Soil-Surface CO_2 Flux and Growth in a Boreal Norway Spruce Stand

Effects of soil warming and nutrition

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Abstract

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Global warming is predicted to affect the carbon balance of forests. A change in the carbon balance would give a positive or negative feedback to the greenhouse effect, which would affect global warming. The effects of long-term soil warming on growth, nutrient and soil-surface CO_2 flux (*R*) dynamics were studied in irrigated (I) and irrigated-fertilised (IL) stands of Norway spruce in northern Sweden. Soil temperature on heated plots (Ih and ILh) was maintained 5 °C above that on unheated plots (Ic and ILc) from May to October, by heating cables.

After six years' soil warming, stemwood production increased by 100% and 50% in the I and IL treatment, respectively. The main production increase occurred at the beginning of the season, probably as an effect of the earlier increase in soil temperature. In the Ih treatment, however, the growth increase was evident during the entire season. The effect of increased nitrogen (N) mineralisation on annual growth appeared to be stronger than the direct effect of warming.

From 1995–2000, the total amount of N stored in aboveground tree parts increased by 100 and 475 kg N ha^{-1} on Ic and ILc plots, respectively. During the same period, 450 kg N fertiliser was added to the ILc plot. Soil warming increased the total amount of N stored in aboveground tree parts by 50 kg N ha^{-1}, independently of nutrient treatment.

Soil warming did not significantly increase *R,* except in early spring, when *R* was 30–50% higher on heated compared to unheated plots. The extended growing season, however, increased annual respiration (R_A) by 12–30% throughout. R_A losses were estimated to be 0.6–0.7 kg C ha^{-1} a^{-1}. Use of relationships between *R* and soil temperature, derived from unheated plots, overestimated R_A on heated plots by 50–80%. These results suggest that acclimation of root or microbial respiration or both to temperature had occurred, but the exact process(es) and their relative contribution are still unclear.

In conclusion, the study showed that soil warming stimulated tree growth, but resulted in only a minor increase of annual *R*, suggesting an increased carbon sink for boreal forests in a warmer climate.

Keywords: biomass production, boreal, climate change, phenology, *Picea abies*, soil respiration

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Appendix

Paper I–V

The present thesis is partly based on the following papers, which are referred to by their Roman numerals:

I Monika Strömgren & Sune Linder. Effects of nutrition and soil warming on stemwood production in a boreal Norway spruce stand. *Global Change Biology* (submitted).

II Monika Strömgren, Sune Linder, Harald Grip & Peter Högberg. Soil-warming effects on nutrient availability in a boreal Norway spruce forest. *Plant and Soil* (submitted).

III Stith T. Gower, Monika Strömgren & Myron Tanner. An automated system to measure soil-surface CO_2 flux. *Soil Science Society of America Journal* (submitted).

IV Monika Strömgren, Stith T. Gower & Sune Linder. Effects of soil warming on soil-surface carbon dynamics in a boreal *Picea abies* forest. *Global Change Biology* (submitted).

V Sune Linder, Monika Strömgren & Stith T. Gower. Long-term soil warming does not increase soil-surface CO_2 flux in a boreal forest. *Nature* (submitted).

Introduction

In recent decades, global warming has been the subject of great concern not only to scientists, but also to politicians and people in general. A global change in climate would affect the life of everyone. Almost every day, headlines in newspapers throughout the world refer to global warming and introduce new facts or speculations about its consequences. Over the past year, there have been more than 600 articles in the New York Times alone that include the words 'global warming' or 'climate change' (6-Sept-2001). Droughts, floods, storms, heatwaves, heavy rain and rising sea levels have all been attributed to global warming or to the greenhouse effect.

International concerns about global warming led, in 1992, to the creation of the United Nations' Framework Convention on Climate Change (UNFCCC) in Rio de Janeiro. In September 2000, the Convention had been ratified by 186 states (UNFCCC, 2001). The ratifying states agreed that high emissions of greenhouse gases, such as carbon dioxide (CO_2), can be harmful, and that the concentration of greenhouse gases in the atmosphere should be stabilised at a level that prevents dangerous, human-induced interference with climate. The Convention requires that each country should implement national programmes to mitigate climate change, and should make an inventory both of greenhouse gas sources (such as emissions of CO_2 from transport and industries), and of sinks (such as forest ecosystems) (UNFCCC, 2001). However, the Convention did not quantify acceptable emission levels of greenhouse gases, and it is still uncertain whether or not sinks and sources of CO_2 connected to changes in landuse and forestry should be included.

The reduction in greenhouse gas emissions was quantified in the Kyoto Protocol. It was decided that emissions of greenhouse gases should decrease by 5% in 2008–2012, compared to the 1990 level (UNFCCC, 2001). According to the Protocol, this goal can be achieved in two ways: (*i*) by decreasing emissions of the gases and (*ii*) by influencing the uptake rate of CO_2 from the atmosphere through deforestation, afforestation or reforestation. However, the Protocol did not specify how the emission abatement should be distributed among the parties to the convention (D'Evie & Taylor, 1999). Furthermore, the Protocol will be enforced only when it has been ratified by at least 55 countries, which account for at least 55% of global CO_2 emissions (UNFCCC, 2001). In late September 2001, only 40 countries had ratified or acceded to the Kyoto Protocol.

What then is the greenhouse effect, and is there global warming? If there were no greenhouse effect, the Earth's temperature would be -18 °C, *i.e.* 33 °C colder than today, a condition that would be catastrophic for life (*cf.* Puhe & Ulrich, 2001). Thanks to the earth's atmosphere, the climate is warmer and more favourable. The Earth's atmosphere reflects one-third of the incoming solar radiation, while 30% of the remainder is trapped in the atmosphere and 70% reaches the soil surface. Approximately 40% of the incoming solar radiation is reflected back from the Earth's surface as infrared radiation (heat). Whereas the atmosphere is relatively permeable to short-wave radiation, such as incoming solar radiation, it absorbs long-wave radiation, such as infrared radiation. Water vapour, carbon dioxide (CO_2), methane, nitric oxides and tropospheric ozone are examples of gases that have a strong capacity to absorb long-wave radiation. They are, therefore, referred to as the greenhouse gases. Among these, water vapour is the most important in terms of abundance, and CO_2 is the second. Combustion of fossil fuels and change of landuse has increased the concentration of atmospheric CO_2, which has reinforced the greenhouse effect. Atmospheric CO_2 increased from *ca.* 280 ppm in pre-industrial times, to *ca.* 320 ppm in 1960, and has now reached 370 ppm (Fig. 1) (Keeling & Whorf, 2000). Atmospheric CO_2 concentration and global mean temperature have covaried closely during the past 420 000 years (Petit *et al.*, 1999), but it is uncertain whether the concentration of CO_2 controls the temperature or *vice versa*. Moreover, during the past centuries, it is not only emissions of greenhouse gases that have increased, but also emissions of aerosols and sulphate-aerosols (*cf.* Charlson *et al.*, 1991). Those emissions counteract the effects of greenhouse gases, and have a cooling effect on the Earth. Nevertheless, climate is complex and is affected by a multitude of factors, such as changes in the Earth's orbit and axial tilt, solar activity, volcanic activity, orogeny and by the relative distribution of land and sea. Has, therefore, the recent increase in greenhouse gases increased the Earth's temperature?

Historically, the northern hemisphere has shifted between glacial and interglacial phases. Changes in temperature have occurred rapidly (Houghton *et al.*, 2001). Since the end of the latest glacial period, the climate has been variable,

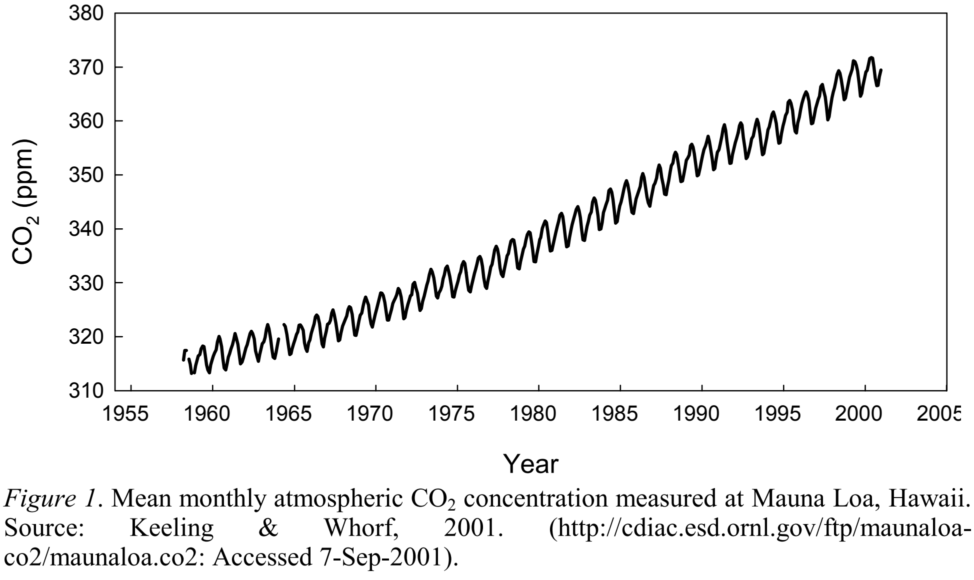

Figure 1. Mean monthly atmospheric CO_2 concentration measured at Mauna Loa, Hawaii. Source: Keeling & Whorf, 2001. (http://cdiac.esd.ornl.gov/ftp/maunaloa-co2/maunaloa.co2: Accessed 7-Sep-2001).

with periods of warmer, colder, wetter, and drier conditions than at present, but the 20th Century was the warmest during the past millennium (Fig. 2). The global surface temperature has increased by 0.6 °C during the past 100 years (Houghton *et al.*, 2001). Moreover, the sea level has risen, snow cover and ice extent have decreased and there is a strong indication that precipitation has increased. Can those changes be explained by natural variations or not? Opinions among scientists differ (compare Karlén, 2001 and Mann *et al.*, 2000), but IPCC states that the increase in temperature is 'very likely' caused by anthropogenic emissions of CO_2 (*cf.* Houghton *et al.*, 2001). In addition, within the 21st Century, since the concentrations of CO_2 are still increasing, the global mean temperature is predicted to increase by 1.4–5.8 °C. The temperature increase will probably be higher for terrestrial ecosystems, and the greatest increases are predicted to take place in northern latitudes.

