Processes Controlling Carbon Fluxes in the Soil-Vegetation-Atmosphere System

David George Hadden
Faculty of Natural Resources and Agricultural Sciences
Department of Ecology
Uppsala

Doctoral Thesis
Swedish University of Agricultural Sciences
Uppsala 2017

Acta Universitatis agriculturae Sueciae
2017:4

Cover: Compilation of eddy covariance equipment on a variety of ecosystems (Photo: D. Hadden & A. Grelle)

ISSN 1652-6880
ISBN (print version) 978-91-576-8781-4
ISBN (electronic version) 978-91-576-8782-1

Print: SLU Service/Repro, Uppsala 2017

Processes Controlling Carbon Fluxes in the Soil-Vegetation-Atmosphere System

Abstract

Increasing emissions of carbon dioxide (CO_2) to the atmosphere have a direct impact on global warming and climate change. The ability of ecosystems to sequester CO_2 is therefore of great importance. The Boreal forest contains one of the world's largest carbon stocks after having acted as a net sink of CO_2 for thousands of years. Carbon is stored within the forest in the form of biomass and soil carbon and has accumulated largely due to the cold climatic conditions which limit respiration for much of the year. However with a changing climate and land use, the fate of the large carbon stores and future sequestration capabilities within the boreal zone are threatened and not fully understood. This thesis aims to improve the understanding of the processes that control fluxes of CO_2 into and out of terrestrial ecosystems within the boreal zones.

Long term continuous high frequency measurements of carbon dioxide fluxes were done using the eddy covariance technique on a variety of forest and agricultural sites within Sweden. This thesis includes studies from six sites: a managed northern boreal forest, a primary unmanaged boreal forest, two agricultural fields of which one was cultivated and one was set aside, and two sites of a chronosequence of pine forests where the carbon use efficiency of mycorrhiza was studied. Four out of six study sites were seen to have a net loss of CO_2 to the atmosphere. Ecosystem and site specific variables such as natural disturbance, change in ecosystem functioning and tillage were found to be strong drivers influencing the carbon fluxes. One common finding from all studies however was that the net carbon balance of an ecosystem is highly sensitive to small changes in either gross photosynthesis or gross ecosystem respiration.

Overall this thesis shows that carbon fluxes are driven by a number of different processes and variables which are highly dependent upon ecosystem type and site conditions such as development stage and disturbances. We further found that site characteristics such as forest heterogeneity and prevailing wind directions could affect the accuracy of annual net budgets of CO_2 measured by the eddy covariance technique. In addition it highlights the importance in correcting for bias within the measurement technique and suggests correction schemes.

Keywords: Carbon dioxide exchange, Eddy covariance, Respiration, Boreal forest, primary forest, organic soil cultivation, set aside

Author's address: David Hadden, SLU, Department of Ecology,
P.O. Box 7044, 750 07 Uppsala, Sweden
E-mail: david.hadden@ slu.se

In memory of my grandads George Lawson & Les Williamson.

Abair ach beagan agus abair gu math e

Say but little and say it well.

Gaelic proverb

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Hadden, D. & Grelle, A. (2016). Changing temperature response of respiration turns boreal forest from carbon sink into carbon source. *Agricultural and Forest Meteorology* 223(2016), 30-38.

II Hadden, D. & Grelle, A. Carbon balance of primary Boreal forest sensitive to small scale disturbances (submitted manuscript).

III Hadden, D. & Grelle, A. The impact of cultivation on organic farmland greenhouse gas fluxes. (submitted manuscript)

IV Hagenbo, A., Hadden, D., Clemmensen, K.E., Grelle, A., Manzoni, S., Mölder, M., Ekblad, A., Fransson, P. Large seasonal variation in mycelial carbon use-efficiency across a Pinus sylvestris chronosequence (manuscript).

Paper I is reproduced with the permission of the publishers.

The contribution of David Hadden to the papers included in this thesis was as follows:

I Main author, fieldwork, data processing and analysis.

II Main author, fieldwork, data processing and analysis.

III Main author, fieldwork, data processing and analysis.

IV Co-author, fieldwork, eddy covariance data processing and analysis.

Abbreviations

CH_4	Methane
CO_2	Carbon Dioxide
EC	Eddy Covariance
GPP	Gross Primary Production
LAI	Leaf Area Index
NBP	Net Biome Production
NEE	Net Ecosystem Exchange
NEP	Net Ecosystem Production
NPP	Net Primary Production
TER	Total Ecosystem Respiration

1 Introduction

1.1 Background

Anthropogenic emissions of Carbon Dioxide (CO_2) are on the rise. This has resulted in the global atmospheric concentration of CO_2 having surpassed 400 ppm (Showstack, 2013). This increase in CO_2 has a direct impact on global warming by changing radiative forcing of the atmosphere (Forster et al., 2007).

As an important part of the carbon cycle, atmospheric concentrations of CO_2 are naturally regulated through ecosystem respiration and uptake by photosynthesis. With increased anthropogenic emissions however, the ability of terrestrial ecosystems to sink carbon dioxide is of high importance. Global forests cover approximate 4.1 billion hectares and are important stores of terrestrial carbon with a capability of sequestering ca. 4.0 Pg carbon year^{-1} (Dixon and Wisniewski, 1995; Pan et al., 2011).

Due to a cold climate for much of the year, the Boreal zone contains one of the globes largest carbon stocks. Having acted as a carbon sink for thousands of years the boreal region is thought to contain ca. 559 Pg carbon in the form of biomass and soil carbon (Lal, 2005). To what extent global warming will affect the carbon stocks of the boreal forest is uncertain.

The net ecosystem exchange *NEE* of CO_2 between the terrestrial system and the atmosphere is a balance between two processes; gross primary production *GPP* and total ecosystem respiration *TER* (Gower et al., 2001; Lindroth et al., 1998). With more carbon stored within global soils than within the atmosphere (Davidson and Janssens, 2006) it is vital to understand the processes controlling carbon fluxes within the soil-vegetation-atmosphere system if we are to predict future scenarios and mitigate any potential losses from terrestrial ecosystems under a changing climate.

1.2 Respiration

Respiration is the process in which carbon is transferred from terrestrial and aquatic ecosystems back to the atmosphere in the form of CO_2.

There are two forms of respiration: autotrophic respiration (R_a) and heterotrophic respiration (R_h). R_a is the return of CO_2 to the atmosphere as a result of plant metabolism. R_a can return more than 50% of the carbon fixed during photosynthesis and is a key regulator of productivity within forest ecosystems. R_a is controlled by the volumes of living biomass, the nutrients available to vegetation and vegetation growth rate. It is also strongly correlated to air temperatures with greater levels of respiration at higher temperatures (Ryan et al., 1997).

R_h is the release of CO_2 to the atmosphere through decomposition of organic material by organisms such as bacteria, fungi and soil animals. R_h is largely dependent upon substrate quality and quantity, moisture and temperature. Globally, R_h from forest ecosystems emits around 76.5 Pg CO_2 C year^{-1} (Raich and Schlesinger, 1992).

