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Seasonal variation and controlling factors of soil carbon effluxes in six vegetation types in southeast of Sweden

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This report concerns a study which was conducted for SKB. The conclusions and viewpoints presented in the report are those of the author and do not necessarily coincide with those of the client.

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Abstract

Soil carbon effluxes of a pine stand, a spruce stand, a lichen rock, two oak stands and a meadow in the Laxemar investigation area in south-eastern Sweden (57°5'N, 16°7'E) have been measured with the closed chamber technique at 14 occasions between 23 of March 2004 and 10th of March 2005. Soil temperature at 10 cm depth, air temperature, soil moisture and photosynthetically active radiation (PAR) were also measured. Exponential regressions with soil respiration against air and soil temperature were used to estimate soil respiration between 15th of March 2004 and 14th of March 2005. A light response curve with Gross Primary Production (GPP) against PAR and a cubic regression with GPP against air temperature were used for modelling GPP in meadow for the growing season, 15th of March to 31st of October 2004. The exponential regressions with soil respiration against air and soil temperature explained on average 30.6% and 47.6% of the variation, respectively. Soil moisture had a linear limiting effect on soil respiration for all ecosystems but spruce, where soil moisture was the limiting factor above a threshold value of about 50%vol. In the forest ecosystems, GPP of the ground vegetation were not reducing soil carbon effluxes, while in meadow it was. In meadow, the light response curve with GPP against PAR explained 32.7% of the variation in GPP while the cubic regression against air temperature explained 33.9%. No significant effect of soil moisture on GPP was detected. The exponential regression equations with air and soil temperature against soil respiration could be used to temporally extrapolate the occasional field measurements. The light response curve with GPP against PAR and the cubic regression with GPP against air temperature could also be used for temporal extrapolation. From the modelled soil respiration, annual soil respiration for the ecosystems in Laxemar, during 15th of March 2004 to 14th of March 2005, were estimated to be between 0.56 and 1.18 kg C m⁻² y⁻¹. Annual GPP of meadow was estimated to be between 0.49 and 0.54 kg C m⁻² y⁻¹, which gives a net ecosystem exchange for the meadow of between 0.38 and 0.66 kg C m⁻² y⁻¹, i.e. a significant loss of carbon to the atmosphere.

Sammanfattning

Kolflöden i markskiktet har uppskattats för sex olika ekosystem i Laxemars undersökningsområde i nordöstra småland (57°5'N, 16°7'E). De ekosystem som undersöktes var ett tallbestånd, ett granbestånd, en lavhäll, två olika ekbestånd och en äng. Vid 14 olika tillfällen mellan den 23 mars 2004 och den 10 mars 2005 uppskattades kolflödena med hjälp av en infrarödgasanalysator som kopplats till en plexiglaskammare. Under tiden som mätningarna pågick mättes även luft- och jordtemperatur, jordfuktighet och den del av solljuset som fotosynteserande växter tar upp (PAR). Markskiktets kolflöden delades upp i markrespirationen och i brutto primär produktionen (GPP). GPP inverkan på markskiktets kolflöden undersöktes. De abiotiska faktorernas påverkan på både markrespirationen och GPP analyserades därefter. Exponentiella regressioner mellan markrespirationen och luft- och jordtemperatur användes tillsammans med ett temperaturdataset för att extrapolera ut markrespirationen från 15 mars 2004 till 14 mars 2005. De modellerade värdena utvärderades sedan gentemot de fältmätta värdena. För det ekosystem där GPP påverkade markskiktets kolflöden användes en ljusresponskurva med GPP mot PAR och en tredjegrads ekvation med GPP mot lufttemperatur för att extrapolera ut GPP över växtsäsongen den 15 mars 2004 till den 1 november 2004. Även denna modell utvärderades gentemot fältundersökningarna.

Luft och jordtemperatur hade en direkt påverkan på markrespirationen för alla ekosystem och under alla säsonger bortsett från lufttemperaturen under vintern för tallbeståndet, ängen och för ett av ekbestånden. Under vintern är markrespirationen låg och andra klimatfaktorer har en starkare påverkan. I genomsnitt förklarade de exponentiella regressionerna markrespirationen bra, där lufttemperaturen förklarade i genomsnitt 30.6 % av variationen medan jordtemperaturen förklarade 47.6 %. Markrespirationen begränsades inte av markfuktigheten så länge den befann sig inom vissa värden, men vid hög markfuktighet begränsades den. Visuellt såg det ut som om markfuktigheten påverkade även vid låga värden, men detta var ej statistiskt signifikant. Vid höga värden hade markfuktigheten en linjärt begränsande påverkan med ökad markfuktighet för alla ekosystem utom granbeståndet. För gran hade markfuktigheten ingen påverkan under 50% vol medan vid högre värden var markfuktigheten den begränsande faktorn.

Utvärderingarna av den modellerade markrespirationen visade på att exponential regressionerna gav rimliga värden på markrespirationen. Med lufttemperaturen modellerades den årliga markrespirationen fram till att vara mellan 0.56 kg kol per m² och år för lav till 0.98 kg kol per m² och år för tallbeståndet. Med jordtemperaturen modellerades den fram till att vara mellan 0.75 kg kol per m² och år för lav till 1.18 kg kol per m² och år för ett av ekbestånden.

Den fotosynteserande markvegetationen i skogsbestånden tog inte upp tillräckligt mycket kol för att detta skulle vara statistiskt mätbart, d.v.s. inte för något av skogsbestånden kunde GPP påvisas. Ängen däremot hade GPP som påverkade markskiktets kolflöden. Här förklarade ljusresponskurvan med GPP mot PAR i genomsnitt 32.7% av variationen i GPP medan tredjegrads ekvationen med GPP mot lufttemperaturen förklarade i genomsnitt 33.9%. Det gick inte att statistiskt belägga någon påverkan av markfuktigheten på GPP, antagligen var för få mätningar genomförts.

Utvärderingen av de modellerade GPP värdena gentemot fältundersökningarna visade att den ljusresponskurva med GPP mot PAR och tredjegrads ekvationen med GPP mot lufttemperaturen kunde användas till att modellera GPP. De modellerade värdena var rimliga. Årlig GPP modellerades till 0.49 kg kol per m² och år med lufttemperatur modellen och till 0.54 kg kol per m² och år med PAR modellen. För ängen innebär detta att man kan beräkna nettoflödet av kol från markskiktet, och marken i ängen förlorar årligen mellan 0.38 kg kol per m² och år till 0.66 kg kol per m² och år.

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1 Introduction

The Swedish Nuclear and Fuels Waste Management Co (SKB) investigates two sites in Sweden for a potentially deep repository of spent nuclear fuel, the Laxemar and the Forsmark investigation areas. In the work of siting a deep repository, extensive site investigations will precede the coming proposal. An important part of the site characterisation is the development of site descriptive models that gives an integrated description of the current state of the regions and the processes that might affect this state in the future /Lindborg 2005/. One process that is important in these site descriptive models is the carbon cycling.

The work of siting a deep repository also includes a safety assessment, where different types of scenarios are analysed. If a future leakage occurs, the radioactive isotopes could then end up in the ecosystems above the repository. The fate of the radionuclides and their possible radiological impacts are then highly determined by ecosystem carbon cycling since radioactive isotopes often follow the same pathway as stable elements vital for the vegetation /Greger 2004/. It could also be that the ecosystems are affected by the handling of the waste and the activity around the repository. To notice this possible change, it is of main importance to have knowledge about the carbon cycle beforehand, both for the understanding of an unaffected ecosystem and to have something to compare the damaged ecosystem with.

In the study of the carbon cycle, forests have been in focus because of their large productivity, while grasslands have received less attention resulting in lack of data for grassland ecosystems /Valentini et al. 2000, Novick et al. 2004/. Approximately 40% of the world's terrestrial surface (excluding Greenland and Antarctica) consists of grassland and they form a significant part of the global carbon cycle as well /White et al. 2000, LeCain et al. 2002/. Most grassland is grazed and it is therefore important to understand the carbon cycle of meadows /LeCain et al. 2002/.

Carbon stored in the soil can be released through soil respiration and it represents between 60 and 80% of total forest ecosystem respiration /Kelliher et al. 1999, Granier et al. 2000, Janssens et al. 2001a/ and is therefore an important part of the total carbon exchange between ecosystems and the atmosphere. Even though soil respiration is such a main part of the total ecosystem respiration, it can be diminished by photosynthetic activity of the ground vegetation. The carbon taken up by the vegetation is the gross primary production (GPP). Some studies show that the influence of ground vegetation photosynthesis can be extensive and have a large influence on soil carbon effluxes /Goulden and Crill 1997, Law et al. 1999a, Morén and Lindroth 2000, Janssens et al. 2001b, Widén 2002/ while others indicate that the uptake is negligible due to regulation of environmental factors /Baldocchi et al. 1997, Kelliher et al. 1999/.

Soil respiration is the sum of respiration from ground vegetation, roots, rhizosphere, mycorrhiza and microbes. There are many different factors that control soil respiration where temperature and sometimes moisture are the dominant factors /Lloyd and Taylor 1994, Kirschbaum 1995, Davidson et al. 2000, Morén and Lindroth 2000, Swanson and Flanagan 2001 etc/. The temperature sensitivity varies for different temperature ranges /Kirschbaum 1995/ and for the different soil respiration components (roots, microbes etc) /Boone et al. 1998, Janssens et al. 2003/. Temperature and respiration from the different components fluctuate seasonally and the temperature sensitivity differs accordingly /Rayment and Jarvis 2000, Widén 2002/. GPP is also affected by abiotic factors, where the part of the spectrum from solar radiation that is used in photosynthesis (PAR), temperature and soil moisture are the most important factors /Lambers et al. 1998/.

There have been several studies attempting to estimate soil carbon effluxes with more or less advanced models /Baldocchi et al. 1997, Fang and Moncrieff 1999, Law et al. 1999b, Rayment and Jarvis 2000, Adams et al. 2004, Novick et al. 2004/. A simple model that has been successful is to use the response of soil carbon effluxes to temperature, moisture and PAR to temporally extrapolate occasional soil carbon efflux measurements /e.g. Morén and Lindroth 2000, Widén 2002, Janssens et al. 2003, Olsrud and Christensen 2004/. This empirical approach is the most frequently used method to simulate soil carbon effluxes, because of its simplicity.

1.1 Aims and hypotheses

This study investigated the carbon cycle of boreal and temperate ecosystems of the Laxemar investigation area in Northeastern Småland. There were two general aims; first to analyse the influence of abiotic factors on soil carbon effluxes in coniferous forests, deciduous forests and a meadow, and secondly, to test whether regression equations with soil respiration and GPP against abiotic factors can be used to model soil carbon effluxes during the time period 15th of March 2004 to 14th of March 2005.

1. Previous studies have indicated that temperature and soil moisture have an effect on soil respiration /Lloyd and Taylor 1994, Swanson and Flanagan 2001, Morén and Lindroth 2000, Davidson et al. 1998, 2000/. The first specific hypothesis was that soil respiration is affected by air temperature, soil temperature and soil moisture.
2. It has been shown that simple regression equations are sufficient to model soil respiration for a longer time period /Janssens et al. 2003, Olsrud and Christensen 2004, Widén 2002/. The second specific hypothesis was that air and soil temperature can be used to model soil respiration 15th of March 2004 to 14th of March 2005.
3. It has been shown that photosynthesis influence soil carbon effluxes of the floor in ecosystems /Goulden and Crill 1997, Widén 2002, Janssens et al. 2001b, Law et al. 1999a, Morén and Lindroth 2000/. The third specific hypothesis was that GPP affects soil carbon effluxes.
4. Precipitation, photosynthetically active radiation (PAR) and temperature are abiotic factors influencing photosynthesis /Lambers et al. 1998/. The fourth specific hypothesis was that GPP is affected by PAR, air temperature and soil moisture.
5. It has also been shown that simple regression equations can be used to model GPP over a longer time period /Maljanen et al. 2001, Olsrud and Christensen 2004/. The fifth specific hypothesis was that PAR and air temperature can be used to model GPP in a meadow during the time period 15th of March 2004 to 14th of March 2005.

