

CO₂ efflux from boreal forest soil before and after clear-cutting and site preparation

Jukka Pumpanen

Academic dissertation

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Abstract

The aim of this study was to quantify CO₂ concentration in soil and soil CO₂ efflux in boreal forests of two different ages over seasons and years and to assess how forest clear-cutting and consequent site preparation affect CO₂ emissions from the soil. Processes underlying soil CO₂ efflux and factors affecting it were studied with a process-based model, simulating the CO₂ production and the movement of CO₂ in the soil. In addition, the reliability of systems used for measuring CO₂ effluxes was examined.

CO₂ concentration in the soil profile followed a seasonal pattern similar to soil temperature. Highest concentrations were usually measured in summer. In the young forest, the CO₂ concentrations ranged from 580 to 780 $\mu\text{mol mol}^{-1}$ in the humus layer to 13 620 - 14 470 $\mu\text{mol mol}^{-1}$ in the C-horizon in the summer. In winter the concentrations were much lower ranging from 498 $\mu\text{mol mol}^{-1}$ in the humus to 1213 - 4325 $\mu\text{mol mol}^{-1}$ in the C-horizon. Occasional peaks were measured in April due to formation of ice crust on the soil surface. In the old forest, CO₂ concentrations in the deeper soil layers were lower than in the young forest due to differences in soil particle-size distribution affecting the diffusion properties of the soil and differences in the thickness of the soil pack.

Soil moisture affected significantly CO₂ concentration in the soil profile, because the transport of CO₂ in the soil was greatly affected by water content related gas diffusion. This was clearly shown by comparing empiric observations to simulations with the process model. If soil moisture was not included in the model, unrealistic high concentrations resulted. Clear-cutting decreased CO₂-concentrations by 29-33% in O- and A-horizons and by 20-26% in B- and C-horizons.

Soil CO₂ efflux was also affected by soil temperature and soil moisture. Under the forest cover, soil temperature explained more than 45% of the temporal variation in soil CO₂ efflux, but in extremely dry conditions, soil water content restricted soil respiration. The efflux showed a seasonal pattern, ranging from a low of 0.0-0.1 g CO₂ m⁻² h⁻¹ in winter to peak values of 2.3 g CO₂ m⁻² h⁻¹ occurring in late June and in July. In the young forest, the daily average effluxes in July were 1.23 g CO₂ m⁻² h⁻¹ in wet climatic conditions, but during extreme drought the fluxes were 0.98 g CO₂ m⁻² h⁻¹. In the old forest the average fluxes in July were 0.51 and 0.49 g CO₂ m⁻² h⁻¹ in wet and dry conditions, respectively. The spatial variation in CO₂ efflux was high (CV 18 – 45%).

The two chamber systems used in the study, flow-through and non-flow-through chamber, showed highly different effluxes when compared to each other on soil *in situ* and tested against artificially generated known CO₂ effluxes. Non-flow-through chamber underestimated fluxes by about 30% whereas the flow-through chamber overestimated the fluxes by about 30%. No major pressure anomalies were observed in chambers, but CO₂ efflux measurements were sensitive to mixing of air inside the chambers and disturbance of CO₂ gradient in the soil when placing the chamber on the soil.

Annual CO₂ effluxes measured by non-flow-through chambers ranged in the young forest between 2787 and 2732 g CO₂ m⁻² and in the old forest between 2096 and 2130 g CO₂ m⁻² during wet and dry years respectively. Annual effluxes measured by flow-through chambers were 12-22% higher during respective years. After the clear-cutting, the annual effluxes remained unchanged on places where litter was removed and increased by 55% on places where litter was left on site. The amount of CO₂ emitted from the decomposition of logging residue during the first year after the clear-cutting was 23% of the total C pool in the logging residue on the soil surface. The estimated annual emissions from the humus layer and from the A- and B-horizons were about 20% of the root mass measured at the site before clear-cutting. The decomposition of the logging residue was at fastest during the first year after the clear-cutting, slowing down in the following years. Based on the measured CO₂ evolution rate and observed reduction of decomposition rate along with the aging of decomposing material, it seems that the decomposition of the logging residue may take longer than the time needed for the new forest stand to act as a carbon sink again. Thus in the long, over subsequent forest crop rotation periods, the amount of carbon accumulated in the soil may be larger than the amount of carbon released into the atmosphere in decomposition.

Key words: boreal forest soil, soil respiration, CO₂ efflux, chamber, forest clear-cutting, site preparation, dynamic model, diffusion

List of original articles

This thesis is based on the following articles, which are referred to by their Roman numerals:

- I.** Pumpanen J., Ilvesniemi H., Keronen P., Nissinen A., Pohja T., Vesala T., and Hari P. 2001. An open chamber system for measuring soil surface CO₂ efflux: Analysis of error sources related to the chamber system. *Journal of Geophysical Research-Atmospheres. Journal of Geophysical Research.* Vol 106. No. D8: 7985-7992.
- II.** Pumpanen J., Ilvesniemi H. and Hari P. 2003. A process-based model for predicting soil carbon dioxide efflux and concentration. *Soil Science Society of America Journal.* 67: 402-413.
- III.** Pumpanen J., Ilvesniemi H., Perämäki M. and Hari P. 2003. Seasonal patterns of soil CO₂ efflux and soil air CO₂ concentration in a Scots pine forest: comparison of two chamber techniques. *Global Change Biology* 9: 371-382.
- IV.** Pumpanen J., Westman C. J. and Ilvesniemi H. Soil CO₂ efflux from a podzolic forest soil before and after forest clear-cutting and site preparation. Accepted by *Boreal Environment Research*.

Jukka Pumpanen participated in planning the research, was responsible for data collection, data analysis, modelling, literature searches and was the main author in all studies. Hannu Ilvesniemi and Pertti Hari advised in modelling, participated in planning the research and in discussions and commented on the manuscript in studies I-III. Carl Johan Westman and Hannu Ilvesniemi participated in planning the research and in discussions and commented on the manuscript in study IV. Petri Keronen, Toivo Pohja and Ari Nissinen participated in the construction and maintenance of the measurement system and commented on the manuscript in study I. The computer program of Martti Perämäki was used in calculating the fluxes in study II. Timo Vesala participated in planning the measurement system and commented on the manuscript in study I.

1. Introduction

1.1. Background

Global climate warming and attempts to restrain the emissions of greenhouse gases by using forests for carbon sequestration has raised interest in the carbon balance of forest ecosystems and factors affecting this balance. Carbon fluxes between terrestrial ecosystems and the atmosphere is one of the key interests in the Kyoto Protocol, which aims to quantify the reductions in greenhouse gas emissions. However, the factors controlling carbon exchange between forest soil and the atmosphere, its magnitude and location are still uncertain and under a debate (IGBP Terrestrial working group 1998; Valentini *et al.* 2000).

Several studies have suggested that in the northern hemisphere forest ecosystems act as a carbon sink (Kauppi *et al.* 1992; Nabuurs *et al.* 1997; Fan 1998). However, these estimates are still controversial (Malhi *et al.* 1999). Also tropical and temperate forests have been considered to be potential carbon sinks. Nevertheless, boreal ecosystems are potentially important in driving changes in atmospheric CO₂ because of their large carbon pools. Current estimates of the world's soil carbon pool average 1500 Gt (C). Boreal forest soils are among the largest terrestrial carbon pools, estimated to contain approximately 15% of the soil C storage world wide (Schlesinger 1977; Post *et al.* 1982). Because climate warming is predicted to be greatest in the north, these C pools can cause a positive climate feedback, which would speed up the increase in the atmospheric CO₂ concentration. Different climate scenarios predict 1 – 3.5 °C increase in the global mean surface temperature during the next century (IPPC 1995). However, regional temperature changes could differ substantially from the mean global value. Current warming predictions for the boreal zone are 1.5°C higher than for the rest of the world. (Moore 1996 in Gullledge and Schimel 2000).

The two most important processes affecting the carbon balance of a forest ecosystem are photosynthesis and respiration. CO₂ is assimilated in photosynthesis by trees and ground vegetation and translocated to soil through several pathways (Fig. 1.). Significant amounts of carbon is allocated to the root systems for root growth and root maintenance. When roots die, the carbon is added to the forest floor and mineral soil as dead organic matter. Carbon is added to the forest floor and humus from above ground biomass through litter fall and leaching of dissolved organic matter from the canopy (Edwards and Harris 1977; Kalbitz *et al.* 2000) and from roots (Högberg *et al.* 2001). Carbon is released from the soil to the atmosphere through the decomposition of dead organic matter and through the respiration by roots, root mycorrhizal fungi and other soil micro-organisms (Gaudinski *et al.* 2000; Chapin III and Ruess 2001). Some carbon is also leached out of the ecosystem dissolved in ground water especially in peatlands (Urban *et al.* 1989; Sallantaus 1992). However, in podzolized mineral soil the amount of dissolved organic carbon leached to ground water is very small (Easthouse *et al.* 1992; Lundström 1993).

The relationship between production and decomposition determines whether a system is a sink or a source of atmospheric CO₂. In old forests these two fluxes are of similar magnitude and changes in climate and the length of growing season can shift a forest from being a sink to be a source of carbon (Valentini *et al.* 2000). It is still not well known what are the absolute and relative contributions of these fluxes on the forest carbon balance, and how climatic factors affect them. In order to partition the net carbon exchange of a forest ecosystem accurately into different components, more understanding is needed on the quantity of soil CO₂ efflux, and factors controlling it.

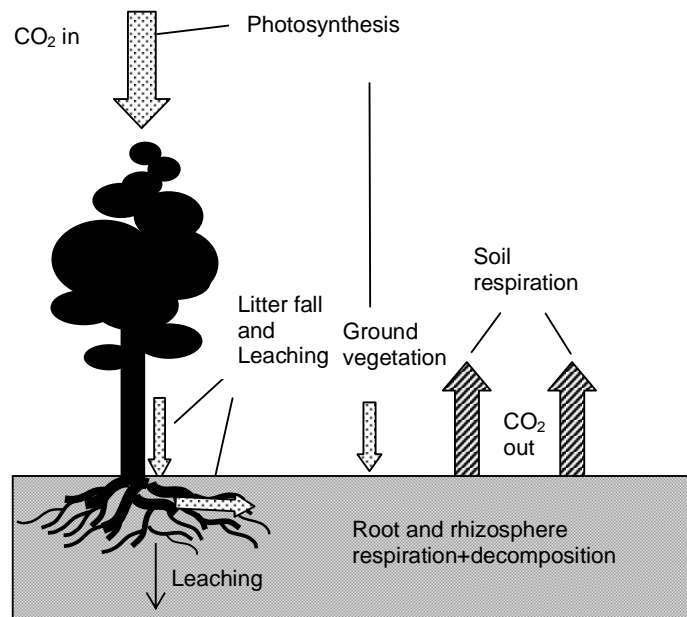


Figure 1. Carbon fluxes and factors controlling them in forest ecosystem. The two major fluxes generated by photosynthesis and respiration, which are of similar magnitude, determine whether the forest is a sink or a source of carbon.

1.2. CO₂ concentration in soil and soil CO₂ efflux

CO₂ concentration in the soil air space between soil particles is often an order of magnitude higher than in the atmosphere (Fernandez and Kosian 1987; Suarez and Simůnek 1993) resulting in a large concentration gradient between the soil and the atmosphere. The primary mechanism for transporting CO₂ from the soil to the atmosphere is molecular diffusion (Freijer and Leffelaar 1996). According to Fick's first law, the gas flux is dependent on the concentration gradient and the diffusivity of the soil. Thus the CO₂ flux in the soil is usually upwards resulting in a CO₂ efflux out of the soil.

CO₂ can also move between the soil layers as dissolved in water (Simůnek and Suarez 1993). Also mass flow of CO₂ by convection caused by wind or atmospheric pressure fluctuations may affect the gas movement in soil especially in deep soils.

However, other mechanisms of gas movement than concentration controlled diffusion have been shown to account for less than 10% of the CO₂ lost from the upper soil and even less for the deeper unsaturated zone (Wood and Petraitis 1984).

CO₂ is produced within the soil by heterotrophic microbial respiration and by autotrophic root respiration. Soil microorganisms release CO₂ by oxidizing organic debris and return the carbon assimilated by the plants back to the atmosphere. Major factors affecting microbial respiration are the amount and quality of organic carbon in the soil, soil temperature and soil moisture (Kirschbaum 1995; Davidson *et al.* 1998; Prescott *et al.* 2000a). These factors are highly variable, depending on the geographical location of the site, the physical and chemical properties of the soil, and the age and species composition of the forest.

In boreal forests the decomposition is often slow due to unfavorable climate: low temperature and high humidity. Soil temperature remains between 0-5 °C most of the year. Podzolic soils are also low in pH mainly because of the formation of plant-derived acidic organics in litter decomposition (Lundström *et al.* 2000).

Root and rhizosphere respiration is the second major component of soil CO₂ efflux. Estimates on the contribution of root and rhizosphere respiration are highly variable, ranging from 10 to 90 % (Nakane *et al.* 1983, 1996; Ewel *et al.* 1987b; Bowden *et al.* 1993; Hanson *et al.* 2000; Maier and Kress 2000). Direct measurements of root and rhizosphere respiration are difficult because the measurements themselves usually affect respiration by e.g. wounding the roots. Moreover, instantaneous measurements of root respiration are difficult to scale up to the ecosystem level because of large spatial variation in root distribution (Buchmann 2000).

The amount of root and rhizosphere respiration is dominated by the root biomass of a specific soil layer. Pietikäinen *et al.* (1999) and Widén and Majdi (2001) found highest respiratory activities in boreal forest in organic soil layer close to the soil surface where also the amount of fine root biomass was highest. However, the rate of CO₂ production by roots at different depths depends also on the proportion of new and old roots. As the root tissue mature there is gradual decline in respiration. (Singh and Gupta 1977).

