Methane exchange in a boreal forest: : the role of soils vegetation and forest management

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ELIN SUNDQVIST Methane exchange in a boreal forest

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The role of soils, vegetation and forest management

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Methane exchange in a boreal forest

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Abstract

Forests have a positive impact on the level of greenhouse gases in the atmosphere because they absorb carbon dioxide through photosynthesis and store carbon in the soil. Moreover, many forests function as a sink for the greenhouse gas methane (CH_4). The uptake of CH_4 takes place in well-aerated soils through oxidation by methanotrophic bacteria. However, there is a net production of CH_4 in anaerobic soils, such as submerged soils, by microorganisms, archaeans. CH_4 dissolved in ground water can be taken up by trees and discharged through stems or foliage. CH_4 can also be formed in green plants and emitted, which mainly occurs when plants are exposed to high UV radiation, high temperature, or if the foliage is damaged. The work in this thesis focus on the CH_4 exchange in a boreal forest, at the research station Norunda, in central Sweden. The aim is to quantify the net CH_4 exchange at the site and investigate what factors constitute the main control of the exchange in soil and vegetation. The impact of clear-cutting, stump harvesting and thinning on the CH_4 exchange was also studied.

Chamber measurements in undisturbed and thinned forest show that the soil is a sink of CH4. The uptake generally benefits from a large groundwater depth, low soil moisture and high temperatures. Chamber measurements on clear-cut and stump harvested plots show net emissions, which is associated with increased groundwater levels and increased soil moisture as a result of harvesting. Branch chamber measurements on shoots of spruce, pine, birch and rowan also show an uptake of CH4, which is in contrast to previous studies, mostly done in laboratories, which found net emissions from plants. Uptake by vegetation correlated with photosynthetically active radiation, which indicates a coupling to photosynthesis. Unlike our measurements on soil and vegetation, results from our micrometeorological measurements above the canopy showed net emissions from the forests to the atmosphere. These measurements represented a larger area than the chambers and differences could therefore be explained by large CH4 production in small wet areas, which exceeds the uptake in the rest of the soil. However, scaling of soil chamber measurements based on elevation data, indicate that the soil in the main study area was a sink of CH4 regardless of some minor areas with CH4 production. CH4 emissions from vegetation or transport of CH4 from surrounding source areas are other possible explanations for this discrepancy.

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Methane exchange in a boreal forest

The role of soils, vegetation and forest management

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A doctoral thesis at a university in Sweden is produced either as a monograph or as a collection of papers. In the latter case the introductory part constitutes the formal thesis, which summarizes the accompanying papers already published or manuscripts at various stages (in press, submitted or in preparation)

Cover photo by Elin Sundqvist: The Norunda forest

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Paper IV Sundqvist E, Persson A, Vestin P and Lindroth A. Upscaling of soil methane exchange in a boreal forest using chamber measurements and high-resolution LiDAR elevation data. *Manuscript.*

Contribution

Paper I ES was responsible for data analysis, led the writing of the manuscript and contributed to field measurements.

Paper II ES was responsible for data analysis, led the writing of the manuscript and contributed to field measurements.

Paper III ES was responsible for data analysis and writing of the manuscript. MM made flux-calculations and data processing. NK made footprint analyses.

Paper IV ES was responsible for upscaling of fluxes, led the writing of the manuscript, developed empirical model used for upscaling. AP generated topographic wetness indexes and water tables for the study area.

Sammanfattning

Skogar har en positiv inverkan på halten av växthusgaser i atmosfären eftersom de binder koldioxid via fotsyntesen och lagrar kol i marken. Dessutom utgör många skogar en betydande sänka för växthusgasen metan. Upptaget av metan sker i väl syresatta marker genom oxidation utförd av metanotrofa bakterier. Däremot sker en nettoproduktion av metan i syrefattiga skogsmarker när mikroorganismer, s.k. arkéer bryter ner organiskt material. Metan löst i markvatten kan tas upp i träd och sedan avges genom stammar eller bladverk. Metan kan också bildas i gröna växter och emitteras, vilket främst sker när växter utsätts för hög UV-strålning, höga temperaturer eller skador på bladverken. Avhandlingen fokuserar på metanutbytet i ett borealt skogsområde vid forskningsstationen Norunda i mellansverige. Syftet är att genom fältmätningar kvantifiera nettoutbytet av metan i skogen och undersöka vilka faktorer som utgör den huvudsakliga kontrollen av utbytet i mark och vegetation. Effekter av slutavverkning, stubbskörd och gallring på metanutbytet studeras också.

Kyvettmätningar på ytor i ostörd och gallrad skog visar att marken i Norunda är en sänka av metan. Metanupptaget gynnas generellt av ett stort avstånd från markytan till grundvattnet, en låg markfukt, och höga marktemperaturer. Kyvettmätningar på en slutavverkad och en stubbskördad yta visar däremot på nettoemissioner av metan från marken, vilket hänger samman med en höjd grundvattennivå och ökad markfukt till följd av avverkningen. Grenkyvettmätningar på skott av gran, tall, björk och rönn visar också på ett upptag av metan vilket står i kontrast till tidigare studier, mestadels utförda i laboratorier, som funnit nettoemissioner från växter. Upptaget i vegetationen korrelerar med det fotosyntetiskt aktiva ljuset vilket tyder på en koppling till fotosyntesen. Till skillnad från våra mätningar på mark och vegetation så visar resultat från våra mikrometerorologiska mätningar ovanför trädkronorna på nettoemissioner från skogen till atmosfären. Då dessa mätningar representerar ett större område än de ytor som kyvettmätningarna är gjorda på skulle skillnaden kunna förklaras med att metanproduktionen i små blöta områden är så hög att den dominerar upptaget i den övriga marken. En uppskalning av markmätningarna baserat på höjddata indikerar dock att marken i det centrala studieområdet är en sänka av metan trots en del mindre partier med produktion. Emissioner från vegetationen eller transport av metan från omkringliggande källområden är andra tänkbara förklaringar till skillnader mellan mätningarna.

Abstract

Forests have a positive impact on the level of greenhouse gases in the atmosphere because they absorb carbon dioxide through photosynthesis and store carbon in the soil. Moreover, many forests function as a sink for the greenhouse gas methane (CH_4). The uptake of CH_4 takes place in well-aerated soils through oxidation by methanotrophic bacteria. However, there is a net production of CH_4 in anaerobic soils, such as submerged soils, by microorganisms, archaeans. CH_4 dissolved in ground water can be taken up by trees and discharged through stems or foliage. CH_4 can also be formed in green plants and emitted, which mainly occurs when plants are exposed to high UV radiation, high temperature, or if the foliage is damaged. The work in this thesis focus on the CH_4 exchange in a boreal forest, at the research station Norunda, in central Sweden. The aim is to quantify the net CH_4 exchange at the site and investigate what factors constitute the main control of the exchange in soil and vegetation. The impact of clear-cutting, stump harvesting and thinning on the CH_4 exchange was also studied.

Chamber measurements in undisturbed and thinned forest show that the soil is a sink of CH_4. The uptake generally benefits from a large groundwater depth, low soil moisture and high temperatures. Chamber measurements on clear-cut and stump harvested plots show net emissions, which is associated with increased groundwater levels and increased soil moisture as a result of harvesting. Branch chamber measurements on shoots of spruce, pine, birch and rowan also show an uptake of CH_4, which is in contrast to previous studies, mostly done in laboratories, which found net emissions from plants. Uptake by vegetation correlated with photosynthetically active radiation, which indicates a coupling to photosynthesis. Unlike our measurements on soil and vegetation, results from our micrometeorological measurements above the canopy showed net emissions from the forests to the atmosphere. These measurements represented a larger area than the chambers and differences could therefore be explained by large CH_4 production in small wet areas, which exceeds the uptake in the rest of the soil. However, scaling of soil chamber measurements based on elevation data, indicate that the soil in the main study area was a sink of CH_4 regardless of some minor areas with CH_4 production. CH_4 emissions from vegetation or transport of CH_4 from surrounding source areas are other possible explanations for this discrepancy.

Contents

1. Introduction

Well-aerated forest soils play an important role in the global methane (CH_4) budget by acting as a net sink for atmospheric CH_4 through consumption by methanotrophic bacteria (Born et al., 1990; Crill, 1991). Boreal forests covers approximately one third of the Earth's forested land surface area and their influence on the CH_4 budget is therefore of high importance. Although boreal forests generally are considered net sinks of CH_4 (Saari et al., 2004; Whalen et al., 1992), a production by single-cell microorganisms called archaeans dominates the CH_4 exchange in anaerobic soils, such as submerged soils (Christiansen et al., 2012; Fiedler et al., 2005). CH_4 consumption and production rates depend on temperature and soil water conditions (Aronson et al., 2013), which make the CH_4 budget sensitive to climate change. This is of particular importance for boreal regions as temperature and precipitation are expected to increase more at higher latitudes (IPCC, 2013).

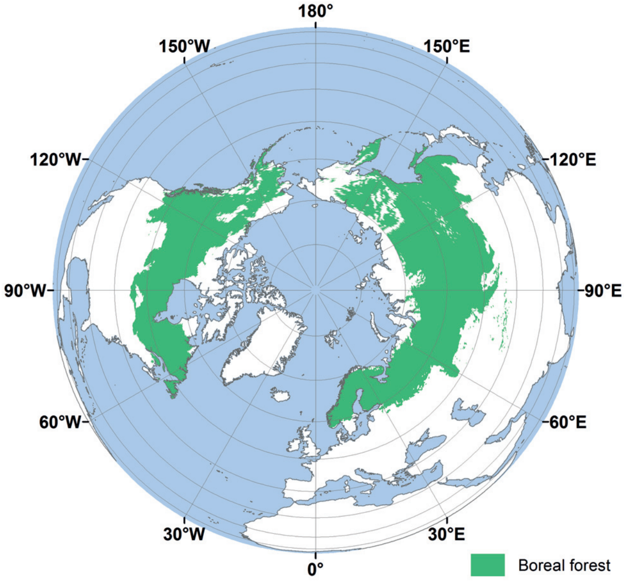

Figure 1. Map of boreal forests of the world (Hansen et al., 2010)

Boreal forests belong to regions with sub-arctic and cold continental climate, holding relatively few species of which most are conifers. Water bodies of different characters like bogs and shallow lakes are often scattered therein. Soils are rich on organic matter since decomposition is slow due to low temperatures (Burton et al., 2003). The heterogeneity of boreal forests soils and the strong seasonality causes spatial and temporal variability in CH_4 exchange. Clear-cuts is another important feature of boreal forests and their impact on hydrological and nutrient cycles may alter the CH_4 budget (Bradford et al., 2000; Castro et al., 2000). Adding to the complexity of CH_4 budget in forests, trees have been found to transport CH_4 in soil water which is released through the stem or foliage (Terazawa et al., 2007). Aerobic formation of CH_4 in green plants has also been observed (Keppler et al., 2006). However, it is still unclear to what extent these emissions affect the CH_4 budget of boreal forests.

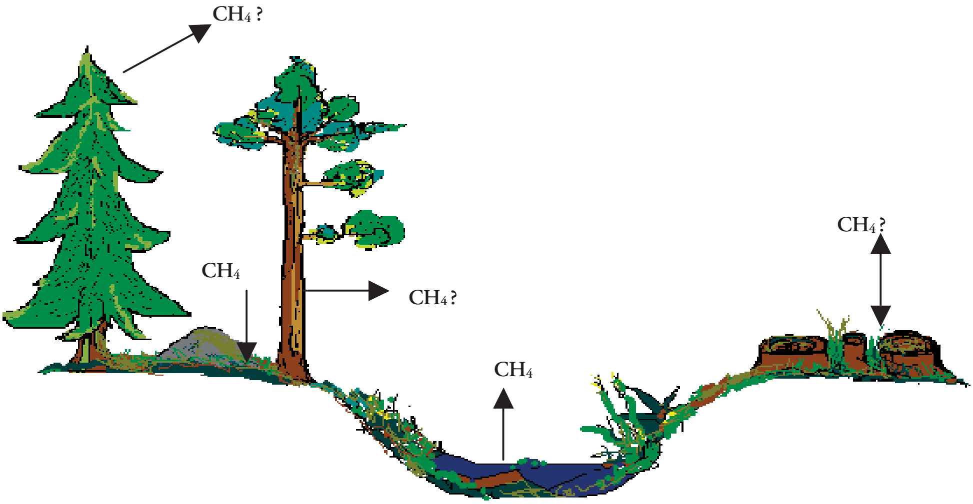

Figure 2. Well-known and potential sources and sinks of CH_4 in a boreal forest.

1.1 Global sources and sinks of CH_4

Globally, decomposition of organic material in wetlands is the largest natural source of CH_4, and accounts for 60-80 % of all natural emissions (Kirschke 2013). Other natural sources are termites, wild animals, oceans, geological sources, hydrates and wild fires. Anthropogenic sources, dominated by agriculture and fossil fuel exploitation accounted for 50-65 % of the global emissions during the decade of the 2000s (Ciais et al., 2013).

Compared to the number of CH_4 sources there are few CH_4 sinks. Oxidation by OH radicals in the troposphere and stratosphere is the major CH_4 sink responsible for about 90 % of the removal of CH_4 from the atmosphere (Ciais et al., 2013). The only net biospheric sink for atmospheric CH_4 is oxidation by methanotrophic bacteria in well-aerated soils, which represents only about 5 % of the global sink (Kirschke, 2013). Relatively dry and warm areas, such as semi-arid steppe and tropical savannah accounts for the largest soil uptake (Potter et al., 1996; Ridgwell et al., 1999). Other minor CH_4 sinks are reactions with chlorine radicals in the stratosphere and in the marine boundary layer (Kirschke, 2013). The different sources and sinks contributing to the global CH_4 budget are not yet well quantified (IPCC et al., 2007) and new sources of CH_4, for example vegetation (Keppler et al., 2006) and geological seepage of CH_4 (Etiope, 2010) are still discovered.

1.2 CH_4 in the atmosphere

CH_4 has a relatively short lifetime in atmosphere (12 years) because of its propensity to react with hydroxide (OH) radicals in the atmosphere (Reay et al., 2010). However, due to its efficiency in absorbing infrared radiation its global warming potential is 28 times that of CO_2 in a 100-year perspective (without inclusion of climate-carbon feedback) (Myhre et al., 2013). Besides direct climate forcing, CH_4 in the atmosphere also indirectly contributes to global warming by affecting concentration of ozone and stratospheric water vapor levels (Lelieveld et al., 1993). The atmospheric concentration of CH_4 is higher in the northern hemisphere (Dlugokencky et al., 1994) since the majority of all CH_4 sources are located there (Fung et al., 1991).

The atmospheric concentration of CH_4 increased rapidly due to industrialization from 830 ppb in 1850 to 1799 ± 2 ppb in 2010 (Kirschke, 2013). There was a temporal decline in growth rate of atmospheric CH_4 between 1997 and 2007 (Rigby et al., 2008), but the causes for this are unclear. Decreases in wetland sources (Bousquet et al., 2006), reduction in fossil fuel sources (Aydin et al., 2011), variations in atmospheric concentrations of OH radicals (Rigby et al., 2008) and reduced rice agriculture (Kai et al., 2011) are a few theories aiming to explain the observed decline.

1.3 Soil CH_4 exchange

CH_4 uptake by soil was discovered by Harriss et al, in 1982. The uptake rates in forest soils are generally higher than in grassland and arable land (Boeckx et al., 1997; Dutaur and Verchot, 2007) and conversion of natural forests to agricultural land is believed to have substantially decreased the global soil sink over the last 100 years (Ojima et al., 1993). CH_4 consumption is the result of methanotrophic bacteria combining oxygen and CH_4 to form formaldehyde from which they can gain energy and biomass (Mancinelli, 1995). The sink capacity of all soils types was recently estimated to 28 Tg CH_4 y^{-1} by a bottom up approach and 32 Tg CH_4 y^{-1} by a top down approach (Kirschke, 2013).

In wet soils, CH_4 production dominates the CH_4 exchange (Le Mer and Roger, 2001), but CH_4 production can also take place in well-aerated forests soils at anaerobic micro sites (Fischer and Hedin, 2002; Kammann et al., 2009) and in deeper soil layers where anaerobic conditions occur (Kammann et al., 2001). CH_4 produced in soils is an end product from decomposition of organic material in anaerobic environments. At first, organic compounds are degraded to H_2, CO_2, formate and acetate by fermentative and acetogenic bacteria. The formation of CH_4 from these substrates is then carried out by methanogens, which are single cell microorganisms belonging to the group Archea (Stams and Plugge, 2010). Methanogens are sometimes passively present in oxic soils, which means that an area can make a rapid shift from a sink to a source of CH_4 as soon as anaerobic conditions arises (Yavitt et al., 1995). Shifts from CH_4 sinks to sources have been observed in forest ecosystems following rainfall (Hudgens and Yavitt, 1997; Sakabe et al., 2012).

1.3.1 Soil CH_4 consumption

Soil diffusivity is an important factor controlling CH_4 oxidation in forest soils, since the uptake is often limited by the rate at which atmospheric CH_4 and oxygen is supplied to the bacteria. Most important is the molecular diffusivity in the air filled pore space of the soil, although diffusivity in soil water is also possible. Soil moisture (Billings et al., 2000; Gulledge and Schimel, 1998; Whalen and Reeburgh, 1996) and soil texture (Dorr et al., 1993; Dutaur and Verchot, 2007) therefore influence the rate of CH_4 oxidation by altering soil diffusivity. While a decrease in soil moisture generally leads to an increased CH_4 uptake by methanotrophs the microbial activitity can be limited by physiological water stress if the soil becomes too dry (Gulledge and Schimel, 1998). Temperature is not considered to be a major factor controlling CH_4 oxidation, but a positive correlation is generally found (Crill et al., 1994; King and Adamsen, 1992; Koschorreck and Conrad, 1993). N-fertilization might inhibit CH_4 consumption in forest soils with high N-concentration (Börjesson and Nohrstedt, 1998) whereas it has no long term effect in N-limited soils (Börjesson and Nohrstedt, 1998; Saari et al., 2004). The inhibition is due to competition for CH_4 by nitrifiers, which have an enzyme similar to methanotrophs and are able to oxidize CH_4 but at a lower rate (Hutsch et al., 1993). The highest CH_4 oxidation activity is often found in the mineral soil (Börjesson and Nohrstedt, 1998; Kahkonen et al., 2002; Saari et al., 1998), even though the concentration of CH_4 is higher closer to the soil surface. A possible explanation would be that the concentration of inhibitory compounds, like ammonium and nitrate, are higher near the soil surface (Schnell and King, 1994).

Methanotrophic bacteria are generally divided into two groups, high affinity methanotrophs able to consume CH_4 at low atmospheric concentrations and low affinity methanotrophs consuming CH_4 at high concentrations (Shukla et al., 2013). Low affinity methanotrophs are therefore found near source areas of CH_4 (Bender and Conrad, 1992) such as aerobic zones of bog soils where they consume much of the CH_4 produced by methanogens before it diffuses to the atmosphere (Mancinelli, 1995). Methanotrophs responsible for oxidation of atmospheric CH_4 are difficult to isolate from soil particles (Prieme et al., 1996) and are therefore poorly known.

1.3.2 Soil CH_4 production

Anaerobic condition is a prerequisite for soil CH_4 production, but once it occurs, other factors such as the availability of organic matter, soil temperature and water table depth control the CH_4 production. Input of organic material has been shown to enhance CH_4 production in several studies (Segers and Kengen, 1998) and the quantity and quality of the substrate seem to have a higher influence on CH_4 production rate than density of methanogens (Joulian et al., 1996). CH_4 production is more temperature dependent than CH_4 consumption (Dunfield et al., 1993), respiration and photosynthesis (Yvon-Durocher et al., 2014), with higher temperatures leading to higher CH_4 production. Changes in water table depth influence CH_4 production since it alters the relative extent of anaerobic and aerobic zones in soil (Kammann et al., 2001; Whalen and Reeburgh, 1990), but at a water table depth of 10 cm and above, other factors, such as temperature and substrate availability become more important (Christensen et al., 2003).

1.4 CH_4 exchange by plants

Keppler et al (2006) were first to report aerobic CH_4 emissions from living plants. These results attracted wide attention in the scientific community and were soon confirmed in several subsequent studies (McLeod et al., 2008; Messenger et al., 2009; Wang et al., 2008). Although a few studies did not find evidence for substantial emissions (Beerling et al., 2008; Dueck et al., 2007), the phenomenon is now widely accepted. The CH_4 emissions from foliage might stem from pectic methyl ester group in the cell wall of the plants. CH_4 is emitted when the pectic methyl ester groups are under influence of reactive oxygen species which in turn have been activated by UV radiation (Messenger et al., 2009), or other environmental stress factors like high temperatures (Vigano et al., 2008), or physical damage to plant tissue (Wang et al., 2009). Various extrapolations of plant emissions indicate that they are not of major importance for the global CH_4 budget (Bloom et al., 2010; Butenhoff and Khalil, 2007; Houweling et al., 2006).

Tree trunks can also emit CH_4 which originates from soil (Gauci et al., 2010; Pangala et al., 2013; Terazawa et al., 2007) or is produced in anaerobic environments within the stem, caused by fungus infection (Covey et al., 2012) or by wet heartwood (Zeikus and Ward, 1974). CH_4 originating from soil can reach the atmosphere dissolved in soil water by transpiration or possibly in gaseous form via mediation through internal air spaces in tree bodies (Terazawa et al., 2007).

The only well-understood uptake process of CH_4 in forest vegetation is consumption by Sphagnum spp. mosses by symbiosis with partly endophytic methanotrophic bacteria (Larmola et al., 2010; Raghoebarsing et al., 2005). Carbon dioxide (CO_2) produced from oxidation of CH_4 is then fixed to the plant during photosynthesis (Raghoebarsing et al. 2005).

1.5 Forest management impact on soil CH_4 exchange

Management practices in forests are mostly driven by wood demand (Carroll et al., 2012). In Sweden and many other boreal regions, clear-cutting is the most common form of forest management which leads to age-homogenous forest stands that are harvested every 50-150 years depending on species and climate (Skogforsk, 2011). In order to fully utilise the biomass potential in a harvested forest area, there is a growing interest for stump harvesting. Stump harvesting is expected to take place at 5-10 % of harvested area in Sweden, which results in an energy contribution of 1.3-2.6 Twh per year (Skogforsk, 2013). A clear-cut is expected to be a source of carbon during the first 10-30 years after harvest (Carroll et al., 2012). Relatively few studies have been made on forest management effects on CH_4 exchange and these studies focus on different management practices and different types of forests. It is therefore hard to draw any conclusions on, for example the impact of clear-cutting on the CH_4 budget in comparison to thinning. Several studies have reported a reduced net soil CH_4 uptake or shifts from soil CH_4 sinks to sources due to both clear-cutting (Bradford et al., 2000; Castro et al., 2000; Jen and Wu, 2008; Steudler et al., 1991; Zerva and Mencuccini, 2005) and thinning (Dannenmann et al., 2007; Keller et al., 2005; Thibodeau et al., 2000). A few studies observed no impact on CH_4 exchange by clear cutting (Huttunen et al., 2003) and thinning (Sullivan et al., 2008; Wu et al., 2011). Increased soil moisture (Castro et al., 2000), raised water tables (Zerva and Mencuccini, 2005), increased nitrogen availability (Bradford et al., 2000) and compaction of soil by machinery (Keller et al., 2005) are some of the causes for a reduced CH_4 uptake. So far there are no publications on the effects of stump-harvesting on CH_4 exchange.

1.6 Objectives

Various sources and sinks contribute to the CH_4 budget of forests, and CH_4 fluxes are known to vary both spatially and temporally. CH_4 exchange in forests is also sensitive to climate change and disturbances such as forest managemenent. The complexity of CH_4 exchange in forests is a challenge when CH_4 budgets are to be quantified. The main objectives of this PhD project were to:

* Quantify the CH_4 exchange at a boreal forest site (paper I-IV),

* Investigate the role of vegetation in the CH_4 budget of a boreal forest (paper II),

* Investigate the controls of spatial and temporal variability of CH_4 exchange in a boreal forest (paper I-IV),

* Investigate the impact of forest management on soil CH_4 exchange in a boreal forest (paper I).

2. Methodology

2.1 The study site

The in situ measurements that form the basis for this thesis were conducted at the Norunda research site, 60˚5 N, 17˚29 E, in central Sweden, 30 km north of Uppsala (Figure 2). The site is situated on the southern edge of the boreal zone. Climate records from Uppsala for 1980-2010 show an average annual air temperature of 6.5°C, and an average annual precipitation of 576 mm. 120 year old pine (*Pinus sylvestris*) and spruce (*Picea abies*) trees dominates the site, but some birch trees (*Betula pubescens*) can also be found. Ground vegetation consists mainly of bilberry (*Vaccinium myrtillus*) and feathermosses (*Hylocomium splendens and Pleurozium schreberi*). The soil is a glacial till, rich in stones and boulders (Lundin et al., 1999) and the depth of the organic soil layer is about 3-10 cm. The area is relatively flat with an elevation ranging from around 40 m - 52 m above sea level. Drainage of the area has been done several times which has resulted in a lowered water table. The last drainage of the area was done 1980.

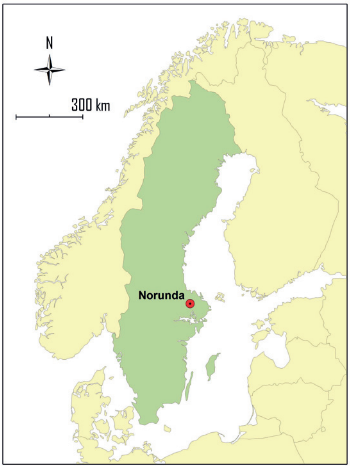

Figure 3. Map showing the location of Norunda in central Sweden.

The Norunda field station was established in 1994 with the primary goal to study forest atmosphere exchange of carbon and energy by micrometerological measurements in a 100 meter tower. Since 2012, Norunda site is part of the Integrated Carbon Observation System (ICOS), which is a European research infrastructure providing long term observations to better understand the greenhouse gas balance of the European continent. Norunda site is also part of the Integrated non-CO_2 Greenhouse gas observation system (InGOS), which focuses on monitoring the greenhousegases CH_4, nitrous oxide, sulphur hexafluoride, halocarbons and hydrogen.

Forest management has been carried out in the area for at least 200 years. The land cover in the SW to NE sectors surrounding the tower consists of forest which has not been thinned or fertilized in a few decades, while the forest in the NE to SW sectors were thinned in 2008 which decreased the leaf area index from 4.8 to 2.8 m^2m^{-2}. To the west of the tower, at a distance of about 500 m, there is a clear-cut area of about 6.5 hectars of wich about 2 hectar have been stump harvested. The thinning was done in November 2008, the clear-cutting in February 2009 and the stump harvesting in May 2010. Both the clear-cut and the stump-harvested area were mounded and planted in May 2010.

2.2 Overview of field work

CH_4 exchange was studied at Norunda forest site by gradient measurements above canopy in the 100 meter tower (Figure 4a), by soil chamber measurements at undisturbed and managed plots (Figure 4b), by branch chamber measurements of shoots from different tree species (Figure4c) and by a floating chamber on a small pond. All CH_4 concentration measurements were made with a laser gas analyser (LGR-Los Gatos Research). Fluxes measured by soil chambers were up-scaled to facilitate the comparison with gradient measurements, since gradient measurements represent a large area. The impact of forests management on CH_4 exchange was studied by soil chamber measurements on a thinned forest plot, on a clear-cut plot and on a stump harvested plot. Environmental variables such as soil and air temperatures, soil moisture, water table depth and radiation were also measured at the site so that their influence on the CH_4 exchange could be studied. Since only one gas analyser and one set of chambers were available for soil and branch chamber measurements, the setup was moved between the different plots. Timing of the different measurements are found in Table 1 and a map showing the different plots along with the Norunda tower is found in Figure 5.

Figure 4. Photos of Norunda tall tower (upper left), the branch chamber (upper right) and soil chambers at the thinned plot (bottom).

Table1. Description of measurements periods.

Time period	Method	Plot description
1 August 2009 -31 May 2010	4 soil chambers, 1 branch chamber, 1 floating chamber	Thinned forest
16 June 2010 - 31 December 2011	Gradients above canopy	Undisturbed and thinned forest
7 July - 4 October 2010	5 soil chambers, 1 branch chamber	Undisturbed forest
7 October - 20 October 2010	5 soil chambers	Stump harvested
21 October to 4 November 2010	5 soil chambers	Clear-cut

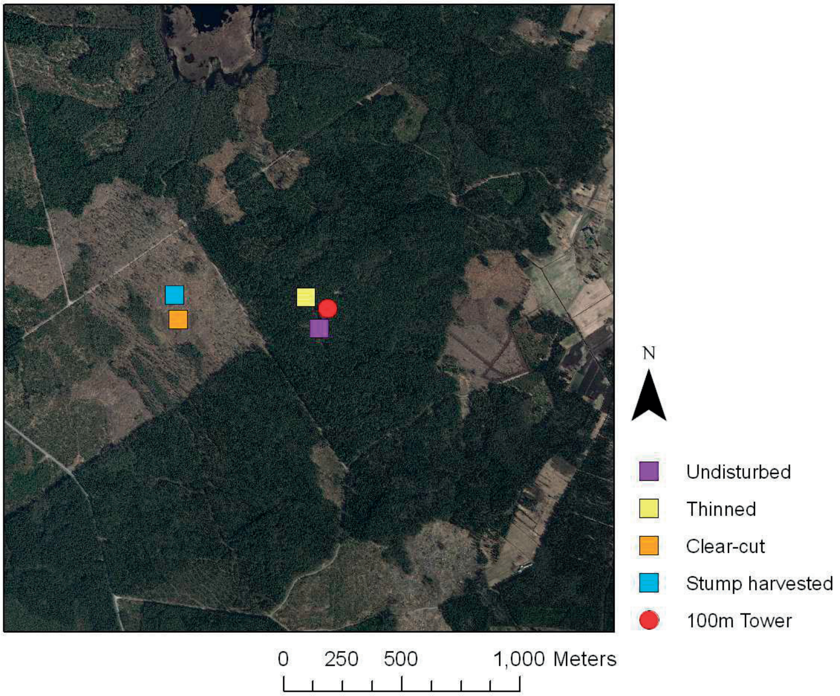

Figure 5. The different measurement plots and the 100m tower at Norunda site (Lantmäteriet, 2013).

