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61

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The effects of elevated humidity, extreme weather conditions and clear-cut on greenhouse gas emissions in fast growing deciduous forests

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CONTENTS

ORIGINAL PUBLICATIONS

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

I **Hansen, R.**, Mander, Ü., Soosaar, K., Maddison, M., Lõhmus, K., Kupper, P., Kanal, A. and Sõber, J. 2013. Greenhouse gas fluxes in an open air humidity manipulation experiment. Landscape Ecology 28: 637–649, doi 10.1007/s10980-012-9775-7.

II Rosenvald, K., Tullus, A., Ostonen, I., Uri, V., Kupper, P., Aosaar, J., Varik, M., Sõber, J., Niglas, A., **Hansen, R.**, Rohula, G., Kukk, M., Sõber, A. and Lõhmus, K. 2014. The effect of elevated air humidity on young silver birch and hybrid aspen biomass allocation and accumulation – Acclimation mechanisms and capacity. Forest Ecology and Management 330: 252–260.

III **Torga, R.**, Mander, Ü., Soosaar K., Kupper P., Tullus, A., Rosenvald, K., Ostonen, I., Kutti, S., Jaagus, J., Sõber, J., Maddison, M. and Lõhmus, K. 201X. Weather extremes, humidity manipulation, and tree species shape soil greenhouse gas emissions. Submitted.

IV Becker, H., Uri, V., Aosaar, J., Varik, M., Mander, Ü., Soosaar, K., **Hansen, R.**, Teemusk, A., Morozov, G., Kutti, S. and Lõhmus, K. 2015. The effects of clear-cut on net nitrogen mineralization and nitrogen losses in grey alder stand. Ecological Engineering 85: 237–246.

Author's contribution:

	I	II	III	IV
Original idea	*		*	
Study design	*		*	
Data collection	*	*	*	*
Data analysis	*		*	*
Manuscript preparation	*	*	*	*

ABSTRACT

Elevated humidity, heat waves and summer drought are some possible scenarios for future climate in northern Europe. Therefore it is important to know how forest – the main ecosystem type in northern Europe, will react and adapt to changes, and whether there is a positive feedback on soil-atmosphere greenhouse gas fluxes. Short rotation forestry in fast-growing deciduous stands is one possible solution to reduce the use of fossil fuels and to mitigate further climate change. On the other hand, clear-cutting and the following stand establishment are considerable disturbances for the forest soil, hence these disturbances, as well as the selected tree species, may have an effect on greenhouse gas fluxes. However, the effects of climate change, such as increased humidity, heat waves, and drought, on fast-growing deciduous forest ecosystems and the soil-atmosphere greenhouse gas fluxes of ecosystems, and the effects of forest management, such as tree species, stand establishment, and clear-cut on greenhouse gases are not sufficiently well studied.

This thesis focused on the effects of climate change and forest management on soil greenhouse gas fluxes in fast-growing deciduous forest ecosystems: (i) the free air humidity manipulation experiment (FAHM) was used to study the effect of elevated humidity, heat waves, summer drought and forest management and (ii) the Agali site was used to study the effect of clear-cut. CO_2, CH_4 and N_2O fluxes were measured with static chambers from three control and three humidified plots from young silver birch and hybrid aspen stands in the FAHM site and from a mature grey alder forest and adjacent clear-cut plot in the Agali site. In both study sites, soil temperature and soil water potential (SWP) were monitored and various soil environmental parameters measured. In addition, in the FAHM site, the growth dynamics and biomass allocation of both tree species and the understory were measured to distinguish the effect of humidification and tree species on greenhouse gas fluxes.

CO_2 was the dominant greenhouse gas compared to CH_4 and N_2O. Small amounts of methane were taken from the atmosphere by the soil and mainly small amounts of N_2O were released. CO_2 emission was related to soil temperature and CH_4 uptake, to SWP. Therefore these greenhouse gases had a typical seasonal pattern. N_2O emission did not correlate to measured soil environmental parameters and therefore a distinct seasonal pattern was missing, but there were some peaks during moister conditions.

Humidity manipulation may have opposite effects on CO_2 emission, depending on weather conditions, as well as tree species and biomass allocation in the stands. In an extremely warm summer with normal precipitation, elevated humidity inhibited CO_2 emissions in silver birch but not in hybrid aspen stands, whereas in an extremely warm and dry summer, elevated humidity enhanced CO_2 emissions in both tree stands and also microbial activity in silver birch stands. Due to the lower growth and smaller canopy of hybrid aspens, the aboveground understory had better light conditions than under silver birch. Higher aboveground biomass of understory before the clear-cut may be one

reason for the respective higher CO_2 emissions in aspen stands. After the clear-cut, silver birch stands tended to have higher CO_2 emissions than aspen stands, which may be related to slower development of planted birches compared to naturally regenerated aspens. CO_2 emissions were the highest in an extremely warm summer when moisture was not limiting, and the lowest in a warm and dry summer strongly affected by drought stress. Drought is a strong stress factor and may affect greenhouse gas fluxes even in the following year(s), which was also proved in the present study.

Elevated humidity increased SWP by altering the transpiration and growth of trees. Methane uptake was in good accordance with soil water potential. Therefore elevated humidity mostly decreased methane uptake compared to the control. Tree species coped differently with elevated humidity, hence the FAHM site had a tree-species-specific effect on the SWP; soils were drier under silver birches than hybrid aspens before the clear-cut, causing higher methane uptake under birches. However after clear-cut of silver birch, forested hybrid aspen stands had higher methane uptake than clear-cut silver birch stands in 2012. Maximum annual methane uptake occurred during the warm and dry summer as a result of a heat wave and drought. Minimum annual CH_4 uptake occurred in moister soil conditions; probably one cause was decreased evapotranspiration at lower air temperatures. Elevated humidity tended to inhibit N_2O emissions in hybrid aspen stands, but not in silver birch stands.

In addition to young deciduous stands, clear-cut as a significant disturbance of a forest ecosystem was studied in a mature grey alder stand. Harvesting affected all the measured greenhouse gas fluxes: CO_2 emissions were higher, CH_4 uptake and N_2O emissions were lower in a clear-cut, compared to adjacent grey alder forest.

This thesis was a pilot study of several climate and management factors possibly affecting greenhouse gas fluxes. Elevated humidity, clear-cut and tree species affected all the measured greenhouse gas fluxes. Extreme weather conditions and stand establishment affected CO_2 emissions and CH_4 uptake. Elevated humidity had various effects on CO_2 emissions, depending on abiotic and biotic factors. At the same time, CH_4 uptake from both tree stands and N_2O emissions in hybrid aspen stands were often decreased by humidity treatment. Clear-cut of grey alder forest decreased N_2O loss but enhanced gaseous C losses. The results of this thesis provide a useful insight into future deciduous forest greenhouse gas dynamics. However, more tree species should be involved for a longer period with a higher frequency of measurements in order to draw more general conclusions about all of these factors.

1. INTRODUCTION

1.1. Climate change: increasing greenhouse gas concentrations in the atmosphere, warming, changes in the water cycle, extreme climatic events

Greenhouse gases like CO_2, CH_4 and N_2O are the main drivers of climate change and the increase is caused mainly by anthropogenic emissions (Ciais et al., 2013). Climate is warming and changes in the global water cycle are therefore expected. Increased temperature will enhance evaporation and warmer air can hold more water vapour. Near-surface specific humidity (amount of water in the atmosphere expressed as weight of water vapour per unit weight of moist air) has been increasing since the 1970s (Hartmann et al., 2013). According to climate models, specific humidity will rise 20 % in the coming decades (Meehl et al., 2007) in the troposphere and the amount of water vapour in the atmosphere will increase by 5 to 25 % by the end of the century (Collins et al., 2013). However, relative humidity is expected to decrease over most land areas in all seasons as the temperature increases (Collins et al., 2013). On land areas north of 30°N, annual precipitation has increased since 1900 up to 2005 (Hartmann et al., 2013), and further increase is expected in high latitudes by the end of the century (Collins et al., 2013). The change in precipitation may not be uniform over all seasons, as some models predict increase (near future, up to 2035) and others, decrease (long-term, up to 2200) for the summer (Collins et al., 2013; Kirtman et al., 2013). Most models predict wet winters and dry summers in high latitudes (Collins et al., 2013); dry summers increase the risk of drought, which may be interspersed with intense downpours since the warmer atmosphere is capable of holding more water (Meehl et al., 2007). Climate warming increases the risk of more frequent and longer heat waves (Meehl et al., 2007). For Estonia, climate models predict the rise of air temperature by 3–4 ºC, and of mean precipitation by 10–20 % by the end of the century (Kont et al., 2003; Jaagus and Mändla, 2014).

1.2. Forest greenhouse gas fluxes and factors affecting them

Forests have an important role in the global C cycle and soil CO_2 emission is a key flux in a forest ecosystem C budget. Boreal and temperate forests are essential carbon sinks and therefore affect atmospheric CO_2 negatively. The growth of boreal forest is temperature- and lightlimited and depends on the length of growing season; shorter growing season as well as stress factors which decrease photosynthesis can turn boreal deciduous forest from carbon sink to source (Baldocchi, 2008). Most of the C pool is in the soil, but also in biomass, litter and dead wood (Pan et al., 2011). In boreal forests even more C is reserved in the soil than in plants when compared with temperate forests. One reason for higher C sequestration in boreal forest soils is 2–2.5 times lower heterotrophic

respiration when compared to temperate forests (Lorenz and Lal, 2010). There can be significant tree-species-related differences in the C-sequestration pattern within the same region, e.g. C is stored mainly in woody biomass for silver birch stands and in the soil for grey alder stands (Uri et al., 2014; Varik et al., 2015), however these differences are still not thoroughly considered.

Even though N_2O and CH_4 have high global warming potential in 100-year time (298 and 34 respectively when compared to CO_2), CO_2 is still the most important well-mixed greenhouse gas in all types of ecosystems, followed by CH_4, dichlorodifluoromethane and N_2O (Ågren and Andersson, 2012; Myhre et al., 2013). All three studied greenhouse gases (CO_2, N_2O and CH_4) have life-times long enough to be relatively homogeneously mixed in the troposphere.

Soil carbon dioxide release to the atmosphere occurs by autotrophic (from living root systems) and heterotrophic respiration (from decomposers); the soil-atmosphere C exchange by abiotic processes is minor (Lovett et al., 2006). Thus the size and activity of the soil microbial community is crucial, as well as the litter input flux into the soil, which provides the substrate for decomposers. Carbon dioxide emission has a strong temperature dependency and therefore has clear seasonal dynamics in boreal and temperate forests (Ambus and Robertson, 2006; Ullah et al., 2009). The soil water regime is also important; the optimal water-filled pore space for soil CO_2 emissions is 20–60 % (Schaufler et al., 2010). In addition to the characteristics above, soil chemical and physical properties, vegetation type, biomass growth, as well as the interaction of all these components are important for CO_2 emissions (Lukac and Godbold, 2011). The forest C cycle in a boreal deciduous forest is sensitive to climate change, i.e. it has been found that spring warming increased gross primary production by 74 % and ecosystem respiration by 61 %; summer drought decreased gross primary production by 12 % and increased ecosystem respiration by 21% (Welp et al., 2007).

Methane flux in forest soil is a result of two processes: methanotrophy and methanogenesis. Methane fluxes are controlled mainly by soil moisture: high soil moisture decreases the gas diffusivity and additionally favors methanogenic activity, which leads to increased CH_4 productivity (Wu et al., 2011). These processes require opposite soil moisture conditions; so, usually, well-drained soils are sinks and poorly drained soils are sources for methane (Ullah and Moore, 2011). In upland forests, methane uptake mainly occurs (Megonigal and Guenther, 2008; Ullah et al., 2009; Gundersen et al., 2012), whereas forests on organic soils mostly emit methane (Takeuchi et al., 2003; von Arnold et al., 2005). In addition to soil moisture, methane flux may be affected by soil tem-perature, pH, N availability, extreme precipitation events and other environ-mental parameters and their interactions (Ambus and Robertson, 2006; Weslien et al., 2009). Forests have one of the highest methane uptake rates compared to other natural terrestrial ecosystems (Mander et al., 2010; Tian et al., 2010; Jacinthe et al., 2014).