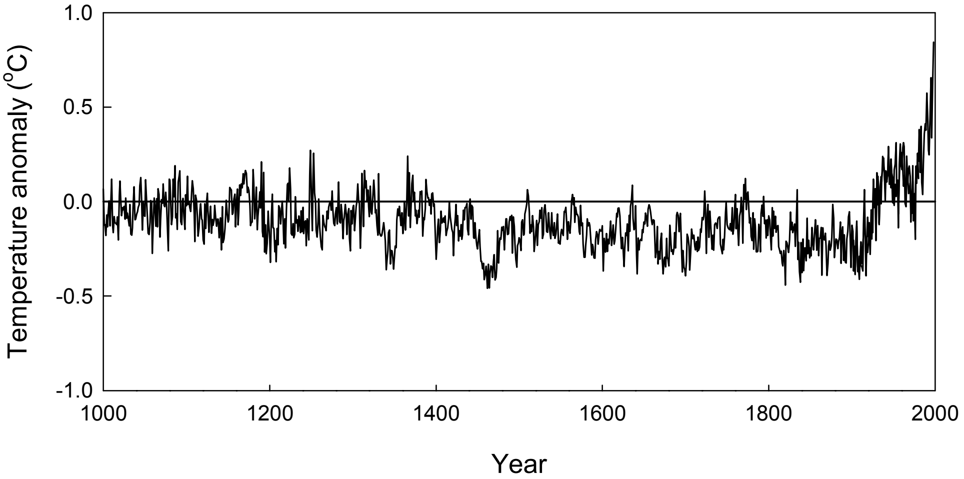

Figure 2. Annual Northern hemisphere mean temperature during the past millennium. The years 1000-1980 are based on reconstructed data, and 1902-1998 is based on instrumental data. Source: Mann *et al.*, 1999 (http://ngdc.noaa.gov/paleo/ei/ei_pdf.html: Accessed 25-Oct-2001).

Global warming and the boreal forests

Boreal forests constitute 40% of the world's forests and they are of great economic importance to many northern countries (*cf.* FAO, 2001, Jarvis *et al.*, 2001, Gower *et al.*, 2001). The global forests contain the Earth's largest terrestrial carbon pool, most of which is in the northern forests (Dixon *et al.*, 1994). A warmer climate can affect the forests and alter the carbon balance, which in turn will feed back to the greenhouse effect (*cf.* Luxmoore *et al.*, 1993; Wang & Polglase, 1995; Kirschbaum, 2000a).

The carbon balance of a forest can mainly be described in terms of photosynthesis and respiration. Carbon is assimilated in the forest through photosynthesis by the tree canopy and ground vegetation. Carbon is released again by respiration from foliage, stems, branches, roots, and mycorrhizae, which is referred to as *autotrophic respiration*. In addition, carbon is released by microbes and microfauna during decomposition of organic matter, which is referred to as *heterotrophic respiration*. Both photosynthesis and respiration are sensitive to changes in temperature. Photosynthesis increases with temperature until it reaches an optimum temperature, whereafter it begins to decrease (DeLucia & Smith, 1987; Teskey *et al.*, 1994), and respiration is usually described by an exponential relationship on temperature.

Both photosynthesis and respiration are large components of the carbon balance; the difference between them decides whether the ecosystem will act as a sink or a source of carbon. Therefore, the carbon balance of a boreal forest is very sensitive to temperature changes and, during certain periods, the forest can even act as a carbon source (*cf.* Wang & Polglase, 1995; Lindroth *et al.*, 1998). Nevertheless, the northern forests usually absorb more carbon than they release (Dixon *et al.*, 1994). In a global perspective, however, there is a net flux of CO_2 from the forests to the atmosphere, which represents 15–40% of anthropogenic carbon emissions (Raich & Schlesinger, 1992; Dixon *et al.*, 1994). This net loss is a consequence of changes in landuse, forest status and forest carbon cycling (Dixon *et al.*, 1994).

An increase in temperature directly affects plant growth or net primary production (NPP), through changes in respiration and photosynthesis (*cf.* Wang & Polglase, 1995; Kirschbaum, 2000a). There is evidence for increases in plant growth, caused by increased temperature, and longer growing seasons in recent decades (Myneni *et al.*, 1997). This is particularly pronounced in northern latitudes. Temperature is an important factor in controlling biomass production in boreal forests (Havranek & Tranquillini, 1995). Despite high solar radiation, gross primary production (GPP) is limited by frozen or cold soils, which not only prevent water uptake and therefore photosynthesis, but also induce physiological damage to the needles of evergreen trees (*cf.* Jurik *et al.*, 1988). About 40% of the potential GPP[1] in a boreal Norway spruce forest may be lost each year due to low temperatures (Bergh *et al.*, 1998).

Increases in temperature will also increase the rate of nutrient mineralisation in the soil (Bonan & Van Cleve, 1992; Kirschbaum, 2000b). Growth in a boreal forest is primarily limited by low nutrient availability (Tamm, 1991). An increased temperature can, therefore, stimulate biomass production and carbon uptake in the ecosytem. How nutrient dynamics in the soil is affected, is critical for improving long-term predictions of carbon sink strength (Medlyn *et al.*, 2000). On the other hand, a temperature increase will also increase CO_2

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[1] The GPP which could be achieved if the plants had been able to use all light radiation

emissions *via* the decomposition of organic matter (Jenkinson *et al.*, 1991; Kirschbaum, 1995, 2000b; Wang & Polglase, 1995). The soil contains far more carbon than does living biomass (Dixon *et al.*, 1994; Gower *et al.*, 1997; Kauppi *et al.*, 1997), and soil-surface CO_2 flux from terrestrial ecosystems releases 15–40% of total CO_2 emissions to the atmosphere (Raich & Schlesinger, 1992; Dixon *et al.*, 1994). A temperature increase could stimulate respiration of CO_2, caused by increased rates of decomposition, more than it would stimulate NPP (Kirschbaum, 2000b). This could convert the forest ecosystem into a carbon source. However, the response of soil carbon dynamics to global warming is complex, and further research is needed to understand all of the processes involved (Mooney *et al.*, 1999).

There are other factors which complicate the outcome of a global warming. The forest ecosystem may acclimate to higher temperatures (Dewar *et al.*, 1999; Mooney *et al.*, 1999; Kirschbaum, 2000a; Atkin *et al.*, 2000; Oechel *et al.*, 2000), and the species distribution may change (Kirschbaum, 2000a).

Results from experiments that simulate a warmer climate show shifts in species composition (Chapin III *et al.*, 1995; Harte & Shaw, 1995; Saleska *et al.*, 1999) and increased biomass production (Arft *et al.*, 1999; Rustad *et al.*, 2001), but also decreased production (Marion *et al.*, 1997). An increase in soil respiration and nitrogen mineralisation has been observed (see the recent review by Rustad *et al.*, 2001). However, in many warming experiments it is difficult to distinguish moisture effects from warming effects (*cf.* Saleska *et al.*, 1999). A decrease in soil moisture due to soil warming has been reported in some soil-warming experiments (*cf.* Peterjohn *et al.*, 1993; Harte & Shaw, 1995; Rustad & Fernandez, 1998; Rustad *et al.*, 2001). A warmer climate will increase evapotranspiration, but in northern mid- and high latitudes, precipitation and water vapour concentration may increase during the present century (Houghton *et al.*, 2001), which makes the prediction of soil moisture still more uncertain.

How to simulate a warmer climate in a mature forest?

One of the ways of increasing understanding of a system is to study one parameter, while the other parameters are kept constant. For this kind of study, laboratory experiments are perfect, and have provided an insight into how plants and soils are affected by different environmental factors. However, for practical reasons, most studies in laboratories are performed on seedlings or young trees. Models can link studies made on different compartments to a larger scale, but a mature tree does not always show the same response as a young tree or a seedling. Laboratory studies must therefore be complemented with field studies. In addition, simulation models have been used to predict the response of an entire ecosystem, but there is still a need for long-term field experiments to verify the models (Luxmoore *et al.*, 1993).

Various techniques have been used in the field to study the effects of a warmer climate. Chambers of various shapes have been used (Shaver *et al.*, 1986; Marion *et al.*, 1997), but they often cover only a small area, usually up to a few square metres. Overhead radiators (Harte *et al.*, 1995) and heating cables (Van Cleve *et al.*, 1990; Peterjohn *et al.*, 1993; Rustad & Fernandez, 1998) can cover larger areas. Some studies have used natural climatic gradients, such as altitudinal (Ineson *et al.*, 1998) or latitudinal (Janssens *et al.*, 2001) transects. Few *in situ* studies have been made to study the effects of global warming on wood production in mature trees (see review by Rustad *et al.*, 2001), since such studies require large areas and a long duration, or large-scale experimental facilities.