2.3 Soil chamber measurements

Chambers are widely used for measuring soil CH_4 exchange since they are relatively inexpensive and easy to handle. They are useful for investigating spatial variability of soil CH_4 exchange and its site specific controlling factors (Livingstone and Hutchinson, 1995). A disadvantage is that they only cover a small soil surface area and since CH_4 exchange varies spatially the measurements might not be representative for a larger area and not even for a particular site (Denmead, 2008). Chambers are also criticized because they may interfere with the environment at the sampling plot, for example by altering the soil temperature or the soil evaporation rates (Denmead, 2008). Sometimes gas concentration inside the chamber changes so much in comparison to ambient air that it influences the fluxes (Davidson et al., 2002). Pressure fluctuations are another problem related to chamber measurements (Denmead, 1979).

We used closed dynamic chambers (Denmead, 2008) which means that the volume of the chamber is fixed and air is circulated between the chamber and the analyser so that the flux can be calculated from the rate of change in CH_4 concentration in the chamber headspace. In between the measurements the lid of the chambers were open. The chambers were automated, which enabled measurements once every hour. They had a volume of 110 liters and covered a surface-area of 0.2 m^2. During the measurements the air being sucked from the chambers to the analyzer is sent back to the chambers to avoid pressure changes and a fan is responsible for mixing of the air inside the chamber. Concentrationes were sampled every 2-10th seconds. Measured concentrations were corrected for dilution effects by water vapour. Due to the enclosed environment in a chamber, water vapor from evapotranspiration will cause an increase in water vapour concentrations and dilute the air so that CH_4 concentrations are underestimated, if not corrected for.

A linear model was used to describe the relation between CH_4 concentration and time. Since the concentration is measured as a dimensionless mixing ratio (ppm), it has to be converted to a per mole basis (µmol /m^3) using the ideal gas law. Thereafter CH_4 flux ($F_{CH4flux}$) can be calculated as $F_{CH4flux} = \frac{dC}{dt}\frac{V}{A}$, where F is the flux (µmol m^{-2} h^{-1}), C is the measured concentration (µmol /m^3), V (m^3) is the chamber volume, A (m^2) is ground surface-area and t is time.

Apart from CH_4 , the gas analyser also measured CO_2 and H_2O. Soil moisture and soil temperature were measured in the chambers, making it possible to study their influence on the CH_4 exchange. Soil moisture was measured at 0-5 cm depth with a Ml-2x ThetaProbe from DeltaT Devices while the soil temperature was measured at 5 cm depth using a type-T thermocouple.

2.4 Branch chamber measurements

A branch chamber was used to measure CH_4 exchange from shoots of spruce (*Picea abies*), birch (*Betula pubescens*), rowan (*Sorbus aucuparia*) and pine (*Pinus sylvestris*). Due to practical limitations, measurements could not be performed at the top of the canopy, but were instead made on branches near the ground and on smaller plants, but on relatively sunny locations. The functioning of the branch chamber is similar to the soil chambers in the way that changes of headspace concentration are measured after closure of the chamber by recirculating the air through the gas analyzer. Measurements were conducted once every hour for a 6 minutes time period with a measuring frequency of 0.1 Hz. In-between the mearuements periods the lid of the chamber was open to let ambient air in. The chamber had a volume of 5.7 litres and the leaf area of the enclosed shoots varied between 0.0019 m^2 and 0.031 m^2. Leaves and needles were not damaged by the measurements. The sides of the branch chamber exposed to the sun were made out of quartz glass, which is transparent to ultraviolet (UV) radiation. This was important since plant emissions are though to be stimulated by UV-radiation (Vigano et al., 2008). To avoid temperature changes inside the chamber during measurements a Peltier cooler was used, which kept air inside the chamber to within $\pm 1^{\circ}C$ of the ambient air. A fan was installed in the chamber to mix headspace air.

Air temperature, photosynthetically active radiation (PAR) and UV radiation were also measured within or nearby the chamber. Because of the strong correlation between radiation and temperature, under natural conditions, additional laboratory measurements were made on horticultural specimens of spruce and pine, which gave us the opportunity to examine the impact of one variable at a time.

2.5 Micrometeorological measurements

Micrometeorology broadly describes the exchange of mass and momentum between the land surface and the atmosphere and is generally applied to the 10% of the atmospheric boundary layer that is closest to the ground (Moncrieff et al., 1997). In contrast to chamber measurements, micrometeorological measurements can estimate the exchange of e.g. CO_2 and CH_4 for a larger forest area without disturbing the environment. Two main categories of micrometeorological methods exist, the eddy covariance (EC) method and the gradient method. For studies of net ecosystem CO_2 exchange between forest and atmosphere, gradient methods have been applied frequently since around 1970 while EC methods have been used since around 1990 (Baldocchi et al., 2001). However, CH_4 exchange is more challenging to measure in a forest due to the small magnitude of the fluxes (Nicolini 2013), so chambers are still the most common method for forest CH_4 exchange studies.

With the EC method the vertical transport of a gas can be measured directly. Parcels of air are transported in the atmosphere both horisontally and vertically by turbulent eddies of different sizes. The air parcels have a certain concentration of the gas of interest. By measuring with high frequency, often 10-20 times per second, how much of the gas is transported upwards and downwards along with the vertical wind speed, the net average flux can be calculated for a certain time period (Burba and Anderson, 2005). A sonic anemometer is usually used to measure the vertical wind speed while a fast response gas analyser measures the concentration of the gas.

While EC measurements are made at only one height, gradient measurements are made at two heights so that a concentration gradient can be calculated. Gradient methods are sometimes prefered over EC measurements beacause fast response analysers are not required. A drawback with measurements at two different heights is that the source area, which is the area that contributes to the measured concentrations, differ between the heights. If the forest is not homogenous the difference in source area at two different heights will influence the concentration gradient and hence the magnitude and maybe even the direction of the flux (Denmead, 2008; Meyers et al., 1996).

In this study two different type of gradient methods were used to measure the CH_4 exchange between the canopy and the atmosphere above; the combined EC and gradient method and the modified Bowen ratio method. Gradients were measured in Norunda tower between 31.7m and 58.5m and between 31.7m and 101.6m with the laser gas analyser. The combined EC and gradient method makes use of turbulent diffusivities obtained from EC mesurements at 33m height in the tower and the CH_4 exchange can be calculated as the product of the turbulent diffusivity and the vertical concentration gradient of CH_4 (Denmead, 2008). The modified Bowen ratio method assumes that turbulent diffusivites for scalars are similar. The CH_4 exchange F_{CH4} is calculated from EC measurements on CO_2 as $F_{CH_4(Bowen)} = F_{CO_2} \frac{\Delta C_{CH_4}}{\Delta C_{CO_2}}$ (Meyers et al., 1996).

2.6 Upscaling of soil chamber measurements

Upscaling of soil CH_4 exchange at the site was made using an empirical model based on chamber observations in combination with LiDAR ground elevation data. The upscaling was made for every square meter in a 100 hectar area surrounding Norunda tower. The empirical model was driven by soil temperature, soil moisture and water table depth. Since measurements of soil temperature at the site have shown to be relatively constant in space only temporal variations in temperature were accounted for. Spatial information of soil moisture and water table depth were estimated based on LiDAR elevation data. Airborne LiDAR for the Norunda site was acquired with support from the British Natural Environment Research Council (N. Kljun, pers. Comm 2014).

At first a topographic wetness index was derived from the LiDAR data. TWI is calculated as $TWI = \ln(A / \tan\beta)$, where A is the upslope area (m^2) being drained through the position of interest, and β is the slope angle at that position (degrees) (Beven and Kirkby 1979). TWI was then converted to soil moisture through a relationship found by linear regression between TWI and data on soil moisture mesaured at 12 locations in Norunda.

LiDAR data was also used to estimate spatial variation in water table depth. Since the water table is expected to roughly follow the ground surface at a larger scale, filtering of small scale variations in the topography left a smoothed surface that was assumed to represent the water table. This surface was adjusted with actual measurements of the water table depth at one position near the Norunda tower.

2.7 DNA-analyses of spruce and pine needles

CH_4 oxidising bacteria in the leaf or on the leaf surface could be an explanation of the CH_4 uptake measured by shoots of trees at Norunda (Holland and Polacco, 1994; Raghoebarsing et al., 2005; Van Aken et al., 2004). Possible also ammonia oxidising bacteria could help in this process since they have been found to consume CH_4 in soils (Hutsch et al., 1993). To investigate if these bacteria were present on pine and spruce needles at the study sites, 9 samples of each plant were sent for DNA analyses at the Department of Microbiology at the Swedish Uiversity of Agricultural Sciences in Uppsala. DNA were extracted from 0.3 g of each pine sample and 0.6 g of each spruce sample. The larger weight needed for the spruce needles were probably because they were drier than the pine. The FastDNA® Spin Kit for Soil and the FastPrep ® Instrument (MP Biomedicals, Santa Ana, CA) were used for the extractions. Abundances of methanotrophic bacteria and ammonia oxidizing bacteria were determined using real-time quantitative polymerase chain reaction (qPCR).

3. Results and Discussion

3.1 Quantification of CH_4 exchange

According to chamber measurements at the undisturbed and thinned forest plots, soils and vegetation are sinks of CH_4 (paper I, II), while gradient measurements above canopy indicate that the site as a whole is a net source of CH_4 (paper III). Upscaling of soil CH_4 exchange for a 100 ha area surrounding the tower where the gradient measurements were conducted indicates just like chamber measurements that the soil is a net sink of CH_4 (paper IV).

The undisturbed forested plot was on average a net soil sink of CH_4 of -10 µmol m^2h^{-1}, which was the same value shown by the upscaling (paper I, IV). The CH_4 sink at the thinned plot was reduced in comparison to the undisturbed sector to an average of -5 µmol $m^{-2}h^{-1}$ (paper I). These uptake values are of the same order of magnitude as reported by other forest soils (Jang et al., 2006; Smith et al., 2000). The one chamber location on shallow standing water showed average emissions of 40 µmol $m^{-2}h^{-1}$. According to gradient measurements the whole ecosystem, soil and vegetation, is a net source of CH_4 of 1.48 to 4.57 µmol $m^{-2}h^{-1}$, depending on which gradient method used for flux calculations (paper III).

Results from the in situ branch chamber measurements on shoots of spruce, pine, rowan and birch showed a significant average CH_4 uptake of 0.7 µmol $m^{-2}h^{-1}$ per unit of leaf area (paper II). This is in sharp contrast to other studies, although mainly laboratory studies, which has shown that green plants, also woody plants, can emit CH_4 (Keppler et al., 2009; Vigano et al., 2008; Wang et al., 2008). A simple upscaling by just multiplying the average value with the leaf area index, i.e., square meter of leaf surface per square meter ground surface, of the site gives a net uptake of -3.4 µmol $m^{-2}h^{-1}$, which is in the same order of magnitude as forest soils (Jang et al., 2006).

At the clear-cut and stump harvested plots the soil was a net source of CH_4 of 13.6 µmol $m^{-2}h^{-1}$and 13.1 µmol $m^{-2}h^{-1}$, respectively (paper I). However, a large spatial variation was found for the different chamber locations ranging from sinks of -2.9µmol $m^{-2}h^{-1}$ to sources of 53.8 µmol $m^{-2}h^{-1}$. The shift from CH_4 source to CH_4 sink is supported by combined eddy covariance and gradient measurements on CH_4

exchange which have been running in Norunda on two plots at the clear-cut area and two plots at the stump harvested area since May 2010 (Vestin et al., 2014).

3.2 Drivers of soil CH_4 exchange

According to soil chamber measurements at the undisturbed and thinned plots, the net CH_4 uptake generally increased with decreasing soil moisture, a lowered water table and increasing soil temperatures (paper I). This is consistent with existing literature. A decrease in soil moisture facilitates the diffusion of CH_4 and oxygen to the methanotrops (Whalen and Reeburgh, 1996), a lowered water table increases the impact of the methanotrophic oxidation zone in relation to the methanogenic production zone (Kammann et al., 2001) and increases in soil temperature stimulates the microbial activity (Born et al., 1990; Crill, 1991). Although the gradient measurements in general showed net emissions, they were decreased in late summer of 2010 and 2011 which could be due to decreased soil moisture and a lowered water table (paper III). Peak emissions shown by gradient measurements coincide with a high water table following precipitation in June 2010 and September 2010 and snowmelt in April 2011. According to soil chamber measurements it seemed like the impact of the different variables on the CH_4 exchange was dependent on the relatively dryness of the soil (paper I). The soil temperature influence was more pronounced during relatively dry time periods, for example in September 2010 at the undisturbed plot when there were no major precipitation events. Moreover, the soil temperature was in general more influential on the undisturbed plot than on the thinned plot which might be due to the on average higher soil moisture at the thinned plot that made CH_4 consumption to a larger extent limited by the diffusion rate of CH_4 and oxygen to the bacteria. A higher temeprature response at higher soil diffusivities was also found by Mosier et al., (1996). At two of the measurement locations on the thinned site, there was a shift from a net uptake to net emissions at a few occasions which were probably related to temporally higher soil moisture contents and water tables due to heavy rainfall and snowmelt (paper I). A rise in water table and an increase in soil moisture at the clear-cut and stump harvested plots as a result of a decreased evapotranspiration following harvest, were thought to be responsible for the shift from a net sink of CH_4 to a net source of CH_4. In October and November 2010 when soil chamber measurements were conducted at the clear-cut and stump harvested plot, the water table was on average more than 1m higher at these plots than at the undisturbed forest plot and the soil was almost saturated with water at many of the measurement locations (paper I). The recovery time for soil sink capacity of abondoned agricultural land can be more than 100 years (Prieme et al., 1997; Smith et al., 2000). One reason for this is that transpiration and interception increase with the age of the forest which results in dryer condititons on the forest floor, which in turn enhance the methanotrophic activity (Hiltbrunner et al., 2012). Other possible explanations for the slow recovery are the long time it takes for the soil structure to be restored (Prieme et al., 1997; Ruser et al., 1998) and the low growth rate of methanotrophs (Prieme et al., 1996). This reasoning can probably hold also for a clear-cut. The combined eddy covariance and gradient measurements on CH_4 exchange at the clear cut and stump harvested plots (Vestin et al., 2014) are expected to continue for at least a few more years. Results from these measurements can give an indication on the long-term effects of clear-cutting and stump harvesting.

3.3 CH_4 exchange by plants

The net CH_4 uptake by plants significantly increased with increasing levels of photosynthetically active radiation (PAR) for most of the plants studied in situ (paper II). Also, in laboratory, when keeping the air temperature fixed, a statistically significant correlation between PAR and CH_4 uptake was found. This indicates that there might be a coupling between CH_4 uptake and stomatal conductance. Stomatal conductance increases practically linearly with light at the range of PAR encountered in this study and CH_4 might diffuse in through the stomata of the leaves. The sink could then be positioned within the leaves, or the CH_4 could be transported downwards through the tree and be released through the trunk, or transported through the tree trunk to the soil the opposite way as found by other studies (Terazawa et al., 2007). One possible sink of CH_4 would be the presence of endophytic or epiphytic bacteria with the ability to consume CH_4 (Raghoebarsing et al., 2005; Van Aken et al., 2004). However, the DNA analyses of shoots of spruce and pine could not demonstrate the presence of methanotrophs or ammonium oxidisers. Diel pattern of the CH_4 exchange shown by gradient measurements, with minimum emissions in the afternoon that correlates with gross primary production (GPP) and vapour pressure deficit (VPD), support the CH_4 uptake by vegetation found by chamber measurements. The decreased emissions in the afternoon could be due to an increased soil uptake which was found by (Sakabe et al., 2012; Wang et al., 2013), but the soil CH_4 exchange measured by chambers in this study did not find a consistent diel pattern.

3.4 Sink or a source?

Is the Norunda site as a whole a sink of CH_4 or a source of CH_4? In several other studies where both soil chamber measurements and micrometeorological measurements were available, the results have been consistent (Querino et al., 2011;

Wang et al., 2013; Yu et al., 2013). One possible cause for the discrepancy at Norunda site between the uptake in soils and vegetation measured by chambers (paper I, II), and the emissions measured by gradients above canopy (paper III), can be large emissions from small source areas, such as ponds or bogs, within the footprint (Fiedler et al., 2005; Sakabe et al., 2012; Simpson et al., 1997). However, upscaling of the soil CH_4 exchange only showed net average emissions for 1.75 % of the 100 ha that the upscaling covered (paper IV). With the assumption that there is a net uptake of –10 µmol $m^{-2}h^{-1}$ in well aerated soils and emissions of 40 µmol $m^{-2}h^{-1}$ in wet soils, 20 % of the total area would have to be classified as wet for the site to shift from a sink to a source.

Although we measured a net uptake by shoots from different tree species (paper II) it can not be ruled out that vegetation contributes to the net emissions measured by gradients. It is possible that uptake and emissions by leaves occur simultaneously and depending on e.g. the UV level either one of the processes dominates the CH_4 exhange. In a laboratory experiment, Vigano et al (2008) found CH_4 emissions from the coniferous tree Pinus ponderosa that was exposed to UV irradiance. However, this is not consistent with the diel pattern shown by gradient measurements where CH_4 emissions peak at night when UV-radiation is low (paper III). Therefore, CH_4 formation in leaves is not likely to explain all the net emissions measured above canopy. Transport of CH_4 from soil water subsequently released through the trunks of the trees is another possible contribution to the emissions (Gauci et al., 2010; Terazawa et al., 2007).

It is possible that the footprint area for the gradient measurements (paper III) should be extended. This would result in that more of the clear-cut area, which has shown to be a strong CH_4 source, and possibly also areas with lakes and bogs, would contribute to the meaured emissions. The footprint refered to in this study is a flux footprint which is normally used for eddy-covariance measurements, but according to (Horst, 1999) it can also be used for gradient measurements. If, however, a concentration footprint is more suitable, the footprint would be extended (Vesala et al., 2008). Contribution from more distant source areas could also explain the diel pattern shown by gradient measurements. The contribution from these source areas would be larger at night than during daytime due to reduced turbulence at night.

3.5 Further research

Soil CH_4 exchange measurements at multiple locations would be valuable to get more information on the spatial variability of CH_4 exchange and to test how well the model manage to upscale the CH_4 exchange at the site. Four transects with in total 100 chamber frames each have recently been installed at Norunda site and are currently used for measuring CO_2 soil respiration. A portable system for measuring CH_4 exchange together with soil moisture and soil temperature will be introduced in summer 2014.

The role of vegetation for the CH_4 budget at the Norunda site, and for forests in general, is still an open question. CH_4 exchange by plants needs to be studied in situ at different locations, on different species and at different heights in the forest at Norunda site and elsewhere. It is of great interest to investigate if CH_4 uptake by plants can be confirmed at other sites. The CH_4 uptake process needs to be explained. A way to start would be to feed labelled CH_4 to plants and try to find out if it is allocated in the plants.

Another option to investigate the role of the canopy in the CH_4 exchange would be to utilize within-canopy profiles of CH_4 concentrations in combination with Lagrangian inverse modelling. This approach requires also turbulence measurements in the canopy for parameterisation of the air flow and the dispersion of air parcels (M. Mölder, pers. Comm 2014).

CH_4 exchange between tree trunks and the atmosphere at the Norunda site is another study area of interest. A pilot study by (Reinelt, 2013) was carried out on one pine and one spruce for one day in April 2013. Both emissions and uptake were measured. Fluxes were very small, -0.12 to 0.19 μmol $m^{-2}h^{-1}$, possibly below the flux detection limit of the analyser. It could not be excluded that any leakage of the chamber could have considerable impact on the fluxes. Improved measurement technology and measurements over longer time periods, including periods with warmer soils, would give more information about the importance of trunk emissions at Norunda site.

4. Conclusions

Contradictory results from chamber measurements on soils (paper I), vegetation (paper II) and gradient measurements above canopy (paper III) make it difficult to determine if Norunda site as a whole is a sink or a source of CH_4. According to chamber measurements well areated soils were sinks of -5 μmol $m^{-2}h^{-1}$ and -10 μmol $m^{-2}h^{-1}$ at the thinned and undisturbed forest plots respectively (paper I) and vegetation was a sink of CH_4 of -0.7 μmol $m^{-2}h^{-1}$ per unit of leaf area (paper II). Gradient measurements however indicated net emissions of 1.48 to 4.57 μmol $m^{-2}h^{-1}$ (paper III). The clear-cut and stump harvested plots were net sources of CH_4 (paper I) and it is possible that contributions of emissions from these areas can explain part of the discrepancy between chamber measurements and gradient measurements. Emissions from vegetation and source areas located further away from the tower, such as bogs and lakes, might also contribute.

Further studies on plant CH_4 exchange in the area is needed before any conclusions about the role of vegetation in the CH_4 budget can be drawn. Although we measured a net uptake by shoots of different trees, it is possible that CH_4 emissions from leaves or tree trunks occur simultaneously. If a net uptake by plants of the same order of magnitude as measured at Norunda site (paper II) were confirmed in subsequent studies, the sink capacity of plants would be comparable to that of the soil. No methanotrophic or ammonium oxidising bacteria was found during DNA analyses of spruce and pine needles. This indicates that CH_4 could be either physiologically incorporated into the plant or that CH_4 removed by leaves simply is transported down through the tree to the soil, or released through the tree trunk.

The variables whose influence on CH_4 exchange have been studied most intensively are soil temperature, soil moisture and water table depth (paper I, III, IV), all of which seem to be of importance for spatial as well as temporal variability of soil CH_4 exchange. Soil moisture and water table depth seem to be heirarchically superior to soil temperature (paper I). Increases in soil moisture and raised water tables can lead to temporal shifts from sinks to sources observed at the thinned forest plot, or more permanently shifts observed at the clear-cut and stump harvested plot (paper I).

The recovery time of the soil at the clear-cut and stump harvested plot might be several decades, but it is impossble to tell from this short term study. Increased soils moisture and raised ground water table as a consequence of clear-cutting are not unusual, and should be considered in the CH_4 budget of managed forests. In this study the effects of thinning on the CH_4 exchange were not as pronounced as the clear-cutting, although the net uptake was reduced in comparison to the undisturbed plot (paper I). Any forest management practice that reduces disturbance and leaves a continuous forest cover might be a better alternative from a global warming perspective.

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Paper I

Short-term effects of thinning, clear-cutting and stump harvesting on methane exchange in a boreal forest

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Abstract

Forest management practices can alter soil conditions, affecting the consumption and production processes that control soil methane (CH_4) exchange. We studied the short-term effects of thinning, clear-cutting and stump harvesting on the CH_4 exchange between soil and atmosphere at a boreal forest site in central Sweden, using an undisturbed plot as the control. Chambers in combination with a high precision laser gas analyser were used for continuous measurements. Both the undisturbed plot and the thinned plot were net sinks of $CH_{4,}$ whereas the clear-cut plot and the stump harvested plot were net CH_4 sources. The CH_4 uptake at the thinned plot was reduced in comparison to the undisturbed plot. The shift from sink to source at the clear-cut and stump harvested plots was probably due to a rise of the water table and an increase in soil moisture, leading to lower gas diffusivity and more reduced conditions which favour CH_4 production by archea. Reduced evapotranspiration after harvesting leads to wetter soils, decreased CH_4 consumption and increased CH_4 production, and should be accounted for in the CH_4 budget of managed forests.

1. Introduction

Methane (CH_4) is the second most important carbon greenhouse gas, with a radiative forcing at least 25 times higher than carbon dioxide from a 100-year perspective (Shindell, et al., 2009). Consumption of CH_4 by methanotrophic bacteria in the aerobic part of the soil profile (Harriss et al., 1982) and production of CH_4 by archaeans in the anaerobic water-saturated part of the profile (Ehhalt, 1974) and at anaerobic micro-sites (von Fischer and Hedin, 2002; Kammann et al., 2009) often occur simultaneously (Le Mer and Roger, 2001; Megonigal and Guenther, 2008). Generally, well-aerated forest soil is a net sink of atmospheric CH_4 (Van Amstel 2012). Consumption in soils is the second largest sink of CH_4 after tropospheric oxidation by hydroxyl radicals with a global sink capacity estimated recently at 28-32 Tg CH_4 y^{-1} (Kirschke et al., 2013). The soil sink capacity is higher in forest soils than in grasslands and arable land (Dutaur and Verchot, 2007), and therefore the global CH_4 budget is sensitive to disturbances in forests. Conversion of natural forests to arable land, increased N deposition from the atmosphere, and N-fertilization of agricultural lands are estimated to have reduced the global CH_4 soil sink by about 30 % between 1880 and 1980 (Ojima et al., 1993).

Disturbances, including forest management practices, can also have an impact on the soil CH_4 exchange by altering soil conditions such as soil moisture (Zerva and Menucuccini, 2005; Castro et al., 2000), water table depth (Zerva and Menucuccini, 2005) bulk density (Mojeremane et al., 2012), soil temperature (Zerva and Menucuccini, 2005; Thibodeau et al., 2000), nutrient content (Smolander et al., 1998) and pH (Smolander et al., 1998). CH_4 oxidation in soil has been observed to be controlled by diffusivity (Koschorreck and Conrad, 1993; Whalen and Reeburgh, 1996; Gulledge and Schimel, 1998). A well-drained coarse soil facilitates the exchange of oxygen and CH_4 between the atmosphere and the deeper soil levels where CH_4 is consumed (Verchot et al., 2000). By contrast, increased soil moisture and soil compaction reduce the diffusivity, and promotes anoxic environments in which CH_4 can be produced (Koschorreck and Conrad, 1993; Whalen and Reeburgh, 1996; Gulledge and Schimel, 1998). Changes in water table depth also influence the CH_4 exchange by altering the relative extent of anaerobic and aerobic zones in the soil (Whalen and Reeburgh, 1990). Temperature is also an important driver of CH_4 production, with higher temperatures leading to higher CH_4 production, while consumption by methanotrophs is less strongly enhanced (Dunfield et al., 1993).

Increased nitrogen content in the soil has been shown to inhibit CH_4 consumption in several studies (Steudler et al., 1989; Hutsch et al., 1993; Wang and Ineson, 2003). This is due to competition by certain nitrifiers, which might occupy the same niche in the soil. These nitrifiers have an enzyme similar to methanotrophs and are also able to oxidize CH_4, though possibly at a lower rate (Hutsch et al., 1993).

Summarizing the effects of forest management practices on CH_4 exchange is difficult since relatively few studies have been made on this topic, and they have covered a range of management practices, soil types and forests. However, several studies reported that clear-cutting led to reduced CH_4 uptake, possibly due to increased soil moisture (Wu et al., 2011), increased nitrogen availability (Steudler et al., 1991; Bradford et al., 2000), changes in pH, (Bradford et al., 2000) and erosion (Kagotani et al., 2001). A shift from soil CH_4 sink to soil CH_4 source has been reported due to a rise in water table depth combined with increases in substrate availability (Zerva and Mencuccini, 2005) and due to increases in soil moisture (Castro et al., 2000). The same shift from sink towards emission has been seen following soil compaction by skid trails and machinery, as a part of clear-cutting (Teepe et al., 2004) and thinning (Keller et al., 2005). One study on a clear-cut drained peat soil showed no substantial changes in CH_4 exchange (Huttunen et al., 2003).

Site preparation by mounding at clear-cuts can have a negative impact on CH_4 exchange from a climate perspective. In one study, compaction of the soil by excavators during mounding increased CH_4 emissions (Mojeremane et al., 2012). CH_4 emissions from stagnant water in hollows created during mounding can sometimes exceed the consumption in the mineral soil on top of the mounds (Mojeremane et al., 2010). However, bedding after clear-cutting has resulted in reduced CH_4 emissions (Castro et al., 2000). Drainage can also reduce CH_4 emissions following clear-cutting, but its positive effect on CH_4 emissions was outweighed by increases in CO_2 emissions when drainage was conducted on saturated peaty soils (Mojeremane et al., 2012).

Stump harvesting for bioenergy production has recently been proposed as a way of substituting fossil fuel CO_2 emissions in Sweden. To our knowledge there are no publications on the effects of stump harvesting on CH_4 exchange, although it is likely to have a similar effect to other clear-cutting and site preparation actions. There are a few studies on the effect of thinning on CH_4 exchange in a forest. Reduced CH_4 uptake due to increased nitrogen availability has been reported (Thibodeau et al., 2000). A study at three thinned plots in a temperate beech forest reported slightly reduced emissions at one plot, whereas the other two were not significantly different from the control plots (Dannenmann et al., 2007). Another study in a temperate forest actually showed an increased CH_4 uptake after thinning, as opposed to a decrease at two adjacent clear-cut areas (Bradford et al., 2000). Some studies found no significant changes in CH_4 exchange after thinning (Wu et al., 2011; Sullivan et al., 2008).