The photosynthetic activity of leaves influences the rate of root and rhizosphere respiration (Singh and Gupta 1977; Högberg *et al.* 2001). According to Högberg *et al.* (2001) soil respiration decreased by about 54% within 1-2 months and about 37% within 5 days when the supply of photosynthates to roots and their mycorrhizal fungi was stopped by girdling i.e. stripping the bark to the depth of the xylem.

In addition to biological processes, abiotic processes such as carbonate dissolution and chemical oxidation may contribute to soil CO₂ efflux (Burton and Beauchamp, 1994). This is however a minor source of CO₂ in boreal forests in Scandinavia due to the mineral composition of soil, mainly acidic minerals such as granodiorite and gneiss and almost complete lack of lime stone (Wahlström *et al.* 1992).

Despite large number of studies there is still a considerable uncertainty about the magnitude of CO₂ efflux from soil and factors controlling it. In order to estimate soil

CO₂ efflux more accurately more understanding is needed on processes controlling soil respiration. For example it is not well known what is the contribution of deeper soil horizons to total soil respiration and its seasonal variation, and what is the combined effect soil temperature and soil moisture on soil respiration. Moreover, little is known about the pattern of CO₂ concentration within the soil profile and its dependence on soil physical properties such as porosity, temperature and moisture.

1.3. Effect of disturbance on soil carbon balance

Due to their large land area and large carbon pool forests have an important role in the management of soil carbon stocks. Land use, such as forest harvesting affects soil carbon pool, and it has been suggested that carbon stocks can be managed by silvicultural practices (Karjalainen 1996b; Johnson and Curtis 2001; Liski *et al.* 2002). Upon such disturbances as forest fire or clear-cutting, the carbon balance of a forest is profoundly changed. First the carbon assimilation in photosynthesis of trees is ceased and secondly a large amount of fresh litter is released to the soil (Gordon *et al.* 1987; Millikin *et al.* 1996; Nakane *et al.* 1996; Lytle and Cronan 1998). When the tree canopy is removed, the solar radiation on the soil surface is increased resulting in higher diurnal temperature fluctuation in the soil. Daytime high temperatures at the clear-cut site have been shown to increase (Leikola 1974; Edwards and Ross-Todd 1983). Furthermore, because of decreased transpiration soil water content usually increase (Edwards and Ross-Todd 1983; Seuna 1986). Because the decomposition of soil organic matter is dependent on soil temperature and soil moisture, an increase in these factors can increase the decomposition rate of organic matter. The ground vegetation re-colonizing on the clear-cut site may also affect the carbon balance of the soil by adding fresh organic matter into the soil. Moreover, carbohydrates introduced into the soil through root exudates may affect the decomposition of soil organic matter (Cheng 1996).

Johnson and Curtis (2001) carried out a meta-analysis based on studies carried around the world in different forest ecosystems and concluded that on average forest harvesting had little effect on carbon in mineral soil. However, in coniferous forests saw log harvesting seemed to cause a significant increase in soil carbon due to the logging residue left on the soil surface. On the other hand, studies of Olsson *et al.* (1996) showed little or no effect of residues on soil carbon. According to Covington (1981) the soil carbon pool decreases after harvesting. The time since harvest seems to be an important factor. Several studies have shown soil carbon stocks to increase temporarily after harvesting. This increase can last from 4 to 18 years (Johnson and Curtis 2001). The net effect of the clear-cut on soil CO₂ efflux is ambiguous, because of the concomitant change in root and rhizosphere respiration. According to Ewel *et al.* (1987a), Gordon *et al.* (1987) and Lytle and Cronan (1998) soil CO₂ efflux increased after harvesting, but Edwards and Ross-Todd (1983) and Nakane *et al.* (1996) found the opposite.

In addition to clear-cutting and residue removal, the site preparation used for promoting the germination of seeds and helping the survival of planted seedlings also affects the decomposition of soil organic matter. The area exposed to this kind of treatment is significant. For example, in Finland about 120 000 hectares is annually prepared mechanically after harvesting (Finnish Statistical Yearbook of Forestry 2001). In site preparation the organic layer at the soil surface is partially mixed with mineral soil. Usually 40 - 60% of the soil surface is exposed in site preparation (Saksa *et al.* 1990). Large mounds of soil and shaded pits have different microclimate than that of the undisturbed soil (Beatty and Stone 1986; McClellan *et al.* 1990; Millikin 1996). Because the decomposition of soil organic matter is affected by temperature (Kirschbaum 1995; Davidson *et al.* 1998), the soil CO₂ efflux from different micro sites can be highly variable. Because of the complex interaction of biological processes and physical changes in the forest floor upon forest harvesting, the consequences of forestry practices on soil carbon balance and CO₂ emissions from soil are still unclear.

1.4. Accuracy in measuring soil CO₂ efflux

Soil CO₂ efflux is usually measured with different types of chamber techniques. The two major chamber types used widely for measuring soil fluxes are non-steady-state and steady-state chambers according to the nomenclature of Livingston and Hutchinson (1995). In non-steady-state chambers the CO₂ efflux is calculated from the concentration change over time in the chamber headspace (Singh and Gupta 1977; Rochette *et al.* 1992; Jensen *et al.* 1996). In steady-state chambers, the CO₂ efflux is calculated from the difference between the CO₂ concentration at the inlet and the outlet of the chamber.

Comparisons between the chambers have shown relative differences between various chamber types (Raich *et al.* 1990; Norman *et al.* 1997; Janssens *et al.* 2000) or demonstrated biases related to chambers (Nay *et al.* 1994; Fang and Moncrieff. 1998; Gao and Yates 1998). Non-steady-state chambers have been shown to give systematically lower fluxes than steady-state chambers, the underestimation ranging from 10% (Rayment and Jarvis 1997; Rayment 2000) to about 40-50% (Norman *et al.* 1997). Differences have also been found between non-steady-state chambers (Janssens *et al.* 2000).

No single method has been established as a standard, because different methods have not been compared to known CO₂ effluxes. Despite intensive work to develop more reliable chambers, the chamber itself always affects the object being monitored and each type of chamber has its distinctive problems. In non-steady-state chambers increasing concentration in the chamber headspace influence the CO₂ efflux from the soil by altering the natural concentration gradient between the soil and the atmosphere (Nay *et al.* 1994; Davidson *et al.* 2002). Moreover, pressure anomalies caused by placing the chamber on the soil surface may disturb the CO₂ concentration gradient in the soil.

In steady-state chambers, unless properly controlled, differences between the inflow and outflow rates can cause pressure difference between the chamber and the ambient air, which can generate additional airflow between the chamber and the soil. Even pressure differences of 1 Pa have been shown to cause errors in CO₂ efflux measurements (Kanemasu *et al.* 1974; De Jong *et al.* 1979; Fang and Moncrieff 1996; Kutsch 1996, Fang and Moncrieff 1998; Lund *et al.* 1999).

Uncertainties involved in measuring the fluxes cause significant errors for flux estimations, which makes the estimations of forest carbon balance less reliable. Because of this, the accuracy of the chambers used for measuring soil CO₂ efflux should be determined properly. Sensitivity analysis and profound testing of these error sources is a way to overcome these problems. To be able to determine the accuracy of different systems the systems should also be tested against known CO₂ efflux.

2. Aims of the study

The overall aim of this study was to quantify soil CO₂ efflux from boreal forests of two different ages over the seasons and years and to study how forest clear-cutting and site preparation affect CO₂ efflux from soil. Because soil CO₂ efflux depends on temperature and moisture conditions and consequently, since clear-cutting influences both of them, CO₂ emissions from soil should change in clear-cutting. There is also a major shift from autotrophic to heterotrophic respiration due to the removal of trees. Accordingly, I wanted to know what are the consequences of these major changes in forest ecosystem on soil carbon storage i.e. should the carbon stocks of the soil decrease after the clear-cutting.

Four sub-studies were conducted to clear out these issues. In order to understand the environmental factors and physical processes controlling soil CO₂ efflux, a process-oriented model was developed in sub-study II. The importance of soil temperature and soil moisture on soil respiration and diffusion of CO₂ from the soil to the atmosphere were examined with the model. In addition, the contribution of various soil horizons to soil respiration, its seasonal variation and the pattern of CO₂ concentration within the soil profile were studied with the model.

The aim of sub study III was to quantify the seasonal pattern of soil CO₂ efflux and CO₂ concentration in the soil profile and to compare different systems used for measuring soil CO₂ efflux. In addition, the effects of soil temperature and moisture on CO₂ efflux and soil air CO₂ concentration were studied empirically. The accuracy and precision of the chamber systems used for measuring the effluxes and factors affecting them were studied in detail in paper I.

Finally, the effects of clear-cutting, removal of logging residue and site preparation on CO₂ emissions from soil were assessed in sub study IV. In addition, annual CO₂ emissions from the logging residues and their effect on the long-term carbon balance of the forest are discussed in paper IV.

3. Material and methods

3.1. Conceptual model of respiration and CO₂ transport within the soil

Processes involved in soil CO₂ efflux and the effects of soil temperature and soil moisture were studied with a process based model (II). The model simulates CO₂ concentration of the air in soil pore space and the transport of CO₂ within the soil and from the soil to the atmosphere using hourly values for soil temperatures, volumetric soil water content and ambient CO₂ concentration. A schematic picture of the model is presented in figure 2.

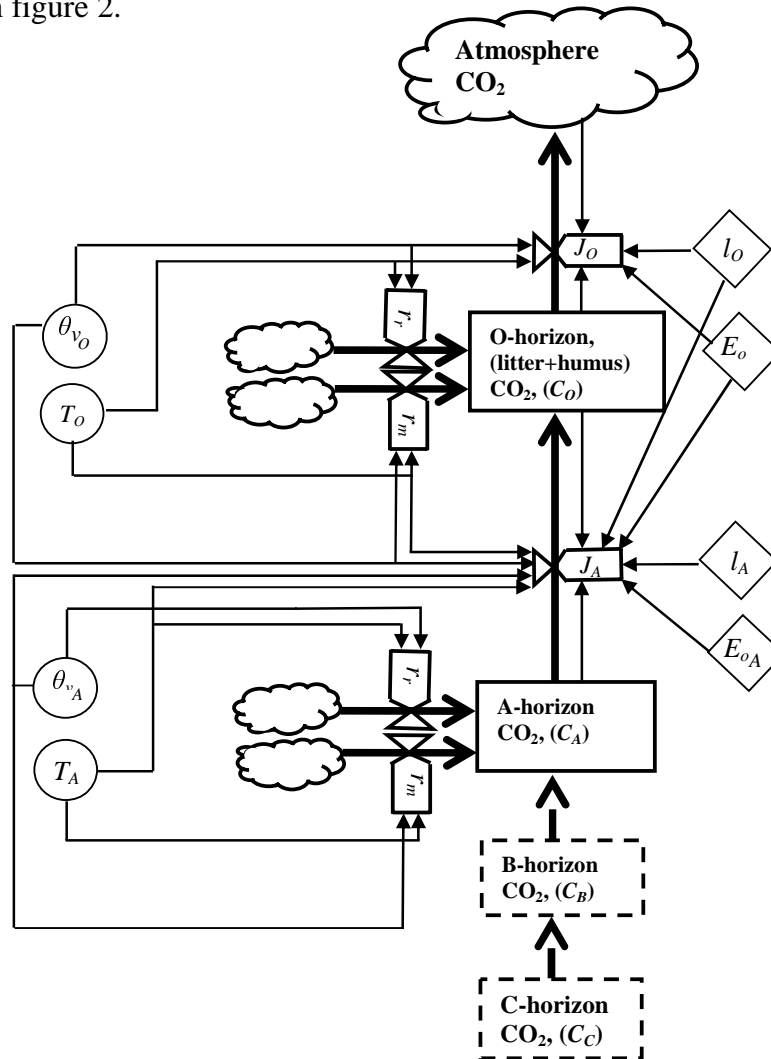


Figure 2. Soil CO₂ fluxes and pools. CO₂ is produced in each layer by microbial respiration (r_m) and by root respiration (r_r), which are affected by temperature (T) and by soil water content (θ_v). The transport of CO₂ between the layers is driven by diffusion and the CO₂ flux (J) depends on the total porosity of the soil (E_o), the thickness of the layers (l) and the concentration gradient between the layers. The CO₂ effluxes are denoted by thick arrows, and thin arrows represent effects between parameters and processes. The amount of CO₂ in a soil horizon is denoted by C and soil layers are denoted with capital letters O , A , B and C .

The model is based on the following assumptions: Soil is divided in successive layers, an approach that suits well for boreal forest soils with distinct horizon boundaries. All processes and soil properties are described separately for each layer. O-horizon is a separate organic layer above mineral soil. The mineral soil is divided into A-, B- and C-horizons. CO₂ is produced in each layer by microbial and root respiration. The contributions of both sources are assumed to be equal, in accordance with recent studies in coniferous forests that estimated the contribution of root and rhizosphere respiration to range from 33 to 73% (Maier and Kress 2000; Högberg *et al.* 2001; Widén and Majdi 2001). The oxidation of carbon compounds in biological organisms is determined by temperature and by soil moisture. The respiration rate of each layer depends exponentially on temperature and nonlinearly on soil moisture of the corresponding layer (Fig. 3). The dependence of respiration rate on temperature, $r(T)$ is:

$$r(T) = \alpha e^{\beta T} \quad (1)$$

where T is the temperature (°C). α and β are parameters determined separately for each soil layer (Fig 3a). The effect of soil moisture on soil respiration is:

$$f(\theta_v) = \text{Min} \{a \theta_v^d, b (E_o - \theta_v)^g, 1\} \quad (2)$$

where $f(\theta_v)$ represents the CO₂ efflux evolved from soil, θ_v is the volumetric water content (m³ m⁻³) and E_o is the total porosity (m³ m⁻³). The equation is taking into account both the effects of drought and anoxic conditions in wet soils approaching the water saturation (Fig. 3b). Parameters a , b , d and g are empirical constants that are fixed for a given soil type (Skopp *et al.* 1990).

