

MAI KUKUMÄGI

Factors affecting soil respiration and
its components in silver birch and
Norway spruce stands



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LIST OF ORIGINAL PUBLICATIONS

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

- I **Kukumägi M**, Ostonen I, Kupper P, Truu M, Tulva I, Varik M, Aosaar J, Sõber J, Lõhmus K. 2014. The effects of elevated atmospheric humidity on soil respiration components in a young silver birch forest. *Agricultural and Forest Meteorology* 194: 167–174.
- II Uri V, Varik M, Aosaar J, Kanal A, **Kukumägi M**, Lõhmus K. 2012. Biomass production and carbon sequestration in a fertile silver birch (*Betula pendula* Roth) forest chronosequence. *Forest Ecology and Management* 267: 117–126.
- III Varik M, **Kukumägi M**, Aosaar J, Becker H, Ostonen I, Lõhmus K, Uri V. 2015. Carbon budgets in fertile silver birch (*Betula pendula* Roth) chronosequence stands. *Ecological Engineering* 77: 284–296.
- IV Uri V, Aosaar J, Varik M, Becker H, **Kukumägi M**, Ligi K, Pärn L, Kanal A. 2015. Biomass resource and environmental effects of Norway spruce (*Picea abies*) stump harvesting: An Estonian case study. *Forest Ecology and Management* 335: 207–215.
- V **Kukumägi M**, Ostonen I, Uri V, Helmisaari H-S, Kanal A, Kull O, Lõhmus K. Stand age affects soil respiration and its components in a Norway spruce chronosequence. (submitted manuscript).

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The participation of the author in preparing the listed publications is as follows:

- paper I – was responsible in developing the idea and experimental design, collected and analyzed soil respiration data and was leading author in writing the paper;
- paper II – participated in processing of model trees and in collection of litter data and participated in writing the paper;
- paper III – contributed to developing the idea and experimental design, collected and analyzed soil respiration data and participated in writing the paper;
- paper IV – contributed to developing the idea and experimental design, collected and analyzed soil respiration data and participated in writing the paper;
- paper V – was responsible in developing the idea and experimental design, collected and analyzed soil respiration and above-ground litter data and was leading author in writing the paper.

LIST OF ABBREVIATIONS

Rs	soil respiration, the sum of heterotrophic (decomposition of dead organic matter by decomposers) and autotrophic (root and rhizosphere) respiration
Rh	heterotrophic respiration
Ra	autotrophic respiration
Rh/Rs	contribution of heterotrophic respiration to soil respiration
Ra/Rs	contribution of autotrophic respiration to soil respiration
C	carbon
Ts	soil temperature
Q₁₀	temperature sensitivity of respiration, the proportional increase in respiration when temperature increases by 10 °C
SWC	soil moisture
FRB	fine root biomass
FRNPP	fine root net primary production
MB	microbial biomass
FAHM	free air humidity manipulation experiment

I. INTRODUCTION

Soil CO₂ efflux (i.e. soil respiration (Rs)), globally 68–98 Pg C yr⁻¹, is the second largest flux in the global carbon (C) cycle (Raich and Schlesinger, 1992; Schlesinger and Andrews, 2000; Raich et al., 2002; Bond-Lamberty and Thomson, 2010b), and thus is the key process in the terrestrial C cycle. Forests store vast pools of C, over two-thirds of the C in forest ecosystems is contained in soils (Dixon et al., 1994). The C balance is a very delicate equilibrium between photosynthesis and respiration. Although many European forests act as C sinks (Valentini et al., 2000) the influence of climate, growing-season length and disturbance can cause significant shifts in an ecosystem (Goulden et al., 1998; Lindroth et al., 1998; Hyvönen et al., 2007). Rs comprises a large part of the C fluxes of a forest ecosystem, accounting for up to 80% of total ecosystem respiration (Raich and Schlesinger, 1992; Janssens et al., 2001; Davidson et al., 2006). Even small changes in the magnitude of Rs could severely alter the balance of atmospheric CO₂ concentration, with potential feedbacks to climate change. The topic is relevant also at the national level as data about the forest soil CO₂ effluxes is scarce in Estonia; however, the government is obliged to report on C pool changes in forests, which in turn affects the development of a national climate policy. Hence, the knowledge of the dynamics of soil CO₂ effluxes is essential for a better understanding of the C balance of terrestrial ecosystems and the main issues are quantification and modelling of the main C fluxes of different forest types.

Rs is influenced by various biotic and abiotic factors at different temporal and spatial scales. In this thesis, attention is paid to the effects of climatic factors (elevated air humidity, soil temperature (Ts) and soil water content (SWC)), below-ground biomass and activity, litter input, forest age and management type on the soil CO₂ effluxes; which all have been found to be important factors affecting the C cycling of forest ecosystems (Raich and Schlesinger, 1992; Pregitzer and Euskirchen, 2004; Hibbard et al., 2005; Ryan and Law, 2005; Peng et al., 2008; Bahn et al., 2010; Harmon et al., 2011). Nevertheless, a complete understanding of soil respiration is still unclear due to the complexity of the processes and the interaction of the affecting factors involved.

Climate change scenarios predict warmer and wetter conditions for northern forests in this century (Kont et al., 2003; IPCC, 2007a). Changes in precipitation frequency and intensity vary on a regional scale; up to a 40% increase of precipitation has been estimated in northern Europe (IPCC, 2007b). This will impact soil water content and affect forest nutrient cycles (Johnson et al., 2003). Changes in precipitation patterns are associated with increased water vapour in the atmosphere, caused by an increase in temperature (IPCC, 2007a); thus a higher amount of precipitation will raise air humidity. A climate manipulating experiment at an ecosystem-scale is an important tool enabling us to simulate, investigate and predict changes in the C balance of forest ecosystems. Rs has been found to increase in elevated CO₂ (FACE) and warming experiments

(Rustad et al., 2001; King et al., 2004; Wu et al., 2011). The knowledge about the possible effect of elevated humidity on CO₂ efflux is lacking. As forests at high latitudes are considered to be vulnerable to changes in climate and as Rs is the main determinant of C balance in northern hemisphere forests (Valentini et al., 2000), it is necessary to understand the influence of environmental factors on Rs, including increasing air humidity, in order to predict the future C budget.

Forest age plays an important role in determining the distribution of ecosystem C fluxes and sequestration (Pregitzer and Euskirchen, 2004), but relevant findings are contradictory. There have been reported an increase (Wiseman and Seiler, 2004) and a decrease (Saiz et al., 2006a) of Rs with stand age, as well as non-linear responses of Rs to stand age (Wang et al., 2002; Tang et al., 2009). However, to develop long-term models, it is crucial to understand the impact of stand age on forest C dynamics in association with a changing climate (Tang et al., 2009).

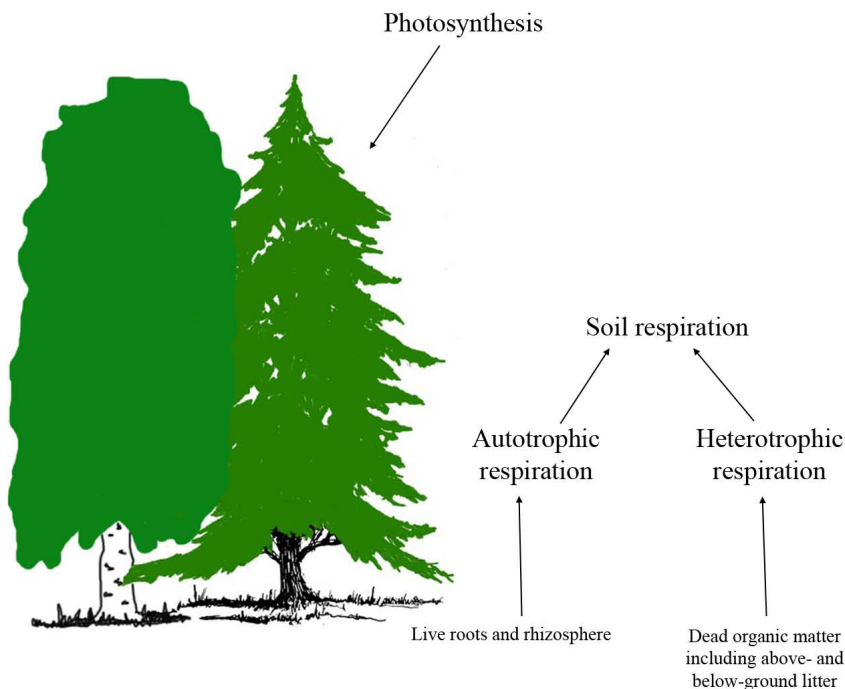


Figure 1. Simplified scheme of the carbon cycle of a forest ecosystem, which shows the basic components of soil CO₂ efflux and its sources.

Rs, as the sum of autotrophic (root and rhizosphere) (Ra) and heterotrophic (mainly microbial) (Rh) respiration (Hanson et al., 2000; Subke et al., 2006), is affected by several biotic factors (Fig. 1). A significant positive correlation

between R_s and fine root biomass (FRB), fine root production (FRNPP) and microbial biomass (MB) has been found (Xu and Qi, 2001; Lee and Jose, 2003; Knohl et al., 2008). Fine root production and biomass dynamics vary spatially and temporally and are greatly influenced by forest type, climate, soil nutrient status, stand age, etc. (Block et al., 2006; Finér et al., 2007; Yuan and Chen, 2012). However, below-ground biomass and turnover are yet often inadequately or discordantly estimated part of the C budget of forest ecosystems. Life in below-ground is largely supported by substrates from above-ground. Substrate supply from photosynthesis (primary source of R_a) can strongly influence R_s (Högberg et al., 2001; Ryan and Law, 2005; Kuzyakov and Gavrichkova, 2010; Hopkins et al., 2013). Photosynthetically recently fixed C may account for 60–80% of R_s during the peak growing season (Högberg et al., 2001; Pregitzer et al., 2006). Furthermore, R_s is positively related to above-ground litterfall (substrate for microbes) (Hibbard et al., 2005; Sulzman et al., 2005). Because of the complex interactions between below- and above-ground processes, for several reasons, it is highly important to examine the components of R_s (R_a and R_h) separately:

- The relative contribution of R_a or R_h to R_s can vary greatly, from 10% to 90%, although the variability depends on the type of the ecosystem, the season of the year and the measurement technique (Hanson et al., 2000).
- Substrate supply and availability (photosynthates for R_a , litter for R_h) vary seasonally (Högberg et al., 2001; Hopkins et al., 2013; Zhang et al., 2014).
- R_a and R_h are thought to respond differently to environmental factors (Boone et al., 1998; Högberg et al., 2001; Wei et al., 2010; Ma et al., 2014).
- R_a and R_h may vary differently with stand age (Bond-Lamberty et al., 2004b; Saiz et al., 2006a; Luan et al., 2011; Ma et al., 2014).
- R_h is a major process releasing globally about 60 Pg of C per year into the atmosphere (Shao et al., 2013). Quantification of the R_h flux is essential for C budgeting and thus for estimating C sequestration, i.e. net ecosystem productivity.