Aims

The UN Convention on Climate Change, in Rio de Janeiro in 1992, raised a problem: the consequences of global warming are uncertain and not fully understood. The Convention therefore encourages scientific research into climate change. Moreover, the 186 countries that have ratified the Convention, agreed to make further inventories of sinks and sources of greenhouse gases in natural ecosystems. The present thesis is based on a soil-warming experiment in a Norway spruce stand in Northern Sweden, growing under conditions of both low and high availability of soil nutrients. It contributes to the understanding of causes and effects on elevated soil temperature in a forest ecosystem. The specific aims of this project were to study the effects of soil warming and nutrient availability on (*i*) phenology, (*ii*) stemwood production, (*iii*) nutrient dynamics, and (*iv*) the seasonal dynamics of soil-surface CO_2 flux.

Materials and methods

Site description

The present soil-warming study was performed in a long-term nutrient optimisation experiment at Flakaliden (64°07′N; 19°27′E; alt. 310 m a.s.l.) in Northern Sweden, during the years 1995–2000. The principal aim of the nutrient experiment was to demonstrate the potential yield of Norway spruce (*Picea abies* (L.) Karst.), under given climatic conditions and non-limiting soil water, by optimising the nutritional status of the stands, at the same time as leakage of nutrients to the groundwater was avoided (*cf.* Linder & Flower-Ellis, 1992; Linder, 1995).

Flakaliden is situated in the Boreal Zone (*cf.* Sjörs, 1963) and has an annual mean temperature of 2.3 ºC. The mean annual precipitation is 600 mm, one-third of which falls as snow. The soil was a thin podozolic, sandy, glacial till with an average thickness of *ca.* 120 cm. The thickness of the humus layer varied between 2 and 6 cm, with a mean thickness of 4.3 cm. The ground cover was dominated by feather mosses, but there were also some *Sphagnum* species and reindeer lichens (*Cladina ssp.*). The field layer is dominated by dwarf shrubs such as

Table 1.*Mean of air and soil temperature, total precipitation and total global radiation during the growing seasons 1995–2000. Mean and standard deviation for the period 1990–1999 are shown at the bottom of the table*

Year	Air temperature (°C)	Soil temperature (°C)	Precipitation (mm)	Global radiation (MJ m^{-2})
1995	11.6	8.5	205	1850
1996	12.0	7.7	209	1820
1997	15.4	10.8	243	1810
1998	10.3	7.9	455	2000
1999	11.8	8.8	234	2050
2000	10.3	8.9	473	1860
1990–1999	11.7 ±1.5		269 ±99	1930 ±210

Vaccinium myrtillus and *Vaccinium vitis-idaea*. In the fertilised treatments, the canopy had closed, which resulted in a diminishing groundcover and an increase of grasses such as *Deschampsia flexuosa,* and herbs, such as *Epilobium angustifolium* and *Maianthemum bifolium*.

The growing season usually starts in mid-May and lasts until the last week in September, *i.e.* a duration of *ca.* 134 days. Six years' climate data for the experimental period are given in Table 1, and the seasonal variation of soil temperature from 1995–2000, in Fig. 3.

In general, the first snow fell in October and persisted until May. The maximum snow depth, attained in March (1995–2000), was more than 1 m. Since the canopy had closed on the fertilised treatments, the snow depth at the beginning of the winter period was thinner, and the snow cover was less deep there than on the controls. This caused slightly lower soil temperatures and an increased depth of

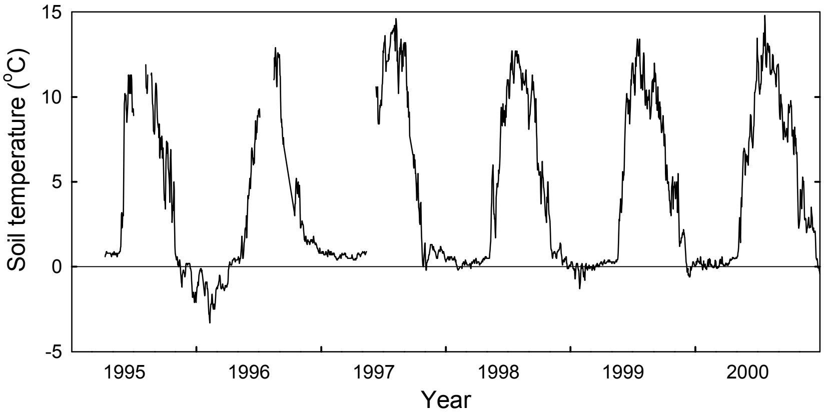


Figure 3. Daily means of soil temperature in the first centimetre of the mineral soil on the irrigated plots at the Flakaliden research site 1995–2000.

frozen soil on the fertilised plots. Weather conditions at the beginning of winter are important for the development of frozen soil. An early, thick snow cover on unfrozen soil, may prevent soil freezing (Odin, 1992). When the snow has reached a certain depth, the effect of air temperature on soil temperature is very small. Odin (1992) found that six years out of ten had hard-frozen soil to a maximum depth of at least 10 cm in an old spruce forest 20 km from Flakaliden. Between 1995–2000, however, only one winter (1995/1996) was cold enough to cause a soil temperature consistently below 0 °C at Flakaliden (Fig. 3), and the depth of frozen soil was only a few centimetres on control plots, but could be 10–20 cm on the fertilised plots.

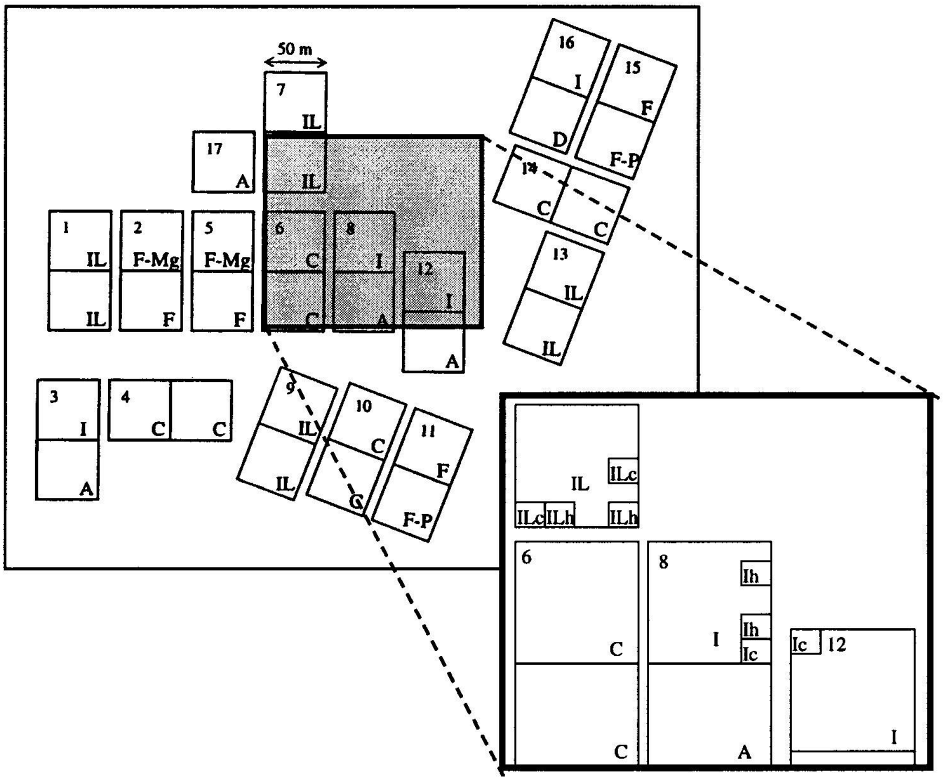


Figure 4. Design of the soil-warming experiment at the Flakaliden research site, where I denotes irrigation, IL irrigation and fertilisation, c unheated and h heated. Other treatments in the main experiments are annual fertilisation with solid fertilisers (F), fertilisation with all essential nutrients except phosphorus (F-P) or magnesium (F-Mg), nitrogen fertilisation supplemented with wood ash (A) and control (C). One plot is used for a water exclusion treatment (D). For information regarding the main experiment, see Bergh *et al.* (1999).

The nutrient treatments

The experiment was established in 1986 in a young Norway spruce stand planted in 1963, after prescribed burning and soil scarification, with four-year-old seedlings of a local provenance. The nutrient treatments, which began in 1987, included untreated control plots, irrigated plots, and two nutrient optimisation treatments. Treatments were replicated four times in a randomised block design, and each replicate consisted of 50 × 50 m plots. In the present study, only irrigated (I) and irrigated-fertilised (IL) plots were included. In the IL treatment, all essential macro- and micronutrients were supplied every second day during the growing season (mid-June to mid-August), and water was supplied to the plots to maintain a soil water potential above −100 kPa. In 1996, the annual increment of stem volume was *ca.* 3 m^3 ha^{-1} in the C and I treatments, and 14 m^3 ha^{-1} in the F and IL treatments (Bergh *et al.*, 1999). Water is not normally limiting for tree growth at Flakaliden. For further details regarding treatments, see Linder (1995).