Soil respiration (r) is obtained by multiplying $r(T)$ with $f(\theta_v)$:

$$r = r(T) f(\theta_v) \quad (3)$$

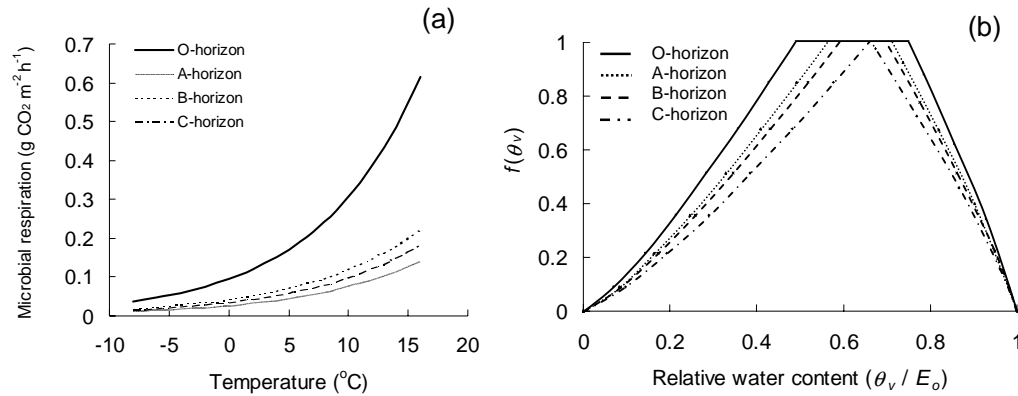


Figure 3. The relation between (a) soil respiration and soil temperature and (b) between soil respiration and soil water content in O-, A-, B- and C-horizons.

CO₂ transport within the soil and out of the soil is driven primarily by diffusion, which depends on the total porosity of soil layers, soil-water content, layer thickness, and the concentration gradient between the layers. The CO₂ flux driven by diffusion between A- and O-horizon is described with the following equation:

$$J_{AO} = -D_{AO} \frac{C_O - C_A}{(l_O + l_A)/2} \quad (4)$$

where J_{AO} is the flux from A- to O-horizon (g CO₂ m⁻² s⁻¹), D_{AO} is the diffusion coefficient of CO₂ between O- and A-horizons (m² s⁻¹), C_O , C_A , l_O and l_A are the CO₂ concentration (g CO₂ m⁻³) and thickness (m) of O- and A-horizons, respectively. The diffusion coefficient D_{AO} , is obtained as the weighted average of the layer specific coefficients weighted by the thickness of the soil layers. The fluxes between other horizons were calculated in a similar way with parameters determined separately for each layer. The amount of CO₂ in each layer was obtained using a CO₂ mass-balance equation with time discrete formalism (Eq. 10 in II).

3.1.1. Parameterization and testing of the model

Parameterization of the model was mostly based on process measurements carried out at the field measurement station SMEAR II in Hyytiälä and in the literature. Values for parameters used in temperature response functions (Eq. 1.) were obtained from core samples taken in July 1998 and reaching 0.5 - 1.0 m into the soil. Samples were divided according to soil horizons and temperature response curves were determined in laboratory separately for each layer Kähkönen *et al.* (2001), Pietikäinen *et al.* (1999) and Ilvesniemi (Ilvesniemi, unpublished data, 1996). Parameters for the moisture function were obtained from the studies of Skopp *et al.* (1990), Mecke and Ilvesniemi (1999) and Glinski and Stepniewski (1985). Total porosity of the soil was obtained from soil water retention curves determined for each soil horizon.

The model was tested against CO₂ effluxes measured from soil surface and soil profile CO₂ concentrations in a young Scots pine forest (II). A period of 19 months from 1 May 1998 to 30 November 1999 excluding winter months from December to April was chosen to study the performance of the model. The importance of water content on soil CO₂ efflux and CO₂ movement in the soil were studied by running the model with two configurations using the same data set. In the first simulation, water content was taken into consideration in respiration functions, whereas in the second simulation, the effect of water was left out. The performance of the model was analyzed by comparing measured CO₂ effluxes and CO₂ concentrations to those predicted by the model (Fig. 6 and Table 2 in II).

3.2. Measurement sites

All experiments in this study were carried out in Hyytiälä in Southern Finland (61° 51' N lat., 24° 17' E long.). In papers I, II and III measurements were carried out at field station for measuring forest ecosystem-atmosphere relations (SMEAR II). For details of the measurement station see Vesala *et al.* (1998). The site was sown with Scots pine seeds in 1962 after prescribed burning and soil scarification. The soil is glacial till having podzolic horizons partially mixed in some points and a newly formed O-horizon. The soil is confined to a homogeneous bedrock. In 1999, when the field measurements of this study were carried out, the stand had a dominant height of 13 m and 2100 stems per hectare with a stem volume of 119 m³ ha⁻¹ (Ilvesniemi and Liu 2001).

In paper IV, the study was carried out in a 130-year old Scots Pine – Norway Spruce stand 2-3 km apart from Hyytiälä. The site extends over a 100-m long catena, which covers a dry-mesic gradient. The tree stand was dominated by Scots pine (*Pinus sylvestris* L.) at the dry end of the catena, and by Norway Spruce (*Picea abies* L. Karsten) at the mesic end. The parent material of the soil at the site is glaciofluvial deposit with a texture varying from coarse to fine sand. According to FAO-Unesco soil classification system the soil is a Haplic podzol (FAO-Unesco 1990). The soil deposit is several meters deep and the surrounding bedrock is mainly acidic granite, granodiorite, and mica-gneiss with some small intrusions of gabbro and peridotite.

3.3. Soil CO₂ efflux measurements

In the young forest (1-III), soil CO₂ efflux was monitored over two and a half years by two different chamber methods. Continuous measurements were carried out hourly throughout the year by two automated chambers located at the same place. Spatial variation in soil CO₂ efflux was studied by sampling CO₂ efflux with manual chamber three times a year from ten randomly selected locations.

The automated system is a hybrid between steady-state flow-through and non-steady-state flow-through chambers and it has been described in detail in paper I and by Hari *et al.* (1999). In the system, compensation air with known CO₂ concentration was introduced into a cylindrical chamber made of polycarbonate (diameter and height 200 mm) at 3 L min⁻¹ flow rate and equal amount of air was pumped from the chamber to the CO₂ analyzer (URAS 4, Hartmann & Braun, Frankfurt am Main, Germany). The compensation air was taken from above the tree canopy and pumped through a 0.05 m³ steel container to eliminate possible fluctuations in CO₂ concentrations. The flow rates of the compensation air and the sample air were regulated by two separate pumps and mass flow controllers (5850E, Brooks Instrument, Veenendaal, Netherlands). Air in the chamber was mixed by a small fan installed in the middle of the chamber.

The chamber was equipped with a pneumatically operating lid mechanism keeping it closed during the measurement periods and open between them. During the

70-seconds measurement period the CO₂ concentration was monitored continuously with infrared CO₂ analyzer and the readings were saved every 5 s. The same analyzer was used for measuring the compensation air CO₂ concentration immediately before and after each measurement period. The chambers were installed permanently on the soil so that the lower edge of the chamber was pushed to a depth of 10 mm into the top humus layer. Plants were removed from the chambers.

The manual chamber was a non-steady-state non-flow-through chamber. During the measurement the chamber (diameter 200 mm and height 300 mm) made of polycarbonate and covered with aluminium foil was attached for ten minutes to a collar installed permanently to a depth of 50 mm in the soil. A small fan was used to mix the air within the chamber's headspace. Gas samples (50 cm³ in volume which was 0.9% of the chamber headspace) were taken by polyethylene syringes (BD Plastipak 60, BOC Ohmeda, Helsingborg, Sweden) equipped with a three-way valve (BD Connecta™ Stopcock, Becton Dickinson, NJ, USA) manually 0, 2, 6, and 10 min after the chamber attachment. The CO₂ concentration of the air samples was determined within 6 h by infrared gas analyzer (URAS 3G, Hartmann & Braun, Frankfurt am Main, Germany). The CO₂ efflux was calculated from the linear fit between CO₂ concentration in the chamber and time.

3.3.1. Accuracy and precision of soil CO₂ efflux measurements

Because two different chamber systems were used for measuring CO₂ effluxes and various systems have been shown to give highly different results, they were tested and compared to each other. The automated chambers were tested for two major sources of error; pressure differences caused by differences between the flow rates of incoming and outgoing air in the chamber, and the effect of mixing the air inside the chamber. Tests were carried out in the field on natural soil. We varied the flow rate of compensation air to test the sensitivity of the chamber system to possible pressure differences generated by differences between in and out flow rates. In addition, we estimated the concentration of air entering the chamber in mass flow of air from the humus in case of under pressure in the chamber. This is discussed in detail in paper I, but a short summary of the tests is presented here.

The automated chamber was not very sensitive to differences between the flow rates of compensation air and the air sucked to the analyzer. During low effluxes (0.07 - 0.11 g CO₂ m⁻² h⁻¹) a more than 30% difference between the flow rates was needed to produce a statistically significant effect on the flux measurement. (Table 1. in I). When the compensation air flow rate was lower than the analyzer air flow rate, the measured effluxes were higher than the control effluxes, because air was mainly drawn into the chamber through the humus (Fig. 4). When the compensation airflow rate was set higher than the analyzer flow, the measured effluxes were lower than the control effluxes, because part of the CO₂ produced in the soil escaped from the chamber before entering the analyzer. The chamber seemed to be less sensitive to over pressure than to under pressure especially during higher effluxes (0.25-0.37 g CO₂ m⁻²

h^{-1}) than during low effluxes. These sources of error were negligible in normal measurements, because the difference between the flow rates was always less than 1%.

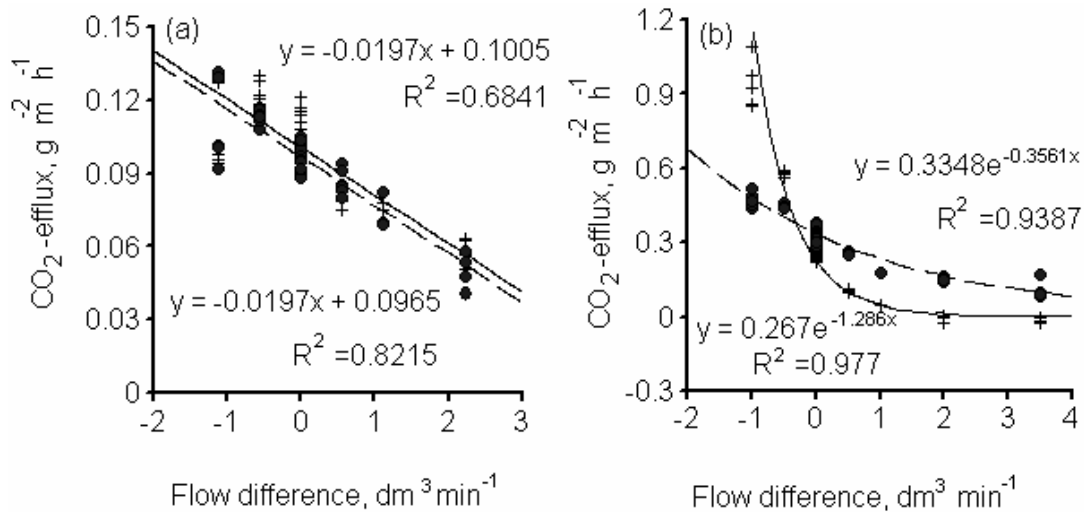


Figure 4. The relationship between measured CO_2 effluxes and flow rate differences during extremely low efflux in late autumn (a) and (b) in spring. Measurements with flow rate difference of $0 \text{ dm}^3 \text{ min}^{-1}$ are control measurements. Solid and dotted lines refer to two automated chambers used in the test.

Sufficient mixing of air in the chamber was crucial for proper measurements of CO_2 efflux in the automated chambers. The speed of the fan, i.e. the turbulence inside the chamber affected the measured CO_2 efflux and the deviation of the measurements. When the fan was switched off, the measured effluxes were lower and more variable than those measured when the fan was on. When the speed of the fan was increased, also the measured efflux increased. The efflux leveled off at about 70% of the fan speed normally used in the measurement suggesting that the mixing of air was sufficient in these chambers.

We also tested if the measurement principle affected the efflux values. This was done by converting the automated chamber from a flow-through chamber to a non-flow-through chamber by disconnecting the compensation air and the sample air tubes from the chamber and by determining the flux with similar method to that of the manual chamber. The flow-through method gave on average 11% higher efflux than the non-flow-through method (Table 4. in I). Differences between the two methods were larger with high effluxes than with low effluxes. The measurements with non-flow-through technique showed a higher coefficient of variation (ranging from 0 to 11%) than flow-through measurements (ranging from 0 to 7%) suggesting that the accuracy of measurements with the flow-through technique may be better than that with the non-flow-through technique.

In paper III, the automated chambers and manual chambers were compared in situ on forest soil, and with a diffusion box method developed by Widén & Lindroth

(2003). The non-flow-through chamber gave ~50% lower efflux values than the flow-through chamber during high efflux in summer (Fig. 7a in III). When compared to known CO₂ effluxes generated artificially and ranging from 0.4 to 0.8 g CO₂ m⁻² h⁻¹, the flow-through chamber gave equal effluxes at the lower end of the range, but overestimated high effluxes by 20%. The non-flow-through chamber underestimated the CO₂ efflux by 30% (Fig. 7b in III). These differences should be taken into consideration when interpreting the results of this study.

3.4. CO₂ concentration in soil

The seasonal pattern of CO₂ concentration in the soil air space was studied with air samples collected from gas samplers installed permanently in the humus (O-horizon), eluvial (A-horizon), and illuvial layers (B-horizon) and in the parent material (C-horizon) (II-III). The gas collectors were made of punctuated, hollow bars, covered with Gore-Tex™ PTFE 0.45- μ m membrane. Gas samples were drawn into similar syringes to those used in manual chambers simultaneously with manual CO₂ efflux measurements. The CO₂ concentration of gas samples was measured by infrared gas analyzer (URAS 3G, Hartmann & Braun, Frankfurt am Main, Germany) within 6 h upon sampling.

