Effects of Fertilisation on Rhizospheric and Heterotrophic Soil CO₂ Efflux in Boreal Norway Spruce Stands

Per Olsson

Faculty of Forest Sciences
Department of Forest Ecology
Umeå

Department of Forest Ecology

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Abstract

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There are strong indications that the global mean temperature is rising. The increase in temperature is mainly attributed to the increase in the atmospheric CO_2 concentration, $[CO_2]$, the result of anthropogenic emissions from burning fossil fuels and changes in land-use, mainly deforestation. The total emissions of CO_2 cannot be accounted for by the measured increase in $[CO_2]$, nor by the amounts estimated to be taken up by oceans and terrestrial ecosystems, hence there is a missing sink for CO_2, where the boreal forest may play an important role.

The tree growth in boreal forests is limited by climate and nutrients, hence could a warmer climate, and more available nutrients, increase production. Increased temperature may, however, also accelerate decomposition of soil organic matter. Since production and decomposition is affected by the availability of nutrients, increased N-deposition or forest fertilisation may mitigate the effects of global warming.

The main objective of the present study was to determine the effects of nutrient supply on soil respiratory components in a boreal Norway spruce forest, especially the effects on heterotrophic and rhizospheric activity. To partition soil respiration into these components, tree-girdling, which terminates the carbohydrate supply from photosynthesis to the rhizospheric component, was used. The study was conducted in 40-year-old Norway spruce stands in Northern Sweden, which were growing at growth-limiting and optimised availability of soil nutrients, respectively.

During the period of annual maxima of soil respiration, fertilisation decreased rhizospheric soil CO_2 efflux by approximately 50%. Also heterotrophic soil CO_2 efflux was approximately 40% lower in fertilised plots, than in non-fertilised plots, despite a three-fold higher above-groundproduction in the fertilised plots.

In conclusion forest fertilisation contributes to C sequestration by increasing biomass production as well as retarding decomposition of soil organic matter.

Key words: autotrophic respiration, girdling, *Picea abies*, soil respiration, soil organic matter, starch

Author's address: Per Olsson, Department of Forest Ecology, SLU, SE-901 83 Umeå. Sweden.

Contents

Appendix

Papers I-II

This thesis is based on the following papers, which will be referred to by their Roman numerals:

I. Olsson, P., Linder, S., Giesler, R. & Högberg, P. 2005. Fertilization of boreal forest reduces both autotrophic and heterotrophic soil respiration. *Global Change Biology* 11, 1745–1753.

II. Högberg, P., Nordgren, A., Ottosson-Löfvenius, M., Bhupinderpal-Singh, Olsson, P. & Linder, S. 2005 Fractional contributions by autotrophic and heterotrophic respiration to soil-surface CO_2 efflux in Boreal forests. In: *The Carbon Balance of Forest Biomes.* (Eds. H. Griffiths & P.G Jarvis), Francis & Taylor, pp. 249-265.

Introduction

The global carbon balance

The global carbon (C) budget is not in balance. Input to the atmosphere is greater than output from the atmosphere, thus carbon dioxide, CO_2, is accumulated in the atmosphere, at a rate of 2.8 Pg C a^{-1} (Fan *et al.,* 1998) (Peta=10^{15}). To a large extent this increase is attributed to the human induced transfer of geological C to atmospheric CO_2, emitting 5.5 Pg C a^{-1} (Schimel, 1995); the total world consumption of fossil fuel increased from 3431 Mega ton oil equivalents (Mtoe) in 1973, to 4839 Mtoe in 2003 (IEA, 2005). The addition of CO_2 to the atmosphere has in the last century increased CO_2 concentration in the atmosphere from pre-industrial values of 280 ppm, to 360 ppm in 2001 (IPCC, 2001).

A group of gases, referred to as greenhouse gases (GHG) absorb outgoing long wave radiation from the Earth, thereby energy is restrained at the crust-troposphere continuum. This property of GHG increases the mean global surface temperature by 33 °C (IPCC, 2001). After H_2O, CO_2 is the second most important GHG. Hence, an increased concentration of CO_2 will change the radiation budget of Earth. This is called radiative forcing and is currently accounting for 1.46 W m^{-2} for CO_2 (IPCC, 2001). There is a wide concern that the extra energy near the surface of the planet will have far-reaching consequences for climate and life on Earth. The countries who have ratified the United Nations Framework Convention on Climate Change (UNFCC), the Kyoto protocol, have taken a first step to counteract further anthropogenic interference with the climate (cf. Steffen *et al.,* 1998). A total of 157 countries have accepted the Kyoto protocol and in November 2005 it had been ratified by 84 nations.