The objective of this study was to quantify the short-term CH_4 exchange at four sites: an undisturbed forest plot, a thinned forest plot, a clear-cut plot with stumps remaining, and a clear-cut plot with stumps removed. The comparison between the different treatments is facilitated because all four sites are within a defined area and have a common soil type. We also wanted to investigate how soil moisture, soil temperature and water table depths influenced the soil CH_4 exchange.

2. Methods

2.1 Site description

The CH_4 exchange measurements took place in a forested area on the southern edge of the boreal zoon, at Norunda research station in central Sweden, 60˚05 N, 17˚29 E. Hourly automated chamber measurements were made using a system that was moved between 4 differently managed plots. One plot contained undisturbed 120-year-old mixed pine (*Pinus sylvestris*) and spruce (*Picea abies*) forest, which had not been thinned or fertilized in several decades. The other three plots were recently (2009-2010) impacted by either thinning, clear-cutting or stump harvesting. Thinning was done in order to stimulate continuous forestry cover, rather than to increase growth.

Measurements were made using four chambers at the thinned plot, and five chambers at each of the other plots. The chamber locations were named U1-U5 at the undisturbed plot, T1-T4 at the thinned plot, C1-C5 at the clear-cut plot and S1-S5 at the stump harvested plot. At the clear-cut and stump harvested plots half of the chamber frames were positioned on bare soil, where organic and mineral soil layers were mixed. The disturbance was caused either by stump harvesting, or by site preparation to facilitate the establishment and growth of new plants. The remaining frames were placed on soil surfaces with intact vegetation. The clear-cut and stump harvested plots had been fertilized in 1976, 1988 and 1998.

Ground vegetation was sparse and dominated by bilberry (*Vaccinium myrtillus*) and feather mosses (*Hylocomium splendens* and *Pleurozium schreberi).* There were more shrubs and grass at the clear-cut site, following the soil's disturbance. The soil was a glacial till (Lundin et al., 1999) with an organic layer of 3-10 cm depth. For the period 1980-2010, the mean air temperature was 6.5 °C, and the mean annual precipitation was 576 mm (measured 30 km south of Norunda).

2.2 Timing of measurements

Thinning took place in November 2008, the clear-cutting in February 2009 and stump harvesting in May 2010. Both the clear-cut plot and the stump harvested plot were mounded and planted in May 2010. The chamber frames were installed in 2005 at the undisturbed and thinned plots, and in June 2010 at the clear-cut and stump harvested plots, to allow time for soil and vegetation to recover from the disturbance.

Due to equipment limitations, measurements were conducted at one plot at a time. Measurements at the thinned plot were made from 1 August 2009 to 31 May 2010, at the undisturbed plot from 07 July 2010 to 04 October 2010, at the stump-harvested plot from 07 October 2010 to 20 October 2010 and at the clear-cut plot from 21 October to 9 November 2010. Winter data at the thinned plot from 01 December 2009 to 14 April 2010 were not used in the analyses due to uncertainties in the measurements caused by snow and frost.

2.3 Equipment

We used automated, transparent chambers of Polymethyl methacrylate in combination with a high precision off-axis integrated cavity output spectroscopy (ICOS) laser gas-analyser (DLT-100, Los Gatos Research (LGR)) for simultaneous concentration measurements of CH4, CO2 and H2O. The chambers had a volume of 110 litres and covered a surface-area of 0.2 m2. Gas concentrations in the chambers were measured after closure by recirculating the air through the gas analyser for 6 min. The flow rate between chambers and manifolds was 8-10 l/min. This air stream was sub-sampled and passed through the analyser at a flow rate of 1.2 l/min. A fan was installed in each chamber, designed to ensure sufficient mixing of chamber headspace air without disturbing the laminar boundary layer at the ground. Soil moisture was measured in the chambers at 0-5 cm depth with a Ml-2x thetaProbe from DeltaT Devices. The soil temperature was measured at 5 cm depth inside the chambers using a type T thermocouple. Soil temperature measurements at the thinned plot did not work properly and so temperature data from the undisturbed plot, 125 meters away, was used instead.

2.4 Water table

There were differences in height between the chamber frames relative to the ground water table. One pipe with continuous measurements of the ground water table was located 125 m from the thinned plot and 30 meters from the undisturbed plot. The groundwater table at these plots was treated as horizontal. At the clear-cut and stump harvested plots, the ground water table was measured manually in seven pipes at each plot, on the 8th and 20th of October 2010 and 2nd of November 2010. An inverse distance-weighting model was used to calculate the height of the ground water table in relation to the ground surface for 40 m2 areas surrounding the chamber frames. The ground water table was also measured continuously at one position on the clear-cut plot.

2.5 Soil sampling

Soil samples were taken in order to determine carbon (C) and nitrogen (N) content and pH in the top 20 cm of the soil including the humus layer, where the chambers had been positioned. The litter layer was not taken into account. Sampling was done in November 2010 at the clear-cut and stump harvested plots and in September 2012 at the undisturbed and thinned plots.

At the clear-cut and stump harvested plots, humus layer samples were taken, down to the border between organic and mineral soil layers, using a 10 cm x 10 cm quadratic frame. The mineral soil was sampled with a 15.9 cm2 steel corer to a depth of 20 cm, but was subdivided in the field into 0-10 and 10-20 cm layers. Humus samples were treated individually, while the mineral soil samples were pooled plot-wise for each soil layer. The samples, folded in plastic bags, were transported in cooling boxes to the laboratory, where they were kept fresh at 4-5°C during the preparation process before the final analyses. Soil samples were passed through either a 5 mm (humus samples) or a 2 mm (mineral soil) mesh. Stones and gravel >2 mm diameter not passing the mesh was always rejected, as were any roots. The sieved soil material from each sample was carefully mixed and divided into a number of sub-samples for determination of soil pH (H_2O), and total C and N content. Fresh weight/dry weight ratios were determined after drying the sub-samples at 105 °C for 24 h. Soil layer pH was determined with a glass electrode in the supernatant after shaking for 2 h on a rotary shaker, and sedimentation in an open flask for another 22 h. The proportion of fresh soil to distilled water was 1:1 by volume, compared to about 1:10 for dry matter to water for humus, and 1:2.5 for mineral soil). Total C and N content were determined, using vacuum-dried soil samples at 60 °C for 24 h, in a Carlo-Erba NA

1500 Analyser. Because soil pH was always below 6, we assumed that there was no carbonate C, and all C analysed was assumed to be organic C.

At the undisturbed and thinned plots a cylindrical metal corer with an 11 cm2 opening was pressed horizontally into the humus layer, and also at 5 cm and 10 cm depth in the mineral layer. At some of the measurement locations (T1, T4, U2, U6) large stones, rocks and roots occupied a large volume of the mineral soil so that sampling at 10 cm depth in the mineral soil was not possible. The soil samples were kept below 5°C until they were analysed. The total amount of C and N in the soil samples was analysed with an element analyser (Elementar Analysensysteme GmbH, Germany). The pH value was measured after two hours equilibration with a 0.1 M barium chloride solution (Orion Research model Microprocessor ionalyzer/901). The extractions were made on fresh material. Before determining the bulk density, the samples were oven dried for 48 hours at 100 °C and then sieved through a 2 mm mesh.

2.6 Data analyses

The rate of change of CH_4 concentration (dC_CH_4/dt) within the chamber was calculated using a linear fit to the first two minutes of concentration data measured by the gas analyser, beginning immediately after chamber closure. We calculated the r^2 values for the fits of five different slopes, which were lagged at 10 seconds intervals after chamber closure. The fit with the highest r^2 value was then selected. The CH_4 flux ($J_{CH4flux}$) was calculated as $J_{CH4flux} = \frac{dC}{dt}\frac{V}{A}$, where C is the molar density (µmol m^{-3}), V (m^3) is the chamber volume and A (m^2) is ground surface area. All fluxes with an r^2 value higher than 0.3 and a root mean square error less than 0.1 were kept for further analyses. This corresponded to 99 % of the data at the undisturbed plot, 97 % of the data at the thinned plot, 82 % of the data at the clear-cut plot and 73 % of the data at the stump harvested plot. Correction of the measured CH_4 concentrations for dilution by water vapour was only possible at the undisturbed, clear-cut and stump harvested plots after water vapour measurements started in June 2010. This means that daytime data (global radiation > 20 W/m^2) from the thinned plot had to be excluded from the analyses. During night the dilution effect had very little impact. The impact of the environmental variables on CH_4 exchange was analysed by Spearman linear correlations using the corr function, and by multilinear regression on standardized data using the function stepwisefit (both Matlab version R2009b). The significance of mean values at the measurement locations was calculated with the ttest function (also Matlab version R2009b).

3. Results

3.1 Environmental conditions

There were differences in soil moisture and soil temperatures among the plots. On average the undisturbed forest plot, with measurements exclusively from the summer season, July through September, had the driest and warmest records, and also the measurement locations were further above the ground water table than at other plots (Fig.1, Table 1). The clear-cut plot, which was measured in October and November, showed the coldest and wettest conditions including the highest water table. Four of the five measurement locations at this plot were on average less than 15 cm above the ground water table (Fig.1, Table 1). The thinned plot and the stump harvested plot had similar average moisture and temperature conditions, but the measurements at the thinned plot proceeded over a longer time period and thus the conditions varied more. The thinned plot also had a generally lower ground water table than the stump harvested plot (Fig.1, Table 1). Soil N and C content and pH were higher at the clear-cut and stump harvested plots than at the undisturbed and thinned plots (Table 1).

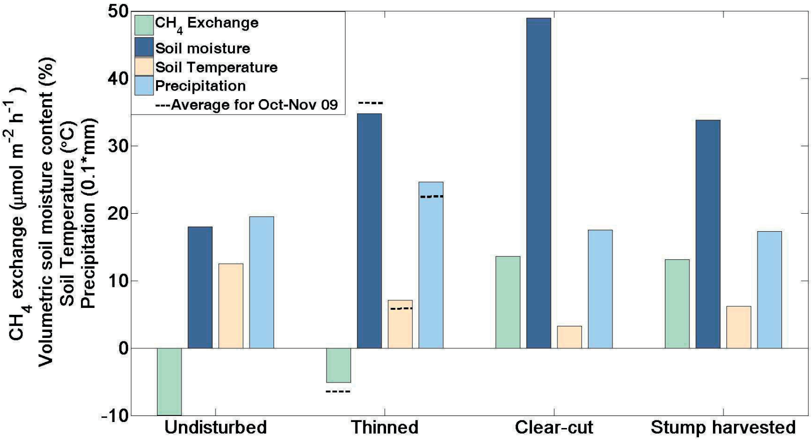
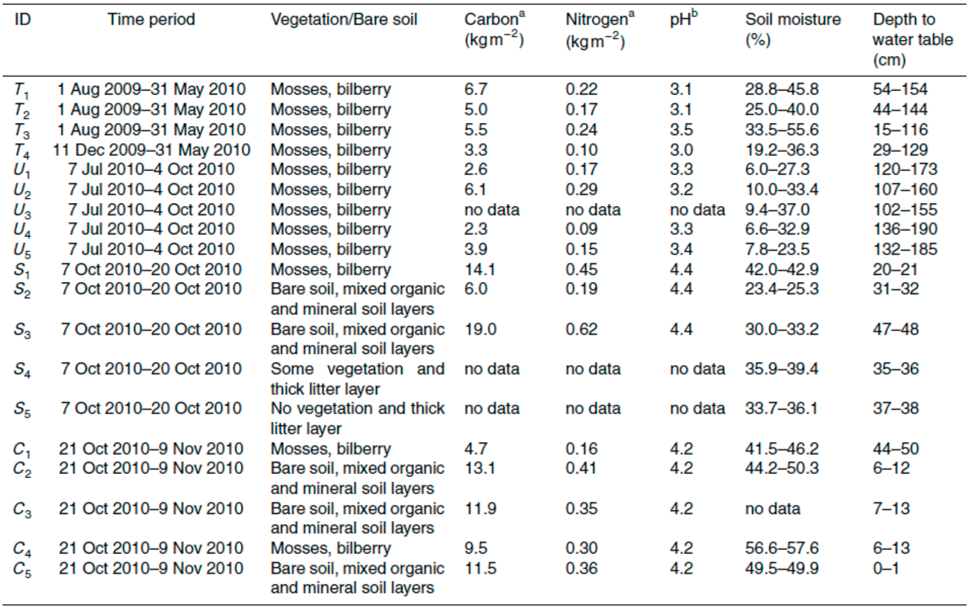


Fig.1. Average CH_4 exchange rates, soil moisture and soil temperature at the four sampling plots. Data from the entire measurement period at each plot is included. The dashed line at the thinned plot represents average values for October and November, since measurements at the clear-cut and stump harvested plots were conducted during this part of the year.

Table 1. Information regarding vegetation, C and N pool, pH, soil moisture (5th and 95th percentiles) and depth to water table at the individual chamber locations. Chamber locations were named U1-U5 at the undisturbed plot, T1-T4 at the thinned plot, C1-C5 at the clear-cut plot and S1-S5 at the stump harvested plot.

a) C and N pool to a depth of 20 cm in the mineral soil (litter layer excluded).

b) pH (BaCl2) for the undisturbed and thinned plots and pH (H2O) for the clear-cut and stump harvested plots were measured at 0-10 cm depth in the mineral soil.



ID	Time period	Vegetation/Bare soil	Carbon[a] (kgm^{-2})	Nitrogen[a] (kgm^{-2})	pH[b]	Soil moisture (%)	Depth to water table (cm)
T_1	1 Aug 2009–31 May 2010	Mosses, bilberry	6.7	0.22	3.1	28.8–45.8	54–154
T_2	1 Aug 2009–31 May 2010	Mosses, bilberry	5.0	0.17	3.1	25.0–40.0	44–144
T_3	1 Aug 2009–31 May 2010	Mosses, bilberry	5.5	0.24	3.5	33.5–55.6	15–116
T_4	11 Dec 2009–31 May 2010	Mosses, bilberry	3.3	0.10	3.0	19.2–36.3	29–129
U_1	7 Jul 2010–4 Oct 2010	Mosses, bilberry	2.6	0.17	3.3	6.0–27.3	120–173
U_2	7 Jul 2010–4 Oct 2010	Mosses, bilberry	6.1	0.29	3.2	10.0–33.4	107–160
U_3	7 Jul 2010–4 Oct 2010	Mosses, bilberry	no data	no data	no data	9.4–37.0	102–155
U_4	7 Jul 2010–4 Oct 2010	Mosses, bilberry	2.3	0.09	3.3	6.6–32.9	136–190
U_5	7 Jul 2010–4 Oct 2010	Mosses, bilberry	3.9	0.15	3.4	7.8–23.5	132–185
S_1	7 Oct 2010–20 Oct 2010	Mosses, bilberry	14.1	0.45	4.4	42.0–42.9	20–21
S_2	7 Oct 2010–20 Oct 2010	Bare soil, mixed organic and mineral soil layers	6.0	0.19	4.4	23.4–25.3	31–32
S_3	7 Oct 2010–20 Oct 2010	Bare soil, mixed organic and mineral soil layers	19.0	0.62	4.4	30.0–33.2	47–48
S_4	7 Oct 2010–20 Oct 2010	Some vegetation and thick litter layer	no data	no data	no data	35.9–39.4	35–36
S_5	7 Oct 2010–20 Oct 2010	No vegetation and thick litter layer	no data	no data	no data	33.7–36.1	37–38
C_1	21 Oct 2010–9 Nov 2010	Mosses, bilberry	4.7	0.16	4.2	41.5–46.2	44–50
C_2	21 Oct 2010–9 Nov 2010	Bare soil, mixed organic and mineral soil layers	13.1	0.41	4.2	44.2–50.3	6–12
C_3	21 Oct 2010–9 Nov 2010	Bare soil, mixed organic and mineral soil layers	11.9	0.35	4.2	no data	7–13
C_4	21 Oct 2010–9 Nov 2010	Mosses, bilberry	9.5	0.30	4.2	56.6–57.6	6–13
C_5	21 Oct 2010–9 Nov 2010	Bare soil, mixed organic and mineral soil layers	11.5	0.36	4.2	49.5–49.9	0–1

3.2 CH_4 exchange

The mean CH_4 exchange of all measurement locations within the plots were as follows: the undisturbed plot and the thinned plot were net CH_4 sinks of -10 μmol m^{-2} h^{-1} and -5 μmol m^{-2} h^{-1} respectively, while the clear-cut plot and at the stump harvested plot were net sources of 13.6 μmol m^{-2} h^{-1} and 13.1 μmol m^{-2} h^{-1}, respectively (Fig.1). However, the CH_4 exchange varied within the plots. At the clear-cut and stump harvested plots, both net sources and net sinks existed (Fig.2). Plot T_3 and T_4 at the thinned plot shifted between net daily CH_4 sinks and net daily CH_4 sources on a few occasions (Fig.3b). Fluxes ranged from -7.2 to -11.4 μmol m^{-2} h^{-1} at the undisturbed plot, from -0.3 to -8.6 μmol m^{-2} h^{-1}at the thinned plot, from -2.9 to 29.6 μmol m^{-2} h^{-1}at the clear-cut plot and from -2.8 to 53.8 μmol m^{-2} h^{-1} at the stump harvested plot (Fig.2). The measurement locations at the managed plots showed a large variability in CH_4 exchange ranges and temporal behaviour (Fig.3b-3d). The measurement locations at the undisturbed plot were consistently CH_4 sinks throughout the measurement period (Fig.3a).

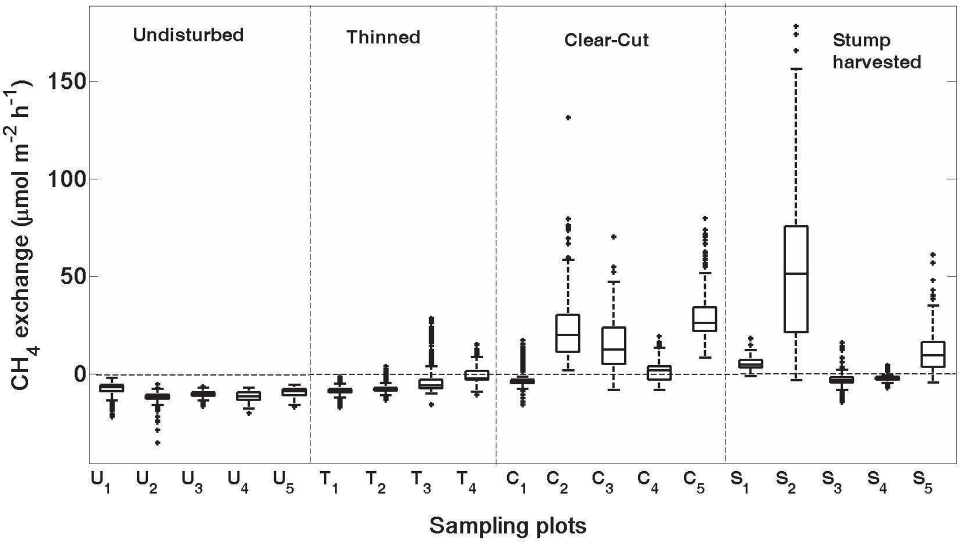
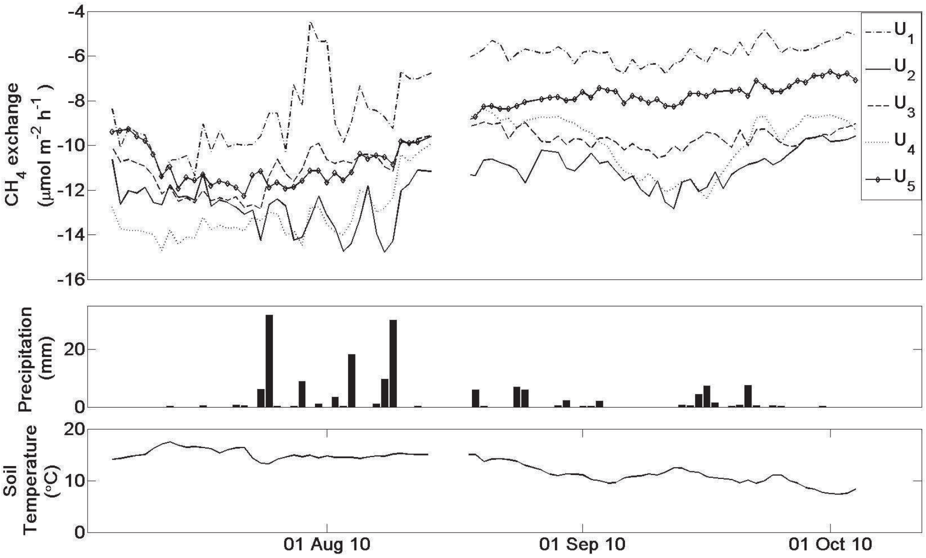
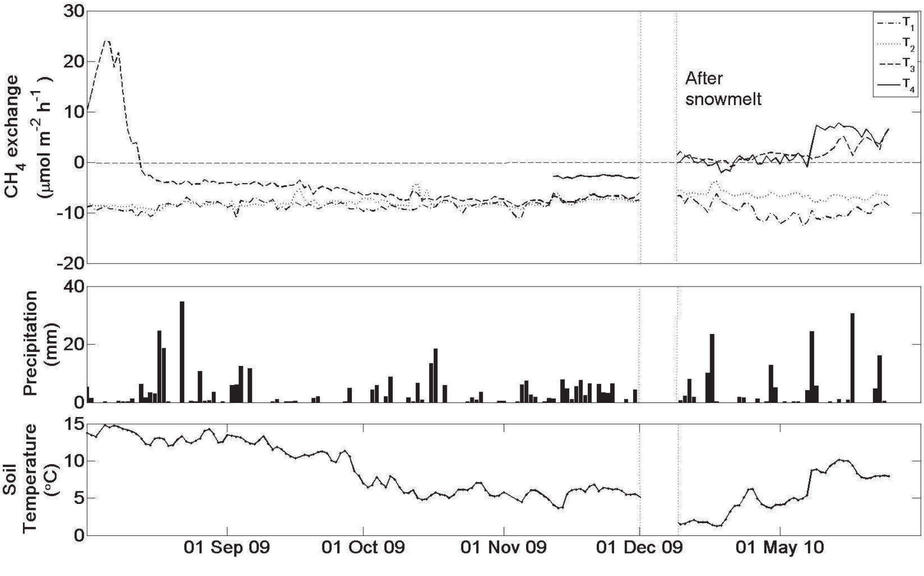


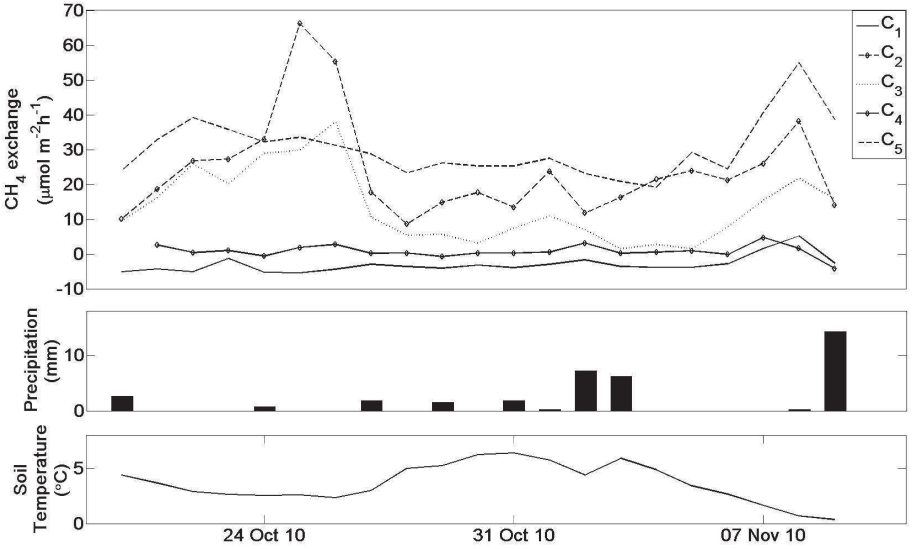
Fig.2. Boxplots of CH_4 exchange (µmol m-2 h-1) at all individual measurement locations. The middle line of the box and whisker plot represents the median of all recordings including night-time measurements. The edges of the box are the 25th and 75th percentiles, the whiskers, (black dotted lines) are the extreme values not considered outliers. Values larger than q3 + w (q3–q1) or smaller than q1–w (q3–q1) are considered outliers, where q1 and q3 are the 25th and 75th percentiles, respectively, and w = 1.5 is the whisker length. The median values are all significantly different from zero at the 99% significance level except for T4, which is significant at the 95% significance level.


-4
-6
-8
-10
-12
-14
-16
CH4 exchange (μmol m-2 h-1)
U1
U2
U3
U4
U5
Precipitation (mm)
20
0
Soil Temperature (°C)
20
10
0
01 Aug 10
01 Sep 10
01 Oct 10

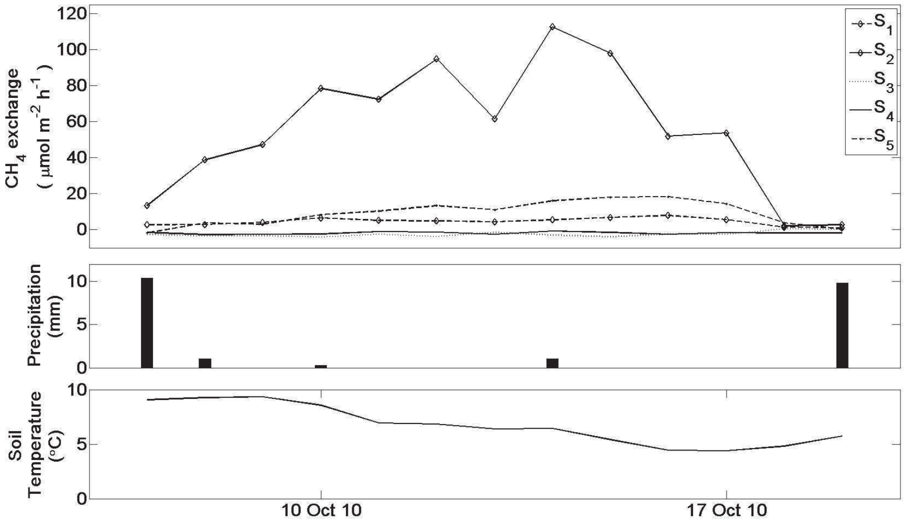
3a)


30
20
10
0
-10
-20
CH4 exchange (μmol m-2 h-1)
T1
T2
T3
T4
After snowmelt
Precipitation (mm)
40
20
0
Soil Temperature (°C)
15
10
5
0
01 Sep 09
01 Oct 09
01 Nov 09
01 Dec 09
01 May 10

3b)



3c)



3d)

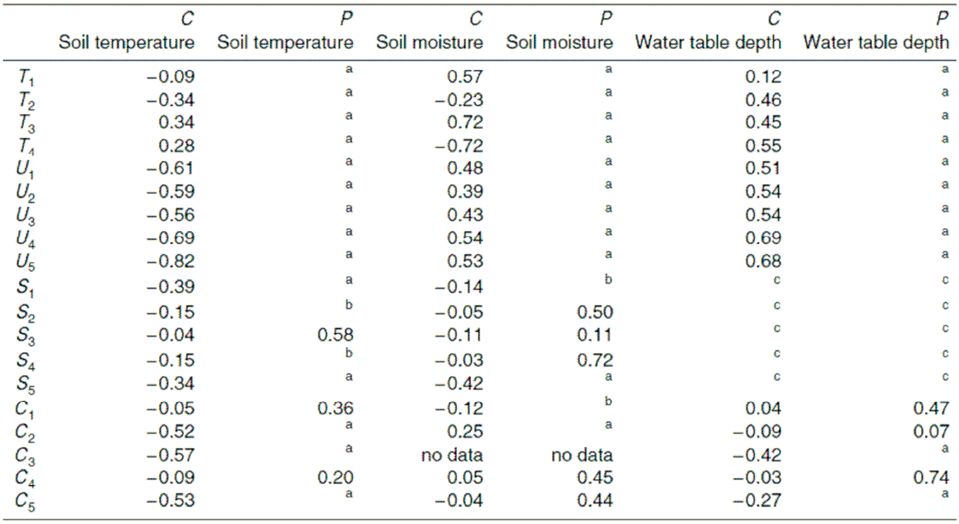
Fig.3. Time series of daily mean CH$_4$ exchange, daily precipitation and daily mean soil temperature at the measurement locations. **3a**) Undisturbed plot, **3b**) Thinned plot, **3c**) Clear-cut plot and **3d**) Stump harvested plot.

3.3 Drivers of CH_4 exchange at the undisturbed and thinned plots

Linear regression analyses between CH_4 exchange and climatic variables showed that for most measurement locations at the undisturbed and thinned plots, consumption significantly ($p<0.001$) increased with decreasing soil water content, decreasing water table depth and increasing temperatures. Exceptions to this were net CH_4 uptake at locations T_3 and T_4 which decreased with increasing temperatures, and net CH_4 uptake at locations T_2 and T_4, which decreased with decreasing soil moisture (Table 2). Figure 4 shows an example of the CH_4 exchange response to temperature and soil water conditions at plot U_2.