3.5. Soil temperature and soil moisture

In the young forest, soil temperature was measured in each soil horizon at 15-minute intervals with silicon temperature sensors (Philips KTY81-110, Philips Semiconductors, Eindhoven, The Netherlands) and soil water content at one-hour intervals by the TDR-method (Tektronix 1502 C cable radar, Tektronix Inc., Redmond, USA) (II and III). Sensors were installed permanently in the soil at five locations in each soil horizon close to the gas samplers.

In the old forest, soil temperature in O-horizon was measured in each collar immediately after the CO₂ efflux measurement by manual thermometer (Fluke 52/KJ, Fluke Electronics, Everett, WA, USA) and on hourly basis by thermocouples connected to a data logger (Delta-T, Delta-T Devices Ltd, Cambridge, UK). Soil matric potential was measured by tensiometers (Soil Measurement Systems, TX, USA) and Tensicorder (Soil Measurement Systems, TX, USA) once a week at respective depths (IV). Thermocouples and tensiometers were installed permanently in the soil, close to the gas samplers at 9 locations in each soil horizon.

3.6. The effect of clear-cutting and site preparation on soil CO₂ efflux

The effect of clear-cutting and different site preparations on soil CO₂ efflux were studied in a 130 year-old mixed Scots pine - Spruce forest (IV). The monitoring of soil CO₂ efflux was started in 1997, one year before clear-cutting. During that year CO₂

efflux was measured weekly with the manual chamber method from three collars installed permanently in the still uncut forest.

In March 1998, half of the forest was clear-cut (Fig 1. in IV). We removed logging residue from the measurement points and continued CO₂ efflux monitoring between 1998 and 2000 in the same places. The effect of the removal of trees and logging residue on soil CO₂ efflux was studied by comparing the effluxes to those of the adjacent control forest.

The effect of site preparation was studied on eight square blocks 10 m x 15 m in size established on the clear-cut site in May 1998. On each block, soil was treated with four different site preparations simulating the methods commonly used in silviculture in Finland. The site preparations were mounding where the organic layer (O-horizon) on top of the soil and the uppermost 0.2 m of the mineral soil were excavated and placed upside down next to the excavated pit (Fig. 2. in IV). A mound was formed where B-horizon was on the top followed by A-horizon and organic layer inside the mound. In the pit, soil was exposed down to the top C-horizon above which most of the roots were confined. We also established measuring points, where only the surface of the mineral soil was exposed by removing the O-horizon. Finally, measuring points where the soil surface was left untreated and litter of harvested trees was left on site, were established. The total amount of points where effluxes were measured was 39 (Fig. 1 in IV).

The seasonal pattern in soil CO₂ efflux was studied on all treatments in the summers of years 1998 and 1999 by sampling in the control forest and on blocks 1 and 8 biweekly (Table 1. and Fig.1. in IV). An intensive sampling where the effluxes in all 39 points were measured to study the internal variation within the site was done twice in the summer of 1998 and three times in the summers of 1999 and 2000. CO₂ efflux measurements were carried out between 8 and 11 in the morning.

Annual effluxes from the control forest and from the clear-cut site were obtained by integrating hourly effluxes obtained by a temperature regression (Eq. 1 in IV) fitted for biweekly measured fluxes and average temperatures in O- and A-horizons. On the clear-cut site, fitting was done for measuring points where the logging residue was removed and for points where the logging residue was left on site. Soil CO₂ effluxes were estimated for each hour based on hourly measured soil temperatures and temperature response functions of the respective treatments.

Instantaneous CO₂ effluxes measured on different site preparations were compared by T-test to those measured in the control forest. The sources of variances between site preparation treatments and between blocks were studied by nested random effect analysis of variance SAS 6.12. Statistical software (SAS Institute Inc., Cary, NC) was used in the analysis.

The components of soil respiration before and after clear-cutting were estimated with a process model simulating the autotrophic and heterotrophic respiration, the decomposition of soil organic matter and the litter input into the soil at weekly intervals. In the model, soil is divided into organic layer and mineral soil (Fig.5.). Soil organic matter in both layers consists of three compartments describing the

decomposition stages: litter, partly decomposed litter and humus. Carbon is transferred out of the system in decomposition at a rate, which depends exponentially on the temperature of the respective layer (Eq. 1). A fraction of carbon is transferred from one compartment to the subsequent compartment (R3-R5) at a rate depending on the mass loss of litter Prescott *et al.* (2000b) modified from Liski *et al.* (1998). These rates determine the amounts of carbon that are removed from the compartments during each simulation time step. The respiration originating from the root metabolism was considered autotrophic respiration (R6). A large proportion of the carbon allocated by plants to roots was assumed to leach out of the roots in root exudates (R7) (Boone *et al.* 1998, Högberg *et al.* 2001), and to become decomposed by root associated micro-organisms (R8). Annual litter fall (R1) and root growth (R2) were divided for each week according to the seasonal pattern in soil temperature the peaks occurring in August. The only mechanism of carbon movement between the soil layers was dissolved organic carbon in the soil water percolating from the organic layer to the mineral soil (R12).

Parameterization of the model was based on field measurements carried out in Hyytiälä. Annual litter fall, $0.146 \text{ kg C m}^{-2}$ was obtained from needle biomass (0.51 kg C m^{-2}) measured in Hyytiälä by Ilvesniemi and Liu (2001) assuming that the turnover rate of the needle biomass was 3.5 years. Root growth was obtained from Ilvesniemi and Liu (2001). It was estimated that the annual amount of carbon allocated to root growth was $0.225 \text{ kg C m}^{-2}$ of which 60% occurred in mineral soil and 40% in organic soil. This division was based on the measurements of root biomass distribution in the soil Pietikäinen *et al.* (1999). The turnover rate of fine roots was assumed to be 3 years, thus the total fine root biomass in the soil when the model was at steady state was 0.37 kg m^{-2} . The proportion of carbon allocated to root exudates was assumed to be equal to the amount of carbon allocated to root growth. The amount of carbon transported in water from organic to mineral soil was $0.017 \text{ kg C m}^{-2}$ annually Pumpanen (1995). The decomposition rate of root exudates (R8) was assumed to be about 3 times higher than that of the litter on the soil surface.

The temperature responses for decomposition of different organic components (R9-R11) were determined from soil samples collected from the site. Samples were incubated at different temperatures ranging from 4 to 20 °C and the amount of emitted CO₂ was determined by gas chromatograph. Parameters α and β for temperature responses are presented in Appendix 1. The total amount of carbon in the soil simulated by the model at steady state was about 5.5 kg C m^{-2} which is of the same magnitude than that measured by Liski (1995) for similar soils in Hyytiälä in Finland.

In the clear-cut the root growth was assumed to decrease by 99%. After clear-cutting root growth and aboveground litter fall were assumed to increase annually by 20%. The amount of carbon released in the soil in the logging residue was 4.7 kg C m^{-2} of which about 36% was in tree crowns, 26% in stumps and 38% in roots. The respiration in different soil compartments was simulated with the model for one year before and three years after clear-cutting by using weekly average temperatures in O-horizon and in the mineral soil measured at the site.

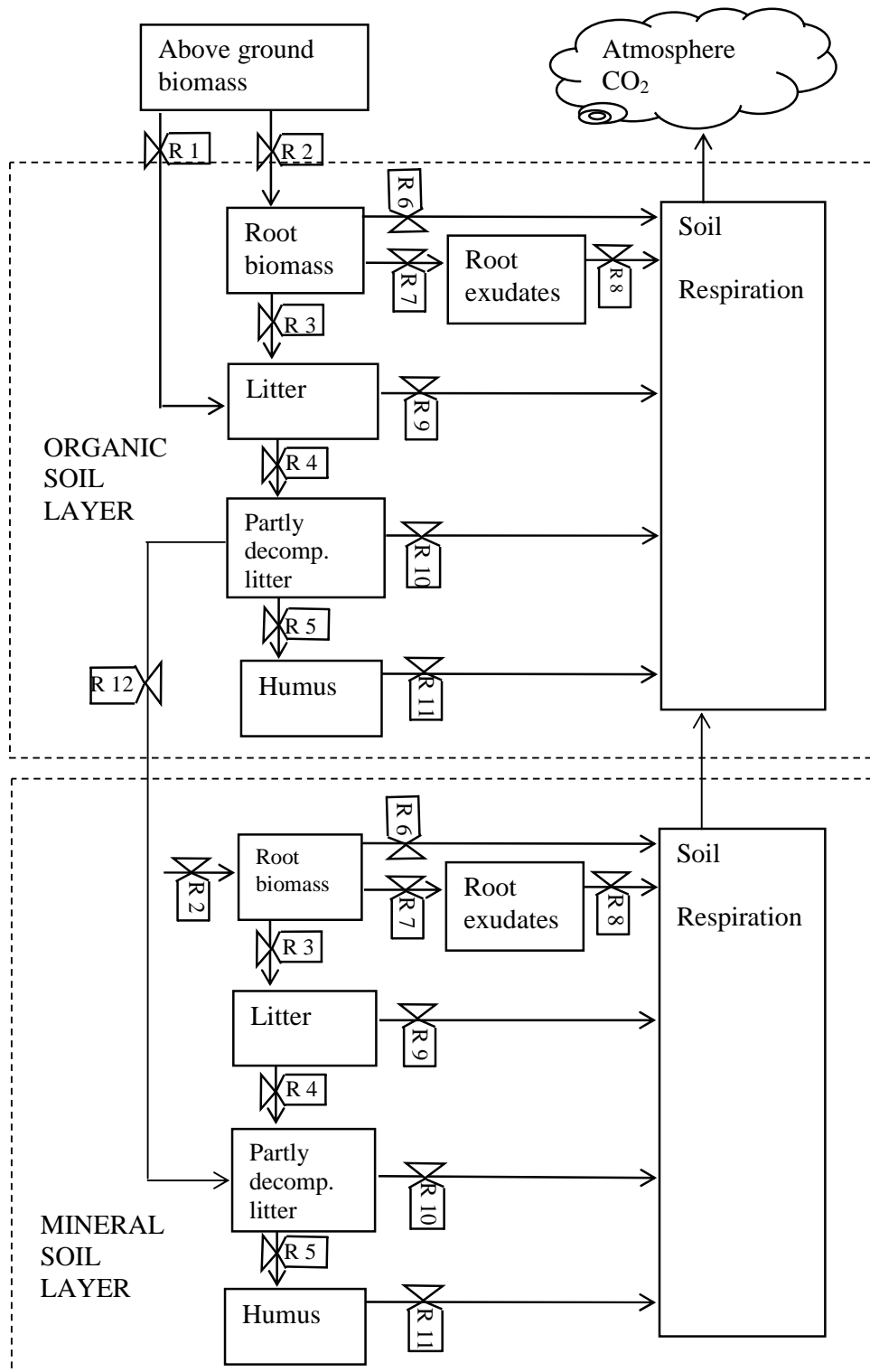


Figure 5. Schematic presentation of the process-model used for estimating the different contributions of soil respiration in the forest and at the clear-cut site.

4. Results

4.1. CO₂ concentration in soil

Soil CO₂ concentration showed a seasonal pattern that followed the soil temperature (Fig. 6). Highest concentrations in the soil profile were measured in the summer ranging in young forest from 580-780 $\mu\text{mol mol}^{-1}$ in O-horizon to 14470 $\mu\text{mol mol}^{-1}$ in C-horizon (Fig. 6a). High concentrations were also measured occasionally in O-horizon in April because of the formation of ice crust on the soil surface. In winter the concentrations were much lower ranging from 498 $\mu\text{mol mol}^{-1}$ in O-horizon to 1213-4325 $\mu\text{mol mol}^{-1}$ in C-horizon.

In the old forest, the concentrations in B- and C-horizons were lower than in the young forest being on average 3270 $\mu\text{mol mol}^{-1}$ in B-horizon and 3860 $\mu\text{mol mol}^{-1}$ in C-horizon in June and July. However, in O- and A-horizons the concentrations were of the same magnitude than those in the young forest. High concentrations in April were also measured in the old forest, CO₂ concentrations peaking at 14254 $\mu\text{mol mol}^{-1}$ and 9530 $\mu\text{mol mol}^{-1}$ in O- and A-horizons, respectively (Fig. 7a.). After clear-cutting the CO₂ concentrations in all soil horizons were substantially lower than before clear-cutting. In O- and A-horizons the average CO₂ concentrations between June and July in 1998 were 29% and 33% lower than those before clear-cutting. In B- and C-horizons the concentration decreased less, 20-26 % respectively.

CO₂ concentrations predicted by the model agreed quite well with measured values, especially in A-, B- and C-horizons. The coefficient of determination (r^2) for predicted CO₂ concentrations ranged from 67% in A-horizon to 82% in C-horizon (Fig. 8 in II). There was a gradient in CO₂ concentration the concentrations being highest in deeper soil layers throughout the year indicating that there was biological activity in the soil profile all year round (Fig. 6. in III). According to model simulations, most of the CO₂ production occurred in the humus layer throughout the year (Fig. 7. in II). However, the relative contribution of deeper layers to total respiration was at its highest in late autumn, because of low temperature at the soil surface.