Soil temperature has been shown to be one of the main variables to influence R_h (Fang and Moncrieff, 2001). With large carbon stocks stored within boreal forest soils and the sensitivity of R_h to temperature, there is potential for global warming to accelerate the decomposition of carbon stocks which would result in a positive feedback to atmospheric CO_2 concentrations. Currently there is uncertainty regarding future carbon stock scenarios under a warmer climate. This scenario has led to numerous studies being carried out with the focus being on the temperature sensitivity of R_h.

1.3 Photosynthesis

Forests remove CO_2 from the atmosphere through photosynthesis. Net primary production NPP is equal to the difference between gross primary production GPP minus autotrophic respiration R_a. NPP is directly associated with carbon storage in forest ecosystems. Of the CO_2 that is photosynthesised from the atmosphere, only around 25-60% goes towards NPP, the remainder is respired back to the atmosphere in the form of R_a (Ryan et al., 1997).

Environmental variables such as humidity, temperature, solar radiation levels, atmospheric CO_2 concentrations and nutrient availability have an effect on photosynthetic rate. The response of photosynthesis to these environmental variables is not the same as the response of R_a to the same variables, thus a change in climate may impact on NPP and carbon sequestration (Ryan et al., 1997). NPP is correlated to leaf area index LAI as abiotic factors such as resource availability influence *LAI* and thus also influence *NPP* (Gower et al., 2001). A higher *LAI* leads to more photosynthesis. *LAI* varies substantially depending upon forest type and stand structure. Typically, boreal forests have a smaller *LAI* than deciduous forests and foliage distribution is more clustered in coniferous forest stands (Chen et al., 1997). These traits influence the interception of photosynthetically active radiation *PAR* and thus *NPP*. Uptake of forest ecosystems also varies with stand age. Once the forest canopy closes, young forests typically act as small carbon sinks. The sinking capabilities increase as the forest reaches maturity and eventually as the forest becomes old the carbon balance moves towards neutrality (Pan et al., 2011).

1.4 Managed Boreal forest stands

The majority of northern Europe's Boreal forests are managed for timber production (FAO, 2005). Managed boreal forests can be characterised as being homogenous in structure with little diversity in tree species and even aged stands. Managed forests are generally seen to act as large net carbon sinks due to their high basal area, high levels of net ecosystem production *NEP* and low levels of dead biomass within forest stands (Magnani et al., 2007). *NEP* is defined as the difference between *GPP* and total ecosystem respiration *TER*.

The carbon balance of managed forests is however dependant on numerous factors and varies depending upon stand age (Hyvönen et al., 2007).

The prevalent forest harvesting method in northern Europe is by clear-cutting (Lundmark et al., 2013). After clearcutting the ecosystem is seen to be a net source of CO_2 to the atmosphere due to reduced sink capabilities by the removal of living biomass, and increased soil respiration. However, once vegetation has re-established and gross photosynthesis outweighs gross respiration the forest can be seen to act as a net carbon sink again (Amiro et al., 2010).

1.5 Unmanaged primary forests

Much of the global Boreal forest is unmanaged and can be classed as primary forest. This is particularly true for Russia with 31% and Canada with 53% of the forest classified as unmanaged primary forest (FAO, 2005). With such a large area of unmanaged forest, it is important to have an understanding of how the primary boreal forests impact the global carbon balance.

The characteristics of primary forests differ significantly from those of managed forests. The ecology of primary forests is driven largely by natural disturbances such as fire, storms, insect attacks and age related mortality. This results in a distribution of tree species and age, a variation in canopy structure and significant volume of coarse woody debris *CWD* (Hansen et al., 1991). *CWD* plays an important part of the carbon balance of primary forests. The volumes of *CWD* are much greater in unmanaged forests compared to managed forests for a number of reasons. Firstly, mature trees are not harvested and thus when they eventually die they are left in-situ to decompose over a long period of time (Spies et al., 1988). Secondly, a significant proportion of *CWD* within unmanaged forests is derived from self-thinning (Mäkelä, 1997; Peet and Christensen, 1987), whereas managed forest stands undergo a thinning regime and a large percentage of the thinned biomass is removed from the ecosystem.

How effective primary boreal forests are in sequestering carbon is still widely debated. In recent years the consensus is leaning towards the view that the forests are moderate carbon sinks (Luyssaert et al., 2008). However the counter view of this is that old growth forests should be carbon neutral due to equilibrium in growth and mortality within the forest, e.g. Jarvis et al. (1989).

Figure 1. Fiby urskog: an unmanaged primary forest (study II). Photo: D. Hadden

1.6 Agriculture on organic soils

Globally, agriculture is a large contributor to atmospheric greenhouse gas *GHG* concentrations with significant emissions of CO_2, methane (CH_4) and nitrous oxide (N_2O) being emitted annually (Cole et al., 1997).

The global land area used for agricultural practices has increased dramatically in recent times (Lambin and Meyfroidt, 2011) resulting in an escalation of *GHG* emissions to the atmosphere. It is well understood that converting natural peat lands to cultivated land has a detrimental effect on the soil carbon balance (Berglund and Berglund, 2010; Grønlund et al., 2008). Organic soils contain high levels of organic material and when cultivated upon are seen to be a consistent source of CO_2 due to decomposition (Maljanen et al., 2007).

Soil temperature and soil water content are important variables in regulating CO_2 fluxes from organic soils. It is widely accepted that soil respiration increases with an increase in temperature (Fang and Moncrieff, 2001). This is important to consider when evaluating the future carbon balance of peat soils under a changed climate. Before the conversion to agricultural use, natural peat soils were often water logged. However, to be used for cultivation peat soils are drained which leads to increased decomposition of organic material. Studies show that CO_2 fluxes from peat soils can be reduced by increasing the water table as this in turn reduces peat mineralization. However with a higher soil water content, the flux of methane is likely to be larger than from soils where the water content is low (Regina et al., 2015).

Currently the direct effect of tillage on the carbon balance is debated. Studies have shown that tillage is a major driver in causing cultivated land to act as net carbon source, e.g. Ogle et al. (2005), whereas others such as Elder and Lal (2008) found that tillage had little to no effect on the net carbon balance.

2 Aims

The aims of this thesis are:

- To quantify the long-term carbon balance of boreal forest ecosystems (studies I & II)
- To determine the effect of cultivation on the carbon balance of organic agricultural soil (study III)
- To identify processes controlling the ecosystem carbon balance (studies I-III)
- To bridge the gap between small scale processes and the ecosystem carbon balance (studies II & IV)
- To increase the accuracy of ecosystem carbon budget estimates by a data correction scheme (study II)

3 The Eddy Covariance Technique

3.1 Theory

To measure continuous CO_2 fluxes on an ecosystem scale, the Eddy Covariance (EC) technique is arguably the most reliable and accurate method available. The technique not only measures fluxes of gases, but also momentum, and sensible and latent heat fluxes.