In a global perspective, the efflux of C derived from the geological C pool is, however, relatively small, about one tenth of the efflux from the terrestrial respiration (Schimel, 1995). Hence small changes of the terrestrial C efflux will have significant effects for the global radiation balance. The terrestrial efflux of C is mainly derived from plant respiration, and microorganisms decomposing soil organic matter (SOM). In recent years there has been a concern that a warmer climate will increase decomposition of SOM, releasing extra carbon dioxide and accelerate climate change. This assumption is based on the Arrhenius equation, where temperature determines the speed of reactions. Broadly speaking, the scientific community can be divided into two groups, those who predict that the increased decomposition SOM will cause further feedback to global warming (e.g. Kirschbaum, 1995, 2000; Cox *et al.,* 2000; Chapin III *et al.,* 2000; Cramer *et al.,* 2001; Jones *et al.,* 2005; Knorr *et al.,* 2005) and those who do not predict such a strong positive feed back from increased decomposition of SOM, since increased nutrient availability will increase biomass production in nutrient limited ecosystems (e.g. Liski *et al.,* 1999; Giardina & Ryan, 2000; Jarvis & Linder, 2000; Lou *et al.,* 2001; Strömgren, 2001).

Carbon balance of boreal forests

At present most terrestrial ecosystems act as sinks for C (cf. Dixon *et al.,* 1994; Ciais *et al.,* 1995; Schimel, 1995; Malhi, Baldocchi & Jarvis, 1999), and especially notable is the sink capacity of the boreal forest (Fan *et al.,* 1998; Houghton, 2002). The boreal forest covers a circumpolar, vast territory, and after the tropical forests, it is the second largest terrestrial biome in the world covering approximately 15.6 x 10^6 km^2. The climate is cold, and decomposition of SOM is slow (Johansson, Berg & Meentemeyer, 1995; Berg & McClaugherty, 2003), which has mainly been ascribed to low soil temperatures. In comparison with tropical and temperate forests, the slow decomposition in boreal forests has resulted in a disproportionately large soil C pool (Dixon *et al.,* 1994). This is critical since the northern hemisphere is expected to experience the greatest warming, and as previously mentioned, warming may accelerate decomposition of SOM and cause a positive feed back of C to the atmosphere.

Biomass production in most boreal forests is nutrient-limited, and the most limiting nutrient element is nitrogen (N) (cf. Tamm, 1991; Linder, 1995; Nohrstedt, 2001). Human activities, such as combustion of fossil fuels, which forms NO_x and the use of commercial fertilisers, cause a net N input to land ecosystems, which can have contributed to the observed recent increased production in northern temperate and boreal forests (e.g. Kauppi, Mielikäinen & Kuusela, 1992; Spiecker *et al.,* 1996). The human related input of N has more than doubled globally since before the industrialization (Galloway *et al*., 1995; Vitousek *et al.,* 1997), and it has been suggested that increased N deposition on land could lead to an increased storage of 0.1–1.3 Pg C a^{-1}, especially in N-limited high-latitude forests (Townsend *et al.,* 1996; Holland, 1997). Contradictory results have, however, been reported from chronic N-addition studies in temperate and boreal forests, which have shown declining tree growth (Aber *et al.,* 1995). In a more recent study, based on analyses of ^{15}N tracer added to forests and the C:N ratios of the pools, i.e woody biomass, non-woody biomass, forest floor, and mineral soil, in which the tracer was later found, Nadelhoffer *et al.* (1999) suggested that N deposition makes a minor contribution to C sequestration in northern temperate forests. However, since N-deposition is very low in northern Sweden, and not expected to increase in the near future (SMHI, 2005), the focus of this thesis is on the effects of fertilisation.

The soil carbon pool in boreal forests is also affected by N-inputs. Fertilisation of temperate and boreal forests has clearly demonstrated that N-input increases the soil carbon pool (cf. Johnson & Curtis, 2001; Johnson *et al.,* 2002; Freeman *et al.,* 2005). This increase of C storage in soils is a result from increased input of litter, which follows upon the greater overall biomass production, but is also attributed to a negative effect of N on decomposition of soil organic matter (e.g. Fog, 1988; Berg & Matzner, 1997; Olsson, 2001; Franklin *et al*., 2003; Sjöberg *et al.,* 2004). Thus additions of N to N-limited ecosystems have a considerable potential to enhance both forest production and soil C storage (cf. Tamm, 1991; Bergh *et al.,* 1999; Nohrstedt 2001; Paper I). Soil rhizospheric respiration (by roots and associated microorganisms), on the other hand, would be expected to decline when trees decrease their allocation of C to roots in response to a higher nutrient availability (e.g. Linder & Axelsson, 1982; Cannell & Dewar, 1994). Suggesting

that C losses from below-ground plant respiration will be reduced and more C will be stored in above-ground biomass.

Apart from climate and N-input, land use, land-use change, and forest management have crucial roles in balancing the C budget of boreal forests (cf. Covington, 1981; Schulze *et al.,* 1999; IPCC, 2000; Valentini *et al.,* 2000; Houghton & Hackler, 2001; Goodale *et al.,* 2002; Freeman *et al.*, 2005; Zerva & Mencuccini, 2005).