Concerning the methodological aspect of soil respiration partitioning, the trenching approach is the most widely used root exclusion technique for separating R_a and R_h components of R_s , although it has various limitations (Kuzyakov, 2006; Subke et al., 2006). Neglecting the decomposition of detached roots and increased soil water content in trenched plots leads to overestimation of R_h . On the other hand, lack of fresh inputs of above- and below-ground litter leads to underestimation of R_h (Epron, 2009). Therefore, several corrections should be considered while estimating the contribution of R_h to R_s , but still few studies have taken them into account.

T_s and SWC are the most relevant climatic factors associated with seasonal and interannual changes in R_s rates (Raich and Schlesinger, 1992; Lloyd and Taylor, 1994; Davidson et al., 1998; Hibbard et al., 2005; Luo and Zhou, 2006; Wang et al., 2006; Bahn et al., 2010; Gaumont-Guay et al., 2014). SWC limits

Rs usually at the lowest and at the highest levels (Davidson et al., 1998; Xu and Qi, 2001; Curiel Yuste et al., 2003; Luo and Zhou, 2006). Therefore, Ts is usually the main driving variable for seasonal changes in Rs at optimum SWC conditions in northern forests (Hibbard et al., 2005; Luo and Zhou, 2006). The sensitivity of respiration processes to Ts is frequently described by the Q_{10} value – the relative increase of respiration with a temperature increase by 10 °C. Despite the growing information on the temperature sensitivity of respiration processes, Rh and Ra can have different Q_{10} values (Boone et al., 1998; Hartley et al., 2007; Luan et al., 2011; Ma et al., 2014) and there is no consensus on which Rs component is more sensitive to Ts. Furthermore, recent studies have revealed the dependence of Q_{10} on substrate supply and quality (Gershenson et al., 2009; Hopkins et al., 2013; Erhagen et al., 2015). Above-ground litterfall and fine root turnover are the two dynamic fluxes of C cycling and the main sources of C for soil decomposers in forest ecosystems, and both have a clearly expressed seasonal (especially at higher latitudes) and age-dependent cycle (Varik et al., 2013; Zhang et al., 2014). Therefore, substrate supply has a confounding effect on the temperature response of Rs and can mask its direct correlation with Ts. During forest succession, environmental conditions change and the temperature sensitivity of Rs and its components may change also with stand age. For example, Rs was more responsive to Ts and SWC in a younger stand than in an older stand (Jassal et al., 2012). Heterotrophic respiration was more sensitive to temperature in a mature larch stand compared to a sapling stand (Ma et al., 2014). Wang et al. (2013) found that Q_{10} of Rh and Ra increased with stand age in larch stands, but for Mongolia pine, only Q_{10} of Rh increased with stand age, whereas Ra showed no significant relationship with Ts. Nevertheless, less attention has been paid to the effect of stand age on the different components of Rs and on their temperature sensitivity. Another important aspect is varying temperature sensitivity of different soil organic matter (SOM) fractions. Karhu et al. (2010) found that the most labile C was least temperature sensitive, while more recalcitrant, intermediate C (mean residence time from years to decades) was highly temperature sensitive, and old, centennially cycling C was again less temperature sensitive, indicating a stronger positive feedback to global warming compared with current estimates.

Forest management has a great potential for controlling the C storage of forest (Hyvönen et al., 2007). Considering the need to reduce CO₂ emissions, more intensive utilization of biomass has become a major issue worldwide. A quite novel prospective source of renewable energy is the biomass of stumps. In Finland uprooting of tree stumps is a common management practice (Finnish Statistical Yearbook of Forestry, 2013). In Estonia, stump harvesting is not yet a common forestry practice. Large-scale stump harvesting requires relevant research to determine potential environmental risks (decrease of soil fertility) and to avoid the possible failure of sustainable forest management. Several studies have explored the effect of harvesting on the forest soil CO₂ efflux but the results are contradictory (Mallik and Hu, 1997; Striegl and Wickland, 1998;

Wiseman and Seiler, 2004; Payeur-Poirer et al., 2012). Moreover, estimations of soil respiration rates vary greatly ($171\text{--}2600\text{ g m}^{-2}\text{ yr}^{-1}$) in different studies depending on the harvesting method, climatic conditions and the forest type (Luo and Zhou, 2006). Also, different site preparation methods can significantly affect the soil CO_2 efflux. For example, soil respiration rate increased at a site where logging residue was left on site, but decreased to pre clear-cutting level when logging residue was removed (Pumpanen et al., 2004). While the effect of clear-cutting, thinning, burning, fertilization, litter removal and site preparation on the forest soil CO_2 efflux has been investigated by several authors (Pumpanen et al., 2004; Luo and Zhou, 2006; Peng et al., 2008), little is known about the consequences of tree-stump harvesting on the soil CO_2 effluxes. The effect of stump harvesting on R_s may be different. Stump uprooting disturbs soil structure in the upper layer, which may have a significant effect on mineralization and R_s (Walmsley and Godbold, 2010). On the one hand, CO_2 emission in an uprooted area may decrease since the amount of decomposing organic matter (dead roots) is reduced. On the other hand, soil disturbance may induce more intensive mineralization of C and thereby initiate CO_2 emission, which may reduce the stable soil C storage (Grelle et al., 2012).

Aim of the thesis. There are three novel aspects in this thesis. First, in the light of global climate change, the knowledge about the effect of elevated air humidity on soil CO_2 effluxes will help to predict and understand the consequences of a changing pattern of humidity on the forest carbon cycle (**I**). Second, the first results are obtained about soil respiration partitioning into the heterotrophic and autotrophic components in Estonian silver birch and Norway spruce forests (**III**, **V**). Third, stump harvesting for biomass is a new forest management practice in Estonia and paper **IV** reports the first results of this research in relation to soil respiration partitioning. The results of the above studies could be used both in absolute and relative terms in the carbon cycling models of forest ecosystems.

The general aim of the thesis was to study the effect of several factors: abiotic (elevated air humidity, soil temperature and moisture); biotic (stand age and development stage, fine root biomass and turnover, above-ground litter input, soil microbial biomass and activity) and forest management (stump harvesting) on total soil respiration and its autotrophic and heterotrophic components in silver birch and Norway spruce stands of different ages (**I**, **III**, **IV**, **V**). The results of paper **II** were used as background information and for compiling C budgets for silver birch stands. Special attention was paid to the temperature sensitivity of the soil respiration components and to the improvement of trenching methodology (**III**, **V**).

The specific objectives were:

- to investigate the impact of elevated air humidity on R_s in a young silver birch plantation;

- to examine the seasonal dynamics of R_s and the contribution of R_h and R_a to R_s in relation to abiotic and biotic factors in silver birch and Norway spruce forest chronosequences;
- to analyse age-related changes of R_s and its components in silver birch and Norway spruce stands;
- to estimate the temperature sensitivity of R_s and its components, R_h and R_a , in silver birch and Norway spruce stands of different ages;
- to assess the contribution of R_h to R_s in silver birch and Norway spruce stands considering the disadvantages of the trenching method and improving the methodology;
- to estimate the effect of stump harvesting on R_s and R_h at a clear-cut site of Norway spruce.

The hypotheses tested in the thesis:

- R_s will be higher at increasing air humidity mainly as a result of greater above-ground+below-ground NPP of the understorey and the respective litter input into the soil.
- The effect of stand age on soil CO_2 effluxes is related to changes in biotic factors rather than to changes in abiotic factors.
- The effect of soil moisture on soil CO_2 effluxes is minor and R_s is driven mainly by soil temperature.
- Soil respiration components (R_h and R_a) differ in their response to temperature.
- Post-clear-cut Norway spruce stump harvesting does not cause significant increase of R_s .

2. MATERIALS AND METHODS

2.1. Study sites

All study sites are situated in the hemiboreal forest zone characterized by a moderately cool and moist climate. The long-term average annual precipitation is 650 mm, the average temperature is 17.0 °C in July and –6.7 °C in January. The growing season usually lasts 175–180 days. The studied tree species were silver birch (*Betula pendula* Roth) and Norway spruce (*Picea abies* (L.) Karst), both growing in fertile site types. Silver birch and Norway spruce are economically and ecologically important tree species widely distributed in Northern Europe (Krüssmann, 1976; Evans, 1984). Silver birch is a fast-growing, light-demanding early-successional deciduous tree colonizing open areas soon after clear-cut (Hynynen et al., 2010). Norway spruce is a shade tolerant tree species often growing in the second layer of birch stands. Some stand and soil characteristics of the studied sites are given in Table 1.

Table 1. Stand characteristics. Age (at the beginning of the study), height (H), diameter at breast height ($D_{1.3}$) (*stem basal diameter for silver birch at age 3), basal area, forest site type, soil type, pH_{KCl} , carbon-to-nitrogen ratio (C:N) and organic C (C_{org}) for 0–10 cm soil layer. Letters c and h represent treatments with increased air humidity (h) and control (c); letters E and R represent study sites of Elva and Røuge.

Tree species	Age (yr)	H (m)	$D_{1.3}$ (cm)	Basal area ($m^2 ha^{-1}$)	Forest site type	Soil type	pH_{KCl}	C:N (%)	C_{org}
Silver birch	3(c)	2.44*	2.20*			<i>Endogleyic Planosol</i>	4.2	12.1*	1.27
	3(h)	2.26*	2.23*			<i>Endogleyic Planosol</i>	4.4	12.6*	1.34
	13	10.9	5.8	20.1	<i>Oxalis</i>	<i>Albeluvisol</i>	5.4	15.2	1.49
	32	17.0	10.8	29.2	<i>Oxalis</i>	<i>Gleyic Umbrisol</i>	3.9	13.6	3.08
	45	25.6	20.1	29.8	<i>Oxalis</i>	<i>Albeluvisol</i>	4.6	15.8	2.26
Norway spruce	4(E)				<i>Oxalis</i>	<i>Endogleyic Arenosol</i>	3.6	19.5	2.73
	4(R)				<i>Myrtillus</i>	<i>Endogleyic Albic Podzol</i>	3.3	23.5	4.94
	30	9.1	7.6	23.7	<i>Oxalis-Myrtillus</i>	<i>Eutric Spodic Gleysol</i>	2.6	26	34.3
	39	19.2	16.7	39.3	<i>Oxalis-Myrtillus</i>	<i>Eutric Reductigleic Gleysol</i>	3.2	27	45.0
	87	30.0	30.2	34.0	<i>Oxalis-Myrtillus</i>	<i>Gleyic Carbic Podzol</i>	2.6	31	84.6

* Height and stem basal diameter of silver birch stand at age 3, planted on former agricultural land after Sellin et al. (2013) and C:N ratio after Hansen et al. (2013).