The technique can be used in a wide variety of applications; however there currently is no single standardised configuration that can be universally applied to all environments and therefore the method must be tailored to individual site characteristics (Burba, 2013).

The method calculates the exchange rate of CO_2 between a surface such as a plant canopy and the atmosphere by means of the covariance between CO_2 concentrations and the vertical wind velocity. Atmospheric turbulence in the form of eddies results in a vertical upward and downward movement of airflow which transports molecules of CO_2 between the plant canopy and the atmosphere. Transporting eddies vary in size from large (hundreds of meters) to small (centimetres) and are affected largely by surface roughness, atmospheric stability, wind speed, and physical landscape characteristics. Due to the variation in eddy size and the chaotic characteristics of a turbulent atmosphere, sampling must be conducted at a high sample rate (often around 20 Hz) in order to capture the small-scale vertical transportation of CO_2, and over a set period of time in order to include large-scale mixing. This vertical movement (or flux) can then be calculated as:

$$flux = \overline{\rho_c \cdot w}$$

Where ρ_c is the density of the air constituent CO_2, and w is the vertical wind velocity.

Within the atmospheric boundary layer where measuring occurs, the airflow is turbulent and stochastic. With the use of Reynold’s decomposition, the atmospheric turbulence can be conveyed as the mean and its deviation over time. This can be presented as:

$$\overline{flux} = \overline{\left(\overline{\rho}_c + \rho_c{}'\right)\left(\overline{w} + w'\right)}$$

And expanded as:

$$\overline{flux} = \overline{\overline{\rho_c} \cdot \overline{w}} + \overline{\rho_c{}' \cdot \overline{w}} + \overline{\overline{\rho_c} \cdot w'} + \overline{\rho_c{}' \cdot w'}$$

Where the mean is denoted by an accent and the deviation of the mean is denoted by a prime.

The deviation of the mean corresponds to the turbulence and stochasticity of airflow within the atmospheric boundary layer.

This equation can be further simplified as the Reynolds decomposition results in the average of the mean deviation being zero. Further simplifications result from two assumptions. Firstly, that there is little to no variations within the air density during the averaging period. Secondly, that the vertical air flow does not undergo any divergence or convergence and that measurements occur over a flat homogeneous surface and therefore the mean vertical flow must be zero.

With these assumptions the equation can be simplified to:

$$Flux = \overline{\rho_c{}' \cdot w'}$$

The CO_2 density ρ_c can be expressed as mean air density multiplied by CO_2 mixing ratio. The eddy flux can thus be described as the mean air density and the covariance between deviations in the mean vertical wind velocity and mixing ratio (Baldocchi, 2003; Burba, 2013).

3.2 Application of the Eddy Covariance technique

An eddy covariance system consists basically of a three dimensional sonic anemometer (short “sonic”), a rapid infrared gas analyser (IRGA) and often a selection of auxiliary sensors for measuring environmental variables such as solar radiation, and soil temperatures.

The sonic anemometer is used to measure the wind speed and direction. This is done by measuring the speed of sound between transducers. The speed of sound in static air is known, thus a fixed distance between the transducers means that the time it takes for sound to pass from the sending to the receiving transducer under static conditions is known. Movement of air however will cause a change in the expected time for sound to pass between the transducers. This change can then be calculated into wind speed. The sampling rate of a sonic used for EC is typically 10 or 20 Hz (Aubinet et al., 1999).

The high sampling rate of the EC technique results in special requirements needed from the gas analyser. There are a number of high frequency gas analysers designed for use with the eddy covariance technique currently on the market. Studies I, III & IV in this thesis used a closed path system whilst study II used an open path system.

A closed path system requires air to be drawn through tubing to a sampling chamber that is entirely concealed from the surrounding atmosphere. An open path analyser on the other hand is entirely open to the atmosphere and measures gas concentrations as the air passes through the sampling space. Each of these systems has their individual advantages and disadvantages (Burba, 2013).

The selection of analyser is often driven by the ecosystem type where measurements will occur. One of the main criteria in analyser selection is power availability. Closed path systems have a higher power consumption than open path systems, largely due to the need for an external pump that can draw air through an inlet and down a tube to the analyser (Aubinet et al., 1999). This must be done at a high flow rate in order to minimise damping of concentration signals. Another disadvantage of the closed path system is that maintenance (e.g., air filter exchange, pump maintenance) is usually higher than for the open path system. Closed path analysers are sometimes of differential type, i.e. they measure gas concentrations relative to a continuously supplied reference gas which can be hard to transport and thus maintenance in remote locations can be difficult.

Figure 2. A closed path system where air is drawn through a tube from an inlet next to the sonic down to the analyser that is housed at the bottom of the mast. Photo: D. Hadden

Open path systems do not need any pumps or a supply of reference gas and therefore are preferred for remote locations. Open path systems are however more susceptible to data loss and measurement interference than the closed path systems. Precipitation can interfere with the sampling in an open path system, which may result in poorer data quality (Burba, 2013). A closed path analyser on the other hand is not affected by precipitation as it is protected by weather proof housing.

The spatial separation between the sonic sampling area and the sampling area of the open path analyser or inlet of a closed path system is important to consider. The vertical separation of the sampling areas should not be more than 15 cm so that the same air sample is measured by both apparatus. Although it is important to limit the spatial separation of the apparatus, care should be taken not to create convergence or divergence of the airflow due to distortion from the analyser if placed too close to the sonic (Aubinet et al., 1999; Burba, 2013).

Accounting for fluctuations of temperature and water vapour is especially important when using an open path gas analyser. An open path analyser measures the amount of CO_2 molecules within the sampling volume between the sensors. However temperature and water content have a direct impact on air density, in that warm moist air has a lower density than cool dry air. Thus, if the measured upward flow was warmer and wetter than the measured downward flow then measured CO_2 in the upward flow would have a lower density than that of the downward flow. This results in a measured flux as a consequence of variation in air density rather than the result of respiration or photosynthesis. This effect can be corrected for using the Webb-Pearman-Leuning *WPL* correction (Webb et al., 1980). It should also be noted that the heat fluxes are measured by the sonic anemometer and thus the air density may vary between the gas analyser and the sonic anemometer due to energy fluxes deriving from surface heating of the gas analyser and the spatial separation between the two instruments. This effect cannot be completely mitigated by the *WPL* correction alone. However by adding a fine wire thermometer to the measuring volume of the gas analyser the effect of surface heating and spatial separation could be removed (Grelle and Burba, 2007). In recent years an integrated open path gas analyser and sonic anemometer (IRGASON) has come to the market (Campbell Scientific inc, Logan, UT, USA). This is designed so that the sampling volume of the gas analyser and the sonic are combined. This eliminates the error created by surface heating of the instruments.

Data quality is highly dependent upon atmospheric conditions. Periods with poor mixing, stable stratification and low wind speeds may result in poor data quality. These conditions are especially typical during night time. Under stable conditions, a build-up of CO_2 can occur under the measurement system (known as storage). If conditions remain stable then horizontal advection and the ‘drainage’ of CO_2 away from the measurement system can occur.

