	Coarse root biomass increment	1.03	1.18	0.88	0.99
	9	Tree fine root production	0.71	0.66	0.57	0.94
	10	Fine root and rhizome production of herbaceous plants	0.12	0.12	0.66	0.73
		Soil				
C outputs	11	Heterotrophic respiration	4.46	4.13	4.84	4.16
	12	Leaching	0.01	0.01	0.01	0.01
	13	C input to the soil (4 + 5 + 6 + 7 + 9 + 10)	2.95	2.92	3.46	4.05
	14	Soil C exchange (13-(11 + 12))	−1.5	−1.2	−1.4	−0.1
		Productivity				
	15	NPP = (1 + 2 + 3 + 4 + 7 + 8 + 9 + 10)	8.89	9.74	8.59	9.50
	16	NEP = 15-(11 + 12)	4.43	5.60	3.75	5.34

uptake in the thinned stand was slightly higher compared to the unthinned stand.

In both stands, thinning had a significant effect on the forest aboveground C storage (Table 9) rather than on the annual C fluxes (Table 11). However, since thinning affects several stand characteristics, among them herbaceous plants, fine roots, soil respiration etc., a more sophisticated understanding of the effect of thinning on C cycling, as well as on the functioning of the ecosystem is needed. For this purpose, C budgeting serves as a relevant tool, demonstrating how the forest ecosystem is functioning after thinning in changed environmental conditions. NEP is a widely used informative parameter characterizing the functioning of the forest ecosystem as a C sink or as a C source (Chapin et al., 2006; Waring and Running, 2007). In the present study C budgeting was applied to estimate the effect of thinning on ecosystem's C cycling and to clarify the role of each particular C flux in shaping NEP.

Earlier studies conducted in boreal forest demonstrate that the reduction of the basal area of stand by 26% does not lead to significant differences in NEE between the unthinned and the thinned sections, as the increased C uptake by the ground vegetation compensates for reduced canopy photosynthesis (Vesala et al., 2005). Also in the present study thinning stimulated the growth of the herbaceous plants (Tables 8 and 9). Still, this did not compensate for the decrease of the production of the trees on the stand level; in the pole stand the total production of the trees decreased 1.1 t C ha yr^{-1}, while the production of the herbaceous plants increased only 0.2 t C ha^{-1} yr^{-1}; in the middle-aged stand the respective values were 1.3 and 0.3 t C ha yr^{-1}. Thus, considering short-term post-thinning effects, the increased biomass of the herbaceous plants compensated for only a modest part of the reduced C sink of the tree layer. Of course, the biomass and species composition of herbaceous plants depends on many factors among which soil fertility and light conditions play the major role. It should be noted that the shrub layer, which may also account for an essential part of the stand C storage (Vogel and Gower, 1998), was absent from the studied stands.

The C balance of an ecosystem depends on the C input fluxes, on the one hand, and on the C output fluxes, on the other hand. Cumulative heterotrophic respiration (Rh) represents the main C efflux in the studied stands; the average contribution of Rh to Rs varied between 0.56 and 0.70, which is in accordance with other studies (Cheng et al., 2015; Lei et al., 2018). The annual Rh flux was of the same magnitude across the treatments, being only slightly higher in TPs and contributing modestly to the decrease of NEP (Table 11).

Studies estimating the effect of thinning on Rs have shown inconsistent results. When some authors report enhanced Rs after thinning (Cheng et al., 2015; Shabaga et al., 2015), then others have found a decrease of Rs (Tang et al., 2005; Sullivan et al., 2008) or no change at all (Ma et al., 2004; Campbell et al., 2009). A recent meta-analysis concluded that in broadleaved forests thinning significantly increased Rs (Zhang et al., 2018). Soil temperature and soil moisture are considered the best environmental predictors of changes in soil respiration (Raich and Schlesinger, 1992). Usually, thinning has been shown to increase soil temperature (Peng and Thomas, 2006; Cheng et al., 2014; Shabaga et al., 2015; Zhang et al., 2018) as a result of increased soil insolation after canopy thinning and understorey removal (Lei et al., 2018). In this study, thinning altered the soil environment through increasing soil temperature mainly in spring and summer (S1). Soil temperature increase for the studied months varied between 0.1 and 1.5 °C. In late autumn and winter (December) (S1) thinning resulted in lower soil temperatures (0.3–1 °C) because of enhanced radiation related cooling. The thinning treatments were generally drier than the unharvested sites probably because of the higher evaporation of the surface soil layer. It has been found that during 3 years after thinning, soil moisture can be lower in thinned *Pinus massoniana* stands (Lei et al., 2018) and in mixed deciduous forests (Shabaga et al., 2015). Thinning intensity can play an important role in soil moisture. According to a meta-analysis based on 53 publications, only moderate and heavy thinning significantly increased soil moisture (Zhang et al., 2018).

In this study soil temperature explained 64–87% of the variation in Rs and 50–78% of the variation in Rh (except in 2016 for CP and in 2017 for TP in the pole stand), while soil moisture had no significant effect on the soil CO_2 effluxes. In general, thinning did not significantly influence the soil CO_2 effluxes at the early post-thinning stage: modelled mean Rs and Rh were similar in CP and TP in both stands. Estimation of differences between the parameters of the exponential model showed that thinning did not significantly change the response of Rs and Rh to soil temperature, which is in accordance with studies by Tang et al. (2005) and Sullivan et al. (2008). The effect of forest thinning on Rs is a combined result of changes in the microclimate, caused by both thinning and inter-annual climate variability, and changes in the substrate supply, i.e litterfall and fine root biomass and production (Tang et al., 2005), which are all expected to change by forest thinning (Peng and Thomas, 2006; Zhang et al., 2018). In the current study litterfall and fine root production did not change after thinning, which may be a possible reason for the non-response of Rs and Rh to thinning.

Litterfall is the major aboveground input of C and nutrients to the soil in forest ecosystems (Starr et al., 2005; Neumann et al., 2018) and affects also Rh (Scott-Denton et al., 2006). The annual leaf litter input was not markedly smaller after thinning (Table 5), which can be explained by low thinning intensity, as well as by the removal of largely suppressed trees with relatively short crowns and small leaf mass. The annual leaf litter flux across both stands and treatments varied from 1.7 to 3.1 t ha^{-1} yr^{-1}, which falls in the range for silver birch and downy birch stands of different ages in Estonia (Uri et al., 2012, 2017b). Leaf litter dynamics demonstrated an expected trend during the three-year study period (2016–2018) for the middle-aged stand, i.e. the annual litter flux was not statistically different between TP and CP.

Another major C input to the soil is fine root production (FRP) (Finér et al., 2011; Lukac, 2012). When FRB is a relatively small C pool, then FRP can make up to 75% of annual NPP (Finér et al., 2011). However, the belowground C flux is the main bottleneck in the study of forest ecosystem's C cycling (Leppälammi-Kujansuu et al., 2014): FRP and FRB are often underestimated or even excluded from these studies. In the current study FRB varied between 2.4 and 2.7 t ha^{-1} across the studied stands and plots (Table 7), being of the same magnitude as reported for silver birch boreal forests (Ding et al., 2019), and similar to the general average value of FRB (2.3 t ha^{-1}) reported for boreal forests (Jackson et al., 1997). These results are also in good accordance with earlier estimations for young and middle-aged Estonian birch stands (1.9–2.4 t ha^{-1}) (Varik et al., 2013). The annual FRP values were close to the earlier results for silver birch stands estimated by the ingrowth core method (Varik et al., 2015). In the second post-thinning year, the level of FRP was the same as in the unthinned plot (0.71 and 0.66 t C ha^{-1} yr^{-1}, respectively) in the pole stand, which indicates that the remaining trees did not respond to thinning by intensified FRP. The turnover rates across the stands ranged from 0.44 to 0.75, which is also consistent with an earlier study of Estonian silver birch stands (Varik et al., 2015). An increase of fine root necromass after thinning (due to removed trees), contributing to the additional organic C input to the soil and to the rise of Rh, is expected. However, in the current study increased necromass was seen only for the middle-aged stand in the first post-thinning year (Table 6). According to Vesala et al. (2005), birch leaves and dead fine roots are a major new source of C for microbes to decompose at the early post-thinning stage. In the current study the above- to belowground litter ratio indicated that aboveground leaf litter was a larger C flux to soil compared with the C input from FRP. Thus, the results of FRB and FRP are in line with the results of Rh, i.e. there was no significant increase of FRB or FRP in the subsequent post-thinning years, which could have been a source of labile soil C and increased Rh.

C leaching was very low (Table 11), which is consistent with earlier similar studies (Uri et al., 2017a; Becker et al., 2016). Because of its negligible share of the leached TOC flux in the whole budget, it is often ignored in C budgeting (Varik et al., 2015).

Regarding soil C exchange, the output and input fluxes were more or less balanced in the CP of the middle-aged stand. In the other treatment plots, soil C loss through Rh exceeded the C input into the soil through organic litter (Table 11). This could be explained by the fact the production and turnover of extrametric mycorrhizal mycelia is not taken into account in C budgets (Wallander et al., 2013). Moreover, Wallander et al. (2004) suggested that the C inputs from fine roots and mycorrhizal hyphae were even of the same order of magnitude. A similar imbalance was noted also in our earlier silver birch chronosequence study (Varik et al., 2015). Also the estimation of different C pools and fluxes is often erroneous, which affects the balance of C budgets.

5. Conclusions

Although thinning reduced NEP in the studied silver birch stands, the whole ecosystems still remained C sinks. The effect of thinning on NEP was more evident in the middle-aged stand than in the young stand, decreasing 1.6 and 1.2 t C ha yr^{-1} (i.e. 23–30%), respectively. Owing to the high biomass production ability of birches, fast recovery of NEP is expected, which means that the decrease of the C sink is short-term. The C accumulation by the herbaceous plants increased after thinning, but it did not compensate for the decreased C accumulation by the trees. Compared to the unthinned stands, the effect of thinning on the soil output fluxes was weak, and possibly associated with minor changes in the input fluxes (leaf litter flux, fine root production).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118660.