Silver birch

FAHM (I). The study site FAHM (Free Air Humidity Manipulation) is located at Rõka village, Järvselja Experimental Forest District (58°14'N, 27°18'E), in southeastern Estonia. The experimental area (2.7 ha) was established on an abandoned agricultural field in 2006–2007. The relief of the site is gently sloping with a maximum difference in elevation of about 8 m. One-year-old bare-root transplants of silver birch were planted in the spring of 2006 with a 1 m spacing in 9 study plots (Kupper et al., 2011). Silver birch occupied half of each experimental plot. The other half was occupied by hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.), not analysed in this study. To clarify the impact of soil biota and understorey species diversity on the functioning of the ecosystem, two different types of understorey were established in the plots. The “early successional community” was relatively species-poor and was created by sowing timothy-grass (*Phleum pratense* L.). The “forest community” consisted primarily of meadow and forest plants transplanted in 0.5×0.5×0.2 m patches collected from a nearby forest clear-cut. The transplantation of forest floor species was carried out in May and June 2006. Additionally, seeds of forest understorey species were sown in the plots in autumn of 2006. The prevailing species in transplanted plots were *Aegopodium podagraria* L., *Rubus idaeus* L., *Fragaria vesca* L., *Stellaria holostea* L. etc. However, dominating species in the “forest community”, formed in misting and control plots by the time of this study, were *Ranunculus repens* L., *Lathyrus pratensis* L., *Festuca rubra* L., and *Veronica chamaedrys* L. (Parts et al., 2013). Study was carried out in six experimental plots. Air humidity was increased by 7% on average above ambient level in three experimental plots (misting plots) by fumigating trees with mist in the years 2008 and 2009. Misting was applied daily (Sundays excluded) from 9.00 to 17.00 h from mid-May to the 31st of August in 2008; and from 9.00 to 19.00 h from the 5th of May to the 25th of September in 2009. The other three experimental plots were control areas where misting was not applied. The experimental design is described in detail in Kupper et al. (2011).

Chronosequence (II and III). The study sites of the three silver birch stands were located at Kambja (58° 3'N, 27° 1'E), at Alatskivi (58° 37'N, 27° 2'E) and at Erastvere (57° 8'N, 26° 56'E) in southeastern Estonia. Studied *Oxalis* silver birch stands aged 13 (pole), 32 (middle-aged) and 45 years (premature) grew in a flat landscape. Stands on this site type are highly productive; acidic soils have a relatively thick A-layer, moisture conditions for plant growth are suboptimal, the soils are well drained and the steady forest floor is missing in most cases (Lõhmus, 1984). The youngest stand was growing on abandoned agricultural land, the other stands were growing on forest land. All stands had closed canopies; in the oldest stand the second layer of Norway spruce was growing. Understorey was negligible in the oldest stand.

Norway spruce

Clear-cut (IV). Two Norway spruce clear-cut sites with automorphic fertile soil were located at Elva (58° 19' N, 26° 31' E) and at Rõuge (57° 42' N, 26° 45' E) in southeastern Estonia. Sites were clear-cut in winter 2010/2011 and stumps were harvested in October of 2011. In the spring of 2012 both study sites were reforested by planting four-year-old bare-root spruce transplants; initial density was 3000 plants per hectare.

Chronosequence (V). The study sites of the three Norway spruce stands were located at Järvselja (58° 15' N, 27° 16' E) in southeastern Estonia. Studied Norway spruce stands aged 30 (pole), 39 (middle-aged) and 87 years (mature) grew in a flat landscape. All stands grew on forest land. The sites, although drained, are characterized by a periodically high groundwater table. Less impermeable *Gleysols* retain water saturated close to soil surface and remain wet longer compared with *Gleyic Podzols*. Silver birch was a co-dominant tree species in the mature stand. In the pole and middle-aged stands the understorey was practically missing because of poor light conditions under the tree canopy. The dominating understorey species in the oldest stand were *Vaccinium myrtillus* L., *Maianthemum bifolium* F.W.Schmidt, *Trientalis europaea* L., and *Oxalis acetosella* L. The dominating moss species were *Pleurozium schreberi* Mitt. and *Hylocomium splendens* B., S. et G., in the pole stand also patches of *Sphagnum* sp. occurred.

2.2. Soil respiration, soil temperature and soil moisture measurements

Soil CO₂ effluxes were measured monthly during growing seasons (from May to October (**I, V**) and from May to November (**III, IV**)) using a closed dynamic chamber method (PP *Systems* SRC-1 chamber with gas analyser CIRAS-2 (Differential CO₂/H₂O Infrared Gas Analyzers)). The chamber area was 78.5 cm² and the volume was 1170 cm³. The CO₂ rate was expressed as μmol CO₂ m⁻²s⁻¹. Soil respiration is measured when a chamber of known volume is placed on the soil and the rate of increase in CO₂ within the chamber is monitored. PVC collars (inner diameter 10 cm, height 5 cm) were installed to a soil depth of 1–2 cm. To measure only respiration from soil, green plants were cut if necessary.

Soil temperature (Ts, °C) was measured simultaneously with respiration using an attached soil temperature probe STP-1 (PP Systems International, Inc., USA) inserted at ~5 cm depth. Volumetric soil moisture (SWC, %) was measured at ~5 cm depth using a HH2 Moisture Meter Version 2 (Delta-T Devices Ltd, UK). In addition, in **I** Ts (ST1 soil temperature probe; Delta-T Devices, Burwell, UK) was measured in 3 replications at 15 cm depth in each experimental plot. Precipitation was measured continuously (TR-4 tipping bucket rain gauge; Texas electronics, Dallas, TX) and recorded in 4–5 replications in

each experimental plot above the understorey (Kupper et al., 2011). Data was stored with a data logger (DL2e; Delta-T Devices). In **III–V** soil temperature (model 1425, Technologies, Inc, USA) and soil moisture (Watermark soil moisture sensor 6450WD, Technologies, Inc, USA) were measured every hour at a depth of 10 cm and data was stored with a data logger (WatchDog 1425, Spectrum Technologies, Inc, USA).

The trenching method with insertion of PVC cylinders to a depth of 45–50 cm was applied to distinguish heterotrophic respiration from total soil respiration (**III, IV, V**). This depth is sufficient for excluding root respiration since most of the fine root biomass of trees is located in the forest floor and in the top 20 cm mineral soil (Ostonen et al., 2005; Uri et al., 2007; Varik et al., 2013). The above-ground vegetation was carefully removed from inside a trench with minimum soil disturbance and the trenched plots were kept free of the green vegetation throughout the study. Soil CO₂ efflux from the trenched plots was used to estimate heterotrophic respiration (Rh) because of the root exclusion; total soil respiration (Rs) was measured in the control plots.

2.3. Estimation of fine root biomass and production

Fine root biomass (FRB) of Norway spruce (**V**) and the understorey (**I**) was estimated using soil cores. The cores were divided into the organic layer (average 10 cm) (**V**) and the 0–10, 10–20 and 20–30 cm mineral soil layers (**I, V**). The roots of a soil core layer were carefully washed free of soil manually. Fine roots of spruce (**V**) or the understorey and roots of silver birch (**I**) were separated under a microscope. In study **I** the main part of the below-ground biomass was formed by rhizomes and fine roots of the understorey; the share of fine roots of silver birch was approximately 10% of the total fine-root fraction. Biomass samples were dried at 70 °C for 48 h and weighed to 0.001 g.

Fine root and rhizome net primary production (FRNPP) (g m⁻² yr⁻¹) of the understorey (**I**) was estimated by maximum-minimum method (1) by subtracting the value of the lowest biomass (FRB_{min}) from the value of the highest biomass (FRB_{max}) (Brunner et al., 2013). Root turnover rate was calculated by dividing below-ground net primary production (FRNPP) by mean FRB (2).

$$\text{Annual FRNPP} = \text{FRB}_{\text{max}} - \text{FRB}_{\text{min}} \quad (1)$$

$$\text{Root turnover rate (yr}^{-1}\text{)} = \text{FRNPP} / \text{mean FRB} \quad (2)$$

FRB for silver birch stands was estimated by the ingrowth core method (**III**). Mean FRB was estimated as an average of live root biomass during the sampling period; the third year ingrowth core biomass data were considered to be representative of the actual fine root pool.

In silver birch and Norway spruce stands FRNPP was estimated by ingrowth cores (d=40 mm, mesh size 6 mm) (Ostonen et al., 2005), which were installed

systematically in random transect groups all over the stands. Sampling was carried out three times per vegetation period, in June, August and October. The annual FRNPP in the ingrowth cores was calculated by balancing living and dead root biomass according to Fairley and Alexander (1985). FRNPP was calculated on the basis of the third year data of the ingrowth cores. Turnover rate was calculated by dividing the annual production by the mean biomass from ingrowth cores (III, V).

2.4. Microbiological analysis

Soil samples for microbiological analysis were taken in all stands with a soil corer (\varnothing 2 cm) from the 0 to the 10 cm layer in October and composite samples were formed per stand (III, V) or per treatment (I). Fresh soil samples were sieved ($d < 2$ mm) to obtain the fine earth fraction (Löhmus et al., 2006). Soil samples were used for measurements of microbial biomass C (MB) and basal respiration. Cross contamination of samples was carefully avoided at sampling and at sample processing. The Substrate Induced Respiration (SIR) method was applied in order to evaluate metabolically active microbial biomass in the soil. The SIR was determined via the Oxitop® manometric system (Oxitop®, WTW). The oxygen consumption per gram of dry soil was calculated according to a recommended procedure by Platen and Wirtz (1999) and microbial biomass carbon (mg C per g of dry soil) was calculated according to Beck et al. (1996). Microbiological methods are thoroughly described in papers I and III.

2.5. Chemical analysis of soil

Soil pH in 1 M KCl suspensions was measured using the ratio 10g:25 ml (I, II, IV, V). Total soil C content was determined by the dry combustion method using a varioMAX CNS elemental analyser (II, IV). Soil nitrogen (N) was determined according to the Kjeldahl method (I, II, IV, V). The analyses were performed at the Laboratory of Biochemistry of the Estonian University of Life Sciences.

2.6. Above-ground tree litter flux

In the silver birch stands, ten litter traps (collecting area 0.25, 0.33 and 0.53 m²) were placed in the pole, middle-aged and premature stands (II, III). Litter was sampled fortnightly during the period June 2004–May 2005 in the youngest stand and during May 2008–June 2009 in the two older stands. In the Norway spruce chronosequence, ten litter traps (collecting area 0.5 m²) were placed in the pole stand and eight litter traps (collecting area 1 m²) were placed in the middle-aged and mature stands in November 2003 (V). Litter was sampled monthly during the period November 2003–December 2004. Litter samples were divided into spruce needles, deciduous tree leaves, branches and other

material (in Norway spruce stands only) and corresponding masses (g m^{-2}) were calculated.

2.7. Stump harvesting technique

All sites were divided into four subplots with an equal area: two control plots and two stump harvesting plots. For rooting, a Pallari KH 160 stump extractor combined with a hydraulic excavator was used. Selectively, only spruce stumps were uprooted, the stumps of deciduous trees and pine stumps were left on site. For better drying as well for more complete removal of soil particles, the stumps were shaken and cut after uprooting. The aboveground harvesting residues (branches, tops) were left on site everywhere. Thus, this study is not a classical “whole-tree harvesting” research but rather a conventional “stems-only” harvesting study with stump removal (IV).