The soil-warming treatment

The soil-warming experiment was set up in I and IL stands. The reason for using treatments including irrigation was to reduce the risk of drying the soil as an effect of warming. The experiment consisted of two 10 × 10 m heated plots on each nutrient treatment (Ih and ILh; Fig. 4). Every heated plot had a paired control plot (Ic and ILc), chosen for its similarity in basal area. The warming system was tested in autumn 1994 and the treatment started in April 1995.

The soil was warmed by heating cables inserted at intervals of *ca.* 20 cm. The soil warming started in April each year, about five weeks before the soil thawed in the unheated plots. The soil temperature was increased 1 °C per week, until a 5 ºC difference between the warmed and control plots was reached. In late autumn, when the soil temperature on the control plots approached 0 ºC, the soil temperature of the warmed plot was reduced by 1 °C a week. A detailed description of the soil-warming system is provided in paper I and by Bergh & Linder (1999).

The soil-warming system maintained a temperature difference of 5 °C between heated (Ih and ILh) and control plots (Ic and ILc) during the growing season (Fig. 5). The difference was somewhat higher than 5 °C during a few days in spring. On these occasions, the snow had melted on the heated plots, but the control plots were still snow-covered. The temperature peak was a consequence of warming by solar radiation. On a smaller temporal scale, such as a few days, the soil temperature was 5±0.2 ^{o}C (Fig. 6). A large proportion of the soil was affected by the warming. At a mineral soil depth of 50 cm, warming maintained a 4 ^{o}C difference in the middle of summer (see paper I).

The soil on the heated plots was in general drier than that on control plots during the first years of warming. From July 1997 and onwards the heated plots were given extra irrigation relative to their control plots, to maintain the soil water

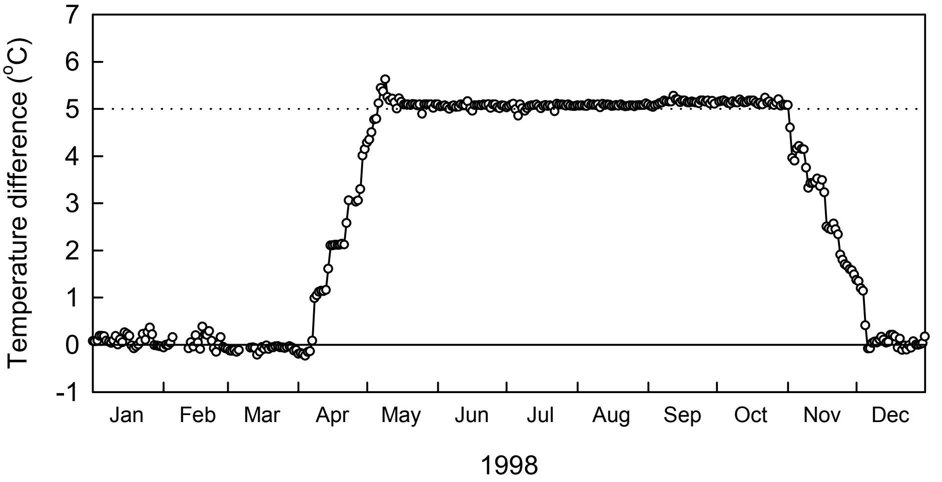


Figure 5. Difference in soil temperature, measured in the first centimetre of the mineral soil, between irrigated heated (Ih) and unheated (Ic) plots in 1998. Each data point is a mean of two plots.

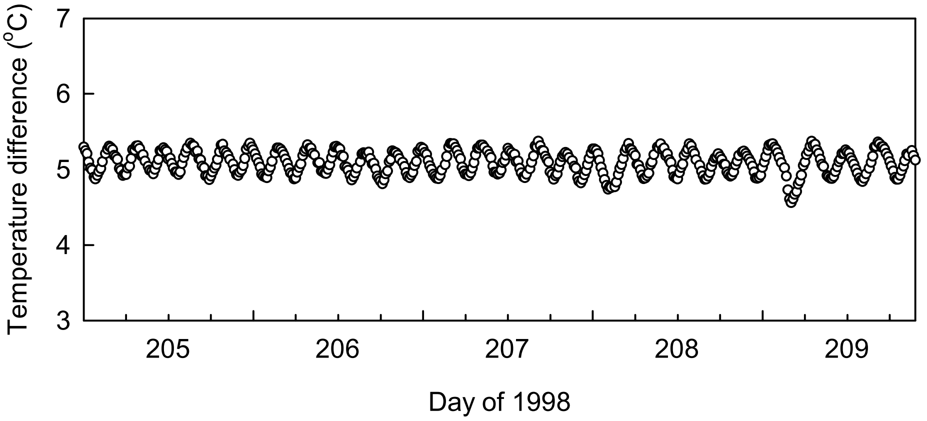


Figure. 6 Difference in soil temperature, measured in the first centimetre of the mineral soil, between one irrigated-fertilised heated (ILh) and unheated (ILc) plot during five days in July 1998.

potential above −100 kPa. Since the start of extra irrigation, the difference in soil moisture has been small or absent (paper I).

The vertical and horizontal variation in temperature and soil moisture, in relation to distance from the heating cable, was studied in early June 2001. This was done before irrigation started; the mean air temperature during the day was 17 °C. Soil temperature decreased with depth in the soil, but was not affected by the horizontal distance to the heating cable in the mineral soil (0–10 cm; Fig. 7). The temperature in the humus layer (0 to +2 cm) decreased by 0.5 °C at a distance of

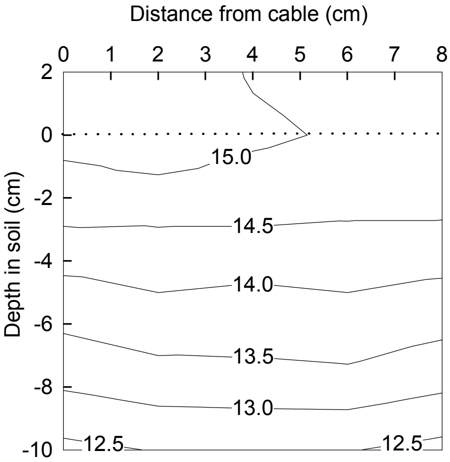


Figure 7. Spatial variation of temperature (°C) on a heated plot in relation to the distance to the heating cable, measured 8 June 2001. Air temperature was *ca.* 17 °C. The dotted line corresponds to the border between the humus layer and mineral soil. The heating cable was situated at 0 cm.

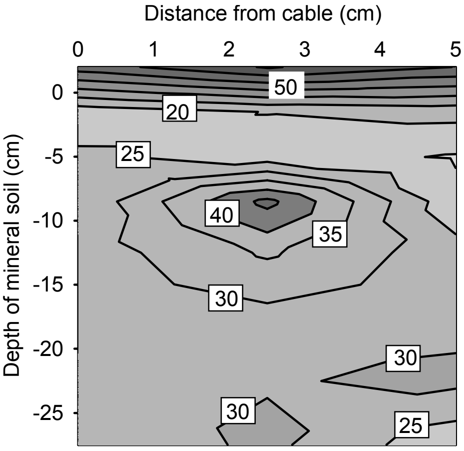


Figure 8. Spatial variation of soil moisture (Mass%) in relation to the distance from the heating cable in early June 2001. The heating cable was situated at 0 cm.

5 cm from the cable. The difference was small and cannot be stated to be a consequence of the heating cable. No vertical and horizontal soil moisture gradients were observed in relation to the distance to heating cable, neither in the mineral soil nor in the humus layer (Fig. 8). This indicates that after installation of the heating cables, the disturbance due to soil warming was small. Temperature and soil moisture profiles were similar on warmed plots compared to their control plots. In addition, there were only small differences in snow and frost depth between warmed and control plots. ILh had less snow than ILc, but it was already lower in the winter before the start of soil warming. Since weather conditions at the beginning of the winter are important for the development of frozen soil (Odin, 1992), there could be differences between individual years.

Measurements

Phenology

The date of budburst for south-facing apical buds was monitored during spring 1997–1999 on Ic, Ih, ILc and ILh plots. All spruces more than 2 m from the edges of the plots were monitored. The buds of the second-order branches (*cf.* Flower-

Ellis, 1996) in whorl 6 were observed in 1997 and the buds of the first-order branches in whorl 3 in 1998–1999.

The increase in basal area development at breast height was studied by band dendrometers, installed on the same spruces used for monitoring budburst. The dendrometers were measured manually once a week from April–May to September in 1997 and onwards. In June 1998, twenty of the manual dendrometers were replaced by automatic band dendrometers (ELPA–93, University of Oulu, Finland). The automatic dendrometers, which were connected to a logger and measured hourly, were installed on four plots (one plot per treatment), in total five bands per plot. The circumference increment was recalculated to weekly basal area increment (ΔB). Relative weekly basal area increment (ΔB_r) was obtained by dividing ΔB by the basal area measured before growth started. For further details, see paper I.

Stem volume production (paper I)

Tree height (H) and diameter at breast height (D) were measured annually in autumn after diameter growth ceased. Stem volume on bark was estimated by a function derived by Andersson (1954). Total stem volume per unit soil surface was calculated for each plot, trees less than 1 m from the edges of the plots being excluded. The annual volume growth in year t (G_t) was then calculated. Differences in standing volume between the plots could be accounted for by normalising G_t to volume growth in 1994 (G_{94}), the year before the warming treatment started.

$$G_{rel} = 100 \cdot \left(\frac{G_t}{G_{94}} - 1 \right) \qquad (1)$$

where G_{rel} is relative volume growth in per cent. Relative growth of basal area (B_{rel}) and relative height growth (H_{rel}) were estimated in the same way.