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III

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Short-term effect of thinning on the carbon budget of young and middle-aged Scots pine (*Pinus sylvestris* L.) stands

K. Aun [a,*], M. Kukumägi [a,b], M. Varik [a], H. Becker [a], J. Aosaar [a], M. Uri [a], G. Morozov [a], M. Buht [a], V. Uri [a]

[a] *Estonian University of Life Sciences, Institute of Forestry and Rural Engineering, F. R. Kreutzwaldi 5, 51006 Tartu, Estonia*
[b] *University of Tartu, Institute of Ecology and Earth Sciences, Vanemuise 46, 51014 Tartu, Estonia*

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ABSTRACT

Thinning is the main silvicultural method for improving stand growth and wood quality, however, despite the relevance and extensive use of thinning in forest management, its effect on stand carbon (C) balance is still poorly studied at the ecosystem level. The present case study estimated the two-year post-thinning effect on the C balance of a pole stand and a middle-aged Scots pine stand growing on mesotrophic sandy soils. Moderate thinning from below reduced the stand C storage by 21–24%, however, the amount of C accumulated in woody biomass, which was removed by logging, is expected to recover in both stands in the following four years. The reduced biomass of the trees contributed to the decreased annual net primary production (NPP) of the stand by 9–11%. The absolute value of net ecosystem production decreased by 0.9 and 0.7 t C ha^{-1} yr^{-1} in the pole and the middle-aged stand, respectively; still, both thinned plots maintained their C sink status. The production of the herbaceous understorey as well as the production of needles increased in the younger stand after thinning, but this could not compensate for C loss at the stand level. The effect of thinning on the production of mosses and dwarf shrubs was not expressed in either stand, probably due to the too short post-thinning period. Thinning did not significantly affect either total soil respiration or the heterotrophic respiration (Rh). However, it increased the contribution of Rh to total soil respiration, which can be attributed to decreased fine root biomass and root respiration, while the aboveground litterfall was not significantly changed after thinning. Fine root production, which accounted for the main belowground litter input, was significantly lower in both thinned plots. Moderate thinning in the pole and the middle-aged Scots pine stand did not change the ecosystem into a C source and the induced C loss will be compensated during a short post-thinning period.

1. Introduction

Climate change and carbon (C) sequestration are important issues in the light of increased concentration of atmospheric carbon dioxide (CO_2) (Nabuurs et al., 2007) and forest ecosystems have an important role in C cycling and mitigation of climate changes at the global and regional levels, accumulating C in biomass, as well as in the soil (Mund et al., 2002; Laiho et al., 2003; Pan et al., 2011; Bravo-Oviedo et al., 2015). Although almost half of total organic C in terrestrial ecosystems is stored in forest soils (Mayer et al., 2020), the proportion of C stored in biomass and in the soil may still be highly variable in different forests, depending on tree species, soil type and land use history (Vesterdal et al., 2002; Uri et al., 2014, 2017ab; Mayer et al., 2020). Also forest management plays an important role in C accumulation and although globally unmanaged forests may have about 50% larger C stocks compared to managed forests, their net ecosystem productivity (NEP) is usually lower (Noormets et al., 2015).

Among different silvicultural methods, thinning is a principal management practice for improving stand growth and wood quality, especially in naturally regenerated dense stands where stem properties are highly variable (Rytter and Werner, 2007; del Río et al., 2017). However, thinning brings out changes of various degree in the C storages and fluxes of the forest ecosystem. Several studies report minor effects of thinning on C sequestration in forest and the recovery time from thinning within a couple of years (Misson et al., 2005; Vesala et al., 2005; Dore et al., 2010; 2012; Saunders et al., 2012; Trant, 2013). Others claim that forest ecosystems need longer time to recover from the loss of C uptake due to thinning (Scott et al., 2004; Lindroth et al., 2018) and that

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* Corresponding author.
E-mail address: kristiina.aun@emu.ee (K. Aun).

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thinning can greatly affect the C storages and fluxes of the forest ecosystem (Jandl et al., 2007; Pang et al., 2013; Bravo-Oviedo et al., 2015; Çömez et al., 2019).

However, the results of various studies indicate that the response of ecosystems to thinning is highly multifaceted, being related to changes in above- and belowground processes and microclimatic conditions. C balance of an ecosystem results from gross primary production and ecosystem respiration, which in turn consists of respiratory losses from plant metabolism (autotrophic respiration: above- and belowground plant respiration) and microbial respiration from the decomposition of dead organic matter (heterotrophic respiration (Rh)). Belowground plant respiration and Rh are components of total soil respiration (Rs) which can contribute two thirds of ecosystem respiration in Scots pine forest (Kolari et al., 2009). Heterotrophic respiration, representing the main C efflux in forest ecosystems (Uri et al., 2017ab; Kukumägi et al., 2017; Kriiska et al., 2019), is inevitably affected by thinning (Lei et al., 2018) through changes in the microclimate and substrate availability such as litterfall (Zhang et al., 2018; Chen et al., 2020). Input of harvest residues and dead roots via potentially increased soil temperature and soil moisture, as well as changes in fine root biomass and production (Lei et al., 2018; Zhang et al., 2018; Zhao et al., 2019), can affect the balance between the soil respiration components, i.e. Rh and belowground plant respiration.

Although studies of C cycling have been especially highlighted in recent decades for a better understanding of C sequestration capacity and dynamics of different forest ecosystems, studies of whole C budgets at the ecosystem level are still rare and their results are somewhat contradictory.

The current case study was carried out in a 25-year-old and in a 45-year-old Scots pine stand in Southern Estonia, growing on mesotrophic sandy soils, which is a common type of the pine ecosystem in the Northern and Baltic countries. As Scots pine is a native widespread species in Eurasia and the most dominant tree species in Northern European as well as in Estonian forests, it has great ecological and economical importance in the forestry of many countries. In Estonia, Scots pine stands cover over 31% of forest land, being the most widespread tree species (Yearbook Forest, 2019).

The aim of the present case study was to estimate the short-term effect of thinning on C balance in pole stage and middle-aged Scots pine stands. For that purpose, all main C fluxes and storages of the ecosystem were evaluated and C budgets were compiled for the thinned and unthinned stands. We hypothesized that although annual net primary production (NPP) decreases after moderate thinning from below due to the removal of trees and the potential increase of heterotrophic respiration, the whole ecosystem will still remain a C sink.

2. Materials and methods

2.1. Study sites

Two naturally regenerated Scots pine stands in southeastern Estonia, a 25-year-old (pole) and a 45-year-old (middle-aged) stand, were included in the study (Table 1). Both pure stands were even-aged and growing in a *Myrtillus* site type according to a local classification (Lõhmus, 1984). In both studied stands two sample plots were established in 2015 and thinning from below was carried out in one plot (September 2015), the other plot remained the control. All stumps and harvest residues were left at the site and the stems were collected for commercial use according to local forest management practices. The area surrounding the thinned plot was also thinned in a similar mode to avoid the edge effect. Buffer zone allowed the harvesting of model trees without disturbing the sample plots.

The thinning intensity was 31% and 24% of the basal area for the pole stand and for the middle-aged stand, respectively, which follows local forest management practices. The size of the sample plots was 0.08–0.09 ha. The main stand characteristics were measured after thinning (Table 1).

Table 1
Characteristics of the study sites in 2017; $D_{1,3}$ – average stand diameter at breast height, H – average stand height, BA – basal area of stand, Mean ± standard error (SE) is presented.

Stand	Treatment	Stand density, trees ha^{-1}	$D_{1.3,}$ cm	H, m	BA, m^2 ha^{-1}
Pole	Thinned	1178	14.2 ± 0.3^a	13.7 ± 0.4^a	18.8
	Control	2722	11.3 ± 0.2^b	14.2 ± 0.9^a	27.2
Middle-aged	Thinned	813	19.5 ± 0.5^a	18.9 ± 0.4^a	24.2
	Control	1373	17.2 ± 0.5^b	18.1 ± 0.5^a	31.8

Statistically significant difference between the treatments within stand is denoted by letters ^{a} and ^{b}.

2.2. Estimation of biomass and production

2.2.1. Aboveground biomass and production of trees

The model tree method (Bormann and Gordon, 1984; Uri et al., 2017ab) was used for determining aboveground biomass. In August 2017, in both stands, 5 model trees were felled per treatment (outside the intact plots), following the diameter distribution of the remaining trees. The model trees were processed as described in our parallel study (Aun et al., 2021); the stems of the model trees were separated into 5 stem sections: 0–1.3 m, 1.3 m until the beginning of the living crown and the crown in turn was divided into 3 equal sections. A stem disc was taken from each section for determining the proportion of the stemwood and stembark, as well as, dry matter content and for measuring radial growth. The stems and the branches were weighed in field and one model branch was selected from each crown section, which was thereafter fractionated in the laboratory into current year needles, current-year shoots, older needles and older branches. Subsamples were taken from each fraction for determining dry matter content. For that purpose, they were weighed, dried at 70 °C and reweighed to 0.01 g in the laboratory and dry mass for each fraction was calculated using dry matter content.

Allometric equation (1) was created for estimation of the aboveground biomass and stemwood production of the sample plot (Uri et al., 2017ab)

$$y = ax^b \tag{1}$$

where y is the aboveground biomass or annual stemwood production of tree (g), x is breast height diameter (cm), a and b are the parameters of the model (Supplementary material 1 (S1)). For more statistically reliable biomass models, the data of the model trees from thinned and control plots were pooled, assuming that for the short (2 year) post-thinning period, the allometric relationship between tree dimensions and biomasses was similar for the thinned and the control plots (Aun et al., 2021).