Monthly multilinear regression analyses (Table 3) added some temporal information to the CH_4 exchange at the undisturbed and thinned plots. At the undisturbed plot the water table depth affected CH_4 consumption in August. In September 2010 temperature was the most influential variable at all measurement locations. In July 2010 the result was less distinct, showing some measurement locations with a higher dependency on water table depth and soil moisture, and some measurement locations with a higher dependency on temperature. The clearest result at the thinned plot was a strong dependency on soil moisture at measurement locations T_1 and T_3 in August 2009 and at locations T_1 and T_2 in April 2010 (Table 3). Soils were wetter than average in August and April due to heavy rains in June and July 2009, and snowmelt in spring 2010.

Table 2. Correlation coefficients C and corresponding P-values for the linear regressions between CH_4 exchange and soil temperature, soil moisture and water table depth.
a) significant, $p < 0.001$,
b) significant, $p < 0.05$
c), At the time for measurements on the stump harvested plot, the water table depth was only measured manually on a few occasions and therefore no linear regression could be made for this period.



	C Soil temperature	P Soil temperature	C Soil moisture	P Soil moisture	C Water table depth	P Water table depth
T_1	−0.09	a	0.57	a	0.12	a
T_2	−0.34	a	−0.23	a	0.46	a
T_3	0.34	a	0.72	a	0.45	a
T_4	0.28	a	−0.72	a	0.55	a
U_1	−0.61	a	0.48	a	0.51	a
U_2	−0.59	a	0.39	a	0.54	a
U_3	−0.56	a	0.43	a	0.54	a
U_4	−0.69	a	0.54	a	0.69	a
U_5	−0.82	a	0.53	a	0.68	a
S_1	−0.39	a	−0.14	b	c	c
S_2	−0.15	b	−0.05	0.50	c	c
S_3	−0.04	0.58	−0.11	0.11	c	c
S_4	−0.15	b	−0.03	0.72	c	c
S_5	−0.34	a	−0.42	a	c	c
C_1	−0.05	0.36	−0.12	b	0.04	0.47
C_2	−0.52	a	0.25	a	−0.09	0.07
C_3	−0.57	a	no data	no data	−0.42	a
C_4	−0.09	0.20	0.05	0.45	−0.03	0.74
C_5	−0.53	a	−0.04	0.44	−0.27	a

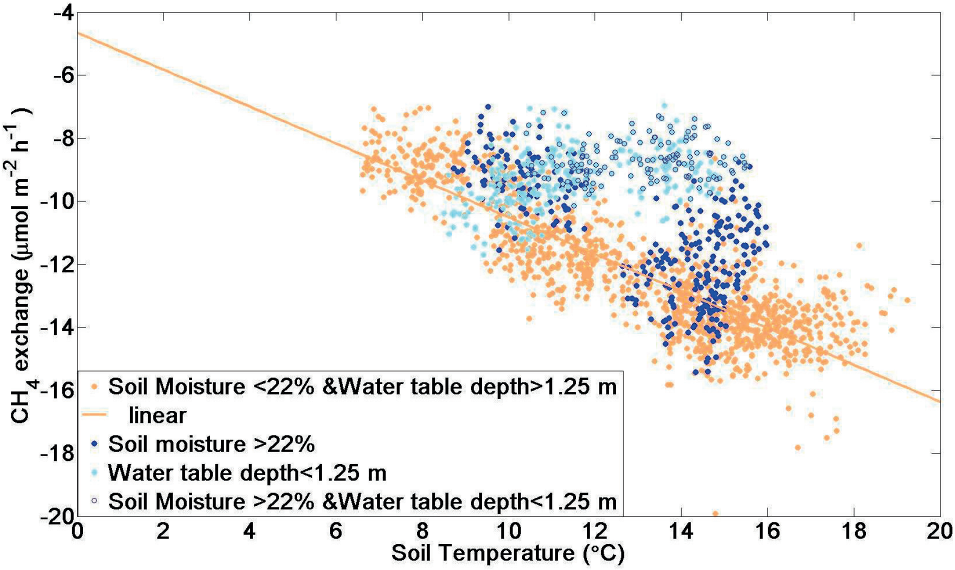
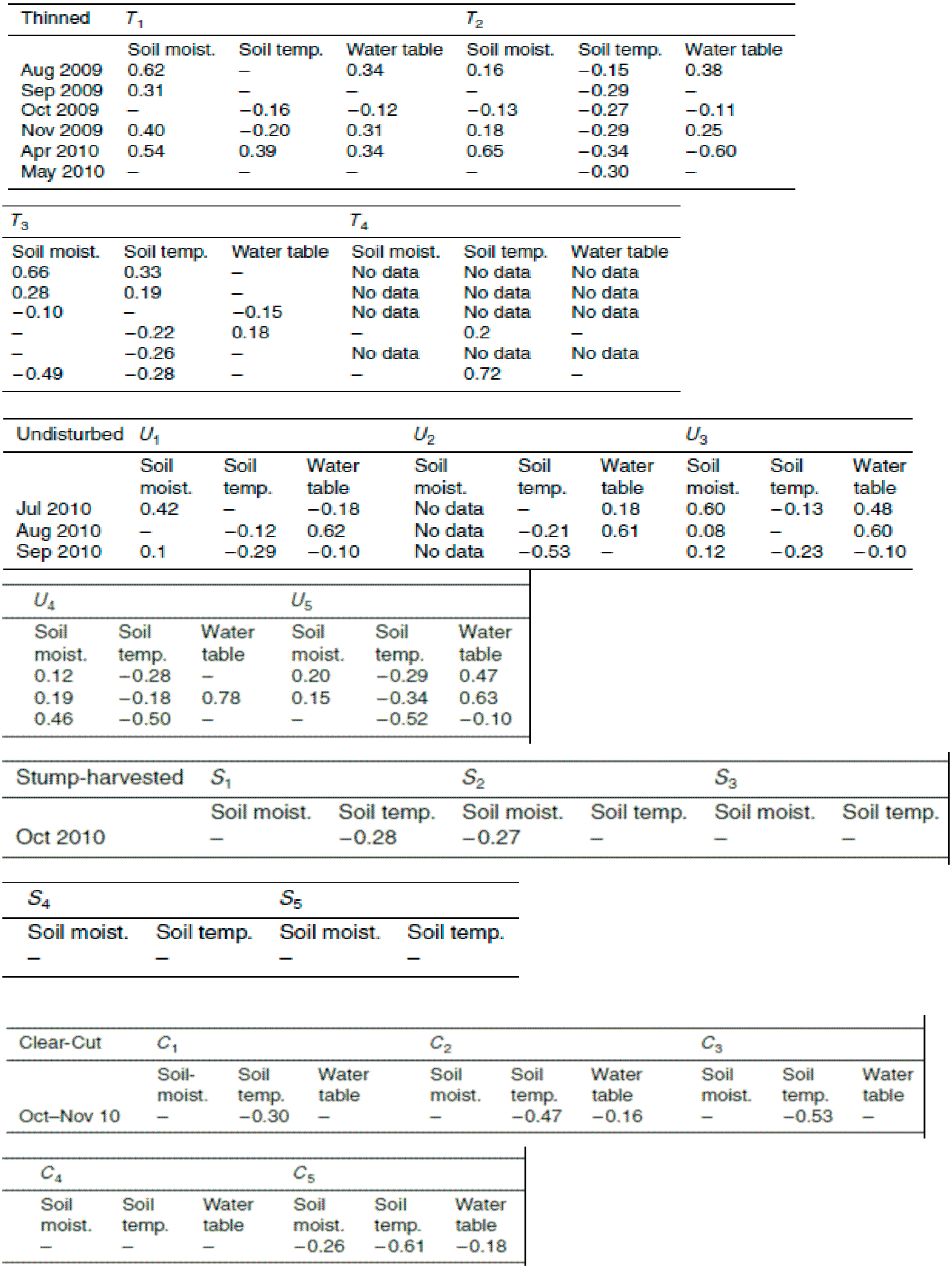


Fig.4. Correlation between CH_4 exchange (µmol m-2 h-1) and soil temperature (˚C) at measurement location U2. The different colours represent different soil moisture and water table depths.

Table 3. Coefficients from multilinear regression analyses. A value is given only if the variable significantly contributes to explain the variation in the CH_4 exchange.



Thinned	T_1			T_2			T_3			T_4		
	Soil moist.	Soil temp.	Water table	Soil moist.	Soil temp.	Water table	Soil moist.	Soil temp.	Water table	Soil moist.	Soil temp.	Water table
Aug 2009	0.62	–	0.34	0.16	−0.15	0.38	0.66	0.33	–	No data	No data	No data
Sep 2009	0.31	–	–	–	−0.29	–	0.28	0.19	–	No data	No data	No data
Oct 2009	–	−0.16	−0.12	−0.13	−0.27	−0.11	−0.10	–	−0.15	No data	No data	No data
Nov 2009	0.40	−0.20	0.31	0.18	−0.29	0.25	–	−0.22	0.18	–	0.2	–
Apr 2010	0.54	0.39	0.34	0.65	−0.34	−0.60	–	−0.26	–	No data	No data	No data
May 2010	–	–	–	–	−0.30	–	−0.49	−0.28	–	–	0.72	–

Undisturbed	U_1			U_2			U_3			U_4			U_5		
	Soil moist.	Soil temp.	Water table	Soil moist.	Soil temp.	Water table	Soil moist.	Soil temp.	Water table	Soil moist.	Soil temp.	Water table	Soil moist.	Soil temp.	Water table
Jul 2010	0.42	–	−0.18	No data	–	0.18	0.60	−0.13	0.48	0.12	−0.28	–	0.20	−0.29	0.47
Aug 2010	–	−0.12	0.62	No data	−0.21	0.61	0.08	–	0.60	0.19	−0.18	0.78	0.15	−0.34	0.63
Sep 2010	0.1	−0.29	−0.10	No data	−0.53	–	0.12	−0.23	−0.10	0.46	−0.50	–	–	−0.52	−0.10

Stump-harvested	S_1		S_2		S_3		S_4		S_5	
	Soil moist.	Soil temp.	Soil moist.	Soil temp.	Soil moist.	Soil temp.	Soil moist.	Soil temp.	Soil moist.	Soil temp.
Oct 2010	–	−0.28	−0.27	–	–	–	–	–	–	–

Clear-Cut	C_1			C_2			C_3			C_4			C_5		
	Soil-moist.	Soil temp.	Water table	Soil moist.	Soil temp.	Water table	Soil moist.	Soil temp.	Water table	Soil moist.	Soil temp.	Water table	Soil moist.	Soil temp.	Water table
Oct–Nov 10	–	−0.30	–	–	−0.47	−0.16	–	−0.53	–	–	–	–	−0.26	−0.61	−0.18

3.4 Drivers of CH4 exchange at the clear-cut and stump harvested plots

Generally at the clear-cut and stump harvested plots, the measurement locations with net emissions of CH_4 had either a relatively short distance to water table, or were disturbed by site preparation, or both, although there were exceptions. Plot S_4 and S_5 had the same water table depth and were not disturbed by preparation, but plot S_4 was a CH_4 sink while plot S_5 was a CH_4 source (Fig.5).

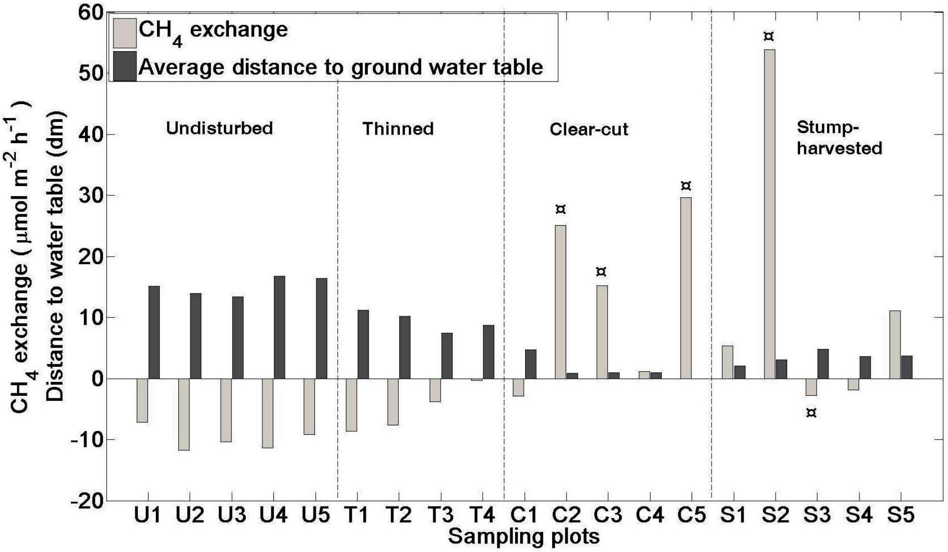


Fig. 5. CH_4 exchange (µmol m-2 h-1) at all individual measurement locations with associated level of ground water table. The water table depth at plot C5 is close to zero and that is why the bar is not visible in the diagram.

¤ Measurement locations where soil surface was disturbed during site preparation.

At the majority of the measurement locations on the clear-cut and stump harvested plots, higher temperatures correlated significantly ($p<0.05$) with lower CH_4 emissions, or in one case with a higher net uptake. Both negative and positive significant correlations between CH_4 exchange and soil moisture was found at a few measurement locations but the soil moisture range at those measurement locations was very small. At two measurement locations with net emissions at the clear-cut plot, there was a significant ($p<0.05$) negative correlation between CH_4 exchange and water table depth, so that a lower water table depth gave higher CH_4 emissions (Table 2). The multilinear regression confirmed the significantly negative correlation between CH_4 exchange and temperature at 5 measurement locations.

4. Discussion

All measurement locations at the undisturbed forest plot were sinks of CH_4 throughout the measurement period, which is consistent with the generally drained, drier and warmer soil conditions at the plot (Fig.1). The measurement locations at the thinned plot were also net sinks of CH_4, although reduced in comparison to the undisturbed plot. By contrast, the clear-cut and stump harvested plots were net sources of CH_4. Since the measurements at the different plots were conducted at different times of year, seasonality and annual variations can probably explain some of the differences in CH_4 exchange and soil conditions. However, it is not likely that differences in water table depth between the plots are due solely to seasonal variations. In the autumn of 2010 the water table was on average more than 1 m higher at the clear-cut and stump harvested plots than at the undisturbed plot. In addition to this, the mean CH_4 exchange for the autumn period October to November at the thinned site did not differ much from the mean CH_4 exchange for the whole measurement period, indicating that average seasonal variations are small (Fig.1). Precipitation was on average higher during the measurement period at the thinned site than during measurements at the other plots, which did not cause a switch from CH_4 sink to CH_4 source.

Water table depth, soil moisture and soil temperature were all shown to be important drivers of CH_4 exchange, as demonstrated by the linear and multilinear regression analyses. However it appears that the rise of water table and increased soil moisture caused some of the measurement locations to shift to CH_4 sources. This is consistent with results by Zerva and Menucuccini (2005) and Castro et al, (2000). Temporal shifts to CH_4 emissions after snowmelt and summer precipitation, as were seen at measurement locations T_3 and T_4, were also reported by Wang and Bettany, (1995).

A majority of net emitting measurement locations at the clear-cut and stump harvested plots (C_2, C_3, C_4, C_5, S_1) were positioned less than 21 cm above the water table, and had a volumetric soil moisture content above 40% (Table 1). Also measurement location T_3, when it had temporarily shifted to a CH_4 source, had volumetric soil moisture content above 40%. Net emissions were also measured at measurement location S_2 and S_5 with water table depths at 30-40 cm and volumetric soil moisture contents of 23-40%. Fiedler and Sommer (2000) found a threshold value of water table depth at 15 cm, below which only minor annual emissions were measured. The three measurement locations at the clear-cut and stump harvested plots which showed net consumption of CH_4 were further than average above the water table for those plots (Fig.4).

Temperature seemed to have a stronger impact on CH_4 exchange in drier conditions. Figure 5 illustrates a high correlation, $r^2 = 0.74$, between soil temperature and CH_4 exchange at measurement location $U_{2,}$ when excluding data points with soil moisture above 22% and a distance to the water table of less than 1.25 m. The threshold value of 22% was selected after visual inspection of the data. If all the data from wetter conditions were included (volumetric soil moisture content > 22 % and water table < 1.25 m away), the corresponding r^2 equals 0.47. This is consistent with the results from the multilinear regression analyses showing that water table depth had a significant impact on the CH_4 exchange at all measurement locations in August 2010, when the water table depth varied strongly. In contrast, during September, there were no major precipitation events and soil temperature was the most influential variable. Soil moisture was rarely below 30 % at the thinned plot, thus the temperature dependence was less. In autumn, September to November 2009, all measurement locations at the thinned plot were stable sinks of $CH_{4,}$ even though the soil temperature was at times below 5˚C.

At the clear-cut and stump harvested plots, where most measurement locations were net sources of CH_4, we would expect a positive correlation between soil temperature and CH_4 exchange, so that higher temperatures led to higher net emissions of CH_4. Methanogens generally respond better than methanotrophs to increased temperatures (Dunfield et al., 1993). However this was not the case: a majority of the measurement locations showed a significantly negative correlation between temperature and CH_4 exchange.

Higher N content in the soil at the clear-cut and stump harvested plots could also possibly contribute to reduced consumption and shifts to emission of CH_4 (Thibodeau et al., 2000; Bradford et al., 2000), although we did not measure the fraction of total N that was freely available. Overall the total N content was higher at the clear-cut and stump harvested plots than at the undisturbed and thinned plots (Table 1), which is possibly due to fertilization that took place in 1976, 1988 and 1998. However at measurement location S_2, which showed the highest emissions of CH_4, the N content was relatively low.

The highest CH_4 emissions were found at four of the five disturbed measurement locations: that is, sites of bare soil where organic and mineral soils were mixed. The soil at disturbed measurement locations seemed less compact than at measurement locations with intact vegetation, so the disturbance probably did not inhibit diffusion. Possibly the availability of fresh organic material was higher at disturbed measurement locations. Fresh, labile organic matter would promote heterotrophic uptake of O_2 and increase the soil's water retention, thereby promoting the activity of methanogenic archeans (Wachinger et al., 2000). The one disturbed measurement location, which showed net CH_4 consumption, S_3, was positioned on top of a mound with relatively large distance to the ground water table (Fig.4).

Since this is a study of the short-term effects of forest management practices on CH_4 exchange, there are no data on how long-lived these effects are. Sudden shifts from sinks to sources and back again due to changes in soil water conditions are evident, as we have seen at the thinned plot (Fig.3b). It might take from years (Tate et al., 2006) to several decades for a soil to regain its full sink capacity. The recovery time for the soil CH_4 sink strength of forests on abandoned agricultural land was more than 100 years (Prieme et al., 1997; Smith et al., 2000). Hiltbrunner et al, (2012) found that the soil CH_4 sink capacity of abandoned agricultural land increased with stand age up to 120 years, due to the increased transpiration of older forests and their ability to shield the forest floor from precipitation, which resulted in more favourable conditions for methanotrophic activity.

Uptake rates by upland forests might be overestimated (Grunwald et al., 2012; Fiedler et al., 2005). A study by Grunwald et al, (2012) found that wet forests were as important as wetlands for the CH_4 budget of European forests, and Fiedler et al, (2005) found that if 2.3% of a forest area consisted of wet soil the forest could turn from a sink to a source of CH_4. As mentioned, after clear-cutting, water table depth decreased and soil moisture increased. Wetter soils and a higher ground water table are common consequences of clear-cutting, and it is therefore important to consider their impact on the CH_4 budget in managed forests, especially if the recovery time for the soil CH_4 sink is several decades. In this study the effects of thinning on the CH_4 exchange were not as pronounced as for clear-cutting, although the plot average consumption was reduced in comparison to the undisturbed plot. Any forest management practice that reduces disturbance and leaves a continuous forest cover might be a better alternative from a global warming perspective.

5. Conclusions

Our study on the short term effects of boreal forest management on CH_4 exchange shows that the undisturbed plot and the thinned plot remained net CH_4 sinks, while the clear-cut and stump harvested plots were net CH_4 sources. Linear regression analyses between CH_4 exchange and climatic variables showed that for most measurement locations at the undisturbed and thinned plots, net CH_4 uptake increased significantly with decreasing soil moisture, decreasing water table depth and increasing temperatures. A higher water table and increased soil moisture were likely to be responsible for the shift to CH_4 emissions at the clear-cut and stump harvested plots. At most of the measurement locations, which showed net emissions, the soil was almost saturated and the water table was within a few decimetres of the soil surface. Clear-cutting of the forest resulted in a raised ground water table and in increased soil moisture. These effects should be accounted for in the CH_4 budget of managed forests.

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Paper II

GEOPHYSICAL RESEARCH LETTERS, VOL. 39, L21806, doi:10.1029/2012GL053592, 2012

Atmospheric methane removal by boreal plants

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[1] Several studies have proposed aerobic methane (CH_4) emissions by plants. If confirmed, these findings would further increase the imbalance in the global CH_4 budget which today underestimates CH_4 sinks. Oxidation by OH-radicals in the troposphere is the major identified sink followed by smaller contribution from stratospheric loss and oxidation by methano- and methylotrophic bacteria in soils. This study directly investigated CH_4 exchange by plants in their natural environment. At a forest site in central Sweden, *in situ* branch chamber measurements were used to study plant ambient CH_4 exchange by spruce (*Picea abies*), birch (*Betula pubescens*), rowan (*Sorbus aucuparia*) and pine (*Pinus sylvestris*). The results show a net uptake of CH_4 by all the studied plants, which might be of importance for the methane budget. **Citation:** Sundqvist, E., P. Crill, M. Mölder, P. Vestin, and A. Lindroth (2012), Atmospheric methane removal by boreal plants, *Geophys. Res. Lett.*, *39*, L21806, doi:10.1029/2012GL053592.

1. Introduction

[2] The first report of CH_4 emissions by green plants by *Keppler et al.* [2006] proposed global CH_4 emissions by vegetation in the range of 62 to 236 Tg each year, which would comprise 10–30% of the total CH_4 entering the atmosphere [*Lowe*, 2006]. Several subsequent studies supported the findings of aerobic CH_4 emissions [e.g., *Wang et al.*, 2008; *McLeod et al.*, 2008; *Vigano et al.*, 2008; *Messenger et al.*, 2009], but the extrapolation of the results by Keppler using net primary production as a scalar has been criticized. A more conservative estimate was made using biome leaf biomass and photosynthesis as scaling factors, which resulted in emissions in the range of 10–60 Tg yr^{-1} [*Kirschbaum et al.*, 2006]. A number of other extrapolations have been made [*Houweling et al.*, 2006; *Butenhoff and Khalil*, 2007; *Ferretti et al.*, 2007] all resulting in a lower range than that of Keppler et al. Ultraviolet (UV) radiation has been shown to drive an aerobic production of CH_4 from plant tissue and pectin [*McLeod et al.*, 2008; *Vigano et al.*, 2008]. Estimates of global foliar CH_4 emissions from UV-irradiated pectin resulted in a value of 1 Tg yr^{-1} [*Bloom et al.*, 2010]. UV driven demethylation of the methoxyl groups of pectin in the cell wall of the plant has been suggested as a potential source of CH_4 [*McLeod et al.*, 2008; *Keppler et al.*, 2008; *Messenger et al.*, 2009]. UV radiation is indicated to act on a photosensitizer, which generates reactive oxygen species (ROS), which in turn attack pectic polysaccharides so that CH_4 formation occurs [*Messenger et al.*, 2009]. Besides UV-radiation, physical injury of the plant [*Z.-P. Wang et al.*, 2009] and other environmental stress factors might also stimulate ROS activity [*Z.-P. Wang et al.*, 2009; *Qaderi and Reid*, 2011; *Wishkerman et al.*, 2011]. At the same time it is well established that ROS can react with water to form OH [*Logan et al.*, 1981], the principal atmospheric sink of CH_4. The CH_4 emissions from plants have also been suggested to stem from dissolved CH_4 in the water drawn into the plant and subsequently released through diffusion [*Dueck et al.*, 2007] or transpiration [*Nisbet et al.*, 2009].

[3] The importance of the emissions and the mechanisms through which they are released are still discussed [*Bruhn et al.*, 2012]. Some studies have not found evidence for substantial aerobic CH_4 emissions [*Dueck et al.*, 2007; *Beerling et al.*, 2008; *Kirschbaum and Walcroft*, 2008]. There is also little evidence from in-situ studies on plant emission. Comparison of soil chamber measurements between plots with intact vegetation and removed vegetation led to increased production of CH_4 in the intact plot at a tropical savanna [*Sanhueza and Donoso*, 2006] and at two alpine grasslands [*Cao et al.*, 2008; *S. Wang et al.*, 2009]. However Cao et al. also found in their study that alpine shrubs instead consumed CH_4 and *S. Wang et al.* [2009] explained the discrepancy found in their study with differences in soil water content and soil temperature. There have also been a few studies on methane exchange by canopies. *Mikkelsen et al.* [2011] found indications of periodic canopy emissions using a gradient-based method whereas two studies using eddy covariance measurements didn't find any significant emission from the canopy [*Bowling et al.*, 2009; *Smeets et al.*, 2009].

[4] Sphagnum spp. mosses are the only plants so far reported to consume CH_4 by symbiosis with partly endophytic methanotrophic bacteria. Carbon dioxide (CO_2) produced from oxidation of CH_4 is then fixed to the plant during photosynthesis [*Raghoebarsing et al.*, 2005].

[5] Numerous plants have epiphytic bacterial associations, in this case pink-pigmented facultative methyltrophs (PPFMs) that can consume methanol emitted by plants [*Holland and Polacco*, 1994]. One strain of these bacteria, methylobacterium sp. BJ001T that was isolated from poplar tree tissue has been reported to be able to use CH_4 as a sole source of carbon and energy [*Van Aken et al.*, 2004]. This report was not considered definitive [*Dedysh et al.*, 2004].

2. Method

[6] We directly measured CH_4 exchange by boreal plants with the ambient atmosphere in a boreal forest (Table 1).

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Table 1. Details on Measurement Periods[a]

Plant Type	Type of Measurement	Measuring Period	Measuring Frequency	Number of Recordings Available for Analysis (n)	Plant Height (m)	Shoot Leaf Area (m^2)	Temperature Range (°C)	PAR Range (μmol m^{-2} s^{-1})	GPP Range (μmol m^{-2} s^{-1}) for PAR > 2	UV Range (μmol m^{-2} s^{-1})
Spruce1	In situ	13/8–15/9 2009	1/hour	285	~20	0.031	7−19	0−435	−11−0	0−2.8
Birch1	In situ	16/9–19/10 2009	1/ hour	361	~2.5	0.019	−3−16	0−140	−6−4	0−1.5
Spruce2	In situ	7 /7–28/7 2010	1/ hour	399	~20	0.017	13−30	0−117	−7−2	0−1.1
Spruce3	In situ	29 /7–12/8 2010	1/ hour	281	~1	0.026	13−22	0−76	−7−1	0−1
Rowan	In situ	27/8–10/9 2010	1/ hour	279	~4.5	0.008	5−16	0−80	−13−2	0−0.8
Birch2	In situ	10/9–24/9 2010	1/ hour	203	~1	0.011	6−17	0−33	−5−1	0−0.4
Pine1	In situ	29/9–4 /10 2010	1/ hour	97	~0.4	0.003	1−12	0−36	−10−6	0−0.5
Spruce4	Lab	24 hours Feb 2011	4/ hour	65	~0.5	0.008	5−25	0−382	−25−8	-
Spruce5	Lab	24 hours Feb 2011	4/ hour	61	~0.5	0.0147	5−25	0−358	−17−4	-
Spruce6	Lab	72 hours Feb 2011	4/ hour	198	~0.5	0.0168	5−26	0−380	−11−2	-
Pine2	Lab	24 hours Feb 2011	4/ hour	70	~0.3	0.005	5−25	0−327	−25−4	-
Pine3	Lab	24 hours Feb 2011	4/ hour	139	~0.3	0.0019	5−26	0−375	−100−14	-

[a] Information on plant sample and ranges of temperature, PAR, GPP and UV-radiation. 90% of the data fall within the Temperature, PAR, GPP and UV-radiation ranges that are shown in the table.

Semi-continuous field measurements on branches of different plants were made to study direct CH_4 exchange by plants and its dependence on photosynthetically active radiation (PAR), ultraviolet radiation (UV-radiation), temperature and photosynthesis. Because of the strong correlation between different environmental parameters, e.g., radiation and temperature, under natural conditions, additional laboratory measurements were also made to study the controlling factors. The CH_4 exchange measurements were made on spruce (*Picea abies*), birch (*Betula pubescens*), rowan (*Sorbus aucuparia*) and pine (*Pinus sylvestris*) in the 100-year-old Norunda forest stand in central Sweden at 60°5′ N, 17°29′ E. In 2009, the measurements took place in a forest stand that was thinned in 2008, whereas measurements in 2010 were in an untouched part of the forest. The measurements on birch in 2009 were made during the senescent period because environmental stresses had been posited to play an important role in affecting emissions [*Z.-P. Wang et al.*, 2009; *Qaderi and Reid*, 2011; *Wishkerman et al.*, 2011] (see Table 1 for details on measurements periods). Since the branch chamber measurements were integrated in a larger system with measurements of methane oxidation in the soil and methane gradients within the forest, the branches had to be selected within a limited area with the requirement of being reachable from the ground, but in a position that is reached by the sun at least part of the day. This explains the low PAR range for part of the measurement periods.