2.8. Data analysis

Statistica 7.1 software was used to perform all statistical analyses; level of significance $\alpha=0.05$ was accepted in all cases. The normality of variables was checked using Lilliefors and Shapiro-Wilk’s tests on datasets. Rs data deviating from the normal distribution were log-transformed to normalize for statistical analysis. The effects of treatment (misting (increased air humidity) or trenching), time (month, year) and forest age on respiration rates, Ts and SWC were examined using the General Linear Models (GLM) module and repeated measures or factorial ANOVA. In case of significant effects ($P<0.05$), means were compared with the Tukey Unequal N HSD test or with t-test. Multiple stepwise regression analysis was performed to evaluate the relationships between respiration and Ts and soil moisture. General model has the following form:

$$\text{Flux} = ae^{bT_s}ce^{d\text{SWC}} \quad (3)$$

where:

a, b, c and d are coefficients,
 Ts is soil temperature ($^{\circ}\text{C}$) and
 SWC is volumetric soil moisture (%).

Relationship between Rs and Ts and temperature sensitivity (Q_{10}) were calculated using exponential function. Functions (4) and (5) were used in I

$$\text{Flux} = ae^{bT_s} \quad (4)$$

$$Q_{10} = e^{10b} \quad (5)$$

Modified equation (6) was used in **III** and **V**

$$\text{Flux} = R_{10}Q_{10}^{((T_s-10)/10)} \quad (6)$$

where:

R_{10} is respiration rate at temperature 10 °C,

Q_{10} is the relative increase of respiration with a temperature increase to 10 °C.

Cumulative R_s and R_h of the snow-free season (April–November) were modelled for all stands using monthly mean T_s from the data loggers (**III**, **V**). The T_s values for April and November, if necessary, were calculated using regressions between T_s for each stand and T_s measured in the experimental area of Free Air Humidity Manipulation of the forest ecosystems (Kupper et al., 2011). R_a was calculated as the difference between R_s and R_h . To discard the confounding effect of T_s on R_s , partial correlation analysis was used and the effect of SWC on R_s was analysed.

The trenching method influences environmental conditions inside deep PVC cylinders. SWC increases due to eliminated water uptake and transpiration by plants; as insertion of cylinders cuts off tree roots, the value of the CO_2 efflux from the decomposing detached roots has to be subtracted from the R_h value (Subke et al., 2006; Ngao et al., 2007; Comstedt et al., 2011); simultaneously, fine root growth and litter production are interrupted. Neglecting the effect of decomposing detached roots and increased SWC would lead to overestimated values of R_h and the lack of fresh inputs of intact roots would lead to underestimation of R_h (Epron, 2009). Therefore, corrections which take into account root exclusion and increased moisture effects were applied. See more detailed calculations in **III** and **V**.

3. RESULTS AND DISCUSSION

3.1. Effect of increased air humidity (I)

Soil respiration was measured in two consecutive growing seasons in experimental plots with increased air humidity (misting) and ambient conditions (control). Rs rates ranged from 1.3 to 9.9 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ over two growing seasons (May–Oct) being in the range of published data about European forest ecosystems (Matteucci et al., 2000). Misting decreased Rs in the second study year, however, remarkably only in July (Fig. 2, $P < 0.05$). Cumulative Rs of the growing season 2009 was 11 and 8.8 t C ha^{-1} in the control and misting plots, respectively.

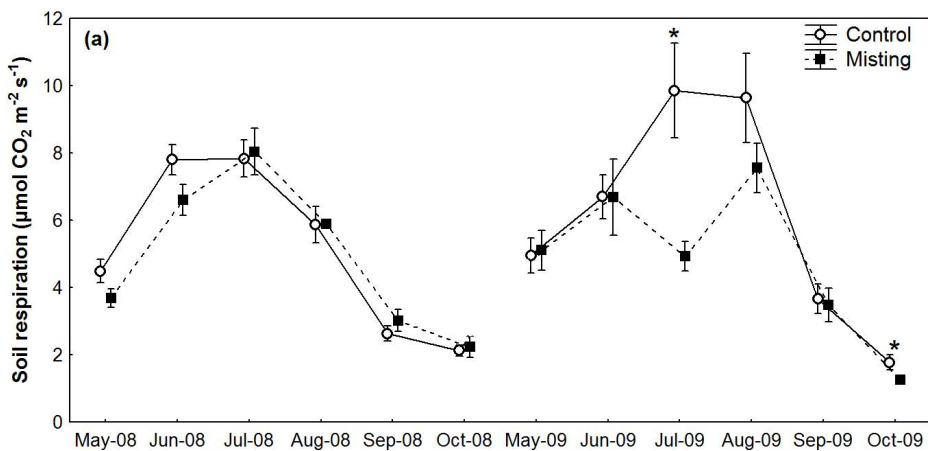


Figure 2. Soil respiration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) in the control and misting plots in the silver birch stand during the growing seasons 2008–2009. Error bars represent the standard error of the means. * represents significant differences $P < 0.05$. (I)

Soil temperature, explaining up to 75% of the variation of Rs, was the dominant climate variable driving the seasonal variation of Rs (Fig. 2 in I, $P < 0.0001$). The majority of Rs studies have found high correlation between Ts and Rs (Rustad et al., 2001; Hibbard et al., 2005; Luo and Zhou, 2006; Bronson et al., 2008; Gaumont-Guay et al., 2014). Nevertheless, Ts could not explain the difference in Rs between the control and misting plots in the midsummer, because Ts were very similar in the control and misting plots throughout this period (Fig. 1b in I, $P > 0.05$). Nor could this difference be attributed to SWC, although it was 1.3–1.6 times higher in the misting plots than in the control plots (Fig. 1c in I, Table 2 in I) but overall had a weak negative effect on Rs ($P < 0.05$). Generally, in forest ecosystems where SWC is usually not limiting, Rs is more sensitive to changes in Ts than to changes in moisture (Lloyd and Taylor, 1994; Davidson et al., 1998). As the study was carried out during two relatively wet summers a

stronger effect of SWC on Rs in the misting plots would therefore be expected in drought conditions.

The impact of the root and rhizome biomass and production of the understorey and microbial activity on Rs was analysed. In literature, a significant positive correlation has been found between Rs and FRB and MB (Xu and Qi, 2001; Lee and Jose, 2003; Knohl et al., 2008). Substrate supply can strongly influence Rs (Ryan and Law, 2005; Kuzyakov and Gavrichkova, 2010; Hopkins et al., 2013). Furthermore, Rs has been found to be related to ecosystem production (Janssens et al., 2001). At FAHM, the understorey NPP represents most of ecosystem NPP and its litter forms the main part of substrate for decomposers. Although misting did not affect MB ($P>0.05$), microbial respiration activity was increased by 28% (Table 2 in I, $P<0.05$), indicating higher Rh under increased air humidity conditions (supported by the higher annual understorey litter flux). The products of photosynthesis serve as the main substrate for Ra (Kuzyakov and Gavrichkova, 2010; Hopkins et al., 2013). Concerning the trees, stomatal conductance of birch leaves was significantly lower in the misting plots in July, possibly leading to reduced carbohydrate supply from leaves to roots. Moreover, a considerable decline in photosynthetic capacity has been found at this experimental site (Sellin et al., 2013). However, 90% of below-ground biomass was formed by rhizomes and fine roots of the understorey, thus the main part of the substrate for Ra originates from the understorey. The effect of changes in carbohydrate supply from tree leaves should be less important. Interestingly, the above-ground biomass of the understorey was similar for the misting and control plots (Table 2 in I, $P>0.05$), whereas the fine root and rhizome biomass and NPP of the understorey were approximately two times higher in the misting plots compared to the control plots (Table 2 in I, $P<0.05$). This indicates poorer assimilate support for Ra per root biomass unit in the misting plots. Therefore, lower Rs at increased air humidity could be related to lower proportion of Ra compared with ambient conditions. Hence, increased air humidity affects not only total Rs, but the proportion of soil respiration components.

3.2. Soil respiration in silver birch and Norway spruce chronosequences (III, V)

3.2.1. Seasonal dynamics of soil CO₂ effluxes in relation to abiotic and biotic factors

Soil respiration. Significant seasonal variation of Rs was observed in three birch (pole, middle-aged and premature) and spruce (pole, middle-aged and mature) stands ($P<0.05$) (Fig. 3; a middle-aged stand of birch and a pole stand of spruce are used as an example). In general, mean Rs (May–Nov) ranged about 1 to 8 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in both tree species, being comparable to the results measured in other boreal and temperate forests (Khomik et al., 2006; Vincent

et al., 2006; Korhonen et al., 2009; Wang et al., 2013; Gaumont-Guay et al., 2014). R_s , irrespectively of stand age, increased in spring and peaked in summer, and declined thereafter in autumn following the seasonal dynamics of T_s rather than changes in SWC (Fig. 2 in III and V). Such dynamis is commonly observed in boreal and temperate forests (Borken et al., 2002; Elberling and Ladegaard-Pedersen, 2005; Luo and Zhou, 2006; Gaumont-Guay et al., 2014). Seasonal variation of R_s is largely driven by changes in T_s , SWC, substrate availability, and their combinations, however, the main controlling factor depends on the type of the ecosystem and climate (Luo and Zhou, 2006).

Soil temperature. T_s was the main driver of the temporal variation in R_s . R_s and T_s were strongly and positively correlated in all stands ($r=0.79$ – 0.81 in spruce stands, $r=0.81$ – 0.89 in birch stands, $P<0.0001$). For example, in 2010 across stands of different ages, T_s alone explained 67–89% of the variation in R_s in birch stands and 74–91% of the variation in R_s in spruce stands ($P<0.001$ in all stands). The strong relationship between R_s and T_s over the seasonal course observed in this study is consistent with the results of studies conducted in European forests where up to 90% of variation in R_s was explained by T_s (Matteucci et al., 2000; Janssens et al., 2003). Seasonal dynamics of T_s was very similar in each stand for both tree species (for spruce Fig. 2b in V). In the birch stands, the lowest T_s were measured in November (around 6 °C in 2010 and 2–4 °C in 2011) and maximum T_s were measured in July (18–20 °C in 2010 and 17–18 °C in 2011). In the spruce stands, T_s was measured during 6 growing seasons (2004–2006, 2009–2010 and 2013) and the results showed that the summer of 2010 was the warmest ($P<0.05$). Maximum T_s in spruce stands reached generally 12–14 °C, but 15–16 °C in 2010. Low T_s were similar for the birch and spruce stands, but maximum T_s , measured in summer 2010, were 3–4 °C lower in the spruce stands than in the birch stands because of the dense canopy of spruce, which prevents solar radiation from reaching the ground.

Soil moisture. Across all measured data, SWC improved the regression model only in the oldest stands of both tree species: by 7% in a birch stand (45-year-old) and by 6% in a spruce stand (87-year-old). To eliminate the confounding effect of T_s , partial correlation was used to estimate the effect of SWC on R_s . SWC had a weak positive effect on R_s , which, however, was significant only for the oldest spruce stand and for the oldest birch stand ($r=0.36$, $P=0.006$ and $r=0.53$, $P=0.01$, respectively), considering all measured data for the studied stands. Also the driest soil was observed in the oldest stands of both tree species. The stimulating effect of SWC on R_s during the growing season was found in a Sitka spruce chronosequence in Ireland, whereas an opposite effect was revealed in the dormant season (Saiz et al., 2006b). Limiting effect of SWC on R_s has been reported frequently as caused by drought or by excessive SWC (Davidson et al., 1998; Borken et al., 2002; Vincent et al., 2006; Gaumont-Guay et al., 2006; Nikolova et al., 2009). More detailed analysis of the effect of SWC

on R_s is challenging because T_s and SWC often co-vary (Davidson et al., 1998).