Estimates of ANPP

ANPP was assumed to be directly related to the increase in biomass of the tree (*cf.* Gower *et al.*, 2001). By the use of a carbon content of 50% for different fractions of the tree, the total uptake of carbon can be estimated. A carbon content of 50% agrees with analyses of C content in biomass in Flakaliden (*cf.* Nurmi, 1993).

Allometric relationships based on on biomass samplings at Flakaliden were used to estimate the dry weight of branches and needles for I and IL treatments (*cf.* Flower-Ellis, 1996). The allometric relation derived for the I treatment was used both for Ic and Ih trees, and that derived for IL treatments was used on ILc and ILh trees.

Since the plots were small, the mean diameter (D) and height (H) of the plots had a variation which was not an effect of the treatment *per se*. To remove this interference, the mean H, D, ΔH and ΔD from each I and IL treatment (in the Flakaliden base experiment) were assumed to correspond to the characteristics of a mean tree of each Ic and ILc in 1994. Height and diameter for Ic, Ih, ILc and ILh plots were then calculated in relation to their different relative growth rates (equation 1) in height and basal area for different years (paper I). Initial values of D and H in 1999 are given in Table 2.

To scale up from carbon content per tree to carbon content per hectare, a modified version of the method described by Madgwick (1981) was used, whereby stem volume was used instead of basal area.

Table 2. *Initial values and annual growth in 1999 for the Norway spruce stand used in the estimate of ANPP. Dry mass of the biomass was estimated from stem diameter and height, using linear relationships obtained from biomass samplings (Flower-Ellis, pers. comm.)*

Parameter	Initial values				Annual growth			
	Ic	Ih	ILc	ILh	Ic	Ih	ILc	ILh
Height (dm)	66	70	89	84	3.0	4.5	3.7	4.9
Diameter (mm)	85	92	134	140	2.2	4.2	4.9	6.7
Volume (m^3 ob ha^{-1})	49	59	144	152	4.0	7.5	13.3	17.5
Biomass (Mg ha^{-1})	50	61	136	143	4.5	8.4	13.9	18.5

Foliar chemistry (paper II)

For carbohydrates, nutrients, and isotope ^{15}N analysis, a few shoots from whorl 7 were sampled from 5 trees in the centre of each plot. After sampling, all shoots were immediately immersed in liquid nitrogen and then stored at −18 °C until they were dried at 85 °C for 48 hours. For details concerning the analysis of carbohydrates, nutrients and ^{15}N, see paper II. The following studies were performed on shoots from Ic, Ih, ILc and ILh plots:

- *Age-class of needles:* To study the effects of age on nutrients and carbohydrates, different age-classes of needle were sampled from five branches per treatment in February 2001. Shoots from the current year (C) and up to six-year-old shoots (C+5) were taken from each branch.
- *Seasonal dynamics*: To observe the seasonal dynamics of nutrients and carbohydrates, shoots were sampled on two and three occasions for C and C+1 shoots respectively.
- *Annual dynamics*: To study the long-term trend of nutrients and carbohydrates, shoots were sampled each year after the middle of September.
- *A simple N budget*: A nitrogen (N) budget for the aboveground fractions of the trees was estimated for each year, 1995–2000. For estimates of the aboveground biomass, allometric relationships were used. For further details see paper II.

Soil-surface CO_2 flux

Soil-surface CO_2 flux (R) was measured on top of the soil, and included CO_2 fluxes from the soil compartments as well as the ground vegetation. Two closed respiration systems, one portable and one automatic, stationary unit, were used to measure the soil-surface CO_2 flux. The portable system consisted of an infrared gas analyser (Li-Cor 6250, Licor Inc. Lincoln, NE, USA) connected to a dark chamber (LI–6200–09, Li-Cor Inc., Lincoln, NE, USA). The automatic and stationary system consisted of an infra-red gas analyser (LICOR 6252, Licor Inc. Lincoln, NE, USA) and eight circular chambers made from transparent acrylic plastic, with a lid on the top. Each chamber was measured every 50 minutes. To minimise chamber effects on the microclimate, the lids were closed only during measurements (3 min). The automatic system is further described in detail in paper III.

Spatial variation

Spatial variation in R was studied on a small scale in the I treatment in autumn 1997. The measurements were performed with the portable system. Soil-surface CO_2 fluxes were measured every 10 cm over a total area of 60 × 60 cm.

Effects of soil warming and fertilisation

To study differences between the treatments (Ic, Ih, ILc and ILh), the portable system was used to measure soil-surface CO_2 flux (*paper V*). On each plot, 10 collars were installed in June 1998; five collars at locations with only moss present and five at locations with dwarf shrubs or herbs. The first measurement started two weeks after installation of the collars. Measurements were made monthly during the growing seasons in 1998–1999. Soil temperature and soil moisture were measured adjacent to the measurement point. Respiration was also measured in two locations on top of the snow in January 1999 and 2000.

Seasonal dynamics

Soil-surface CO_2 flux was measured continuously in ILc and ILh by the automatic respiration system. Four chambers were installed in July 1998 on one of the ILh plots and four on an ILc plot. Each chamber was placed in representative locations in terms of the ground-layer vegetation. The chambers were moved to new locations in May 2000. Adjacent to each chamber, soil temperature was measured at 10-cm depth from the soil surface.

The automatic respiration system allowed continuous measurements of soil-surface CO_2 flux, and was used for estimating total soil-surface CO_2 flux (R), net soil-surface CO_2 flux (F) and total photosynthesis of the forest floor (P).

$$F = R - P \qquad (2)$$

Since the chambers were transparent, only measurements of *F* were performed, while *R* and *P* had to be estimated. During the dark hours, however, *F* equals *R,* because no photosynthesis occurs in darkness. Only measurements made between 22:00 and 02:00 (photosynthetic radiation <30 µmol m^{-2} s^{-1}) were used to fit functions for estimating *R* during the remainder of the day. The temperature effect on *R* can be explained by a simple exponential function, $R = R_0e^{kT}$, where R_0 is the estimated respiration at 0 °C, *T* is the soil temperature in °C, and *k* is a fitted constant. The relative increase in *R* when temperature increases by 10 °C during a limited time period, is called Q_{10}, and is related to *k* by the following function; $Q_{10}=e^{10k}$.

In *paper V*, different ways of modelling *R* were tested. All models used the simple exponential function as a base. The parameterisation of model runs A and B was done in SAS statistical software. Details concerning the model runs are given in paper V, but a brief description is given here:

- Model run A: *R* was assumed to be dependent on temperature only within each treatment, *i.e.* one exponential temperature relationship was fitted for a whole year of data for each treatment.
- Model run B: Temperature sensitivity and basal respiration were allowed to vary from one month to another within each treatment, *i.e.* one exponential temperature relationship was fitted per month and per treatment.
- Model run C: The reliability of using temperature responses derived in an ambient temperature, to estimate *R* in an elevated temperature, was tested in model run C. In this run, the functions derived on the ILc treatment in model run B were used on the temperature regime in the ILh treatment.
- Model run D: The effect of using a fixed R_0 and Q_{10} was tested. A Q_{10} of 2.4 was taken from the literature (Raich & Schlesinger, 1992), and a value of R_0 derived for the ILc plot in run A was used to parameterise the exponential function.

Annual soil-surface CO_2 flux

Measurements from the automatic system were used to estimate annual *F* (F_A), *R* (R_A) and *P* (P_A) for 1999. Since measurements of *F* were made only during the snowfree period, the following simplifications were made:

- *R* equals 0.35 µmol CO_2 m^{-2} s^{-1} when the temperature of the soil is below 0.5 °C (*paper V*). The value is a mean of the CO_2 flux measurements made on top of the snow in 1999 and 2000.
- In spring and autumn, when no measurements were made but when the soil temperature exceeded 0.5 °C, estimates of *R* from model B were used. The period during which the soil temperature rose above 0.5 °C before the measurements started, was assumed to have the same temperature sensitivity as in

June. In autumn, from the end of the measurements until the soil temperature declined below 0.5 °C, the temperature sensitivity for October was used.

- *P* was assumed to equal 0 before and after the measurement period, since the snow disappeared only a few days before the measurement period started and photosynthesis was very small or absent at the end of the measurement period.
- There was a large variation in *P* between different chambers as a consequence of the large variation in the biomass of forest floor. Therefore, the amount of *P* was assumed to be the same on both heated and unheated plots.

F and *R* were estimated from the actual measurements. The nocturnal measurements of *R* were assumed to be valid within 24 hours. *P* was then calculated as the difference between *F* and *R*. On average, data were missing during less than 5% of the time in 1999. If data were missing for a short period (*e.g.* 2 hours), a mean of one hour before and one hour after was used. For missing data during longer periods, an interpolation based on linear regression between chambers was used. However, on two occasions (26–28 June and 17–19 July), data were missing from all chambers at the same time. The fluxes for these periods were assumed to be a mean of the fluxes on the day before and after the interruption.

Since there was no difference in temperature response for *R* between Ic compared to ILc, and Ih compared to ILh (see Fig. 15), the model derived for ILc and ILh was used on Ic and Ih, respectively. Photosynthesis (*P*) could not be assumed to be the same, however, since the ground- and field-layer vegetation was more abundant on the Ic and Ih plots. Therefore, *P* was assumed to equal *P* at those locations on the IL plot with rich vegetation.