Soil respiration and the 'black box'

On a global basis, soil respiration is the largest component of respiration from forests (Janssens *et al.,* 2001; Ryan & Law, 2005). Soil respiration is the efflux of CO_2 from the soil surface, and is the result of all biological soil processes in which carbon dioxide is produced. To estimate the amount of C lost, or gained, as a result of decomposition of SOM and input of litter, we must, however, subtract the fractional contribution of respiration by living roots from total soil respiration. This is expressed in the equation modified from Hanson *et al.* (2000):

Net change of soil C = Litter inputs − (total soil carbon efflux − root respiration).

In this sense the soil can be considered a 'black box', where we have to define and quantify the fractional contributions from the autotrophic- and heterotrophic components of soil respiration.

Autotrophic organisms, e.g., green plants (photoautotrophs) utilise inorganic matter (CO_2, H_2O) and sunlight to build organic material and store energy. If we consider higher plants, organisms with differentiated cells and well developed organs, this strict definition would even exclude the plant roots from being autotrophic, since they do not fix their own energy, but use recently fixed organic C from the green parts of the plant. Roots can, however, not be considered heterotrophic (heterotroph = an organism that cannot synthesise organic compounds from inorganic) since they are part of an autotrophic organism. Mycorrhizal fungi, and other microorganisms in the vicinity of the roots, also use recently fixed organic C from the plant, and the mycorrhizal fungi can be seen as extensions of the roots. Further arguments for mycorrhizal fungi to be included among the autotrophs is that almost all root tips in boreal forests are covered by ectomycorrhizal fungi, ECM (eg. Arnebrant & Söderström, 1992; Wallenda & Kottke, 1998; Taylor, Martin & Read, 2000), and the roots and mycorrhiza are in practice physically inseparable. Moreover, roots and ECM produce considerable amounts of dissolved organic C, which is supplied to microorganisms living in the vicinity of ECM roots (e.g. Garbaye, 1994; Högberg & Högberg, 2002). In this sense the rhizosphere concept is a more functional term, since the rhizosphere includes roots, mycorrhizas and other microorganisms utilising recently fixed C (Hiltner, 1904, Sulzman *et al.,* 2005). The definition of rhizospheric respiration used here and in Sulzman *et al.* (2005) is analogous with the definition of autotrophic respiration used in Högberg *et al.* (2001), Bhupinderpal-Singh *et al.* (2003), and in Papers I and II.

Many attempts have been made to estimate the fractional contributions from autotrophic and heterotrophic soil respiration (cf. Hansson *et al.,* 2000, Kuzyakov & Larionova, 2005). The variation reported for the autotrophic part is huge, ranging from 10-90%. This variation is attributed to differences between ecosystems, but also to a large extent to the different techniques that were used. The techniques to separate soil respiration into autotrophic and heterotrophic soil respiration have until recently been divided into three broad categories (Hanson *et al.,* 2000);

i)   *integration of components*; the soil system is disintegrated into its different parts, and the respiration from each component is measured separately. The sum of the components is then, preferably compared with in situ measurements of total soil carbon efflux;

ii)   *use of physical barriers* to exclude roots, e.g., trenching;

iii)   *isotopic methods*, often based on labelling of photosynthates with radioactive ^{14}C or stable ^{13}C.

Further elaboration on the advantages/disadvantages with the different techniques are presented in Paper II.

Recently Högberg *et al.* (2001) successfully applied a fourth technique, where large-scale tree-girdling was used to separate the two major soil respiratory components. Tree-girdling is a simple physiological manipulation, where the phloem is removed around the stem to prevent any further C transport to the roots. As described above, the delicate connection between roots and microorganism does not allow any brutal separation, where the different components respiration are measured separately, and then scaled up to stand level. Tree-girdling allow us to separate the soil respiratory components, with the soil profile left intact, and therefore this method that was chosen for the present study.

Objectives

The purpose of the present thesis was (i) to determine the compartmental components of soil CO_2 flux in a boreal Norway spruce (*Picea abies* (L.) Karst.) forest, and (ii) to quantify the effects of nutrient additions on the components of soil respiratory activity. For this purpose a large-scale girdling experiment was conducted in a long-term nutrient optimisation experiment of a boreal Norway spruce plantation (Paper I).

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Materials and Methods

Site description

To study the compartmental contribution to total soil respiration, a large-scale tree girdling experiment (cf. Papers I & II) was performed in a long-term nutrient optimisation experiment, in a 40-year-old Norway spruce stand, at Flakaliden, northern Sweden (64°07'N; 19°27'E, altitude 310 m a.s.l.). The nutrient optimisation experiment was commenced in 1987, and the main purpose of the experiment was to demonstrate the potential yield of Norway spruce under the prevailing climate by optimising the nutritional status of the stands (cf. Bergh *et al.,* 1999).

Flakaliden has long winters and short cool summers. The mean annual temperature is 2.3 °C, the monthly mean temperature varies from -8.7 °C in February, and 14.4 °C in July, respectively (Bergh *et al.,* 1999). Snow usually covers the ground from mid-October to mid-May. The mean annual rainfall is approximately 600 mm, of which more than a third falls as snow. Soil parent materials are silty-sandy tills, and the soil is classified as a Haplic Podzol (FAO system).