SWC in the upper 5 cm soil layer fluctuated markedly during the growing seasons depending on the pattern of precipitation (Fig. 3 in **III** and Fig. 2c in **V**). In general, SWC is higher in spring due to the melting of snow, decreases thereafter in summer and increases in autumn at the end of the growing season. But, for example, the summer of 2004 was rainy and SWC fluctuated less than in the other study years. SWC was measured during 4 growing seasons in the spruce stands and the results showed a significantly moister soil in 2004 and in 2013 than in 2006 and in 2010 ($P < 0.05$). At the stand level, the smallest variation in SWC throughout the growing season was observed in the oldest stands of birch and spruce. For example, SWC of the birch stands ranged from 10 to 28% in the pole stand, from 9 to 40% in the middle-aged stand and from 7 to 21% in the premature stand in 2011. In the spruce stands SWC varied the most during the growing season of 2013 and ranged from 6 to 48% in the pole stand, from 10 to 58% in the middle-aged stand and from 19 to 34% in the mature stand

Although T_s was the main driver of the temporal variation of R_s , the effect of SWC can be revealed in very dry soil conditions. For example, the decline in R_s rates in all birch stands in July 2011 was probably related to very low soil moisture content at that time, with a simultaneous T_s maximum (Fig. 3a, c, e, Figs. 2 and 3 in **III**). The limitation in R_s observed at the time of high T_s may be attributed to drought stress on microbial communities and root activities (Lavinge et al., 2004; Borken et al., 2006; Moyano et al., 2009; Suseela et al., 2012), especially in the top soil layer. However, the response to water stress may be different for roots and for soil microbes as roots can extract water from deeper soil horizons. Furthermore, the response to drought can be tree species-specific. Nikolova et al. (2009) found a stronger decline in R_a in Norway spruce forest than in European beech forest, applying to the contrasting strategies in beech and spruce of coping with drought.

Heterotrophic and autotrophic respiration. The relative contribution of both R_a and R_h to R_s can vary greatly depending on the season of the year (Hanson et al., 2000; Lavinge et al., 2003; Ruehr and Buchmann, 2009; Tomotsune et al., 2013; Wang et al., 2013). Measured R_h followed a pattern similar to that of R_s showing higher values in summer and lower in spring and autumn in both birch and spruce stands (Fig. 3a, b). There was a positive correlation between R_h and T_s ($r = 0.79$ – 0.87 for the spruce stands and $r = 0.74$ – 0.92 for the birch stands, $P < 0.0001$). Although the seasonal dynamics of R_a (calculated as $R_s - R_h$) was relatively similar to that of R_s in the birch stands, R_a had a more variable pattern in the spruce stands (Fig. 3a, b). A significant positive correlation was found between R_a and T_s for the birch stands ($r = 0.60$ – 0.80 , $P < 0.0001$); correlation between R_a and T_s was not significant for the spruce stands.

Ts was the main climatic factor explaining the variation of Rh: 80–84% in the birch stands and 72–84% in the spruce stands ($P < 0.0001$). Ts and SWC together explained as much as 86–93% of variation of Rh in the birch stands and 80–99% in the spruce stands ($P < 0.0001$ for both species). In general, the descriptive force of Ts was weak or, in spruce stands even missing, for Ra ($P > 0.05$) (Table 4 in V) with an exception for the pole birch stand where Ts explained 80% of variation of Ra ($P < 0.0001$).

Strong seasonality is characteristic of the boreal zone; not only Ts and SWC but also growth and activity of roots and microbes vary seasonally. The increase of SWC by 23–30% in the trenched plots in birch stands and by 40% in the trenched plots in spruce stands ($P < 0.05$) (Fig. 3e, f) is the direct consequence of root exclusion (Subke et al., 2006; Comstedt et al., 2011). When Rh fluxes for the year 2010 were recalculated using the moisture correction per each month (Apr–Nov), a different pattern of contribution of **Rh to Rs** was found for the birch and spruce stands. Across the stands, the Rh/Rs ratio varied between 0.37 and 0.75 for the birch stands, while the contribution of Rh to Rs was higher in spring and autumn. The Rh/Rs ratio for the spruce stands was more evenly distributed throughout the period from April to November ranging between 0.52 and 0.68. The peak of litterfall for deciduous tree species is in autumn, but Norway spruce litterfall is more evenly distributed throughout the year in Estonia and in Finland (Frey, 1981; Ukonmaanaho, 2013). Considering the growing season period, small peaks of needle litterfall were observed in early summer and autumn in a mature Norway spruce stand in Estonia (Frey, 1981; Kukumägi unpublished data). Rh contributes relatively more to Rs in late autumn and early spring during the peak of newly fallen easily decomposable litter (Lavinge et al., 2003).

As FRNPP varies during the year it influences the contribution of **Ra to Rs**. Fine root growth of silver birch started in spring, reached a maximum biomass in midsummer and decreased thereafter (Fig. 1 in III). The main growth of <1 mm Norway spruce roots in the region has been shown to occur in August (Ostonen et al., 2005). In southern Sweden, fine root growth was the largest in late summer for both silver birch and Norway spruce (Hansson et al., 2013a). Ra contributed the most to Rs in late August and September in a mature Norway spruce forest (Comstedt et al., 2011). To sum up, Ra contributes more to Rs in the period of the highest fine root production (Lavinge et al., 2003). This is consistent with studies in different forest ecosystems (Lee et al., 2003; Irvine et al., 2008; Högberg et al., 2009; Korhonen et al., 2009; Tomotsune et al., 2013) reporting high seasonal variation in the Ra/Rs ratio.

Rs is influenced by substrate availability through the impact of photosynthates and above- and below-ground litter on soil autotrophic and heterotrophic activity (Högberg et al., 2001; Ryan and Law, 2005; Hopkins et al., 2013). Hence, changes in fine root and microbial growth and activity, influenced by both environmental factors and substrate availability, can modify the proportion of Ra and Rh during the growing season.

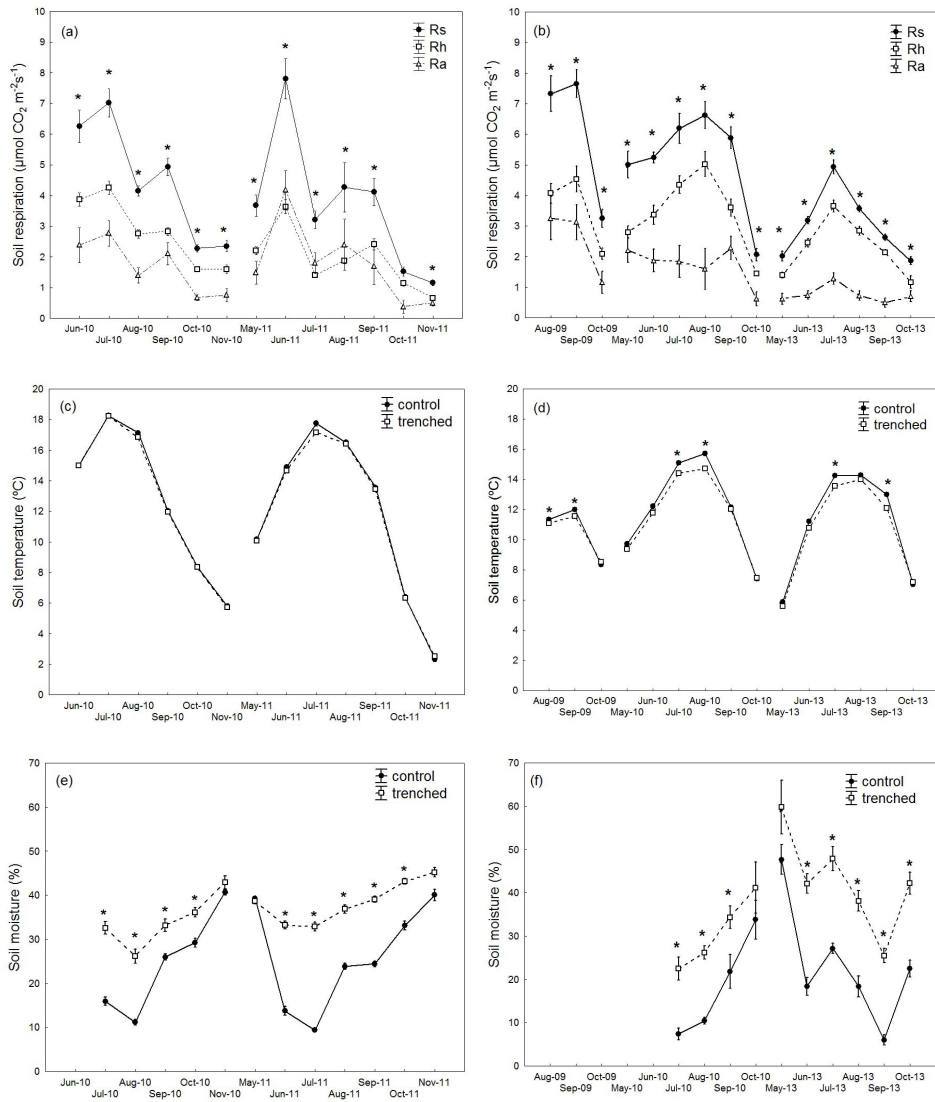


Figure 3. Seasonal dynamics of soil respiration (Rs), heterotrophic respiration (Rh), autotrophic respiration (Ra) (a, b), soil temperature (c, d) and soil moisture (e, f) in control and trenched plots in a 32-year-old silver birch (a, c, e) and in a 30-year-old Norway spruce (b, d, f) stands across the study years. Error bars represent the standard errors of the means.

* represents significant differences between measured Rs and Rh (a, b) or between control and trenched plots (c-f).

3.2.2. Temperature sensitivity of soil respiration and its components

The obtained Q_{10} values of R_s (2.4–3.5), derived from the growing season, remained within the range (2.0–6.3) reported for European and North-American forest ecosystems (Davidson et al., 1998; Janssens et al., 2003). In this study Q_{10} values represent the apparent temperature sensitivity as it includes the seasonality of several factors (such as substrate supply, SWC) (Davidson et al., 2006; Davidson and Janssens, 2006; Subke and Bahn, 2010), but use of this parameter allows convenient comparison with the results of similar studies.