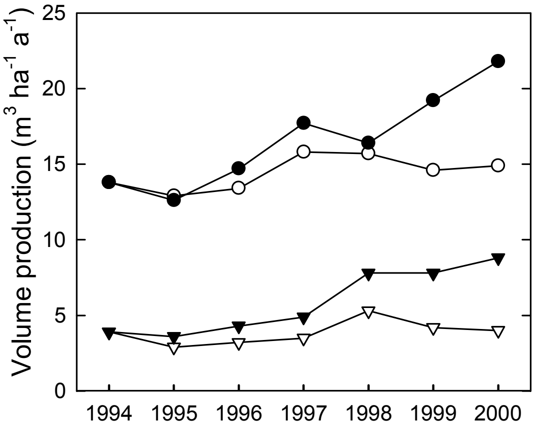
Results and Discussion

Effects on tree growth (paper I)

Soil warming increased stemwood production. The annual stemwood production was significantly higher on Ih plots compared to Ic plots in all years after the first year with warming (Fig. 9). ILh tended to have a higher stemwood growth compared to ILc in all years, except the first year of warming (Fig. 9). The difference was significant only in 1999 and 2000. Growth in basal area relative growth to growth in 1994 (B_{rel}) showed similar treatment effects, but height growth (H_{rel}) had no clear trend (paper I). The height increments were, however, affected by snow damage, especially on IL plots with high leaf-area indicies.

The annual growth of stemwood and basal area was closely related. Study of the seasonal development of basal area showed that the heated plot had a higher basal area growth than the control plots. Furthermore, it showed that Ih had con-

Figure 9. The annual increment of stem volume in Norway spruce stands. The treatments were irrigation unheated (open triangles), irrigation heated (filled triangles), irrigated-fertilised unheated (open circles) and irrigated-fertilised heated (filled circles). The nutrient experiment started in 1987 and the soil warming experiment started in 1995.



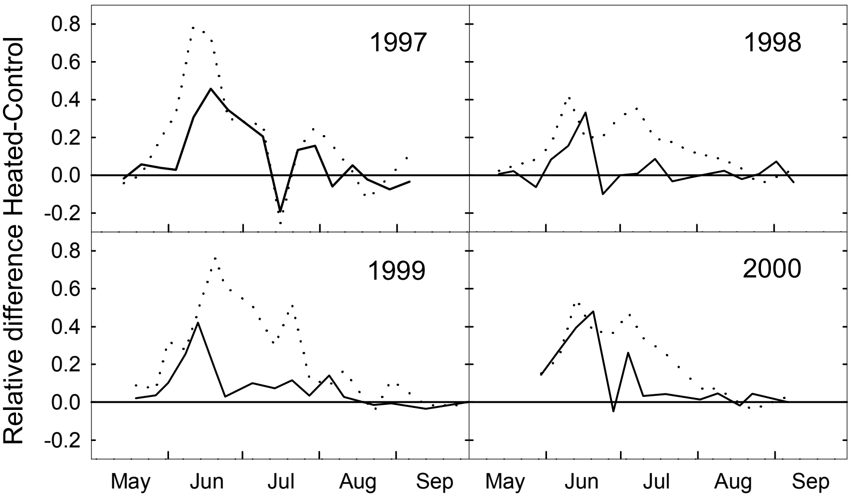


Fig 10. Difference in relative increment of basal area between heated and unheated plots in irrigated (dotted line) and irrigated-fertilised (solid line) treatment during the growing seasons of 1997-2000. Relative increment of basal area is expressed in per cent, as weekly basal area growth divided by the basal area before growth started in spring.

tinuously higher basal area growth than Ic during the whole season, but that ILh grew more than ILc only in June (Fig. 10). The difference between Ih and Ic was, however, greatest in June.

An increase in growth may be explained by two main factors: the first is the prolonged period of unfrozen soil, hence increased availability of water for plants; the second is increased nutrient mineralisation in the soil, caused by soil warming (*cf.* Van Cleve *et al.*, 1990; Lükewill & Wright, 1997), leading to higher nutrient uptake by trees. Low soil temperature has a negative effect on photosynthesis (*cf.* DeLucia, 1986; DeLucia & Smith, 1987; Wan *et al.*, 1999), photosynthetic recovery during spring (*cf.* Bergh & Linder, 1999) and root production (Camm & Harper, 1991). Frozen or cold soils during spring also inhibit water uptake (*cf.* Bergh & Linder, 1999; Zweifel, 1999; Mellander, 2001), which prevents photosynthesis. The effect of warming should therefore be most pronounced at the beginning and end of the season. The increase in growth was largest at the beginning of the season when the soil was cold, but aboveground growth ceased at the same time in the beginning of August, on both heated and unheated plots. The increase in growth during the whole season on the Ih plots is a response to increased nutrient mineralisation. Although aboveground biomass production began and ended at the same time, the production of roots continued during a longer period on the heated than on the unheated plots (Majdi, pers. comm.).

Assuming that the IL treatment had an optimum nutrient status and was not limited by nutrient availability (Linder, 1995), production would be limited by low soil temperature. When soil temperature increased, stemwood production increased by 20−30%, which may be interpreted as a ‘warming effect’ or the response to a longer period of unfrozen or warmer soil. The increase of about 80−100% in the Ih treatment is, however, a result of both warming and increased mineralisation. This indicates that the effect of nutrient mineralisation, as a result of soil warming, is more important for growth on low fertility sites, than is the direct temperature effect of a prolonged growing season. However, we cannot be sure that the IL treatment was not limited by nutrients. Since there was no N leakage from the IL plots, and fertilisers were not given in excess, trees on the IL treatment could still increase their growth in response to increased nutrient availability. This would indicate that the mineralisation effect can be even more important. However, the forest soil on this site was seldom very cold and the frost depth was shallow, which led to an increase in soil temperature as soon as the snow cover disappeared in spring. A prolonged growing season may, therefore, be more important at sites with hard-frozen, fertile soils.

Effects on nutrient dynamics (paper II)

The production of stem biomass increased on the warmed plots. One hypothesis was that nitrogen mineralisation had increased on the warmed plots. Is this hypothesis in accordance with the nutrient studies?

There was a significant increase of N in one-year-old needles in the first year of soil warming on the Ih plots, compared to the Ic plots (Fig. 11). Van Cleve *et al.* (1990) also found an increase in [N] in the first year of soil warming. One possible explanation for the increase of needle [N] could be increased N mineralisation. However, this increase in N availability resulted in increased biomass production, which was first significant in the second year of soil warming (*cf.* Fig.

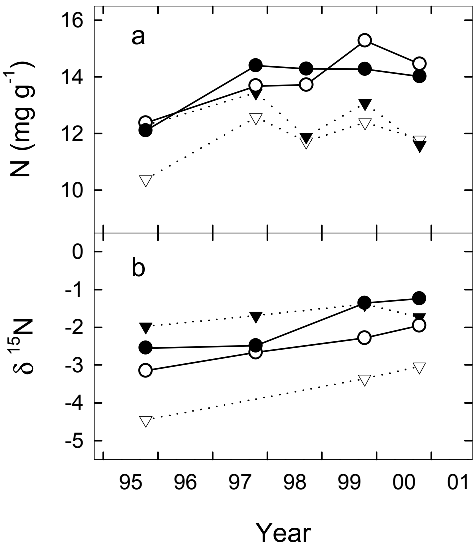


Figure 11. Nitrogen content (N) and natural abundance of isotope ^{15}N (δ ^{15}N) in one-year-old Norway spruce needles. Symbols: irrigated plots (triangles) irrigated-fertilised plots (circles). Open symbols unheated control plots, filled symbols heated plots.

9); this is to be expected in boreal and temperate conifers (*cf.* Linder, 1995). The increase in biomass production may have diluted the [N] in the needles.

There has also been a shift in the abundance of the δ^{15}N in the needles (Fig. 11). The plants should have three major sources of N in this experiment: (*i*) soil N derived only at ambient soil temperature, which is valid for all treatments, (*ii*) increased availability of soil-N, caused by increased temperature, which is relevant for the warmed plots, and (*iii*) soil N from the fertiliser for ILc and ILh only. Soil warming increased the abundance of δ^{15}N significantly. This suggests an increased availability of N from deeper soil layers, which had a significantly higher δ^{15}N than the upper soil layers (paper II, *cf.* Högberg *et al.*, 1996, 1999; Högberg, 1997). There was little or no increase caused by soil warming in the fertilised treatment.

There was a tendency for decreasing concentrations of phosphorus (P), potassium (K) and boron (B) in current needles on the Ih plots compared to the Ic plots (paper II). This may be a result of increased biomass production on the warmed plot. There is, however, a considerable between-year variation in foliar nutrients as an effect of variations in weather conditions (*cf.* Linder, 1995). Lower concentrations of organic-N and P in the soil solution were also observed, which may be a consequence of the increased nutrient uptake of the plants (*cf.* Näsholm *et al.*, 1998). Otherwise, there were no effects, or small effects only, on soil chemistry in the soil solution, caused by soil warming (paper II).