The biomass of the needles, current shoots and branches, as well as the proportion of the stemwood and bark were calculated on the basis of the percentage distribution of the fractions of the model trees separately for the thinned and the control plots.

Stemwood production was calculated on the basis of the width of the annual rings which were measured from the stem cross-section discs. Dried discs were polished and the width of the annual rings were measured to 0.001 mm using the software WINDENDRO (Regent Instruments Inc.). The Whittaker and Woodwell (1968) Eq. (2)

$$W_i = W_0\left(r^2 - (r - i)^2\right) / r^2 \tag{2}$$

was used to calculate annual stemwood production for the different sections of the model trees where, W_i is the annual dry mass increment of stemwood (g), W_0 is the dry mass of the stemwood (g), r is the radius of the analysed disc (mm), i is the thickness of annual ring (mm). The stemwood production of the model tree was calculated by summing up the production of each stem section.

The relative increments of the wood and bark fractions were assumed to develop proportionately and the production of the branches was determined using the relative increment of the stemwood (Uri et al., 2012). The C storage for the different fractions was calculated using C concentrations for the different fractions of the Scots pine stand (Uri et al., 2019).

2.2.2. Aboveground biomass and production of understorey plants

Ten random samples were taken from each plot for estimation of the aboveground biomass of the understorey plants, at the end of July 2017 when maximum aboveground biomass was achieved. The aboveground biomass of all understorey vegetation was taken from a 0.5 m^2 quadrat (cut as close to the ground surface as possible), dried at 70 °C to constant weight and weighed in the laboratory (Uri et al., 2017ab). The samples were collected randomly along the diagonal traversing the sample plot (five samplings per one diagonal and five per the other diagonal). Additionally, for estimation of the biomass of mosses, a metal frame (25 × 25 cm) was placed randomly in the quadrat and all mosses within the frame were collected. The dry mass of moss samples was estimated.

The annual production of the herbaceous plants was assumed to be equal to their biomass, since the biomass of herbs is annual (Uri et al., 2017ab). For estimation of the production of the dwarf shrubs (mainly *Vaccinium myrtillus*), subsamples were taken and the current-year growth (shoots, leaves) was separated and considered as annual production. The annual production of moss biomass at the ecosystem level was calculated by using the average share (%) of annual increment in the total biomass of the mosses (Uri et al., 2019).

A C concentration of 43.4% was used to calculate the C storage of the herbaceous plants (Uri et al., 2017b, 2019). C concentrations of 46.4% and 44.5% were used to calculate the C storages of the dwarf shrubs and mosses, respectively (Uri et al., 2019).

2.2.3. Stump and coarse root biomass and production of trees

The belowground biomass of the stump and coarse roots was assumed to be 19.9% of aboveground woody biomass according to a regional study carried out in a similar heath forest (Külla, 1997). Annual coarse root production was calculated on the basis of the equal relative increments of wooden aboveground biomass; the proportional increments of the aboveground and belowground woody biomass fractions were assumed to be equal (Uri et al., 2017ab). A C concentration of 45.8% was employed for different belowground biomass fractions to estimate the belowground C storages and accumulation (Uri et al., 2019).

2.2.4. Fine root biomass and production of trees and understorey plants

The fine root (diameter < 2 mm) biomass (FRB) of the pine and dwarf shrubs as well as the belowground biomass of the herbaceous plants were estimated using the soil coring method (Vogt and Persson, 1991; Stober et al., 2000; Ostonen et al., 2005). Sampling was carried out in October 2017 when fifteen soil monoliths were collected randomly along the diagonal traversing the sample plot from both stands to a soil depth of 40 cm. The monoliths were separated into depth layers (0–10; 10–20; 20–30 and 30–40 cm), then packed, labelled and transported to the laboratory, where the samples were stored in the freezer at −5 °C until further processing. In the laboratory, the samples were defrosted and washed carefully for extracting roots from the soil. The samples were sorted under the binoculars into the different fractions: the living and dead fine roots of pine and dwarf shrubs, and the roots and rhizomes of the herbaceous plants. The sorted samples were dried at 70 °C to constant weight and weighed to 0.001 g for calculating FRB.

For estimation of fine root production (FRP), an average turnover rate of 0.84 yr^{-1} was used for Scots pine stands (Brunner et al., 2009) and 0.20 yr^{-1} was used for dwarf shrubs (Uri et al., 2019). FRP was considered to be equal to the input of both annual belowground litter and the C flux to the soil (Kleja et al., 2008; Varik et al., 2015; Ding et al., 2019). Since the production, dying and decomposition of fine roots in closed canopy forests are continuous and long-lasting processes, annual FRP is considered a steady state C flux into the soil (Meyer et al., 2013). An average C concentration of 50.1% (Uri et al., 2019) was used for calculation of the C storage in the fine roots of the pine trees. For calculation of the C storage in the fine roots of the dwarf shrubs, a C concentration of 46.4%, was used, as established by the dry combustion method with a varioMAX CNS elemental analyser (ELEMENTAR, Germany). The total belowground biomass of the dwarf shrubs was not estimated, since soil coring is not an appropriate method for estimating the biomass of coarser root fractions.

For the belowground fraction of the herbaceous plants, the turnover rate was assumed to be 1 year (Lõhmus et al., 2002; Uri et al., 2011) and an average C concentration of 43.4% (Uri et al., 2019) was used for calculation of the C storage.

2.3. Aboveground litter flux of trees

Seven litter traps with a collecting area of 0.36 m^2 each were used for estimation of the aboveground litter flux of the trees, which were installed randomly in the thinned and control plot of studied stands in early spring 2016. Litter samples were collected once a month during the two-year study period (2016–2017). The samples were dried at 70 °C to constant weight, separated into needles, branches and other material (e.g. seeds, pieces of bark, buds etc.), and weighed in laboratory.

2.4. Soil

2.4.1. Soil analyses

In 2016, in both studied stands, seven soil pits (depth 1.0 m) were excavated and the soil profile was described, as well as the soil type of the study sites was prescribed according to the IUSS Working Group WRB (2006). Bulk density samples were taken from each soil pit to a soil depth of 50 cm, using a stainless steel cylinder (Ø 40 mm; V = 50 cm^3). In the laboratory, all samples were dried to constant weight at 105 °C and weighed. Samples were taken from depths of 0–10 cm and 10–20 cm from twelve random points across the study plot with a soil auger (Uri et al., 2017ab), for estimation of pH, soil nutrient and C concentration for chemical analyses (Table 2). There was no statistically significant difference in soil nutrient or C content between the treatments ($M - W$, $p > 0.05$).

For estimation of the C storage in the organic soil layer (forest floor), samples from 10 random points over the plot were taken with a soil corer (Ø 108 mm). The cutting edge of the soil corer was sharpened and the internal diameter of the upper part of the auger was 2 mm larger than the diameter of the cutting edge to avoid compression of the organic layer. The formed monolith of the organic layer was divided into the O_1 and O_2 horizons according to decomposition rate. The thickness of layers was measured in forest and all samples were packed into plastic bags and transported to the laboratory where they were dried to constant weight at 70 °C and weighed. The content of C and ash was analysed from composite samples separately in the O_1 and O_2 layers (Table 2). For calculating the mass of the forest floor and C storage for the whole horizon, the dry weight of the soil was corrected by taking ash content into account.

In the soil samples, total N by the Kjeldahl method was analysed using a Tecator ASN 3313. To assess available ammonium lactate extractable phosphorus in the soil, the flow injection analysis with Tecator ASTN 9/84 was used. The flame photometric method was used to analyse available potassium from the same solution. Soil pH in 1 M

Table 2
Soil characteristics for the studied stands; N – Kjeldahl nitrogen (%), P – available (AL) phosphorus, K – available (AL) potassium, Ca – calcium, Mg – magnesium, OM – organic matter content. All characteristics are presented for the 0–20 cm mineral topsoil layer. No statistically significant differences were found between the treatments within stands.

Stand	Treatment	Soil type	pH_{KCl}	N	P	K	Ca	Mg	Bulk density	OM
				%	mg kg^{-1}				g cm^{-3}	%
Pole	Thinned	*Endogleyic Podzol*	3.9	0.10	34.2	31.2	104	9.6	1.05	4.15
	Control		4.0	0.11	31.4	38.8	87.7	8.2	1.05	3.85
Middle-aged	Thinned	*Endogleyic Albic Podzol*	3.5	0.02	9.5	13.2	45.9	7.9	1.01	5.01
	Control		3.7	0.03	13.4	16.4	49.5	10.8	1.02	5.12

KCl suspensions was measured at a ratio of 10 g:25 ml. The dry combustion method and a varioMAX CNS elemental analyser (ELEMENTAR, Germany) were used to determine carbon content of oven-dried samples. All chemical analyses were performed at the Biochemistry Laboratory of the Estonian University of Life Sciences (Table 2).

2.4.2. Soil respiration and the microclimate

Total soil respiration (Rs) and heterotrophic respiration (Rh) rates (μmol CO_2 m^{-2} s^{-1}) were measured monthly from April to October 2016 and from May to November 2017, using the closed dynamic chamber method (PP *Systems* SRC-1 chamber (volume 1.170 cm^3, enclosed soil surface 78 cm^2), with a gas analyser CIRAS-2 (Differential CO_2/H_2O Infrared Gas Analyzers)). To distinguish Rh from Rs, the trenching method was applied with insertion of 12 deep PVC cylinders (Ø20 cm, height 50 cm) to a depth of 40–45 cm in each treatment (thinned and control) plot in November 2015. To avoid any CO_2 leakage from the soil respiration chamber PVC collars (Ø 10 cm, height 5 cm) were inserted at a depth of 3 cm for Rs measurements and inside the trenched plots for Rh measurements. The herbaceous vegetation was carefully removed from the deep cylinder and the collar with minimum soil disturbance, and both were kept free of the live vegetation throughout the study. Each soil respiration measurement lasted 120 s or automatically ended if the system CO_2 concentration increased more than 60 ppm.