Rh vs Ra. In this study R_a includes root, rhizomicrobial and mycorrhizal respiration and R_h includes the SOM-derived flux. The Q_{10} value is dependent on the partitioning of R_s . Intriguingly, birch and spruce behaved inversely. When in the pole spruce stand R_h was more sensitive to T_s compared with R_a , than in the birch stands Q_{10} values of R_a were higher than Q_{10} values of R_h (Table 2). This result highlights the importance of partitioning soil respiration components and estimation of their temperature sensitivity, especially as published results about the temperature sensitivity of R_h and R_a are controversial. Some studies show higher seasonally derived Q_{10} for R_a than for R_h (Boone et al., 1998; Gaumont-Guay et al., 2008; Ma et al., 2014), while others report opposite (Hartley et al., 2007; Lalonde and Prescott, 2007; Luan et al., 2011) or equal values (Bååth and Wallander, 2003). Most probably, R_a is dependent more on substrate provision from photosynthesis than on T_s (Högberg et al., 2001; Hartley et al., 2007; Wei et al., 2010; Hopkins et al., 2013), which could explain the higher Q_{10} values of R_a . More pronounced phenological seasonality is more characteristic of birch than of spruce. Nevertheless, through influencing the seasonality of substrate supply, especially in deciduous forests at higher latitudes, temperature affects soil CO_2 effluxes indirectly as well.

Chronosequence. Stand age impacted the Q_{10} of R_h , although T_s was similar between the stands in the trenched plots. In the birch stands Q_{10} of R_h increased with stand age: 1.9, 2.1 and 3.0, respectively; a significant difference was found between the middle-aged and the premature stands ($P < 0.05$) (Table 2). In the spruce stands, Q_{10} of R_h was the highest in the pole stand (4.6) and the lowest in the middle-aged stand (2.9) ($P < 0.05$). One possible explanation for this could be differences in the quantity and quality of litter which change with stand age (Table 3, Table 8 in II) (Saiz et al., 2006a; Ma et al., 2014). The Q_{10} of R_h has found to be dependent on substrate quality and availability (Conant et al., 2008; Gershenson et al., 2009; Erhagen et al., 2015). Decomposition of recalcitrant substrates can be more sensitive to temperature than labile substrates (Conant et al., 2008). Spruce needle litter creates an acidic environment favouring slower decomposition and SOM formation. Norway spruce stands had larger C stocks

in soil than silver birch stands, mainly in the organic layer (Hansson et al., 2013b). In the premature birch stand, the second layer of Norway spruce produced 21% of total tree litter flux annually (Table 3). In the spruce stands needle litter accounted for 86% of the total litter flux in the pole stand and 35% in the mature stand. Also the relative amount of branch litter increased with stand age.

Table 2. Temperature sensitivity (Q_{10}) of soil respiration (Rs), heterotrophic respiration (Rh) and autotrophic respiration (Ra) in silver birch and Norway spruce stands in 2010. Letters a and b represent significant differences between differently aged stands ($P < 0.05$).

	Silver birch			Norway spruce		
	13 (yr)	32 (yr)	45 (yr)	31 (yr)	40 (yr)	88 (yr)
Rs	2.4 ^a	2.4 ^a	2.9 ^b	3.5 ^a	3.1 ^a	2.6 ^b
Rh	1.9 ^a	2.1 ^a	3.0 ^b	4.6 ^a	2.9 ^b	3.6 ^c
Ra	3.1 ^a	3.1 ^a	4.3 ^b	3.2	–	–

Climate change scenarios predict an increase in air temperature (by 2.3–4.5 °C) in the Baltic region (Kont et al., 2003). Soil warming experiments can cast light on possible changes in the soil CO₂ effluxes in a changing climate. A significant enhancement of the response of Rs and Rh to warming has been found in several studies (Bronson et al., 2008; Schindlbacher et al., 2009; Aguilos et al., 2013). Furthermore, an overview of different ecosystems in China indicated that the temperature sensitivity of Rs is higher in cold, high-latitude forest ecosystems compared with warm, temperate areas (Peng et al., 2009). Enhanced temperature sensitivity of Rh, found in a soil warming experiment in cool-temperate forested peatland by Aguilos et al. (2013), emphasizes the importance of partitioning Rs. However, some warming studies report either a decrease or no significant change in Q_{10} values (Niinistö et al., 2004; Bronson et al., 2008). In this study the respiration of mycorrhizal roots and mycelia in the soil was not separated. However, as the majority of fine root tips in boreal and temperate spruce forests (Taylor et al., 2000) and over 95% of the short roots (distal roots with primary structure, i.e. the most active part of the fine roots) of silver birch (Uri et al., 2007) are colonized by ectomycorrhizal fungi, it is important to consider the mycorrhizal mycelium and its response to environmental factors in further studies of Rs models (Heinemeyer et al., 2007; Moyano et al., 2007). Furthermore, a fifty percent decrease in ectomycorrhizal root biomass per stand basal area with an increase of 2 °C annual mean temperature is predicted for the boreal zone (Ostonen et al., 2011), which may affect both Rs and its partitioning. An increase of temperature might change the carbon balance and temperature sensitivity of Rh, indicating the importance of component partitioning. The more so as there is some evidence that ectomycorrhizal colonization can alter the temperature dependence of Rs (Koch et al., 2007) and as temperature

sensitivity of soil CO₂ effluxes is continually major uncertainty in predicting soil respiration in the conditions of global warming. However, currently there is a lack of a mechanistic understanding of mycorrhizal respiration and specifically of the impact of mycorrhizal colonization on the scaling parameters used to predict Rs (Hughes et al., 2008).

3.2.3. Age-related changes in soil respiration and its components

Total soil respiration, heterotrophic and autotrophic respiration. The cumulative soil respiration rates (581–914 g C m⁻² in the birch stands and 561–773 g C m⁻² in the spruce stands) for the snow-free season (Apr–Nov) of the warmest year of 2010, found in this study represent most of the annual fluxes and remain in the range of values published for boreal and temperate coniferous forests (383–900 g C m⁻² yr⁻¹) (Janssens et al., 2001; Saiz et al., 2006a; Korhonen et al., 2009; Bond-Lamberty and Thomson, 2010a; Wei et al., 2010; Gaumont-Guay et al., 2014; Ma et al., 2014). Cumulative Rh for the snow-free season of 2010 was similar in the birch and spruce stands (ranging from 279 to 402 g C m⁻²); Ra ranged between 302 and 518 g C m⁻² in the birch stands and between 256 and 371 g C m⁻² in the spruce stands. Based on different studies, winter Rs (Dec–April or Nov–April) can account for 5–19% of total annual Rs (Wang et al., 2002; Mo et al., 2005; Vogel et al., 2005; Schindlbacher et al., 2007). As changes in winter temperatures cause inter-annual variation in winter soil CO₂ effluxes, the proportion of winter soil respiration in annual soil respiration can vary as well.

Non-linear relationship was found between the respiration fluxes and stand age. Modelled respiration fluxes of the birch stands increased in the pole stage reached a maximum in the middle-aged stage and decreased in the premature stage (III). In the spruce stands the respiration fluxes increased after clear-cut, increased in the pole stage, and decreased thereafter in the middle-aged stage and increased again in the mature stage (Fig. 1 in V). Several studies have found a significant effect of stand age on Rs (Wang et al., 2002; Pregitzer and Euskirchen, 2004; Bond-Lamberty et al., 2004b; Saiz et al., 2006a; Tang et al., 2009; Luan et al., 2011). Environmental factors Ts and SWC were not able to explain this variation as Ts was similar for the stands and the effect of SWC on Rs was weak. Hence, the underlying reason for the variation in the respiration fluxes must be biotic factors. In the birch stands, cumulative Rs of the snow-free period was the highest in the middle-aged stand. Estimated FRB increased with stand age and FRNPP was the highest in the middle-aged stand, suggesting a significant effect of fine root dynamics on Rs; also soil MB increased with stand age (Table 3). This result is consistent with studies reporting a significant positive correlation between FRB or FRNPP and Rs (Lee and Jose, 2003; Knohl et al., 2008). The increase of Rs with stand age was related to FRB in a loblolly pine chronosequence aged 1 to 25 years (Wiseman and Seiler, 2004). In the spruce stands, both FRB and FRNPP were lower in the middle-aged stand than

in the pole stand; this is consistent with the finding by Klopatek (2002) who studied 20-year-old, 40-year-old and old-growth Douglas fir stands and reported significantly lower R_s in the 40-year-old stand, which was related to the lowest FRNPP. Saiz et al. (2006a) reported the highest R_s rates in a 10-year-old stand in a Sitka spruce chronosequence and linked the decrease of R_s in older stands to decreasing FRB. In the present study, the highest cumulative R_s for the snow-free season in the mature spruce stand can be attributed to a considerably larger share of the roots of deciduous trees, as well as of shrubs and of the understorey in this stand, owing to better light conditions under the tree canopy. In the mature stand, FRNPP of Norway spruce made up 67% of the total FRNPP while in the pole stand 95% of the total FRNPP was made up by spruce (data not shown). R_h as well as MB were similar in the pole and mature stands. Positive correlation between R_s and MB has been found by Xu and Qi (2001) and by Lee and Jose (2003).

Partitioning of soil respiration is an important step towards the understanding of C cycling at the ecosystem level. Moreover, quantifying heterotrophic respiration allows to calculate the net ecosystem production (NEP). Net ecosystem productivity and respiration change during forest succession (Goulden et al., 2011). The results of this study highlight the importance of considering forest age in C budgeting studies.

Average seasonal R_h/R_s ratio. The contribution of R_h to R_s was similar in the studied stands varying between 0.43 and 0.48 in the birch stands and between 0.52 and 0.54 in the spruce stands (Table 3). This is consistent with studies reporting average contribution to be approximately between 50–60% (Hanson et al., 2000; Epron et al., 2001; Schuur and Trumbore, 2006; Comstedt et al., 2011). However, annual contribution of R_a or R_h to R_s in forests can vary greatly (10–90%) (Hanson et al., 2000; Bond-Lamberty et al., 2004a; Wei et al., 2010). Some studies examining changes in the contribution of either component to R_s during stand development have found both an increase and a decrease of the R_h/R_s ratio with stand age (Saiz et al., 2006a; Luan et al., 2011; Ma et al., 2014). Bond-Lamberty et al. (2004b) studied a boreal black spruce chronosequence at well-drained and poorly drained sites and reported a significant change (5–40%) in the R_a/R_s ratio across the chronosequence (age 4–152 years). Still, the authors emphasize that these figures represent minimum values, pointing also to the shortcomings of the trenching method. Although the R_h/R_s ratio was similar for studied stands in this study, age-related effects on the R_h/R_s ratio might be revealed in case a longer chronosequence of stands is considered.

Table 3. Mean characteristics of the studied stands: FAHM in ambient conditions (age in 2009: 4 yr), silver birch (age in 2010: 13, 32 and 45 yr) and Norway spruce (age in 2010: 31, 40 and 88 yr), clear-cut sites of Norway spruce (age in 2013: 5 yr) in Elva (E) and Røuge (R). Corrected average Rh/Rs ratio for the snow-free period (Apr–Nov), * uncorrected Rh/Rs ratio for clear-cut sites for the period May–October.

Soil respiration (R_s , $\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$) and measured heterotrophic respiration (R_{h_m} , $\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$), cumulative soil respiration and heterotrophic respiration for the snow-free period ($R_{s_{cum}}$ and $R_{h_{cum}}$, t C ha^{-1}) in silver birch and Norway spruce chronosequences; in clear-cuts and in FAHM for May–October. Abiotic factors: soil temperature (T_s , $^{\circ}\text{C}$) and soil moisture (SWC, %). Below-ground biotic factors: fine root biomass (FRB, g m^{-2}), fine root production (FRNPP, $\text{g m}^{-2}\text{yr}^{-1}$), root turnover rate (yr^{-1}), microbial biomass (MB, mg Cg^{-1}). Above-ground biotic factors: total tree litter flux ($\text{g m}^{-2}\text{yr}^{-1}$), and flux of needles, deciduous tree leaves and branches ($\text{g m}^{-2}\text{yr}^{-1}$).