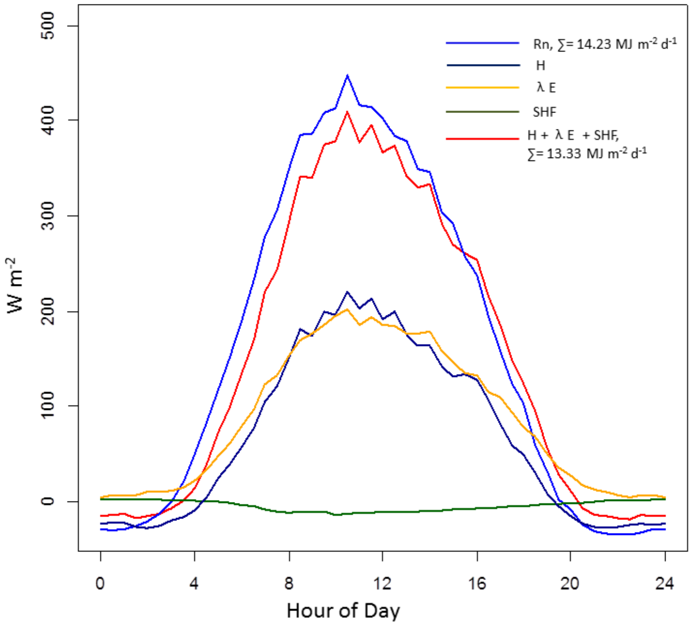

Figure 3: average diurnal energy fluxes (W m^{-2}) during June and July 2008 from a managed boreal forest. Rn = net radiation, H= sensible heat flux, λE= latent heat flux and SHF = soil heat flux. Here we can account for 93.7% of the energy budget.

3.2.1 Energy balance

When net radiation is absorbed by an ecosystem it is converted into sensible heat flux *H*, latent heat flux *λE* and soil heat flux *SHF*. This is commonly referred to as the energy balance. A common way of validating that the eddy covariance system works appropriately is by closing the energy balance. The eddy covariance system measures the sensible heat flux and latent heat flux. With the addition of soil heat flux measurements then an energy budget can be constructed. If the sum of these components is equal to the measured net radiation (which is measured by an independent apparatus) then it can be assumed that the measurement system is measuring correctly and thus the measured CO_2 fluxes also are correct. Fig. 3 is an example of the average diurnal energy balance during the summer of 2008 from a managed boreal forest (study I). Here the measured energy components accounted for 93.7% of the net radiation. The 6.3% that is not accounted for may be a result of a variation in the source areas of the energy fluxes that are measured by the eddy covariance equipment and the source area of the measured net radiation. Variation may have also occurred due to processes such as advection and storage and thus some the energy fluxes may not have been measured by the eddy covariance equipment.

3.3 Field implementation

The EC technique typically consists of a three path-way sonic anemometer and a fast response infrared gas analyser mounted within the boundary layer above a plant canopy or other measuring surface (Aubinet et al., 1999). The Sonic and the open path gas analyser or intake leading to a closed path analyser are placed above the plant canopy in order to capture the entire gas exchange between the ecosystem and the atmosphere during periods with sufficient mixing. For example, if the sampling volume was situated below the canopy then a potential carbon sink would not be measured correctly and the net ecosystem exchange *NEE* would not be representative of the entire ecosystem.

3.3.1 Footprint

The height in which the system is situated above the canopy plays a large role in determining the flux source area (typically called the ‘footprint’). The footprint is further determined by the canopy roughness length (z_0) and atmospheric stability (Rebmann et al., 2005). Canopy roughness can be thought of as a proxy for the variations within vegetation canopy height. For example a forest has a larger roughness length than a grass field. A high z_0 reduces the footprint area due to greater friction which creates more atmospheric turbulence. Under stable atmospheric conditions, turbulence is minimal and the footprint increases in diameter and distance. The footprint of an EC system is not static and continually varies depending on site and atmospheric conditions. This can lead to a source of error, particularly when the ecosystem within the footprint is heterogeneous (Göckede et al., 2006). It is therefore important to consider the landscape and physical properties of the intended measurement site when selecting a suitable area for EC measurements (Baldocchi, 2003; Papale et al., 2006).

4 Methods

This section summarises the methods used in the four studies of this thesis.

4.1 Study Areas

All four studies were located in Sweden. Study III focused on the carbon balance of agricultural systems, papers I and II looked at the carbon balance of boreal forests and paper IV focused on the carbon use efficiency of mycorrhizal fungi over a pine forest chronosequence. All studies used the eddy covariance technique to measure the exchange of carbon dioxide between the terrestrial system and the atmosphere.

4.2 Eddy covariance systems

Studies I, III & IV used closed path eddy covariance systems. Study II used an open path system. The selection of closed or open path gas analyser for each study was driven primarily by the availability of mains power.

Studies I, II and IV all had the possibility of running the eddy covariance system off of mains power and therefore a closed path system was used. Study II however had no mains power and therefore was powered by solar panels in combination with an EFOY Pro fuel cell (SFC Energy AG, Brunnthal, Germany). Because of the requirement for low power consumption, an open path system was used in Study II.

Figure 4. Open path system within a primary forest (study II) where power supply was limited to solar panels and fuel cells. Photo: A. Grelle.

Study I used an LI-6262 closed path infrared gas analyser (LI-COR inc, Lincoln Nebraska, USA) in combination with a Solent 1012R2 sonic anemometer (Gill Instruments. Lymington, UK). Study IV and the cultivated site of study III used the same gas analyser but in combination with a Solent 1012R3 sonic anemometer.

For study II an LI-7500 open path infrared gas analyser (LI-COR inc., Lincoln, NE, USA) combined with a CSAT-3 sonic anemometer (Campbell Scientific, Logan, UT, USA) was used.

The set-aside site of study III consisted of a fast response GGA-EP Off-Axis Integrated Cavity Output Spectroscopy (OA-ICOS) analyser (Los Gatos Research Inc., San Jose, CA, USA) from 2012 to 2014 followed by an LI-6262 during 2015 to 2016. The sonic was a Solent 1012R3 for the entire duration of measuring. The OA-ICOS analyser was used due to its capability of measuring CH_4. After two years however, the analyser malfunctioned and was replaced by the LI-6262.

The overall calculation and correction of the measured fluxes was in line with the EUROFLUX methodology (Aubinet et al., 1999). Data gaps were filled with a combination of linear interpolation and bin-averaging.

4.3 Partitioning of the NEE

The EC technique measures the net ecosystem exchange *NEE* of CO_2 between the atmosphere and the terrestrial ecosystem. The *NEE* is the balance of total ecosystem gross respiration *TER* minus gross photosynthetic productivity *GPP*.

It can often be of interest to have an understanding of these components as it is the gross fluxes and not the net fluxes that are driven by biophysical and biochemical processes. We must therefore separate them from the measured *NEE*.