Soil temperature (°C) was measured simultaneously with soil respiration in the untrenched and trenched plots using an attached soil temperature probe STP-1 (PP Systems International, Inc., USA) inserted at a depth of 5 cm. Volumetric soil moisture (%) was also measured at a depth of 5 cm using a HH2 Moisture Meter Version 2 (Delta-T Devices Ltd, UK). In addition, soil temperature (model 1425, Spectrum Technologies, Inc, USA) and volumetric soil moisture (Water Scout sensor model SM 100, Spectrum Technologies, Inc, USA) were measured continuously every hour from April 2016 to December 2017 in the thinned and the control plots. Data was stored with a data logger (WatchDog 1425, Spectrum Technologies, Inc, USA).

2.5. Carbon leaching

C leaching was measured using stainless steel plate lysimeters in both studied stands (Roots and Voll, 2011; Uri et al., 2011; Becker et al., 2015; Morozov et al., 2019). Lysimeters were installed and water was sampled as described in our parallel study (Aun et al., 2021): 7 stainless steel plate lysimeters were installed at random points across the area to a soil depth of 40 cm to both sample plots in studied stands. Water was sampled monthly from April to December using a peristaltic vacuum pump. The annual cumulative leaching flux was determined by summing up the amounts of leached C for the different months (Uri et al., 2017b; Morozov et al., 2019).

2.6. Carbon budgeting

A C budget was compiled separately to each sample plot by balancing the input and output C fluxes for 2017, i.e. for the second post-thinning year (Fig. 1). Net ecosystem production (NEP) (3) was defined as the difference between net primary production (NPP) and C loss through

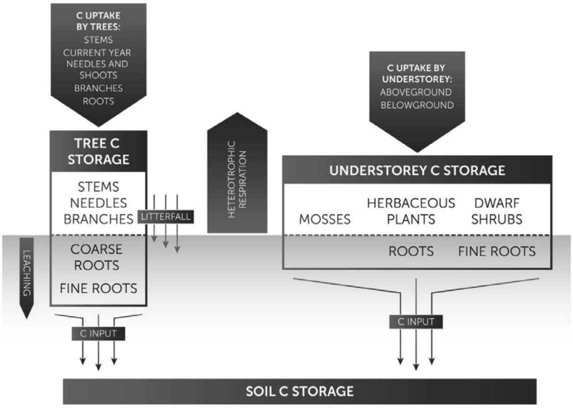

Fig. 1. Estimated carbon storages and fluxes in studied forest ecosystems.

heterotrophic respiration (Rh) and leaching (L) (Clark et al., 2001; Lovett et al., 2006; Meyer et al., 2013).

$$\mathrm{NEP} = \mathrm{NPP} - (\mathrm{Rh} + \mathrm{L}), \tag{3}$$

where NEP serves as the amount of C accumulated in the ecosystem. In the present study a positive value of NEP was treated as a net transfer of C from the atmosphere into the forest (C sink), but a negative NEP is considered as C loss. NPP was estimated by adding up the annual production of all biomass fractions of the trees and the understorey plants (Varik et al., 2015; Uri et al., 2017ab, 2019).

2.7. Statistics

The normality of variables was analyzed with the Lilliefors-test and the Shapiro-Wilk test. Statistical analyses were done separately for the two pairs of study plots for comparing stand or soil characteristics. Statistical differences of the means were investigated by the *t*-test. The Mann Whitney *U* test was used for comparing the data that did not follow a normal distribution. Allometric regression models were created for estimating relationships between model tree biomass or stemwood production with tree diameter. The quality of the fit of the models was assessed by coefficient of determination (R^2) and level of probability (p).

Soil respiration data were normalised by log-transformation. The effects of treatment (thinning), time (month) and their coeffect on Rs, Rh, soil temperature and soil moisture were tested using repeated measures ANOVA followed by Tukeýs post-hoc test. The T-test was used to estimate significant differences in soil temperature and soil moisture between the trenched and untrenched plots. An exponential model (4) was used to describe the relationship between Rs (or Rh) and soil temperature at a depth of 5 cm:

$$\mathrm{Rs}\ (\mathrm{or}\ \ \mathrm{Rh}) \ = \ ae^{bTs} \tag{4}$$

where a and b are the fitted parameters, and Ts is soil temperature (°C). Pearson correlation coefficient between Rs (or Rh) and soil moisture was calculated; to eliminate the confounding effect of temperature, partial correlation analysis was further used. In case the correlation with soil moisture was significant ($p < 0.05$), a multiple linear regression, with temperature and moisture being the two independent variables, was conducted. The cumulative Rs and Rh fluxes for the period April-December and the annual fluxes for 2017 were modelled using the daily mean soil temperature and soil moisture values from the data loggers.

3. Results

3.1. Biomass and production of trees

The biomass of the trees was smaller in the thinned plot than in the control plot of both studied stands (Table 3), contributing to lower annual production of woody biomass at the stand level. Stemwood accounted for 63–68% of tree biomass allocation across the treatment plots, representing also the largest share in the annual tree production (39–51%). Stemwood production was 1.2 t ha^{-1} yr^{-1} and 0.8 t ha^{-1} yr^{-1} lower in the thinned plot compared to control plot of the pole and middle-aged stands, respectively (Table 3). In the pole stand, the annual production of the needles and current-year shoots was higher in the thinned plot, however, an opposite trend was revealed in the middle-aged stand (Table 3).

3.2. Aboveground litter flux of trees

Thinning had no effect on annual litterfall; two years after thinning there were no statistically significant differences in the aboveground litter fluxes between the thinned and control plots of either studied stand (M-W, $p > 0.05$) (Fig. 2). Needles formed the largest share of tree litterfall (68–77%), being 5–7% larger in the thinned than in the control plots. The share of the branches and other material fractions in aboveground litterfall was around 11% higher in the control than in the thinned plot of both stands.

3.3. Aboveground biomass of understorey vegetation

The species composition of the understorey vegetation of the studied stands was different: in the pole-stage stand dwarf shrubs were almost absent and herbaceous plants and mosses were prevalent. In the middle-aged stand the situation was the opposite: dwarf shrubs and mosses were dominant and the share of herbaceous plants was moderate (Table 4). Thinning had a strong effect on the growth of the herbaceous plants in the pole stand (M-W, $p < 0.05$), where the aboveground biomass of the herbaceous understorey was almost three times higher compared to the control plot. Differences in the aboveground biomass of the mosses and

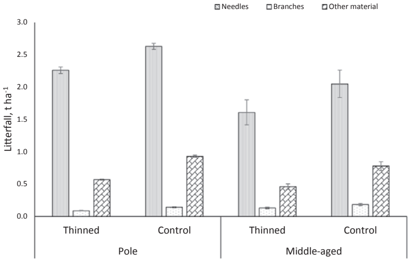

Fig. 2. Annual aboveground tree litter fluxes of the studied stands in 2017; bars indicate standard error; no statistically significant difference was found between the treatments within stand, litter traps n = 7 per plot.

Table 3
Fractional distribution of the biomass and production of the trees in the studied stands in 2017, two years after thinning.

Fraction	Biomass, t ha^{-1}				Annual production, t ha^{-1} yr^{-1}			
	Pole		Middle-aged		Pole		Middle-aged	
	Thinned	Control	Thinned	Control	Thinned	Control	Thinned	Control
Stemwood	58.9	82.8	98.0	121.4	4.1	5.3	5.2	6.0
Stembark	6.9	9.7	9.3	11.5	0.4	0.6	0.5	0.5
Current year needles	2.7	2.2	1.9	2.4	2.7	2.2	1.9	2.4
Current year shoots	1.0	0.7	0.6	0.7	1.0	0.7	0.6	0.7
Old needles	1.6	1.4	1.7	2.3	–	–	–	–
Old branches	7.9	6.3	9.2	14.2	0.5	0.4	0.5	0.7
Stump and coarse roots	15.0	19.6	22.9	28.1	1.7	1.8	1.6	2.0
Total	94.0	122.7	143.5	180.5	10.4	11.0	10.2	12.3

Table 4
Aboveground biomass of the understorey vegetation in the studied stands in 2017; Mean ± standard error (SE) is presented.

Stand	Treatment	Aboveground biomass		
		Herbaceous	Mosses	Dwarf shrubs
			$t\ ha^{-1}$	
Pole	Thinned	0.55 ± 0.10^{a}	0.45 ± 0.24^{a}	0.02 ± 0.04^{a}
	Control	0.17 ± 0.06^{b}	0.69 ± 0.37^{a}	0.04 ± 0.03^{a}
Middle-aged	Thinned	0.06 ± 0.04^{a}	1.83 ± 0.47^{a}	0.68 ± 0.22^{a}
	Control	0.09 ± 0.04^{a}	1.91 ± 0.43^{a}	0.45 ± 0.08^{a}

Statistically significant difference between the treatments within stand is denoted by letters [a] and [b].

Table 6
Carbon storages of the studied stands.

Component	Pole		Middle-aged	
	Thinned	Control	Thinned	Control
	C storage, $t\ C\ ha^{-1}$			
Aboveground biomass				
Trees	37.7	49.1	57.5	72.7
Understorey plants	0.5	0.4	1.2	1.1
Total	38.2	49.5	58.6	73.8
Belowground biomass				
Trees	8.1	11.1	11.3	14.1
Understorey plants	0.6	0.3	0.1	0.3
Total	8.6	11.4	11.4	14.4
Plant biomass total	**46.8**	**60.9**	**70.1**	**88.2**
Mineral soil (0–20 cm)	23.4	25.4	28.9	30.1
Forest floor	8.7	8.3	35.3	34.7
Soil total	32.1	33.7	64.2	64.8
Ecosystem total	**78.9**	**94.6**	**134.3**	**153.0**

dwarf shrubs between the thinned plot and the control plot were not statistically significant for either stand (M-W, $p > 0.05$) (Table 4).