[7] A temperature controlled, automated branch chamber was used in combination with a high precision off-axes ICOS lazer (LGR-Los Gatos Research) to determine changing mixing ratios of CH_4 in the chamber headspace. The sides of the branch chamber exposed to the sun were quartz glass, which is transparent to UV radiation. The volume of the chamber was 0.0057 m^3. The chamber sealed around the stems of the leaves or needles being studied so that the leaves remained intact throughout the measurements. Changes of headspace concentration were measured after closure of the chamber by recirculating the air through the gas analyzer during a period of 5 min every hour. During closure, the air inside the chamber was kept to within ±1°C of the ambient air, and a fan was used to mix the headspace air. The cooling of the air was provided with a peltier cooler controlled by a CR 1000 data logger (Campell Inc., Logan, USA). The measuring frequency was 0.1 Hz in 2009 and 1 Hz in 2010. Besides CH_4, the analyzer measured CO_2 in 2009 and CO_2 and H_2O in 2010. The flow rate through the analyzer was 1.2 l/min.

[8] Before the measurements started, the chamber was put in an oven for 48 hours at 70°C to prevent possible CH_4 emissions from the chamber itself. The chamber was also run empty, but with equal procedures as the rest of the measurements, for a couple of weeks in 2009 to make sure there is no spurious CH_4 flux. The mean of the CH_4 exchange for this period was not significantly different from zero.

[9] In February 2011, laboratory measurements were made on horticultural specimens of spruce (Picea glauca conica) and pine (Pinus mugo var. pumilio). Samplings of the same species as measured in the field where not available at this time of the year. Exactly the same equipment was used as for the *in situ* measurements. The only difference was that flux measurements were performed four times per hour. The CH_4 exchange was tested at three temperature intervals, 3–7°C, 13–17°C and 23–27°C and four different

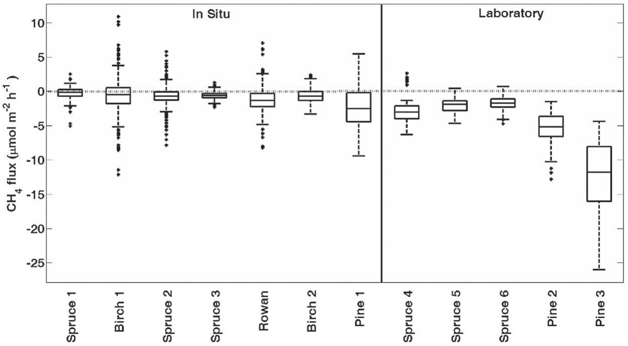

Figure 1. CH_4 exchange (μmol m^{-2} h^{-1}) for 12 measuring periods. The data are expressed per unit (m^2) of leaf area. The middle line of the box and whisker plot represents the median of all recordings including nighttime measurements. The edges of the box are the 25th and 75th percentiles, the whiskers, (black dotted lines) are the extreme values not considered outliers. Values larger than q3 + w (q3–q1) or smaller than q1–w (q3–q1) are considered outliers, where q1 and q3 are the 25th and 75th percentiles, respectively, and w = 1.5 is the whisker length. Negative values represent a flux from the atmosphere towards the branch. The median values are all significantly different from zero at 99% significance level.

intervals of PAR, 0 μmol m^{-2} s^{-1}, 50–150 μmol m^{-2} s^{-1}, 250–350 μmol m^{-2} s^{-1} and 350–450 μmol m^{-2} s^{-1}. The measured CH_4 concentrations had to be corrected for dilution effects by water vapor, but since the water vapor was not measured in 2009 it had to be calculated . We used the Ball-Berry equation, to calculate the stomatal conductance to CO_2, g_s (μmol m^{-2} s^{-1}), as: $g_s = g_0 + \frac{m \cdot A \cdot h}{C_s}$ where $g_0 = 0.01 \cdot 10^6$ (μmol m^{-2} s^{-1}) is the stomatal conductance [*Collatz et al.*, 1991], $m = 8.75$ (dimensionless) is a fitting parameter [*Xu and Baldocchi*, 2003]. A (μmol m^{-2} s^{-1}) is photosynthesis rate, h (dimensionless) is relative humidity and C_s (μmol CO_2 (mol air)$^{-1}$) is the mixing ratio of CO_2 in air at the leaf surface. C_s is calculated as $C_s = C_a - A \cdot \frac{1.37}{g_b}$ [*Liu et al.*, 2009], where C_a (μmol CO_2 (mol air)$^{-1}$)) is the ambient CO_2 concentration in the air and $g_b = 0.075$ m s^{-1} is the boundary layer conductance of the shoot, assuming 1 m s^{-1} wind speed in the chamber [*Martin et al.*, 1999]. The transpiration rate E (μmol m^{-2} s^{-1}) is calculated as: $E = g_s' \cdot \frac{(e_s(T_a) - e_a)}{P_a}$, where $g_s' = 1.6 \cdot g_s$ and g_s (μmol m^{-2} s^{-1}) is the stomatal conductance to water vapor, e_s (kPa) is the saturation vapor pressure at air temperature, T_a (°C), e_a (kPa) is the ambient vapor concentration and P_a (kPa) is the air

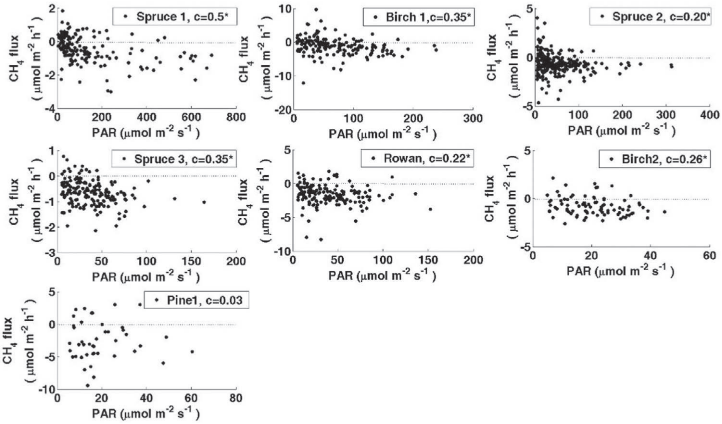

Figure 2. The correlation of CH_4 flux (μmol m^{-2} h^{-1}) with PAR (μmol m^{-2} s^{-1}) for the seven different shoots studied *in situ.* Only PAR values larger than 5 μmol m^{-2} s^{-1} are included in the plots. The c-value is the correlation coefficient. * Indicates that the correlation is significant at 95% significance level.

Table 2. Correlation Between CH_4 Exchange and PAR, CH_4 Exchange and Temperature and CH_4 Exchange and UV Radiation for *in Situ* Measurements[a]

Plant Type	n	Correlation Coefficient, CH_4 and PAR	Correlation Coefficient, CH_4 and Temperature	Correlation Coefficient, CH4 and UV-Radiation
Spruce1	165	-0.5^{b}	-0.46^{b}	-0.52^{b}
Birch1	170	-0.35^{b}	-0.25^{b}	-0.42^{b}
Spruce2	251	-0.20^{b}	−0.09	−0.26
Spruce3	173	-0.35^{b}	-0.32^{b}	-0.42^{b}
Rowan	151	-0.22^{b}	−0.14	-0.19^{b}
Birch2	88	-0.26^{b}	−0.016	-0.24^{b}
Pine1	44	−0.03	0.04	−0.04

[a] The correlation with PAR and UV is calculated for PAR-values larger than 5 μmol m^{-2} s^{-1}.

[b] Significant at 95% level.

pressure. We then used the measured ambient water vapor mixing ratio in the nearby tower as the initial concentration at time for chamber closure and then we added transpired water to calculate the successively increasing water vapor concentration in the chamber. As the next step, we calculated the dry concentration of CH_4 for each time step as $C_{dry} = C_{wet} \cdot \frac{1}{\left(1 - \frac{w}{1000}\right)}$, where w (mmol mol^{-1}) is the water vapor molar ratio. In 2010 w was measured and the correction could be done directly.

[10] The CH_4 mixing ratio obtained by the analyzer and after dilution corrections, c (μmol mol^{-1}), was then converted to C (μmol m^{-3}) by $C = c \cdot P/(R \cdot T)$, where $P = 101325$ Pa is the standard atmospheric air pressure, $R = 8.314$ J mol K^{-1} is the gas constant and T (K) is the chamber temperature.

[11] From the concentration data, a linear fit was made for a two-minute interval beginning immediately after chamber closure to retrieve dC/dt. We calculated the r^2 values for the fits of five different intervals, which were slightly offset to each other and selected the fit with the highest r^2 value. All fluxes with an r^2 value significant at 95% level where kept for further analyses. The CH_4 flux ($J_{CH4flux}$) was calculated as $J_{CH\,4\,flux} = \frac{dC}{dt}\frac{V}{A}$, where V (m^3) is the chamber volume and A (m^2) is the projected leaf area of the enclosed shoot.

[12] Mean CH_4 exchange and spearman correlations between CH_4 exchange and PAR, temperature, UV and GPP were calculated. The whisker length of 1.5 in the box and whisker plot (see Figure 2) is suggested by *McGill et al.* [1978].

3. Results

[13] The results from the branch chamber measurements show a significant mean uptake of CH_4 by all studied plants (Figure 1).

[14] There was a consistent, small but significant negative correlation between CH_4 exchange and PAR for six of the seven species measured *in situ* with increasing CH_4 uptake for higher values of PAR (Figure 2 and Table 2). The measurements on Pine1 were not significantly correlated with PAR. The correlation coefficients for CH_4 exchange and UV-radiation were similar to those of PAR with increasing CH_4 uptake for higher values of UV-radiation (Table 2). Only three of the seven *in situ* measurements, Spruce1, Spruce2 and Birch1, were significantly and positively correlated with temperature (Table 2). The average CH_4 uptake per unit of leaf area across all species and environmental conditions for the *in situ* measurements was 0.7 μmol m^{-2} h^{-1}.

[15] In the laboratory measurements, CH_4 exchange was significantly (95%) correlated with PAR (range 0–450 μmol m^{-2} s^{-1}) for all measurements with correlation coefficients of −0.23, −0.28 and −0.22 for temperature intervals 3–7, 13–17 and 23–27°C, respectively (Table 3). CH_4 uptake was positively correlated with temperature at 90% significance level with correlation coefficients 0.14 and 0.19 for PAR intervals -5-5 and 250–350 respectively, and negatively correlated with temperature with correlation coefficients −0.01 (p = 0.9), and −0.19 (p = 0.1) for PAR intervals 50–150 and 350–450 respectively (Table 4).

[16] The correlation of CH_4 exchange with GPP was better for the laboratory measurements than for the *in situ* measurements. Of the *in situ* measurements, only Spruce1 and Birch1 showed a significant positive correlation between CH_4 exchange and GPP with correlation coefficients of 0.57 (Figure 3) and 0.52 respectively (Table 5).

4. Discussion

[17] In contrast to earlier studies of CH_4 exchange by plants, we find a net consumption by all plants studied both *in situ* and in the laboratory. The presence of endophytic or epiphytic bacteria with the ability to consume CH_4 would be a possible explanation for this [*Raghoebarsing et al.*, 2005;

Table 3. Correlation Between CH_4 Exchange and PAR at Fixed Temperature Intervals for All Species Measured in Laboratory

Temperature Range (°C)	n	Correlation Coefficient, CH_4 and PAR	p
3–7	109	−0.23	0.02
13–17	119	−0.28	0.002
23–27	80	−0.22	0.05

Table 4. Correlation Between CH_4 Exchange and Temperature at Fixed PAR Intervals for All Species Measured in Laboratory

PAR Range (μmol m^{-2} s^{-1})	n	Correlation Coefficient, CH4 and Temperature	p
−5–5	149	0.14	0.08
50–150	60	−0.01	0.9
250–350	202	0.19	0.01
350–450	74	−0.19	0.1

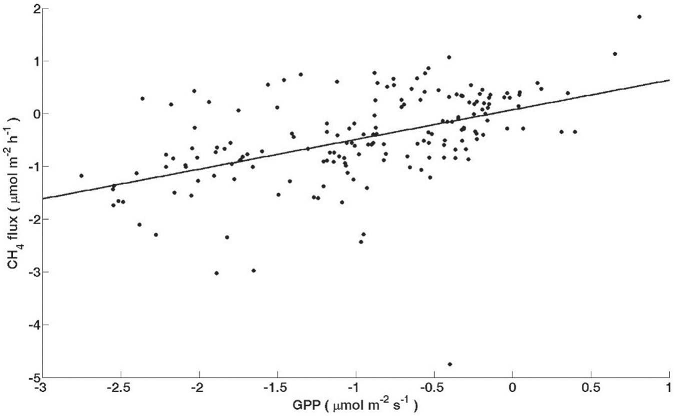

Figure 3. Correlation between CH_4 (μmol m^{-2} h^{-1}) exchange and GPP (μmol m^{-2} s^{-1}) for Spruce1. The correlation coefficient is 0.57. Notice that a negative GPP means uptake from the atmosphere.

Van Aken et al., 2004]. The timescale of the atmospheric OH sink is too large for it to be an explanation.

[18] The strong correlation between PAR and temperature *in situ* makes it difficult to sort out which parameter has the strongest control. The laboratory measurements gave more distinct results: the uptake increased consistently with increasing PAR while there was no consistent control on the uptake by temperature (Tables 3 and 4). This indicates that the CH_4 sink is located somewhere inside the leaves and that the diffusion rate is controlled by the stomatal conductance. Stomatal conductance increases practically linearly with light at the range of PAR encountered in this study. The temperature response found for a several PAR intervals with a decreasing uptake for increasing temperatures could also be explained by a response to vapor pressure deficit (VPD) with stomata responding in the opposite direction, i.e., closing when temperature (and VPD) increases.

[19] What speaks against a microbial process is the negative correlation between CH_4 consumption and temperature found in the laboratory studies since bacterial activities are normally favored by increasing temperatures. However, if it is the diffusion rate through the stomata that is the limiting factor for bacterial consumption, this hypothesis could still be valid.

[20] The emissions of CH_4 by plants that have been reported in several studies are thought to depend on environmental stresses that activate ROS. It is possible that this emission process occurs simultaneously with a consumption of CH_4 by bacteria. High levels of ROS would then control the CH_4 exchange leading to net emissions. Most plants in their natural environment however, might not experience such a high stress level. The absence of UV radiation in the laboratory might explain the higher CH_4 uptake and the higher correlation of the uptake with GPP in this particular environment.

[21] Our observations also contain positive CH_4 fluxes particularly at low GPP (or PAR), but this is mainly attributed to the uncertainty in the measurements. Under the condition of very low fluxes, the uncertainty in measured concentrations caused by signal noise, become significant.

[22] If we scale up our observed *in situ* uptake of CH_4 by multiplying the mean value of 0.7 μmol m^{-2} h^{-1} with the leaf area index of the Norunda forest (4.8) we obtain a value of 3.4 μmol m^{-2} h^{-1}. This is close to the mean CH_4 soil oxidation rate in various forest soils based on 28 studies, which is 4.0 μmol m^{-2} h^{-1} [*Jang et al.*, 2006], this indicates that the canopy might play an equally important role as the soil in the global context.

[23] Two recent studies give alternative explanations to the slow-down in the growth rate of atmospheric methane in the last decades. One of them indicates that it is due to a stabilization of fossil-fuel emissions [*Aydin et al.*, 2011] whereas the other explains it by a decrease in microbial methane sources in the northern hemisphere [*Kai et al.*, 2011]. Our results offer a third explanation: that an increasing amount of CH_4 has been taken up by vegetation during the last decades as a consequence of increased greenness

Table 5. Correlation Between CH_4 Exchange and GPP for All Plants Studied[a]

Plant Type	n-Value	Correlation Coefficient, CH4 and GPP
Spruce1	171	0.57[b]
Birch1	176	0.52[b]
Spruce2	273	0.1
Spruce3	184	0.1
Rowan	162	0.06
Birch2	102	−0.03
Pine1	47	−0.3[b]
Spruce4	49	0.38[b]
Spruce5	47	0.14
Spruce6	144	0.31[b]
Pine2	47	0.51[b]
Pine3	97	0.67[b]

[a] GPP is calculated for PAR > 2.

[b] Significant at 95% level.

[*Myneni et al.*, 1997], NPP [*Nemani et al.*, 2003] and GPP [*Chen et al.*, 2006] as observed by satellite remote sensing.

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Paper III

Methane exchange in a boreal forest estimated by gradient method

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Abstract

Forests are generally considered to be net sinks of atmospheric CH_4 because of oxidation by methanotrophic bacteria in well-aerated forests soils. However, emissions from wet forest soils, and sometimes canopy fluxes, should also be considered when quantifying the CH_4 budget of a forest. We used a modified Bowen ratio method and combined eddy covariance and gradient methods to estimate net CH_4 exchange at a boreal forest site in central Sweden. Results show that the site is a net source of CH_4. This is in sharp contrast to soil and leaf chamber measurements indicating that the site is a net sink. Wetter soils within the footprint are thought to be responsible for the discrepancy. We found no evidence for canopy emissions *per se*. However, the diel pattern of the CH_4 exchange with minimum emissions at daytime correlated well with GPP, which supports an uptake in the canopy, as was recently observed with branch chamber measurements on shoots from different tree species from the same site.

1. Introduction

Forests cover about 30% of the world's land surface area and due to their heterogeneity can host both CH_4 consuming (Harriss et al., 1982) and CH_4 emitting (Ehhalt, 1974) soil environments. A well-aerated forest soil is a net sink of atmospheric CH_4 because of oxidation by methanotrophic bacteria (Born et al., 1990; Crill, 1991; Whalen and Reeburgh, 1990). This does not necessarily mean that a forest site is a net sink of CH_4. Production of CH_4, by archaea, takes place in anoxic environments such as water-saturated soils and small ponds scattered in the forest and in anaerobic micro sites within otherwise well drained soils (Fischer and Hedin, 2002; Hudgens and Yavitt, 1997; Kammann et al., 2009). It is possible that the CH_4 uptake rate in forests, especially in moist forests, is overestimated since emissions from wet soils are not adequately accounted for (Grunwald et al., 2012). Even if CH_4 emissions are sporadic and limited to restricted areas, their occurrence frequency and source strength might turn a forest site from a net sink to a net source of CH_4 (Fiedler et al., 2005; Sakabe et al., 2012) depending upon the scale. The capacity of plants with roots in CH_4 rich water saturated soils, even woody plants, to transport and release CH_4 (Gauci et al., 2010; Terazawa et al., 2007) adds another level of the complexity to the analyses.

Soil moisture, soil texture and water table depth are crucial in determining whether the soil will act as a CH_4 sink or a CH_4 source. Soil moisture and soil texture influence the soil diffusivity and thus the flux of CH_4 and oxygen from the atmosphere to the soil depths where CH_4 is consumed (Born et al., 1990; Koschorreck and Conrad, 1993; Whalen and Reeburgh, 1996), while water table depth alters the relative extent of anaerobic and aerobic zones in the soil (Whalen and Reeburgh, 1990). Soil moisture and water table depth varies spatially due to e.g. topography, which result in spatial variations of CH_4 exchange (Lessard et al. 1994, Yu K. W. et al. 2008). There is also a temporal variability in CH_4 exchange, mainly due to changes in temperatures and precipitation (Castro et al., 1994; Guckland et al., 2009). CH_4 production is strongly favored by increasing temperatures, while CH_4 oxidation is not as sensitive (Dunfield et al., 1993; Yvon-Durocher et al., 2014). Soils have been observed to switch from sinks to sources following precipitation (Hudgens and Yavitt 1997, Keller and Reiners 1994, Sakabe et al. 2012, Wang F. L. and Bettany 1995).

Most in situ measurements have been made with chambers e.g. (Bradford et al. 2000, Crill et al. 1994, Guckland et al. 2009). They are suitable for detailed studies of processes controlling CH_4 exchange but they might not be spatially representative for a larger area (Denmead, 2008) and semi-continuous measurements are possible only with automated chambers. Micrometeorological (MM) methods, such as gradient methods and eddy covariance (EC) methods can better capture spatial and temporal variability of CH_4 exchange over forests at ha or larger scales. Net ecosystem carbon dioxide (CO_2) exchange between forests and the lower atmosphere has been measured with gradients since 1970 and with EC since the early 1990s (Baldocchi et al., 2001). Measuring CH_4 exchange is more challenging due to low flux rates from spatially restricted areas within a forest and therefore relatively few MM studies have been made (Nicolini 2013). MM methods that have been used for CH_4 exchange between forest stands and the atmosphere are EC (Shoemaker et al., 2014; Smeets et al., 2009) relaxed EC (Sakabe et al. 2012, Ueyama et al. 2012), profile method (Bowling et al. 2009) and gradient method (Querino et al., 2011; Simpson et al., 1997).

We used a gradient method to study CH_4 exchange at a boreal forest site in central Sweden. The aim was to quantify the CH_4 exchange between the canopy and the overlaying atmosphere and to investigate the reasons for variability in CH_4 exchange over time. We also wanted to compare the result from micrometeorological methods with soil CH_4 exchange measured by chambers in the same area during part of the measurement period.

2. Method

2.1 Site description

The CH_4 gradient measurements used in the exchange calculations were made from 16 June 2010 to 31 December 2011 at a boreal forest site, at the Norunda research station, 60˚5 N, 17˚29 E in central Sweden. A forest stand consisting of 120 year old mixed pine (Pinus sylvestris) and spruce (Picea abies) trees surrounded the measurement tower within a 500 m radius. The south west (SW) to north-east (NE) directions had not been thinned or fertilized in a few decades, while NE to SW quadrants were thinned in 2008 which decreased the leaf area index from 4.8 to 2.8. Forest stands of various ages covered most of the area within a 500-800 m radius around the tower, apart from a clear-cut area of 6.5 ha in the west and a smaller clear-cut area in the south. Tree heights at the site were generally around 25 m. At distances greater than 800 m, agricultural lands, wetlands and lakes contributed to the mosaic of the landscape (Figure 1).

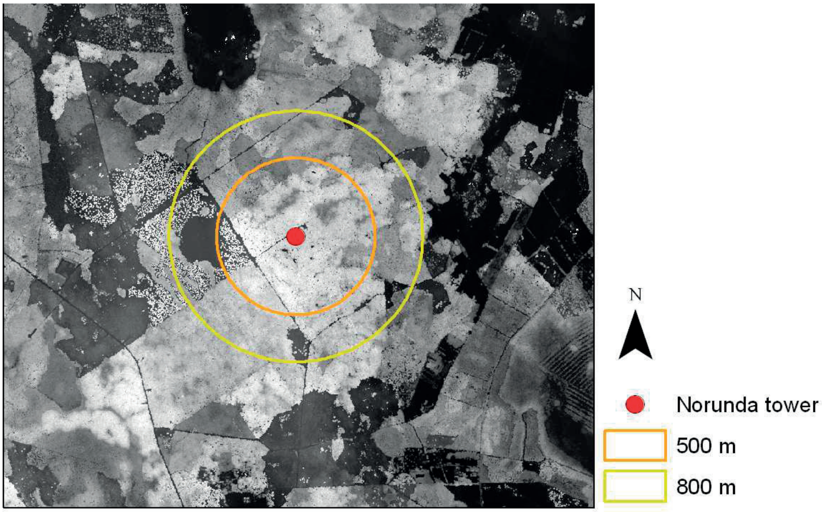

Figure 1. Digital surface model (DSM) of Norunda site. Areas within 500m and 800m radiuses from the tower are defined.

Ground vegetation at the site was sparse and dominated by bilberry (Vaccinium myrtillus) and feathermosses (Hylocomium splendens and Pleurozium schreberi). The soil was a glacial till (Lundin et al., 1999) with an organic layer of 3-10 cm depth. The mean air temperature was 6.5°C and the mean annual precipitation was 576 mm, from 1980-2010, measured 30 km south of Norunda at the Uppsala climate station.

2.2 Instrumentation

Concentrations of CH_4 and CO_2 were measured at three heights, 31.7 m, 58.5m and at 100.6 m above ground, with an off-axis integrated cavity output spectroscopic (ICOS) laser analyser (DLT-100, Los Gatos Research (LGR)). All intake heights were above the canopy. The 31.7 m intake was within the rougness sublayer while the other two intakes were in the semi logarithmic layer. Displacement height was estimated to be 21.1 meter.

Air was pulled down to the analyser through 4 mm high density polyethene tubing. An individual membrane pump was used for each level. A 8 l mixing volume was installed in each line and a perma pure dryer was used to drying the air before the analyser. Each level at the tower was sampled for 5 min. The first minute was omitted from the calculation of the average concentration (see below). The gas analyser measured at a frequency of 1 Hz. The flow rate through the tubing was 3 l min-1 but the subsampling rate through the analyser was 0.7 l min-1. The excess flow was vented through a T-connector.

EC measurements of CO_2 were conducted at 33 m height with a 3-D sonic anemometer (USA-1, Metek GmbH) and an infrared gas analyser (LI-7000, Li-Cor Inc.) The air was drawn to the gas analyser through 6 m of 4 mm high density polyethene tubing at a rate of 8-9 l min-1. The measuring frequency of both wind and concentration was 10 Hz and fluxes were calculated on the basis of 30 averaging periods. Linear detrending was used and the time lag between wind and gas concentrations measurements was determined by maximum correlation. No frequency correction due to tube dampening was done. This correction would be small at such a high measurement height.

Chamber measurements were made 100 m to the NW of the tower from 7 July 2010 to 4 October 2010 (Sundqvist et al., 2014). We used five automated, transparent chambers of polymethyl methacrylate which covered a surface-area of 0.2 m2 and had a total volume of 110 liters. CH_4 concentrations were measured with a high precision off-axis integrated cavity output spectroscopy (ICOS) laser gas-analyser (DLT-100, Los Gatos Research (LGR)) that was located at a minimum of 4 m and a maximum of 15 m from the chambers. During the 6 minutes of each measurement, the chambers were closed and air was recirculated through the gas analyser. A fan was installed in each chamber to ensure sufficient mixing of chamber headspace air. Chamber frames were installed in 2005 so by 2010 there had been time for soil and vegetation to recover from the disturbance.

Continuous measurements of soil temperature, air temperature, precipitation, water table depth and soil moisture were made and logged at 10 s intervals. Air temperature was measured at 33 m height on the tower with a type T thermocouple placed in a ventilated radiation shield. Soil temperature was measured at 5 cm depth with a type T thermocouple. Soil moisture was measured at 5 cm depth with permittivity sensors (Ml-2x ThetaProbe, Delta-T Devices Ltd). Precipitation was measured using a tipping bucket rain gauge (RM Young Company), at an open site at 80 m E of the tower. Water table depth was measured at 80 m N of the tower.

2.3 Gradient methods

CH_4 exchange was calculated using two different methods, a modified Bowen ratio method (BR) and the combined EC and gradient method (ECG). CH_4 exchange was calculated from gradients between 31.7 m and 58.5 m and from gradients between 31.7 m and 100.6 m height.

Fluxes calculated by the modified Bowen ratio method using gradients between 31.7 m and 58.5 m will be referred to as BR1 and BR2 will be used when the fluxes are based on gradients between 31.7 m and 100.6 m. Similarly, fluxes calculated by the ECG method will be referred to as ECG1 when using gradients between 31.7 m and 58.5 m and ECG2 when based on gradients between 31.7 m and 100.6m.

The ECG method is described in detail by Denmead, (2008) and Simpson et al., (1997), among others. Similar to Ficks law of diffusion, the vertical turbulent transport of CH_4 in the atmosphere F_{CH4} is given by:

$$F_{CH4}(ECG) = -\frac{1}{V} K_c \frac{\Delta C}{\Delta z},$$

where the turbulent diffusivity Kc , valid for a layer in the atmosphere, is derived from Monin Obukhov similarity theory,

$$K_c = \frac{k u_* \Delta z}{\left[\ln\frac{z_2}{z_1} - \psi_t\left(\frac{z_2}{L}\right) + \psi_t\left(\frac{z_1}{L}\right) - \int_{z}^{z^*} \Phi_t (1-\phi_t) \frac{dz}{z} \right]}$$

where ρ (kg m^{-3}) is air density , u_* (m s^{-1}) is friction velocity, $k = 0.4$ is von Karman's constant, C is CH_4 concentration (µmol mol^{-1}), z_2 (m) is upper air intake height, z_1 (m) is lower air intake height and ψ_h is the diabatic correction function for heat that applies for profiles. The function Φ_t is also the diabatic correction function but this applies for gradients. The roughness sublayer effects are expressed through ϕ_t (Mölder et al., 1999; Physick and Garratt, 1995). The integration goes from a certain height inside the roughness sublayer to the top of the roughness sublayer ($z_* = 35.9$ m). All heights are counted from the displacement height d. The diabatic correction function for heat depends on stability, which is height divided by the Obukhov length L. We used the diabatic correction function of Högstrom, (1988). V (m^{3}mol^{-1}) is volume of one mole of air.