Concerning the N cycling of forest ecosystems, available N is often a limit-ing key element, as it is vital for biological activity, but the role of N_2O in the

forest N budget is minor. However, N_2O as greenhouse gas may be important. Nitrous oxide in forest soil is generated by microbial processes (nitrification and denitrification) as a byproduct. Treatments (reactive N addition, increased temperature, changes in precipitation regime), soil moisture, soil C/N ratio and pH can significantly affect N_2O emissions in forest soils (Gundersen et al., 2012). N_2O fluxes are affected by pH in several ways: during denitrification, lower pH promotes N_2O production, but autotrophic nitrifiers are sensitive to pH <4.5 (Ågren and Andersson, 2012).

Among factors affecting denitrification, soil oxygen supply and N availability are essential. In general, more N_2O is formed when more reactive nitrogen is available (Ciais et al., 2013). However, extra N might be consumed in an ecosystem by competitive N uptake processes before it can affect greenhouse gas fluxes (Ambus and Robertson, 2006). Likewise, Soosaar et al. (2011) and Mander et al. (2014) have found that in less loaded riparian grey alder forests, N_2O emissions were low and the potential of N_2 emission was high, whereas in analogous grey alder stands downslope of intensively fertilized fields the N_2O emissions were similar to previous stands, but the potential of N_2 emission was significantly lower. It has been found that soil moisture has a considerable positive effect on N_2O emissions (Schaufler et al., 2010; Benanti et al., 2014), e.g. heavy rainfall can increase N_2O emissions (Ambus and Robertson, 2006). Hence a pattern of extreme climatic events and disturbances strongly affects annual global N_2O emission (Zhuang et al., 2012). Freeze-thaw events can be major sources of N_2O emission (Maljanen et al., 2003; Wu et al., 2010), but high-latitude and drought-region ecosystems are small sources of N_2O globally, since tropical soils are the major sources (Zhuang et al., 2012). In summary, N_2O emissions are affected by a large number of environmental variables, which makes it hard to distinguish one major determinant of the flux. Of natural terrestrial ecosystems, forest and agricultural lands are the main N_2O sources (Tian et al., 2010). However, Schaufler et al. (2010) found highest N_2O emission in grasslands followed by forests.

1.3. The effect of clear-cut on forest greenhouse gas fluxes

Clear-cut is a considerable disturbance in a forest ecosystem, which will change overall species composition, microclimate, water and nutrient availability and also soil greenhouse gas emissions (Bergeron et al., 2008; Kim, 2008; Lavoie et al., 2013). Generally, harvest turns forests from C sinks to C sources, particularly in the first years (Page et al., 2011). Typically soil temperature and soil moisture and/or water table level will increase, but not always (Huttunen et al., 2003; Luo and Zhou, 2006). Clear-cut provides dead plant material part of it easily decomposable, but on the other hand decreases the photosynthetic capacity of the site (Page et al., 2011). However if trees regenerate from root suckers and/or stump sprouts then root system stays active and there occurs an input of aboveground forest residues mainly. Changes in soil nutrient cycle, soil mois-

ture and soil temperature caused by clear-cut may increase N_2O emissions and decrease CH_4 uptake. However, the effect on CO_2 emissions depends on effects on autotrophic and heterotrophic respiration, which may respond differently (Page et al., 2011); there have been studies showing results ranging from increased (Kim, 2008) to decreased CO_2 fluxes (Laporte et al., 2003).

As methane flux depends mainly on soil moisture, a decrease in CH_4 uptake or an increase in emission is expected after clear-cutting (Castro et al., 2000; Page et al., 2011). However Bradford et al. (2000) justified the decrease in CH_4 uptake with changes in soil pH and the N cycle. Clear-cutting reduced methane uptake also in a temperate coniferous forest, and a recovery in CH_4 uptake began more than five years after the clear-cut (Wu et al., 2011). Though the effect of clear-cut on CH_4 flux is not always clear (Huttunen et al., 2003).

For N_2O emissions Gundersen et al. (2012) found clear-cutting to have the largest positive treatment response (compared with fertilization, increased temperature, more/less precipitation), with the maximum on the second year after harvest in mineral soil. However, the effect of clear-cut on N_2O emission is also not always clear. An increase in N_2O flux usually lasts for the first few years after the clearcutting (Page et al., 2011).

1.4. Fast growing deciduous forest ecosystems

As climate change has become a pressing issue, bioenergy has become an important renewable energy source. Forest covers 51.1 % of Estonia and is therefore the most common land category in the country (Estonian Environment Agency, 2014). It is predicted that the share of deciduous trees at higher latitudes will increase together with climate change. Therefore gas emissions in deciduous forests were considered in this thesis. Moreover, deciduous trees are more resilient to wind-breakage, root rot and acid rain than conifers and considered native tree species in the thesis are pioneers able to regenerate naturally (Johansson, 1999). Silver birch, grey alder and hybrid aspen are all fast-growing tree species suitable for short-rotation forestry. Short-rotation forestry provides biomass suitable for energy, construction wood, and the pulp and paper industry (Weih, 2004; Rytter and Stener, 2014).

Birch is the most important deciduous tree in Northern Europe (Hynynen et al., 2010; Hytönen et al., 2014). Silver birch (*Betula pendula* Roth.) has wide natural distribution in Eurasia (Hynynen et al., 2010). In Estonia the area of birch forests has almost doubled in half a century and they make up 31.2 % of the total forest area (Estonian Environment Agency, 2014). The financial maturity, according to internal rate of return, of silver birch is 34–45 years (Tullus et al., 2012b). Silver birches are pioneers that grow mostly on upland soils and are shade intolerant (Hytönen et al., 2014). They successfully regenerate when seeds and a site with abundant light conditions are available. However, planting should be preferred for the production of high-quality timber (Hynynen et al., 2010).

Grey alders (*Alnus incana* (L.) Moench) are highly productive fast growing trees, an important source for woody biomass production with a rotation length of 15 to 20 years in suitable conditions (Johansson, 1999; Aosaar et al., 2012). After clear-cut new trees will grow from stump sprouts; therefore no new forest planting is required. The Baltic region is very suitable for grey alders (Aosaar et al., 2012) because of good adaptation of the species to temperate and boreal climate (Rytter, 1996) and good cold hardiness (Weih, 2004). The area of grey alders has more than tripled within half a century (from 1958 to 2012) and they account for 8.7 % of the total forest area in Estonia (Estonian Environment Agency, 2014). In addition to high productivity, grey alder stands are known to improve soil quality. Grey alders accumulate C and N into the soil when growing on newly forested land (Uri et al., 2014). The trees have a symbiotic relationship with N_2 fixing bacteria. *Frankia* can fix N_2 up to 200 kg ha^{-1} yr^{-1}, however, this is very energy costly activity (Ågren and Andersson, 2012). Nitrogenase activity in root nodules is probably self-regulating and N_2 fixation will likely decrease when the ecosystem has enough available N (Rytter, 1996). It is also related to assimilate availability, being lower in mature less productive stands (Lõhmus et al., 2002). As N_2 symbiotic fixation is a soil-acidifying process, grey alders have a potential to decrease soil pH (Uri et al., 2014). Concerning substrate availability for denitrifiers, the soil N pool in grey alder stands is high and net nitrification is close to 100% net N mineralization.

Hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) is a hybrid of European and American aspen; the financial maturity is 26–34 years (Tullus et al., 2012b). Hybrid aspen has higher annual growth rate, related to a longer vegetative period, than European aspen and American aspen (Yu et al., 2001; Tullus et al., 2012c). However, longer growing time may increase the risk of frost damage (Yu et al., 2001). Hybrid aspen is also capable of vegetative regeneration, renewing mainly from root suckers. The new generation formed after clear-cutting has a higher stemwood production at the beginning of the growth cycle, but the difference decreases with stand age (Rytter and Stener, 2014).

1.5. The effect of elevated humidity on fast-growing deciduous forest ecosystems

Various effects of climate change on ecosystems have been studied in numerous free-air experiments: free-air CO_2 enrichment experiments (FACE) have been conducted in grasslands, in prairies, on agricultural land, in deciduous and coniferous forests (Williams et al., 2000; Phillips et al., 2001; Mosier et al., 2002; Zak et al., 2003; Müller et al., 2009; Lam et al., 2011); a combination of summer drought, increased CO_2 and temperature was applied to temperate heathland (Mikkelsen et al., 2008; Selsted et al., 2012); a combination of additional water and nitrogen fertilization in FACE plots in grassland (Mosier et al.,

2003); a combination of elevated CO_2 and O_3 in grassland (Kanerva et al., 2007); and an irrigation experiment in larch forest (Koide et al., 2010).

The effect of humidity on forest ecosystem functioning was not studied in free air manipulation experiments until 2008 when a unique free-air humidity manipulation experiment (FAHM) was initiated in Estonia to investigate the effect of elevated humidity on young deciduous forests (Kupper et al., 2011). In the troposphere, water vapour can absorb considerable amounts of long wave radiation and can therefore exacerbate the greenhouse effect (Ågren and Andersson, 2012). Water vapour is responsible for the largest contribution to the natural greenhouse effect (two to three times more than CO_2) however, the amount of water vapour in the atmosphere is controlled by air temperature and the residence time in the atmosphere is about ten days (Myhre et al., 2013). In the thesis, however, the direct effect of elevated humidity on deciduous forest ecosystems, which particularly shape soil greenhouse gas fluxes (CO_2, CH_4 and N_2O), was considered.

In order to analyze the effect of elevated humidity, investigations were carried out within a complex free-air experiment. Increasing humidity was assumed to have an impact on evapotranspiration, plant growth, biomass allocation and several soil processes that are directly responsible for greenhouse gas fluxes (Fig. 1). Humidity manipulation decreased the transpiration of silver birches and hybrid aspens in moist years (Kupper et al., 2011). Nutrient uptake from soil to leaves was reduced due to lower transpiration induced by increased humidity, which in turn diminished photosynthetic capacity and tree above-ground growth in both tree stands (Tullus et al., 2012a; Sellin et al., 2013). Reduced transpiration and tree growth affected soil water content: soils were moister in humidified plots compared to control plots (Parts et al., 2013; Kukumägi et al., 2014). However, the effect of elevated humidity was not uniform. The transpiration rate was higher in the increased humidity treatment in the silver birch stand with moderate water deficit, but with severe water deficit there was even no difference between treatments (Sellin et al., 2014). The effect of humidification on trees' water exchange depended to great extent on weather conditions during the vegetation period. Still regardless of variability in meteorological conditions during different vegetation periods, the effect of humidity manipulation on ecosystem processes was significant (Kupper et al., 2011; Tullus et al., 2012a; Sellin et al., 2013; Sellin et al., 2014).

Trees in the silver birch stands adapted to elevated humidity by forming longer and thinner short roots to increase the absorptive area (Parts et al., 2013). A similar morphological stress response was found for hybrid aspens (I. Ostonen personal communication). Contrary to the stress reaction of trees, soil microbial activity was increased by 28 % in elevated humidity conditions after two years of manipulation in silver birch stands (Kukumägi et al., 2014). Also there was a shift in the fungal community: hydrophilic fungal morphotypes dominated in humidified plots and hydrophobic in control plots (Parts et al., 2013).