Soil carbon effluxes and abiotic factors were investigated in a pine stand, a spruce stand, a lichen rock, two oak stands and a meadow. To investigate the first specific hypothesis soil respiration was analyzed against abiotic factors. A regression with soil respiration against air and soil temperature was used to temporally extrapolate soil respiration for the period 15th of March 2004 to 14th of March 2005. Comparing the models with field measurements were done to test the second specific hypothesis. If GPP influenced soil carbon effluxes were tested to control the third specific hypothesis. For the ecosystems where GPP had an effect on soil carbon effluxes, regression analysis with GPP against abiotic factors tested the fourth specific hypothesis. PAR and air temperature were used for modelling GPP 15th of March to 31st of October and comparing the models with the field measurements tested the fifth specific hypothesis.

2 The carbon cycle in terrestrial ecosystems

All living tissues are composed of carbon and all life on Earth is depending on processes in the carbon cycle. Photosynthesis and respiration are together with mortality and different disturbance regimes (fire, storms, drought etc) the processes of main importance for the carbon cycle /Schlesinger 1997/. The main constituents of the carbon cycle are briefly described in the following sections (Figure 2-1).

2.1 Gross primary production, GPP

The total uptake of carbon through photosynthesis is the gross primary production, GPP, of the vegetation. Photosynthesis is the biogeochemical process that transfers carbon from the atmosphere and its oxidized form, carbon dioxide, into the biosphere and its organic form, carbohydrates.



It is the process of capturing sunlight, which provides life with energy and results in plant growth. The photosynthesis provides the atmosphere with the oxygen necessary for all animal life.

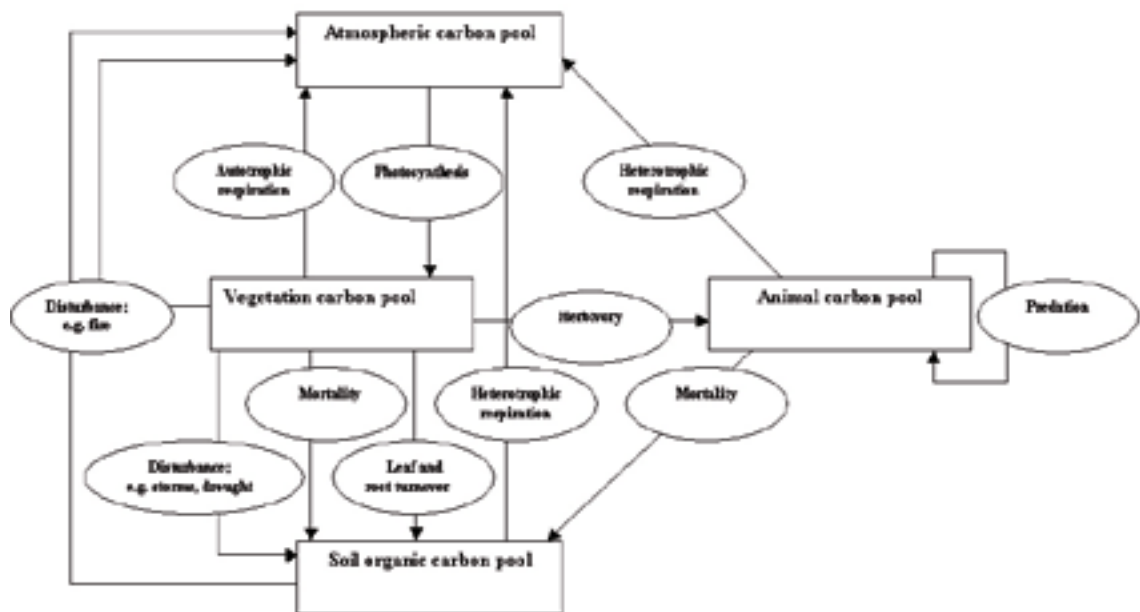


Figure 2-1. Flowchart describing the carbon cycle in terrestrial ecosystems. Squares are carbon pools; arrows and circles are processes moving carbon between the pools.

2.2 Respiration

Energy stored by photosynthesis is later used for maintenance, growth or reproduction by living organisms. The process responsible for the breakdown of the carbohydrates is respiration.



The plants use about half of GPP for their own maintenance /Schlesinger 1997/ and this carbon dioxide is released back to the atmosphere through autotrophic respiration, while the plants accumulate the rest. Parts of GPP accumulated by vegetation is consumed by herbivores and becomes a part of the animal carbon pool, this carbon is either released to the atmosphere through heterotrophic respiration or transported to the soil through mortality. The rest of the carbon taken up by plants will either be released to the atmosphere through disturbance, such as fire, or transported to the soil through mortality of the vegetation. Part of the carbon transported to the soil is decomposed and released to the atmosphere through heterotrophic soil respiration.

Soil respiration varies as a function of soil temperature, soil moisture and chemical composition of material to be decomposed /Schlesinger 1997/. Soil respiration and soil temperature has an exponential relationship in the soil temperature range found in the field; higher soil temperature gives more soil respiration /Widén 2002/. Soil respiration and soil moisture has different relationships at different moisture ranges /Davidson et al. 2000, Janssens et al. 2003/. In dry soils there is a positive linear relationship. Soil respiration can be inhibited due to dryness. In waterlogged soils decomposition is reduced due to anaerobic conditions and there is a negative linear relationship between soil moisture and soil respiration. In between these conditions is a plateau where soil respiration is not affected by soil moisture /Heal 1981/. Nitrogen and lignin content in litter will speed up respectively slow down the breakdown processes /Yao et al. 2003/. In soil organic matter there are different acids that are more or less easy to decompose /Schlesinger 1997/.

2.3 Net Primary Production, NPP

Net Primary Production, NPP, is here defined as the rate at which plants accumulate carbon in their living tissues, GPP minus autotrophic respiration.

$$NPP = GPP - R_p$$

where R_p is autotrophic respiration.

Net Ecosystem Production (NEP) is net primary production on an ecosystem level.

$$NEP = GPP - R_t$$

where

$$R_t = (R_p + R_h + R_d)$$

where R_t is total respiration, R_d is heterotrophic soil respiration and R_h is herbivore respiration.

In ecosystems being young or exposed to disturbances, most of the NEP goes to the production of new plant tissues /Giese et al. 2003/. In old and stable ecosystems GPP mainly goes to the maintenance of the vegetation and any extra NEP will be allocated to the soil organic carbon pool /Giese et al. 2003/.

Temperature, precipitation and photosynthetically active radiation (PAR) are abiotic factors influencing primary production /Lambers et al. 1998/. High temperature gives a longer growing season increasing annual production of the ecosystems /Hasenauer et al. 1999/. A raise in temperature can have a negative effect due to a rise in evapotranspiration, which is lowering photosynthesis if water is a limiting factor /Sitch et al. 2003/. Biomass contains 80–95% water and insufficient water in the soil can be a limiting factor for biomass production /Lambers et al. 1998/. PAR and primary production has a positive relationship at low irradiance due to PAR being the limiting factor in the transport of electrons in photosynthesis /Lambers et al. 1998/. At higher PAR it is the uptake of carbon dioxide that is the limiting factor and PAR does not have any effect on GPP /Lambers et al. 1998/.

2.4 Vegetation carbon pool

The terrestrial biosphere has an important role in the global carbon cycle. Ecosystems can be sources and release carbon to the atmosphere, or they can be sinks and take up carbon from the atmosphere. Different amount of carbon is accumulated by the vegetation depending on biotic factors like species composition, LAI, and age of the ecosystem. Abiotic factors of importance are temperature, humidity, nutrients, incoming solar radiation and disturbances /Schlesinger 1997/.

2.5 Soil organic carbon pool

NEP accumulated in the vegetation is sooner or later delivered to the soil organic carbon pool as litter fall. Litter is undecomposed dead organic material. Decomposition of litter is a two-part process. It is the breakdown of litter at the soil surface and it is the accumulation of soil organic matter /Olsson et al. 2002/. Decomposition results in release of carbon dioxide, water and nutrients. Soil organic matter is highly resistant humus and it can be divided into two parts /Olsson et al. 2002/. A minor part of the soil organic matter is in the bulk of the soil, slowly decomposing and having an age of thousands of years and the remaining is closer to the surface, fast decomposing and of much more recent origin /Schlesinger 1997/.

2.6 Human influences

Humans have influenced the carbon cycle since they started to use land for rising crops /IPCC 2001/. Carbon stored in the soil can be released back to the atmosphere when land-use is changed and forests are clear-cut. Since industrial revolution, humans have started a large-scale influence on the carbon cycle. By using fossil fuels, carbon stored in the lithosphere is released back to the atmosphere. Carbon dioxide is a greenhouse gas and it has impact on the global climate. The mean global temperature increased 0.8°C 1860–2000 /IPCC 2001/. A reason could be the rise in concentration of greenhouse gases due to anthropogenic emissions.

3 Materials and method

3.1 Site description and setup

The investigation took place from March 2004 to March 2005 at six localities in the Laxemar investigation area. The Laxemar investigation area, where SKB performs site investigations, is situated 25 km north of Oskarshamn in southern Sweden (57°5'N, 16°7'E). The mean annual temperature from 15th of March 2004 to 14th of March 2005 was 7.4°C, with the warmest month temperature of 17.8°C for August and the coldest month being February with -1.4°C. Climate is temperate and the growing season (threshold 5°C) started on the 15th of March and ended on the 31st of October 2004. The Laxemar investigation area contains a large variety of ecosystems, where the main ecosystems are coniferous forests, deciduous forests and cultivated land.

Six representative ecosystems for the examined area were used in this investigation, a Scots pine (*Pinus sylvestris*) stand (pine), a Norway spruce (*Picea abies*) stand (spruce), a lichen dominated rock with sparsely distributed Scot pines (lichen), two different Pedunculate oak (*Quercus robur*) stands (oak 1 and oak 2) and a seminatural grassland (meadow). In Table 3-1, characteristics of the ecosystems can be seen. A homogeneous area within each ecosystem was divided into nine equally large plots. Within each of these plots, a spot for soil carbon efflux measurements was selected by taking a certain number of steps into each part spinning around and throwing a stick randomly. The measurement was done where the stick landed. If the stick landed at places where measurements could not be taken, the closest possible place was chosen instead. In cases when there were branches or obstacles on the ground, which prevented soil carbon efflux measurements to be made, these were removed. The stick was left to mark the exact location of the spot.



Figure 3-1. Map of the investigated localities in the Laxemar investigation area. Red dots mark the site of the ecosystems investigated and the yellow triangle is Åspö climate station.

Table 3-1. Characteristics for the different ecosystems. LAI is maximum leaf surface area per ground surface area divided by two and green biomass is autumn ground layer green biomass. Litter is in kg dry weight m⁻², total carbon content in kg C m⁻², humus layer in cm, basal area in m² ha⁻¹, tree height in m, tree age in years and green biomass is in g dry weight m⁻². /Lundin et al. 2004/, measured humus layer and total carbon content. /Tagesson 2006a/ measured basal area, tree height, stand age and LAI. Litter and green biomass were taken from /Löfgren 2005/. The ASM codes are the SKB ID-codes used by SKB for identification of the different sites. For litter and green biomass, standard deviations are also given.

Ecosystem	Litter	Total carbon content	Humus layer	Basal area	Tree height	Stand age	LAI	Green biomass
Pine ASM001429	–	20.3	16	21.0	19.6	96	3.20	–
Spruce ASM001440	1.60 ± 1.08	48.7	44	15.5	21.0	55	3.58	8 ± 7
Lichen ASM000210	1.22 ± 0.54	–	10	22.5	–	–	3.47	41 ± 22
Oak 1 ASM001426	0.49 ± 0.17	6.3	21	15.0	17.1	112	1.55	88 ± 26
Oak 2 ASM001427	–	12.8	24	19.5	19.4	133	4.63	–
Meadow ASM001430	0.48 ± 0.45	27.6	28	–	–	–	–	156 ± 65

3.2 Soil carbon efflux measurements

The soil carbon efflux measurements were made on fourteen occasions during 20th of March 2004 to 10th of March 2005 (Table 4-4). The measurements were made during the hours of daylight, but started in the morning and ended in the afternoon at different times depending on time of the year and when the sun rose and set. The measurements were done at exactly the same places all fourteen times for all ecosystems but meadow, where sticks could not be left in place because of grazing animals. In February and March some places could not be found due to snow cover and in these cases a random place in the vicinity were chosen instead. Lichen was not measured in March 2004 and spruce was not measured in January 2005 because of bad weather conditions.