The Bowen ratio is the ratio of sensible to latent heat exchange $\beta = H / LE$. If assuming that the diffusivities for sensible and latent heat are identical, the Bowen ratio can be determined as a ratio of temperature (T), and humidity (e) gradients, $\beta = \gamma\delta T / \delta e$, where γ is the psychometric constant. If fluxes and corresponding gradients of e.g. sensible heat, latent heat or as in this case, CO_2, are available from EC measurements the CH_4 exchange F_{CH4} can be calculated by the modified Bowen ratio (Moncrieff et al. 1997) as $F_{CH4}(BR) = F_{CO2} \frac{\Delta C_{CH4}}{\Delta C_{CO2}}$

2.4 Data processing of gradient measurements

Measurements at a specific level were conducted for five minutes at each height at the tower before the sampling was shifted to next level. The first minute at each level was always removed from the analyses due to the time it takes for the air to be exchanged in the tubing and the analyser cell. The remaining 4 minutes of measurements were averaged into 4 one-minute mean values. The 11 min long gaps in data series for a certain level were filled by interpolation before 30 minute mean concentrations were calculated.

Before calculating the fluxes, the input data were examined and concentration data with values exceeding 3 ppm for CH_4 and 800 ppm for CO_2 were removed. De-spiking of CO_2 data from EC measurements was also done. If more than 3000 errors were found in a 30 minutes data sequence consisting of 18000 values, CO_2 flux was not used because the removal of too many data might have a negative impact on the covariance (Foken, 2008). Data from January and February 2011 were excluded from the analyses due to a time synchronization problem.

When the fluxes had been calculated error estimation were made and fluxes with an estimated total error less than 20 µmol m^{-2} h^{-1} for CH_4 fluxes and 1 µmol m^{-2} s^{-1} for CO_2 fluxes value were kept for further analyses. Total errors in fluxes calculated by the BR method were estimated based on errors in CH_4 and CO_2 gradients and errors in CO_2 fluxes measured by EC method. Total errors in fluxes calculated by ECG method were estimated using errors in CH_4 gradients and errors in heat flux and friction velocity measured by EC. The maximum allowed error was 0.5 µmol m^{-2} s^{-1} for CO_2 fluxes from EC measurements, 0.3 ppm for CO_2 gradients and 0.8 ppb for CH_4 gradients, 0.05 ms^{-1} for u* and 10 Wm^{-2} for sensible heat flux.

After processing the CH_4 flux data, 40 %, 56%, 20% and 47% of data remained from BR1, BR2, ECG1 and ECG2, respectively. For CO2 fluxes, 73 % remained from ECG1 and 86 % from ECG2. Most of the daytime data had to be dismissed, due to small gradients. When data had been processed 93% of the dataset of BR2 and ECG2 consisted of nighttime data and 87 % of the dataset of BR1 and ECG1 consisted of nighttime data. Nighttime data is here defined as times when global radiation < 50 Wm^{-2}.

Multilinear regression analyses on standardized data were used to investigate the impact of environmental variables on CH_4 exchange on a seasonal time scale (Draper and Smith, 1998).

2.5 Data processing of chamber measurements

Soil CH_4 exchange by chambers ($F_{CH4soil}$) was calculated as $F_{CH4soil} = \frac{dC_{soil}}{dt}\frac{V_c}{A}$, where C_{soil} is the molar density (µmol m^{-3}), V_c (m^3) is the chamber volume and A (m^2) is ground surface-area. A linear fit of a two-minute interval of the concentration data obtained with the gas analyser, beginning immediately after chamber closure was used to retrieve dC_CH_4/dt. We calculated the r^2 values for the fits of five sequential slopes, which were lagged by 10 s intervals after chamber closure. The fit with the highest r^2 value was then selected. All fluxes with an r^2 value higher than 0.3 and root mean square error less than 0.1 were kept for further analyses. 99 % of the data passed this quality control.

2.6 Footprint analyses

An improved version of the flux footprint parameterization of (Kljun et al., 2004) was used to estimate temporally varying footprint areas to the tower instrumentation. This footprint parameterization is based on the Lagrangian stochastic particle model LPDM-B (Kljun et al., 2002) and is valid for a much broader range of atmospheric conditions than analytical footprint models are. This is especially important for measurements at heights well above the tree canopy as in the current study, where measurements can be frequently outside the surface layer.

The footprint parameterization was run based on input data from i) the Norunda flux tower at 33-m height at hourly temporal resolution: wind direction, standard deviations of the vertical and lateral wind velocity, and friction velocity; and ii) data based on an airborne LiDAR survey of the site in 2011: high spatial resolution maps of roughness length and displacement height surrounding the tower.

Here, we follow the suggestion of Horst, (1999) that the flux footprint methodology can be applied to the flux gradient approach, whereby the ‘representative measurement height‘ of the fluxes is calculated as the arithmetic mean of the two concentration measurement heights for stable stratification, and based on the geometric mean for unstable conditions. Note that Horst (1999) further pointed out that in the case of the Bowen ratio method, the flux footprint could only be derived for horizontally homogeneous fluxes.

3. Results

Errors in CH_4 concentration gradients caused the largest error in calculated CH_4 fluxes. Gradients were small most of the time, especially during the day (Figure 2a) due to strong turbulence. At night the turbulence is weak and gradients are more easily distinguished and the concentrations at different levels are distinctly different (Figure 2b). The distribution of the sizes of CH_4 concentration gradients during day and night for the processed datasets are shown in histograms in Figure 3.

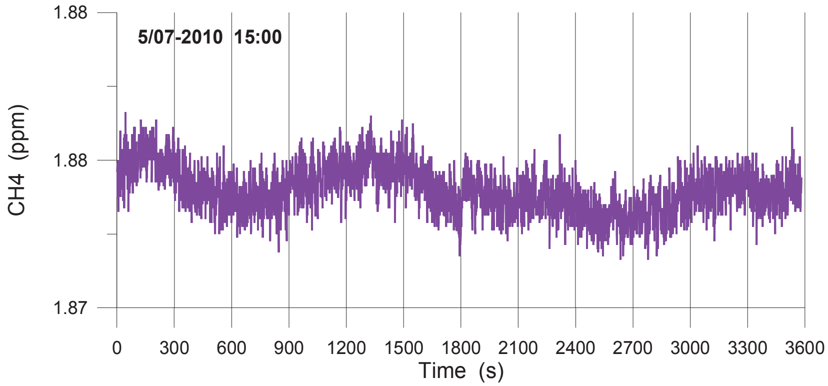

Figure 2a) Daytime CH_4 concentrations. 5 min=300s at each level starting with level 1 (=31.7 m).

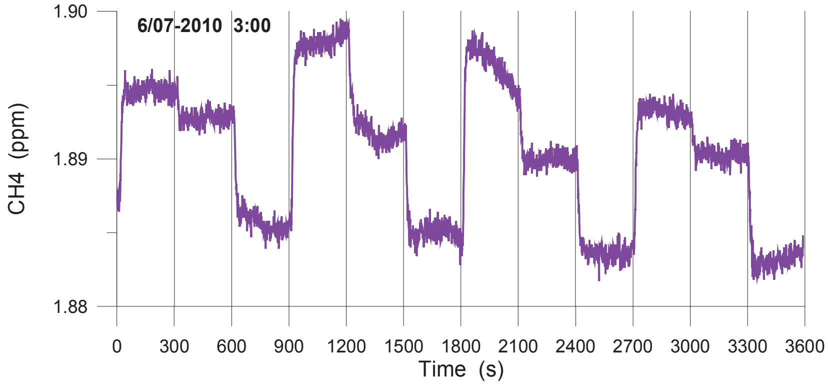

Figure 2b) The same as figure 2a, but nighttime.

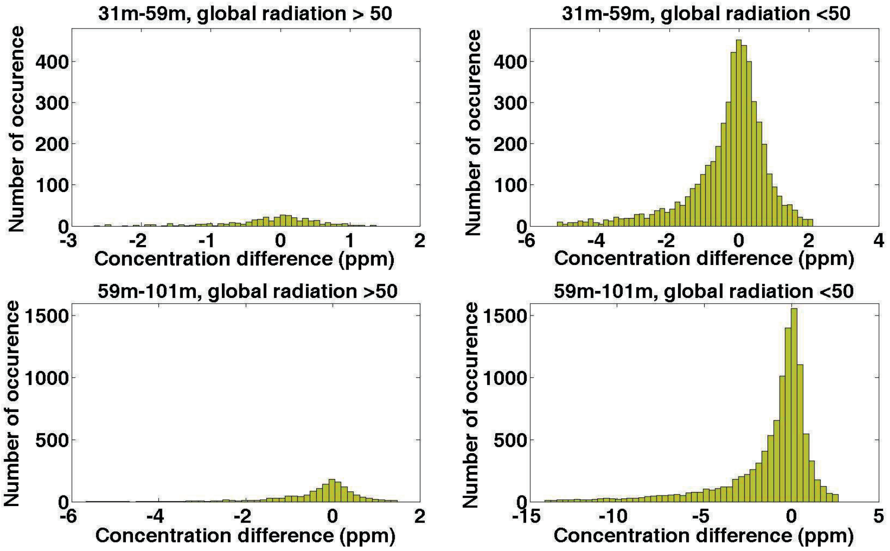

Figure 3. Occurrence of CH_4 concentration differences for different height intervals and for day and night. Data between the 2nd and 98th percentiles are shown.

Good agreements between CO_2 fluxes calculated by ECG method and CO_2 fluxes from EC measurements can be seen in figure 4. The ECG method captures seasonal and diel variations, although it tends to overestimate peak respiration values. Fluxes from the two methods are significantly correlated, $p < 0.001$ with a Pearson correlation coefficient of 0.80.

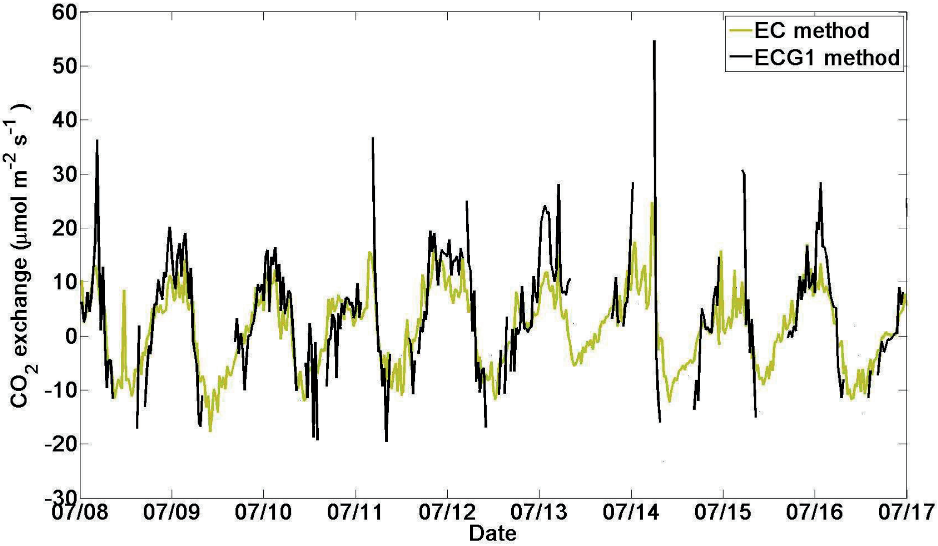

Figure 4) Comparison between net CO_2 exchange measured by the EC at 33 m and net CO_2 exchange calculated from gradients between 31m and 59 m by combined EC and gradient method in July 2010. For the ECG method, only values with good accuracy (see text), total error < 20 µmol m-2h-1, are shown.

Taking the entire measurement period and all wind directions into account the Norunda site is a net source of CH_4 according to both flux calculation methods. Mean emissions at the site were 2.57, 4.57, 1.48, 2.99 µmol m^2h^{-1} for BR1, BR2, ECG1 and ECG2 respectively. The main wind directions at the site was S to SW (Figure 5). Emissions from this direction were lower in comparison with peak emissions at NW to NE wind directions (Figure 6). The 90 % level of the footprint for gradients measured between 31.7 and 58.8 m were within 500 meter from the tower (Figure 7a) while the footprint for gradients measured between 31.7 and 100.6 m reached almost 1 km from the the tower so that part of the clear-cut was within the 50 % level of the footprint (Figure 7b), i.e. emissions from the clear-cut had a high probability to be measured from the higher level.

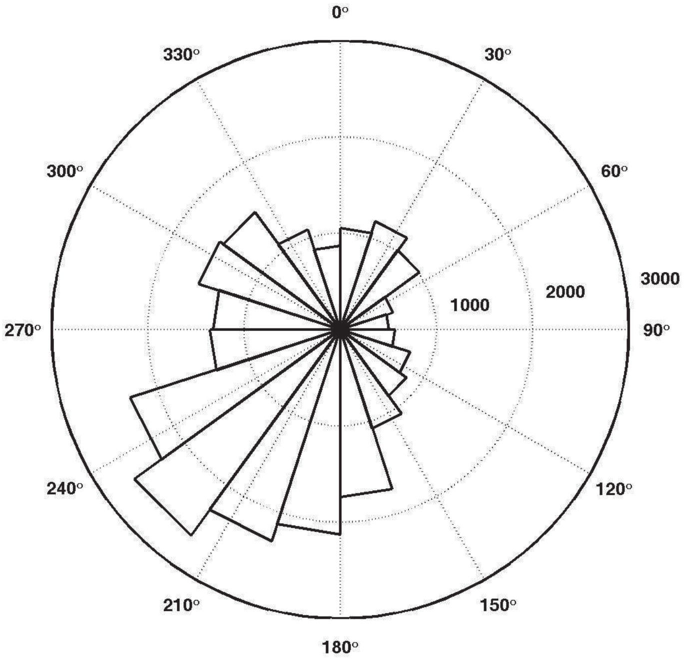

Figure 5. Distribution of the numbers of measurements observed at the tower according to wind direction quadrant.

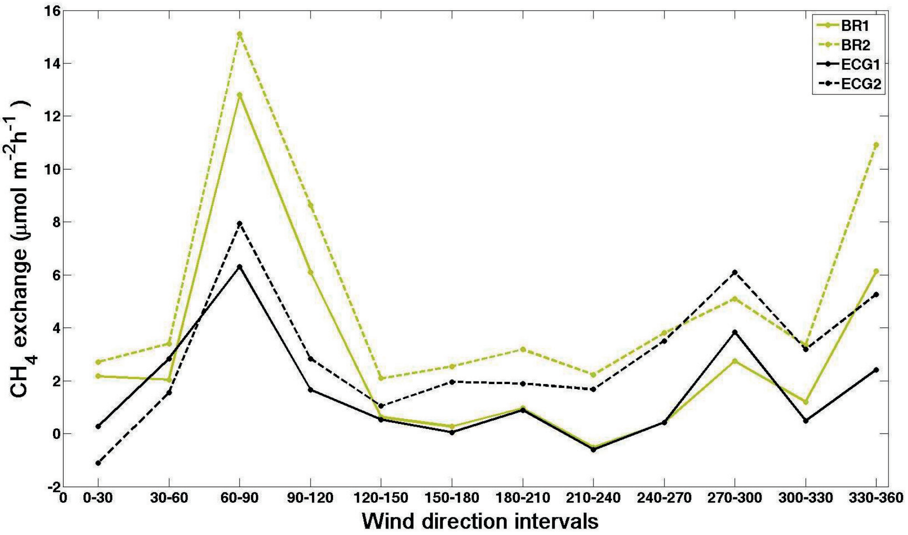

Figure 6. Average CH_4 exchange for wind directions binned in 30 degrees intervals.

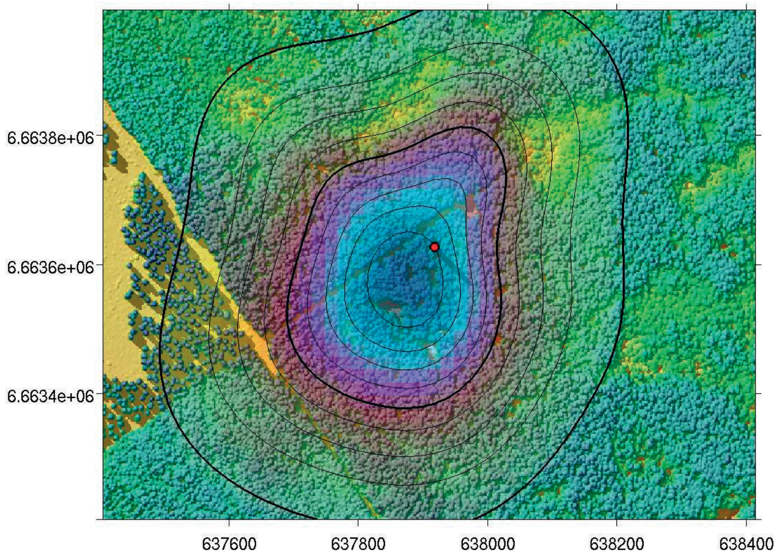

Figure 7a. Cumulative footprint climatology for the entire measurement period for gradients between 31.7 m and 58.5 m. The area between each circular line represents 10 % of the footprint. The color of the background map symbolises the canopy height, the darker the green, the higher the canopy. Coordinates: UTM, Tower location: Red dot

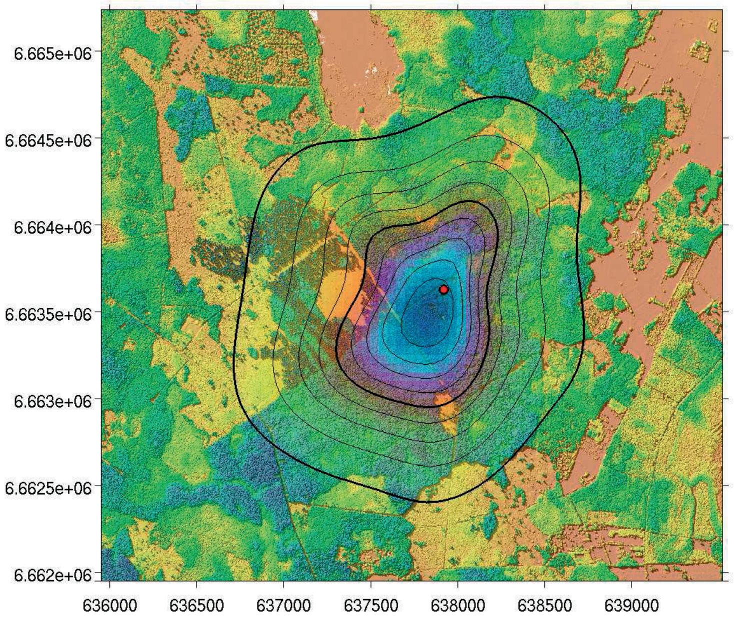

Figure 7b. Same as figure 7a but here calculated for gradients between 31.7 m and 100.6 m.

Monthly mean values of CH_4 exchange measured by the gradient method from the main wind direction, SW, where no emission peaks were found, as well as monthly mean chamber measurements from July to September 2010 are listed in Table 1. Chamber measurements indicate that the soil is a sink of CH_4 of around -10 µmol $m^{-2}h^{-1}$, which is similar in magnitude to previously reported forest soil uptake rates (Smith et al., 2000). The mean monthly chamber fluxes were in the range -9.0 to -11.7 µmol $m^{-2}h^{-1}$ during July to September 2010 while the gradient methods during the same period ranged between -2.7 µmol $m^{-2}h^{-1}$ (ECG1 August 2010) and +5.9 µmol $m^{-2}h^{-1}$ (BR2 & ECG 2 September 2010). For the whole measurements period, the CH_4 exchange measured by gradient methods ranges from a minimum uptake of -4.0 µmol $m^{-2}h^{-1}$ in August 2011 by BR1 to maximum emissions of 8.7 µmol $m^{-2}h^{-1}$ in June 2010 by BR2. According to BR1 and ECG1 there is a net average CH_4 uptake for the months August 2010, December 2010, May 2011, July to September 2011 and November to December 2011 (Table 1). BR2 and ECG2 show reduced emissions for most of these months except for summer 2011 (Table 1).Weekly average values of CH_4 exchange by BR1 and ECG1 from the main wind direction and environmental conditions at the site for the entire measuring period are shown in figure 8. There was no clear correlation between CH_4 fluxes and the different environmental drivers although there was a tendency that negative fluxes mostly coincided with the minimum in ground water table and that the largest positive fluxes in 2011 coincided with the peak in ground water table.

Table 1. Monthly mean values of CH_4 exchange for main wind directions, 180°-240° , which are free from well-known larger source areas.

	BR1	BR2	ECG1	ECG2	Chambers
	CH_4 exchange (µmol m^{-2} h^{-1})	CH_4 exchange (µmol m^{-2} h^{-1})	CH_4 exchange (µmol m^{-2} h^{-1})	CH_4 exchange (µmol m^{-2} h^{-1})	CH_4 exchange (µmol m^{-2} h^{-1})
Jun 2010	7.5	8.7	4.0	8.0	-
Jul 2010	1.95	5.6	1.2*	3.8	-11.7
Aug 2010	-1.7	2.1	-2.7	2.4	-9.8
Sep2010	3.9	5.9	2.5	5.9	-9.0
Oct 2010	2.7	5.3	4.1	5.5	-
Nov2010	0.7*	2.8	-0.7*	3.0	-
Dec2010	-1.6	1.7*	-1.9	1.1*	-
Mar 2011	0.3*	3.5	1.0	2.2	-
Apr 2011	3.1	3.9	5.9	6.6	-
May 2011	-0.3*	1.7	-1.4*	1.2	-
Jun 2011	0.2*	5.2	1.1*	3.9	-
Jul 2011	-1.2*	1.3*	-1.2*	0.1*	-
Aug 2011	-4.0	1.1*	-3.7	1.8	-
Sept2011	-2.7	1.1*	-1.6*	0.4*	-
Oct 2011	0.3*	0.9*	0.1*	0.2*	-
Nov 2011	-1.1	-0.1*	-1.4	-1.4	-
Dec 2011	-1.4	0.4*	-3.1	-0.4*	-

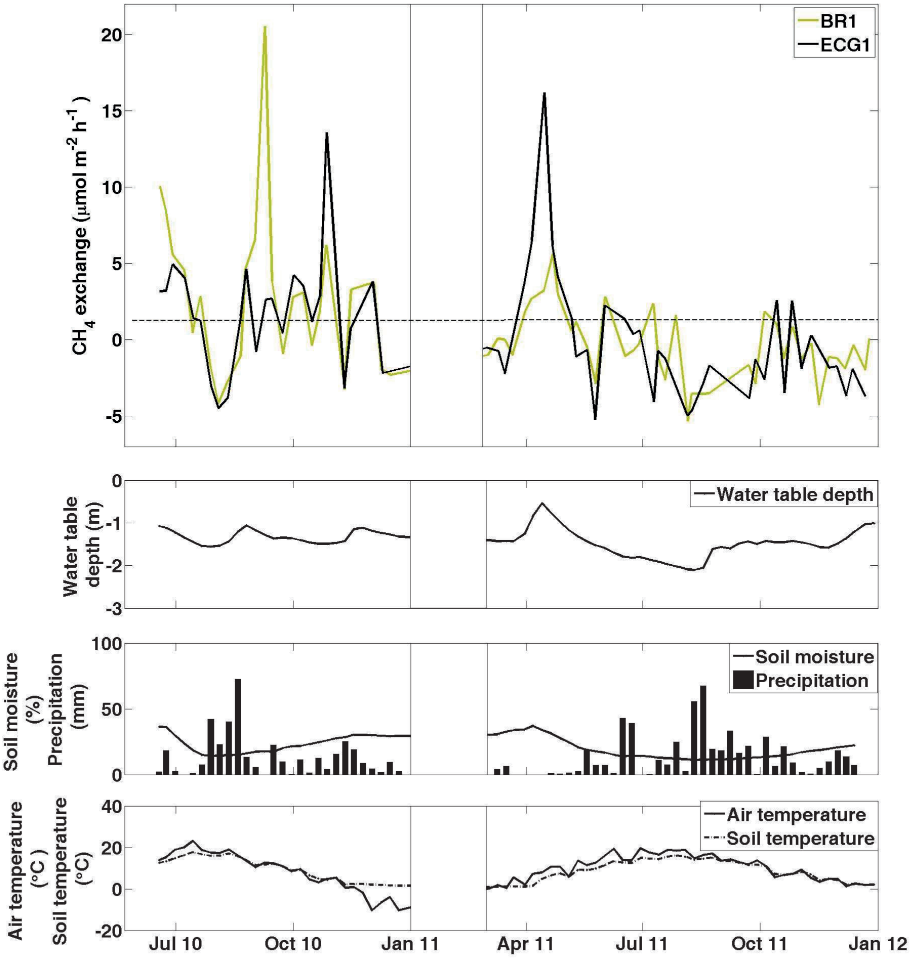

Figure 8. Weekly mean values of CH$_4$ exchange, water table depths, soil moisture, precipitation, air temperature and soil temperature.

Diel variations in CH_4 exchange were apparent when data were binned hourly (Figure 9). CH_4 emissions were maximum just before dawn (ca 05:00) local time and then decreased during the day to minima in late afternoon 15:00-18:00 local time. The diel pattern was evident in fluxes derived by both BR method and ECG methods but was most pronounced for BR1. The amplitudes of the diel variation in CH_4 exchange curves were on the order of 5-8 $\mu molm^{-2}h^{-1}$. We looked closer at diel variations of BR1 since it has a more homogenous footprint than BR2 and ECG2 and because more daytime values of CH_4 exchange (n=xx) passed the data filter than for ECG1 (n=yy). Seasonal variations in diel pattern of BR1 are illustrated in Figure 10. Correlations between hourly-binned CH_4 exchange for BR1 and hourly-binned soil temperature, air temperature, gross primary production (GPP) and vapor pressure deficit (VPD) are listed in table 2. Significant correlations, $p<0.05$, were found for all variables depending on season. Correlations were strongest for air temperature and GPP. Soil CH_4 exchange measured by chambers does not show a consistent diel pattern (Figure 11).

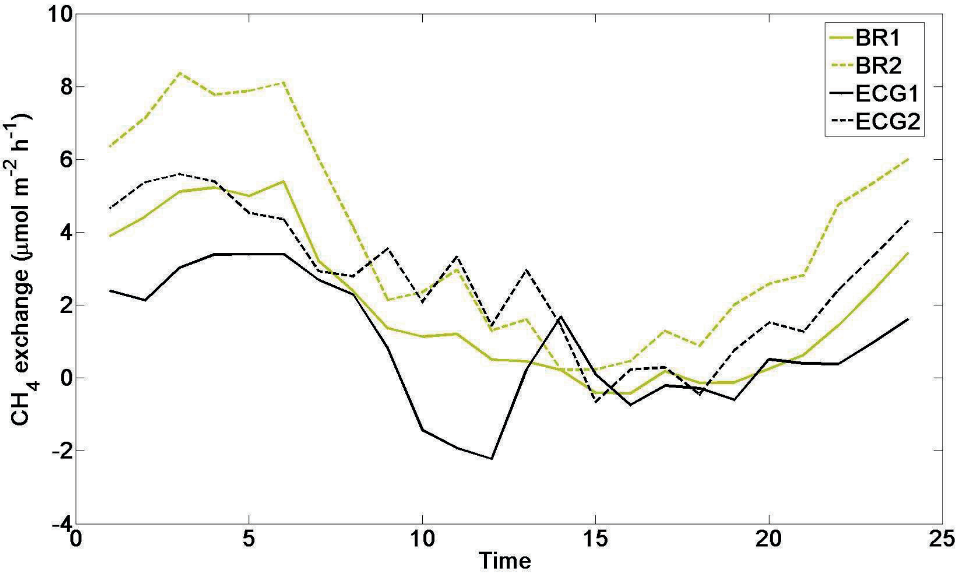

Figure 9. Diel pattern of CH_4 exchange binned hourly for the entire measurement period.

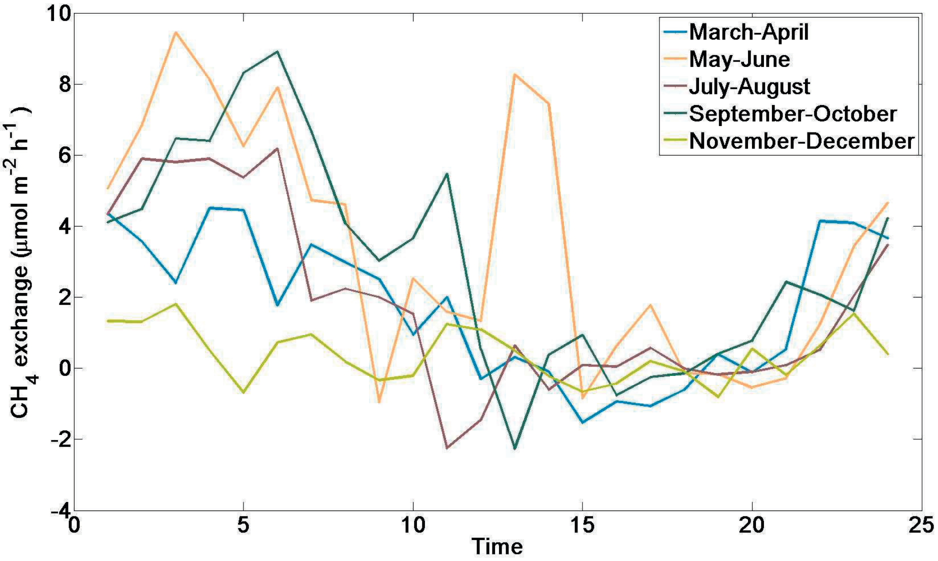

Figure 10. Seasonal diel patterns of CH$_4$ exchange.