Elevated humidity has been found to relieve drought stress (reduced stomatal limitation to photosynthesis) of hybrid aspen (Niglas et al., 2014), but changes found in the physiology of silver birches grown under elevated humidity will make trees more vulnerable to water deficit (Sellin et al., 2014). Results in the FAHM experiment indicate that increased humidity, even with a longer growing period due to increased temperature, has a negative or no effect on the growth rate of northern latitude forests (Sellin et al., 2013).
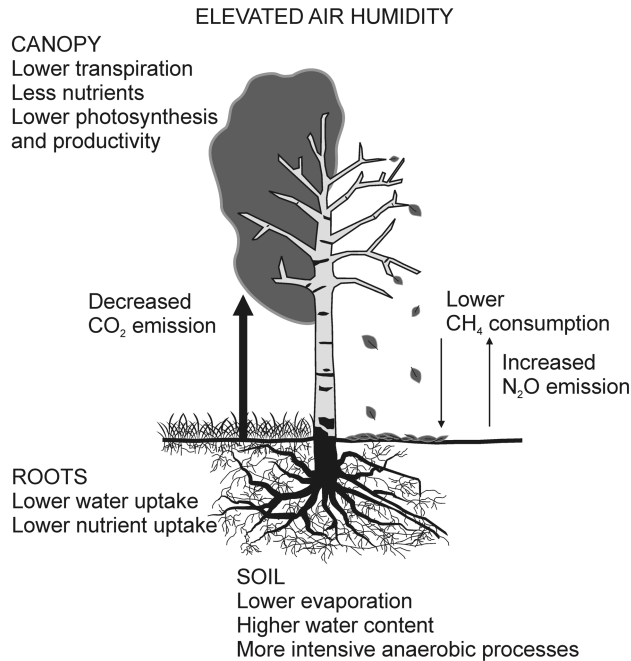
ELEVATED AIR HUMIDITY

CANOPY
Lower transpiration
Less nutrients
Lower photosynthesis
and productivity

Decreased
CO_2 emission

Lower
CH_4 consumption

Increased
N_2O emission

ROOTS
Lower water uptake
Lower nutrient uptake

SOIL
Lower evaporation
Higher water content
More intensive anaerobic processes

Figure 1. Conceptual scheme of the expected main impacts of elevated humidity on greenhouse gas fluxes and relevant ecosystem parameters in a young boreo-nemoral deciduous forest on automorphic soil (Publication I).

The main aim of the thesis was:
to analyze the effect of climate change (elevated air humidity, extreme climate events) and forest management (clear-cut, stand establishment, tree species) on soil greenhouse gas (CO_2, CH_4, and N_2O) emissions in fast-growing deciduous stands.

Specific objectives were:
(1) to ascertain the influence of elevated air humidity on the seasonal and annual variations in soil greenhouse gas (CO_2, CH_4, and N_2O) fluxes in fast-growing young deciduous forests (I,II);

(2) to analyze how extreme weather conditions (high temperature and drought) and tree species, interactively with elevated air humidity, influence soil greenhouse gas (CO_2, CH_4, and N_2O) fluxes (II,III);

(3) to ascertain the effect of clear-cut on soil greenhouse gas fluxes in a mature grey alder stand (IV)

The hypotheses of the study were:

(1) elevated humidity and tree species have a significant impact on greenhouse gas emissions (I, II, III);

(2) heat waves and drought decrease soil CO_2 and N_2O emissions and increase CH_4 oxidation (III);

(3) clear-cut of a mature grey alder stand initiates larger soil greenhouse gas fluxes (IV);

2. MATERIALS AND METHODS

2.1. Study sites and set-up of experiments (FAHM, Agali)

All studies were conducted in south-eastern Estonia in silver birch and hybrid aspen experimental stands in FAHM (58º14´ N, 27º18´ E, altitude 44–50 m) and in grey alder stands in Agali (58º17´ N, 27º17´ E, altitude 32–37 m) study sites. The typical length of the growing season is 175–180 days. Long-term (1966–2010) air temperature and precipitation were measured at the Meteorology Station of the Tartu Observatory (58º15'55'' N, 26º27'58'' E), 50 km west of both study sites. The 30-year average temperature in the region for 1981-2010 was 5.8 ºC (17.6 ºC in July, which was the warmest month and -5.3 ºC in February, which was the coldest month); average annual precipitation was 680 mm (427 mm from May to October) and relative humidity was 80 % (77 % from May to October) according to the Estonian Weather Service. Additionally, meteorological parameters were measured in the FAHM site. Vegetation periods in all study years were warmer than the long-term average (Fig. 2). 2010 and 2011 were extremely warm summers and 2013 had an exceptionally warm May and June, and 2012 was the coldest of the six measurement years. Precipitation in 2010 and 2014 was in same order of magnitude as the long-term average; 2011, 2012 and 2013 were drier and 2009 was moister. However, precipitation from June to August is most important for carbon dioxide flux due to the intense plant growth in this period. June in 2011 and July in 2010–2012 were low in precipitation.
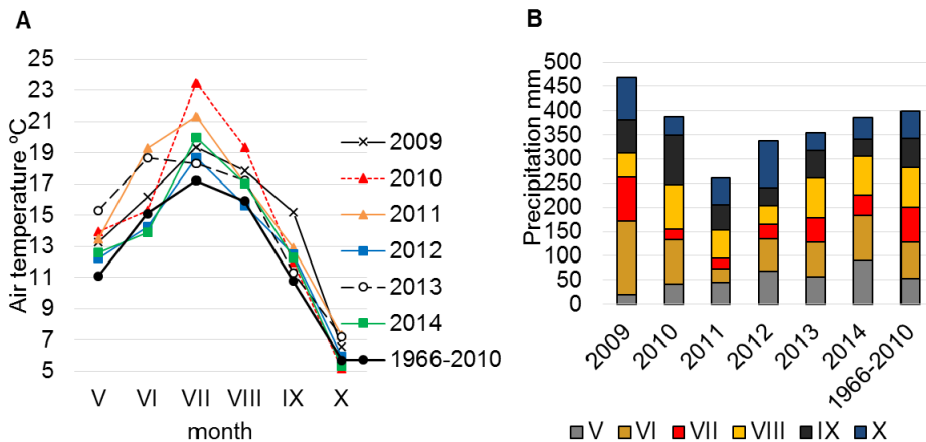

Figure 2. Monthly mean air temperatures (A) and monthly precipitation (B) in the FAHM site from May to October from 2009–2014, compared to regional long-term average monthly precipitation and mean temperature (Publication III).

2.1.1. Free Air Humidity Manipulation experiment (FAHM)

The FAHM experimental site is located on former arable land on Endogleyic Planosol (IUSS Working Group WRB, 2007). The A horizon (0–27 cm) has a sandy loam texture and the subsoil (50 cm), a sandy clay loam texture, which means that the finer texture of the subsoil is more effective in preserving available water in the soil during water shortage (Hansen et al., 2013 – Publication I). The porosity of the soil is similar in humidification and control treatments, ranging between 56.7–59.6 % by volume (Publication I). Some soil chemical characteristics are presented in Table 1. In FAHM plots, soil chemical characteristics did not differ between control and humidified plots, except soil pH. However, after seven years of stand growth, topsoil N % was higher under silver birch than hybrid aspen.

The study site is a fenced area of 2.7 ha. Measurements for publications I, Rosenvald et al. (2014) – II and Torga et al. (201X) – III were conducted in six hexagonal 14 × 14 m experimental plots: three humidified plots and three control plots. All study plots were divided into four segments: two adjacent according to tree species and two perpendicularly according to understory vegetation (Fig. 3). Selected silviculturally important tree species were silver birch (*Betula pendula* Roth) and hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.). One-year-old birch seedlings were planted in spring 2006 and mono-clonal aspens were also first planted at the same time, but did not survive due to the poor quality of the planting material and had to be replanted in autumn 2006. Therefore the heights of the aspens were smaller than those of the birches. Trees were planted with 1 × 1 m spacing inside the study plots. The buffer zone around the study plots was planted with hybrid aspens with 2 × 2 m spacing. Seven-year-old birches and aspens from the control and humidified plots were harvested after the end of 2011 and 2012 respectively, because the trees got too high to humidify the whole canopy. After harvesting, monoclonal silver birches were planted in spring 2012; aspens regenerated vegetatively by stump and root sprouts. All study plots were established with two types of understory vegetation: dominated either by early-successional grasses or by forest understory. The early-successional grass understory had low diversity and contained mainly grasses common to set-aside arable land. The forest understory was formed by planting 0.5 × 0.5 × 0.2 m soil patches originating from clear-cut forest and by sowing forest plant seeds. The understory is described in more detail in: Kupper et al. (2011); Parts et al. (2013); Kukumägi et al. (2014).

Humidity manipulation began in 2008. For the humidity treatment, 0.1 m^3 of water for a plot per hour was pumped from the nearby pond. Small droplets of water, which were previously filtered (20 µm) and softened with a DME demineralizer (Prominent Dosiertechnik GMBH, Heidelberg, Germany), were sprayed into the air over the experimental plot. In 2008 and 2009 mist droplet size was 50 µm, but in 2010 and 2011 the size was reduced to 10 µm to avoid wetting the leaves (Kupper et al., 2011; Tullus et al., 2012a). Humidity was increased only during the daytime, when wind speed was <4 m/s, relative humidity <75 % and

air temperature >10 ºC from May to September. Average increase of relative humidity by the manipulation was 7%, and in suitable weather conditions, even up to 18% according to Kupper et al. (2011).

Table 1. Soil characteristics (0–10 cm) in FAHM at felling time (c – control, h – humidification; significant differences between treatments are marked in bold; Publication II); and in Agali; (CC – clear-cut, F – forest; Publication IV).

	Silver birch		Hybrid aspen		Grey alder	
	c	h	c	h	CC	F
pH$_{KCl}$	4.3	**4.5**	4.2	**4.6**	5.8	5.9
N (%)	0.144	0.136	0.131	0.112	0.315	0.364
Organic matter (%)	2.7	2.6	**2.7**	2.4	6.5	7.5

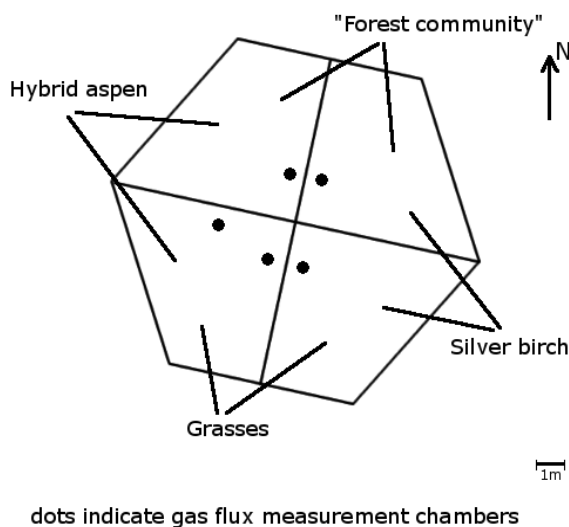dots indicate gas flux measurement chambers

Figure 3. The scheme of a FAHM experimental plot (one of the six). Tree species and understory type in four segments are indicated.

2.1.2. Agali grey alder stand and clear-cut

The Agali experimental site (Becker et al., 2015 − Publication IV) is also located on former arable land on Umbric Planosol soil (IUSS Working Group WRB, 2007). Two 20 × 35 m study plots for publication IV were established in 2011 in a homogeneous mature (32-year-old) grey alder (*Alnus incana* (L.) Moench) forest with mean tree height of 17 m. One plot was clear-cut in May 2011 and the other was left for the control treatment. For soil chemical analysis, 15 soil samples per plot were randomly taken with a soil corer (D = 40 mm)

from different depths of the topsoil; some soil chemical characteristics for 0–10 cm layer are presented in Table 1. No significant differences in soil chemical characteristics were found between grey alder forest and clear-cut in the Agali site (Publication IV).