Soil carbon effluxes were measured using the closed chamber technique. An infrared gas analyzer (EGM-4) together with a canopy assimilation chamber (CPY-2) from PP-systems was used (PP-systems, Hitchin, Hertfordshire, UK). It was measured by placing the canopy assimilation chamber on the ground and continuously measures the change in concentration of carbon dioxide in the chamber either for four minutes or when the difference in concentration of carbon dioxide had changed by 50ppm. Soil respiration was measured directly afterwards by taking a new measurement but this time the chamber was darkened with a lightproof hood. The chamber was flushed for fifteen seconds in between the measurements to clean the chamber of carbon dioxide. The EGM-4 had problems with overestimations of the soil carbon efflux estimates and the data were therefore adjusted according to /Tagesson 2006b/. Finally, GPP was estimated by subtracting soil respiration from the soil carbon efflux measurements. The sign of GPP was changed from being negative to being positive, as GPP is an uptake of carbon by the ground vegetation.

During the soil carbon efflux measurements, air and soil temperature were also measured. Soil temperature was measured at a depth of 10 cm with a STP-1 sensor (PP-system, Hitchin, Hertfordshire, UK). Soil moisture in the humus layer was also measured at a depth of 0–7 cm

with a moisture meter (Delta-T devices, Cambridge, UK (HH2-moisture meter with a Theta probe, type ML2X)). Soil type was set to organic. At each place three different soil moisture measurements were taken and the median value was used on each sampling occasion.

3.3 Statistical methods

3.3.1 Soil respiration

SPSS 12.0.1 for Windows was used for the statistical analysis. The result of the regressions were set to be significant if the p -value was lower than 0.05, a trend if they were between 0.05 and 0.1 and non-significant above 0.1. All soil respiration values were separated into three different seasons; the first half of the growing season (15th of March to 14th of July), the second half of the growing season (15th of July to 31st of October) and winter (1st of November to 14th of March). Exponential regressions were done for the different seasons with soil respiration (R) against air temperature and against soil temperature at 10 cm depth, $R = R_0 e^{kT}$, where R_0 is soil respiration at the reference temperature of 0°C and T is temperature (°C). 1.9% of the soil respiration values were zero or negative and they were excluded to enable the use of exponential regressions. There were problems with the thermometers on the 5th and 6th of July 2004, 14th to 16th of February 2005 and 8th to 10th of March 2005 and in total 13.6% of the air temperature and 3.9% of the soil temperature measurements were excluded. In the exponential equation k is related to Q_{10} , the relative increase in soil respiration when soil temperature is increased by 10°C. Q_{10} were calculated by using the formula $Q_{10} = e^{10k}$ /Strömngren 2001/.

The exponential regression equations with soil respiration against soil temperature at 10 cm depth were used to normalize the soil respiration values, thereby reducing the importance of temperature. A boundary line analysis was done for each ecosystem with normalized soil respiration against soil moisture. In the boundary line analysis, the normalized soil respiration values were sorted after soil moisture and separated into ten different groups. In the groups, all values above average plus one standard deviation were extracted. A One-Sample Kolmogorov-Smirnov test was done to check whether the extracted soil respiration was normally distributed. All ecosystems were normally distributed and linear regressions were hereby done to see whether soil moisture had any limiting effect on soil respiration.

3.3.2 Soil respiration modelling

At Äspö climate station (Figure 3-1) air temperature is measured every half hour /Lärke et al. 2005/. To obtain air temperatures for the different ecosystems, linear regressions with air temperature measured in the field against air temperature measured at Äspö were done. The regression equations were used to calculate air temperature for the different ecosystems 15th of March 2004 to 14th of March 2005. The exponential regression equations with soil respiration against air temperature were used on this dataset to model soil respiration for the same period. No model was done for the months where no significant relationship existed; average values measured in the field were used instead. Annual soil respirations for the different ecosystems were calculated by adding together the modelled effluxes of every hour of the year. Residuals were calculated with modelled soil respiration subtracted from soil respiration measured in the field at the closest half-hour from the time of when the field measurements were done

No soil temperature data set for the entire period 15th of March 2004 to 14th of March 2005 existed and soil temperature was therefore modelled. Soil temperature at 10 cm depth in the pine stand was logged every three hours between 24th of March and 4th of July. The average daily soil temperature was calculated for this period. At Äspö climate station, air temperature is measured and the average daily air temperature was also calculated. A linear regression between daily average soil temperature and daily average air temperature was used to model daily average soil temperature for the period 15th of March 2004 to 14th of March 2005.

To get the diurnal variations of soil temperature, the amplitude (A_0) for every day was calculated by dividing the daily temperature range by two. This was done both for the logged soil temperature and for the measured air temperature at Äspö. A growth regression model between the amplitude of measured air temperature and the amplitude of the measured soil temperature between 24th of March and 4th of July was used to calculate soil temperature amplitude from the air temperature amplitude between 15th of March 2004 to 14th of March 2005. The diurnal variation was received by $\cos(\omega t + 1.7252)$, where 1.7252 was added to adjust for the time lag between soil and air temperature. The soil temperature was then modelled 15th of March 2004 to 14th of March 2005 by:

$$T_{\text{soil}}(t) = T_{\text{average soil}} + A_0(\cos(\omega t + 1.7252))$$

where $T_{\text{soil}}(t)$ is the modelled soil temperature (°C) at day time t , $T_{\text{average soil}}$ is the modelled daily average soil temperature (°C) and A_0 is the modelled amplitude of diurnal variation in soil temperature /Hillel 1980/.

The exponential regression equations with soil respiration against soil temperature were used on the modelled soil temperature set to model soil respiration 15th of March 2004 to 14th of March 2005. Residuals were calculated from modelled soil respiration subtracted from soil respiration measured in the field at the closest half-hour from when the field measurements were done.

3.3.3 Ground Gross Primary Production, GPP

GPP measured during the growing season 15th of March to 31st of October 2004 were included in One-Sample Kolmogorov-Smirnov tests to check whether GPP values fitted a normal distribution. The meadow was normally distributed while the other ecosystems were not. A one-sample t -test for the meadow and Mann Whitney U -tests for the other ecosystems against zero were done. It was only the meadow, where GPP had an effect on the soil carbon effluxes. In the meadow, the effect of abiotic factors on GPP was therefore analyzed for.

To analyse the effect of PAR on GPP, a light response curve was fitted to the GPP data set:

$$GPP = - (GPP_1 + R_d)(1 - e^{(-b_1 \text{ PAR})/(GPP_1 + R_d)}) + R_d$$

Where GPP_1 is saturated GPP, R_d is deduced respiration and k is quantum efficiency. Saturated GPP is where GPP levels out, deduced respiration is GPP at zero PAR and quantum efficiency is the initial slope of the curve. Quantum efficiency gives the efficiency of the vegetation to take up PAR.

A commonly used equation to analyze the relationship between GPP and temperature is the Arrhenius function of temperature /Wang et al. 1996, Lankreijer 1998/. In this study, a cubic regression was fitted to the GPP data set because it has the same sigmoidal shape as the Arrhenius function, but it is mathematically easier to work with.

$$GPP = GPP_0 + b_1 T_a + b_2 T_a^2 + b_3 T_a^3$$

where, GPP_0 is the GPP at 0°C, T_a is the air temperature (°C) and $b_{1,2,3}$, are coefficients of the regression.

A boundary line analysis (see last section under 3.3.1 soil respiration p. 15) was also done with GPP against soil moisture to examine if soil moisture had any effect on GPP. Table-curve Windows v 1.0 was used to find any significant relationships between soil moisture and GPP.

3.3.4 GPP modelling

At Äspö climate station, global radiation is measured every half hour /Lärke et al. 2005/. It is given in $W m^{-2}$, but was changed to micromoles $m^{-2} s^{-1}$ by multiplication by 4.6 (Hickler personal communication). PAR was then calculated by taking 0.45 of the global radiation /Monteith and Unsworth 1990/. To extrapolate GPP throughout the growing season 15th of March to 31st of October, the GPP-PAR regression was used on the PAR values from Äspö. The air temperature set 15th of March to 31st of October for meadow was used with the cubic regression with GPP against air temperature to model GPP. To take away GPP in the air temperature model during the hours of darkness, modelled GPP with zero PAR was set to zero. Residuals were calculated with modelled GPP subtracted from GPP measured in the field at the closest half-hour from when the field measurements were done for both the PAR modelled GPP and the air temperature modelled GPP.

3.3.5 Model evaluations

To evaluate the models and to be able to calculate the error of the obtained results, the standard deviation was needed. For the regression models without propagation errors in them, i.e. modelled air temperature and PAR-modelled GPP, standard deviation was given in SPSS. For the other models, which included several modelled variables, i.e. modelled soil temperature, air temperature modelled soil respiration, soil temperature modelled soil respiration and air temperature modelled GPP the formula for error of propagation was used:

$$\sigma^2(f) = (\partial f/\partial x)^2\sigma^2(x) + (\partial f/\partial y)^2\sigma^2(y) + (\partial f/\partial z)^2\sigma^2(z) + (\partial f/\partial a)^2\sigma^2(a) + 2 \text{cov}(x, y)(\partial f/\partial x)(\partial f/\partial y)$$

where $\sigma^2(f)$ is variance in modelled result, $\sigma^2(x)$ is variance of factor in function, i.e. $T_{\text{average soil}}$, R_0 and GPP_0 , $\sigma^2(y)$ is variance of coefficient in function, A_0 and k , $\sigma^2(z)$ is variance of variable in function, T_{air} , and T_{soil} , $\sigma^2(a)$ is variance from calibration of soil respiration and $\text{cov}(x, y)$ is covariance between the factors and coefficients in the functions.

To calculate the standard deviation of the models the square root of the variances was taken. Finally, to evaluate the results of the model, a t -test were done where residuals were compared against t times the standard deviation of the models to see if field results were within the 95% confidence interval of the model. t is from the Students t -statistics and it was found in a table of critical values for t -distribution.

4 Result

4.1 Effect of air temperature, soil temperature and soil moisture on soil respiration

Air temperature had a significant effect on soil respiration for all ecosystems and during all seasons but for pine, oak 2 and meadow during winter, where no effect could be seen (Table 4-1). For those ecosystems and seasons showing a significant pattern, on average 30.6% of the variation in soil respiration was explained by air temperature and at best 56.9% of the variation was explained (lichen, season 3), (Table 4-1).

Soil temperature at 10 cm depth explained soil respiration better than air temperature did. It was significant for all ecosystems and during all seasons. Soil temperature at 10 cm depth explains on average 47.6% of the variation in soil respiration and in the best case, it explains as much as 73.5% of the variation (meadow, season 1), (Table 4-2).

Q_{10} gives the effect of soil temperature on soil respiration within the temperature range in which the measurements were taken up. On average Q_{10} was 7.4, while the largest value (31.6) was found in the lichen ecosystem in the first half of the growing season and the smallest value (1.9) was found in oak 1 in the second half of the growing season. There were large seasonal differences for Q_{10} , which was generally larger in the first half of the growing seasons and at winter compared to the second half of the growing season (Table 4-3).

Table 4-1. Regression parameters and statistics for measured soil respiration against air temperature. Equations follow the form $R = R_0 e^{kT}$ where R is soil respiration in $g\ C\ m^{-2}\ h^{-1}$, T is air temperature in $^{\circ}C$ and d.f. is degrees of freedom. R_0 is initial soil respiration at $0^{\circ}C$. In season, 1 is 15th of March 2004 to 14th of July 2004, 2 is 15th of July 2004 to 31st of October 2004 and 3 is 1st of November 2004 to 14th of March 2005.