To separate the *NEE*, fluxes measured during periods of darkness were used to estimate *TER*. An exponential temperature response was then fitted to the night time values. This response function could then be used to extrapolate day time respiration, and when combined with night time measurements produced *TER*. *GPP* was then calculated as:

$$GPP = -NEE + TER$$

There are a number of accepted methods for separating the *NEE*. In studies I, II and IV we used the exponential function:

$$TER = a + b \cdot e^{c \cdot Ta}$$

Where a represents an offset and b & c the slope and curve coefficients respectively. Ta denotes air temperature.

For the studies in this thesis we chose to use an exponential function with air temperature as the dependant variable rather than soil temperature as it is coupled to vegetation temperature.

4.4 Leaf Area Index.

CO_2 uptake by photosynthesis is directly correlated to leaf area index *LAI* (Gower et al., 2001). *LAI* measurements can therefore be powerful in helping to understand the processes influencing the carbon balance of an ecosystem.

There is a range of *LAI* measurement systems currently available on the market. An LAI-2000 plant canopy analyser (LI-COR inc, Lincoln, Nebraska, USA) was used to measure the *LAI* within the study sites of this thesis. We found however that the equipment could not differentiate between leaf biomass and dead branches or tree stems. This results in a measurement of vegetation area index *VAI* rather than a measurement of *LAI*. To overcome this, a CI-120 plant canopy imager (CID Bio-Science inc, WA, USA) was tested. This analyser takes digital photos of the plant canopy and allows for post processing of the images. Dead biomass, branches, tree trunks etc. could potentially be excluded by selecting the colours that should be included in the *LAI* measurements. We found however that this was highly subjective and *LAI* outputs varied considerably depending on what colours were selected as representative of the tree canopy.

Figure 5. An example image taken using the CI-120 plant canopy imager. There is a large variation in the foliage colour depending on light conditions. It can further be difficult to distinguish between trunk colour and foliage colour. Photo: D. Hadden

5 Results and discussion

5.1 The carbon balance of boreal forest ecosystems.

Studies I and II focused on the carbon balance of a managed and primary boreal forest respectively. Both forests types were found to be net sources of CO_2 to the atmosphere. We found that a managed spruce forest stand turned from being a net carbon sink into a net carbon source within a relatively small time scale and that the net losses were driven by an increase of total ecosystem respiration during the spring and autumn periods.

The unmanaged primary forest had been an annual carbon source for the entire ten years of measurements. It was found that small scale disturbances resulting in an increase of dead biomass were sufficient in causing the ecosystem to be a net source of CO_2 to the atmosphere. The potential carbon sink capabilities of primary boreal forests have been widely debated (e.g. Desai et al., 2005; Jarvis et al., 1989), however the consensus in recent years has been that primary forests can have the potential to sequester large volumes of carbon (Knohl et al., 2003; Luyssaert et al., 2008). Our findings however are supported by Gough et al. (2007) who found that in mature forests the respiration from coarse woody debris had a significant impact on the net carbon balance.

Both of these findings are contrary to much of the literature currently available. It is widely accepted that managed boreal forests are large carbon sinks of CO_2 and are important for sequestering carbon (Magnani et al., 2007; Pan et al., 2011). There are however some studies that have also found managed forests to be a net source of CO_2 to the atmosphere and that the sink capabilities of the boreal forest may be depleted under future climatic conditions (Piao et al., 2008; Ueyama et al., 2014). In none of our studies did we find a change in temperature to be the main driver for net losses of CO_2 to the atmosphere. Rather we found that in both forest types, a change in ecosystem functioning had the greatest impact on the carbon balance. In general, however, changes in ecosystem functioning may also be caused by climate change. This shows that the interactions between the climate system and the biosphere are manifold and complex, and much process understanding is needed to predict future carbon budgets and climate scenarios.

5.2 The carbon balance of farmland on organic soils

Study III compared the carbon balance of cultivated organic soils and set-aside organic soils. The set-aside site was seen to be a net source of CO_2 to the atmosphere, having lost around 2 tonnes CO_2 per hectare over a 4 year period. The cultivated site was seen to act as a small carbon sink over the same time period.

Although the set-aside field was a source of CO_2 it was simultaneously a sink of CH_4. Within a 32 month period, around 1.4 g m^{-2} was removed from the atmosphere. If we consider the GHG emissions in terms of 100-year global warming potential then 1 part methane is equivalent to 25 parts CO_2. Thus the annual absorption of ca. 500 mg CH_4 m^{-2} corresponds to 12.5 g CO_2 m^{-2} y^{-1} and therefore can be considered to reduce the source strength of the site by around 10%.

The cultivated site was a sacrificial crop for birds and other herbivores and thus some biomass was removed from the system by herbivory. In order for the site to be comparable to the set aside site we must include biomass lost to herbivory. To do this we can consider the term net biome production *NBP* which is equal to net ecosystem production *NEP* minus the carbon lost through, for example, herbivory. The average annual yield of the cultivated site was around 2000 kg ha^{-1} of which approximately 40% was exported from the field due to herbivores. This corresponds to the loss of around 400 kg carbon. Thus if we consider these losses then the annual *NBP* is around -400 kg C ha^{-1} y^{-1} and therefore the cultivated site might be considered as a carbon source to the atmosphere. There was no monitoring of herbivory on the set-aside site; however we estimate that light grazing occurred and around 150 kg C ha^{-1} y^{-1} (or 550 kg CO_2 ha^{-1} y^{-1}) was removed from the site during the measurement period. The *NEP* of the set aside site was around -125 kg CO_2 ha^{-1} y^{-1} and by subtracting losses from herbivory the *NBP* is -675 kg CO_2 ha^{-1} y^{-1}.

5.2.1 Tillage

We found that tillage had a direct impact on the carbon balance by increasing net carbon dioxide losses (fig. 6). The impact of tillage on the carbon balance has been widely discussed but a consensus has not yet been reached (Powlson et al., 2014).

Studies have shown that tillage can lead to increased evaporation due to moist soil being brought to the soil surface and an increase in soil temperatures resulting in increased levels of soil respiration. However this is only thought to be a very short term increase in respiration and the main increase in carbon losses is from the physical release of trapped CO_2 from soil pores once the soil is disturbed (Reicosky et al., 1997). Although we found an increase in net losses of CO_2 after tillage we cannot readily associate this only to increased soil respiration but must also consider the removal of vegetation which reduces the sink capabilities of the site. It can be seen (fig. 6) that peaks of net CO_2 losses were highest during the years with tillage and disc cultivation compared to 2016 where no soil preparation occurred.