2.2. Greenhouse gas sampling and analyses

Soil CO_2, CH_4 and N_2O fluxes were measured manually in all plots with non-transparent white truncated-cone-shaped static PVC chambers (Hutchinson and Livingston, 1993). The headspace of chambers was 65 l, with 50 cm diameter at the base. Samples were collected once a month during the snow free period in July–December 2009, April–October 2010, April–December 2011, May–November 2012, May–December 2013, March–December 2014 in the FAHM site (Publications I, III); and in December 2011, May–November 2012, April–December 2013 in the Agali site (Publication IV). For gas measurements, ventilated chambers were placed on the water-filled collars inserted into the soil. In both sites, each plot had five replicates. In the FAHM site, two replicates were in a birch stand and three in an aspen stand. Three and four samples per hour, for the FAHM and Agali sites respectively, were collected from the middle part of the chamber with a syringe and tube system to 100 ml evacuated glass bottles. Sampled air from the bottles was analyzed with a Shimadzu GC-2014 gas-chromatograph (Loftfield et al., 1997). Linear change in time for CO_2 was expected. The emission rates of greenhouse gases were calculated using the linear increase of gas concentrations with time.

2.3. Abiotic environmental conditions

In the FAHM site, several environmental parameters were measured and recorded continuously in experimental plots (a thorough description of methods is given in Kupper et al., 2011). In publications I, III and IV, continuously measured data on soil temperature, soil water potential (SWP) and relative humidity were used. Every soil parameter was measured with four sensors per plot (two in a birch and two in an aspen stand). Soil temperature was measured at 15 cm depth with an ST1 soil temperature probe (Delta-T Devices, Burwell, UK). Soil water potential was measured at 15 cm depth with an EQ2 equitensiometer (Delta-T Devices, Burwell, UK). Relative humidity was measured at the mean height of the canopy in 3–4 replications with a HMP45A humidity probe (Vaisala, Helsinki, Finland). The amount of precipitation was measured with an automatic weather station (Campbell Scientific, Logan, UK) next to the experiment plots. Precipitation was collected at 10-min intervals.

In the Agali site (Publication IV), soil temperature and soil moisture (kPa) was monitored (WatchDog 1425, Spectrum Technologies, Inc., USA) at a depth of 10 cm with two sensors per plot in 2011 and 2012.

2.4. Biomass allocation and litter fluxes in the FAHM site

2.4.1. Tree growth and biomass allocation

Data on tree growth and biomass allocation were used to characterize the tree species- specific response to humidification and the related differences in soil greenhouse gas emissions at stand level. Tree height was measured with a Nedo mEssfix-S telescopic measuring rod (Nedo GmbH & Co.KG, Dornstetten, Germany), and stem diameter at 30 cm height with a LIMIT digital caliper (Luna AB, Alingsås, Sweden) at the end of the growing season in 2010 and 2011 (Publication III). Biomass allocation of birches and aspens was estimated with dimension analysis based on the model trees method (Bormann and Gordon, 1984; Uri et al., 2007) on 7-year-old trees (Publication II). Twelve randomly selected birch trees from both treatments (6 from humidified and 6 from control plots) were harvested after the growing season in 2011 and the same was carried out for aspens in 2012. The aboveground part of a model tree was separated into four height sections (the stem from the base up to a first live branch and three subsequent sections of equal length of the live crown). Each section was weighed and separated into compartments: stem, current year shoots, older branches, dead branches and leaves. A cross-section subsample for wood and bark was taken from the middle of the stem in each section. Subsamples were taken from each compartment for dry matter content and chemical analysis and dried until constant weight at 70 ºC and weighed to 0.01 g.

The belowground biomass of trees was excavated from 1×1 m squares to a depth of 80 cm around model birches (10) and aspens (14). For birches, fine-root (D<2mm) biomass in the A-horizon was estimated by soil cores, as soil excavation causes fine root loss. Altogether, eighteen soil cores (D=48mm) per treatment were taken. Soil cores were divided into 10-cm layers, washed clean from soil and sorted under a microscope into live and dead tree roots; live belowground parts of the understory were collected as well. The excavating loss of fine roots was assumed to be similar for birch and aspen. The methods to assess the belowground part are described more thoroughly in Publication II.

2.4.2. Tree leaf litter

Tree leaf litter – an important substrate for heterotrophic respiration – was collected from six 0.21 m^2 litter traps per tree species per treatment (control, humidification) at a two-week interval during the whole leaf fall, between the end of July until the first half of November in 2010 and 2011 (Publication III). The total dry weight of the leaf litter per ground surface area (g m^{-2}) was estimated.

2.4.3. Understory biomass allocation and litter

Biomass of the aboveground part of the understory was estimated on the basis of 24 samples harvested at the time of maximum biomass (Publication III). The collecting area was 0.5 m^2 and 0.25 m^2 in 2010 and 2011 respectively. An equal number of samples were taken in both treatments (control, humidification) and in both tree stands (aspen, birch). Peak aboveground biomass gives an estimate for annual aboveground litter flux from the understory.

Twelve soil cores were collected from the A horizon for both treatments in the silver birch stand in autumn 2010 and 2011 (Publication III). Understory roots were manually separated from soil and tree roots (see 2.4.1); for a thorough description of sample processing see Kukumägi et al. (2014). Annual belowground litter fluxes from the understory were calculated using the measured root biomasses and turnover rates presented in Kukumägi et al. (2014). Tree root litter flux was not considered here as it was 6.5 and 3.8 times smaller than the litter flux of understory roots and rhizomes in control and humidified plots respectively.

2.5. Soil microbiological analyses

Soil samples were collected randomly with a soil corer (cutting edge 20 mm) from 0–10 cm soil layer from silver birch stands in the FAHM site in October 2011 (Publication III) and from the mature grey alder stand and clear-cut in the Agali site in October 2013 (Publication IV). In the FAHM site, 15 field-moist random samples were taken per segment of a plot and compiled (six composite samples from control and six from humidified plots). In both Agali plots the random samples were taken in three replications (20 samples per replication were compiled). The corer was carefully cleaned to avoid sample contamination. The composite soil samples were put in sealed polyethylene bags and protected from light by black plastic bags. Composite samples stayed for a day at the outside temperature. Next day, roots and rhizomes were carefully removed by hand from the field-moist composite samples and the soil was passed through a 2 mm mesh sieve to obtain a homogenized fine earth fraction.

Manometric respirometers (Oxitop®, WTW) were used to measure soil microbial respiration (Substrate Induced Respiration (SIR)) by determining the sample oxygen consumption (Publications III, IV).

Oxygen consumption in dry soil (mg O_2 kg^{-1} DW h^{-1}) was calculated with the Platen and Wirtz (1999) method. Microbial biomass (mg C g^{-1} DW) was calculated in glycose-enriched moist soil with the Beck et al. (1996) method. In Agali soil samples, enzyme activities (dehydrogenase activity, N-mineralization, potential nitrification, acid phosphatase activity) were additionally measured; the microbiological methods are thoroughly described in Publications III and IV. The enzyme activities were analyzed in connection with nitrous oxide emissions.

2.6. Statistical analyses

The normal distribution of variables was checked with Lilliefors' and Shapiro-Wilk's tests. If necessary, data were log or square-root transformed to get the normal distribution. The effects of humidification and type of understory on tree characteristics were analyzed by factorial ANOVA. The significant effect of factors (humidification, type of understory vegetation, and tree species) on growth and biomass of trees was checked with the t-test. Allometric relationships between the model tree biomass compartments and diameter were found and the Generalized Linear/Nonlinear Model (GLZ) was used to check the significance of humidification in allometric regression models.

For greenhouse gas fluxes, repeated measures ANOVA, t-tests for dependent and independent samples, and the Wilcoxon matched pairs test were used. In statistical analyses, the effect of different type of understory on greenhouse gas fluxes was not significant when both tree species were involved, hence understory type was not included as a fixed factor in further analysis. The relationships between greenhouse gas emissions and environmental variables (soil temperature, SWP, relative humidity) measured on the same day were checked using stepwise regression analysis. Soil respiration depended exponentially on soil temperature and, at low soil water availability, additionally on square root-transformed SWP ($\sqrt{}$-SWP); for methane flux the last variable was used as a predictor in the regression model. The level of significance $\alpha = 0.05$ was used throughout the analyses. Data analyses were performed with STATISTICA 7 (StatSoft, Inc., 2013) and Excel 2010 programmes.

3. RESULTS AND DISCUSSION

3.1. The effects of elevated humidity on young deciduous forest ecosystems

3.1.1. The effect of increased air humidity on environmental conditions

Relative humidity was significantly increased in humidified plots compared to control plots on gas sampling days in 2009–2014 (Wilcoxon test, p<0.005). The mean monthly relative humidity values for May to October from 2009 to 2011 are presented in Parts et al. (2013) and the values were consistently higher in humidified plots than in control plots.

Soil temperature was not significantly different between treatments on gas sampling days in 2009, 2010, 2011 and 2013 (Fig. 4A, Publication I, III), nor in 2008–2009 (Kukumägi et al., 2014). The only revealed differences were caused by clear-cut: in humidified plots, soil temperature was significantly higher than in control plots in birch stands in 2012 (the year after clear-cut) and in aspen stands in 2014 (in the second year after clear-cut; t-test, p<0.05). Also, birch stands had slightly higher soil temperature than aspen stands in humidified plots in 2012 (t-test, p<0.05 one-sided hypothesis) and in control plots in 2014 (t-test, p<0.05). The reasonable explanation is the missing or smaller tree canopy in birch stands after clear-cut and the respective reduced shading.

In 2010 and 2011, monthly mean values were used to estimate the effect of humidity manipulation on soil water potential (Publication III). Elevated humidity significantly increased soil water potential under both tree species in humidified plots compared to control plots (Wilcoxon test, p<0.05); however, for birch stands, the one-sided hypothesis was proved. The likely main reason was reduced transpiration, discussed in Kupper et al. (2011). The impact of tree species on soil moisture conditions was significant: birch stands had significantly lower soil water potential than aspen stands in humidified plots in 2010, and in both treatments in 2011 (Wilcoxon test, p<0.05). Soil water potential on gas sampling days was significantly higher in humidified plots compared to control plots in both tree stands over all the years (Wilcoxon test, p<0.0005, Fig. 5A, Publication I, III). Also, birch stands had significantly lower soil water potential compared to aspen stands on gas sampling days (years 2009–2014, Wilcoxon test, p<0.0005). In both cases (aspen vs birch, humidified vs control plot), the difference was almost two fold. Also, soil moisture (%) in 2008–2009 was higher in humidified plots (Kukumägi et al., 2014).

There was no difference in soil organic matter between control and humidified plots in birch stands before the humidification started (Publication II) nor in the first two misting years (Kukumägi et al, 2014). However, in aspen stands, control plots had more organic matter than humidified plots in 2012 (t-test, p<0.05, Table 1, Publication II). The C/N ratio was 12.6 in humidified plots and 12.1 in control plots (Publication I). Tree species affected soil N content, which was significantly higher under birch than aspen. The values of soil nitrogen content were higher in control plots compared to humidification plots, but the

difference was never significant (Publications I, II; Kukumägi et al., 2014). Before humidification there was no significant difference in top-soil pH between treatments (pH was 4.5), but there was a small significant increase in topsoil pH after 4 years of humidification under both tree species (Table 1, Publication II). The likely reason for the pH change is the rise of water with higher pH from deeper soil due to increased soil moisture in humidified plots.