Ecosystem	Season	d.f.	R_0	k	F -value	p -value	R^2
Pine	1	32	0.032	0.069	17.08	0.000	0.348
	2	44	0.134	0.026	5.36	0.025	0.108
	3	18	0.052	-0.006	0.01	0.913	0.001
Spruce	1	27	0.014	0.103	15.21	0.001	0.360
	2	42	0.080	0.043	5.26	0.027	0.111
	3	26	0.021	0.148	10.34	0.004	0.285
Lichen	1	23	0.002	0.146	16.56	0.001	0.419
	2	43	0.057	0.056	12.32	0.001	0.223
	3	27	0.015	0.194	35.70	0.000	0.569
Oak 1	1	33	0.024	0.065	6.61	0.015	0.167
	2	43	0.126	0.040	10.20	0.003	0.192
	3	36	0.014	0.229	33.96	0.000	0.485
Oak 2	1	24	0.027	0.027	4.47	0.045	0.157
	2	42	0.043	0.074	16.76	0.000	0.285
	3	27	0.023	0.100	1.37	0.254	0.056
Meadow	1	31	0.040	0.067	33.79	0.000	0.521
	2	42	0.076	0.046	23.78	0.000	0.362
	3	31	0.038	-0.022	1.43	0.241	0.044

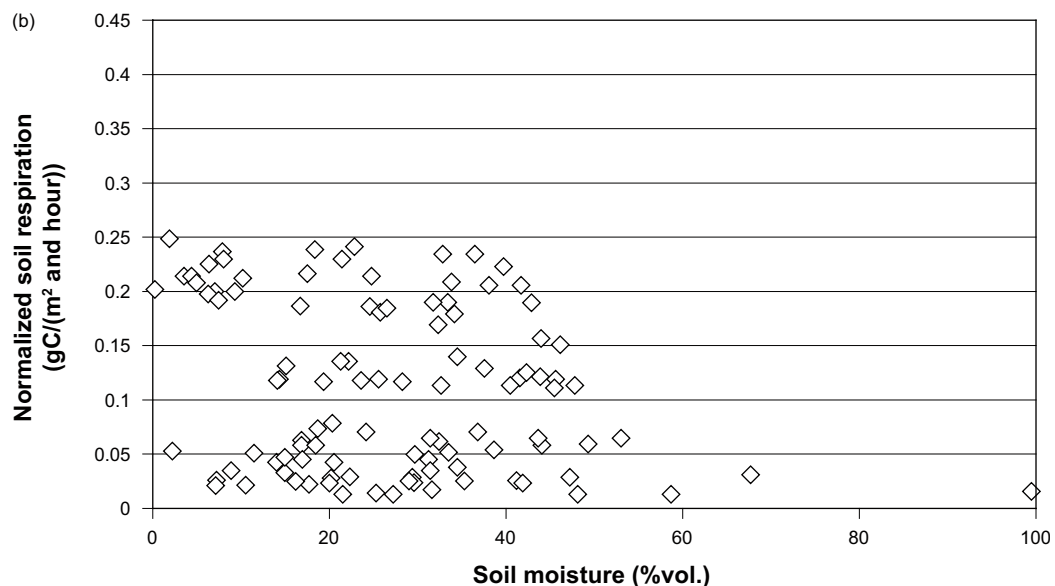
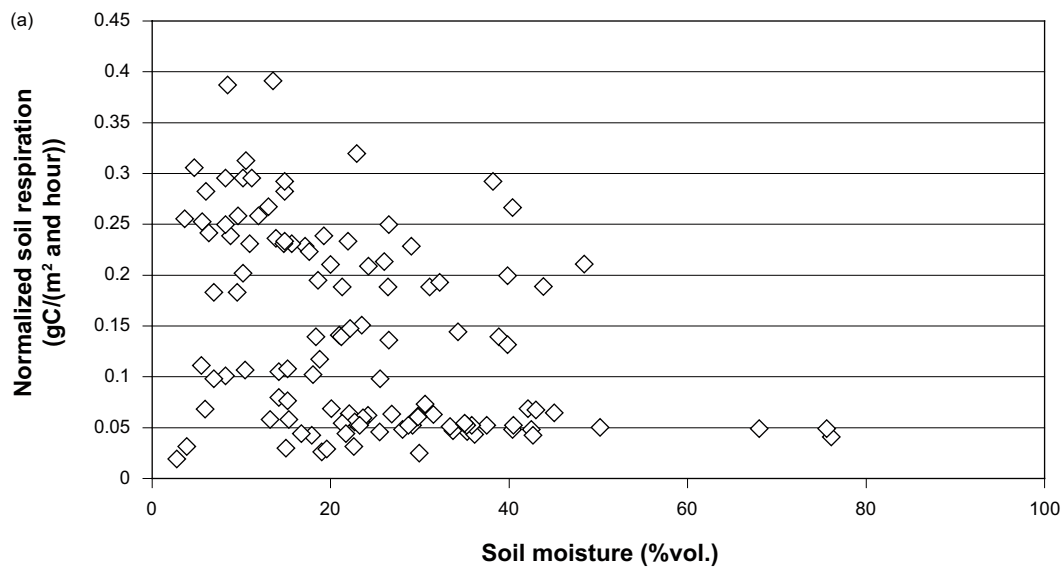
Table 4-2. Regression parameters and statistics for measured soil respiration against soil temperature. Equations follow the form $R = R_0 e^{kT}$ where R is soil respiration in $\text{g C m}^{-2} \text{h}^{-1}$, T is soil temperature in $^{\circ}\text{C}$ and d.f. is degrees of freedom. R_0 is initial soil respiration at 0°C . In season, 1 is 15th of March 2004 to 14th of July 2004, 2 is 15th of July 2004 to 31st of October 2004 and 3 is 1st of November 2004 to 14th of March 2005.

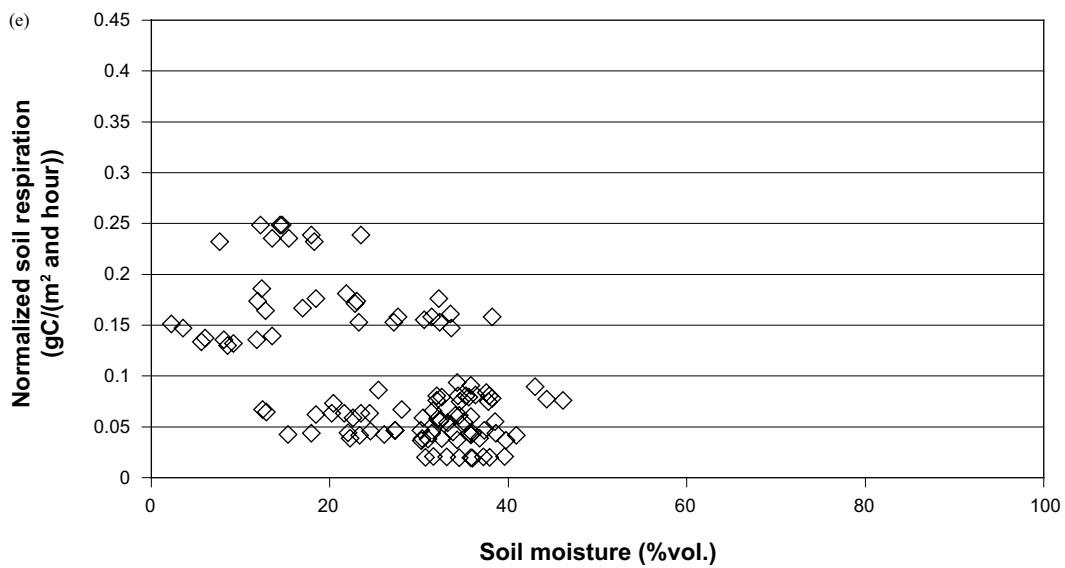
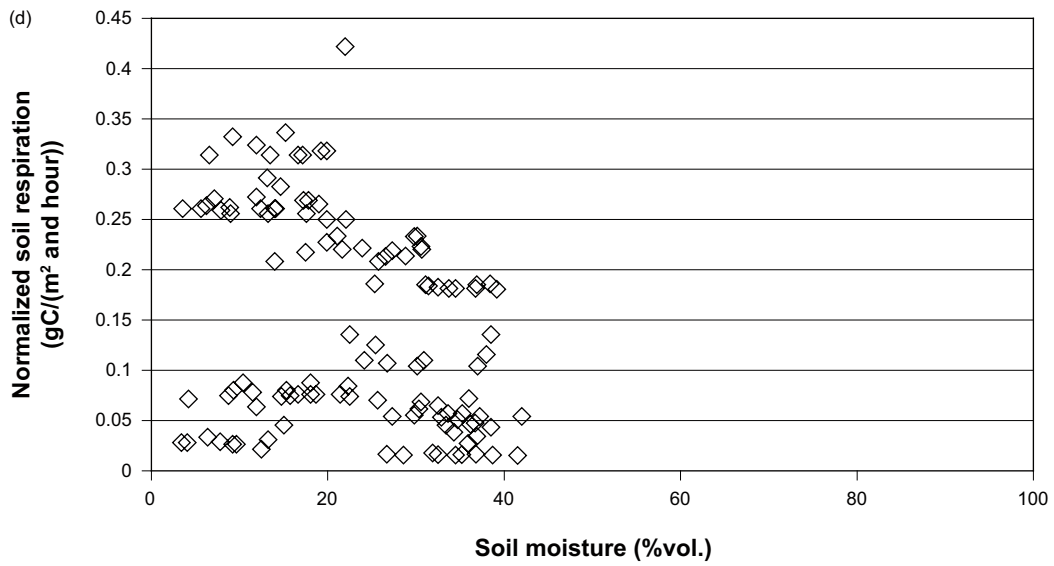
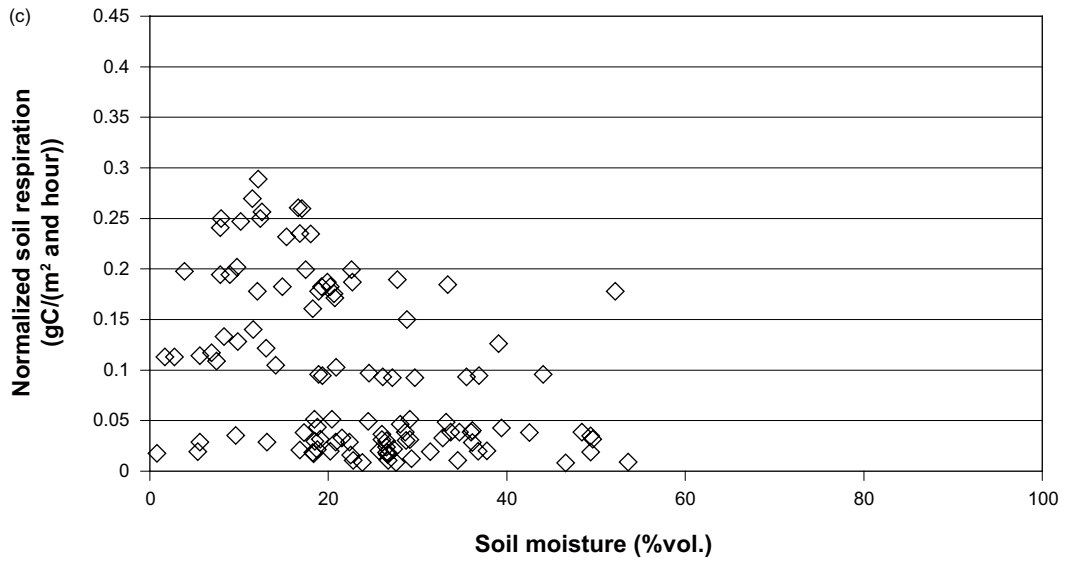
Ecosystem	Season	d.f.	R_0	k	F -value	p -value	R^2
Pine	1	35	0.029	0.139	31.98	0.000	0.477
	2	44	0.048	0.112	24.95	0.000	0.362
	3	41	0.019	0.210	31.45	0.000	0.434
Spruce	1	32	0.013	0.191	64.09	0.000	0.667
	2	43	0.047	0.100	16.11	0.000	0.273
	3	26	0.019	0.213	21.07	0.000	0.448
Lichen	1	23	0.001	0.345	41.22	0.000	0.642
	2	42	0.029	0.126	17.09	0.000	0.289
	3	36	0.016	0.200	46.04	0.000	0.561
Oak 1	1	33	0.008	0.228	66.98	0.000	0.670
	2	43	0.102	0.062	8.61	0.005	0.167
	3	33	0.022	0.263	97.31	0.000	0.747
Oak 2	1	33	0.015	0.179	54.61	0.000	0.623
	2	43	0.023	0.138	18.09	0.000	0.296
	3	32	0.024	0.142	7.19	0.011	0.170
Meadow	1	34	0.041	0.137	94.20	0.000	0.735
	2	42	0.031	0.126	47.22	0.000	0.529
	3	39	0.021	0.242	36.46	0.000	0.483

Table 4-3. Seasonal Q_{10} , the relative increase in soil respiration when soil temperature is increased by 10°C . $Q_{10} = e^{10k}$, k is from the exponential regression equations and d.f. is degrees of freedom.