	Silver birch				Norway spruce				
	4	13	32	45	5 (E)	5 (R)	31	40	88
R_s	6.24	3.09	4.50	5.17	2.37	3.07	5.17	3.92	5.07
R_{h_m}	–	1.77	2.82	3.66	1.46	1.58	3.43	2.82	2.99
$R_{s_{cum}}$	10.9	5.9	9.2	7.8	5.1	3.9	7.1	5.6	7.7
$R_{h_{cum}}$	–	2.8	4.0	3.4	3.2	2.5	3.8	3.1	4.0
Rh/Rs	–	0.48	0.43	0.44	0.62*	0.64*	0.53	0.54	0.52
T_s	12.8	13.1	12.8	12.3	13.4	14.4	11.6	12.4	12.1
SWC	22.7	27.0	24.6	18.1	17.5	28.2	18.4	17.0	10.4
FRB	702	135	195	257	–	–	1110	839	870
FRNPP	518	89	144	131	–	–	650	587	592
Turnover rate	1.2	0.66	0.71	0.51	–	–	0.6	0.7	0.7
MB	1.34	0.38	0.64	1.05	–	–	4.85	3.51	4.90
Total litter flux	–	324	322	358	–	–	187	233	349
Needles	–	–	–	76	–	–	161	144	122
Leaves	–	296	308	206	–	–	9	25	101
Branches	–	28	14	76	–	–	5	35	6

The trenching method is widely used for separating the heterotrophic and autotrophic component of soil respiration in forest ecosystems, however, this method has some disadvantages (Hanson et al., 2000; Kuzyakov, 2006). Problems related to the trenching method are the higher CO_2 efflux from cutoff decomposing roots, potentially higher soil water content in trenched soil volume and the lack of fresh below-ground litter input (Hanson et al., 2000; Ngao et al., 2007; Epron, 2009). Without any correction Rh would be more or less overestimated (Subke et al., 2006; Ngao et al., 2007; Comstedt et al., 2011); also estimation of NEP and the Rh/Rs ratio would be biased. Soil moisture increased approximately 30–40% in the trenched plots compared to the control plots

because of elimination of tree transpiration. For example, in the spruce stands 23% was derived from increased soil moisture only, which is consistent with the result by Comstedt et al. (2011). Root-related correction depends on the difference between fine root standing biomass and production. All applied corrections decreased the Rh/Rs ratio by 13–33% for the birch stands and by 28–31% for the spruce stands. Based on our results and findings in the literature, the shortcomings of the trenching method should be considered in the partitioning calculations.

3.3. Effect of stump harvesting (IV)

It is highly important to consider the harvesting effect on forest C cycle as harvesting can potentially affect Rs through impacting soil physical properties, microclimate, vegetation and root dynamics (Jalonen and Vanha-Majamaa, 2001; Pumpanen et al., 2004; Peng and Thomas, 2006; Peng et al., 2008; Payeur-Poirer et al., 2012). First results of an Estonian pilot study showed that stump harvesting at the studied fertile Norway spruce sites, with high nutrient and carbon storages, did not increase the intensity of Rs. Rh fluxes were also estimated and different results were obtained for the two study sites. At the Rõuge study site Rh was lower in the harvested area than in the control area (1.8 and 2.5 t C ha⁻¹ yr⁻¹, respectively, Fig. 4, P<0.05), indicating reduced CO₂ emission because of the absence of decomposing stump biomass, and hence supporting the assumption that CO₂ emission decreases from uprooted areas. However, at the Elva study site stump harvesting had no effect on the Rh flux: the measured values in the harvested and control plots were almost of the same magnitude (Fig. 4, P>0.05). As trenching had no significant effect on SWC and the share of decomposing detached roots should be minor in the trenched plots, corresponding corrections for the Rh fluxes were not used in this study.

The values of the estimated soil respiration fluxes are consistent with those reported in a Swedish study where average annual C emissions from clear-cut areas were estimated at 4–5 t C ha⁻¹ yr⁻¹ (Grelle et al., 2012). Few studies from Sweden have not found a significant effect of stump harvesting on soil CO₂ effluxes, either (Grelle et al., 2012; Strömgren et al., 2012; Strömgren and Mjöfors, 2012). Strömgren et al. (2012) showed that the effect of stump harvesting on CO₂ flux or soil decomposition processes was similar compared to site preparation such as mounding in a short-term perspective. Grelle et al. (2012) found that during the first year soil CO₂ effluxes were reduced in relation to mounding due to the lack of decomposing stumps, but at the end of the experiment both sites emitted similar amounts of C.

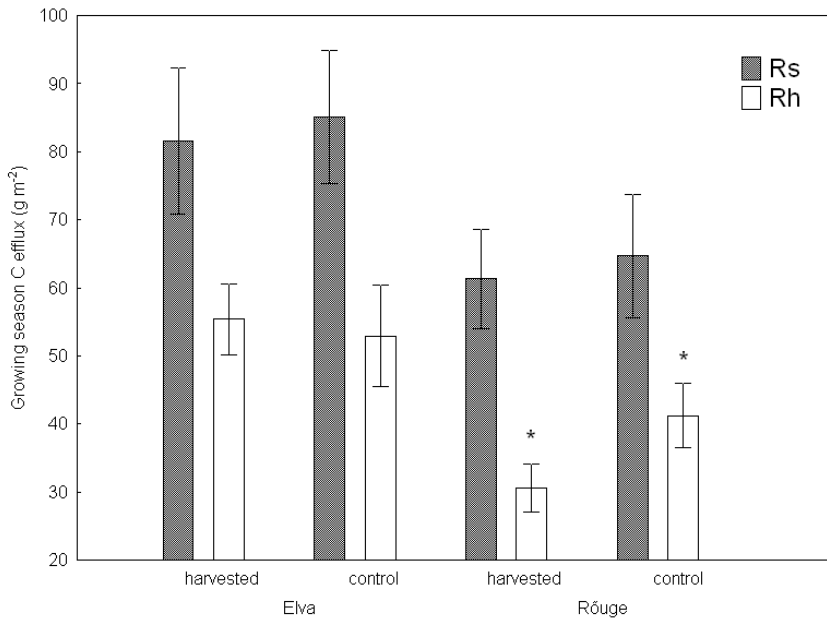


Figure 4. Soil (Rs) and heterotrophic (Rh) respiration rates (g C m^{-2}) in the stump harvested and control clear-cuts of Norway spruce in Elva (*Oxalis*) and Røuge (*Oxalis-Myrtilus*) study sites in growing season (May–October) of 2013. Error bars represent the standard error of the means. *indicates significant differences between the treatments ($P < 0.05$). (IV)

4. CONCLUSIONS

The overall objective of the thesis was achieved. The hypotheses, except for the first one, were proved. During the research one new hypothesis was raised (see conclusion 1). This thesis demonstrates the complexity of below-ground respiration processes and the importance to consider the effect of several natural and anthropogenic factors into prediction of the carbon cycle of a forest ecosystem in a changing climate. Summing up, soil temperature was the main climatic factor explaining the seasonal variation of R_s while soil moisture had a weak effect on R_s .

1. New hypothesis that heterotrophic respiration is higher at increasing air humidity was raised owing to a significant increase of basal respiration of microbes. Although the above-ground biomass of the understorey was similar for the misting and control plots, fine root and rhizome biomass and production were approximately two times as high in the misting plots compared with the control plots. This indicates that lower R_s at increased air humidity could be related to the lower proportion of R_a than in ambient conditions.
2. Stand age affected soil CO_2 effluxes both in the silver birch and Norway spruce chronosequences, which could be explained by changes in fine root dynamics, microbial biomass and above-ground litter flux rather than by changes in soil temperature and soil moisture. The seasonality of fine root and microbial growth and activity, influenced by environmental factors and substrate availability, can modify the proportion of autotrophic and heterotrophic respiration during the growing season. From the methodological point of view, it is essential to consider the effect of disturbances, such as an increased amount of detached decaying roots, an increase of soil moisture and missing fine root turnover, in calculation of soil respiration partitioning in trenched-based respiration studies. All applied corrections decreased the contribution of R_h to R_s by up to one-third in the silver birch and Norway spruce stands. The average contribution of R_h of the growing season to R_s was similar for differently aged stands, varying between 0.43 and 0.48 in the birch stands and between 0.52 and 0.54 in the spruce stands.
3. Soil temperature explained most of the seasonal variation of R_s as well as of R_h , while the descriptive force of temperature was weak for R_a for the silver birch and Norway spruce stands. Overall, soil moisture had a weak positive effect on R_s .
4. The temperature sensitivity of soil respiration components was dissimilar showing opposite responses for deciduous and coniferous tree species. R_h was more sensitive to T_s compared with R_a in the pole spruce stand; contrary results were obtained for the birch stands, which highlight the importance of

partitioning soil respiration and estimating temperature sensitivity for both components.

5. First results of Estonian case study imply that stump harvesting does not affect soil respiration at fertile sites, although it might influence the partitioning of soil respiration. Heterotrophic respiration was lower in uprooted plots, indicating reduced CO₂ emission because of the absence of decomposing stump biomass. However, this result was obtained at one study site only while at the other site harvesting had no effect on Rh. The present results are preliminary and long-term studies would gain a better understanding of environmental responses following large-scale stump harvesting. Also further research is needed focusing on poorer sites.

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SUMMARY IN ESTONIAN

Mullahingamist ja selle komponente mõjutavad tegurid arukase ja hariliku kuuse puistutes

Mulla süsinikuvoogude uurimine metsades on viimastel aastakümnetel märgatavalt kasvanud peamiselt selle tõttu, et muutused mulla CO₂ voogudes ehk mullahingamises võivad oluliselt mõjutada nii regionaalset kui ka globaalset süsinikuringet. Kliimamuutuste seisukohalt on põhjapoolkera kõrgemate laiuskraadide metsad oma suure mulla süsinikuvaruga ühed olulisemad ökosüsteemid globaalses süsinikuringes. Prognoositud temperatuuri ja sademete tõus võib potentsiaalselt mõjutada selle piirkonna metsade süsiniku sidumise ja eraldumise vahelist tasakaalu. Kui atmosfääri veeauru kontsentratsioon kõrgematel laiuskraadidel kliima soojenemise tõttu tõuseb, võib kliima veelgi kiiremas tempos soojeneda. Kõrgendatud CO₂ ja temperatuuri mõju ökosüsteemi erinevatele protsessidele on uuringutega suhteliselt hästi kaetud, aga suurenenud suhtelise õhuniiskuse mõju on paljuski teadmata. Kuna hemiboreaalse regiooni (sh Eesti) metsad on heterogeensed ning mullahingamine moodustab suure osa kogu ökosüsteemi hingamisest, on mulla CO₂ voogude kvantitatiivne hindamine erinevates metsa arengustaadiumites jätkuvalt aktuaalne teema. Mullahingamise kui kompleksse protsessi mõistmine ei ole lihtne ülesanne, kuna see on mõjutatud mitmetest erinevatest abiootilistest, biootilistest ja inimtegevusest tulenevatest teguritest ning nende omavahelisest koosmõjust.