The nutrient optimisation treatment included a complete solid fertiliser nutrient-mix (*F*), which was applied in early June each year. The amount of nutrients supplied was determined each year on the basis of foliar nutrient analysis, the nutrient concentrations in the soil water, and the predicted growth response (cf. Linder, 1995). Controls (*C*) plots that were not given any fertiliser were also included in the major experiment, the treatments were replicated four times, each replicate consisting of a double plot composed of two 50 x 50 m subplots. Each subplot contained a net plot (1000 m^2) surrounded by a buffer zone. Six of the eight subplots from the control (*C*) and six of the eight subplots from the solid fertiliser (*F*) treatments were used for the girdling study presented in Paper I, The plots (after girdling) are referred to as follows: non-fertilised, non-girdled plots *CC* (Control–Control); non-fertilised, girdled plots *CG* (Control–Girdled); fertilised, non-girdled plots *FC* (Fertilised–Control), and fertilised, girdled plots *FG* (Fertilised–Girdled). The total amounts of nutrients supplied to the *F* plots, 1987–2001, are found in Table 1. For further details regarding the treatments see Linder (1995).

Table 1. Total amounts of macro- and micronutrient elements (kg ha^{-1}) added to fertilised plots at Flakaliden during the period 1987-2001. The elements were supplied annually in rates adjusted to an estimated demand (cf. Linder, 1995).

N	P	K	Ca	Mg	S	Mn	Fe	Zn	B	Cu
1275	195	547	68	122	28	4.2	7.4	0.3	4.1	0.3

Girdling

On the 11th and 12th of June 2002, all trees in the net plots of three *F* plots and three *C* plots, respectively, were girdled (a total of 1412 trees). Girdling was performed using a hand-operated Sabre-Cut saw (Ultimate Survival, Seattle, WA, USA) to cut two 5 mm wide rings under the green crown, spaced approximately 5-15 cm apart (Fig. 4d), through the outer bark and phloem and a few mm into the xylem.

The *C* and *F* plots differed substantially in stand characteristics, e.g., the standing volume in *F*-plots was almost three times higher than in *C*-plots (Table 2).

Table 2. Stand characteristics before the girdling in June 2002. The treatments were, non-fertilised control plots (*CC*), non-fertilised girdled plots (*CG*), fertilised control plots (*FC*), and fertilised girdled plots (*FG*). Values shown are means for three plots per treatment.

	CC	*CG*	*FC*	*FG*
Diameter at breast height (mm)	87	85	144	137
Height (m)	7.3	6.7	10.0	9.5
Basal area (m^2 ha^{-1})	14.8	12.9	33.1	33.3
Volume (m^3 ha^{-1})	61.5	51.2	172.6	172.0
Stand density (trees ha^{-1})	2497	2250	2040	2250

Soil respiration

Soil-surface CO_2 efflux was measured in a closed system using an infrared gas analyzer (IRGA), EGM-3 (PP systems, Stotfold, UK), equipped with a dark soil respiration chamber (SRC-1). To allow precisely the same places to be monitored on each sampling occasion, PVC-collars (110 mm in diameter, 50 mm in height) were inserted on each experimental plot. Five PVC-collars were placed in the central part of each plot, with the pattern of a five on a dice, with 10 m spacing between the corners. The collars were gently pushed into the first centimeter of the mor layer. For further information about soil respiration measurements see Paper I

A problem when measuring soil CO_2 efflux during day-time is the ground vegetation, where the use of transparent chambers can result in negative fluxes (photosynthesis). Therefore a dark chamber was used, and shoots of shrubs and grass were removed from the spots where soil CO_2 efflux was to be measured.

Autotrophic soil respiration (Paper I and II) was calculated by subtracting the soil respiration in girdled plots from soil respiration in control plots, (i.e. *CC–CG* and *FC–FG*) for *C* and *F* treatments, respectively (cf. Högberg *et al.,* 2001). Soil respiration in girdled plots, *CG* and *FG* were, hence, used as proxies for heterotrophic respiration. For further details regarding the measurements, and statistical analyses, see Paper I.

Starch analysis

Root and needle samples were collected 40 days after girdling the trees. One-year-old needles were collected from the 7th whorl (from the top) and roots were taken from three randomly selected bulk soil samples per plot. Each soil sample was collected by cutting a square approximately 10 x 10 cm of the mor layer, and depending on the mor-layer thickness the total mor-layer volume (circa 0.5 litre) were brought to the lab. Roots were picked out and gently rinsed under running water, and divided into coarse roots and fine roots (>2 mm and <2 mm in diameter, respectively). To prevent any further physiological processes the fresh plant material was immediately immersed in liquid N for 30 s. Thereafter the plant material was dried in a ventilated oven (85 °C, 48 h), and stored at room temperature until analysed. The dry samples were ground to a fine powder and starch was analysed using an enzymatic method according to Steen & Larsson (1986).