Ecosystem	Season	d.f.	Q_{10}	Soil temperature range ($^{\circ}\text{C}$)
Pine	1	35	4.0	2.5–16.0
	2	44	3.1	9–18.7
	3	41	8.1	0.3–6.8
Spruce	1	32	6.7	0.1–15.4
	2	43	2.7	8.7–16.8
	3	26	8.4	0.4–6.6
Lichen	1	23	31.6	6.1–16.4
	2	42	3.5	9.1–17.6
	3	33	7.4	0.7–5.7
Oak 1	1	33	9.7	2.7–17.3
	2	43	1.9	9.1–19.1
	3	33	13.9	0.3–7.0
Oak 2	1	33	6.0	1.3–13.2
	2	43	4.0	8.5–17.2
	3	32	4.1	0.3–7.1
Meadow	1	34	3.9	1.2–15.6
	2	42	3.5	9.6–18.6
	3	39	11.3	0.3–5.0

Normalized soil respiration did not follow humus layer soil moisture, and there must therefore be some other factor that affects soil respiration. Visually, it appeared like there was a slight decrease in soil respiration in the dry regions while a more pronounced effect could be seen in the wetter parts (Figure 4-1a-f). The highest soil respiration rates occurred at soil moisture values of 15–20%vol while the rates drop to practically zero when soil moisture was about 60%vol. Soil moisture reached these high values since measurements were taken up in the humus layer and not in the mineral part of the soil. The slight decrease in soil respiration in dry soils was not shown in the boundary line analysis while a linear limiting effect on soil respiration, as the soils were getting wetter, was shown for all ecosystems but spruce. For spruce, a threshold effect at about 50%vol. could be seen above which soil respiration was strongly reduced (Figure 4-1a-f).





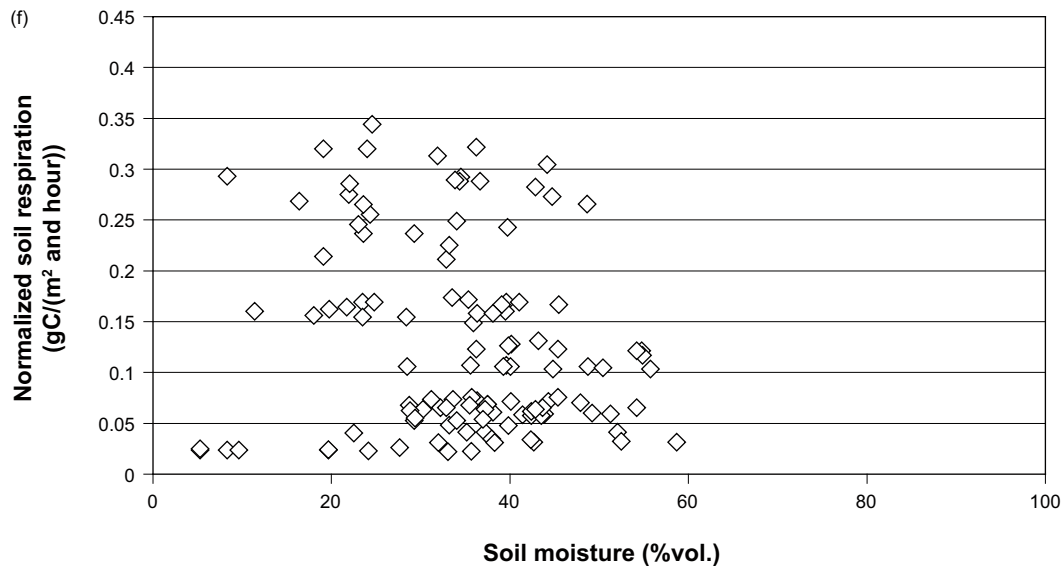


Figure 4-1a-f. Normalized soil respiration in $\text{g C m}^{-2} \text{ h}^{-1}$ against soil moisture for (a) pine, (b) spruce, (c) lichen, (d) oak 1, (e) oak 2 and (f) meadow. Soil moisture is in %vol.

4.2 Evaluation of soil respiration regression models

The comparison between soil respiration measured in the field and air temperature modelled soil respiration (Table 4-4) indicated that they were reasonably close to each other. In total the residuals indicated that the model was slightly underestimating soil respiration.

The comparison between soil respiration measured in the field and soil temperature modelled soil respiration (Table 4-5) indicated that this model also were close to the field measurements. None of the residuals were outside the 95% confidence interval of the soil temperature modelled soil respiration. In total, the model was underestimating soil respiration but less than the air temperature modelled soil respiration was.

4.3 Seasonal and annual soil respiration

There was large seasonal variation in modelled soil respiration. Both air temperature and soil temperature based models peaked in August. Generally, it took longer for air temperature modelled soil respiration to start up in spring than for the soil temperature model (Figure 4-2a-f, Table 4-6 and 4-7).

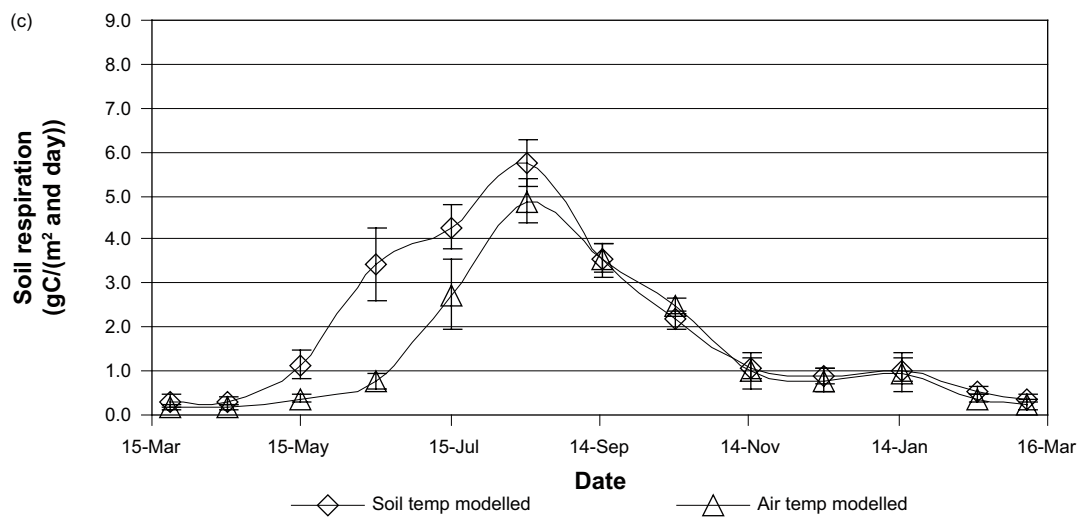
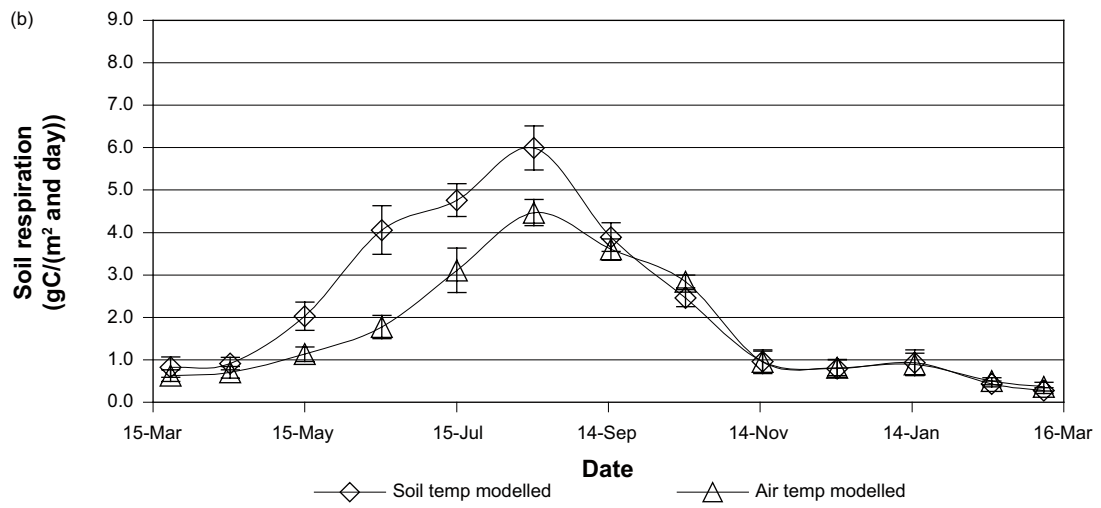
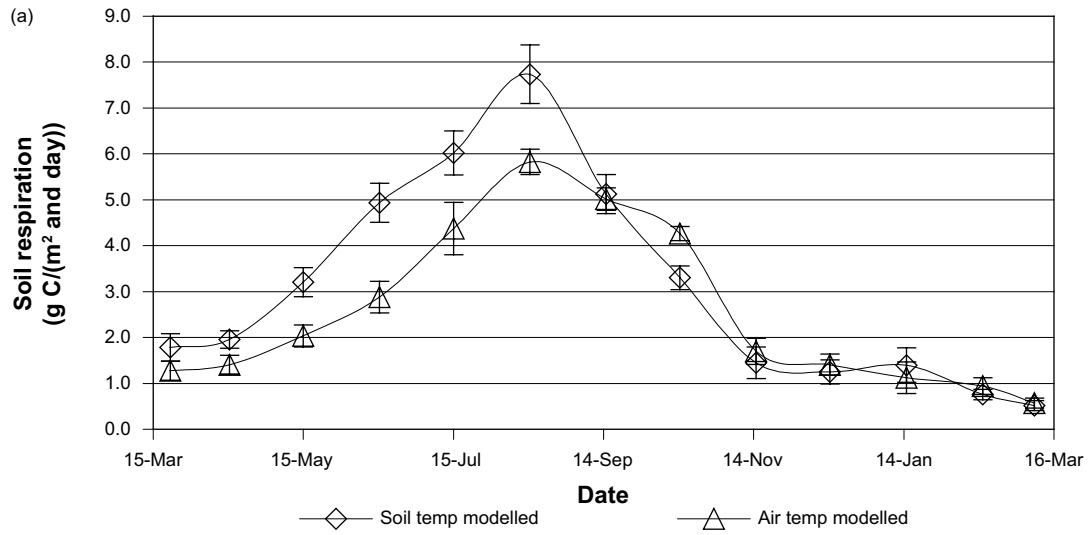
Total annual soil respiration in the air temperature model was between $0.56 \text{ kg C m}^{-2} \text{ y}^{-1}$ for lichen to $0.98 \text{ kg C m}^{-2} \text{ y}^{-1}$ for pine. For the soil temperature model the range was between $0.75 \text{ kg C m}^{-2} \text{ y}^{-1}$ and $1.18 \text{ kg C m}^{-2} \text{ y}^{-1}$. Lichen had the lowest soil respiration and oak 1 had the largest (Table 4-8).

Table 4-4. Average residuals of air temperature based model in $g\ C\ m^{-2}\ h^{-1}$, model values were subtracted from measured value. All residuals but the one with ¹ were inside the 95% confidence interval of the air temperature modelled soil respiration. ¹ means that the model was underestimating soil respiration. Missing data means that no comparison could be done because of non-significant relationship between soil respiration and air temperature or that no field measurements were done.

Date	Pine	Spruce	Lichen	Oak 1	Oak 2	Meadow
23–25 March	0.027	0.005	–	–0.008	–0.011	–0.003
13–15 April	–0.019	–0.011	–0.014	–0.035	0.011	–0.014
10–13 May	–0.008	0.019	0.011	0.044	0.022	0.071
5–6 July	0.150	0.172	0.186	0.224	0.172 ¹	0.139
26–27 July	0.000	0.093	0.011	0.057	0.120	0.060
17 August	0.079	0.074	0.052	–0.038	0.011	0.087
7–8 September	0.104	–0.008	0.057	0.046	–0.019	–0.019
28–29 September	–0.046	0.011	0.030	–0.005	–0.060	–0.057
19–20 October	–0.019	0.003	–0.005	0.022	0.052	–0.016
9–11 November	–	–0.003	–0.019	0.000	–	–
14–16 December	–	0.011	0.005	–0.025	–	–
12–13 January	–	–	–0.025	–0.057	–	–
14–16 February	–	–0.003	0.016	0.016	–	–
8–10 March	–	–0.008	–0.005	–0.011	–	–
Total	0.030	0.027	0.025	0.016	0.033	0.027

Table 4-5. Average residuals of soil temperature based model in $g\ C\ m^{-2}\ h^{-1}$, model values were subtracted from measured value. All residuals were inside the 95% confidence interval of the soil temperature modelled soil respiration. Missing data means that no comparison could be done since no field measurements were done.