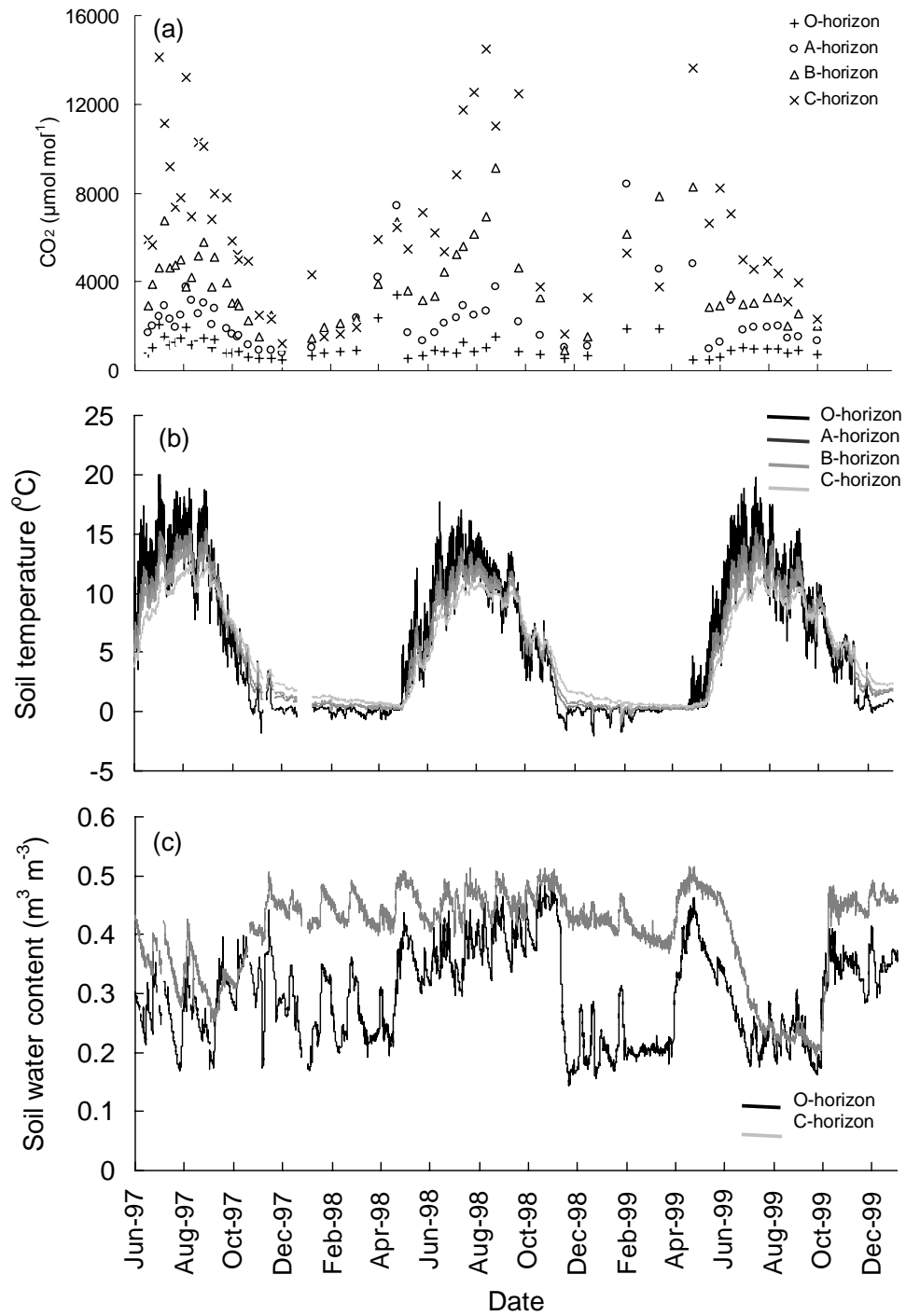


Figure 6. (a) Soil CO₂ concentration in O-, A-, B- and C-horizons in young forest, (b) soil temperature and (c) soil water content in respective horizons.

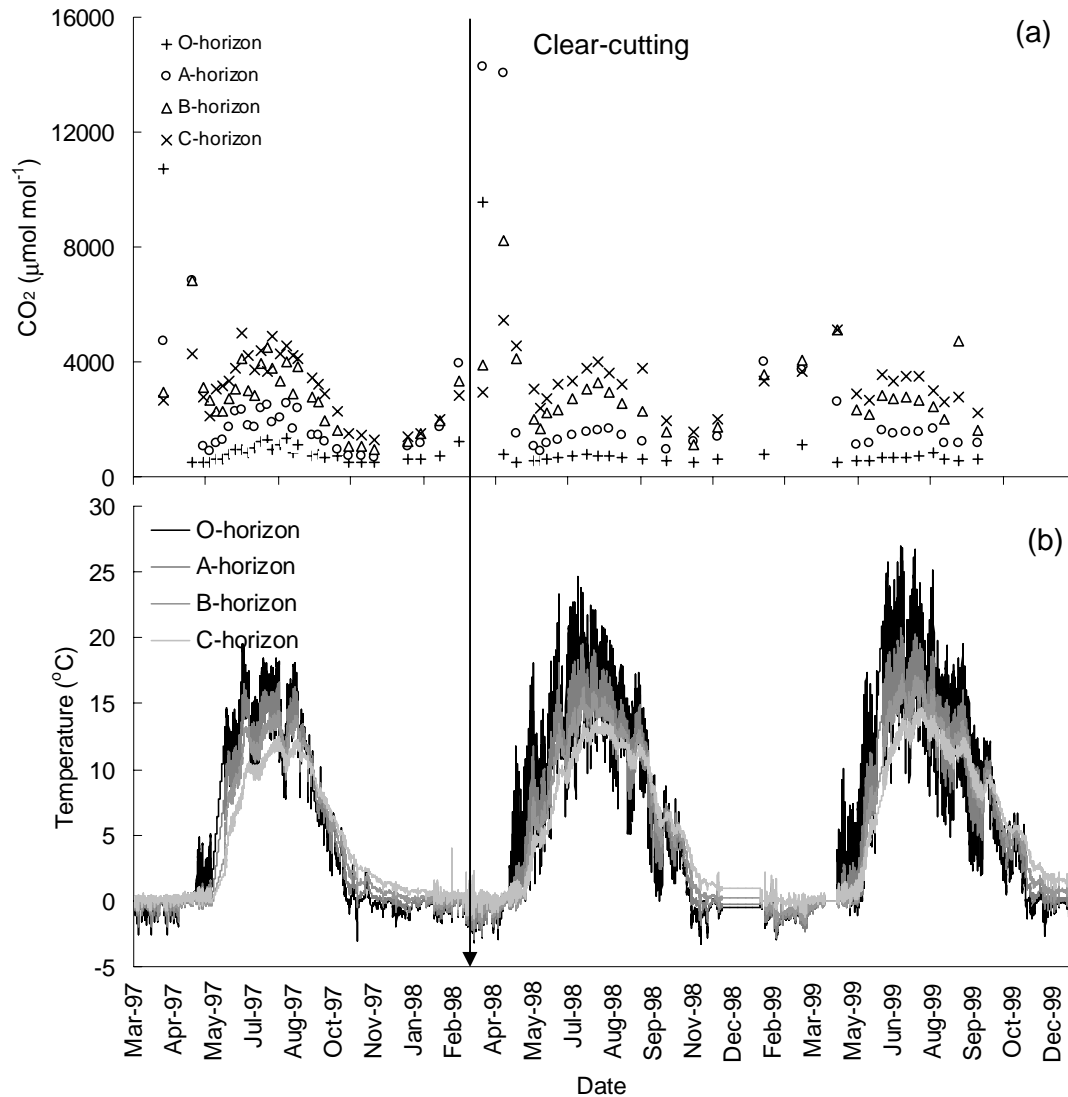


Figure 7. (a) Soil CO₂ concentration in O-, A-, B- and C-horizons and (b) soil temperatures in respective horizons in the old forest before clear-cutting and at the clear-cut site.

The three years studied represented extreme variation concerning soil water content. The late summers of 1997 and 1999 were very dry whereas the summer of 1998 was exceptionally wet (Fig 6c). In 1998 the soil was near field capacity most of the summer; in the humus layer soil water content varied between 0.35-0.4 m³ m⁻³ (-0.02 to -0.08 MPa) and in the B- and C-horizons between 0.4 and 0.5 m³ m⁻³ (-0.004 to -0.001 MPa).

Soil water content affected substantially CO₂ concentration in the soil. In the young forest, soil air CO₂ concentration was much lower during the drought than when the soil was wet (Fig. 6a). However, in the old forest CO₂ concentrations in both

years were on the same level (Fig. 7a). The concentration increased in the spring, partly because of increased soil moisture by thawing and formation of ice crust on the soil surface.

4.2. Soil CO₂ efflux

Variation in soil temperature induced changes in soil CO₂ efflux both on daily (Fig. 1 in III) and annual time scale (Fig. 8). Soil surface temperature explained 69-85% of the temporal variation in soil CO₂ efflux in the young forest and 45-73% in the old forest used for control in the clear-cut experiment. In the young forest, highest CO₂ effluxes were measured in July and in August the daily average effluxes measured by automated chambers being 1.23 and 0.98 g CO₂ m⁻² h⁻¹ in 1998 and 1999, respectively. In winter the average effluxes were much lower, only between 0.0 and 0.1 g CO₂ m⁻² h⁻¹. The spatial variation of CO₂ efflux was high, the coefficient of variation varied between 18 and 45% being highest during high efflux.

Simulations with the process-model showed, that the model could predict soil CO₂ effluxes measured by automated chambers quite accurately. The coefficient of determination (r^2) for the regression of modeled vs. predicted CO₂ efflux was 82-86% (Fig. 9.). However, the model slightly overestimated low effluxes and underestimated high effluxes.

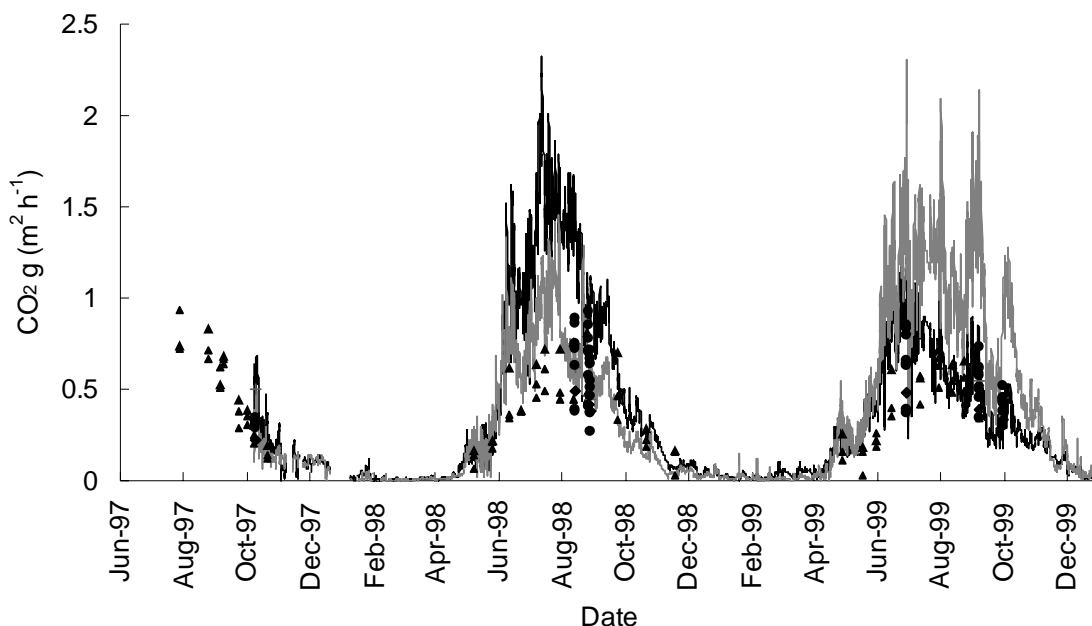


Figure 8. Soil CO₂ efflux measured by automatically operated chambers (lines) and manual chambers (▲, ●).

CO₂ efflux measured by manual chambers showed a similar seasonal pattern to the efflux measured by the automated system. However, the average efflux was lower, only 59% and 73% of that measured by the automatic system in 1998 and 1999

respectively. Temperature responses of soil respiration (Q_{10} value) determined from effluxes measured by automated chambers and humus temperature were 6.29 and 3.30 for respective years and those measured by manual chambers were 3.72 and 2.94, respectively. In the uncut control forest the average effluxes in July were 0.51 and 0.49 $\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ during wet and dry years, respectively (Table 3 in IV). Corresponding temperature responses were 3.29 and 2.92.

Soil water content affected substantially also the CO_2 efflux. This was shown both by the model simulations and by the field measurements. When soil moisture was not taken into account, the model overestimated soil CO_2 effluxes significantly (Fig. 9.). In the young forest, soil CO_2 efflux was substantially lower during the drought than when the soil was wet, even though the temperatures were higher during the dry period. The average effluxes measured manually also showed similar pattern. When the soil was rewetted after a long dry period in 1999, a CO_2 flush resulted. An increase in humus volumetric water content from $0.15 \text{ m}^3 \text{ m}^{-3}$ to $0.37 \text{ m}^3 \text{ m}^{-3}$ more than doubled the soil respiration (Fig. 5 in III).

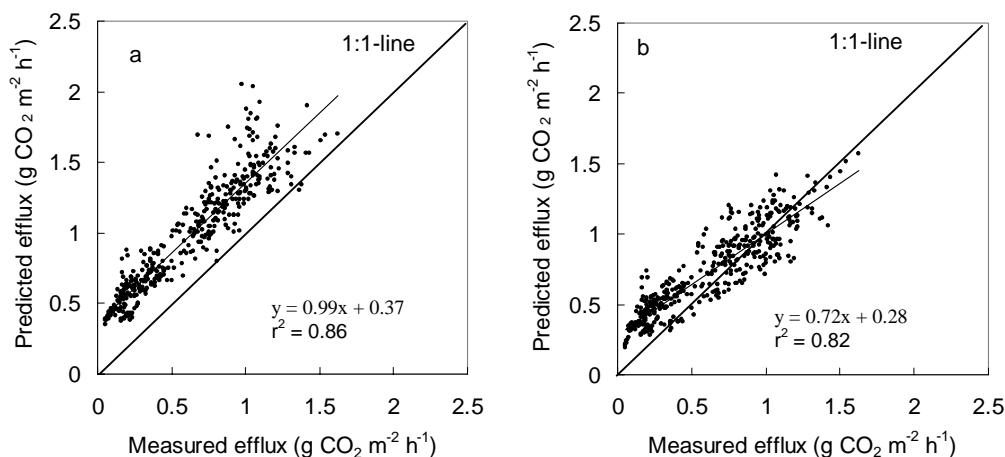


Figure 9. Relationship between measured and predicted CO_2 efflux (a) without the moisture and (b) with the moisture in the model simulation.