3.4. *Fine root biomass and production of trees and understorey vegetation*

Tree fine root biomass (FRB) and fine root production (FRP) at the stand level were lower in the thinned than in the control plot of both studied stands (Table 5). However, average FRB per tree was around 2 kg $tree^{-1}$ across the stands, being slightly higher in the thinned plots. In all cases, 77–79% of the pine fine roots were located in the upper 0–20 cm mineral soil layer. In the pole stand, the biomass of the roots of the herbaceous understorey was higher in the thinned plot compared to the control plot. In the middle-aged stand, the biomass and production of the fine roots of the dwarf shrubs were lower in the thinned than in the control plot.

3.5. *Ecosystem carbon storages*

After thinning, the C storage of plant biomass was reduced by 14 and 18 $t\ C\ ha^{-1}$ in the pole stand and in the middle-aged stand, respectively (Table 6). The soil C storage formed a slightly smaller share of the total ecosystem's C storage, compared to the C storage accumulated in plants. In the pole and in the middle-aged stands, the share of the soil C storage varied in the range 36–41% and 42–48% of the total ecosystems C storage, respectively.

3.6. *Soil respiration and the microclimate*

The seasonal dynamics of soil temperature was very similar in the thinned and control plots of both the pole and the middle-aged stand (Supplementary material 3 (S3)). The coldest month was February and the warmest months were July and August (S2) and trenching did not affect soil temperature ($p > 0.05$). The difference in overall mean soil temperatures between the thinned plot and the control plot varied between 0.1 and 0.3° (S2). Comparison of the periods May-August and October-March revealed different patterns of soil temperature in the thinned and control plots. Moreover, an opposite trend in soil temperature was evident for the two sites: in the pole stand the soil was warmer in the thinned than in the control plot in May-August and cooler in October-March, whereas in the middle-aged stand the soil was warmer in the thinned than in the control plot in the autumn-winter period and cooler in spring and summer (S2, S3).

The seasonal dynamics of soil moisture was also similar for the thinned and control plots, but without a clear season specific trend (S4). In general, soil moisture showed no significant response to trenching ($p > 0.05$), except for the middle-aged stand in 2017; mean soil moisture in control plot was higher in the trenched plots than in the untrenched plots, at 44.1% vs 33.2% ($p < 0.05$), respectively. The control plot was significantly drier than the thinned plot throughout the study period (S2, S4; $p < 0.05$). The pole stand was drier than the middle-aged stand (S2).

Rs and Rh demonstrated distinct seasonality with maximum values in summer (Fig. 3) and the dynamics of the soil CO_2 effluxes was similar to that of soil temperature. Thinning had no significant effect on Rs or Rh (Table 7, $p > 0.05$). For the middle-aged stand, the values of Rs and Rh were slightly lower compared to the pole stand.

The fluxes of cumulative Rs for April-December across all studied stands varied between 5.4 and 7.6 $t\ C\ ha^{-1}$ and the fluxes of cumulative Rh varied between 2.8 and 4.8 $t\ C\ ha^{-1}$ (Table 8). The annual soil respiration fluxes were calculated for the second post-thinning year. Although annual Rs was higher in the control than in the thinned plot for both stands (8.6 vs 7.9 $t\ C\ ha^{-1}$ for the pole stand and 6.4 vs 5.9 $t\ C\ ha^{-1}$ for the middle-aged stand), the mean modelled soil C effluxes were not significantly different between the thinned plot and the control plot (Table 8, *t*-test, $p > 0.05$). The annual Rh fluxes were very similar in the thinned and control plots for both stands (5.3 vs 5.5 $t\ C\ ha^{-1}$ for the pole stand and 4.4 vs 4.3 $t\ C\ ha^{-1}$ for the middle-aged stand). Thinning increased the average contribution of Rh to Rs (Table 8).

Soil temperature was the main driver of seasonal variation in the soil CO_2 effluxes, describing 61–87% of the variation in Rs and Rh (S5). In

Table 5
Fine root biomass and production and necromass of the pine trees, fine root biomass of the dwarf shrubs and belowground biomass of the herbaceous plants in the studied stands two years after thinning (2017); FRB-fine root biomass ($t\ ha^{-1}$), FRP-fine root production ($t\ ha^{-1}\ yr^{-1}$); Mean ± standard error (SE) is presented; n = 15 per plot.

Stand	Treatment	Trees		Understorey		FRP	
		FRB $t\ ha^{-1}$	Necromass	Dwarf shrubs FRB	Herbaceous plants belowground BM	Trees $t\ ha^{-1} yr^{-1}$	Dwarf shrubs
Pole	Thinned	2.72 ± 0.05^{a}	0.84 ± 0.02^{a}	n.e	1.25 ± 0.08^{a}	2.28	n.e
	Control	4.68 ± 0.09^{b}	0.92 ± 0.03^{a}	n.e	0.59 ± 0.03^{b}	3.93	n.e
Middle-aged	Thinned	2.01 ± 0.17^{a}	0.50 ± 0.05^{a}	0.24 ± 0.07^{a}	0.07 ± 0.01^{a}	1.69	0.05
	Control	3.00 ± 0.25^{b}	0.62 ± 0.08^{a}	0.55 ± 0.10^{a}	0.14 ± 0.03^{a}	2.52	0.11

Statistically significant difference between the treatments within stand is denoted by letters [a] and [b].

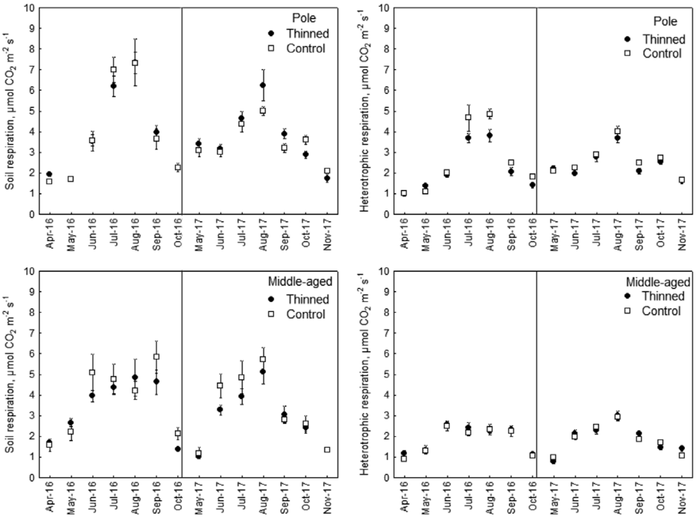

Fig. 3. Seasonal dynamics of total soil respiration and heterotrophic respiration of the studied stands in 2016 and 2017; data represent mean (±SE).

Table 7

Mean (±SE) of measured total soil respiration (Rs) and heterotrophic respiration (Rh) (µmol CO$_2$ m^{-2} s^{-1}) over the two study years for the pole and the middle-aged pine stands.

Stand	Treatment	Rs	Rh
Pole	Thinned	3.79 ± 0.19	2.29 ± 0.09
	Control	3.68 ± 0.17	2.58 ± 0.11
Middle-aged	Thinned	3.12 ± 0.15	1.89 ± 0.07
	Control	3.27 ± 0.23	1.82 ± 0.07

Table 8

Fluxes of cumulative total soil respiration (Rs) and heterotrophic respiration (Rh) (t C ha^{-1}) and the Rh to Rs ratio for the studied stands in April-December 2016 and 2017. Data in brackets represents mean (±SE).

		2016			2017		
Stand	Treatment	Rs	Rh	Rh/Rs	Rs	Rh	Rh/Rs
Pole	Thinned	7.6 (0.85 ± 0.13)	4.0 (0.44 ± 0.07)	0.52	7.3 (0.81 ± 0.14)	4.8 (0.53 ± 0.06)	0.66
	Control	5.6 (0.62 ± 0.11)	2.8 (0.31 ± 0.05)	0.51	7.4 (0.82 ± 0.10)	4.6 (0.51 ± 0.06)	0.62
Middle-aged	Thinned	6.3 (0.70 ± 0.12)	3.9 (0.43 ± 0.06)	0.62	5.4 (0.60 ± 0.12)	3.9 (0.43 ± 0.07)	0.71
	Control	6.8 (0.76 ± 0.16)	3.7 (0.41 ± 0.07)	0.54	6.0 (0.67 ± 0.16)	3.9 (0.44 ± 0.07)	0.65

general, there was no significant difference in parameters a and b of Eq. (4) between the thinned plot and the control plot except for Rs in the pole stand in 2017 ($p = 0.04$) (S5). In this stand soil moisture had a significant positive effect on Rs and Rh (S6). Both soil temperature and soil moisture were included in the regression model to calculate the cumulative or annual soil respiration fluxes, which improved the statistical fit of the regression models. Soil temperature and soil moisture described 78–83% of the variation in Rs and 67–92% of the variation in Rh. In the middle-aged stand the effect of soil moisture on Rs and Rh was nonsignificant.

3.7. *Leaching*

In the pole stand the amount of percolated water and hence also the leaching of total organic carbon (TOC) were very small, being 1.3 and 0.3 kg C ha^{-1} yr^{-1} in the thinned and the control plot, respectively. In the middle-aged stand the amount of leached C was 20.1 and 17.9 kg C ha^{-1} yr^{-1} in the thinned plot and the control plot, respectively.