Date	Pine	Spruce	Lichen	Oak 1	Oak 2	Meadow
23–25 March	–0.038	0.005	–	0.008	–0.003	–0.005
13–15 April	–0.022	–0.014	–0.027	–0.008	–0.022	0.000
10–13 May	–0.038	0.005	–0.003	0.041	0.003	0.019
5–6 July	0.120	0.074	0.131	0.115	0.079	0.035
26–27 July	–0.005	0.074	0.046	0.068	0.134	0.074
17 August	0.000	0.005	0.033	–0.030	–0.008	0.035
7–8 September	0.115	–0.005	0.096	0.063	0.016	0.025
28–29 September	–0.022	0.038	0.074	0.041	–0.016	–0.003
19–20 October	0.030	0.022	0.016	0.038	0.071	0.025
9–11 November	0.027	0.003	0.005	–0.011	0.005	0.046
14–16 December	0.003	0.008	0.000	–0.057	–0.005	–0.008
12–13 January	–0.033	–	–0.027	–0.065	–0.011	–0.060
14–16 February	0.016	0.000	0.005	0.011	0.019	0.011
8–10 March	0.003	–0.005	–0.008	–0.035	–0.011	–0.019
Total	0.011	0.016	0.025	0.011	0.016	0.014



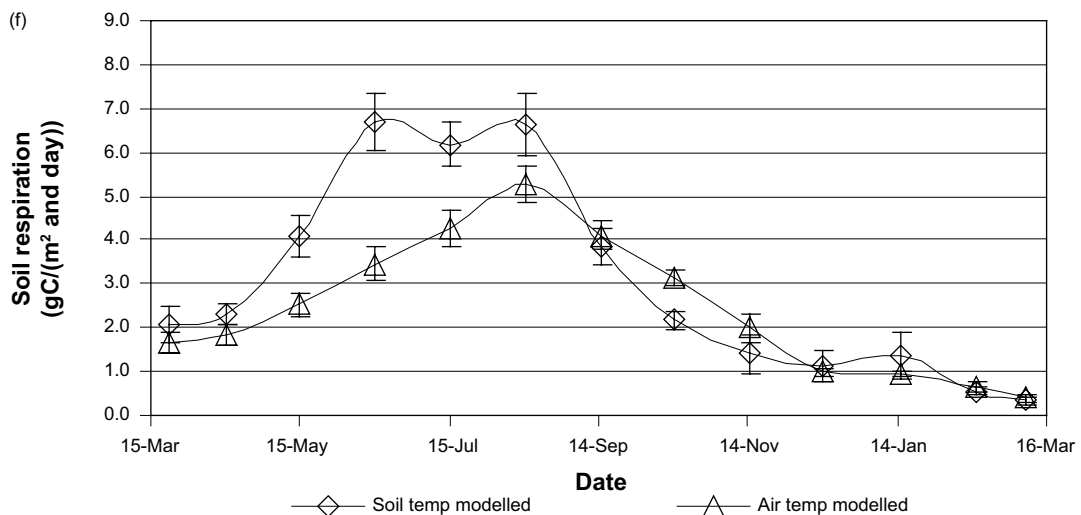
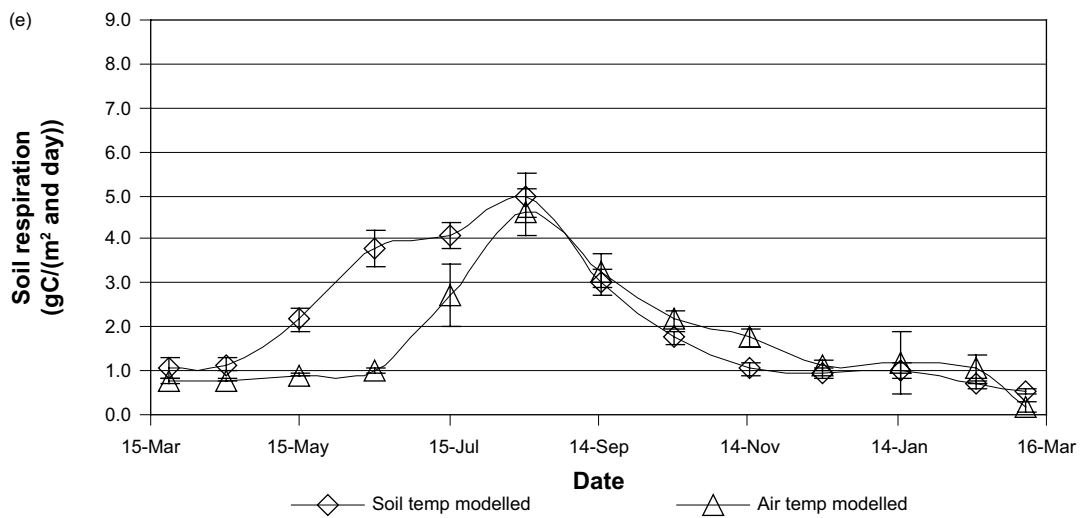
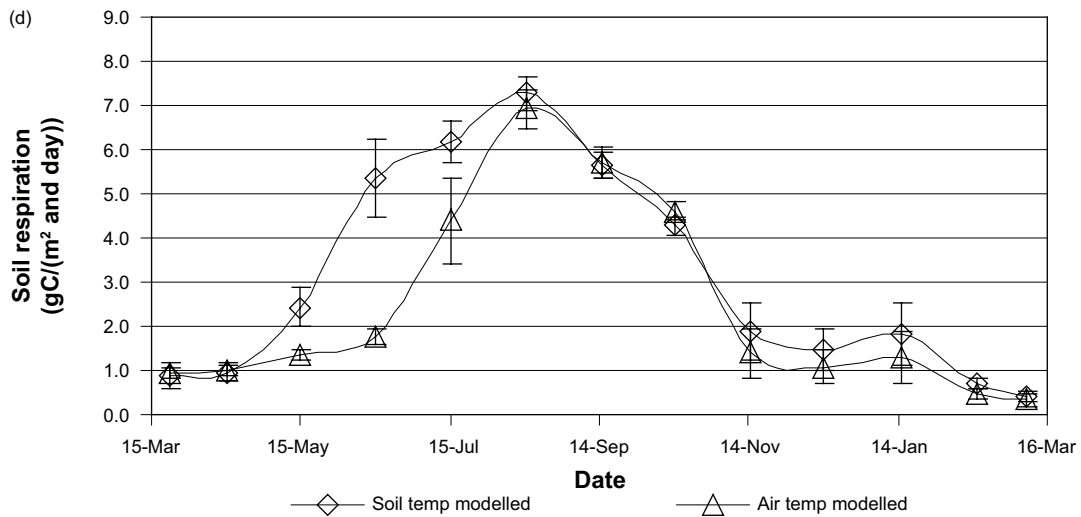


Figure 4-2a-f. Seasonal variation in monthly average air and soil temperature modelled soil respiration 15th of March 2004 to 14th of March 2005 in g C m⁻² day⁻¹ for (a) pine, (b) spruce, (c) lichen, (d) oak 1, (e) oak 2 and (f) meadow. Error bars are one standard deviation of monthly-modelled soil respiration. For air temperature modelled soil respiration in November 2004 to March 2005, average measured values were used for pine, oak 2 and meadow, since no significant relationship to air temperature existed.

Table 4-6. Average monthly soil respiration in g C m⁻² day⁻¹, 15th of March 2004 to 14th of March 2005 for the soil temperature model. The average value for March 2004 is only calculated for the 15th to 31st of March and the average value for March 2005 is only calculated for the 1st to 14th of March.

Date	Pine		Spruce		Lichen		Oak 1		Oak 2		Meadow	
	soil respiration	std. dev.	soil respiration	std. dev.	soil respiration	std. dev.	soil respiration	std. dev.	soil respiration	std. dev.	soil respiration	std. dev.
March 2004	1.781	0.299	0.825	0.239	0.312	0.153	0.889	0.300	1.043	0.232	2.096	0.410
April 2004	1.956	0.191	0.909	0.148	0.318	0.086	0.971	0.182	1.153	0.146	2.312	0.261
May 2004	3.204	0.318	2.029	0.330	1.152	0.307	2.431	0.454	2.177	0.279	4.079	0.465
June 2004	4.932	0.424	4.058	0.575	3.431	0.804	5.350	0.872	3.780	0.420	6.685	0.662
July 2004	6.023	0.480	4.764	0.390	4.281	0.492	6.192	0.456	4.091	0.296	6.166	0.499
August 2004	7.735	0.639	5.992	0.519	5.737	0.542	7.290	0.382	4.983	0.501	6.608	0.710
September 2004	5.125	0.429	3.892	0.342	3.580	0.344	5.628	0.295	3.013	0.309	3.858	0.424
October 2004	3.301	0.254	2.454	0.198	2.162	0.189	4.270	0.211	1.758	0.164	2.168	0.215
November 2004	1.446	0.344	0.958	0.277	1.045	0.242	1.873	0.652	1.040	0.164	1.403	0.461
December 2004	1.246	0.262	0.795	0.204	0.905	0.185	1.487	0.463	0.948	0.132	1.129	0.332
January 2005	1.399	0.377	0.931	0.301	1.010	0.266	1.835	0.700	1.005	0.183	1.370	0.497
February 2005	0.756	0.109	0.431	0.073	0.557	0.079	0.706	0.138	0.685	0.070	0.560	0.105
March 2005	0.513	0.107	0.274	0.069	0.381	0.077	0.422	0.125	0.521	0.073	0.342	0.096

Table 4-7. Average monthly soil respiration in $\text{g C m}^{-2} \text{ day}^{-1}$, 15th of March 2004 to 14th of March 2005 for the air temperature model. In November 2004 to March 2005, soil respirations are average field measured values for pine, oak 2 and meadow, since no statistical significance existed for winter. The average value for March 2004 is only calculated for 15th to 31st of March and the average value for March 2005 is only calculated for the 1st to 14th of March.

Date	Pine		Spruce		Lichen		Oak 1		Oak 2		Meadow	
	soil respiration	std. dev.	soil respiration	std. dev.	soil respiration	std. dev.	soil respiration	std. dev.	soil respiration	std. dev.	soil respiration	std. dev.
March 2004	1.276	0.211	0.629	0.140	0.151	0.059	0.926	0.118	0.765	0.037	1.656	0.244
April 2004	1.407	0.203	0.708	0.136	0.178	0.060	1.003	0.112	0.791	0.035	1.810	0.233
May 2004	2.033	0.238	1.132	0.173	0.365	0.092	1.346	0.124	0.895	0.033	2.527	0.266
June 2004	2.879	0.343	1.776	0.274	0.755	0.190	1.771	0.167	1.000	0.039	3.457	0.372
July 2004	4.374	0.573	3.106	0.526	2.753	0.789	4.393	0.966	2.740	0.701	4.255	0.420
August 2004	5.825	0.278	4.468	0.309	4.860	0.504	6.919	0.428	4.635	0.529	5.245	0.414
September 2004	5.016	0.241	3.600	0.253	3.527	0.374	5.700	0.358	3.261	0.381	4.102	0.329
October 2004	4.265	0.158	2.843	0.150	2.472	0.189	4.614	0.219	2.204	0.183	3.132	0.186
November 2004	1.699	0.283	0.949	0.252	1.026	0.409	1.386	0.558	1.750	0.212	2.004	0.334
December 2004	1.406	0.232	0.815	0.191	0.798	0.279	1.074	0.379	1.120	0.099	0.986	0.109
January 2005	1.124	0.343	0.894	0.262	0.961	0.434	1.298	0.594	1.179	0.712	0.922	0.075
February 2005	0.941	0.181	0.495	0.082	0.365	0.085	0.486	0.114	1.044	0.345	0.665	0.109
March 2005	0.573	0.110	0.367	0.100	0.255	0.107	0.339	0.144	0.172	0.121	0.396	0.105

Table 4-8. Annual soil respiration and standard deviation in kg C m⁻² y⁻¹ for the air temperature and soil temperature based models 15th of March 2004 to 14th of March 2005.

Ecosystem	Air temperature modelled		Soil temperature modelled	
	soil respiration	std. dev.	soil respiration	std. dev.
Pine	0.98	0.62	1.17	0.93
Spruce	0.65	0.61	0.85	0.80
Lichen	0.56	0.69	0.75	1.39
Oak 1	0.94	0.71	1.18	0.98
Oak 2	0.64	0.65	0.78	0.85
Meadow	0.92	0.53	1.15	0.71

4.4 Effect of PAR, air temperature and soil moisture on ground GPP

GPP did not have any effect on soil carbon effluxes in any of the ecosystems but meadow. There was not enough carbon dioxide taken up by the forest floor vegetation to have an effect on soil carbon effluxes. For meadow, where photosynthesis affected soil carbon effluxes, PAR did have a significant effect on the uptake of carbon dioxide and 32.7%, of the variation in GPP was explained by the light response curve. Air temperature had as well an effect on GPP and 33.9% of the variation in GPP could be explained by the cubic regression (Table 4-9). The boundary line analysis with GPP against soil moisture indicated that there was no significant effect of soil moisture on GPP.