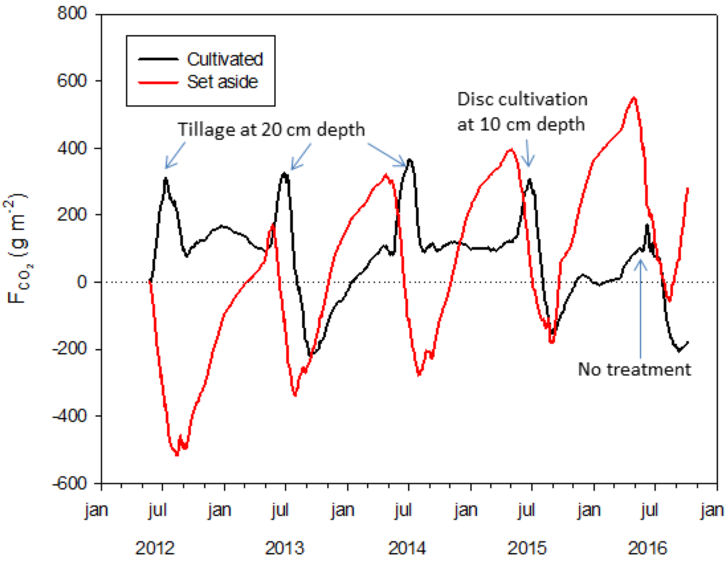

Figure 6. The accumulated flux of CO_2 from the cultivated and set aside sites with the occasions of soil management highlighted.

5.2.2 Should organic soils be set aside to mitigate climate change?

The importance of organic soils for GHG emissions has been widely studied (e.g. Berglund and Berglund, 2010; Elsgaard et al., 2012; Regina and Alakukku, 2010; Regina et al., 2015). To reduce national GHG emissions, Sweden is discussing the possibility of decreasing cultivation intensity on organic soils (Jordbruksverket, 2010).

The aim of study III was to compare the GHG fluxes between a cultivated organic soil and a set aside organic soil. The overall finding was that setting-aside organic soils does not reduce GHG emissions from the ecosystem and in fact the cultivated site was seen to act as a small net carbon sink. When considering *NBP* then both sites were sources of CO_2 to the atmosphere. This study therefore indicates that setting aside organic soils will not lead to fewer emissions and may even result in increased emissions.

5.3 Gross fluxes of carbon dioxide

The net ecosystem exchange *NEE* is the – relatively small - difference between gross primary production *GPP* and gross total ecosystem respiration *TER* (fig. 7).

Biotic and abiotic processes control these gross fluxes and not net fluxes. The net fluxes can be considered a consequence of processes influencing the gross fluxes. A change in either *GPP* or *TER* will impact the *NEE* (Lindroth et al., 1998). It is therefore important to understand the processes that influence these gross components if we are to fully understand ecosystem carbon balances. The understanding of these gross components is further important for the development and improvement of for example, coupled climate models and carbon cycling modelling (Jung et al., 2007). In all of the studies within this thesis we have measured the *NEE*. However, to understand and explain our *NEE* we have studied the gross components and examined the drivers behind these. Studies I, II and III all found that *TER* had the largest impact on the *NEE*. The processes influencing *TER* however were complex and site specific. Study I for example found that a change in the response of respiration to temperature increased *TER* during the spring and autumn periods. Although we could identify that *TER* had the greatest influence on *NEE* and that *TER* had increased due to a change in the respiration response to temperature, we could not identify what was controlling such a change in temperature response.

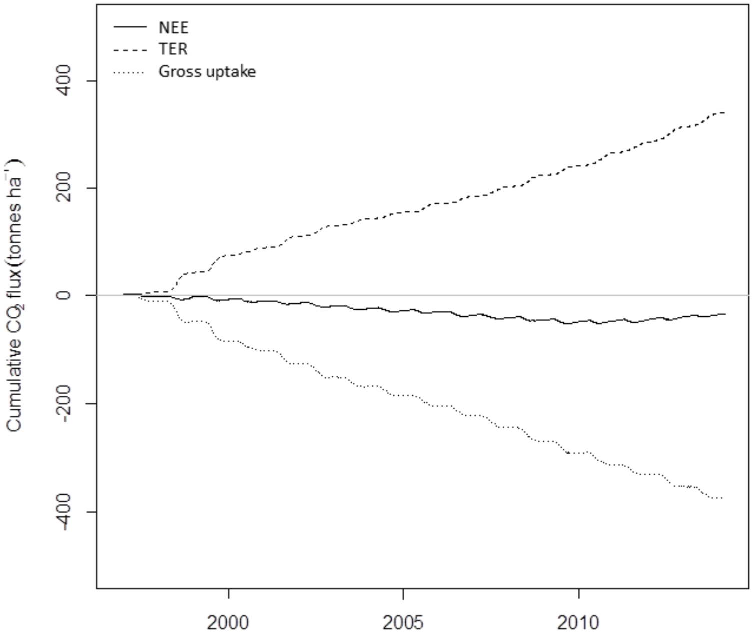

Figure 7. Accumulative flux of CO_2 of a managed forest (study I) shown as *NEE*, *TER* and gross uptake. Negative sign means uptake, positive sign means emission.

The processes influencing the *NEE* occur at different temporal scales. For example, *GPP* and *TER* vary on a diurnal and seasonal scale. These variations are easily correlated to seasonal climatic changes (Falge et al., 2002). However long term gradual changes in either of the gross components are much harder to detect and understand. For example, changes in ecosystem functioning due to forest ageing (fig. 8) or gradual climatic change can only be detected by long term measurements or chronosequence.

Study II measured the *NEE* of a primary forest over a 10 year period. We found that *TER* was greater than *GPP* and thus the forest was acting as a carbon source to the atmosphere. The forest could not however have been a continual carbon source in the past, because its existing carbon stock endorse centuries of carbon uptake. Therefore, a shift in the forest acting as a sink to a source must have occurred before measuring commenced. This indicates that processes influencing the gross components can occur at multi-annual time scales and can have a long term effect on the *NEE*.

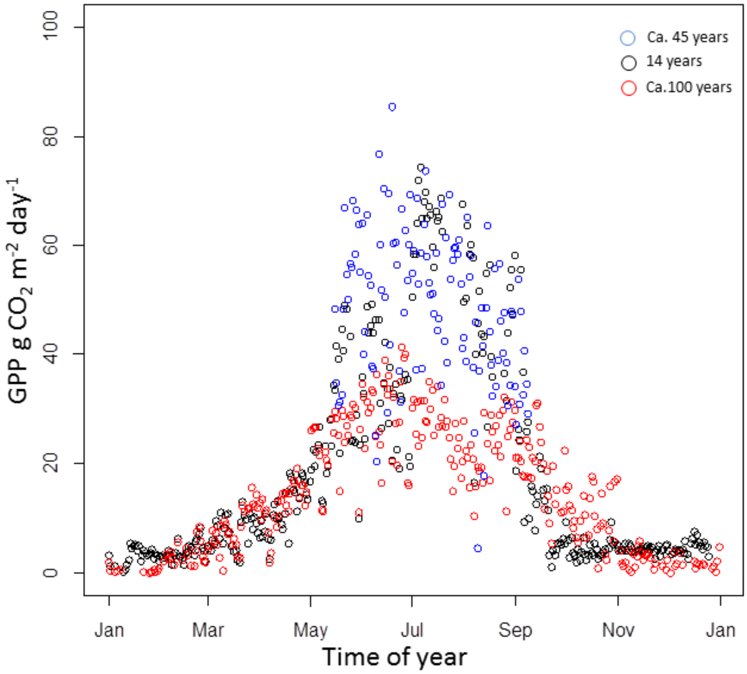

Figure 8. Gross primary production of a boreal forest chronosequence presented as daily averages. The levels of GPP are seen to differ on a seasonal basis and by forest age.