3.8. *Ecosystem carbon budgets*

All studied plots remained C sinks in the second post-thinning year (Table 9); NEP ranged between 1.5 and 3.2 t C ha^{-1} yr^{-1}. Still, thinning reduced NEP by 0.9 and 0.7 t C ha^{-1} yr^{-1} in the pole and in the middle-aged stand, respectively. The largest share of net primary production (NPP) was made up by the stems and needles. The NPP of the pole and the middle-aged stand was 9% and 11% lower in the thinned plot compared to the control plot, respectively. The main C efflux was Rh, which was higher in the pole stand; thinning did not affect Rh in either stand (Table 9). Annual leaching of C was negligible in both stands and did not practically affect C budgets. The annual C efflux from the soil (Rh) exceeded the soil organic C input via aboveground and belowground litter in both stands, regardless of the treatment. The proportions

Table 9
Carbon (C) budgets of the studied pole and middle-aged pine stands two years after thinning; NPP- net primary production, NEP- net ecosystem production.

			Pole		Middle-aged	
			Thinned	Control	Thinned	Control
		Fluxes	t C ha^{-1} yr^{-1}			
C inputs		*Plant aboveground*				
	1	Stems	2.14	2.81	2.68	3.07
	2	Current year needles	1.29	1.04	0.92	1.17
	3	Current year shoots	0.51	0.36	0.30	0.38
	4	Old branches	0.26	0.20	0.85	0.34
	5	Litterfall (needles, branches, other)	1.47	1.87	1.11	1.52
	6	Moss production	0.07	0.11	0.30	0.31
	7	Herbaceous plants	0.24	0.07	0.03	0.04
	8	Dwarf shrub production	0.004	0.007	0.13	0.08
		Plant belowground				
	9	Coarse roots	0.75	0.78	0.70	0.88
	10	Tree fine root production	1.14	1.97	0.85	1.26
	11	Herbaceous plants' roots	0.56	0.27	0.03	0.06
	12	Dwarf shrub fine root production	n.e	n.e	0.02	0.05
		Soil				
C outputs	13	Heterotrophic respiration	5.5	5.3	4.3	4.4
	14	Leaching	<0.01	<0.01	0.02	0.02
	15	C input to the soil=(5 + 6 + 7 + 8 + 10 + 11 + 12)	3.49	4.30	2.46	3.32
	16	Soil C exchange = (15-(13 + 14))	−2.02	−1.01	−1.86	−1.10
		Productivity				
	17	NPP = (1 + 2 + 3 + 4 + 6 + 7 + 8 + 9 + 10 + 11 + 12)	6.96	7.62	6.80	7.64
	18	NEP = (17-(13 + 14))	1.45	2.31	2.48	3.22

of the aboveground and belowground litter fluxes remained in the same magnitude for both stands.

Thinning reduced the C storage accumulated in the woody parts of the trees by 14 t C ha^{-1} and 18 t C ha^{-1}, in the pole and middle-aged stands, respectively. However, the woody biomass production of the trees was estimated at 3.7–4.5 t C ha^{-1} yr^{-1} on the second post-thinning year. Thus, assuming a fixed annual production rate, the loss of the removed C storage of the trees will reach the pre-thinning level during the following four years for both studied stands.

4. Discussion

Thinning is the main forest management practice for shaping stand composition, productivity and quality, as well as growing conditions. Although thinning has been a well-known and widely used silvicultural method in traditional forest management for a long time, its environmental impacts, especially the effect on C cycling, is still inadequately investigated. The current case study was aimed at estimating the C storages and fluxes in young and middle-aged Scots pine stands two years after thinning and at evaluating the short-term effect of thinning on the forest ecosystemś functioning by using C budgeting. In both studied stands, one thinned plot and one unthinned plot were compared without replications, which does not allow to take into account spatial variation of the stands, restricting broader generalization of the results.

4.1. Production of trees

For a pure stand, the main purpose of thinning is to promote the radial growth of remaining trees and to decrease insect and pathogen damages. Thinning reduces the basal area and hence the biomass of the trees at the stand level (Sobachkin et al., 2005; Zhang et al., 2019), which in turn contributes to a temporary decrease of the stand C storage. The immediate post-thinning increase in average diameter at the stand level was the result of thinning with the below method in both studied stands. The estimated aboveground biomass values for the studied stands are comparable with the results from a Scots pine chronosequence study carried out in Lithuania (Armolaitis et al., 2013). Also, the present results for the pole stand are in good accordance with the results reported from Spain for a 22-year-old Scots pine stand, however, the aboveground biomass of the middle-aged stand in the current study was significantly lower than that reported by Ruiz-Peinado et al. (2016), which is probably related to the different thinning intensities used.

The intensity of thinning can be considered modest, since the decrease of the basal area in the pole stand and in the middle-aged stand was 31% and 24%, respectively (del Río et al., 2017). Due to moderate thinning rate, the C storage of the trees was only 21–24% smaller in the thinned plots compared to the control plots. The moderate intensity used in the study is also common in forest management practices in the local region, as forest managers tend to leave stands slightly denser to minimize the high risk of windfall and snow damage. Although thinning decreased the net primary production (NPP) of the two stands by 9% and 11%, respectively, both thinned plots still remained C sinks; their estimated NEP was 1.5 and 2.5 t C ha^{-1} yr^{-1}, respectively. The decrease of NEP was a consequence of the lower standing biomass of the trees, since the main output flux did not increase after thinning.

In the second post-thinning year, NPP was higher in the control plots, but the difference from the thinned plots was moderate and will probably decrease in the nearest future, as tree growth is expected to increase in thinned plots (Mäkinen and Isomäki, 2004; Zhang et al., 2019). At the same time, self-thinning reduces stand density in control plots (Brunet-Navarro et al., 2016). Dore et al. (2012) reported that although thinning markedly reduced net ecosystem exchange in a *Pinus ponderosa* stand, its productivity recovered four years after the treatment, as C accumulation in a thinned stand was slightly higher than in an unthinned stand.

The results of the current study allow to predict that the removed woody C storage of the trees, will reach the preharvest level in the following four years for both studied stands. Actual recovery might even be faster, since the growth of the trees in the thinned stands will accelerate due to improved growing conditions. More favorable environmental conditions will lead to an increase in the production of the remaining trees. This serves as the main compensatory mechanism balancing C accumulation in a post disturbance ecosystem.

4.2. Aboveground litter flux

The annual flux of needle litter across all studied plots varied from 1.6 to 2.6 t ha^{-1} yr^{-1}, which is similar to earlier studies in Estonia (Portillo-Estrada et al., 2013; Kriiska et al., 2019) and coincides with the results of 18-year-long study from southern Finland, where average annual foliage litter production and total litterfall production of 1.6 and 2.6 t ha^{-1} yr^{-1}, respectively, were estimated in a Scots pine stand (Starr et al., 2005). In the present study, the annual litter flux was larger in the pole stand, which can be attributed to its higher density as well as larger foliage biomass.

Although total litterfall was 21–26% lower in thinned plots, no statistically significant differences were found in the litter fractions between the thinned and the control plots in the second post-thinning year, which can be explained by the removal of suppressed trees with relatively short crowns, as well as by the increased needle production in the thinned plots. A similar result was also found in Turkey, where thinnings decreased litterfall by 22% in a mature Scots pine stand (Çömez et al., 2019). Typically, needles account for the bulk (49–75%) of total litterfall in Scots pine stands (Finér, 1996; Starr et al., 2005). The annual production of needles contributes to aboveground litterfall, which serves as the major input of aboveground C and nutrients to the forest soil (Starr et al., 2005; Neumann et al., 2018), affecting in turn Rh (Scott-Denton et al., 2006). In the pole stand the production of needles increased after thinning, which can probably be explained by improved light conditions for the remaining trees. Higher needle production contributed to the annual litter flux whose difference between the thinned plot and the control plot is likely to level out in the nearest future.

4.3. Fine roots

Thinning significantly reduced fine root biomass (FRB) in both studied stands, however, the decrease was larger in the pole stand than in the middle-aged stand, 42% and 33%, respectively. In the middle-aged stand, tree FRB made up only 7–8% of total belowground biomass, which is of the same magnitude as that reported for boreal forests (average 6%) (Vogt et al., 1996). However, in the pole stand, tree FRB accounted for 14–18% of total belowground biomass, being higher in the control plots. At the same time, thinning did not increase fine root necromass in either stand. The above- to belowground litter ratio varied from 0.7 to 1.0 across the studied plots, which shows that above- and belowground litter inputs to the soil were of similar magnitude.

Fine root production (FRP) is considered an essential C input flux to the soil and to the whole ecosystem. At the same time, the belowground C flux is one of the most poorly investigated fluxes in forest ecosystemś C cycling studies (Leppälammi-Kujansuu et al., 2014), being often ignored or modelled by indirect methods. In the current study, FRP varied between 1.7 and 3.9 t ha^{-1} yr^{-1} across the studied stands, forming 12–26% of annual NPP. The estimated FRP values proved to be lower than those reported from middle-aged Scots pine stands in Finland (Makkonen et al., 1999; Helmisaari et al., 2002), but were still of the same magnitude as the corresponding values for older Scots pine stands in Estonia (Kriiska et al., 2019). At the stand level, FRP was higher in the control plots, however, average FRP per tree was 17–25% higher in the thinned plots, which suggests that trees have responded to better growing conditions and sufficient space in the soil for producing more fine roots. The higher FRP in the control plots results from high stand density, as self-thinning had not yet reached its peak in the 25-year-old unthinned stand.

4.4. Understorey vegetation

Several studies have highlighted the reallocation of C sinks after thinning, emphasizing the importance of understorey growth (Vesala et al., 2005; Campbell et al., 2009; Moreaux et al., 2011; Trant, 2013). Thinning stimulated the growth of herbaceous plants in the pole stand, as was also the case in our parallel study of silver birch stands (Aun et al., 2021). In the current study the production of understorey plants made up a moderate share (4–13%) of NPP across all study plots and thinning significantly increased the production of herbaceous plants only in the pole stand. The more abundant growth of herbaceous plants in this stand can be attributed to the better nutrient status of the soil compared with the middle-aged stand. In the thinned plot of the pole stand, the vegetation was quite abundant, with several dominant *Gramineae* species and *Pteridium aquilinum*. However, two years is a too short time to detect changes in the biomass production of mosses and dwarf shrubs, which formed the dominating vegetation in the middle-aged stand. Since the aboveground biomass of herbaceous plants is annual, they respond faster to a more favorable environment, e.g. mainly increased insolation.