4.3. Soil CO_2 efflux before and after clear-cutting and site preparation

4.3.1. Effect of clear-cutting

In 1998, after the clear-cutting, the highest effluxes were measured from the places where the logging residue was left on site and from the mounds (Figure 10.) In 1998 these measuring points showed twice as high effluxes compared to those of the adjacent control forest and sites from which the logging residue was removed. The enhancement effect of the logging residue on CO_2 efflux leveled off rapidly. In 1999 and 2000 the efflux rate in the clear-cut area had dropped to the same level or lower than in the control forest.

When the logging residue was removed from the top of the soil, only root litter and possibly some amount of deteriorated forest floor vegetation remained decomposing in soil. After the clear-cutting, the average efflux rate on this treatment was $0.35 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$; $0.2 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ lower than in the control forest (Table 4 in IV).

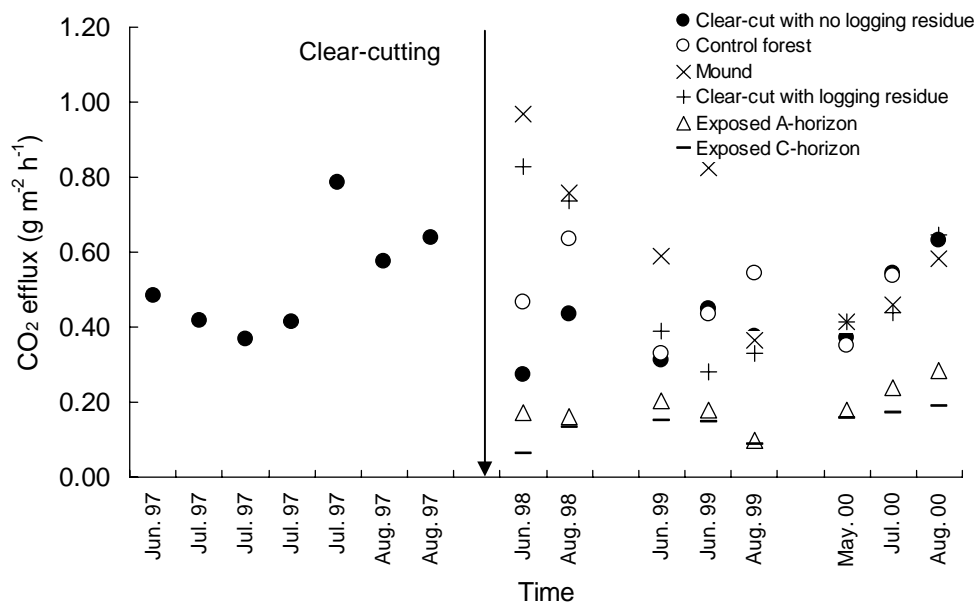


Figure 10. Soil CO₂ efflux from measuring points with different site preparation and from the control forest.

The removal of forest canopy increased daytime temperatures in O- and A-horizons on average by 5°C during the summer following the harvesting. Forest harvesting also affected soil water potential. In 1997 before clear-cutting, matric potentials were more variable and on average lower (less water in the soil) than those during years 1998, 1999 and 2000. Highest matric potentials were measured in 1998. The precipitation varied considerably between the summers. The cumulative precipitation from June 1st to September 30th was 338, 410, 204 and 238 mm in -97, -98, -99 and -00, respectively (Fig. 3c in IV).

4.3.2. Effect of site preparation

Site preparation had a substantial effect on soil CO₂ efflux. The lowest effluxes were measured from places where the organic matter had been removed. On those places, the average effluxes measured between June and September were less than 50% of those in the control forest (Table 4. in IV). The average efflux rates measured from the mineral soil between June and September varied between 0.10 and 0.23 g CO₂ m⁻² h⁻¹. The CO₂ efflux was somewhat higher, if the A-horizon was left on site, and seemed to increase, when the time from the clear-cut increased.

The annual average effluxes from mounds were 0.86, 0.59 and 0.49 and from places with logging residue 0.78, 0.33 and 0.51 g CO₂ m⁻² h⁻¹ in 1998, 1999 and 2000 respectively. The mixing of organic material with mineral soil seemed to increase the rate of decomposition during the two years after the treatment, but in the third year, the effect was not any more detectable.

Differences in CO₂ efflux along the moisture and fertility gradient of the study site were not observed, neither before nor after the clear-cutting. Most of the variation in soil CO₂ efflux originated from site preparation, which accounted for over 75% of the total variance. Forest site type (fertility gradient) accounted for less than 30% of the total variance. The spatial variation increased in the summer and peaked during highest effluxes in July and August. CO₂ efflux was higher and spatially more variable in the forest soil under canopy. At the clear-cut site, on places where no site preparation was applied, the spatial variation was smallest.

4.3.3. Annual CO₂-C losses from the soil

In the young forest, annual CO₂ effluxes obtained from automated chambers were 3117 and 3326 g CO₂ m⁻² in 1998 and 1999 respectively. Annual CO₂ effluxes, integrated over the year from the temperature responses of manual chambers were smaller 2787 and 2732 g CO₂ m⁻² during corresponding years.

Annual CO₂ effluxes from the 130-year-old uncut forest were 1900 g CO₂ m⁻² before clear cutting (Fig. 4 in IV). After the clear-cutting and removal of logging residue annual effluxes remained nearly unchanged 1819, 1960 and 1985 g CO₂ m⁻² in years 1998, 1999 and 2000, respectively. In the adjacent control forest estimated annual effluxes were 2096, 2130 and 2054 g CO₂ m⁻² for respective years.

On places where the logging residue was left on site after clear-cutting the estimated annual CO₂ effluxes were much higher, 3242, 2845 and 2926 g CO₂ m⁻² during the three years following the clear-cutting. Annual CO₂ emissions released from the logging residue during the first year after clear cutting were up to 1423 g CO₂ m⁻², which equals to 388 g C m⁻². The CO₂ emissions originating from the O-, A- and B-horizons and assumed to originate mainly from the decomposition roots of were estimated to be about 352 g C m⁻².

According to the simulations by the process model most of the soil respiration was originated from heterotrophic respiration both in O-horizon and in mineral soil already before clear-cutting (Fig. 11). Before clear-cutting the contribution of heterotrophic respiration was 84 % of the total soil respiration and the contribution of autotrophic root respiration 14%. If the autotrophic respiration and the decomposition of root exudates were pooled and regarded as root and rhizosphere respiration, its proportion would be about 54% of the total soil respiration. Without root exudates, the simulated soil CO₂ efflux in a non-cut forest would have been about 38% lower than that measured in the field.

After the clear-cutting most of the soil respiration originated from heterotrophic respiration in O-horizon, which contributed 63% of the total soil respiration. The

heterotrophic respiration in mineral soil contributed about 35% of the total soil respiration. The respiration originating from root tissue and root exudates almost ceased after the clear-cutting. The proportions of different sources remained quite stable during the three year-period after the clear-cutting, but the total soil respiration decreased almost 17%, which is more than that measured in the field.

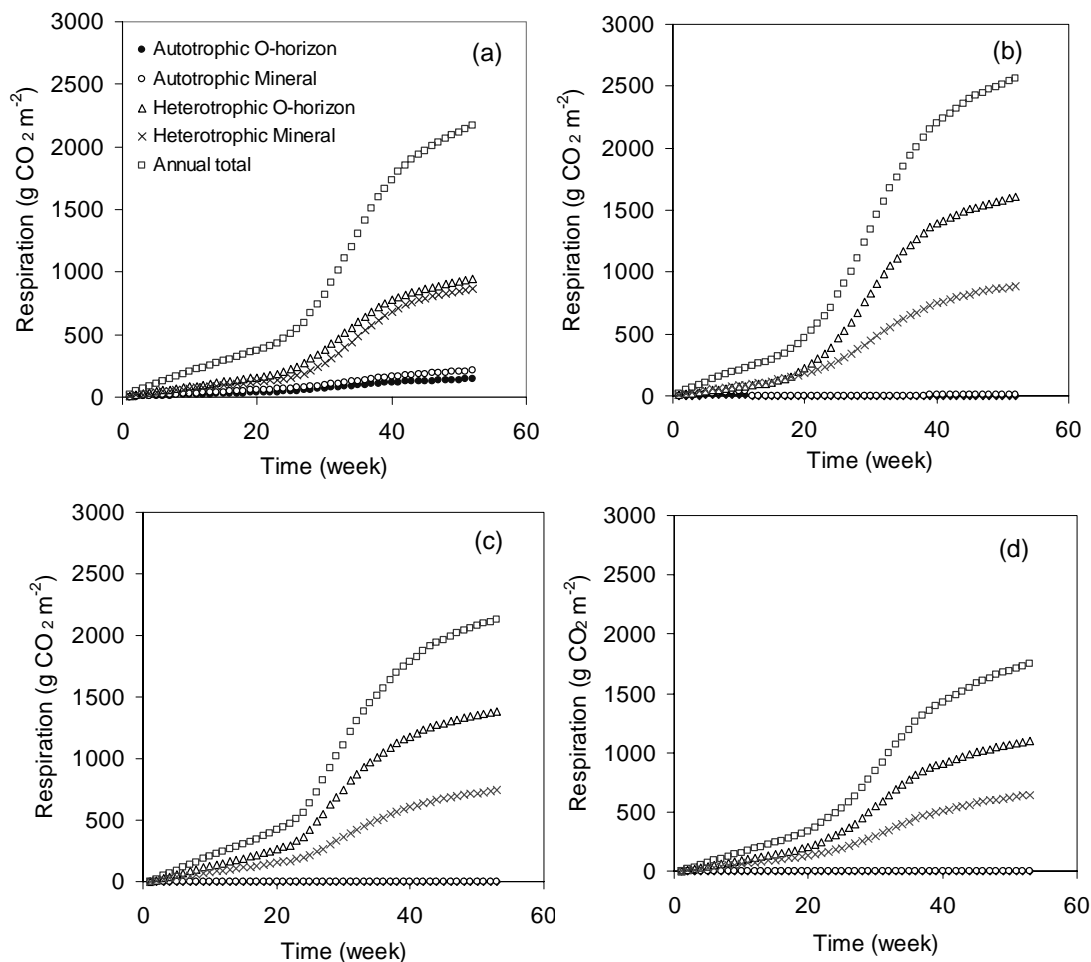


Figure 11. Different components of soil respiration (a) before clear-cutting (b) one year (c) two years and (d) three years after clear-cutting simulated by a process-based model.

5. Discussion

5.1. CO₂ concentration in soil

CO₂ concentrations measured in this study were of similar magnitude to those reported elsewhere (Table 1.). Soil CO₂ concentrations measured in different ecosystems are very variable ranging from 320 - 1000 $\mu\text{mol mol}^{-1}$ in the surface to 17500 - 85000 $\mu\text{mol mol}^{-1}$ in the deep soil. Magnusson (1992) and Billings *et al.* (1998) measured CO₂ concentrations ranging from 1000 - 60000 $\mu\text{mol mol}^{-1}$ in boreal forests (Table 1.).

The concentrations measured in the young forest in B- and C-horizons were higher than in the old forest. This is due to differences in soil particle size distribution. In the old forest, soil was well aerated and well-sorted glacio-fluvial deposit having high proportion of coarse particles (200-2000 μm) whereas in the young forest soil was silty glacial till rich in fine particles (Mecke and Ilvesniemi 1999). Consequently, the pore sizes between soil particles were larger in the old forest than in the young forest. The diffusion coefficient of the soil is affected by the air-filled pore space as well as the continuity and shape of the pores (Glinski and Stepniewski 1985). Fine soil, despite its higher total porosity, may have higher tortuosity, because small soil pores are blocked by capillary water. Thus, the effective diffusion in coarse soil with large pores is higher than in fine soil (Simůnek and Suarez 1993) and due to this the CO_2 concentrations in the old forest remained lower.

Also, in the old forest, soil was deep and thus a vertical movement of air induced by changes in atmospheric pressure was possible. The groundwater level in the old forest lies on average at 2.5 - 5.5 m depth. Thus a 4% change in atmospheric pressure would result in a 0.1 - 0.22 m surface layer involved in the exchange with fresh atmospheric air. During windy conditions this convective transport of CO_2 could reach even deeper in the soil. In the young forest, soil was confined to homogeneous bedrock at a depth of 0.5-1.6 m preventing the vertical movement of air. Therefore the gas movement by vertical airflow was limited only to the very surface of the soil.

Because the diffusion of CO_2 in water is about 10000 times slower than in air, the annual variation in weather conditions and consequent soil water content had a substantial effect on CO_2 concentration in the soil profile. In 1998 the soil in the young forest was close to field capacity and the CO_2 concentrations in deeper soil were nearly twice as high compared to dry conditions in the following summer. High soil water content also affected the CO_2 production in deeper soil layers resulting in a very low respiratory activity. But still, due to slow diffusion even a minor respiration was enough to maintain high CO_2 -concentration. Contrary to this, during the drought the respiration of the C-horizon was higher and exceeded that of the A-horizon, but still the CO_2 concentrations in deeper soil layers decreased because of faster diffusion in increased air-filled pore space. Soil water content may also have affected the soil CO_2 concentration by limiting microbial activity in A- and B- horizons during the extreme drought (Lundgren and Söderström 1983).

Table 1. Soil CO₂ efflux and soil air CO₂ concentration measured simultaneously in various terrestrial ecosystems.