Mullahingamine koosneb autotroofsest ehk juure- ja temaga seotud mükoriisete seente ning risosfääri mikroorganismide hingamisest (Ra) ja heterotroofsest ehk lagundajate (peamiselt mikroobide) hingamisest (Rh). Neid kahte komponenti on oluline eraldi uurida, sest:

- mõlema komponendi (Ra ja Rh) suhteline osakaal mullahingamisest võib olla väga varieeruv (10–90%), sõltuvalt ökosüsteemi tüübist, aastaajast ja meetodikast (Hanson *et al.* 2000);
- substraadi (fotosünteesiproduktid Ra jaoks ja varis Rh jaoks) kättesaadavus varieerub sesoonselt;
- keskkonnategurid (sh mullatemperatuur ja mullaniiskus) ning puistu vanus võivad mõjutada nii autotroofset kui ka heterotroofset hingamist, aga erineval määral;
- heterotroofse hingamise kvantitatiivsed hinnangud on hädavajalikud metsa süsinikubilansi koostamise jaoks ehk teisisõnu saab nii teada, kas ökosüsteem seob või eraldab süsinikku.

Inimene saab metsa süsinikuvaru mõjutada jätkusuutliku metsamajandamise kaudu. Lageraiejärgne kändude juurimine on Eestis veel uudne majandamisviis. Info kändude kui perspektiivse taastuvenergia ressursi kasutuselevõtmise kohta on rakenduslikust aspektist vaadatuna äärmiselt oluline.

Käesolevas doktoritöös käsitleti kolme uutset aspekti. Esiteks suurenenud suhtelise õhuniiskuse mõju mullahingamisele, mis on oluline teave kõrgematel laiuskraadidel prognoositud kliimamuutuse valguses. Seda uuriti metsaökosüsteemi õhuniiskusega manipuleerimise katsealal (FAHM – *Free Air Humidity Manipulation*), mis on maailmas unikaalne eksperiment (Kupper *et al.* 2011). Teiseks saadi Eesti jaoks uued tulemused mullahingamise jaotumisest autotroofseks ja heterotroofseks komponendiks arukase- ja hariliku kuuse puistutes. Kolmandaks analüüsiti Eestis esmakordselt käändude juurimise mõju mulla CO₂ voogudele.

Doktoritöö laiem eesmärk oli uurida erinevate abiootiliste (suurenenud suhteline õhuniiskus, mullatemperatuur ja mullaniiskus) ning biootiliste (puuliik, puistu vanus ja arengustaadium, peenjuurte biomass ja käive, maapealne varisevoog mulda, mulla mikroobne biomass ja selle aktiivsus) tegurite ning metsamajandamise (lageraiejärgne käändude juurimine) mõju mullahingamisele ja selle autotroofsele ja heterotroofsele komponendile erineva vanusega viljakates arukaasikutes ja kuusikutes. Arukask (*Betula pendula* Roth) ja harilik kuusk (*Picea abies* (L.) Karst) on Euroopas laialt levinud puuliigid. Eestis on arukask ja harilik kuusk nii ökoloogiliselt kui ka majanduslikult olulised puuliigid.

Töö kitsamad eesmärgid olid:

- hinnata suurenenud suhtelise õhuniiskuse mõju mullahingamisele noores arukase katsepuistus;
- välja selgitada mullahingamise sesoonne dünaamika ja jaotumine heterotroofseks ja autotroofseks komponendiks seoses abiootiliste ja biootiliste teguritega erineva vanusega arukaasikutes ja kuusikutes;
- analüüsida puistu vanuse mõju mullahingamisele ja selle komponentidele sõltuvalt puuliigist (arukask ja harilik kuusk);
- hinnata mullahingamise ja selle komponentide temperatuuritundlikkust erineva vanusega arukaasikutes ja kuusikutes;
- välja töötada heterotroofse hingamise osatähtsuse (Rh/Rs) parandid, mis on vajalikud eraldatud mullaruumalade meetodi puhul, ning arvutada Rh/Rs suhted kasvuperioodi kohta arukaasikutes ja kuusikutes;
- hinnata käändude juurimise mõju mulla CO₂ voogudele hariliku kuuse lageraie aladel.

Töös kontrolliti järgmisi hüpoteese:

1. Mullahingamine on kõrgem suurendatud suhtelise õhuniiskuse puhul peamiselt alustaimestu suurema maapealse ja maa-aluse produktsiooni ning varisevoo tõttu.
2. Puistu vanuselised muutused mulla CO₂ voogudes on seletatavad eelkõige biootiliste tegurite kaudu.
3. Mullatemperatuur on peamine tegur, mis määrab ära mullahingamise varieerumise ajas; mullaniiskuse mõju on vähemtähtis.

4. Mullahingamise komponentide temperatuuritundlikkused on erinevad.
5. Lageraiejärgne kuusekändude juurimine ei suurenda mullahingamist.

Suurendatud suhteline õhuniiskus vähendas mullahingamise voogu teisel katseaastal. Saadud tulemus lükkas ümber algselt püstitatud esimese hüpoteesi. Regressioonianalüüsi tulemustest selgus, et mullatemperatuur kirjeldas ära kuni 2/3 mullahingamise sesoonsest varieerumisest. Hoolimata sellest, et mullaniiskus oli suurendatud õhuniiskusega katseringides oluliselt kõrgem eelkõige vähenenud transpiratsiooni tõttu (Kupper *et al.* 2011), oli mullaniiskuse mõju mullahingamisele nõrk ja negatiivne. Mõlema uurimisaasta kasvuperiood oli sademeterohke, mistõttu mullaniiskuse tugevam mõju mullahingamisele avaldub tõenäoliselt põua tingimustes. Selgus, et ainult keskkonnateguritega ei saa suurenenud õhuniiskusega katseringides toimunud muutusi seletada. Kuigi mulla mikroobne biomass kontroll- ja suurendatud õhuniiskusega katseringide vahel oluliselt ei erinenud, kasvas mikroobne aktiivsus (teisistõnu heterotroofne hingamine) 28%. Veelgi enam, suurenenud õhuniiskus kahekordistas alustaimestu maa-alust, juurte ja risoomide biomassi, aga mitte maapealset biomassi, mis omakorda viitab sellele, et alustaimestu maa-aluse biomassi ühiku kohta on assimilaatidega varustatus metaboolseteks protsessideks kehvem. Sellest lähtuvalt püstitati uus hüpotees, et heterotroofse hingamise osatähtsus kasvab suurendatud õhuniiskuse tingimustes. Selle hüpoteesi tõestamine vajab aga täiendavaid uuringuid.

Ülejäänud töös püstitatud hüpoteesid (2.–5.) leidsid kinnitust. Puistu vanus mõjutas mulla CO₂ vooge nii arukase kui ka hariliku kuusiku vanuser eas, mullahingamise vood korreleerusid eelkõige muutustega puistute peenjuurte dünaamikas (hüpotees 2). Keskmise Rh/Rs suhe kasvuperioodi kohta oli mõlema uuritud puuliigi puistute vanuseriades sarnane: 43–48% arukaasikutes ja 52–54% kuusikutes. Mullatemperatuur oli peamine tegur, mis kirjeldas ära suurema osa Rs ja Rh sesoonsest varieerumisest, mullaniiskuse mõju mullahingamisele oli positiivne, kuid nõrk (hüpotees 3). Autotroofse hingamise seos mullatemperatuuriga oli nõrk või puudus. Lisaks hinnati Rs, Rh ja Ra temperatuuritundlikkust. Selleks kasutati Q₁₀ väärtust, mis näitab hingamise intensiivsuse muutumist, kui temperatuur tõuseb 10 °C, ja mida kasutatakse juhul, kui hingamise ja temperatuuri vahel on eksponentsiaalne seos. Suurem Q₁₀ väärtus näitab protsessi suuremat temperatuuritundlikkust. Tulemused olid huvitavad selle poolest, et Q₁₀ väärtused Rh ja Ra kohta järjestusid kuusikutes ja kaasikutes erinevalt. Kuusepuistutes oli Rh temperatuuritundlikum kui Ra, kuid kasepuistutes oli tulemus vastupidine (hüpotees 4). Ka kirjanduses on mullahingamise komponentide temperatuuritundlikkuse kohta saadud vastukäivaid tulemusi. See tuleneb sellest, et kasvuperioodi kohta leitud Q₁₀ väärtus on seotud mitmete temperatuurist mõjutatud protsessidega, nagu näiteks fotosüntees. Mitmed uurimused on tõestanud, et Ra sõltub peamiselt fotosünteesi produktidest ning vähem otseselt temperatuurist.

Kändude juurimise mõju mullahingamisele on väga vähe uuritud ning antud uurimustöö omab olulist rakenduslikku tähtsust. Esmased tulemused näitasid, et viljaka kasvukohatüübi korral lageraiejärgne kuusekändude juurimine mullahingamist oluliselt ei mõjuta (hüpotees 5), mis on heas kooskõlas Rootsisis hariliku kuuse katsealal läbi viidud eksperimendi tulemusega (Grelle *et al.* 2012). Siiski on selles valdkonnas vaja teha täiendavaid uuringuid, näiteks kehvemates kasvukohatüüpides.

Käesolevas doktoritöös kasutati mullahingamise autotroofseks ja heterotroofseks komponendiks jagamisel väga levinud eraldatud mullaruumalade meetodikat (“trenching”), mille puudusi püüti parandite rakendamise abil korrigeerida. Selle meetodika puhul välistatakse elusate taimede panus mullahingamisse juurte läbilõikamisega ja mullaruumala mehhaanilise eraldamisega nt vertikaalse toru abil. Läbilõigatud juurtega piirkonnas võib mullaniiskuse sisaldus transpiratsiooni puudumise tõttu märgatavalt tõusta. Läbilõigatud juured moodustavad täiendava varisevoo mulda, samas jääb puudu looduslikes tingimustes pidevalt lisanduv juurevaris – Rh võib vastavalt suureneda või väheneda. Parandite rakendamine vähendas heterotroofse hingamise hinnangut ligikaudu 30% nii kuuse- kui ka kasepuistutes, mis kinnitab teiste samalaadsete uurimistööde tulemust, et antud meetodika kasutamisel tuleb metodoloogilisi puudusi arvesse võtta. Parand, mis arvestaks juurevarise voo katkemist eraldatud mullaruumalas, jäetakse antud meetodika kasutamisel kahjuks enamasti arvesse võtmata (Subke *et al.* 2006).

Metsaökosüsteemi mullahingamine on väga keeruline protsess, mida mõjutavad mitmed ajas ja ruumis varieeruvad tegurid. Doktoritöö tulemused võimaldavad paremini mõista ja prognoosida potentsiaalseid muutusi mullahingamises nii muutuva kliima kui ka metsamajandamise kontekstis.

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