Figure 4. Mean soil temperature (A) and CO_2 fluxes (B) in control (C) and humidified (H) plots in silver birch and hybrid aspen stands in FAHM site in 2009–2014.
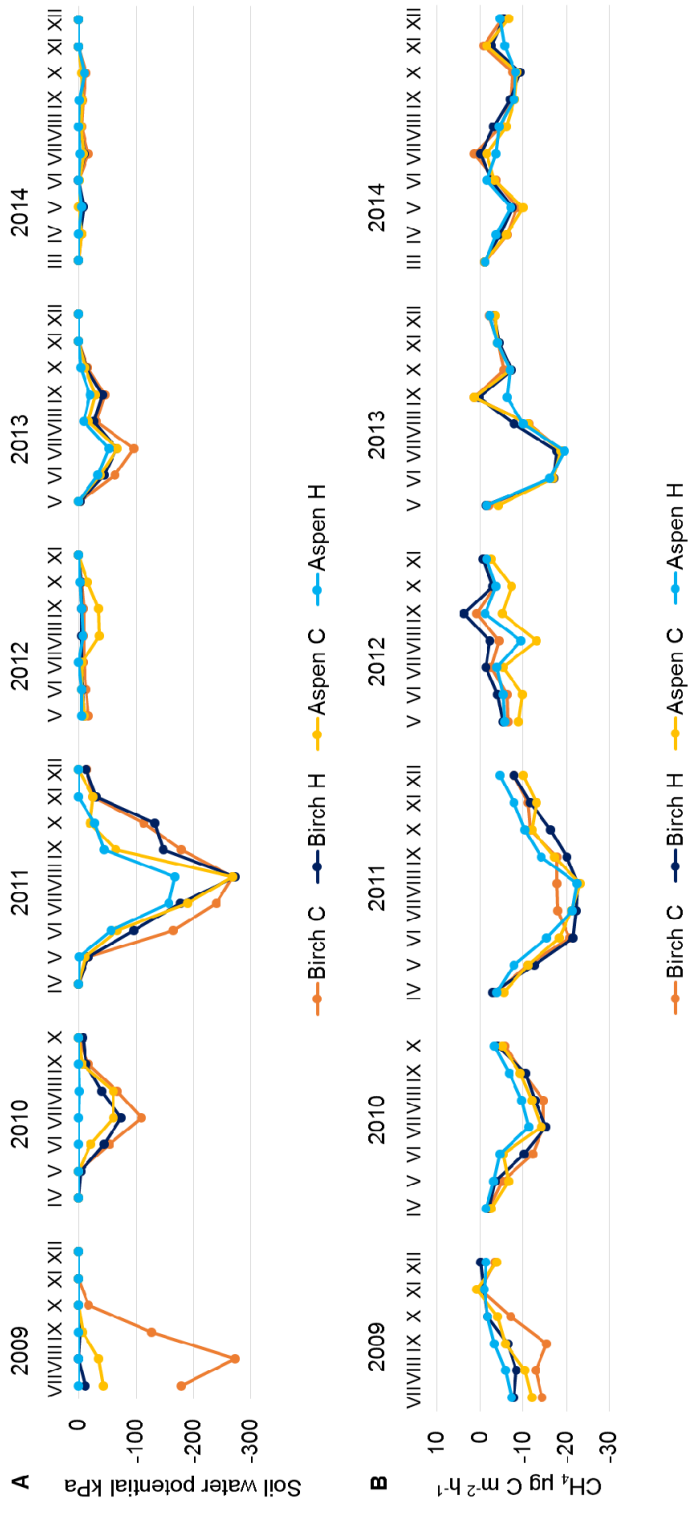
Figure 5. Mean soil water potential (A) and methane fluxes (B) in control (C) and humidified (H) plots in silver birch and hybrid aspen stands in FAHM site in 2009–2014.

3.1.2. The effect of increased air humidity on biomass allocation and litter fluxes of trees and understory

Trees

Generally, humidification treatment inhibited the height growth of both tree species (Fig. 6, Publication II, III). However, humidification treatment did not affect current year height increment in birch stands in 2010, and in aspen stands in 2011 (t-test, $p > 0.05$). Even more, in 2011 with warm and dry growing season humidification enhanced height increment compared to control in birch stands (t-test, $p < 0.05$). Stem diameter at 30 cm height in birch stands was not statistically different between treatments in 2010 and 2011, but the increment of stem diameter was significantly greater in the humidification treatment than in the control in 2011. Aspens were more sensitive to humidity manipulation; stem diameter was significantly smaller in humidified plots compared to control plots and humidification treatment did not have a positive effect on stem diameter increment in either year in aspen stands. Also, tree-species-related differences in acclimation capacity to stress caused by humidification were significant – the silver birch adapted better (Publication II). One possible explanation is that aspens were monoclonal and had lower plasticity for adapting with the changed environment. Birches on the other hand had natural variability and were able to change biomass allocation and accumulation, which enhanced their adaption. After four years of humidity manipulation, birches acclimated to elevated humidity, as there was no difference in biomass accumulation between treatments, but the growth of aspens was still reduced. Petrone et al. (2015) found a high sensitivity to drought in young trembling aspens. So one possible cause why hybrid aspens did not acclimate to elevated humidity was additional stress caused by water limitation in 2011.

Birches, being larger than aspens, had significantly more leaf litter than aspens. Treatment affected tree leaf litter significantly in aspen stands, where control plots had more litter than humidified plots in 2010 (t-test, $p < 0.05$); a similar tendency was found also in 2011. Severe drought in 2011, concurrently with misting, enhanced N and K uptake in silver birches (Publication II). Due to better nutrient status, birch leaves probably provided more assimilates for soil autotrophic respiration and, after senescence, easily decomposable litter. Silver birches had lower leaf temperature in humidified plots compared to control plots and this phenomenon affected photosynthesis (Kupper et al., 2011; Sellin et al., 2014). Increased humidity delayed leaf fall by 2 to 3 weeks in silver birch stands, but not in hybrid aspen stands; on the contrary in 2010 leaf fall was even enhanced (Godbold et al., 2014). Generally, drought advances leaf senescence (Estiarte and Peñuelas, 2015), but tree-species-induced differences are not excluded, as seen from the Bangor FACE and FAHM studies (Godbold et al., 2014). Climate change may alter the dynamics of leaf senescence in different ways: direct effects may occur through alterations in the life-span of leaves, which will modify C uptake; indirect effects may result from changed nutrient retranslocation from senescing leaves, which modifies the nutrient pool for

growth at the beginning of the new growing season (Estiarte and Peñuelas, 2015).

Birches had significantly more fine roots in humidified plots than in control plots in the A horizon (t-test, $p<0.05$, Publication II). Aspens had a similar tendency, but it was not significant. The overall belowground biomass of both tree species did not differ significantly between treatments. However, both tree species in humidified treatments had higher fine root to root (system) ratio and fine root to leaf ratio compared to the control (Publication II). Such an increase in the fine root compartment is in accordance with the extensive foraging strategy to cope with stress conditions (Ostonen et al., 2011).

To mitigate the diminished nutrient uptake due to reduced transpirational flux, the silver birch absorbing roots responded with changes in morphology (Parts et al., 2013), also root hydraulic capacity increased (Sellin et al., 2015).

Understory
The effect of tree species on the understory was significant; aboveground understory biomass in aspen stands was up to three times higher than in birch stands (t-test, $p<0.05$; Table 1 in Publication III). The difference between tree species is probably related to different tree growth and light availability in stands, as aspens were smaller and the shading was not as extensive as under birches. Humidification decreased significantly aboveground understory biomass in the birch stands in 2010 (t-test, $p<0.05$), and a similar trend was seen in 2011. Treatment did not affect aboveground understory biomass in aspen stands.

In birch stands there was significantly more belowground understory biomass in humidified plots than in control plots in 2010 (t-test, $p<0.05$), but with extreme heat and water deficit in 2011 the difference in root biomass levelled off.
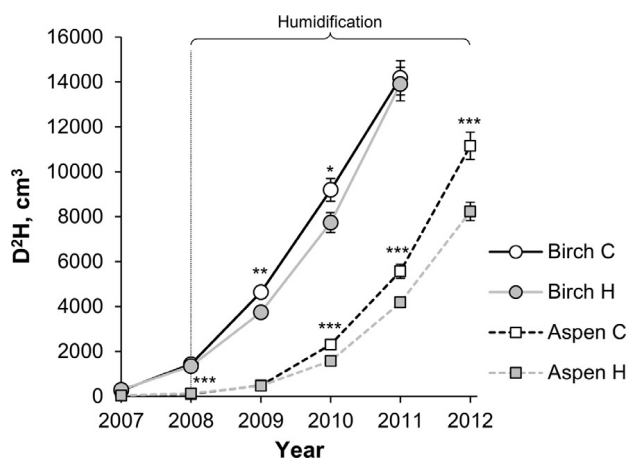

Figure 6. The effect of humidification on the development of stem volume index (D^2H) in silver birch and hybrid aspen stands; humidification treatment was not applied in 2007. Error bars denote standard errors, and asterisks indicate significant differences in group means according to the t-test ($p<0.05^*$, $p<0.01^{**}$, $p<0.001^{***}$; Publication II).

3.1.3. The effect of increased air humidity, tree species, and extreme weather conditions on greenhouse gas fluxes

Carbon dioxide

Soil respiration had clear seasonal dynamics (Fig. 4B, Publications I, III), with the highest emissions in the summer and the lowest in the beginning of spring and in the winter (the exact month depended on the specific year's weather conditions and the length of the measurement season). These seasonal dynamics are typical for CO_2 emissions, with extremely low (less than 8 % of annual flux) winter fluxes (Groffman et al., 2006). During the first year of closed chamber gas measurements the effect of treatment was not clear. However Kukumägi et al. (2014) found that in birch stands in the same year, 2009, with above average precipitation, the control plots had higher CO_2 flux than humidified plots. In 2010, humidified plots had slightly smaller CO_2 flux than control plots in birch stands, which also applies to differences in the aboveground understory. This was the only time when control plots had higher carbon dioxide emission in the FAHM site during the static chamber gas measurements. In 2011, drought in the summer inhibited respiration in control plots and humidification treatment mitigated the heat and water stress, causing significantly higher respiration in humidified plots in both tree stands. During the new rotation from 2012 to 2014, humidified plots continued to be higher CO_2 emitters than control plots in birch stands (the same was true for aspens in 2012 and 2014). Some differences may be explained by higher soil temperature in humidified plots compared to control plots in birch stands in 2012 and aspen stands in 2014. Mean SIR was 0.456 ± 0.024 and 0.515 ± 0.032 mg C g^{-1} DW, and mean basal respiration was 2.42 ± 0.33 and 2.76 ± 0.36 mg O_2 kg^{-1} DW h^{-1} in control plots and in humidified plots respectively (Publication III). Microbial biomass and activity were higher in humidified plots compared to control plots in 2011 (t-test, $p<0.05$ in both cases). A positive effect of misting on microbial activity was found also earlier in the moist year of 2009 by Kukumägi et al. (2014).

There are not many papers about the effects of humidity on CO_2 emissions, but the effect of cloudiness on carbon dioxide exchange in deciduous forest ecosystems has been analyzed. The presence of clouds has been found to en-hance carbon uptake from the atmosphere, either by promoting photosynthesis or by reducing respiration; cloudiness may cause a remarkable decrease in solar radiation (~50%) without reducing carbon uptake capacity in boreal and tem-perate deciduous forest ecosystems (Gu et al., 1999).

CO_2 fluxes differed significantly between tree species: in control plots in 2009, in humidified plots in 2010 and in both treatments in 2011, aspen stands had higher soil respiration than birch stands. After the harvest, CO_2 emission was higher in birch stands than in aspen stands, in humidified plots in 2013 and in both treatments in 2014. The difference in soil respiration between the tree species may be related to the understory biomass, which depended on light con-ditions that were directly affected by tree canopy growth. In the first experi-mental period, before harvest, birches were more viable and bigger than aspens.

In the second period, after harvest, aspens started to grow from stump sprouts and root suckers one year after birch seedlings were planted. The possibility to make use of the former root system of the parent tree enhanced aspen growth compared with birches. Hence CO_2 efflux was affected by forest composition, which shaped the accumulation and the quality of soil organic carbon and soil temperature dynamics (Laganière et al., 2012).