Authors	Chamber/Method [†]	Ecosystem	Age (year) ^{††}	Time period	Efflux (g CO ₂ m ⁻² h ⁻¹) ^{††}	Annual (g CO ₂ m ⁻²) ^{††}	Soil CO ₂ concentration ^{††}
Bajracharya et al. 2000	NSNF	Agricultural soil	-	May 96 - Jul. 97	~0 - 0.230	NA	560 - 20000 µmol mol ⁻¹
Billings et al. 1998	NSNF and DIFF	Boreal mixed forest Boreal flood plain	80 40-100	Jun. 96 - Sep. 96, May 96 - Sep. 97	0.100 - 0.950 0.200 - 1.450	NA	1000 - 12500 µmol mol ⁻¹ NA 2000 - 32000 µmol mol ⁻¹
Burton and Beauchamp 1994	DIFF	Agricultural soil	-	Dec. 98 - Jul. 90 (not in summer)	max 1.340 - 1.710	NA	500 - 5500 µmol mol ⁻¹
Buyanovsky and Wagner 1983	Not measured	Agricultural soil	-	-	-	-	1000 - 85000 µmol mol ⁻¹
Castelle and Galloway 1990	Not measured	Temperate mixed deciduous forest	NA	-	-	-	320 - 17500 µmol mol ⁻¹
Cook et al. 1998	NSF	Sand dune with planted <i>P. radiata</i>	<2	Jul. 94 - Apr. 96	0.058 - 0.580	NA	0.1 - 7.0 kg m ⁻³ · 10 ⁻³
"	DIFF. MODEL	"	"	"	0.232 - 1.627	NA	"
Davidson and Trumbore 1995	NSF	Evergreen forest	NA	May 92, Nov. 92	0.240 - 0.290	NA	8000 - 70000 µmol mol ⁻¹
"	DIFF. MODEL	Pasture	NA	"	0.110 - 0.140	NA	NA
de Jong and Schappert 1972	DIFF	Virgin prairie	NA	May - Oct. 69 and 70	0 - 2.650	2550 May-Oct.	500 - 22600 µmol mol ⁻¹
Fahnestock et al. 1998	DIFF. THR. SNOW	Arctic tundra	NA	Mar. 96 - May 96	0.0006 - 0.036	NA	NA
Fernandez and Kosian 1987	Not measured	Hemiboreal mixed coniferous forest	mature	-	-	-	1000 - 12000 µmol mol ⁻¹
Fernandez et al. 1993	AL	Hemiboreal mixed deciduous forest	NA	Mar. 90 - Oct. 90	0.010 - 0.550	NA	38 - 5620 µmol mol ⁻¹
"	"	Hemiboreal coniferous forest	mature	May 90 - Oct. 90	0.160 - 0.590	NA	500 - 7000 µmol mol ⁻¹
Johnson et al. 1994	DIFF	<i>P. ponderosa</i> seedlings	0	Jul. 92 - Jul. 93	0 - 0.153	1874	1000 - 15000 µmol mol ⁻¹
Magnusson 1992	Not measured	Boreal coniferous forests	53-138	Nov. 85 - Dec. 87	-	-	1000 - 60000 µmol mol ⁻¹
Pinol et al. 1995	SSFL	Mediterranean deciduous forest	40	Jun. 91 - Jun. 92	0.026 - 0.176	~727 - 1069	1500 - 11000 µmol mol ⁻¹
Rustad and Fernandez 1998	NSNF	Hemiboreal mixed coniferous forest	45-130	May 93 - Nov. 95 (not in winter)	0.020 - 0.430	803	1250 - 8000 µmol mol ⁻¹
"	SL	"	"	Jun. 94 - Nov. 95 (not in winter)	0.130 - 0.550	1566	-
Solomon and Cerling 1987	AL and RESP.	Subalpine meadow	NA	Jul. 84 - Jun. 85	0 - 6.8 mmol m ⁻² h ⁻¹	NA	1000 - 13500 µmol mol ⁻¹
Sommerfeld 1993	DIFF. THR. SNOW	Alpine, sparse alpine vegetation	NA	Apr. - May 91, Mar. - May 92	0.7 - 13.7 mmol m ⁻² h ⁻¹	NA	1600 - 3300 µmol mol ⁻¹
Winston et al. 1997	NSF	Boreal coniferous forest	old	Nov. 93 - Apr. 94, Nov. 94 - Apr. 95	~ 0.003 - 0.190	NA	350 - 1700 µmol mol ⁻¹
"	"	"	young	"	~ 0.003 - 0.119	NA	350 - 2100 µmol mol ⁻¹
"	"	"	old	"	~ 0.003 - 0.127	NA	350 - 3500 µmol mol ⁻¹

[†]NSF = non-steady-state flow through, NSNF = non-steady-state non-flow-through, SSFL = steady-state flow-through, AL = alkali trap, SL = soda lime, EC = eddy covariance, DIFF = diffusion

^{††} - not measured, NA = information not available

Test runs with the model showed that soil air CO₂ concentration was even more sensitive to soil water content than the CO₂ efflux (II). If the effect of water was not included in the model, predicted CO₂ concentrations were 3 to 16 times higher than what was actually measured and predicted when the water content was taken into account.

Similar results were also presented by Simůnek and Suarez (1993). Their sensitivity analysis with different water contents showed that, in wet soil CO₂ concentrations were as much as 15 times higher than in dry soil, even if the lack of oxygen was limiting respiration in wet soil. According to Simůnek and Suarez (1993) and Magnusson (1995) soil volumetric water content and ground-water level are dominating factors controlling soil air CO₂ concentration. The soil and air temperatures were normally of secondary importance.

CO₂ concentration in the soil profile was also affected by clear-cutting. After the clear-cutting CO₂ concentration decreased significantly in all soil horizons. This is an indication of decreased biological activity in the soil profile. Evidently, the respiration by living roots decreased shortly after clear-cutting resulting in decreased CO₂ concentration especially in O- and A-horizons, where most of the CO₂ production occurred (Fig. 7 in II).

5.2. Soil CO₂ efflux

Soil CO₂ efflux followed the same seasonal pattern as CO₂ concentration. The efflux started to increase in May along with increasing soil temperature and peaked in July and August. Similar seasonal temperature related pattern for soil CO₂ efflux has been presented by several studies for boreal and temperate forests (Table 2). Fluxes within similar range have also been presented for peatlands (Martikainen *et al.* 1995, Silvola *et al.* 1996ab).

Effluxes previously presented are highly variable (Table 2.). Highest effluxes have been measured in tropical cattle pasture (Davidson *et al.* 2000) and lowest in grasslands (Coxson and Parkinson 1987) and in boreal forests (Gulledge and Schimel 2000). Usually the maximum soil CO₂ effluxes measured in boreal forests are less than 1 g CO₂ m⁻² h⁻¹. However, due to different chamber methods used, the fluxes are not directly comparable. According to the comparison between chamber methods (III), different methods used for flux measurements can deviate by as much as 50% from each other. Moreover, high spatial variation in soil respiration may result in biased estimates of soil CO₂ efflux if the number of sampling points is not large enough. Special attention should be given to the fact that spatial variation increases along with increasing respiration. Therefore the number of sampling points required for reliable estimates of CO₂ effluxes is higher in the summer when the effluxes are high than in the spring and in the autumn.

The temperature responses of soil respiration in this study are within the range of those of other studies in table 2. Boone *et al.* (1998), Borken *et al.* (1999), Davidson *et al.* (1998) and Epron *et al.* (1999a) measured Q₁₀ values ranging between 2.87-5.6 in

temperate forests. Morén and Lindroth (2000) presented a Q_{10} value of 4.75 for boreal forest whereas Gullledge and Schimel (2000) as well as Widén and Majdi (2001) measured much smaller temperature responses in boreal forests, Q_{10} ranging from 0.98 to 2.1. Silvola *et al.* (1996a), measured values of similar magnitude from boreal mires, the average Q_{10} ranging between 2.0 and 2.9 depending on the water table. However, the Q_{10} values were variable ranging from 1.1 to 4.9 depending on the site type and drainage. Raich and Schlesinger (1992) compiled literature values from year-round field studies in various vegetation types and calculated an average Q_{10} of 2.4.

I have not emphasized Q_{10} values in this study, because Q_{10} does not necessarily describe the temperature response of soil respiration in a truthful manner. CO_2 efflux is evolved from the whole soil profile whereas the reference temperature for Q_{10} is usually measured from the soil surface. Thus the temperature responses determined in this way may be biased. Moreover, Q_{10} in the spring and in the autumn reflects merely changes in autotrophic respiration. The proportion of root and rhizosphere respiration is not constant throughout the year. Due to increasing photosynthetic activity in spring the proportion of root and rhizosphere respiration can increase (Boone *et al.* 1998, Högberg *et al.* 2001).

The annual effluxes measured in this study both in the young forest (III) and in the old forest (IV) are high compared to most other studies in boreal and temperate region (Table 2.). However, the comparison of annual effluxes between various studies is difficult because in most cases effluxes have not been measured in winter (Table 2.). In the boreal region the contribution of winter effluxes to annual effluxes is small. In this study only 1.3 - 4.4% of the annual efflux was produced between January and April (III). Thus the “half-year fluxes” presented for boreal forest in table 2 can be considered annual effluxes.

Annual effluxes in the old uncut forest were lower than those measured in the young forest probably because of different biological activity in the two forests. Root and microbial respiration are related to the age of the forest stand and to the fertility of the site (Gullledge and Schimel 2000). A significant part of soil respiration originates from the decomposition of dead organic matter i.e. fresh needle and root litter (Hanson *et al.* 2000), and the amount of litter in terms, is related to the stand age. According to Vanninen and Mäkelä (1999) fine root and needle biomass decline in mature forest stands compared to young stands. This would result in smaller litter fall in old forests and consequently lower soil respiration. Another explanation to higher soil respiration in the young forest could be the fact that the young forest was located on a more fertile site and also the total amount of carbon in the soil was larger than in the old forest. Kolari *et al.* (2002) compared the CO_2 balance of the same young forest as in this study to a 75-year-old forest at 5 km distance with eddy covariance methods and also found significantly higher soil respiration in the young forest than in the old forest. This suggests that the differences were really derived from the forest and not from the chambers used for flux measurements.

Table 2. Soil CO₂ efflux in various terrestrial ecosystems

Authors	Method ⁺	Ecosystem	Age (year) ⁺⁺	Time period	Efflux (g CO ₂ m ⁻² h ⁻¹) ⁺⁺⁺	Annual (g CO ₂ m ⁻²) ⁺⁺	Q ₁₀
Boone et al. 1998	NSF	Temperate mixed deciduous forest	85	Jun. 94 - Jun. 95	0.02 - 0.32	NA	3.50
Borken et al. 1999	NSNF	Norway spruce plantation	65	Sep. - Nov. 93, Apr. - Nov. 94	0.06 - 1.55	1106 - 1171	2.87 - 3.9
"	NSNF	"	65	Dec. 93 - Mar. 94	0.06 - 1.55	1106 - 1171	"
Bowden et al. 1993	SL	Temperate mixed deciduous forest	80	Jun. 91 - Aug. 91	0.229 - 0.420	1360	NA
Buyanovsky et al. 1986	AL	Agricultural soil	NA	May 81 - Dec. 83	0.042 - 0.792	2347	1.62
Casals et al. 2000	AL	Semi-arid Mediterranean forest	40	Nov. 94 - Feb. 96	0.132 - 0.411	NA	NA
Coxson and Parkinson 1987	NSNF	Grassland	NA	Jan., Mar.	0.001 - 0.070	NA	NA
Davidson et al. 1998	NSF	Temperate mixed deciduous forest	60	May. 95 - May 96	0.073 - 0.843	2053 - 2970	4.00 - 4.50
"	"	"	"	"	0.183 - 1.833	2457 - 3043	3.40 - 5.60
Davidson et al. 2000	NSF	Cattle pasture and degraded pasture (Tropical)	30	Feb. 95 - May 96	0.063 - 0.647	6600 - 7330	NA
"	"	Primary and secondary forest (Tropical)	NA	"	0.293 - 1.173	2108 - 2431	3.90
Epron et al. 1999 ^a	NSF	Temperate deciduous forest	30	Jun. 96 - Nov. 97	0.063 - 0.647	2420	NA
Epron et al. 1999 ^b	NSF	Temperate deciduous forest	30	Jan. 97 - Nov. 97	0.175 - 0.400	NA	NA
Ewel et al. 1987	SL and SSFL	Sub tropical slash pine plantations	9 - 29	Apr. 83 - Jul. 84	0.075 - 0.850	3117	NA
"	"	"	"	Mar. 83 - Mar. 84	0.200 - 0.620	NA	NA
Gordon and Schlenner 1987	SL	Boreal mixed coniferous forest	133 <	Aug. 80 - Oct. 80, May 81 - Sep. 81	0.046 - 0.382	NA	NA
Goulden et al. 1998	NSF	Boreal coniferous forest	120	May 94 - Oct. 97	0.020 - 0.150	1023	1.30
Gullledge and Schimel 2000	NSNF	Boreal deciduous forest	85	Jun. - Sep. 92 - 94 (not in winter)	0.020 - 0.070	649	0.98
"	"	Boreal coniferous forest	220	Jun. - Sep. 93 - 94 (not in winter)	0.080 - 0.210	1701	1.90
"	"	Boreal deciduous forest	20	Jun. - Sep. 91 - 92 (not in winter)	0.040 - 0.190	777	1.30
"	"	Boreal coniferous forest	250	Jun. - Sep. 91 - 93 (not in winter)	0.127 - 0.903	2700 - 3400	2.10 - 3.20
Hanson et al. 1993	NSF	Temperate mixed deciduous forest	NA	Mar. - 91 - Nov. 91 and Jan. 92	0.079 - 0.475 ⁺⁺⁺	NA	1.90 - 2.20
Law et al. 1999	EC	Boreal coniferous forest	mixed - age	Jul. 96, Mar. 97, May 97, Aug. 97	0.079 - 0.919	NA	1.80
"	NSF	"	"	May 96 - Aug. 97	0.030 - 0.380	NA	2.09
Londo et al. 1999	SL	Warm temperate deciduous forest	65	Mar. 93 - Jul. 94	0.158 - 0.454	1393 (6 months)	NA
Lytell and Cronan 1998	SL	Cool temperate mixed coniferous forest	40	May 92 - Nov. 92	0.079 - 0.951	4631 - 5779	2.37
Mair and Kress 2000	SSFL	Temperate loblolly pine plantations	8	Apr. 95 - Mar. 96	0.019 - 0.722	NA	NA
Mariko et al. 1994	NSNF and DIFF, THR.	Cool temperate deciduous forest	mature	May 93, Aug. 93	0.016 - 0.673	NA	NA
"	"	"	mature	Apr. 93, Aug. 93	0.010 - 0.702	NA	NA
"	"	Sub alpine coniferous forest	mature	May 93, Sep. 93	0.023 - 0.420	NA	NA
"	"	"	mixed - age	Apr. 91 - Oct. 92	0.320 - 0.750	62.3 - 1320	NA
Martikainen et al. 1995	NSF	Boreal mire	70	May 96 - Oct. 96	max 2.6 - 3.6	4500	4.75
Moren and Lindroth 2000	SSFL	Boreal coniferous forest	70	Jun. 92 - May 93	0.101 - 0.806	3447	3.16
Nakane et al. 1996	AL	Temperate deciduous forest	70	Mar. 80 - Aug. 80, Apr. 80 - Sep. 80	0.150 - 0.660	1359 - 1468 May - Sep.	NA
Schlenner and van Kleeve 1985	SL	Boreal deciduous forest	70	"	0.150 - 0.800	1315 - 1654 May - Sep.	NA
"	"	Boreal deciduous forest	70	"	0.220 - 0.530	1345 - 1358 May - Sep.	NA
"	"	Boreal coniferous forest	70	"	0.210 - 0.630	1446 - 1569 May - Sep.	NA
"	"	Boreal coniferous forest	70	"	0.018 - 1.500	191 - 2267	1.1 - 4.90
Silvola et al. 1996a	SSFL	Boreal mire	NA	May 90 - Oct. 90, May 92 - Oct. 92	0.010 - 0.090	"	"
"	NSNF	"	"	Winter 91 - 92	0.199 - 0.458	1712 - 1720	1.99
Toland and Zak 1994	SSFL	Temperate mixed deciduous forest	mature	Apr. 92 - Nov. 92	0.150 - 0.229	NA	NA
Weber 1985	AL	Boreal coniferous forest	65	May 83 - Nov. 83	"	NA	NA
Widén and Majdi 2001	NSF	Boreal coniferous forest	varying age	May 99 - Oct. 99	0.190 - 1.664	NA	2.10