Table 2. Pearson correlations between hourly-binned CH$_4$ exchange and hourly-binned air temperature, soil temperature, GPP and VPD. * significant at $p<0.05$, ** significant at $p<0.001$

	Air temperature	Soil temperature	GPP	VPD
Mar-Apr	-0.46*	0.48*	0.85**	-0.68**
May-Jun	-0.54**	-0.32	0.49*	-0.46*
Jul-Aug	-0.77**	-0.56*	0.80**	-0.58*
Sep-Oct	-0.81**	-0.46*	0.68**	-0.68**
Nov-Dec	-0.24	-0.16	0.24	-0.17
Total	0.23	0.51*	0.88**	-0.54*

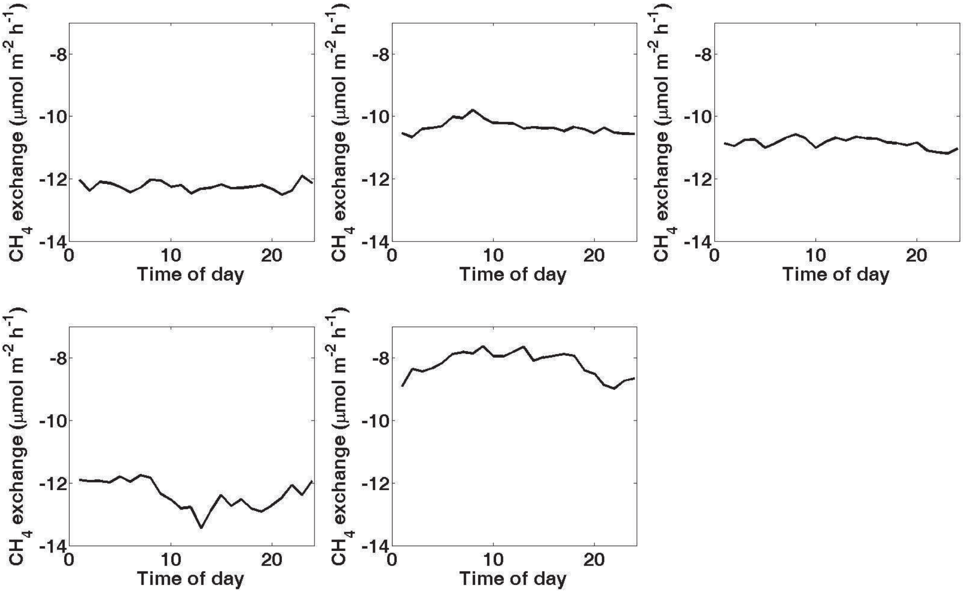

Figure 11. Diel patterns of soil CH_4 exchange measured by chambers, 7 July – 31 September 2010. Each panel illustrates data from a different chamber.

Result from multiple linear regression analyses on CH_4 exchange measured by gradient methods varied depending on method used. Combinations of air temperature, soil temperature, soil moisture, water table depth, CO_2 exchange and GPP could only explain 10-30 % of variations in CH_4 exchange (Table 3). Of the explanatory variables taken into account, CO_2 exchange had the strongest affect on CH_4 exchange for BR1 and BR2, water table depth had the strongest influence on CH_4 exchange for ECG1 and soil moisture had the strongest influence on CH_4 exchange for ECG2 (Table 3).

Table 3. Coefficients calculated by multiple linear regression analyses on standaradised data of daily mean values of CH_4 exchange and the explanatory variables air temperature, soil temperature, soil moisture, water table depth , CO_2 exchange and GPP.

n.s., the variable is not shown to significantly explain any of the variation in the CH_4 exchange.

	ECG1		ECG2		BR1		BR2	
	Jun-Sep, N=55 R^2=0.1	Total, N=190, R^2=0.1	Jun-Sep, N=65 R^2=0.1	Total, N=280, R^2=0.13	Jun-Sep, N=65 R^2=0.26	Total, N=264, R^2=0.23	Jun-Sep, N=72 R^2=0.31	Total, N=299, R^2=0.27
Air temperature	n.s	n.s	n.s	n.s	n.s	n.s	n.s	-0.2
Soil temperature	n.s	n.s	n.s	0.26	-0.25	-0.24	n.s	n.s
Soil moisture	n.s	n.s	0.26	0.41	0.27	0.19	0.24	0.36
Water table depth	n.s	0.31	n.s	n.s	n.s	0.21	n.s	n.s
CO_2	n.s	n.s	n.s	0.16	0.38	0.52	0.49	0.62
GPP	0.3	n.s	n.s	n.s	n.s	0.28	n.s	0.39

4. Discussion

Comparisons of chamber measurements and micrometeorological measurements of CH_4 exchange conducted within the same forest and during the same time period have been shown to agree well (Querino et al., 2011; Wang et al., 2013; Yu et al., 2013). However, in this study, gradient measurements above the canopy indicate that the forest is a net source of CH_4 in contrast to local small spatial scale chamber measurements showing net CH_4 uptake by the soils and leaves. The chambers are not measuring the same things as the gradients that are influenced by much larger areas or the chambers were measuring components that were only contributed weakly to the net flux. Simpson et al., (1997), report a discrepancy between CH_4 exchange measured by gradients above canopy and CH_4 exchange measured below the canopy in the vicinity of their tower. They ascribed the difference to wet patches in the forest emitting CH_4 located throughout the footprint of the above canopy measurements that they had not measured

The clear-cut, which is located within the footprint at 500 m to the WNW from the tower, is a well-characterized source area (Sundqvist et al., 2014) (Figure 7b). Higher emissions were observed when the wind was from that direction. Additional possible sources of CH_4 at Norunda are clear-cuts, lakes and wetlands at 1-2 km distance from the tower. These areas are outside the flux footprint of the gradient measurements. However, at this site, the requirement of horizontally homogeneous fluxes for application of Horst's method (Horst 1999) is not fulfilled. Keeping in mind that footprints for concentration measurements are typically 2-3 times larger than those of flux measurements, the CH_4 sources at larger distances might still contribute to some extent to the measurements. Peak emissions in E and NW directions (Figure 7b) could be explained by distant source areas if seen by both air intakes, but more probably by wet soils within the main footprint.

Emissions from the dominant wind direction are low in comparison to other wind directions and during some months a net uptake is measured using BR1 and ECG1 (Table 1). However, CH_4 uptake measured on soil surface by chambers is much higher. We are aware of patches of wetter soils and small ponds in the main wind direction and it is possible that emissions from these wet areas completely turn the site from a sink of CH_4 to a source of CH_4 as shown by BR2 and ECG2 or temporally when climatic conditions allow as shown by BR1 and ECG1 (Table1). Temporal shifts of soils from net sinks to net sources in wet periods were found in several studies (Hudgens and Yavitt, 1997; Moosavi and Crill, 1997; Sakabe et al., 2012). Observations indicate that large emissions from small source areas can shift a site from a sink to a source (Fiedler et al. 2005, Sakabe et al. 2012).

Reduced CH_4 emissions in summer, as shown in Figure 8, can be due to a decrease in water table and soil moisture that decreases the methanogenic zone in the soil and facilitates diffusion of CH_4 and oxygen to methanotrophs. In summer 2011 the water table depth had dropped on average since the snowmelt in April, which may have resulted in that some typically wet areas shifted from CH_4 source to CH_4 sinks. The positive effect of decreases in water table and soil moisture on methanotrophic uptake might outweigh an increase in CH_4 emission due to increases in soil temperatures which could have been expected otherwise. Peak emissions coincide with a high water table as observed following precipitation and snowmelt that can be seen in June 2010, September 2010 and April 2011. A dependency of the CH_4 exchange on water table depth is shown by multiple linear regression analyses for BR1 and ECG1 considering the entire measurement period.

Quantitative linkages of below canopy processes with measurements that are made above the canopy are difficult to make. In addition, since all air intakes for the gradient measurements are positioned above the canopy it is not possible to distinguish soil emissions from within canopy exchanges. Most MM studies have not detected substantial aerobic CH_4 emissions from vegetation (Bowling et al., 2009; Querino et al., 2011; Ueyama et al., 2012; Wang et al., 2013). However microbial production of CH_4 in wet heartwood of trees have been known for at least 40 years (Zeikus and Ward, 1974) and trees can transport and release CH_4 from soil water (Gauci et al., 2010; Terazawa et al., 2007). Mikkelsen et al., (2011) found indications for CH_4 emissions from a beech forest stand during a period with low wind conditions.

Laboratory studies have shown that aerobic CH_4 emissions from vegetation could be triggered by UV radiation and heating (Vigano et al., 2008), but emissions in absence of UV has also been measured, although at much lower rates (Bruhn et al., 2009). If canopy emissions caused by high UV-radiation were a major contribution to CH_4 exchange at the Norunda site, we would expect the emissions to peak during daytime and not at night as observed in this study (Figure 9).

Diel variations in CH_4 exchange at the site show approximately the same pattern regardless of season, except for November-December where no diel pattern is found. Emissions are highest in the night or early morning and lowest emissions in the afternoon (Figure 10). The nighttime maximum is not likely to be due to venting below canopy storage depletion as was observed by Querino et al., (2011) because CH_4 gradients change gradually. Pattey et al., (2006) measured net CH_4 emissions at a boreal forest site using a gradient method and assigned higher daytime temperatures to be the cause of higher emissions. Since net CH_4 emissions dominate above the canopy at Norunda, we might expect to see the same daytime enhancements due to temperature dependence of methanogens, but for most of the seasons CH_4 exchange is observed to be negatively correlated with temperature (Table 2) suggesting that processes other than temperature dependent production are affecting the net flux.

The lower CH_4 emissions at Norunda site might be due to an increased soil uptake by methanotrophs. Diel trends with maximum CH_4 uptake around noon were found at sites where consumption dominates the CH_4 exchange (Sakabe et al., 2012; Smeets et al., 2009; Wang et al., 2013). Wang et al., (2013) explained the increased daytime uptake with increased turbulence during day that facilitated the transport of CH_4 to the methanotrophs in the soil, while Sakabe et al., (2012) found a dependency of the diel amplitude on air temperature. We know from chamber measurements (Sundqvist et al., 2014) that we have a CH_4 sink in the well aereted forest soil which could benefit from both increased turbulence and increases in soil temperatures. However, the chamber measurements do not show a consistent diel pattern (Figure 11).

Plant uptake could contribute to the observed diel pattern of CH_4 exchange. A net uptake of CH_4 by shoots and leaves of spruce, pine, rowan and birch have been measured at the same site in Norunda (Sundqvist et al., 2012). The uptake increased with increasing photosynthetically active radiation (PAR). Just as with CH_4 emissions we have no means to distinguish an uptake by soil from an uptake by vegetation. However, the diel curve of CH_4 exchange correlates with GPP (Table 2). Because the day to night variation in GPP is largely controlled by radiation, we cannot exclude that the diel CH_4 variations can be affected by an uptake by vegetation.

5. Conclusions

Subtle gradients, especially during daytime, coupled to cumulative error due to ambient variability and instrumentation limitations considerably reduced the number of measurements during data processing. Good agreements between CO_2 fluxes calculated by ECG method and CO_2 fluxes measured by EC method indicate that the ECG method should be reliable also for CH_4 fluxes. Fluxes calculated by BR method and ECG methods are in similar order of magnitudes. According to both BR and ECG methods, the site is a net source of CH_4 of 1.48-4.57 µmol $m^{-2}h^{-1}$. This is not consistent with chamber measurements in the study area which indicate that the soil is a net sink of CH_4 of –10 µmol $m^{-2}h^{-1}$. The only well characterized source area within the footprint of the tower is a clear-cut area, only a minor part of it located within the 50 % footprint level for ECG2 and BR2. Large emissions contributions from smaller wet patches within the forest might turn the site from a sink to a source despite an uptake in the well aerated soil. Since all air intakes are positioned above the canopy it is not possible to distinguish between soil CH_4 exchange and any canopy CH_4 exchange. The CH_4 exchange follow a clear diel pattern, with higher net emissions at night and lower net emissions in the afternoon. The decrease in net emissions during afternoon hours might be a result of an uptake by the canopy since the diel pattern of CH_4 exchange correlates with both GPP and VPD which indicates that there might be a coupling between the CH_4 exchange and photosyntheses.

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Paper IV

Upscaling of soil methane exchange in a boreal forest using chamber measurements and high-resolution LiDAR elevation data

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Abstract

Forest soils are generally considered net sinks of CH_4 but fluxes vary spatially depending on e.g. soil conditions. Measuring CH_4 exchange with chambers, which are commonly used for this purpose, might not give a representative picture of fluxes at the site. Methods for upscaling CH_4 fluxes to site scale are therefore needed. At the boreal forest research site, Norunda, chamber measurements on soils and vegetation indicate that the site is a net sink of CH_4, while tower gradient measurements indicate that the site is a net source of CH_4. Upscaling of soil CH_4 exchange for a 100 ha area was made to obtain a value of the net soil CH_4 exchange valid for the entire site and to further investigate the discrepancy between the measurement methods. The upscaling was made based on an empirical model derived from chamber measurements of CH_4 exchange and measurements on soil moisture, soil temperature and water table depth. High-resolution LiDAR elevation data were used to generate raster of soil moisture and water table depths of the study area, which were used as input data for the upscaling. Despite the simplistic approach, the model predicted fluxes that correlated to chamber fluxes used in the evaluation process. Modeled fluxes were significantly correlated to four out of five chambers with $R > 0.68$. The upscaling showed that the area was a net sink of CH_4 of -10µmol $m^{-2}h^{-1}$, averaged over the entire study area and time period.

1. Introduction

The only well characterized biospheric sink for CH_4 is oxidation by methanotrophic bacteria in soil (Harriss et al., 1982). Globally this soil CH_4 sink was estimated to 28-32 Tg CH_4 yr^{-1}, which is about 5% of the destruction of CH_4 by OH radicals in the troposphere (Kirschke, 2013). Forest soils are generally considered to be net sinks of CH_4 with higher uptake rates than grassland and arable land (Boeckx et al., 1997; Dutaur and Verchot, 2007). However, CH_4 production by archeans usually dominates in anaerobic forest soil environments such as waterlogged soils (Christiansen et al., 2012; Jungkunst et al., 2008; McNamara et al., 2006). CH_4 production also takes place in well-aerated soils at anaerobic micro sites (Fischer and Hedin, 2002; Kammann et al., 2009) and in deeper soil layers where anaerobic conditions occur (Kammann et al., 2001). Hence consumption and production can occur simultaneous at one location and soil conditions will determine what direction the net flux will have. Vegetation might also contribute to the CH_4 exchange of a forest. Trees have been found to transport CH_4 originating from soil water, which is released through the stem or foliage (Terazawa et al. 2007) and aerobic formation of CH_4 in green plants has been observed (Keppler et al. 2006).

Soil CH_4 exchange is further known for large spatial and temporal variability (Christiansen et al., 2012; Ishizuka et al., 2009; Konda et al., 2008; Lessard et al., 1994; Reay et al., 2005; Yu et al., 2008). Spatial variability can be due to e.g. variability in soil moisture, soil texture and water table depths, factors that are dependent on e.g. topography, vegetation and soil type. Soil moisture (Castro et al., 1994; Guckland et al., 2009; Lessard et al., 1994) and soil texture (Dorr et al., 1993; Dutaur and Verchot, 2007; Ishizuka et al., 2009) alters soil diffusivity, which controls the rate at which atmospheric CH_4, and oxygen is supplied to the bacteria. Water table depth alters the relative extent of aerobic and anaerobic zones in soils. A rise of the water table leads to a decreased oxic soil zone and thus a decreased CH_4 uptake (Kammann et al., 2001; Roulet et al., 1992). Changes in soil temperature and precipitation are responsible for temporal variability in CH_4 exchange. Increases in temperature stimulate the activity of both methanogens (Yvon-Durocher et al., 2014) and methanotrophs (Crill et al., 1994; King and Adamsen, 1992), although methanogens benefit more (Dunfield et al., 1993). Other factors that have been found to influence soil CH_4 exchange in forests are soil pH (Weslien et al., 2009) and nitrogen availability (Steudler et al., 1989).

In situ chamber measurements and soil incubations in laboratories have long been the dominating methods for studying CH_4 exchange in forests, although larger scale micrometeorological methods probably will be used more frequently from now onwards (Nicoloni et al., 2013). While CH_4 exchange occurs and is measurable on a centimeter scale, it affects the Earth-system on a much larger scale (Schimel and Potter, 1995). Appropriate scaling of CH_4 exchange from point measurements is desirable to e.g. evaluate micrometeorological measurements, provide data to models and reduce uncertainty in source and sink contributions to regional and global CH_4 budgets (Hashimoto et al., 2011; Marushchak et al., 2013; Schimel and Potter, 1995). Extrapolations of chamber measurements or soil incubations from a few locations by just multiplying with the area of the site or region of interest, is not advisable due to the heterogeneity of forest soils.

Global and regional estimates on soil CH_4 sink strength have been made based on soil texture class (Dorr et al., 1993; Dutaur and Verchot, 2007), land use type (Grunwald et al., 2012) ecosystem class and climatic zones (Dutaur and Verchot, 2007). However, there is a risk for heterogeneity within each class and boundaries between classes might not be well characterized (Matson et al., 1989). Process-based models for global estimates of CH_4 consumption are driven mainly by gaseous diffusion or diffusion in combination with microbial activity (Curry, 2007; Del Grosso et al., 2000; Ridgwell et al., 1999). These models do not account for any production of CH_4 and are not applicable to soils that seasonally shift from net sinks to net sources (Del Grosso et al., 2000). Due to the complexity of many process-based models they require detailed input on climate, vegetation and soil physiochemical properties (Hashimoto et al., 2011). More simple empirical models for site-specific applications are sometimes developed. Castro et al (1994) found that soil moisture, as the only explanatory variable, satisfactory could predict CH_4 fluxes at locations within a temperate forest. Christiansen et al (2012) used spatial variability in soil moisture and water table depths derived from elevation data to upscale CH_4 fluxes from chamber measurements to site scale.

At the Norunda forest site, chamber measurements on soils and vegetation indicate that the site is a net sink of CH_4 (Sundqvist et al., 2012- 2014), while gradient measurements above the forest indicate that the site is a net source of CH_4 (Sundqvist et al, work in progress). The aim of this study was to quantify soil CH_4 exchange, for the entire site (100 ha) by upscaling soil CH_4 exchange using an empirical model based on chamber observations in combination with high-resolution LiDAR elevation data. We also wanted to examine the discrepancy between results obtained from chamber measurements and gradient measurements. Our hypothesis was that emissions from wet patches scattered at the site exceeds the uptake in well-aerated soils. Upscaling of forest soil CH_4 exchange has shown that emissions from wet forests should not be neglected when the CH_4 budget of a region is quantified (Christiansen et al., 2012; Fiedler et al., 2005; Grunwald et al., 2012). Even a relatively small source area can shift a larger area from a sink to a source (Fiedler et al., 2005).

2. Method

2.1 Site description

Upscaling of soil CH_4 exchange was made for a 100 ha area at the Norunda site, 60˚5 N, 17˚29 E, in central Sweden. The study time period was July through September 2010 since both soil chamber measurements and above canopy gradient measurements were available for that time period. The Norunda site is situated at the southern edge of the boreal zone and the forest consists of 120 years old mixed pine (Pinus sylvestris) and spruce (Picea abies) trees. The forest in the NE to SW sectors surrounding the measurement tower were thinned in 2008 which decreased the leaf area index from 4.8 to 2.8 m^2m^{-2} while the forest in the SW to NE sectors has not been thinned nor fertilized in a few decades. The soil is a glacial till, classified as dystric regosol (Lundin et al., 1999) with an organic layer of about 3-10 cm. The area is perceived as relatively flat, the elevation range from 40-52 m above sea level (Figure 1). Since 1843 the water table in the area has been lowered as an effect of several ditchings on a landscape scale, the last known was in 1980. Wet patches are spread in the area. Mean air temperature was 6.5° C and mean precipitation was 576 mm from 1980-2010 measured at Uppsala climate station, 30 km south of Norunda.

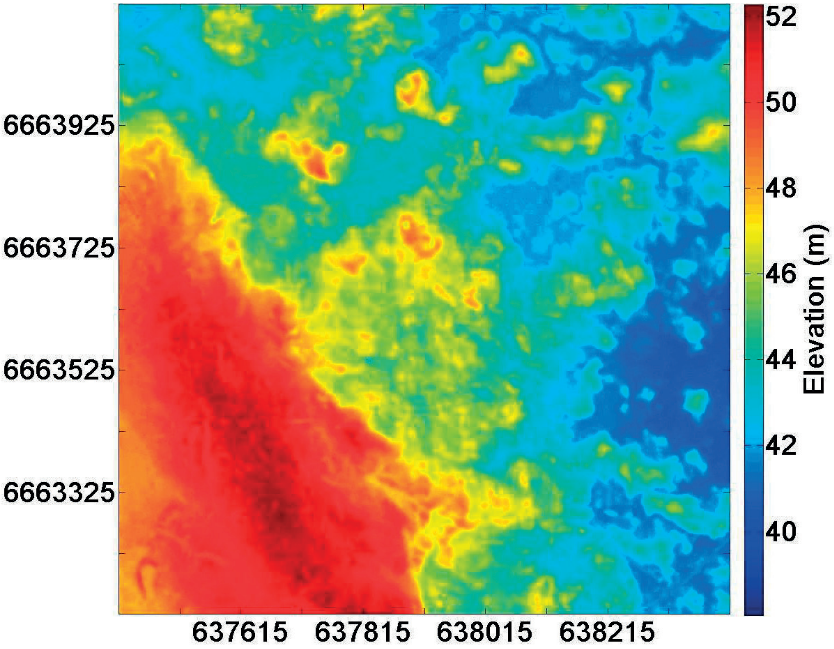

Figure 1. Digital Elevation Model (DEM) of the study area. Coordinates: UTM

2.2 Empirical model for upscaling of CH_4 exchange

The empirical model used for upscaling of soil CH_4 exchange was derived from multiple linear regression analyses (Draper and Smith, 1998) on CH_4 exchange and the main controlling variables; soil temperature, soil moisture and water table depth. Variables included in the analyses were daily averages of hourly chamber measurements conducted at the site. The regression model obtained was assumed to be valid as long as the distance to the water table was larger than 5 cm so that an oxic soil zone could enable CH_4 consumption by methanotrophs. At higher water tables, estimations of CH_4 exchange were based on chamber measurements with a floating chamber at one location on standing shallow water. A median value of 40 µmol $m^{-2}h^{-1}$ for the entire measurement period was assigned to areas with water tables above 5 cm from the soil surface. The mean value of the floating chamber was as high as 120µmol $m^{-2}h^{-1}$ due to several high (>1000µmol $m^{-2}h^{-1}$) flux values, probably related to ebullition.

Measurements from 8 chambers, three located in the thinned section, T1-T3, and five located in the undisturbed section of the forest, U1-U5, were available for developing and evaluating the empirical model. Due to equipment limitations, measurements were conducted at one plot at a time. Daily averages of hourly chamber measurements for the time periods 1 August to 30 September 2009 at the thinned plot and 7 July to 30 September 2010 at the undisturbed plot were included in the analyses. Measurements on standing water were conducted with one floating chamber on shallow water in the thinned sector of the forest. Different combinations of chamber measurement were tested when the empirical model was derived through regression analyses. Three chambers were always used for model development while the other five were used for evaluation. The model that showed the best fit between input data and regression curve and best predicted fluxes in the chambers left for evaluation were used for upscaling. Sensitivity analyses of model parameters were made by local sensitivity analyses by varying one variable at the time and keeping the other fixed (Hamby, 1994). Each parameter was changed with 20% at the time and the change in the model output was quantified.

2.3 Instrumentation

The soil chambers had a volume of 110 liters and covered a surface-area of 0.2 m^2. Concentrations in the chambers were measured with a high precision off-axis integrated cavity output spectroscopy (ICOS) laser gas-analyser (DLT-100, Los Gatos Research (LGR)). For details on the chamber measurements, see Sundqvist et al (2014). Soil temperature was measured continuously at 5 cm depth in the chambers with type-T thermocouples. Soil moisture was measured continuously in the chambers and at 7 other positions throughout the study time period in 2010 and at 9 locations from July to December 2013 (Figure 2). Soil moisture measurements were conducted at 0-5 cm depth with Ml-2x ThetaProbe from DeltaT Devices.

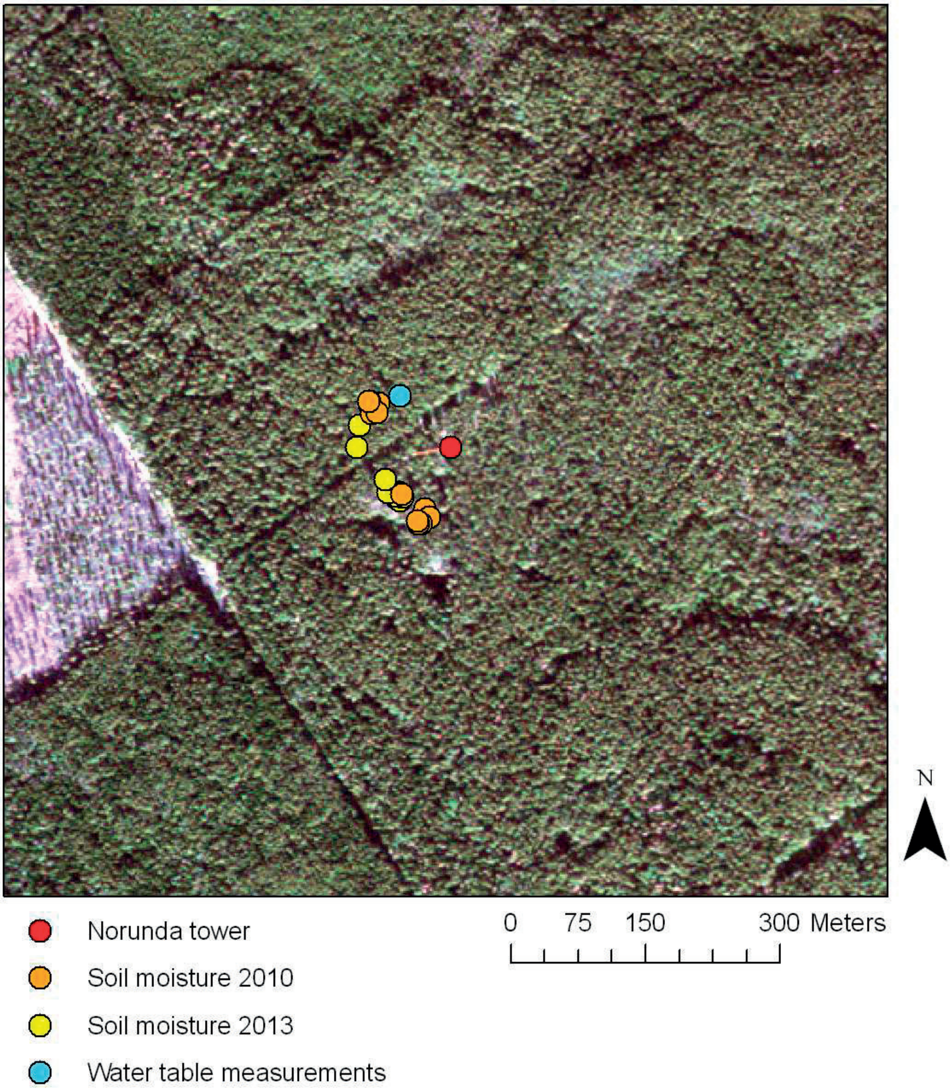

Figure 2. Photo of the study area showing locations for soil moisture measurements, water table measurements and the Norunda tower. The clear-cut can be seen to the left.

2.4 Model input

For upscaling of soil CH_4 exchange to site level, spatial information of soil moisture, water table depth and soil temperature was needed as input. Soil temperature at the site has shown to be relatively constant in space so only temporal variations in temperature were accounted for. Spatial information of soil moisture and water table depth were estimated based on airborne-LiDAR data collected in June 2011.

The LiDAR data had a vertical resolution of <20 cm and was interpolated with an inverse distance weighted algorithm (Hopkinson et al., 2005) to generate a digital elevation model (DEM) with a cell size of 1 x 1 m (Figure 2). A topographic wetness index (TWI) was derived based on this DEM. Since the breakthrough of TWI in modelling (Beven and Kirkby, 1979), it has been used for estimation of many hydrological features, including unsaturated zone soil moisture (Lin et al., 2006; Schmidt and Persson, 2003; Western et al., 1999). Beldring et al., (1999) demonstrated that in the case of forested areas, the spatial patterns of soils moisture can be estimated more accurately by topography alone than with hydrological state measurements, as these provide a too large variability in sparsely distributed measurements. TWI is calculated as $TWI = \ln(A / \tan\beta)$, where A is the upslope area (m^2) being drained through the position of interest, and β is the slope angle (degrees) of that position (Beven and Kirkby, 1979). In the present study the flow routing and the drainage area (A) have been calculated in a multiple flow direction algorithm that take the shape of the slope into account (Pilesjö et al., 2006; Pilesjö et al., 1998). The TWI was converted to soil moisture through a relationship found by linear regression between TWI and soil moisture measured at the 12 positions in 2010 (Figure 2). TWI was also evaluated against the soil moisture measured in 2013 (Figure 2).