Results and Discussion

Girdling reduced total soil respiration by approximately half (Fig. 1a), which is in accordance with other girdling studies (Table 3). In the present study it is, however, for the first time demonstrated that fertilisation of boreal forest reduces both autotrophic and heterotrophic soil respiration.
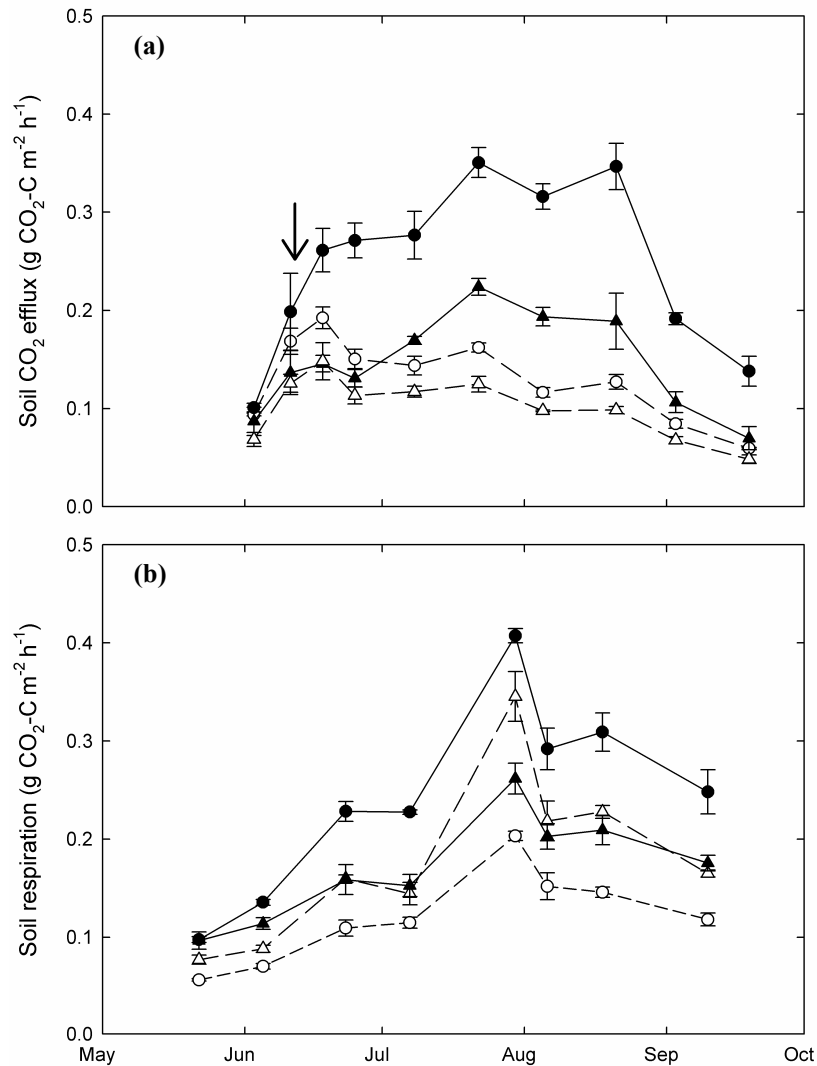

Figure 1. (a) The seasonal course in soil CO_2 efflux (g CO_2-C m^{-2} h^{-1}) in non-girdled control (●) and girdled control (○) (*C*) or non-girdled fertilised (▲) or girdled fertilised (△) Norway spruce stands at Flakaliden in 2002 (a) and 2003 (b), respectively. The annual fertilisation (*F*) commenced in 1987 and the girdling treatment was applied in 2002. The arrow indicates the time of girdling in 2002. Data shown are means ± SE (n=3).

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Table 3. Maximum fractional contribution of rhizospheric respiration to total respiration estimated in tree-girdling experiments. Data from [1]Högberg *et al.* (2001), [2]Bhupinderpal-Singh *et al.* (2003), [3]Paper **I**, [4]Andersen *et al.* (2005), [5]Scott-Denton *et al.* (2005), [6]Högberg (*pers. comm.*), and [7]Subke *et al.* (2004).

Site	Tree species	Stand age	Plot size	Rhizospheric respiration
		Years	m^2	% of total soil C efflux
Sweden				
Åheden[1]	*Pinus sylvestris*	50	900	54
Åheden[2†]	*Pinus sylvestris*	50	900	65
Flakaliden[3]	*Picea abies*	40	1000	63
Flakaliden[3]*	*Picea abies*	40	1000	50
Storskogsberget[6]	*Picea abies*	120	700	50
Germany				
Kranzberger[4]	*Picea abies*	40-50	75-100	51
	Fagus sylvatica	mature	75-100	50
Kranzberger[4†]	*Picea abies*	40-50	75-100	18
	Fagus sylvatica	mature	75-100	30
Wetzstein[7]	*Picea abies*	35	400	50
U.S.A.				
Niwot Ridge[5]	*Pinus contorta*	--	20-40	44
Niwot Ridge[5†]	*Pinus contorta*	--	20-40	17

*fertilised plots; † second year after girdling.