Carbon dioxide emission had a strong correlation with soil temperature (Figs. 4, 7); soil temperature described ≥75 % of CO_2 flux dynamics (Publications I, III). As the ecosystem was changing over the years, and inter-annual weather conditions were remarkable, then study year also affected CO_2 emissions. The highest fluxes were measured in 2010, 2013 and 2014, in that order, with rather warm or even extremely hot (2010) summers and with no clear stress factors. The lowest CO_2 emissions were recorded in 2011, with a hot summer with severe drought. In the case of water limitation, in addition to soil temperature, higher soil moisture affected CO_2 emissions positively; the addition of SWP improved the model by 8 % (Publication III). Soil moisture has been found to regulate CO_2 emissions in drought periods (Ruehr et al., 2010; Selsted et al., 2012) and also to have a strong impact on ecosystem respiration in spring (Welp et al., 2007). However, from June to August the amount of precipitation is crucial, since this is the most active time for CO_2 emissions. Summer drought will inhibit plant growth and microbial activity in the soil and in the long term may change physical soil conditions, which can subsequently cause lower soil respiration (Selsted et al., 2012). Ruehr et al. (2010) and Suseela et al. (2012) found that the water limitation threshold for CO_2 flux started from 15 % soil moisture content. Yet, in some cases, summer drought had a positive effect on ecosystem respiration, when increased temperature enhanced the autotrophic and heterotrophic respiration (Welp et al., 2007). In a warming and drought experiment, 0.4 °C elevated temperature during daytime did not have an overall effect on soil respiration, since it might have been insufficient to induce microbial response, however, soil respiration was reduced by summer drought (14 %) and by the combination of elevated temperature and drought (~50%) (Selsted et al., 2012). Therefore drought can be a major inhibiter for CO_2 emissions, especially when combined with elevated temperature.
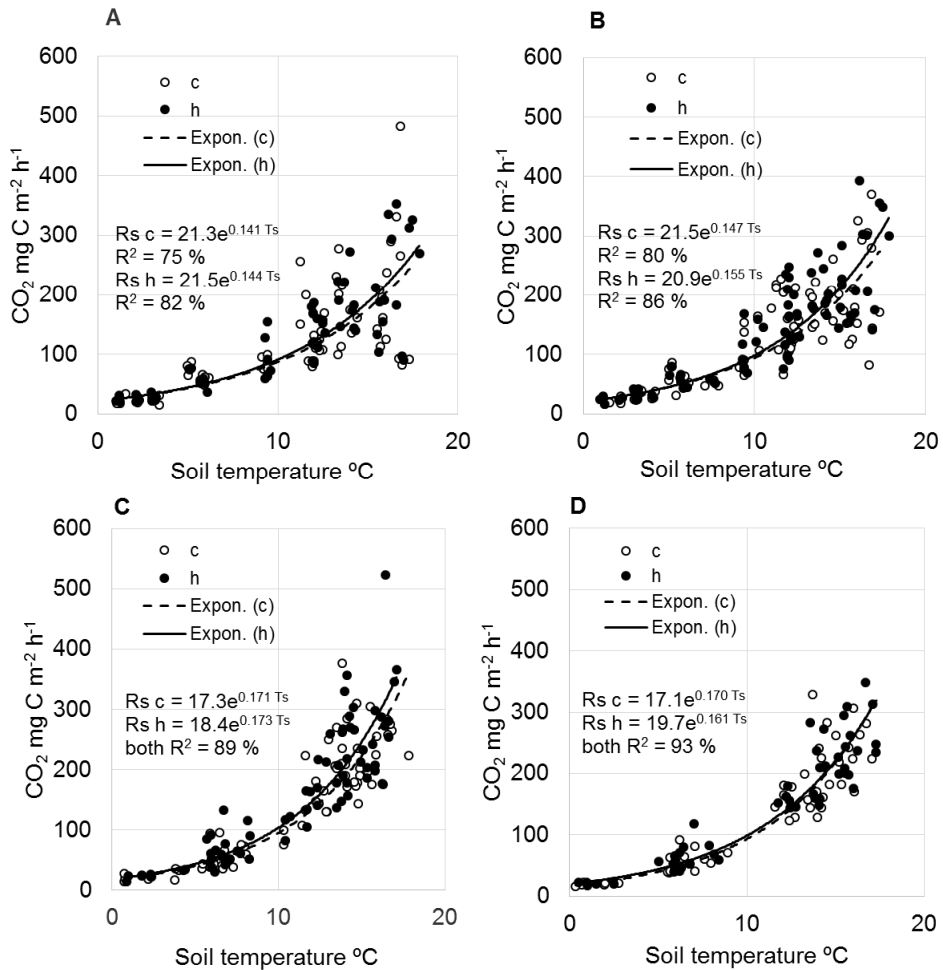
Figure 7. Relationships between carbon dioxide emission (Rs) and soil temperature (Ts) in control (c) and humidified (h) plots in silver birch (A) and hybrid aspen stands (B) before clear-cut, and in silver birch (C) and hybrid aspen stands (D) after clear-cut. In all cases $p<0.000001$.

Methane

Methane was mostly bound from atmosphere to soil in the FAHM site and the flux depended on soil water potential (Fig. 5B, Publications I, III). When SWP was at its lowest, in the summers of 2009–2011, then the methane uptake was higher. This is in good accordance with literature where the seasonal cycle of methane is analyzed: the largest uptake in the summer was found to be related to changes in soil moisture (diffusion) and/or temperature (Ambus and Robertson, 2006; Groffman et al., 2006; Weslien et al., 2009; Wu et al., 2011). However, in some cases other factors may control the uptake, as Lavoie et al. (2013) could not find correlation between environmental parameters (air

temperature and soil moisture) and CH_4 fluxes. The largest mean value of methane emission occurred in September 2012, when measurements were taken in heavy rain. A decrease in CH_4 uptake and an occasional emission of CH_4 after heavy rain in upland soils has been found as well by Savage et al., (1997). A significant decrease in CH_4 uptake has also been shown to be caused by elevated annual precipitation (Wu et al., 2011). In the FAHM site, methane uptake was lower in years with lower air temperature, which may be due to reduced evapotranspiration leaving more water in the soil. Generally, humidification decreased methane uptake. Treatment effect was significant in 2009 and 2012 in both tree stands, also in 2010 and 2011 in aspen stands (t-test, $p<0.05$). However, in 2011 in birch stands, humidification effect was reversed; more CH_4 was consumed in humidified plots than in control plots (t-test, $p<0.05$). In 2011 the birch stand control plots were the driest among the study plots, suffering under severe drought. Extremely dry soil may inhibit methanotrophic activity and therefore depress methane uptake (Wu et al., 2011).

There were distinct differences between tree species in control plots in 2009 (birch stands had higher CH_4 uptake) and in 2014 (aspen stands had higher CH_4 uptake), in humidified plots in 2010 and 2011 (in both years birch stands had higher CH_4 uptake), and in both treatments in 2012 (aspen stands had higher CH_4 uptake, t-test, $p<0.05$). Tree growth affected soil water potential, which in turn controlled methane uptake. After the 2011 growing season, birches were harvested and aspens were left to grow for one year more; therefore, significant differences were expected. Tree species has been found to affect CH_4 uptake. For example, yellow birch was found to have higher CH_4 uptake than sugar maple (Groffman et al., 2006). Plant physiology influences additionally the availability of electron donors and acceptors in soils and may impact CH_4 flux (Megonigal and Guenther, 2008). Tree-species-specific differences in greenhouse gas (CH_4) fluxes could also be related to (methanogenic) archaeal community composition, affected by tree species (Bomberg et al., 2011). Also it has been found that methane emissions can come from the wood of living trees with a ratio of 1:160 between CO_2 and CH_4, which is approximately 4% of annual CH_4 emissions in North Eurasia (Mukhin and Voronin, 2011).

The results of this thesis correspond well with the basic knowledge that dry upland soils are overall net sinks of CH_4 (Del Grosso et al., 2000; Wuebbles and Hayhoe, 2002; Castaldi et al., 2006; Jang et al., 2006). However, upland soils may also contain anoxic microsites where CH_4 is produced (Jang et al., 2006). This is also one of the explanations for the sometimes positive CH_4 emissions in the FAHM site – fluxes to the atmosphere. Importance of dry soil oxidation of CH_4 is clear at global level – it makes up about 5% of the global CH_4 sink (Wuebbles and Hayhoe, 2002).

Nitrous oxide
Nitrous oxide emissions had high temporal and spatial variability but did not have a seasonal cycle (Publications I, III). Groffman et al. (2006) named N_2O fluxes „notoriously heterogeneous". However, the fluxes from young deciduous

forests in FAHM before and after clear-cut mostly remained small. Overall, during the six years of measurements, more than half of all the fluxes remained between -1.6 and 5.6 µg N m^{-2} h^{-1} in both treatments (humidification, control) and both tree stands. The highest variability of N_2O fluxes was found in control plots in aspen stands (from -120 to 120 µg N m^{-2} h^{-1}, Fig. 8) in 2011.

Elevated humidity significantly decreased nitrous oxide emissions compared to the control in aspen stands in 2010 (Wilcoxon test, $p<0.05$). However, in the other years control plots tended to have higher N_2O emissions than humidified plots in aspen stands, and over all measurement years the difference was significant (Wilcoxon test, $p<0.05$). Starting from 2011, control plots tended to have higher N_2O emissions compared to humidified plots in birch stands but the difference was not statistically significant.

Nitrous oxide fluxes did not have a clear correlation with the measured environmental variables. However, humidified treatment had significantly higher pH, lower organic matter (in aspen stand) and somewhat lower N values in the soil. Available N, soil organic carbon and soil pH have a strong influence on N_2O fluxes (Groffman et al., 2006), as soil nitrogen as well as soil organic carbon are substrates for nitrification and denitrification (Zhuang et al., 2012).

Soils in the FAHM site were sources of N_2O in a similar range as was found also in Gundersen et al. (2012), but during the measurement period several negative fluxes were also found. Soil N_2O uptake is nothing unusual but is often dismissed. Schlesinger (2013) found that almost all soils that have high N_2O uptake potential have small mean N_2O emissions. Generally, N_2O uptake is favored by low reactive N and high soil moisture, but there can be numerous processes responsible for N_2O uptake and therefore a wide range of condition may be suitable for uptake (Chapuis-Lardy et al., 2007). Soil organisms might be responsible for consuming half of the produced N_2O (Schlesinger, 2013). Sometimes the boreal conifer forest can even be a net sink of N_2O (Lavoie et al., 2013). The global median N_2O uptake by soils is 4 µg N m^{-2} h^{-1} (highest was 207 µg N m^{-2} h^{-1}), but the sink can be as high as 2 % of the source of N_2O from soil to atmosphere (Schlesinger, 2013).