4.5. Output carbon fluxes

The C budget of an ecosystem depends on the quantity of the C input fluxes and on the C output fluxes. The estimated annual soil C effluxes (5.9–8.6 t C ha^{-1} for Rs and 4.3–5.5 t C ha^{-1} for Rh) remained in the range found for coniferous forests in the boreal and hemiboreal zones (Kolari et al., 2009; Kukumägi et al., 2017; Kriiska et al., 2019).

A meta-analysis of the impacts of forest logging on the soil CO_2 effluxes along with many individual studies confirm that microclimate conditions are among the major biophysical factors influencing the soil CO_2 efflux after forest harvesting (Chen et al., 2020). Soil temperature is expected to increase after thinning because of increased soil insolation, which can be attributed to greater canopy openness (Zhang et al., 2018; Lei et al., 2018). In the present study, mean soil temperatures over the study period varied little (0.1–0.3 °C) between the thinned and the control plots. However, differences in monthly mean soil temperatures of the growing season between the thinned and the control plots reached up to 1.3°, while the differences were greater in the pole stand than in the middle-aged stand.

We also found an opposite trend in soil temperature dynamics between the two stands: in the pole stand the soil was warmer in the thinned plot than in the control plot during the growing season, whereas in the middle-aged stand the soil was warmer during the dormant period. Usually, lower temperatures in thinned stands in winter are caused by enhanced radiation related cooling, but this can also be attributed to different soil moisture conditions. Thinning can increase soil moisture due to reduced evapotranspiration and canopy interception by remaining biomass (Chase et al., 2016; Chen et al., 2020). In the current study, thinning increased soil moisture about two times compared to the control plots in both stands and the soil was significantly moister in the middle-aged pine stand than in the pole stand, owing to the soil cooling effect in the summer and the soil warming effect in the autumn and winter. In the pole stand both soil temperature and soil moisture were significant factors explaining the variation in Rs and Rh, while in the middle-aged stand soil moisture had no effect on the soil respiration fluxes.

Despite of changes in the soil microclimate, thinning had no significant effect on Rh (5.3 in the control plot vs 5.5 t C ha^{-1} in the thinned plot and 4.4 in the control plot vs 4.3 t C ha^{-1} in the thinned plot) in the pole stand and middle-aged stand. The same pattern applies also to Rs, which is in accordance with earlier individual studies (Ma et al., 2004; Campbell et al., 2009; Pang et al., 2013) as well as with a *meta*-analysis by Zhang et al. (2018). Estimation of differences between the parameters of the exponential model showed that thinning did not significantly change the response of Rs and Rh to soil temperature, which was the driving factor of the variation in both soil respiration fluxes.

Both litterfall and fine root biomass influence the soil CO_2 effluxes and are expected to decrease because of forest thinning (Zhang et al., 2018; Chen et al., 2020), which affects also the balance between the respiration components. In the current study, however, thinning had no significant effect on litterfall, nor was there found a significant increase in Rh. A slight initial increase in the first year after thinning in the pole stand might have been induced by an improvement in the growing seasońs microclimate and by an additional input through the dying root system and other organic debris (Olajuyigbe et al., 2012). Rh was the major component of Rs and thinning increased the average contribution of Rh to Rs (Rh/Rs ratio 0.51–0.65 for the control plot, 0.52–0.71 for the thinned plot). This was evidently related to the decline in fine root biomass, resulting in a decrease in root respiration (Pang et al., 2013; Chen et al., 2020).

Besides Rh, soil C loss through leaching is another outgoing flux to be considered when the aim is to compile a carbon budget of stand. However, C leaching was negligible in the pole stand and very low in the middle-aged stand, which is consistent with earlier similar studies (Becker et al., 2016; Uri et al., 2019; Aun et al., 2021). Since the share of the leached C flux in the whole budget is irrelevant, it is often ignored in C budgeting of forest ecosystems (Varik et al., 2015).

4.6. *Carbon storage*

Trees acted as the main C storage in the studied forest ecosystem: 51–64% of the total ecosystem C was accumulated in the trees. The soil C stock in the upper 0–20 cm mineral layer was similar in both studied stands. However, the forest floor layer was thicker in the middle-aged stand and, consequently, the C stock in the organic soil layer was almost twice as large, therefore the total soil C stock was larger in the middle-aged stand. The effect of thinning on the soil C stock might be evident after a longer period, but this issue was not dealt with in the present study. Reduction in the soil C storage may occur through intensified Rh, which is an expected result regarding soil temperature. As discussed above, the effect of thinning on soil Rh was not found in either of the studied stands, which supports the results of an extensive review paper indicating that thinning has a minor effect on the forest soil C stocks (Mayer et al., 2020).

4.7. *Carbon budget*

Although tree biomass plays the most important role in the annual production of forest, thinning affects also other ecosystem components (understorey, soil respiration etc.,). Thus, a wider knowledge of the effect of thinning on C cycling is crucial. For this aim, C budgeting serves as a suitable tool, which allows to demonstrate how the forest ecosystem responds to changed environmental conditions after thinning (Aun et al., 2021). An alternative to it in studies of forest C cycling could be the eddy covariance (EC) method, which provides an accurate estimation of C exchange between the ecosystem and the atmosphere and is based on direct and continuous measurements during a certain period (Baldocchi, 2014). However, EC only provides estimation of the quantity of the input and output fluxes without a detailed specification of the role of different forest ecosystem components, which is its major shortcoming compared to the C budgeting method. Since both methods have their advantages and shortcomings, synthesis of these two methods could yield a result of higher quality and would improve the reliability of a study (Goulden et al., 2011; Peichl et al., 2010; Uri et al., 2019).

Analysis of annual soil C exchange revealed soil C disbalance in both studied stands, regardless of the treatment, meaning that Rh exceeded the C input into the soil via organic litter. Similar results were also found in our earlier studies of silver birch stands (Varik et al., 2015; Aun et al., 2021). A possible reason for this might be the fact that the production and turnover of mycorrhizal mycelia are not taken into account in C budgets, while C inputs through fine roots and mycorrhizal hyphae may even be of the same order of magnitude (Wallander et al., 2004, 2013). Also, annual fine root production might be somewhat underestimated, since it is calculated on the basis of average turnover rate reported in literature sources. In the present study, the annual litter input into the soil from the dwarf shrubs and mosses was not estimated, which may also have affected the above disbalance.

The key issue in relation to thinning and C cycling studies is post-thinning C balance. In other words, will a thinned ecosystem remain a C sink or will it change into a C source? And in the latter case, when will the C budget recover to pre-thinning level? Of course, the management strategies used, primarily thinning intensity, tree species and site fertility, play an essential role in the recovery of C accumulation in the post-thinning period. Although this issue is of great importance in the light of climate change and forest management, there are still very few studies evaluating the effect of thinning at the ecosystem level by taking account of all major C fluxes.

Although the current study is focused on clarifying changes in forest C cycling at the ecosystem level, additional impact upon the effect of thinning on forest C cycling and mitigation of climate changes should also take account of two important aspects: firstly, for managed stands, the proportion of high quality timber output in final felling is higher, which allows to produce products with a longer lifetime, ensuring carbon capture for a longer period. Secondly, the timber collected from thinnings can also be used in the wood industry or in the energy sector, replacing fossil fuels or other materials.

5. Conclusions

Moderate thinning reduced annual NEP 22–37% in the studied Scots pine stands, but after two years the whole ecosystems still acted as C sinks. Thus the proposed hypothesis was proved, despite the decreased NPP, the ecosystem maintained the C sink status. The effect of thinning on the annual C sink was more pronounced in the younger stand than in the middle-aged stand. The decrease of NEP was attributed to the reduced biomass of the trees; at the same time, the annual Rh flux remained almost unchanged by thinning, owing to slight changes in litterfall and overall mean soil temperature.

The response of the understorey vegetation to improved post-thinning environmental conditions was moderate, the growth of herbaceous plants increased only in the younger stand, the production of mosses and dwarf shrubs was similar in the thinned and control plots of both stands. However, thinning reduced significantly fine root biomass, contributing to the decrease of NEP as well as to the belowground organic C input into the soil.

Although moderate thinning from below in the pole and middle-aged Scots pine stands resulted in a decrease of the C storage in tree biomass, the pre-thinning C storage in the trees will recover during the following four years.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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CURRICULUM VITAE

First name: Kristiina

Surname: Aun

Citizenship: Estonian

Date of birth: 08.02.1994

Address: Institute of Forestry and Rural Engineering, Estonian University of Life Sciences, Kreutzwaldi 5, 51006 Tartu, Estonia

Telephone: +372 53312943

E-mail: Kristiina.aun@emu.ee

Education:

2017-2021 PhD studies in forestry, Institute of Forestry and Rural Engineering, Estonian University of Life Sciences

2015-2017 Master studies in forest management, Institute of Forestry and Rural Engineering, Estonian University of Life Sciences

2012-2015 Bachelor studies in natural resources management, Institute of Forestry and Rural Engineering, Estonian University of Life Sciences

2009-2012 Tallinn Gymnasium of Technology

Professional employment:

2018-… Estonian University of Life Sciences, Institute of Forestry and Rural Engineering, Chair of Silviculture and Forest Ecology; junior researcher

Research interests:

silviculture, forest ecology, carbon cycles in forest ecosystem

Foreign languages:

English, Russian

Training and special courses:

2019	EduSaPMan-Network Summer School – “Soil and Water”, National Forestry University of Ukraine, Lviv, Ukraina
2018	SNS & EFINORD Matchmaking day, Alnarp, Sweden
	ELLS, PE&RC, PhD course “Conflicting demands in European Forests a wicked problem?”, Gällivare, Sweden
2017	LLU Forestry doctoral school, Jaunkalsnava, Latvia

Awards:

2019	Scholarship of Estonian University of Life Sciences Raefond
2018	RMK (State Forest Management Centre) Endel Laas scholarship for PhD students
2016	RMK (State Forest Management Centre) Heino Teder scholarship for Master degree students

Projects:

2020-2024	PRG681, Estonian Research Council. The effect of different harvesting methods on ecosystem carbon budget: shelterwood cutting versus clear-cut. Investigator.
2020-2023	T200106MIME.State Forest Management Centre. Effect of selective cutting on the carbon balance of the forest ecosystem and its economic aspects. Principal Investigator.
2020-2022	T200047MIME, Environmental Investment Center. Dynamics of site carbon balance following clear-cut. Principal Investigator.
2019-2021	T180199MIME. Environmental Investment Center. Effect of pre-commercial thinning on development of silver birch stands growing at fertile sites. Principal Investigator.