4.5 Evaluation of GPP regression model

The comparison between PAR modelled GPP and GPP measured in the field indicated that the model fitted well with field measured results. In total, the model tended to overestimate GPP in meadow. The air temperature model also fitted well with GPP measured in the field and it gave smaller residuals than the PAR model did (Table 4-10).

4.6 Seasonal and annual GPP

The light response curve with GPP against PAR indicated that the ground vegetation in meadow annually took up 0.54 ± 0.36 kg C m⁻² y⁻¹. The air temperature model indicated that 0.49 ± 0.42 kg C m⁻² y⁻¹ was taken up annually by ground vegetation. How these were distributed over the growing season can be seen in Figure 4-3 or Table 4-11. For meadow, NEE could be calculated since both GPP and soil respiration was estimated and annually the ecosystem lost between 0.38 and 0.66 kg C m⁻² y⁻¹, i.e. a significant loss of carbon to the atmosphere.

Table 4-9. Regression parameters and statistics for GPP regressions. Equations follow the form $GPP = GPP_0 + b_1T_a + b_2T_a^2 + b_3T_a^3$ for the air temperature regression and $GPP = - (GPP_1 + R_d)(1 - e^{(-b_1 PAR)/(GPP_1 + R_d)}) + R_d$ for the PAR regression. GPP is in g C m⁻² h⁻¹ and d.f. is degrees of freedom. PAR is in $\mu\text{mol photons m}^{-2} \text{s}^{-1}$.

Regression	d.f	GPP _{0,1}	b ₁	R _d , b ₂	b ₃	F-value	p-value	R ²
Air temperature	75	-0.0163	0.0003	-0.0006	9.1E-06	12.5	0.000	0.34
PAR	79	0.2481	0.0008	-0.0084	-	18.7	< 0.001	0.33

Table 4-10. Average residuals, PAR and air temperature based models against field measured GPP for meadow. Residuals are given in $\text{g C m}^{-2} \text{h}^{-1}$. All residuals were inside the 95% confidence interval of the modelled GPP.

Date	PAR	Air temperature
24 March	0.040	-0.003
13 April	0.152	0.002
10 May	-0.006	-0.087
6 July	0.043	-0.006
26 July	0.064	0.014
17 August	-0.037	-0.029
8 September	0.157	0.051
28 September	0.136	0.040
19 October	-0.028	0.029
Total	0.058	0.001

Table 4-11. Average monthly GPP in $\text{g C m}^{-2} \text{day}^{-1}$ during the growing season 15th of March 2004 to 31st of October 2005.

Date	PAR modelled GPP	PAR modelled std. dev.	Air temperature modelled GPP	Air temperature modelled std. dev.
March	1.76	0.46	0.77	0.48
April	2.47	0.49	1.06	0.41
May	2.85	0.37	1.92	0.50
June	3.01	0.40	3.05	0.46
July	2.78	0.57	3.22	0.38
August	2.59	0.48	3.39	0.63
September	2.09	0.30	2.12	0.51
October	1.07	0.48	0.96	0.29

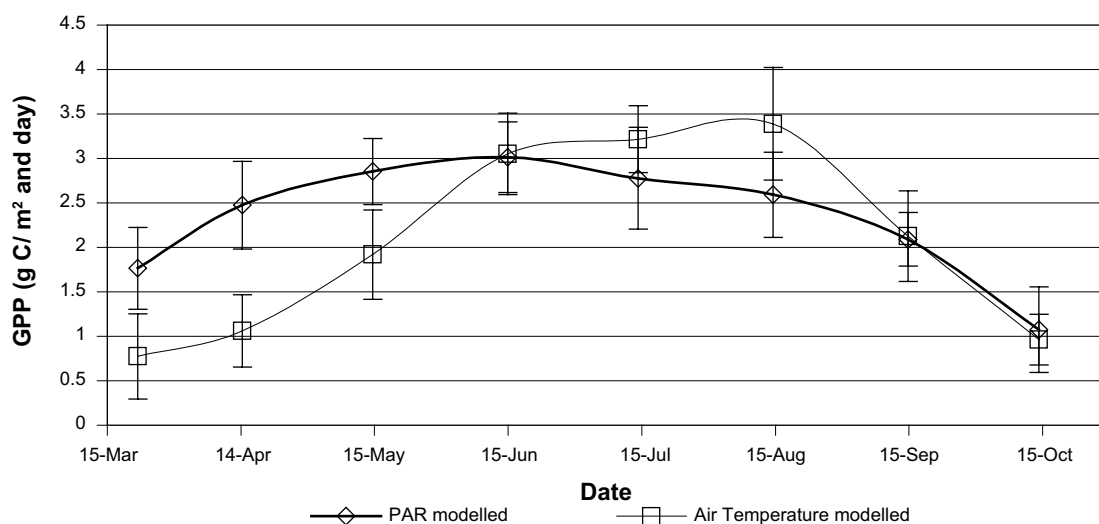


Figure 4-3. Monthly average modelled GPP in $\text{g C m}^{-2} \text{day}^{-1}$ for the growing season, 15th of March 2004 to 31st of October 2004 in meadow. Error bars are one standard deviation of monthly-modelled GPP.

5 Discussion

5.1 Effect of temperature and soil moisture on soil respiration

Studies done in temperate regions have indicated that the main factor to influence soil respiration is temperature /Davidson et al. 1998, Morén and Lindroth 2000, Swansson and Flanagan 2001 etc/, which also can be seen in the ecosystems studied in the Laxemar region. In some ecosystems at winter, air temperature did not affect soil respiration, which can be explained by inactive vegetation and frozen ground. Autotrophic respiration from biomass situated above ground is more affected by changes in air temperature than respiration from decomposers living down in the bulk of the soil and at winter there is no respiration from this aboveground biomass. Secondly, in frozen ground the main part of soil respiration origin from the deeper parts of the soil /Rayment and Jarvis 2000/, which is little affected by shifts in air temperature. Soil temperature still has a large impact on soil respiration in this part of the soil (Table 4-2).

The parameter k is not a constant coefficient; it decreases with an increase in temperature, which results in a decrease in the effect of temperature on soil respiration /Kirschbaum 1995/. Q_{10} , the relative increase in soil respiration when temperature is raised 10°C , therefore differs between the seasons and second half of the growing season with highest soil temperature in general had the lowest Q_{10} . Average Q_{10} in Laxemar was slightly high compared to many other ecosystem studied, where a 10°C increase in soil temperature at soil depths between 2–15 cm gives 2.0–6.0 times the soil respiration /Goulden and Crill 1997, Boone et al. 1998, Davidson et al. 1998, Hollinger et al. 1998, Morén and Lindroth 2000, Pilegaard et al. 2001, Swansson and Flanagan 2001/. Other studies have shown really large Q_{10} though, /Rayment and Jarvis 2000/ found k -values between 0 and 0.5, which is the same as Q_{10} between 0–148, and /Widén 2002/ found k -values between 0.02 and 1.02, which gives Q_{10} up to about 27,000. It is hard to compare Q_{10} between different studies, Q_{10} are derived from measurements taken up in different temperature ranges, and /Kirschbaum 1995/ showed that Q_{10} is temperature-dependent and decreasing with a temperature increase. Secondly, it is important that Q_{10} is derived out of soil temperature taken up at the same depth in the different studies. Q_{10} in Laxemar would differ greatly if they had been derived out of the air temperature set instead. This indicates that Q_{10} can only be used in the same temperature range and against soil temperature taken up at the same depth, as the field measurements that were used to derive Q_{10} were.

Inhibition of soil respiration in drier soils is an effect of desiccation stress while inhibition in more moist areas is a result of the development of anaerobic conditions /Heal et al. 1981, Davidson et al. 1998, Janssens et al. 2003/. But soil respiration from soils with different soil textures and different clay contents respond differently to soil moisture /Heal et al. 1981, Davidson et al. 1998/. In a temperate mixed hardwood forest, where some sites had a swampy character, the linear limitation of soil respiration reached zero at about 90%vol. /Davidson et al. 1998/ and in Douglas-fir stand at Vancouver Island, Canada, it was reached at approximately 35%vol. /Jassal et al. 2005/. For the ecosystems in Laxemar, this limit is reached in between these estimations, at about 60%vol. Even if soil respiration is inhibited by soil moisture in Laxemar, it is not totally compressed. The main explanation for this is that soil moisture measurements were taken up in the humus layer at the soil surface whereas soil respiration also origin from the deeper parts of the soil, where other soil moisture conditions can exist. With regard to spruce in Laxemar, it would appear that some other factor were limiting soil respiration in the lower soil moisture ranges, while it was soil moisture that was the limiting factor above 50%vol.

5.2 Evaluation of soil respiration regression models

The main problem with the modelled soil respiration is that too few measurements were done. The same soil respiration measurements that were used in the model were used to evaluate it; some data should have been separated and used in the evaluation. Another problem is that soil respiration varies over the seasons due to differences in the amount of living biomass, amount of roots, water availability, litter quality and active soil layer /Rayment and Jarvis 2000, Strömngren 2001/ and if there had been more data, the seasons could have been separated narrower. For both growing seasons, measurements done in spring and autumn were in majority in the regression models and this probably explains why residuals were largest in July. The low values in the margin of the growing seasons lower the modelled soil respiration in July, which results in an underestimation (Table 4-4 and 4-5).

5.3 Seasonal and annual soil respiration

The seasonal differences in soil respiration seen in Figure 4-2a–f can be explained by seasonal changes in depth of active soil layer, amount and production of vegetation and roots and changes in microbial activity. The volume of active soil is highly seasonal dependent and it differs due to seasonal changes in temperature, water table and frost /Rayment and Jarvis 2000/. When it comes to root respiration, which is between 50–60% of soil respiration /Högberg et al. 2001, Granier et al. 2000/, it is strongly correlated to soil temperature /Boone et al. 1998/ and photosynthesis of the aboveground biomass /Högberg et al. 2001/. Another cause to the seasonal variation in root respiration is the part connected to growth respiration due to the fine root production, as discussed by /Widén 2002/. When it comes to the heterotrophic respiration, microbial populations do not differ between the seasons but activity and metabolism highly follows temperature and is therefore largest in summer /Blume et al. 2002/.

The annual soil respiration ($0.56\text{--}1.17\text{ kg C m}^{-2}\text{ y}^{-1}$) for the coniferous ecosystems of Laxemar (pine, spruce and lichen) is large compared to the estimated mean for boreal forests of $0.33\text{ kg C m}^{-2}\text{ y}^{-1}$ /Raisch and Schlesinger 1992/. But, there are a large number of studies showing soil respiration well above this estimated mean. /Morén and Lindroth 2000/ and /Lindroth et al. 1998/ found annual soil respiration in Norrunda, Sweden to be $1.23\text{--}1.50\text{ kg C m}^{-2}\text{ y}^{-1}$, /Rayment and Jarvis 2000/ estimated annual soil respiration at $0.90\text{ kg C m}^{-2}\text{ y}^{-1}$ for a black spruce stand in northern Saskatchewan and /Law et al. 1999b/ found a value of $0.68\text{ kg C m}^{-2}\text{ y}^{-1}$ for a pine forest in Oregon. The annual soil respiration for oak 2 ($0.64\text{--}0.78\text{ kg C m}^{-2}$) was about the same as the estimated mean for temperate forests of 0.65 kg C m^{-2} /Raisch and Schlesinger 1992/ while oak 1 ($0.94\text{--}1.18\text{ kg C m}^{-2}\text{ y}^{-1}$) were larger. For deciduous ecosystems, there are also other studies showing soil respiration well above this mean, for example in Northern Wisconsin /Bolstad et al. 2004/ found soil respiration values between 0.82 and $1.21\text{ kg C m}^{-2}\text{ y}^{-1}$. Soil respiration ($0.92\text{--}1.15\text{ kg C m}^{-2}\text{ y}^{-1}$) for meadow was also in the upper regions compared to other studies done. /Novick et al. 2004/ reported for a grass covered field in North Carolina, $1.30\text{ kg C m}^{-2}\text{ y}^{-1}$, while most other studies found lower values. /Suyker and Verma 2001/ and /Suyker et al. 2003/ estimated annual soil respiration to $0.52\text{--}0.54\text{ kg C m}^{-2}\text{ y}^{-1}$ for a tall grass prairie in Oklahoma, /Maljanen et al. 2001/ reported $0.76\text{ kg C m}^{-2}\text{ y}^{-1}$ for an organic field in eastern Finland and in a moist mixed grassland near Lethbridge in Alberta /Flanagan et al. 2002/ did estimate it to be $0.27\text{--}0.30\text{ kg C m}^{-2}\text{ y}^{-1}$.