High N_2O emissions can occur as peaks and are usually caused by strong disturbances such as heavy rain, fertilizer application and freeze-thaw events. In the case of the last disturbance, higher winter fluxes can come from reduced plant N uptake and increased N in the soil (Groffman et al., 2006). However, catching these peaks with manual static chambers is extremely difficult (Osborne et al., 2010). Also, Maljanen et al. (2002) found that N_2O fluxes had a diurnal variation, with up to 1.6-fold higher emissions in daytime than the daily average, which may cause an overestimation, as most of the manual chamber measurements are carried out in daytime.
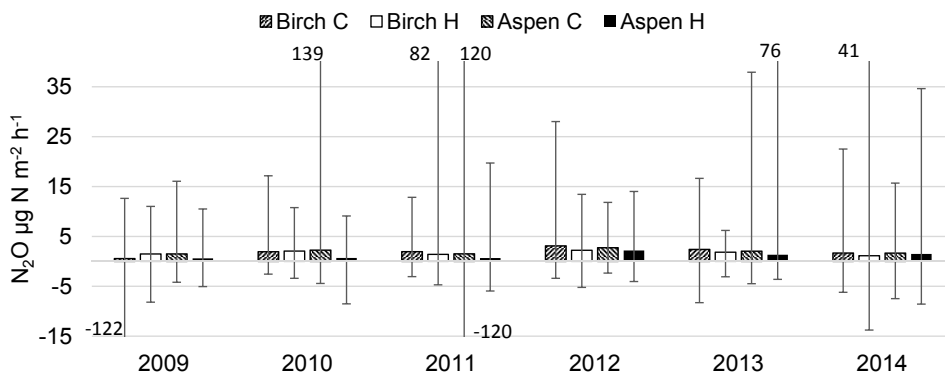
Figure 8. Median N_2O emissions from 2009 to 2014 in control (C) and humidified (H) plots in silver birch and hybrid aspen stands in the FAHM site. Error bars show the minimum and maximum values.

3.2. The effect of clear-cut on the soil in the Agali grey alder site

3.2.1. The effect of clear-cut on soil conditions

Soil temperature was significantly higher in the clear-cut than in the grey alder forest (t-test, p<0.01); the mean difference was 0.7 ºC, but soil moisture and pH were similar in both plots (Publication IV). Clear-cut has an effect on soil parameters. The most common changes are increased soil temperature and soil moisture (Zerva and Mencuccini, 2005; Wu et al., 2011). Clear-cut of boreal conifer forests increased the air temperature and soil moisture, but moisture rose in only half of the clear-cut sites (Lavoie et al., 2013); soil pH may increase after clear-cut as well (Kim, 2008).

3.2.2. The effect of clear-cut on soil greenhouse gas fluxes

The first soil greenhouse gas sampling was performed a half year after the clear-cut and continuous measurements were started one year after the clear-cut. Therefore the first and most rapid effects for CO_2, CH_4 and N_2O emissions are not included.

Carbon dioxide
Carbon dioxide had a typical seasonal cycle in 2012 and 2013. Most intense CO_2 fluxes occurred in the summer, being the highest in July 2012 and in June 2013. Soil CO_2 emission from the clear-cut varied between 11 and 399 mg C m^{-2} h^{-1} and fluxes from alder forest varied between 11 and 176 mg C m^{-2} h^{-1} (Fig. 9). Clear-cut plots had significantly higher CO_2 emissions compared to alder forest plots (means 109 and 69 mg C m^{-2} h^{-1} respectively, t-test, p<0.005). The disturbance enhances CO_2 emissions from litter and the soil carbon pool in

the first few years (Baldocchi, 2008). Kim (2008) found a positive effect of clear-cutting on soil CO_2 efflux in a pine forest. However, Zerva and Mencuccini (2005) showed that clear-cut may reduce CO_2 emissions, which was assumed to be the result of a rise in the water table and/or absence of living tree roots, resulting in the end of tree root respiration. In the Agali site, trees started to regenerate from stump sprouts and the root systems did not die, nor was the soil moister in the clear-cut plot, therefore the opposite effect of clear-cut on soil respiration is explicable. Soil temperature in peaty spruce forest explained up to 90 % of the CO_2 flux, but after clear-cut only up to 45 % (Zerva and Mencuccini, 2005).
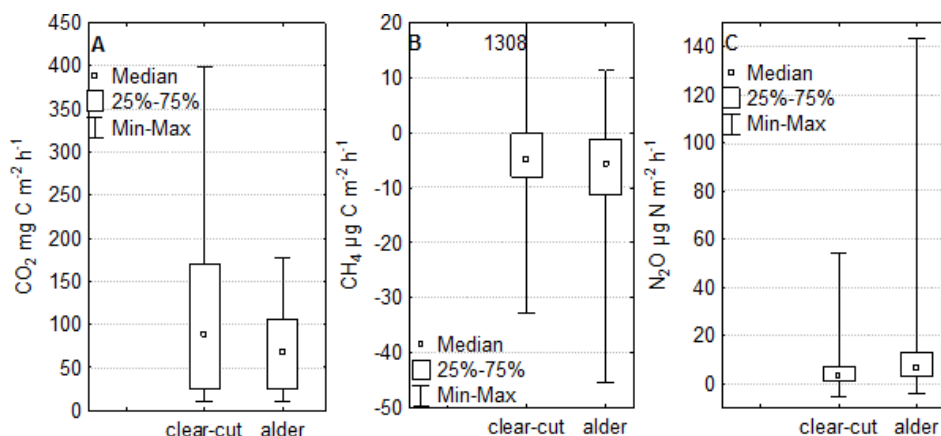

Figure 9. Soil CO_2 (A), CH_4 (B) and N_2O (C) fluxes from clear-cut and grey alder forest in Agali site in 2011–2013.

Methane
Methane emission from the clear-cut varied between -32.8 and 1307.7 µg C m^{-2} h^{-1} and fluxes from alder forest varied between -45.5 and 11.3 µg C m^{-2} h^{-1} (Fig. 9). The clear-cut had lower methane uptake than alder forest (Wilcoxon test, $p<0.005$). Wu et al. (2011) have also found that clear-cut has a negative effect on methane uptake in a temperate spruce forest. Harvest of trees may even turn a negative methane flux into a positive (Zerva and Mencuccini, 2005). However, selective cutting does not have significant impact on CH_4 fluxes (Wu et al., 2011). When temperate forest is situated on a slope, then the 30–40 % decrease in methane uptake after clear-cut may be partially attributed to disturbance and erosion of the soil (Kagotani et al., 2001). Wu et al. (2011) explained the lower uptake with higher soil moisture and higher N turnover rate. However, it does not explain the results in Agali, where the ground is level and soil moisture as well as soil chemical characteristics did not change.

Nitrous oxide

Nitrous oxide emissions from the clear-cut varied between -5.6 and 54.0 µg N m^{-2} h^{-1} and fluxes from the alder forest varied between -4.0 and 143.5 µg N m^{-2} h^{-1} (Fig. 9, Publications IV). Clear-cut significantly decreased nitrous oxide emissions compared to the alder forest (Wilcoxon test, p<0.05). The enzyme activities were analyzed in connection with nitrous oxide emissions, however, significant differences in N transformations were not revealed (Publication IV). Some studies about coniferous forest and the harvest have shown that clear-cut may have a positive (Takakai et al., 2008; Ullah et al., 2009) or an uneven effect (Lavoie et al., 2013), or no clear long-term effect at all (Zerva and Mecuccini, 2005; Tate et al., 2006) on nitrous oxide emission. The enhancement of N$_2$O emissions from the soil after clear-cut are often related to increased inorganic N in interaction with suitable soil moisture, i.e. more available N and an increase in soil moisture contributes to nitrification and denitrification processes (Page et al., 2011). Kellman and Kavanaugh (2008) conducted a vertical profile study that confirmed greater production of N$_2$O in post-harvest sites compared to mature forest, but clear-cuts also had high potential to act as sinks when diffusion in the soil decreased after harvest, and to mitigate the hazardous N$_2$O emissions. Nitrification was a complete process in both treatments: in the grey alder stand and in the clear-cut, and, as fluxes of N$_2$O were small, then denitrification may also have been a complete process. Tate et al. (2006) found peak N$_2$O just after harvest; Gundersen et al. (2012) found a maximum in the second year following the harvest, but more long-term observations are necessary to understand the duration of the effect of a disturbance on soil greenhouse gas emissions. Mature grey alder forest experienced a decrease in N$_2$O emissions after clear-cut but it is not known how long the drop will last.

4. CONCLUSIONS

This thesis provided results of six years of greenhouse gas flux measurements in a free-air humidity experiment with an average increase of 7 % in relative air humidity. Some results are provided on the effect of humidity manipulation on the understory and on tree biomass allocation and accumulation in association with greenhouse gas fluxes, and also on the effect of clear-cut on greenhouse gas emissions. All the set objectives were reached.

The first hypothesis that elevated humidity and tree species have an impact on greenhouse gas emissions was proved. However, the effect of humidification depended on the particular greenhouse gas and on weather conditions, therefore the impact may vary from a decrease to an increase in emissions. Also tree species affected the direction and the size of the impact of humidification on greenhouse gas fluxes. CO_2 emissions were mainly controlled by soil temperature. Soil temperature was predominantly not affected by humidification treatment, therefore other variables were responsible for mediating the effects of elevated humidity on CO_2 emissions. CO_2 emissions were not affected by humidification treatment in the second year of manipulation. In the third year, elevated humidity decreased CO_2 emissions compared to control plots in silver birch stands. After that, elevated humidity mostly increased CO_2 emissions in both tree stands. Methane uptake was usually inhibited by elevated humidity, as humidity treatment increased soil water potential, which was the main environmental factor controlling the methane flux. N_2O emissions were decreased by humidification treatment in hybrid aspen stands, but there was no significant treatment effect in silver birch stands.

   The greenhouse gas fluxes sometimes varied between silver birch and hybrid aspen stands. Hybrid aspen stands tended to have higher CO_2 emissions than silver birches before clear-cut, but vice versa after clear-cut. Differences were probably species-specific and due to different modes of stand establishment after clear-cut. Methane uptake was mostly higher in silver birch stands than in hybrid aspen stands as a result of lower soil water potential in the birch stands before clear-cut. Clear-cut affected methane uptake; clear-cut silver birch stands had lower CH_4 uptake than hybrid aspen forest. For N_2O, a tree-specific effect was only observed in respect to the reaction to humidity treatment.

The second hypothesis about the effect of heat waves and drought on soil CO_2, CH_4 and N_2O emissions was proved for CO_2 and CH_4. For N_2O emissions the effect remained unclear. Heat waves in an extremely warm summer with average precipitation increased CO_2 emissions, but an extremely warm summer combined with summer drought led to a substantial decrease in CO_2 emissions. The year-to-year uptake of methane was affected by the combination of temperature and precipitation, which affected soil moisture. Highest uptake occurred with an extremely warm and droughty summer. However, heat waves in summer and spring also increased methane uptake.

The third hypothesis about the effects of clear-cut on greenhouse gas fluxes was verified for CO_2 and CH_4 but not for N_2O. In the first years, clear-cut enhanced CO_2 emissions, decreased CH_4 uptake, and reduced N_2O emissions compared to mature grey alder forest.

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SUMMARY IN ESTONIAN

Suurenenud õhuniiskuse, ekstreemse ilmastiku ja lageraie mõju kasvuhoonegaaside voole kiirekasvulistes lehtmetsades

Kasvuhoonegaaside sisalduse kasv atmosfääris põhjustab kliimamuutusi, mistõttu on oluline teada: (i) kuidas ökosüsteemid muutuvates tingimustes käituvad ja (ii) mis mõju on ökosüsteemide kohanemisel kasvuhoonegaaside voogudele. Mitmed kliimamudelid, sh Valitsustevahelise Kliimamuutuste Nõukogu (IPCC) poolt kasutatavad, on 21. sajandi lõpuks ennustanud temperatuuri tõusu ja sademete hulga suurenemist Põhja-Euroopas, sh Eestis. Kliimamuutuste tõttu võivad sageneda ekstreemsed ilmastikunähtused nagu näiteks kuumalained, põud ja tugevad hoovihmad. Erinevad ökosüsteemid kohanevad kliimamuutustega erinevalt, mistõttu võib nende elujõulisus, levik ning ühtlasi roll süsiniku ja lämmastiku aineringetes muutuda. Metsad on kõige levinumad ökosüsteemid Põhja-Euroopas kattes näiteks Eestis 51 % maismaast, sellest tulenevalt on nende vastusreaktsioonid kliimamuutustele määrava tähtsusega. Seoses kliima soojenemisega on oodata lehtmetsade osakaalu suurenemist Eestis, mistõttu kasvab kiirekasvuliste lehtpuude roll taastuvenergia tootmisel. Kliimamuutuste leevendamisel on metsad olulised C salvestajad. Metsaökosüsteemid boreaalse ja parasvöötme mineraalmuldadel valdavalt seovad CO_2 ja CH_4 atmosfäärist mulda ja taimedesse ning emiteerivad väheses koguses N_2O, kuid märgade muldadega metsades võib toimuda oluline CH_4 ja N_2O lendumine atmosfääri. Ka süsihappegaasi sidumine majandusmetsades ei ole pidev, vahetult lageraie järgselt muutub ökosüsteem algselt süsiniku salvestajast emiteerijaks.