⁺NSF = non-steady-state flow-through chamber, NSNF = non-steady-state non-flow-through chamber, SSFL = steady-state flow-through chamber, AL = alkali trap, SL = soda lime, EC = eddy covariance

⁺⁺ NA = information not available, ⁺⁺⁺ nocturnal flux

5.3. Effect of clear-cutting and site preparation on soil C-pool

The effects of clear-cutting and site preparation can be viewed based on instantaneous effluxes and on annual effluxes predicted by hourly measured temperatures and temperature responses. The instantaneous effluxes were high immediately after the clear-cutting on places where logging residues were left on soil, but decreased rapidly, and after three years soil CO₂ effluxes measured from the control forest and from the clear-cut site were equal. Probably the easily decomposable organic matter was already consumed by microbes during the first and the second years following the clear-cutting. Berg *et al.* (1984) and Prescott *et al.* (2000 ab) studied the mass loss of broadleaf and coniferous litter on the clear-cut site in boreal forest and found highest (about 28-30%) mass loss in litter during the first year. More than 50% of the mass of litter was lost during the first three years after clear cutting.

The mixing of O-horizon with mineral soil enhanced the decomposition of litter for a short period of time probably because the moisture and temperature conditions became more favorable for decomposing organisms. The increase in soil temperature in mounds was probably the major factor contributing to higher respiration rates (Salonius 1983; Palmer Winkler 1996; Davidson *et al.* 1998).

The exposing of the mineral soil decreased soil CO₂ efflux, because the most active organic soil layer was removed. According to Pietikäinen *et al.* (1999) and Magnusson (1995) the density of fine root biomass was highest in the organic layer and in the A-horizon and decreased rapidly with increasing soil depth. Also the respiratory activity was highest in the organic soil layer. Millikin *et al.* (1996) found similar pattern in soil respiration in pits and mounds in a deciduous forest in Massachusetts. Two years after clear-cutting average soil respiration in mounds and undisturbed soil was twice as high compared to pits with exposed mineral soil. In this study, differences immediately after clear-cutting were much larger compared to those reported by Millikin *et al.* (1996), but after two years differences between the treatments were of the same magnitude.

On places where logging residues were removed, the measured soil CO₂ effluxes decreased significantly immediately after clear-cutting. This was probably due to the fact that the root and rhizosphere respiration ceased when trees were cut, but the decomposition of dying roots was not enough to compensate for the CO₂ efflux emitted from the roots and mycorrhiza. If the logging residue was removed from the top of the soil, only root litter and possibly some amount of deteriorated ground vegetation was decomposing in soil.

Based on the difference in efflux between the control forest and the clear-cut area after the removal of logging residue, the minimum proportion of root and rhizosphere respiration would be at least 36% of the total respiration (Table 4 in IV). Same kind of results have been obtained by trenching method by Ewel *et al.* (1987b), Bowden *et al.* (1993) and Epron *et al.* (1999b) and by Buchmann (2000) who excluded roots by cutting them with collars and by Högberg *et al.* (2001) from a

girdling experiment. However, the separation of root and microbial respiration with these methods is very difficult because of non-normal input of dead roots, which contribute to the CO₂ production. The estimations carried out on the clear-cut site by the process model on the contributions of different components of soil respiration showed high contribution for heterotrophic respiration compared to other studies (Ewel *et al.* 1987b; Bowden *et al.* 1993; Epron *et al.* 1999b; Buchmann 2000; Widén and Majdi 2001). This was probably due to the fact that here, a large proportion of carbon was allocated to root exudates and the decomposition of these exudates was considered to be heterotrophic respiration. In the model, it was assumed that an equal amount of carbon was allocated for root growth and to root exudates. By assuming this, the root biomass and soil respiration simulated by the model were equal to those measured in the field in the old forest. Without root exudates, the total soil respiration would have been about 38% lower than what was actually measured. If the root exudates were accounted to root respiration, its proportion would be about 54%.

After the clear-cutting, the contribution of root respiration and root exudates decreased to almost zero. Still the total soil respiration was higher than before clear-cutting because of the decomposition of organic matter released on the site in the clear-cut. Most of the decomposition occurred in O-horizon. It contributed 63% of the total respiration after the clear-cutting. The increase in soil respiration predicted by this model was however, smaller than the estimated annual efflux (3242 g CO₂ m⁻²). This may be due to the leaching of carbohydrates from the logging residue into the soil, which could enhance the decomposition of humus in the soil, a process not taken into account in the model.

Annual effluxes integrated over the whole year from temperature responses give a different impression on the effect of clear-cutting than the instantaneous effluxes due to the diurnal temperature fluctuation. On the clear-cut site, the daytime soil temperatures were higher than in the forest, and because the prediction was based on temperature response function, high annual fluxes were resulted. Contrary to this, instantaneous effluxes were measured in the morning between 8-11, when temperatures in the forest and on the clear-cut site were still quite equal and the higher daytime temperature on the clear-cut did not affect the effluxes from different treatments.

In places where the logging residue was left on the soil, annual CO₂ emissions during the first year were about 55% higher compared to the uncut control forest. During the first year after clear-cutting the annual emissions from the logging residue were 1423 g CO₂ m⁻², which equals to 388 g C m⁻² if the logging residues were distributed evenly on the soil surface. This was some 23% of the mass of the logging residue above the soil surface. The estimated annual emissions from O-, A- and B-horizons were about 352 g C m⁻², which was about 20% of the root mass. Two years after clear-cutting, the annual effluxes were still higher on the clear-cut site than in the control forest, probably because of higher temperature at the open clear-cut site. However, according to Berg *et al.* (1984) and Prescott *et al.* (200ab) the decomposition rate of litter is not linear, but slows down in time. Moreover, the CO₂

effluxes measured from the logging residue in this study originated mostly from the decomposition of pieces small enough to fit inside the chamber used for flux measurements, such as needles and branches. A large part of the carbon is in coarse woody debris such as thick branches as well as in roots and stumps, the decomposition of which takes considerably longer time than that of fine litter. For example, according model calculations based on literature review by Liski *et al.* (1998) the decomposition rate of fine woody litter such as Scots pine needles is about 3.5 higher than that of branches and 16 times higher than that of boles during the first 5 years of decomposition. Therefore in the long run, the actual mass losses of the logging residue, roots and stumps are probably much lower than those presented here. On the other hand, the method used for measuring CO₂ effluxes on the clear-cut site seemed to underestimate effluxes even by 30% (Fig. 7, in III). If this underestimation was taken into account, the mass losses of the logging residue, roots and stumps would be higher, but still the decomposition that material would take more than 20 years.

According to recent studies clear-cutting and site preparation seem to have controversial effects on the carbon balance of the forest ecosystem over the rotation time. When the forest grows old and achieves its economical rotation length (recommended 90 years in Finland), its capability to sequester carbon slows down, but still remains positive (Liski *et al.* 2001) until it reaches a steady state. Some studies have shown that old forests can be even carbon sources, because respiration in some conditions may exceed carbon accumulation (Lindroth *et al.* 1998).

If the forest is supposed to be a carbon sink in the long run, it has to be regenerated. However, Ewel *et al.* (1987a), Gordon *et al.* (1987) and Lytle & Cronan (1998) showed clear-cut areas to loose carbon in the decomposition of logging residues. Clear-cut site remains a source of carbon dioxide until the regrowth of the vegetation becomes large enough to compensate for the carbon losses in decomposition. Studies on the carbon balance of young forest stands have shown that boreal coniferous forests turn from carbon source to a sink not earlier than at an age of about 15 years (Karjalainen 1996ab; Schulze *et al.* 1999; Liski *et al.* 2001). However, even if clear-cut site loses some carbon before the establishment of a new forest, soil carbon balance in the long run may still be positive. According to Kawagutchi and Yoda (1986), Black and Harden (1995) and Pennock and van Kessel (1997), clear-cut can temporarily increase carbon content in the soil, because carbon in the logging residues becomes incorporated into the soil. Ilvesniemi *et al.* (2002) found 8.4% higher soil carbon pools 12-27 years after the clear-cutting compared to the situation before clear-cutting and suggested that the thriving ground vegetation at the clear-cut site could accumulate significant amounts of carbon.

However, the effects of ground vegetation have been found to be controversial. Carbohydrates introduced into the soil through root exudates may affect the decomposition of soil organic matter (Cheng 1996). Some studies based on experiments using ¹⁴C-labeling methods have shown stimulatory effect of living roots on soil organic matter decomposition (Cheng and Coleman 1990; Helal and Sauerbeck 1984). The break-down of soil aggregates and the stimulation of rhizosphere

microflora were suggested to be the cause of this phenomenon. In contrast, Reid and Goss (1982, 1983) and Sparling (1982) suggested that the competition between the living roots and the rhizosphere microflora for substrates may have a negative effect on organic matter decomposition.

Based on three years of monitoring after clear-cutting, we cannot estimate the decomposition rate and changes in the soil carbon stocks accurately in the long run. However, already with this data, we know that the decomposition of coarse logging residue is likely to take longer than 15 years, i.e. longer than the time required for the new forest stand to start acting as a carbon sink again. Thus, over subsequent forest crop rotations the amount of carbon accumulated in the soil may be larger than the amount of carbon released into the atmosphere in decomposition. However, in order to draw firm conclusions on the effect of clear-cutting on soil carbon stocks, longer monitoring on the carbon dynamics of the clear-cut site and newly established forest as well as the ground vegetation would be necessary.

6. Conclusions

Soil CO₂ efflux measurements are extremely liable to disturbances caused by the measurement devices and the CO₂ efflux values obtained with different measurement devices can be highly variable. Therefore, the systems used for measuring effluxes should always be tested, preferably against known efflux. Moreover, the spatial variation of CO₂ efflux is highly variable and to get a reliable estimate for the CO₂ efflux of a specific area, the number of sampling points should be adequate.

Primary environmental factors determining soil CO₂ efflux are soil temperature and soil moisture. Soil temperature explains most of the temporal variation in soil CO₂ efflux, but soil moisture has a substantial effect on soil respiration in extremely dry conditions. However such conditions are quite rare in boreal forests, but still in order to get reliable predictions, soil water content should be taken into account when analyzing the processes underlying soil CO₂ efflux. Most of the CO₂ is originated from the soil surface layers where majority of the roots and organic material are located, but in winter and during extreme drought the deeper soil horizons have substantial contribution to CO₂ emissions from the soil. This should be taken into account if predicting CO₂ effluxes based on soil surface temperature only. CO₂ concentration within the soil profile is affected more by the air filled porosity of soil than by soil temperature, because the transport of CO₂ in the soil is driven by diffusion, which is very sensitive to soil porosity.

Soil temperature and, to some extent, soil moisture are increased after forest clear-cutting. Higher soil temperature compared to uncut forest and a large amount of fresh organic matter increase annual CO₂ emissions from the soil at the clear-cut site, but when the logging residue is removed the annual emissions are not changed. Site preparation enhances the decomposition by forming mounds with warm temperature and favorable moisture conditions for decomposing organisms. Still, the decomposition of logging residue, roots and stumps may take longer than the time

needed for the new forest stand to act as a carbon sink again. Thus, in the long run, over subsequent forest crop rotation periods soil may be a carbon sink despite some carbon losses into the atmosphere after clear-cutting.

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Appendix 1

Parameters for the model used for simulating the contributions autotrophic and heterotrophic respiration before and after the clear-cutting.

Appendix 1. Decomposition of different soil organic components

Soil layer	Material	Parameter	Parameter
		α	β
Organic soil	Litter	0.0035	0.0648
	Partly decomposed litter	0.0007	0.102
	Humus	0.0004	0.10092
	Root exudates	0.28238	0.0648
Mineral soil	Litter	0.0035	0.0648
	Partly decomposed litter	0.0007	0.102
	Humus	0.0004	0.10092
	Root exudates	0.28238	0.0648