An explanation to that the coniferous forests have larger soil respiration than the estimated mean could be that Laxemar is situated further south than the ecosystems used in the mean estimate by /Raisch and Schlesinger 1992/, Laxemar is on the southern edge of boreal forests. /Lindroth et al. 1998/ explained their high soil respiration estimate with climate variables; the temperature were high and soil moisture were low during periods of large soil respiration. Another explanation could be that the forests of Laxemar are managed and at least the spruce forest is situated on peat-dominated soils that have been subjected to ditching activities. The lowered water

table would start off an increased decomposition due to the high organic soil content. Another explanation given is that the ecosystems are already responding to climate change /Rayment and Jarvis 2000, Bellamy et al. 2005/.

It can be seen that annual soil respiration differs between the ecosystems, tests with soil respiration against different characteristics of the ecosystems could not significantly explain these differences since so few ecosystems were studied. Between soil respiration of the forest ecosystems and the age of the forest, a trend relationship could be seen though (Cubic regression: F -value 84.35; p -value 0.077; R^2 99.4%). This means that soil respiration was low in young and old forest ecosystems and high in between. This is the same relationship that age of a forest has to NPP /Kashian et al. 2005, Binkley et al. 2002, Smith and Long 2001, Gower et al. 1996/ and according to /Janssens et al. 2001a/; NPP is the main factor to determine soil respiration.

A trend relationship was also seen between amount of litter and soil respiration (S-curve: F -value 15.51; p -value 0.059; R^2 88.6%). It was a negative relationship, i.e. the ecosystems with most litter had the lowest soil respiration estimates. The reason for this could be that, the litter measurements were taken up in September /Löfgren 2005/, before the arrival of new litter. The ecosystem with highest soil respiration had already decomposed last year's litter while the ecosystems with low soil respiration had some litter left. Another explanation could be the quality of litter; it might be that the litter is harder to decompose in the ecosystems with much litter.

5.4 Shortages of the closed chamber technique

The measurement of soil carbon effluxes with chambers is the most commonly used technique for estimating soil carbon effluxes. It has been used widely for several decades and the main potential sources of error are hereby well known /Davidson et al. 2002/. The trouble with the closed chamber technique is that the chamber always affects the soil that it does its measurements on. First, since the concentration of carbon dioxide in the chamber is altered and this affects the concentration gradient from the soil /Davidson et al. 2002/. When the concentration in the chamber increases it results in a decrease of the diffusion gradient, which results in an underestimation of the soil carbon dioxide effluxes. This problem can be corrected for by using a quadratic relationship in the curve fitting and by using short measurement periods.

The large problem with the estimates of soil carbon dioxide effluxes is caused by under or overpressure in the chamber /Widén and Lindroth 2003/. Over and under pressure in the chamber can occur due to circulating gases and warming or cooling of chamber air. In an over pressurized chamber soil carbon dioxide effluxes is slowed down while in an under pressurized chamber carbon dioxide is sucked out of the soil /Davidson et al. 2002/. These problems can be avoided with properly designed chambers.

/Pumpanen et al. 2004/ did a study where several different chambers frequently used in the estimations of soil carbon dioxide effluxes were compared to a known CO_2 flux. Their study showed that chambers under and overestimated soil carbon effluxes with between -21 to $+33\%$, depending on type of chamber and method used for mixing the air in the chamber. In average the estimates of the chambers were within 4% of the reference flow /Pumpanen et al. 2002/. Tests were done with SRC-1 chambers from PP-systems and it ranged between underestimates of the soil carbon dioxide effluxes with between -14% to overestimates with $+33\%$. The differences depended on which sand and which soil moisture that the measurements were done on and if collars were used or not.

Most of the times the SRC-1 overestimated the soil carbon effluxes and this were explained by turbulences from the fan. The use of collars also resulted in a larger increase than when no collars were used. In measurements with collars, the chamber gets tightly sealed to the ground

and the better results without the collar could be explained by leakage of CO₂ from under the edges of the chamber, which would compensate for the disturbance of the fan. In the CPY-2 measurements done in Laxemar, collars were not used. Without a collar the estimates of the SRC-1 chamber were between 0.94 and 1.19, with an average of 1.05 of the reference flux. The SRC-1 chamber is different from the CPY-2 chamber though; it is made out of aluminum and it is nontransparent. It is hereby hard to tell if 1.05 is a correction factor, which also could be used for the CPY-2 chamber. The best would be if tests were done with a CPY-2 chamber against a known reference flux.

5.5 Effect of GPP on soil carbon effluxes

In a previous study over the same ecosystems and including the same data, but just for the Spring, /Tagesson 2006c/ found GPP significantly different from zero for all ecosystems but pine. In this study, when data covered the entire growing season, no photosynthesis was found for the ground vegetation in the forest ecosystems of Laxemar. In spruce, there were almost no ground vegetation and in oak 2, ground vegetation existed during spring but disappeared after the development of canopy. For the other forest ecosystems, there were ground vegetation but the amount of carbon dioxide taken up by it was too small to be statistically detectable. Photosynthesis by ground vegetation naturally depends on the structure of the ground vegetation, which then depends on the type of forest. It is also dependent on other factors such as soil moisture, temperature and radiation /Baldocchi et al. 1997, Kelliher et al. 1999/. Some studies have indicated that the forest floor vegetation can be a significant part of the soil carbon effluxes and that they take up a large portion of carbon dioxide /Widén 2002, Morén and Lindroth 2000/. In other studies it have been seen that the uptake of carbon dioxide by the forest floor vegetation is negligible /Baldocchi et al. 1997, Kelliher et al. 1999/.

5.6 Effect of PAR, temperature and soil moisture on ground GPP in meadow

In the meadow in Laxemar, GPP was saturated at 0.248 g C m⁻² h⁻¹, which is in the same range as in several other studies. /Valentini et al. 1995/ found for a California grassland that light saturation occurred approximately between 0.13 and 0.30 g C m⁻² h⁻¹, for plants with sun characteristic leaves, /Rothstein and Zak 2001/ found a levelling off between 0.17 and 0.66 g C m⁻² h⁻¹ and for a grassland and barley fields in Finland, /Maljanen et al. 2001/ found that maximum uptake of CO₂ was between 0.11 and 0.27 g C m⁻² h⁻¹.

The average quantum efficiency, i.e. the efficiency of the vegetation to take up PAR, over the growing season is 0.0052 mol C (mol photons)⁻¹, which is similar to /Flanagan et al. 2002/ and /Ruimy et al 1994/, with quantum efficiencies between 0.0049 and 0.068 and between 0.0019 and 0.0098, respectively.

Former studies have shown that photosynthesis increases exponentially at lower temperatures, to an optimum where after it starts to decrease /Cannell and Thornley 1998, Wang et al. 1996, Lankreijer 1998/. Many studies have used the Arrhenius function of temperature to show this relationship, whereas /Cannell and Thornley 1998/ used a cubic regression since it has the same shape but it is more mathematically transparent. In this study, the cubic regression was chosen since it is easier for the calculation of the standard deviations. The negative part with the cubic regression is though that the underlying processes cannot be interpreted.

No significant effect of soil moisture in the humus layer could be seen on GPP. Visually, it seemed that soil moisture had an effect on GPP in both dry and wet regions but too few measurements were probably done to detect it statistically. Other studies have shown the importance of soil moisture for photosynthesis; /Flanagan et al. 2002/ found that the main

environmental factor to control leaf area index of a temperate grassland was soil moisture and /Suyker and Verma 2001/ showed how the effect of PAR on NEE significantly was reduced under the influence of soil moisture stress.

5.7 NEE in meadow

The uptake of carbon by the ground vegetation in the meadow ($0.49\text{--}0.54 \text{ kg C m}^{-2} \text{ y}^{-1}$) is similar compared to other grassland studies with values between $0.27\text{--}1.21 \text{ kg C m}^{-2} \text{ y}^{-1}$ /Flanagan et al. 2002, Suyker and Verma 2001, Suyker et al. 2003, Novick et al. 2004/. Some of these ecosystems had larger uptake, but this can be explained by the fact that they are situated further south where the growing season is longer. The NEE of $0.37\text{--}0.66 \text{ kg C m}^{-2} \text{ y}^{-1}$ shows that there is a loss of carbon from the meadow to the atmosphere. This is a large loss of carbon and a reason could be if the meadow is a newly drained area containing peat soils. The measurements were taken up within a couple of meters from a ditch and surrounding areas were wet. Recently, it has been shown that soils over England and Wales also lose carbon and the main explanations are changes in land-use and climate /Bellamy et al. 2005/.

5.8 Conclusions

The first general aim of the study was to analyze the influence of abiotic factors on soil carbon effluxes of boreal and temperate forests and a meadow. The study has given further evidence that temperature is a major controlling factor for soil respiration in temperate and boreal ecosystems of the Northern hemisphere. Soil moisture also had a limiting effect on soil respiration for all ecosystems but spruce, where soil moisture was the limiting factor above a threshold value, though. The study also indicates that GPP of ground vegetation were too small to be a part of soil carbon effluxes of the forest ecosystems, but it does have an effect in the meadow. For GPP in the meadow, PAR and temperature affects this part of the soil carbon effluxes.

The second general aim were to test if regression equation with soil carbon effluxes against abiotic factors can be used to model soil carbon effluxes 15th of March 2004 to 14th of March 2005. The exponential regressions with soil respiration against air and soil temperature could be used to extrapolate soil respiration 15th of March 2004 to 14th of March 2005. The light response curve with GPP against PAR and the cubic regression with GPP against air temperature could be used for the growing season, 15th of March to 31st of October 2004. There are many factors that changes over the season that influence the soil carbon effluxes of the temperate and boreal ecosystems and these are not included in a single factor regression. To make better models more data would be needed to be able to separate the seasons into narrower time spans than they have in this study.

The following conclusions can be drawn about the set of hypotheses

1. The first specific hypothesis was verified for all ecosystems but pine, oak 2 and meadow during winter when it comes to that air temperature has an effect on soil respiration, but it was verified for all ecosystems and all seasons when it comes to the effect of soil temperature. It was also verified that soil moisture has an effect on soil respiration.
2. The second specific hypothesis was verified; regression equations with soil respiration against air and soil temperature can be used to model soil respiration 15th of March 2004 to 14th of March 2005.
3. The third specific hypothesis was falsified for all ecosystems but meadow; GPP do not affect soil carbon effluxes for the forest ecosystems. It was verified for meadow, where GPP has an effect on soil carbon effluxes.

4. The fourth specific hypothesis was verified when it comes to PAR and temperature; they have an effect on GPP. It was neither verified nor falsified when it comes to the effect of soil moisture on GPP.
5. The fifth specific hypothesis was verified; PAR and air temperature can be used to model GPP 15th of March to 31st of October 2004.

Generally, most of the hypotheses were verified. Abiotic factors do influence soil respiration; the cases where hypotheses were falsified was for air temperature at wintertime when soil respiration is low and other climatic factors are of larger importance. GPP affected soil carbon effluxes for meadow but not for the forest ecosystems, too little carbon dioxide was taken up by ground vegetation to be detectable. The effect of soil moisture on GPP was neither falsified nor verified since too few data existed to statistically test the hypothesis. Abiotic factors can be used to model soil carbon effluxes and to extrapolate occasional field measurements temporally. Care should be taken to the seasonal variation so that there are not too many other influential factors that change in between the occasions of field measurements. Annual soil respirations in these ecosystems were estimated to be between 0.56–1.18 kg C m⁻² y⁻¹. The ground vegetation in the forest ecosystem did not reduce this net efflux while in meadow it took up between 0.49 and 0.54 kg C m⁻² y⁻¹. For meadow, this gives a positive NEE and the total ecosystem losses 0.37–0.66 kg C m⁻² y⁻¹. For the forest ecosystems, the measurements of soil carbon effluxes show that the floors of these ecosystems also are a large source of carbon.

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