In study IV we did not look at the carbon balance of an ecosystem but rather used the eddy covariance technique to calculate the *GPP* with the aim of understanding the carbon use efficiency *CUE* of mycorrhiza over a chronosequence. It was found that there was a direct relationship between respiration from mycorrhizal fungi and *GPP*. It was also found that mycorrhizal *CUE* had a seasonal variation but was seen to decline with forest age.

Forests are complex ecosystems comprising of many organism types that interact and can influence each other. The ecosystem is further complicated when the interaction of organisms with environmental factors (such as nutrient availability, climate and disturbances) is taken into consideration. Study IV is a good example of an interaction between organisms that impacts the gross uptake and respiration on a short (seasonal) and long (forest life span) time scale.

5.4 Defining the ecosystem carbon balance

The studies presented in this thesis are based largely upon the *NEE* during a specific period of time. Typically we present an ecosystem carbon balance in the form of annual net ecosystem exchange or as the sum of fluxes (ingoing and outgoing) over an entire measurement period. However the measurement periods do not necessarily encompass an entire life cycle of the measured ecosystem.

This raises the issue of time scale and the impact of historical processes that have long term impacts on the gross fluxes. For example, if we compare the carbon balance of study I (a managed forest) and study II (unmanaged primary forest) we find that over the measurement period the managed forest has been a net sink of CO_2 and the primary forest has been a net source of CO_2.

This may however be an incomplete picture. Before measurements commenced, the managed forest was thinned and biomass was removed. If we wish to know the impact forest management has on atmospheric CO_2 then we must consider the fate of the removed biomass.

The primary forest on the other hand has not had any biomass removed from the system which means that within this site we are measuring the net biome production *NBP*. Therefore by comparing the carbon balance of studies I and II we are in fact comparing net ecosystem production *NEP* against *NBP*.

This highlights the issue on the scope and value of studies with eddy covariance data alone which can provide a ‘snapshot’ of the current carbon balance. If however we are to understand the entire ecosystem carbon balance then *NBP* must be considered which will often require the assessment of one or more rotation periods of managed ecosystems.

6 Conclusions and future perspectives

The aim of this study was to increase the understanding of the processes that influence the carbon balance of terrestrial ecosystems. In the studies where we looked at the net carbon balance (studies I, II and III) none of the sites behaved as would be expected and contradicted much of the currently published literature. This highlights the importance of continuing long term measurements of ecosystem greenhouse gas exchange.

Gross total ecosystem respiration has, within studies I, II and III, a larger impact on the *NEE* than gross primary production. We found that the processes driving *TER* were site specific and occurred over short time periods (effect of tillage for example) and over longer time periods, for example in study II where respiration increased due to tree mortality.

If the measurement years from all sites in this thesis are summed then we present 37 years of continual flux data. With this we have been successful in identifying some of the underlying processes that drive the terrestrial carbon balance. However there is scope for continuing in this line of study. It would be especially valuable to focus on the underlying processes behind gross ecosystem respiration as this is complex with many influencing factors and has often the largest impact on the net ecosystem exchange. Although this thesis briefly studied methane fluxes, it would be of great value to study a selection of greenhouse gas species and not be limited to only studying carbon dioxide fluxes. Studying the processes driving fluxes of an array of GHG species would give a more complete overview of the relationship between the terrestrial ecosystem and atmospheric greenhouse gas concentrations.

References

Amiro, B. et al., 2010. Ecosystem carbon dioxide fluxes after disturbance in forests of North America. *J. Geophys. Res*, 115(10.1029).

Aubinet, M. et al., 1999. Estimates of the Annual Net Carbon and Water Exchange of Forests: The EUROFLUX Methodology. In: A.H. Fitter and D.G. Raffaelli (Editors), *Advances in Ecological Research. Academic Press*, pp. 113-175.

Baldocchi, D.D., 2003. Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. *Global Change Biology*, 9(4): 479-492.

Berglund, Ö. and Berglund, K., 2010. Distribution and cultivation intensity of agricultural peat and gyttja soils in Sweden and estimation of greenhouse gas emissions from cultivated peat soils. *Geoderma*, 154(3): 173-180.

Burba, G., 2013. Eddy covariance method for scientific, industrial, agricultural and regulatory applications: *A field book on measuring ecosystem gas exchange and areal emission rates.* LI-Cor Biosciences.

Chen, J.M., Plummer, P.S., Rich, M., Gower, S.T. and Norman, J.M., 1997. Leaf area index measurements. *Journal of geophysical research*, 102(D24): 29-429.

Cole, C. et al., 1997. Global estimates of potential mitigation of greenhouse gas emissions by agriculture. *Nutrient cycling in Agroecosystems*, 49(1-3): 221-228.

Davidson, E.A. and Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, 440(7081): 165-173.

Desai, A.R., Bolstad, P.V., Cook, B.D., Davis, K.J. and Carey, E.V., 2005. Comparing net ecosystem exchange of carbon dioxide between an old-growth and mature forest in the upper Midwest, USA. *Agr Forest Meteorol*, 128(1): 33-55.

Dixon, R.K. and Wisniewski, J., 1995. Global forest systems: An uncertain response to atmospheric pollutants and global climate change? *Water, Air, and Soil Pollution*, 85(1): 101-110.

Elder, J.W. and Lal, R., 2008. Tillage effects on gaseous emissions from an intensively farmed organic soil in North Central Ohio. *Soil and Tillage Research*, 98(1): 45-55.

Elsgaard, L. et al., 2012. Net ecosystem exchange of CO 2 and carbon balance for eight temperate organic soils under agricultural management. *Agriculture, ecosystems & environment*, 162: 52-67.

Falge, E. et al., 2002. Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. *Agr Forest Meteorol*, 113(1–4): 53-74.

Fang, C. and Moncrieff, J.B., 2001. The dependence of soil CO2 efflux on temperature. *Soil Biology and Biochemistry*, 33(2): 155-165.

FAO. Global forest resource assessment (2005). *FAO forestry paper* 147.

Forster, P. et al., 2007. Changes in atmospheric constituents and in radiative forcing. Chapter 2, *Climate Change 2007*. *The Physical Science Basis*.

Gower, S. et al., 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. *Ecological Applications*, 11(5): 1395-1411.

Gough, C.M. et al., 2007. Coarse woody debris and the carbon balance of a north temperate forest. *Forest Ecology and Management*, 244(1): 60-67.

Grelle, A. and Burba, G., 2007. Fine-wire thermometer to correct CO2 fluxes by open-path analyzers for artificial density fluctuations. *Agr Forest Meteorol*, 147(1–2): 48-57.