Kliimamuutuste mõju uurimine erinevatele maismaa ökosüsteemidele on järjest laienev uurimissuund. Seni on peamiselt keskendutud suurenenud CO_2 kontsentratsiooni, tõusnud temperatuuri ja suurenenud või vähenenud sademete hulga mõju väljaselgitamisele. Suurenenud õhuniiskuse mõju lehtmetsadele ja nende kasvuhoonegaasi voogudele on seni vähe uuritud. Ühtlasi mõjutavad kuumalained ja põud nii abiootilisi kui biootilisi tegureid, millel on otsene mõju kasvuhoonegaaside voole lehtmetsas. Nende toime vajab täiendavat analüüsi. Lageraie kui metsamajandamise üks etapp tekitab tugeva häiringu, mille mõju ega ka sellele järgneva metsauuenduse mõju kasvuhoonegaaside voogudele mullast atmosfääri pole piisavalt analüüsitud.

Loetletud mõjusid uuriti 2006. aastal rajatud Metsaökosüsteemi õhuniiskusega manipuleerimise eksperimendi katsealal (FAHM) Järvseljal (Rõkal), kus kiirekasvulises lehtmetsa ökosüsteemides suurendatakse suhtelist õhuniiskust keskmiselt 7 % ja 2011. aastal rajatud lageraie katseala Agalis. Katsealadele valiti kiirekasvulised, Eestile olulised lehtpuuliigid. Arukask on laia loodusliku levikuga Euraasias, olles ühtlasi majanduslikult üks olulisemaid lehtpuuliike Põhja-Euroopas. Hübriidhaab sobib kvaliteetse paberi tootmiseks. Hall lepp on puuliik, millel on lisaks kiirele kasvule võime parandada mullaviljakust. Kliimamuutuste ja lageraie katsed tehti noortes arukase (*Betula pendula* Roth.)

ja hübriidhaava (*Populus tremula* L. × *P. tremuloides* Michx.) puistutes ning täiendav lageraie katse küpses halli lepa (*Alnus incana* (L.) Moench) metsas.

Käesoleva doktoritöö peamiseks eesmärgiks oli analüüsida kliimamuutuste (suurenenud õhuniiskuse, kuumalainete ja põua) ja metsamajandamise (lageraie, metsauuendusviisi, puuliigi) mõju kasvuhoonegaaside voogudele kiirekasvulistes lehtmetsades.

Kitsamad eesmärgid olid:
(1) hinnata suurenenud õhuniiskuse mõju mulla kasvuhoonegaaside (CO_2, CH_4 ja N_2O) voogude dünaamikale noores kiirekasvulistes lehtmetsas;
(2) analüüsida ekstreemsete ilmastikutingimuste (kuumalainete ja põua) ja puuliikide mõju mulla kasvuhoonegaaside (CO_2, CH_4 ja N_2O) voogudele muutunud õhuniiskuse tingimustes;
(3) hinnata lageraie mõju mulla kasvuhoonegaaside (CO_2, CH_4 ja N_2O) voogudele küpses hall-lepikus.

Doktoritöös kontrolliti hüpoteese:
(1) suurenenud õhuniiskus ja puuliik mõjutavad kasvuhoonegaaside voogusid;
(2) kuumalained ja põud vähendavad CO_2 ja N_2O emissioone ja suurendavad CH_4 sidumist mulda;
(3) küpse hall-lepiku lageraie intensiivistab kasvuhoonegaaside vooge.

Doktoritöö põhineb kolmel artiklil ja ühel avaldamiseks esitatud käsikirjal. Artiklite I-III uuringud tehti FAHM-i noortes arukaasikutes ja hübriidhaavikutes ning IV artikli mõõtmised teostati Agali küpses hall-lepikus ja raiesmikul. Kasvuhoonegaaside (CO_2, CH_4 ja N_2O) voogusid mõõdeti suletud pimekambri meetodil kord kuus lumevabal ajal. Kasvuhoonegaaside voogusid ja dünaamikat seostati abiootiliste ja biootiliste keskkonnaparameetritega sh mullamikroobide aktiivsusega. FAHM arukase ja hübriidhaava katsevariantides mõõdeti täiendavalt puude ja alustaimestu biomassi jaotust puistute maapealses ja maa-aluses osas ning varisevoogusid mulda. Taimede biomassi jaotusest sõltub oluliselt autotroofne ja varisevoogudest heterotroofne mullahingamine.

Kõigil katsealadel oli CO_2 ja CH_4 voogudel selge sesoonne käik, CO_2 emissioon sõltus peamiselt temperatuurist ja CH_4 sidumine mullaniiskusest. Süsinikdioksiidi voo moodustab autotroofne ja heterotroofne hingamine, mille aktiivsused sõltuvad oluliselt temperatuurist. Soojem muld põhjustas intensiivsema CO_2 lendumise, mistõttu juulis (harva ka juunis või augustis) oli emissioon suurim ning varakevadel ja hilissügisel kõige väiksem. Talviste lumevaba aja mõõtmiste ja kirjanduse põhjal saab öelda, et talvised CO_2 vood on tühised. Kõik katsealad olid metaani sidujad, kusjuures suvel, kui mullaniiskus vähenes, suurenes CH_4 voog mulda. N_2O voogudel oli suur ajaline varieeruvus, suurimad väärtused mõõdeti valdavalt kevadel või hilissügisel, mil üheks emissiooni soodustavaks faktoriks oli niiskem muld. Selge aastaegadest tulenev N_2O voogude dünaamika puudus.

Suurenenud õhuniiskus mõjutas kõiki mõõdetud kasvuhoonegaaside vooge mullast atmosfääri arukaasikutes ja hübriidhaavikutes. Õhuniiskuse tõus muutis puude transpiratsiooni, veevahetust ja biomassi, mis omakorda mõjutas mulla-parameetreid. Viimased määravad sageli bioloogiliste protsesside kiiruse, mille tulemusel tekivad või seotakse mullas CO_2, CH_4 ja N_2O. Mullatemperatuur enamasti oluliselt ei erinenud niisutatud ja kontrollalal, kuid mulla veepotent-siaal oli enamasti oluliselt suurem niisutatud aladel.

CO_2 ja CH_4 gaasivood erinesid aastate vahel ning ka suurenenud õhuniiskuse mõju gaasi voogudele polnud ühesugune igal aastal. Teisel niisutamise aastal manipulatsioon ei mõjutanud CO_2 voogu. Järgneval, keskmiste sademetega väga kuumal suvel, niisutamine vähendas CO_2 voogu, kuid ainult arukaasikus. Kuumal ja põuasel suvel, 4 aastat peale niisutuskatse algust ning valdavalt ka järgneval kolmel aastal, soodustas niisutamine CO_2 voogu. Manipulatsiooni 3. aastal oli ebatavaliselt kuum vegetatsiooniperiood, mil oli kõige suurem aastane CO_2 emissioon, järgneval aastal oli kuuma ja kuiva koosmõju tõttu kuue mõõ-detud aasta kõige väiksem aastane CO_2 voog. CH_4 sidumine oli enamasti niisu-tuses väiksem kui kontrollis, sest seal oli muld niiskem. Kõige suurem aastane metaani sidumine toimus kuumal ja põuasel suvel. N_2O emissioon oli läbi aas-tate kontrollis suurem kui niisutuses, aga seda ainult hübriidhaavikus.

Arukask ja hübriidhaab käitusid erinevalt muudetud õhuniiskuse tingi-mustes. Mõlemad puuliigid kasvasid kehvemini suurendatud õhuniiskuse tingi-mustes, kuid hübriidhaab oli kasvult oluliselt väiksem. Hübriidhaavikus oli muld oluliselt märjem kui arukaasikus. Erinevus puuliikide kasvus võis olla põhjustatud mõnekuulisest istutamiseaja erinevusest ja/või geneetilise varieeru-vuse puudumisest hübriidhaaval. Arukask suutis 4 aastaga kohaneda muutunud keskkonnatingimustega, kuid hübriidhaava stress aja jooksul suurenes. 6-aastase hübriidhaava stressi suurendas ka põud, mille suhtes see puuliik on väga tund-lik. Kuna hübriidhaab oli väiksem ja selle all oli rohkem valgust, siis selle tule-musel oli hübriidhaava all 2 kuni 3 korda rohkem maapealset alustaimestikku võrreldes arukasega (niisutamise 3. ja 4. aasta). Maapealsed taimeosad mõju-tavad oluliselt autotroofset hingamist ja maapealne varis oli oluline substraat lagundajatele ning heterotroofsele hingamisele. Peale niisutamise 4. ja 5. aastat tehti vastavalt nii arukaasikus kui ka hübriidhaavikus lageraie. Peale raiet kased istutati katsealadele uuesti, kuid hübriidhaavad uunesid ise. Hübriidhaava all oli hingamine sageli suurem enne raiet. Juure- ja kännuvõsudest uunenud hüb-riidhaavad olid kiiremakasvulised kui istutatud kased ning peale raiet oli CO_2 voog suurem arukase all. Enne raiet oli metaani sidumine suurem arukaasikus, sest seal oli muld kuivem. Arukase raie vähendas oluliselt metaani sidumist võrreldes kasvava hübriidhaavikuga. Suurenenud õhuniiskuse mõju CO_2, CH_4 ja N_2O voogudele oli puuliigiti erinev.

Lageraie hall-lepikus mõjutas oluliselt kõiki mõõdetud kasvuhoonegaaside vooge. Esimesel ja teisel aastal peale raiet oli raiesmikul muld soojem, kuid ei mulla keemilised näitajad ega niiskus erinenud hall-lepikus ja raiesmikul. Raies-mikul suurenes oluliselt CO_2 voog, kuid N_2O emissioon ja CH_4 sidumine vähenesid.

Töö andis esialgse ülevaate tuleviku kliima ja metsamajandamise mõjudest kiirekasvuliste lehtmetsade kasvuhoonegaasi voogudele. Põhjalikumate järelduste tegemiseks peaksid edasised uuringud kaasama rohkem puuliike, olema sagedamad pikemate uurimisperioodide vältel. See võimaldaks saada suurema üldisuse astmega tulemusi kõigi muutujate dünaamika kohta ning anda praktilisi soovitusi metsade majandamiseks.

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First author conference presentations:

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- International Summer School, Flux measurement techniques for non CO_2 GHG: methods, sensors, databases and modelling, Poland, 2013
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- Osalemine rahvusvahelises suvekoolis, Measurements Methods in Environmental Biology, Eesti, 2013
- Osalemine rahvusvahelises suvekoolis, Summer school: Flux measurement techniques for non CO_2 GHG: methods, sensors, databases and modelling, Poola, 2013
- Osalemine rahvusvahelises kevadkoolis, Riparian Buffer Zones in Agricultural Catchments: Nutrient Cycling and Management, Eesti, 2010

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2013–2018   Globaalne soojenemine ja maastike aineringe. Maastike struktuuri ja funktsioonide muutused seoses globaalse kliima soojenemise ja inimtegevusega ning aineringe modelleerimine ja ökotehnoloogiline reguleerimine IUT2-16
2013–2016   Süsiniku ja lämmastikuringe muudetud veerežiimiga metsades

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