The simple N budget for the aboveground part of the tree showed that the amount of N in aboveground tree biomass had increased on the warmed plots (Fig. 12). The trees on the Ic plot had taken up *ca.* 100 kg ha^{-1}, *i.e.* N mineralisation had been at least 16 kg N per ha^{-1} a^{-1}. During the first six years of soil warming, the trees on the warmed plots took up 50 kg ha^{-1} more than those on the control plots. The ILc plots fixed 475 kg N ha^{-1} in the aboveground parts of the trees during these six years of warming, which is almost the same amount as the N added by fertilisation (450 kg ha^{-1}).

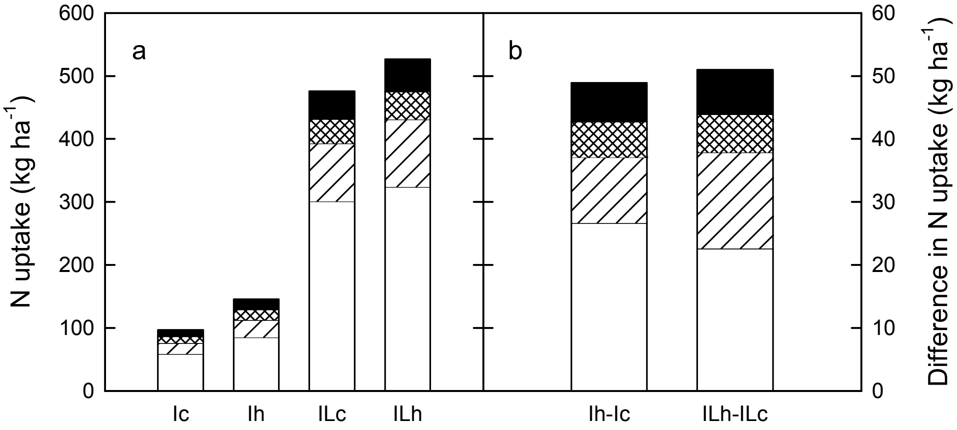


Figure 12. Nitrogen uptake in the aboveground biomass of 35-year-old Norway spruce trees from irrigated unheated (Ic), irrigated heated (Ih), irrigated-fertilised unheated (ILc) and irrigated-fertilised heated (ILh) plots during the first six years of soil warming (1995–2000). Figure (*a)* shows total N uptake for the different treatments and (*b)* shows the difference in N uptake between heated and unheated plots. The fractions were needles (open), branches (hatched), bark (cross-hatched) and stemwood (filled).

Effects on soil-surface CO_2 flux

Spatial variation

The spatial variation in soil-surface CO_2 flux, studied in 1997 in the irrigated treatment, was high within such a small area (0.6 × 0.6 m; Fig. 13). A larger size of chamber may decrease variation between measurements, but the variation would still be high. Soil respiration is dependent on temperature (Lloyd & Taylor, 1994), soil moisture (Seyferth, 1998), organic matter content and substrate quality (*cf.* Rustad *et al.*, 2000 and references therein). Between different locations in the field, it also depends on the amount of roots, ground vegetation, soil structure, depth of soil and soil fauna (*cf.* Stoyan *et al.*, 2000).

It is not always clear why one location has a high or a low flux. For instance, when spatial variation at the small scale was investigated, the highest peak proved to be an anthill. The forest soil is heterogeneous, which emphasises the importance of soil-warming studies which cover areas larger than a few square metres.

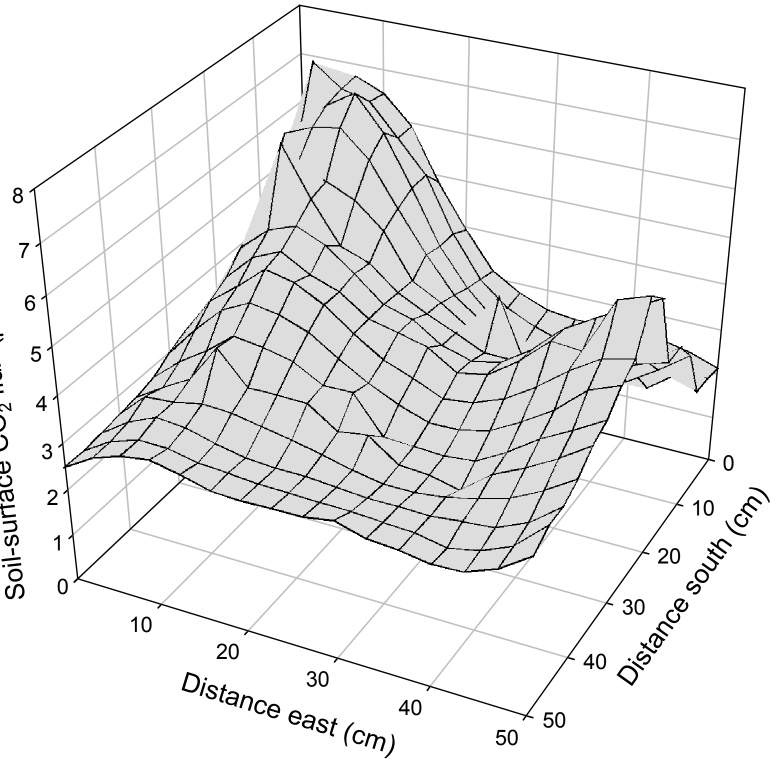


Figure 13. Smoothed spatial distribution of soil-surface CO$_2$ flux in an irrigated treatment on a 0.1 × 0.1 m grid. Each node corresponds to one measurement.

Effects of soil warming (paper IV and V)

Soil warming increased soil-surface CO$_2$ flux by 10–20% during the growing season, but the difference was significant only for the measurement in May 1999 (Fig. 14). For a specific soil temperature, however, soil-surface CO$_2$ flux was always lower on the heated plots (Fig. 15). This reduction in *R* was confirmed when the soil heating was switched off for a week in September 1999; *R* on the heated plot decreased below *R* on the unheated plot (paper IV).

There was no effect of fertilisation on *R* in 1999 (Fig. 15). This was surprising, since it might be assumed that there would be more tree roots on the fertilised plot. This might be explained by the richer field- and bottom-layer on the I plots; the vegetation on the IL plot occurred in patches. However, fertilisation has caused a decrease in *R* in other forests (*cf.* Haynes & Gower, 1995; McDowell *et al.*, 2001). This might be explained by the decrease in total belowground carbon allocation on the fertilised plots, by a decrease in heterotrophic respiration or both.

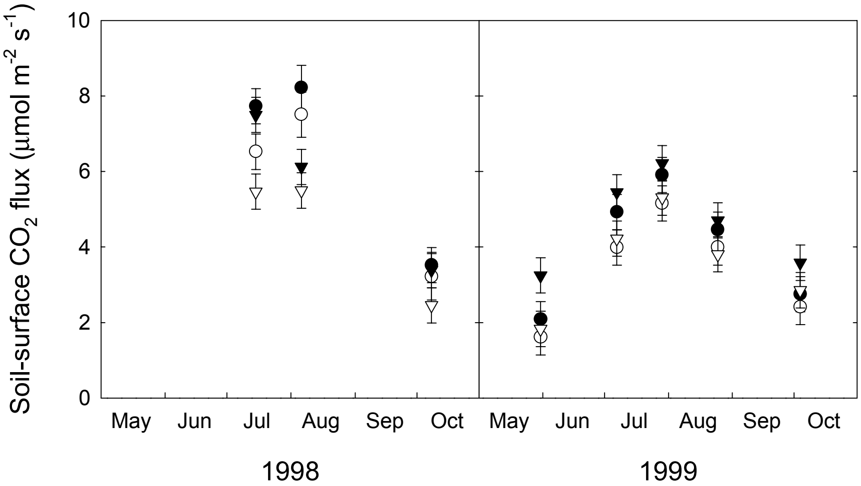


Figure 14. Soil-surface CO_2 flux, during the growing seasons of 1998 and 1999, measured with a portable respiration system. Symbols: irrigated plots (triangles), irrigated-fertilised plots (circles). Open symbols unheated plots, filled symbols heated plots. The error bars correspond to 1 standard error, (*n*=2). For further explantions, see text.

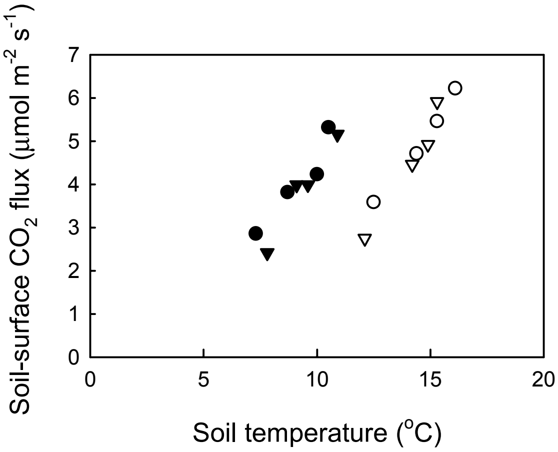


Figure 15. Soil-surface CO_2 flux, measured once a month from July to October. Symbols: irrigated plots (triangles) irrigated-fertilised plots (circles). Open symbols unheated plots, filled symbols heated plots.

An acclimation of soil-surface CO_2 flux has also been seen in a recent soil-warming study on a prairie in the Great Plains in the USA (Luo *et al.*, 2001). In that case study, only temperature sensitivity decreased, whereas in the present experiment, both temperature sensitivity and basal respiration decreased.