Grønlund, A., Hauge, A., Hovde, A. and Rasse, D.P., 2008. Carbon loss estimates from cultivated peat soils in Norway: a comparison of three methods. *Nutrient Cycling in Agroecosystems*, 81(2): 157-167.

Göckede, M., Markkanen, T., Hasager, C.B. and Foken, T., 2006. Update of a Footprint-Based Approach for the Characterisation of Complex Measurement Sites. *Boundary-Layer Meteorology*, 118(3): 635-655.

Hansen, A.J., Spies, T.A., Swanson, F.J. and Ohmann, J.L., 1991. Conserving biodiversity in managed forests. *BioScience*, 41(6): 382-392.

Hyvönen, R. et al., 2007. The likely impact of elevated [CO2], nitrogen deposition, increased temperature and management on carbon sequestration in temperate and boreal forest ecosystems: a literature review. *New Phytologist*, 173(3): 463-480.

Jarvis, P. et al., 1989. Atmospheric carbon dioxide and forests. Philosophical Transactions of the Royal Society of London B*: Biological Sciences*, 324(1223): 369-392.

Jung, M. et al., 2007. Uncertainties of modeling gross primary productivity over Europe: A systematic study on the effects of using different drivers and terrestrial biosphere models. *Global Biogeochemical Cycles*, 21(4): n/a-n/a.

Knohl, A., Schulze, E.-D., Kolle, O. and Buchmann, N., 2003. Large carbon uptake by an unmanaged 250-year-old deciduous forest in Central Germany. *Agr Forest Meteorol*, 118(3–4): 151-167.

Lal, R., 2005. Forest soils and carbon sequestration. *Forest Ecology and Management*, 220(1–3): 242-258.

Lambin, E.F. and Meyfroidt, P., 2011. Global land use change, economic globalization, and the looming land scarcity. *Proceedings of the National Academy of Sciences*, 108(9): 3465-3472.

Lindroth, A., Grelle, A. and Morén, A.-S., 1998. Long-term measurements of boreal forest carbon balance reveal large temperature sensitivity. *Global Change Biology*, 4: 443-450.

Lundmark, H., Josefsson, T. and Östlund, L., 2013. The history of clear-cutting in northern Sweden–driving forces and myths in boreal silviculture. *Forest Ecology and Management*, 307: 112-122.

Luyssaert, S. et al., 2008. Old-growth forests as global carbon sinks. *Nature*, 455(7210): 213-215.

Magnani, F. et al., 2007. The human footprint in the carbon cycle of temperate and boreal forests. *Nature*, 447(7146): 849-851.

Maljanen, M., Hytonen, J. and Makiranta, P., 2007. All m J., Minkkinen K., Laine J. & Martikainen PJ 2007. Greenhouse gas emissions from cultivated and abandoned organic croplands in Finland. *Boreal Env. Res*, 12: 133-140.

Mäkelä, A., 1997. A carbon balance model of growth and self-pruning in trees based on structural relationships. *Forest Science*, 43(1): 7-24.

Ogle, S.M., Breidt, F.J. and Paustian, K., 2005. Agricultural management impacts on soil organic carbon storage under moist and dry climatic conditions of temperate and tropical regions. *Biogeochemistry*, 72(1): 87-121.

Pan, Y. et al., 2011. A large and persistent carbon sink in the world’s forests. *Science*, 333(6045): 988-993.

Papale, D. et al., 2006. Towards a standardized processing of Net Ecosystem Exchange measured with eddy covariance technique: algorithms and uncertainty estimation. *Biogeosciences*, 3(4): 571-583.

Peet, R.K. and Christensen, N.L., 1987. Competition and tree death. *BioScience*, 37(8): 586-595.

Piao, S. et al., 2008. Net carbon dioxide losses of northern ecosystems in response to autumn warming. *Nature*, 451(7174): 49-52.

Powlson, D.S. et al., 2014. Limited potential of no-till agriculture for climate change mitigation. *Nature Clim. Change*, 4(8): 678-683.

Raich, J.W. and Schlesinger, W.H., 1992. The Global Carbon-Dioxide Flux in Soil Respiration and Its Relationship to Vegetation and Climate. *Tellus B*, 44(2): 81-99.

Rebmann, C. et al., 2005. Quality analysis applied on eddy covariance measurements at complex forest sites using footprint modelling. *Theoretical and Applied Climatology*, 80(2): 121-141.

Regina, K. and Alakukku, L., 2010. Greenhouse gas fluxes in varying soils types under conventional and no-tillage practices. *Soil and Tillage Research*, 109(2): 144-152.

Regina, K., Sheehy, J. and Myllys, M., 2015. Mitigating greenhouse gas fluxes from cultivated organic soils with raised water table. *Mitigation and Adaptation Strategies for Global Change*, 20(8): 1529-1544.

Reicosky, D., Dugas, W. and Torbert, H., 1997. Tillage-induced soil carbon dioxide loss from different cropping systems. *Soil and Tillage Research*, 41(1): 105-118.

Ryan, M.G., Lavigne, M.B. and Gower, S.T., 1997. Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate. *Journal Of Geophysical Research*, 103: 28,871-28,883.

Showstack, R., 2013. Carbon dioxide tops 400 ppm at Mauna Loa, Hawaii. Eos, Transactions American Geophysical Union, 94(21): 192-192.

Spies, T.A., Franklin, J.F. and Thomas, T.B., 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology*, 69(6): 1689-1702.

Ueyama, M., Iwata, H. and Harazono, Y., 2014. Autumn warming reduces the CO2 sink of a black spruce forest in interior Alaska based on a nine-year eddy covariance measurement. *Global change biology*, 20(4): 1161-1173.

Webb, E.K., Pearman, G.I. and Leuning, R., 1980. Correction of flux measurements for density effects due to heat and water vapour transfer. *Quarterly Journal of the Royal Meteorological Society*, 106(447): 85-100.

Acknowledgements

I would like to thank **Achim** for giving me the opportunity to do this PhD and for always having the time to discuss any questions that I had. Thanks for being a good supervisor and friend and for making my time as a PhD student enjoyable and stress free. Your time as my PhD handledare may have come to an end but your time as my sailing handledare is just beginning ;)

I would also like to thank **Michael** for making these last few years enjoyable. Thank you for taking time to discuss PhD related issues but also many many other topics and for always asking how I was getting on.

Thank you to the **systems ecology group** as a whole. Your feedback on topics raised during Monday meetings has been valuable.

To **past** and **present PhD students**: There are so many people that I cannot mention you all individually but I would like to thank you all for making it enjoyable to come to work each day. You have always created a cosy atmosphere.

Thank you to my **family** back home for being positive and supporting my decision to make a life abroad.

Thank you **Tenna** and **Hector** for making life great. This thesis would be about 1 page long, if you Tenna had not looked after Hector for all those extra hours, days and weeks. Thank you!

Hector: If you are reading this then you must be really bored **-** put it away now and come find me, let’s go and do something more fun instead!