The DEM was also used to estimate the spatial variation in water table depth. Since continuous measurements of water table depth were available only at a single position within the study area a smoothed ground surface was used to represent the water table. It has been shown in a number of studies that there is a direct relationship, especially in small catchments (Lamb et al., 2001), to a topographical variation in upslope versus downslope areas of the fit between the surface and the groundwater table (Molénat et al., 2005; Seibert et al., 1997). The smoothened ground surface area was lowered in each cell with the water table depth obtained from the one measurement location. The elevation values' spatial autocorrelation were plotted in semi-variograms in which the spatial dependency of elevation was estimated. The geomorphology of the area was studied in aerial imagery and within the DEM. The average measure from valley bottom to hilltop to valley bottom of the ground surface and the results of the spatial auto-correlation formed the base of the smoothing process. The smoothened ground surface was obtained by applying a low-pass filter that averaged the elevation values up to a distance where the spatial auto-correlation of elevation declined.

Tree height derived from the LiDAR data was used to visually evaluate the generated soil moisture and water table depths since trees are known to grow slower in wet soils (Heiskanen and Makitalo, 2002; Koslowski, 1997; Polacek et al., 2006).

3. Results

3.1 Empirical model

The validity of the empirical model differed depending on the combination of chamber data used for developing the model (Appendix 1). This was also the case for the correlation between modeled fluxes and fluxes from chambers used for evaluation of the model. The model with highest fit (R^2) to input data and highest correlation with evaluation data (R), was chosen for upscaling of the CH_4 exchange. The model with the overall best performance had an R^2 of 0.8 and R values of 0.85, 0.72, 0.94, 0.68 and 0.15 (Appendix 1) for U1, U2, U5, T1 and T3, respectively. The R value for T3 was not significant. Uptake values were overestimated for U1, U4 and T3 and underestimated for U5 (Figure 3). Sensitivity analyses showed that the model was equally sensitive for changes in water table depth and soil temperature and less sensitive to changes in soil moisture. A 20 % change in parameter values resulted in 9.1%, 9.2% and 2.7 % change in net CH_4 exchange for water table depth, soil temperature and soil moisture, respectively.

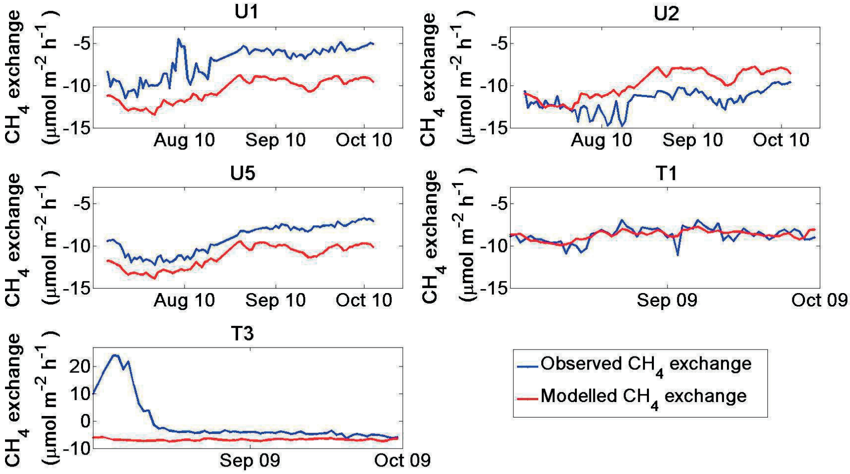

Figure 3. Comparison between modelled and observed CH_4 exchange for the evaluation chambers. * not significant at $p < 0.05$

3.2 TWI and soil moisture

TWI and soil moisture were positively correlated with R values ranging from 0.1-0.7 in 2013 and 0.2-0.7 in 2010 (Figures 4a-b). The correlation coefficients were higher on average in 2013 (Figure 4a). Correlations were not significant due to the limited number of soil moisture measurements. P-values for 2010 were generally < 0.2 (Figure 4c). When soil moisture was decreasing after a precipitation event, the correlation between TWI and soil moisture increased slightly (Figure 4d). A map of TWI is shown in Figure 5. Spatio-temporal variability in soil moisture generated from the relationship between TWI and soil moisture mesurements were on average between 14.7- 22.3 % for 96 % of the data (Figure 6). Daily input data from soil moisture measurements varied between 5-35 %.

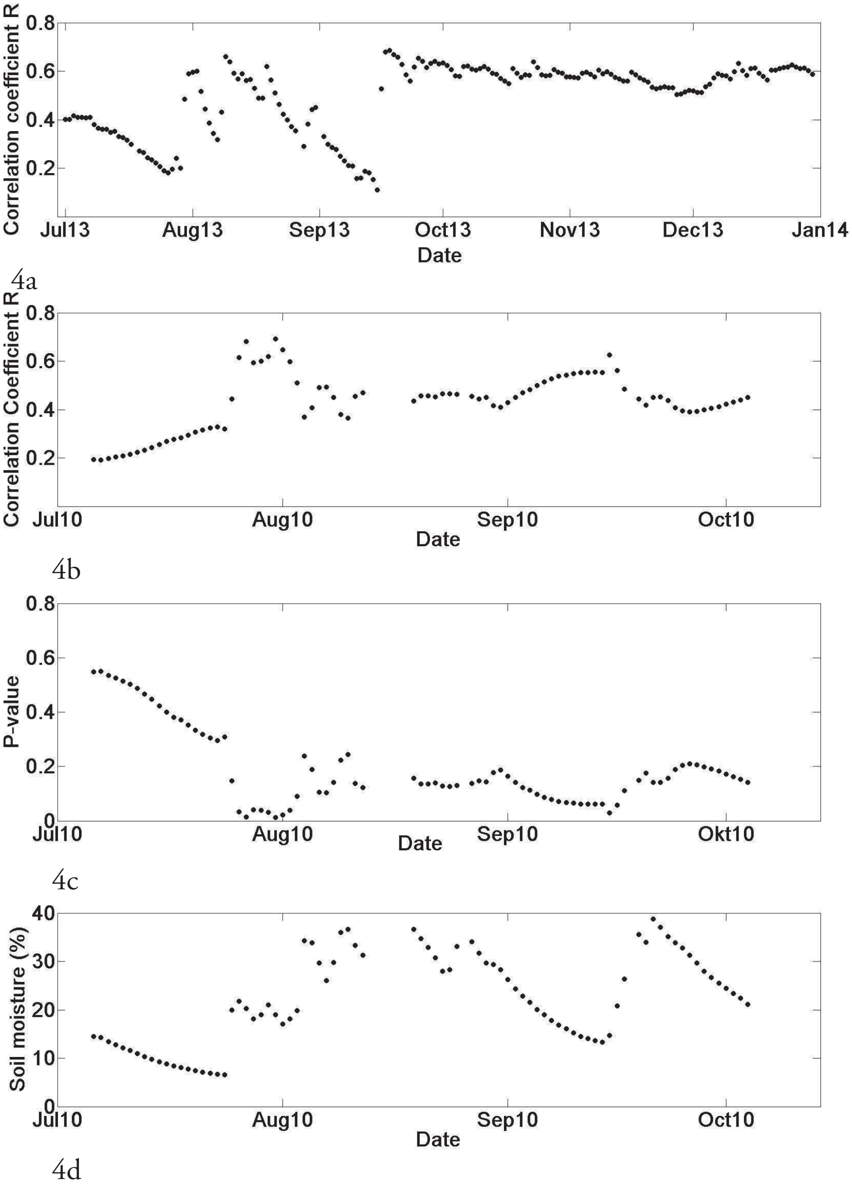

Figure 4. Daily correlation between TWI and soil moisture measured at a) 9 locations July- December 2013; b) 12 locations July-October 2010; c) daily significance level for correlations between TWI and soil moisture measured at 12 locations July-October 2010; and d) daily soil moisture for the time period July-October 2010.

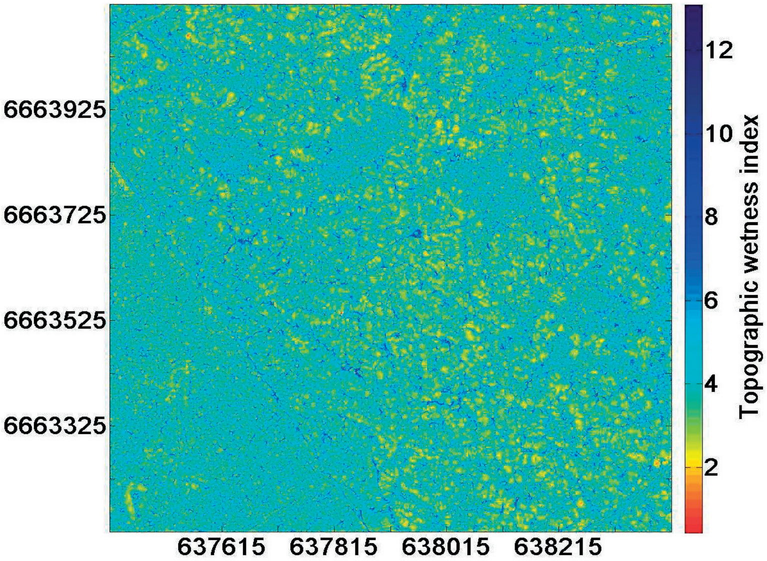

Figure 5. Map of TWI for the entire study area, averaged over the study time period.

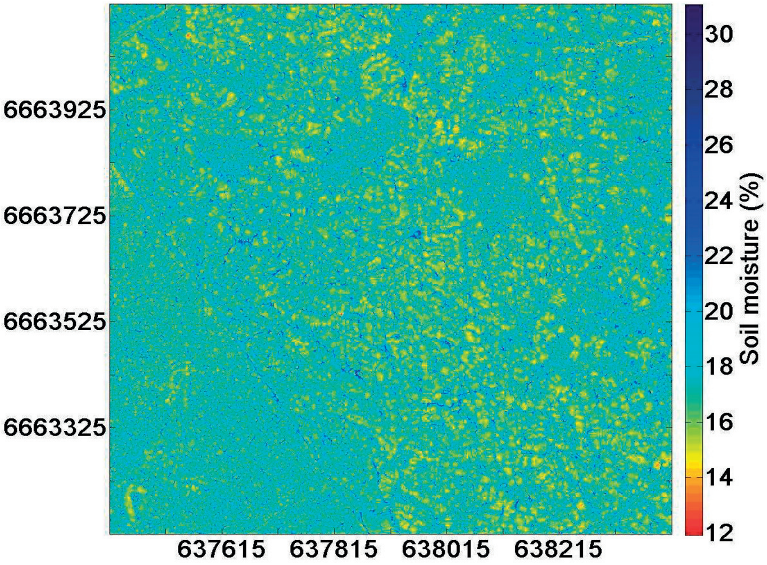

Figure 6. Map of soil moisture for the entire study area, averaged over the study time period.

3.3 Water table depth

For each 1m x 1m cell, the spatial dependency of elevation on the water table was estimated to be 80 meters. A water table surface was generated applying a low-pass filter on the DEM that averaged the elevation values taking 80 m surroundings into account. The ground water measurements were used to let this filtered water table fluctuate temporarily. Spatio-temporal variability in water table ranges on average from -5 m below ground to 0.7 m above ground if excluding outliers, with 2 and 98 percentiles of –2.9 m and –0.27 m. A few wet patches with standing water are shown in the map of modelled water table depth averaged over the study time period (Figure 7). A map of the tree height in the study areas is shown in Figure 8. It can be seeen that areas with lower than average tree heights coincide with areas with higher than average soil moisture and higher than average water tables.

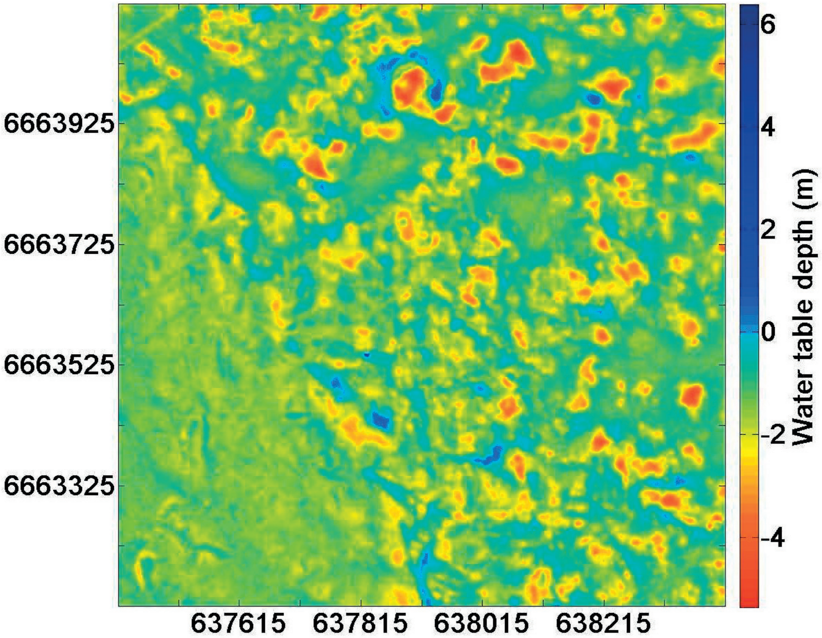

Figure 7. Map of water table depth in the study area, averaged over the study time period.

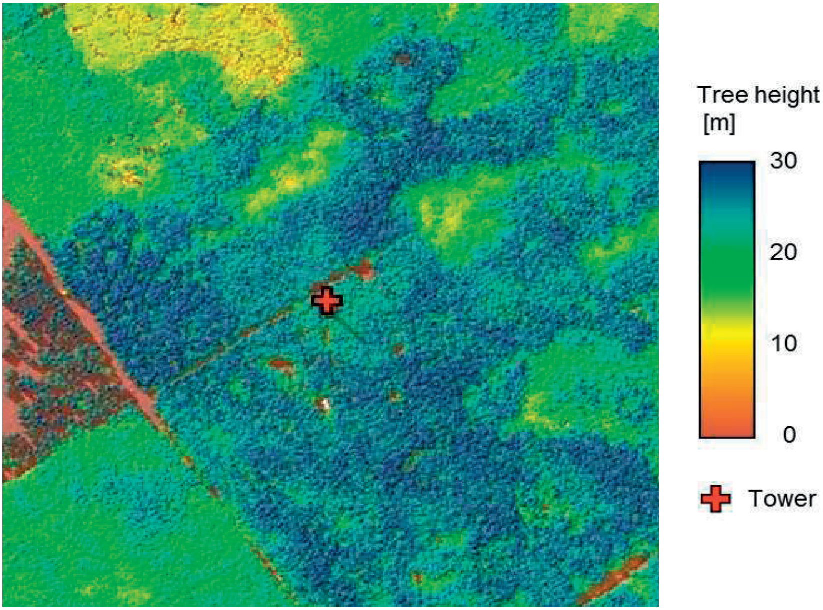

Figure 8. Tree heigh in the study area.

3.4 Upscaled CH_4 exchange

Modelled net CH_4 exchange (derived as described in section 2.2) of the entire study area and time period is –10.0 µmol m^{-2} h^{-1} with a standard deviation of 0.8 µmol m^{-2} h^{-1}. However, the average CH_4 exchange for the entire measurement period varies spatially between uptake values of -21 µmol m^{-2} h^{-1} and the assigned production value of 40 µmol m^{-2} h^{-1} for areas with standing water (Figure 9). Net average emissions are found for 1.75% of the study area. Time series of daily averaged CH_4 exchange, soil moisture soil temperature and water table depth are shown in Figure 10. Over the course of the measurement period, net CH_4 uptake decreased along with decreased soil temperatures.

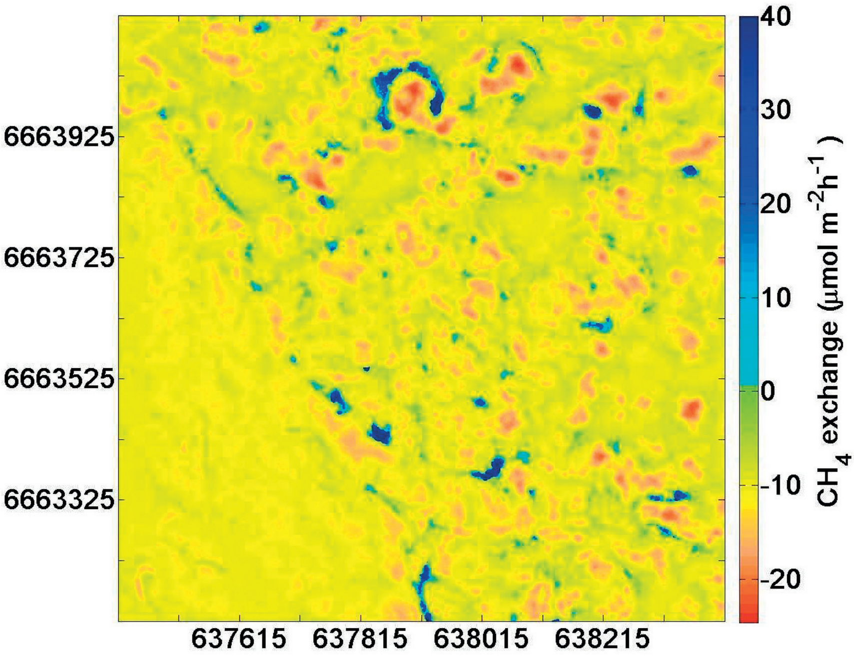

Figure 9. Map of CH_4 exchange in the study area, averaged over the study time period.

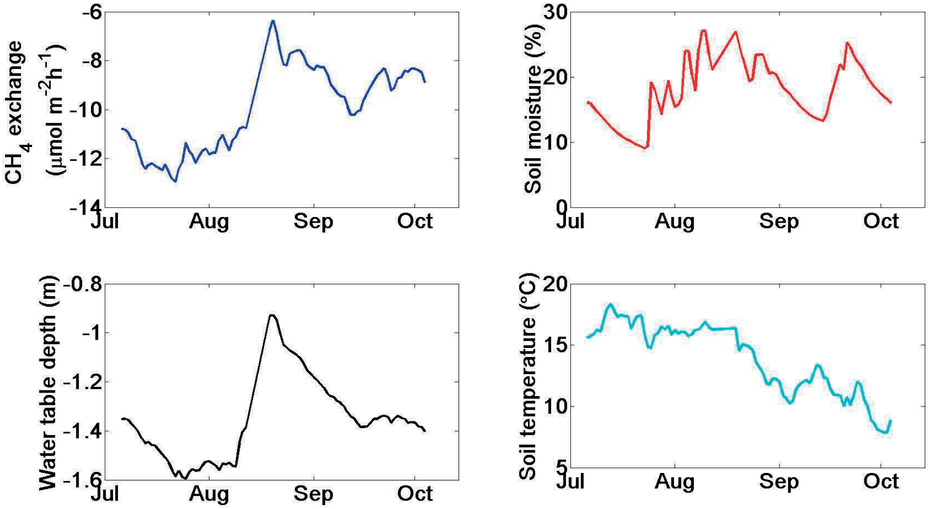

Figure 10. Time series of CH_4 exchange, soil moisture, water table depth and soil temperature, spatially averaged over the study area.

4. Discussion

Although the empirical model for upscaling of CH_4 exchange only includes data from three chamber locations and is driven by the three variables, soil temperature, water table depth and soil moisture it results in good agreement between modelled and measured fluxes. However the model seems unsuccessful in capturing local deviations in CH_4 flux behaviour such as the sudden shift from sink to source of chamber T3 (Figure 3). The shift is probably due to a high soil moisture level following precipitation (Sundqvist et al 2014). Since the model is less sensitive to changes in soil moisture than changes in water table depth and soil temperature, soil moisture driven events might not be fully captured.

The general picture of modelled soil moisture and water table depths derived from LiDAR data agrees well with the qualitative picture we have of the study area. In addition, the lower tree height in areas with higher soil moisture and water tables support the hydrology patterns generated from the DEM (Heiskanen and Makitalo, 2002; Koslowski, 1997; Polacek et al., 2006). In future studies it would be desirable to base the model on more measurements on soil moisture and water table depths for a more quantitative evaluation.

We used filtering of elevation data derived from LiDAR measurements to get the general pattern of the water table in the study area and regulated the absolute depths of the modelled water table with measurements from one single location. Other studies have modelled water tables from TWI, which is highly related to topography. Siebert et al. (1997) concluded that one single location of observation of water table depth was sufficient for the calibration of an index to predict groundwater spatially distributed in a spruce forrested catchment in the west of Sweden. However, we are aware of an area with standing water in summer 2010, which was not accurately captured by the model, although the generated water table map and soil moisture map show higher than average water table depth and soil moisture for this area. The generation of the water table depth is based solely on the DEM. In nature, water table depth is also dependent on soil properties such as large pore structure, impermeable clay layers and sub-surface lateral flow in hillslopes (Grip and Rodhe, 1994; Ward and Trimble, 2004). Clay layers in Norunda soils have been observed at a few positions, but their spatial extent and general depth are unknown.

Moreover, the model was developed under conditions with a water table depth ranging from 0.9m-1.7m below soil surface. Jungkunst et al., (2008) found that CH_4 emissions of a hydromorphic forest soil increases drastically when water table is 10-20 cm from the soil surface and Fiedler and Sommer, (2000) found a threshold value of the water table at 15 cm depth for wetland soils above which production dominated the CH_4 exchange. Since the control of CH_4 production at high water tables differes from CH_4 consumption and mainly depends on substrate availability and soil temperature (Christensen et al., 2003), an additional model developed for high water tables might have improved the upscaling.

Soil moisture was quite well represented during model development with variations between 5% and 35%. However, the average spatial variation of soil moisture generated from TWI was lower. The porosity of the soil in Norunda is around 40% and in areas with standing water, the soil moisture should reach the value of the porosity. Only 0.5 % of the cells had average soil moisture above 24% and no cells had average values above 31%. This might be an effect of that wet areas with standing water are situated in parts of the landscape which are represented as flat or convex in the DEM. The water routing algorithm creates a pattern which is based only on the topography. The model might then disperse water over larger areas rather than concentrating it due to low differences in elevation values. In reality micro-topography and soil properties may drive the water distribution.

The upscaling of CH_4 exchange shows that the study area is a sink of -10.0 µmol $m^{-2}h^{-1}$, which is in the same order of magnitude as shown by chamber measurements. Even if the assigned production areas of 40 µmol $m^{-2}h^{-1}$ (for water tables depths above 5 cm) were extended to water table depths above 30 cm, the area remained a net sink of -9.1 µmol $m^{-2}h^{-1}$. Results from generation of water table depth show that 90 % of the area had a water table lower than -0.7 m, which should be well below the critical levels for CH_4 production. Christiansen et al (2012) found that maintaining a ground water table depth below 50 cm throughout their study area would shift their site from a source of CH_4 to a sink of CH_4. Assuming that an uptake of -10 µmol $m^{-2}h^{-1}$ is reasonable in well areated soils, a net production area of more than 20 % of the total area, with average fluxes of 40 µmol $m^{-2}h^{-1}$, would be necessary to shift the site from a sink to a source. This area would decrease if the production rates approaches the levels of wetland fluxes. Uptake rates decreases over the season (Figure 10) and it is possible that wetter and colder seasons would show another picture. It would be desirable to evaluate the upscaling by measuring CH_4 fluxes with soil chambers at several locations in the area. Further, spatially denser water table and soil moisture data sets would improve the water table estimations.

The results from upscaling of CH_4 exchange shows a net uptake of CH_4. This is in contrast to gradient measurements above the tree canopy in the center of the study area, which shows net CH_4 emissions (Sundqvist et al 2014, work in progress). Part of the study area for upscaling includes the outskirts of a clear-cut (Figure 2). The water table in this part of the study area his risen as an effect of decreased evapotranspiration following clear-cutting, which was not captured by the model since water table depth was calculated from elevation data alone. Chamber measurements on the clear-cut from October -November 2010 showed average emissions of 13 µmol $m^{-2}h^{-1}$ (Sundqvist et al., 2014). Emissions from the clear-cut can be part of the explanation of the discrepancy between the upscaled chamber data and the gradient measurements.

Appendix 1

Results from evaluation of empirical models for upscaling of CH_4 exchange.

a) The combination of chambers used for model devlopement, here given an ID number.

b) R2 shows how well the regression function from multiple linear regression analyses fit the chamber input data. B(T), B(W) and B(SM) are the coefficients for soil temperature, water table depth and soil moisture respectively obtained from the multiple linear regression analyses. I is the interception value. R values show how well the modelled CH_4 exchange correlates with CH_4 exchange of evaluation chambers. *) not significant at p >0.05. n.i) not included since it is does not significantly contribute to the model.

a)

Chambers	ID	Chambers	ID	Chambers	ID
U4, U5, T1	1	U4, U1, T3	12	U3, U1, T1	23
U4, U3, T1	2	U5, U3, T1	13	U3, U2, T2	24
U4, U2, T1	3	U5, U2, T1	14	U3, U1, T2	25
U4, U2, T1	4	U5, U1, T1	15	U3, U2, T3	26
U4, U5, T2	5	U5, U3, T2	16	U3, U1, T3	27
U4, U3 T2	6	U5, U2, T2	17	U2, U1, T1	28
U4, U2, T2	7	U5, U1, T2	18	U2, U1, T2	29
U4, U1, T2	8	U5, U3, T3	19	U2, U1, T3	30
U4, U5, T3	9	U5, U2, T3	20	-	-
U4, U3, T3	10	U5, U1, T3	21	-	-
U4, U2, T3	11	U3, U2, T1	22	-	-

b)

ID	R^2	B (T)	B (W)	B (SM)	I	R (U1)	R (U2)	R (U3)	R (U4)	R (U5)	R (T1)	R (T2)	R (T3)
1	0.68	-0.43	5.8	n.i	4.8	0.79	0.79	0.81	-	-	-	0.71	-0.33*
2	0.80	-0.31	3.1	0.08	3.7	0.80	0.78	-	-	0.96	-	0.63	-0.43*
3	0.58	-0.30	1.9	0.09	-6.3	0.85	-	0.87	-	0.94	-	0.48	0.13
4	0.56	-0.42	7.2	n.i	7.2	-	0.78	0.81	-	0.94	-	0.71	-0.21*
5	0.64	-0.20	2.2	0.03	-4.6	0.84	0.74	0.88	-	-	0.62	-	-0.09*
6	0.80	-0.32	3.5	0.08	-2.8	0.85	0.72	-	-	0.94	0.68	-	0.15*
7	0.58	-0.33	3.6	0.05	-2.4	0.84	-	0.88	-	0.96	0.62	-	-0.09*
8	0.55	-0.46	6.0	n.i	5.8	-	0.79	0.81	-	0.95	0.41	-	-0.34*
9	0.56	n.i	8.1	0.16	0.60	0.69	0.61	0.74	-	-	0.08	-0.03*	-
10	0.55	n.i	6.8	0.22	-4.6	0.71	0.58	-	-	0.67	0.58	-0.04*	-
11	0.65	0.40	4.5	0.30	-15.3	0.43	-	0.36	-	0.18*	0.47	-0.23*	-
12	0.54	n.i	8.9	0.15	2.3	-	0.62	0.74	-	0.68	0.54	-0.02*	-
13	0.52	-0.37	n.i	0.05	-5.9	0.81	0.66	-	0.83	-	-	0.52	-0.46*
14	0.29	-0.39	n.i	0.03	-5.7	0.80	-	0.72	0.80	-	-	0.52	-0.53*
15	0.59	-0.49	4.7	-0.03	5.7	-	0.79	0.73	0.82	-	-	0.62	-0.53*
16	0.54	-0.39	n.i	0.06	-5.7	0.81	0.65	-	0.83	-	0.41	-	-0.42*
17	0.31	-0.42	1.3	n.i	-2.7	0.78	-	0.74	0.80	-	0.19	-	-0.57*
18	0.60	-0.51	2.6	n.i	2.2	-	0.75	0.77	0.83	-	0.24	-	-0.54*
19	0.44	n.i	n.i	0.32	-15.1	0.64	0.44	-	0.52	-	0.59	-0.06*	-
20	0.39	n.i	n.i	0.33	-16.1	0.64	-	0.51	0.52	-	0.59	-0.06*	-
21	0.49	n.i	3.4	0.24	-6.9	-	0.53	0.62	0.65	-	0.60	-0.05*	-
22	0.51	-0.17	2.9	0.08	6.5	0.83	-	-	0.90	0.89	-	0.31	0.53
23	0.26	-0.40	-1.6	0.03	-6.7	-	0.57	-	0.67	0.80	-	0.46	-0.56*
24	0.50	-0.19	4.6	0.05	-3.1	0.80	-	-	0.93	0.89	0.66	-	0.37

25	0.29	-0.42	-1.8	0.05	-7.0	-	0.57	-	0.70	0.81	0.26	-	0.53
26	0.54	0.35	12.0	0.21	-3.4	-0.43*	-	-	-0.49*	-0.78*	0.25	-0.39*	-
27	0.03	n.i	n.i	0.30	-14.2	-	0.44	-	0.52	0.51	0.59	-0.06*	-
28	0.18	-0.44	n.i	n.i	-3.8	-	-	0.68	0.72	0.87	-	0.50	-0.59*
29	0.19	-0.46	n.i	n.i	-3.5	-	-	0.68	0.72	0.87	0.13	-	-0.59*
30	0.35	n.i	5.7	0.20	-4.8	-	-	0.69	0.73	0.66	0.59	-0.04*	-

Acknowledgements

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