The calculated autotrophic respiration in *CC* plots was maximal in late August, when it accounted for more than 60% of total soil respiration (Fig. 2b). In fertilised plots, autotrophic respiration followed a similar trend as in the non-fertilised plots, but accounted for 50% of the total soil respiration (Fig. 2a). This difference was significant in absolute terms (P=0.009).

Table 4. Starch (in percent of dry mass) in fine roots (<2 mm ∅), coarse roots (2-5 mm ∅), and one-year-old needles, in non-girdled (*CC, FC*) and girdled (*CG, FG*) stands, 40 days after girdling. The treatments were non-girdled control (*CC*), girdled control (*CG*), fertilised control (*FC*) and fertilised girdled (*FG*). The significance of differences was tested by *t*-tests. (n=3), ** p<0.001, (*CG* fine roots, n=2).

Organ	*CC*	*CG*	p	*FC*	*FG*	p
Fine roots	7.3	2.5	n.s.	6.8	2.2	0.03
Coarse roots	8.0	0.5	0.01	6.2	1.6	0.01
Needles	10.7	25.7	**	2.9	9.1	**

Already 40 days after girdling root starch reserves were considerably reduced in tree-girdled plots, at the same time there was an increase in starch content of

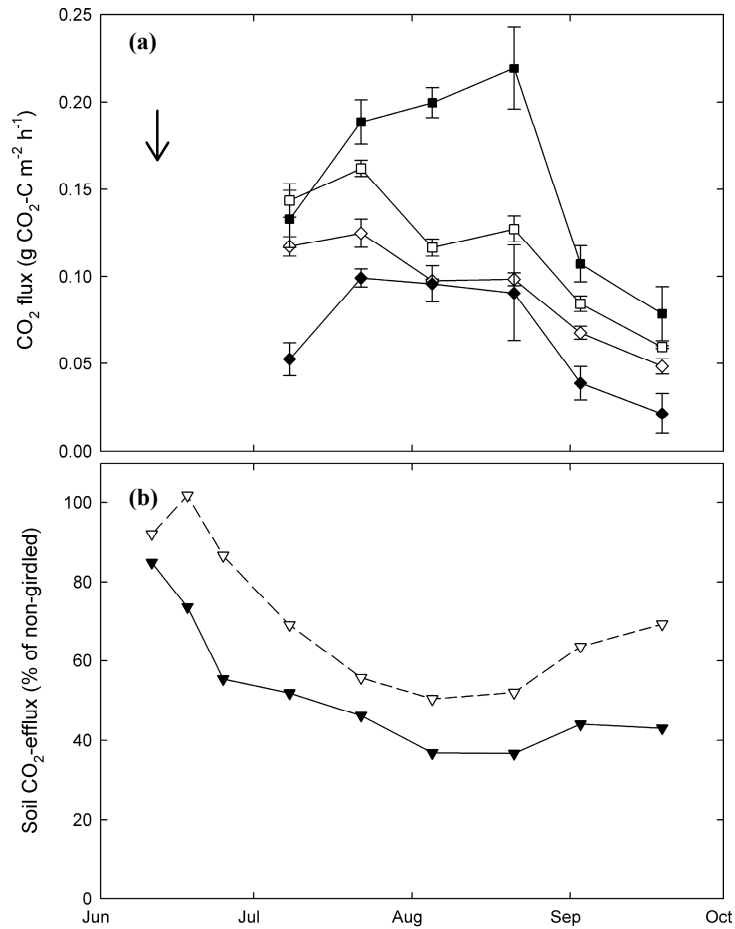needles (Table 4). This is further evidence that the girdling blocked transport of

Figure 2. (a) Calculated autotrophic (■) and heterotrophic (□) respiration in non-fertilised plots, and autotrophic (♦) and heterotrophic (◊) respiration in fertilised plots. (b)   The relative effects of girdling on total soil respiration in non-fertilised (▼) and fertilised plots (▽) at Flakaliden in 2002. The arrow indicates time of girdling. Data are calculated from means (n=3).

carbohydrates from the needles, via the phloem, to the roots, and that the starch reserves in the roots were rapidly depleted, while starch were accumulating in needles of girdled trees.

The close agreement between the curves calculated for autotrophic soil respiration (Fig. 2a, b), suggests that seasonality of C allocation to roots, and depletion of carbohydrates stored in the roots, was similar in both *F*- and *C*-plots, and. that the major part of the C use by below-ground structures takes place in late July and August. This is in accordance with Hansen *et al.* (1997), who suggested that allocation to the roots take place in autumn, when growth of above-ground

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structures has ceased. It is obvious that more resources were allocated below-ground to support respiration in C-plots, as compared to F-plots. This reflects that the relative allocation of resources to roots is larger when there is a shortage of soil available nutrients (e.g. Linder & Axelsson, 1982; Cannell & Dewar, 1994; Ericsson, 1995; Giardina *et al.,* 2003; Lamersdorf & Borken, 2004). Moreover, the C cost of extramatrical mycorrhizal mycelium is also known to be negatively correlated with soil nutrient availability (Wallander & Nylund, 1992; Arnebrant, 1994; Hobbie & Colpaert, 2003; Högberg *et al.,* 2003; Nilsson & Wallander, 2003).