2018-2020	T180044MIME. Environmental Investment Center. Carbon budget in Norway spruce chronosequence stands. Principal Investigator.
2018-2019	P180022MIME, Ministry of Education and Research. The effect of thinnings on the carbon and nitrogen storages and fluxes in middle-aged Scots pine (*Pinus sylvestris*) stands growing in Mesotrophic sites. Principal Investigator.
2014-2019	IUT21-4, Estonian Research Council. The carbon dynamics in Estonian forests affected by sustainable management. Investigator.

ELULOOKIRJELDUS

Eesnimi: Kristiina

Perekonnanimi: Aun

Kodakondsus: Eesti

Sünniaeg: 08.02.1994

Aadress: Metsandus- ja maaehitusinstituut, Eesti Maaülikool, Kreutzwaldi 5, 51006 Tartu

Telefon: +372 53312943

E-mail: kristiina.aun@emu.ee

Hariduskäik:

2017-2021	Eesti Maaülikool, metsandus- ja maaehitusinstituut, metsanduse eriala, doktoriõpe
2015-2017	Eesti Maaülikool, metsandus- ja maaehitusinstituut, metsamajanduse eriala, magistriõpe
2012-2015	Eesti Maaülikool, metsandus- ja maaehitusinstituut, loodusvarade kasutamise ja kaitse eriala, bakalaureuseõpe
2009-2012	Tallinna Tehnikagümnaasium

Teenistuskäik:

2018-…	Eesti Maaülikool, metsandus- ja maaehitusinstituut, metsakasvatuse ja metsaökoloogia õppetool, nooremteadur

Teadustöö põhisuunad:

metsakasvatus, metsaökoloogia, süsiniku ringe metsaökosüsteemis

Võõrkeelte oskus:

inglise, vene

Täiendkoolitused:

2019	EduSaPMan-Network Suvekool – “Soil and Water”, National Forestry University of Ukraine, Lviv, Ukraina
2018	SNS & EFINORD Matchmaking day, Alnarp, Rootsi
	ELLS, PE&RC, PhD kursus “Conflicting demands in European Forests a wicked problem?”, Gällivare, Rootsi
2017	LLU Forestry doctoral school, Jaunkalsnava, Läti

Tunnustused:

2019	Eesti Maaülikooli Raefondi stipendium
2018	RMK Endel Laasi nimeline stipendium
2016	RMK Heino Tederi nimeline stipendium

Projektid:

2020-2024	PRG681, SA Eesti Teadusagentuur. Erinevate raieviiside mõju ökosüsteemi süsinikubilansile - turberaie versus lageraie. Täitja.
2020-2023	T200106MIME, Riigimetsa Majandamise Keskus. Valikraiete mõju metsaökosüsteemi süsinikubilansile ja majanduslikud aspektid. Põhitäitja.
2020-2022	T200047MIME, SA Keskkonnainvesteeringute Keskus. Kasvukoha süsinikubilansi dünaamika lageraie järgselt. Põhitäitja.
2019-2021	T180199MIME, SA Keskkonnainvesteeringute Keskus.Valgustusraiete mõju viljakate kasvukohtade arukaasikute arengule, Põhitäitja.
2018-2020	T180044MIME, SA Keskkonnainvesteeringute Keskus. Süsinikubilanss viljakate kuusikute vanusereas. Põhitäitja.

2018-2019	P180022MIME, Haridus- ja Teadusministeerium. Harvendusraiete mõju keskealiste palumännikute süsiniku- ja lämmastiku varudele ja voogudele. Põhitäitja.
2014-2019	IUT21-4, SA Eesti Teadusagentuur. Eesti metsade süsiniku dünaamika ja jätkusuutlik majandamine. Täitja.

LIST OF PUBLICATIONS

Publications indexed in the Thomson Reuters Web of Science database

1. **Aun, K.;** Kukumägi, M.; Varik, M.; Becker, H.; Aosaar, J.; Uri, M.; Buht, M.; Uri, V. (2021). Short-term effect of thinning on the carbon budget of young and middle-aged Scots pine stands, Forest Ecology and Management,
2. **Aun, K.;** Kukumägi, M.; Varik, M.; Becker, H.; Aosaar, J.; Uri, M.; Buht, M.; Uri, V. (2021). Short-term effect of thinning on the carbon budget of young and middle-aged silver birch (*Betula pendula* Roth) stands. Forest Ecology and Management, 480, 118660. 10.1016/j.foreco.2020.118660 .
3. Aosaar, J.; Drenkhan, T.; Adamson, K.; **Aun, K.;** Becker, H.; Buht, M.; Drenkhan, R.; Fjodorov, M.; Jürimaa, K.; Morozov, G.; Pihlak, L.; Piiskop, K.; Riit, T.; Varik, M.; Väär, R.; Uri, M.; Uri, V. (2020). The effect of stump harvesting on tree growth and the infection of root rot in young Norway spruce stands in hemiboreal Estonia. Forest Ecology and Management, 475, ARTN 118425. 10.1016/j.foreco.2020.118425.
4. Morozov, G.; Aosaar J.; Varik, M.; Becker, H.; Lõhmus, K.; Padari, A.; **Aun, K**.; Uri, V. (2019). Long-term dynamics of leaf and root decomposition and nitrogen release in a grey alder (*Alnus incana* (L.) Moench) and silver birch (*Betula pendula* Roth.) stands. Scandinavian Journal of Forest Research, 34 (1), 12−25. 10.1080/02827581.2018.1521468.
5. Uri, V.; Kukumägi, M.; Aosaar, J.; Varik, M.; Becker, H.; **Aun, K**.; Krasnova, A.; Morozov, G.; Ostonen, I.; Mander, Ü.; Lõhmus, K.; Rosenvald, K.; Kriiska, K.; Soosaar, K. (2019). The carbon balance of a six-year-old Scots pine (*Pinus sylvestris* L.) ecosystem estimated by different methods. Forest Ecology and Management, 433, 248−262. 10.1016/j.foreco.2018.11.012.
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VIIS VIIMAST KAITSMIST

ELINA KARRON
ERINEVATE KASVATUSTEHNOLOOGIATE MÕJU FUSARIUM SPP. ESINEMISELE JA MÜKOTOKSIINIDE TEKKIMISELE TERAVILJADEL
INFLUENCE OF CULTIVATION TECHNOLOGIES ON PATHOGENIC FUSARIUM SPP. OCCURRENCE AND PRODUCTION OF MYCOTOXINS IN CEREALS
Dotsent **Eve Runno-Paurson**, professor **Ülo Niinemets**, emeriitdotsent **Enn Lauringson**
15. juuni 2021

IMBI NURMOJA
SIGADE AAFRIKA KATKU EPIDEMIOLOOGIA EESTIS JA ÜHE VIIRUSTÜVE ISELOOMUSTUS
EPIDEMIOLOGY OF AFRICAN SWINE FEVER IN ESTONIA AND CHARACTERIZATION OF ONE VIRUS STRAIN
Doktor **Arvo Viltrop**, doktor **Sandra Blome**, doktor **Klaus Robert Depner**
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MERILI TOOM
ERINEVATE VAHEKULTUURIDE BIOMASSI MOODUSTAMISE JA LÄMMASTIKU SIDUMISE VÕIME SÕLTUVALT KÜLVIAJAST NING VAHEKULTUURIDE MÕJU SUVIODRA SAAGILE
BIOMASS AND NITROGEN ACCUMULATION BY COVER CROPS DEPENDING ON SPECIES AND SOWING DATE AND THE EFFECT OF COVER CROPS ON SPRING BARLEY YIELD
Dotsent **Enn Lauringson**, dotsent **Liina Talgre**, dr. **Andres Mäe** (Eesti Taimekasvatuse Instituut)
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KAIRE LOIT
PATOGEENSED JA ARBUSKULAARMÜKORIISSED SEENED EESTI KARTULIPÕLDUDEL
PATHOGENIC AND ARBUSCULAR MYCORRHIZAL FUNGI IN POTATO FIELDS IN ESTONIA
Professor **Alar Astover**, dokor **Maarja Öpik** ja doktor **Leho Tedersoo**
22. juuni 2021

NASIME JANATIAN GHADIKOLAEI
HÜDROMETEOROLOOGILISTE JA KLIIMATEGURITE MÕJU JÄRVEDE FÜTOPLANKTONILE: AJASKAALADE OLULISUS
HYDROMETEOROLOGICAL AND CLIMATIC CONTROL OVER LAKE PHYTOPLANKTON: THE IMPORTANCE OF TIME SCALES
Juhtivteadur **Peeter Nõges**, **Biel Obrador**, vanemteadur **Fabien Cremona**, vanemteadur **Alo Laas**
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