In spite of the higher stem wood production (Table 2), and hence higher litter input, the heterotrophic soil respiration was circa 20% lower in fertilised than non-fertilised plots (Fig. 3). It is obvious that litter fall followed leaf area index, which at the time of girdling was more than twice as high in F- compared to C- plots, LAI 7.5 and 3.3, respectively (Sune Linder pers. comm.)
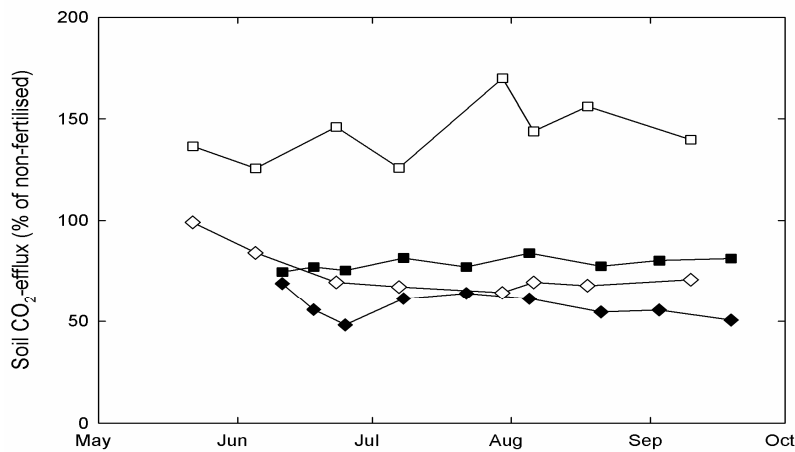

Figure 3. The relative effect of fertilisation (F) on total soil CO_2-efflux in girdled (G), and non-girdled (C) plots in 2002 (filled symbols) and 2003 (open symbols), respectively. FG/CG (■,□), FC/CC (♦,◇). Data are calculated from means n=3.

Franklin *et al.* (2003), working at Norrliden (50 km from Flakaliden), demonstrated that repeated additions of N will cause more C to be sequestered in the litter and mor layers, which is the most respiratory active soil profile (Persson *et al.,* 2000). In addition, Franklin *et al.* (2003) suggested that decomposition was mainly retarded in later stages of decomposition. This is supported by work from many previous studies, suggesting that N has negative effects on decomposition rates in later stages of decomposition (e.g. Fog, 1988; Berg & Matzner, 1997; Butnor *et al.,* 2003).

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There are different explanations for retarded decomposition of soil organic matter after N additions, which can be broadly divided into:

i) *Biological mechanisms*, suggesting that N represses the production of lignolytic enzymes in white root fungi.
ii) *Chemical mechanisms*, by which ammonium and lignin form more recalcitrant products.

A detailed description and discussion regarding these mechanisms can be found in Berg & McClaugherty (2003) and references therein.

In accordance with Townsend *et al.* (1996) and Holland (1997), the results presented above suggest that increased input of N to terrestrial ecosystems will increase C sequestration. The suggestion by Nadelhoffer *et al.* (1999), that *"N deposition only makes a minor contribution to C sequestration in temperate forests"*, overlooks two important things: first, they reported that only a small fraction of the tracer (3%) was found in woody biomass, and up to 80% in forest floor and mineral soil. Nitrogen content of woody biomass is, however, a very poor predictor of forest production, which. is primarily determined by the amount of light that can be harvested, i.e. the amount of leaf area which is related to the available soil nutrient resources (Bergh, *et al.,* 2005) Second, they did not include the negative effect the N-input may have on the decomposition of SOM.

In contrast to a previous girdling experiment in a Scots pine stand in Åheden, 30 km from Flakaliden (Högberg *et al.,* 2001; Bhupinderpal-Singh *et al.,* 2003), The effect of girdling became more complex in the present experiment during the second year after girdling. Already 2-3 months after the girdling of the Norway spruce stands at Flakaliden, a minor yellowing of the needles occurred, possibly caused by water stress induced by resin blocking the water transport (Fig. 4e). This was followed by heavy infestations by bark beetles (Fig. 4c), which killed the trees (Fig 4a, b), and resulted in a heavy input of needle litter as well as root litter to the soil. This is the most probable explanation to why respiration in *FG*-plots exceeded respiration from the corresponding non-girdled *F*-plots in 2003 (Fig. 1b). In 2003 *FG*-plots had approximately doubled their relative contribution in soil respiration compared with 2002 (Fig. 3). This effect was not seen in *CG*-plots, where the input of needle litter was smaller, but since the soil respiration was at the same level as in 2002, the heterotrophic respiration must have increased, since the autotrophic contribution should have been minimal.

As mentioned in the Introduction, global warming is by some models predicted to result in a drastic increase of soil CO_2 effluxes, reducing the soil-C pool (e.g. Kirschbaum, 1995, 2000; Chapin III *et al.,* 2000; Cox *et al.,* 2000; Cramer *et al.,* 2001; Jones *et al.,* 2005; Knorr *et al.,* 2005). A net loss of C from the soil-C pool is the result of heterotrophic activity, but in the total soil CO_2 efflux the autotrophic respiration is also a major component, which has been shown in the present study, as well as other girdling experiments (cf. Table 3). As temperature is often used as a driving variable in models that predict soil carbon dynamics (e.g. Xiao *et al.,* 1998; Yang *et al.,* 2002), it is, hence, of great importance to include different temperature sensitivity of the different soil respiratory components.

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There are experiments that report twice as high temperature sensitivity for roots, than for heterotrophic organisms (e.g. Boone *et al.,* 1998; Epron *et al.,* 2001). These studies overlook the four important factors that have to be considered in estimating the temperature response of the different components of soil respiration: *i*) The effects of seasonality in carbon allocation by trees (Hansen *et al.,* 1997, Yuste *et al.,* 2004). *ii*) Rhizospheric soil respiration seems to be more dependent on irradiance and C assimilation than soil temperature relationship. It is, however, difficult to make a distinct separation since there is a close relationship between irradiance and temperature (Bååth & Wallander, 2003; Langley, Johnson & Koch, 2005; Paper II). *iii*) Time lags, due to long distance phloem transport of carbohydrates from shoots to the roots, causing rhizospheric soil respiration to reflect past weather more than present temperature in the soil (e.g. Ekblad & Högberg, 2000; Bhupinderpal-Singh *et al.,* 2003, Paper II). *iv*) Temperature acclimation of the rhizospheric respiration (e.g. Tjoelker, Oleksyn & Reich 1999 Atkin *et al.,* 2000). In 2002 there were two transient temperature drops during the growing season. This gave us the opportunity to test the temperature responses on the rhizospheric and heterotrophic soil component, respectively. During both temperature drops the estimated heterotrophic soil respiration decreased between 14-33%, while rhizospheric respiration remained steady or increased by up to 100% (Paper II). This suggests that rhizospheric soil respiration should not merely be modelled as a function of temperature. Instead rhizospheric respiration should be modelled as driven by canopy photosynthesis, below-ground allocation of C, and the interaction of these processes with the abiotic environment i.e. irradiance, temperature and soil water content.

Figure 4. Photographs taken in connection to the girdling experiment: Top left (a), girdled trees in *C*-plot summer 2003. Bottom left (b), girdled trees in *F*-plot summer 2003. Top right (c), Spruce trunk after heavy attacksof bark beetles. Mid right (d), girdling of a spruce tree using a survival saw.Bottom right (e), girdled tree from a *C*-plot, cross section just above the girdling (stem was cut and prepared for photographs the winter between 2002/2003). *Photographs a-c: Sune Linder, d-e: Per Olsson.*

Tree girdling is a alternative method to separate rhizospheric from heterotrophic soil respiration (Paper II), but ultimately kills the trees, restricting the time during which the different soil respiratory components can be studied. Furthermore, climate in certain areas may be more or less stable over long time periods, but weather is not. 'Extreme' years of drought or heavy rain may happen within the

short time a girdled stand is studied, which makes interpretation of soil respiratory components very delicate. For example in the second year of the girdling study by Andersen *et al.* (2005), there was a severe summer drought. They saw a decrease in calculated autotrophic soil respiration from 50% to 18% in the girdled spruce stand, which they interpreted as autotrophic respiration being more sensitive than heterotrophic activity to low soil water content. Their results is in contrast to an interpretation by Irvine, Law & Kurpius (2005), who irrigated trees on one side and measured soil respiration on the other. They saw an increase in soil respiration by 211% on the dry side, which they could attribute to root respiration; their partly watered trees could be more photosynthetically active than non-watered trees, and thus sustain considerable root respiration in dry soil, in which heterotrophic respiration, must have been limited.

In the study by Andersen *et al.* (2005) soil respiration in girdled plots approached their control plots during the dry summer the year after girdling. One can assume that this reflects increased heterotrophic activity, as a combined effect of increased soil water content due to reduced water uptake by the girdled trees, and the effect of increased litter input. This is supported by the results from Scott-Denton *et al.* (2005), who reported a similar pattern; where girdled plots became wetter during the second year following girdling, and as a result, calculated root respiration became lower.

Conclusions and suggestions

• Tree girdling provides an effective method to separate rhizospheric and heterotrophic soil respiration.

• The rhizospheric component of the total soil CO_2 efflux in boreal Norway spruce stands, is significant, and negatively affected by availability of nutrients.

• Fertilisation of boreal forests has the potential to increase above-ground biomass production, partly by effects on allocation patterns resulting in lower rhizospheric respiration.

• Additions of N, as fertilisation, have a retarding effect on decomposition rates of soil organic matter.

• Fertilisation of boreal forests has the potential to mitigate climate warming since less C is respired from both autotrophs and heterotrophs, and thus more C will be stored in both biomass and soil.

• The extra biomass produced after forest fertilisation, could be used to substitute fossil fuels, which would help to mitigate the increasing $[CO_2]$ and create new job opportunities.

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