A decrease in *R*, or no effect at all, has been explained in other soil-warming studies by a decrease in soil moisture (*cf.* Saleska *et al.*, 1999). However, soil moisture did not significantly affect *R* in the present study. There may also have been a change in the respiring biomass in the soil. A warmer soil is assumed to increase root growth and root turnover (Pregitzer *et al.*, 2000). This would have led to an increased respiring biomass of roots. However, fine-root production during the growing season was similar on heated and control plots, but the heated plots had production during a longer period (Majdi, pers. comm.). In addition, no decrease has been observed in the microbial biomass in the heated plots (Grayston, pers. comm.).

There are several other possible explanations for the lower respiration at a specific temperature on the warmed plots: (*i*) There could have been a change in substrate quality of the soil organic matter during the previous years of warming (*cf.* Coûteaux *et al.*, 1995; Johansson *et al.*, 1995; Dalias *et al.*, 2001), which could lead to a decrease in decomposition rates, (*ii*) a shift in the function and composition of the microbial communities (Zogg *et al.*, 1997), or (*iii*) one or more ecosystem components may have acclimated to higher temperature (*e.g.* Dewar *et al.*, 1999; Mooney *et al.*, 1999; Kirschbaum, 2000a; Atkin *et al.*, 2000; Oechel *et al.*, 2000).

Soil-surface CO_2 flux is temperature-dependent across space and time, but Raich and Schlesinger (1992) and Janssens *et al.* (2001) found that net primary production (NPP), not temperature, best explained the variation in soil-surface CO_2 flux. Indications that R is correlated with the current photosynthesis of the aboveground vegetation, and that it is less dependent on soil temperature *per se,* has also been suggested in other studies on different ecosystems (*cf.* Fitter *et al.*, 1998; Levy *et al.*, 1999; Pregitzer *et al.*, 2000; Högberg *et al.*, 2001).

Seasonal dynamics (paper IV–V)

The model in which 'month' was included as a factor gave the best agreement with measured R. The factor 'month' covaried significantly with the factor 'temperature' and treatment, showing that basal respiration (R_0) and the slope (k) varied between months (see Fig. 16, *cf.* Epron *et al.*, 1999; Rayment & Jarvis, 2000; Widén, 200X). Model run A, which used one R-soil temperature relationship for a whole year, mimicked the seasonal variation, but gave underestimates in July–August and overestimates in October.

One explaination for the seasonal variation might be that k is different in different temperature ranges (Kirschbaum, 1995; Seyferth, 1998; Atkin *et al.*, 2000), and that different processes incorporated in the soil-surface CO_2 flux have different temperature sensitivities (Boone *et al.*, 1998). In addition, different ages of carbon pool have different temperature sensitivities (*cf.* Liski *et al.*, 1999; Giardina & Ryan, 2000). There is also a natural seasonal dynamic in the amount, production and turnover of ground vegetation, roots, mycorrhizae and microbes, implying that different compartments will give different weight to k and R_0 throughout the season. In addition, if R is correlated with aboveground photosynthesis (see above), and light varies seasonally, this will also affect R seasonally.

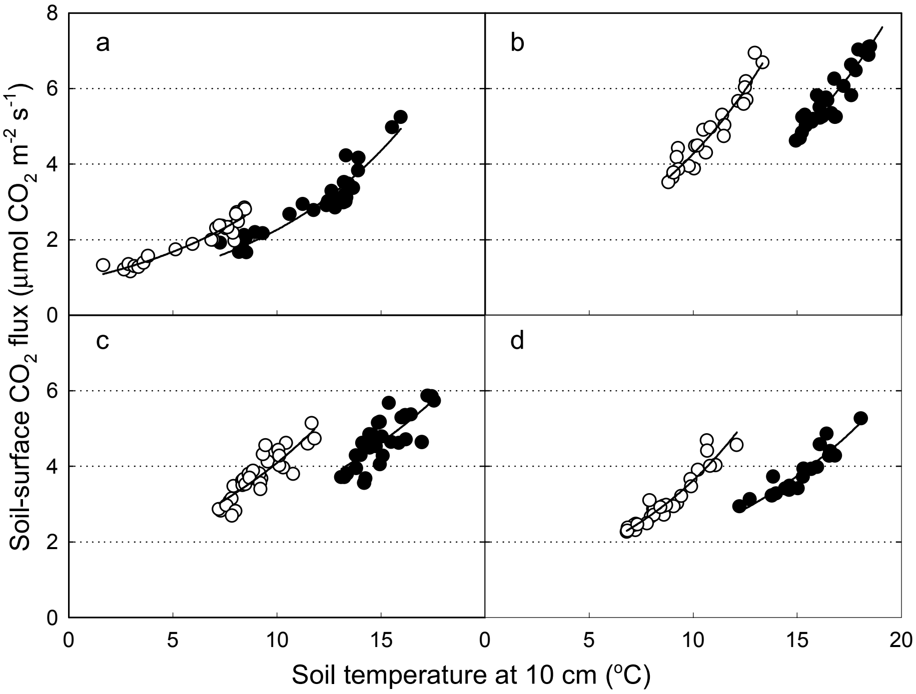


Figure 16. The temporal variation of the relationship between soil-surface CO_2 flux and soil temperature, in a boreal Norway spruce forest, during the snow-free season 1999. The soil-surface CO_2 flux in June (a), July (b), August (c), and September (d), showed significant differences in temperature response in terms of base respiration (R_0) and Q_{10} in both unheated (blue symbols) and heated plots (red symbols). Each data point is a nocturnal (22:00–02:00h) average of three (unheated) and four (heated) respiration chambers.

The use of functions derived at ambient soil temperature on the soil-warming treatment (Model run C) overestimated actual R by 50–80% (Fig. 17). The use of a fixed Q_{10} and R_0 resulted instead in large underestimates (Fig. 17). This highlights the risk of applying an empirical function derived under a certain set of conditions, to new conditions.

Annual soil-surface CO_2 flux (paper IV)

The annual soil-surface CO_2 flux (R_A) was in the same range as reported in other boreal and northern temperate forests (Law *et al.*, 1999; Morén & Lindroth, 2000; Rayment & Jarvis, 2000; Wang *et al.*, 200X; Widén, 200X). Soil warming increased annual soil-surface CO_2 flux (R_A) by 12–30%—depending on year—on ILh compared to ILc (Table 3). The main differerence in R between heated and unheated plots, was in early spring, when the soil was still frozen on the control plots, and in autumn, when the soil on heated plots stayed warmer for a further

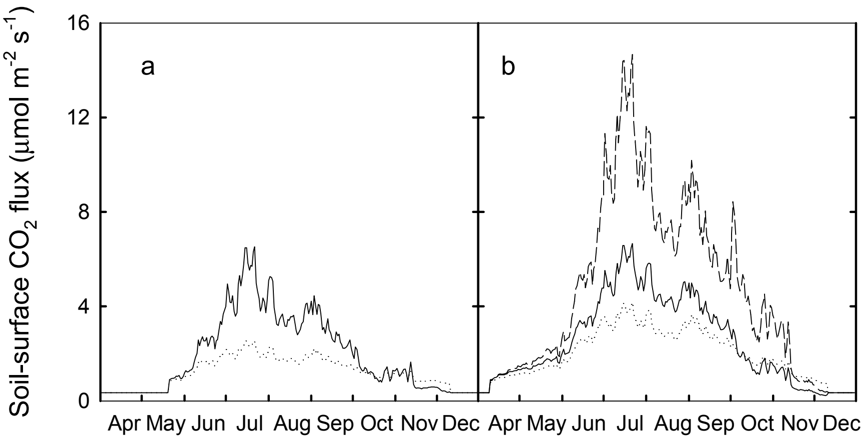


Figure 17. Estimated soil-surface CO$_2$ fluxes, during 1999, in unheated (a) and heated (b) irrigated-fertilised plots, using different models. Solid lines: a monthly adjusted model (Model B); dotted lines: using fixed values of basal respiration (R_0) and Q_{10} throughout the year; broken line in sub-figure (b): Model B fitted to data from the non-heated plot (a) and used in combination with the soil temperatures from the heated plot. For further explantions, see text.

Table 3. *Estimated gross soil-surface CO$_2$ fluxes during 1998, 1999, and 2000, on unheated and heated irrigated-fertilised plots. The estimates were based on (A): A model without monthly adjustments; (B): A model with monthly adjustments; (C): constants derived from the unheated plot and used in combination with soil temperatures from the heated plot, and (D): fixed values of basal respiration (R_0) and Q_{10}. used throughout the year. During winter, when soil temperature was 0.5 °C or lower, a flux of 0.35 µmol CO$_2$ m^{-2} s^{-1} was used. Values for 1998 are shown in italics, to indicate that they are based on a limited number of measurements. For further explanations, see text*

	Irrigated-fertilised (unheated)				Irrigated-fertilised (heated)					
	(kg C m^{-2} a^{-1})			(Δ%)	(kg C m^{-2} a^{-1})				(Δ%)	
Year	A	B	D	D/B	A	B	C	D	C/B	D/B
1998	*0.55*	*0.57*	*0.33*	*−42*	*0.65*	*0.64*	*1.19*	*0.54*	*+86*	*−16*
1999	0.56	0.57	0.35	−39	0.75	0.74	1.31	0.59	+77	−20
2000	0.61	0.61	0.43	−30	0.72	0.73	1.10	0.65	+51	−11

month. However, the net annual soil-surface CO$_2$ flux (F_A) is lower, due to photosynthesis by the field- and bottom-layer vegetation. Where the vegetation was abundant, more carbon was taken up than was released, for some hours during clear days (Fig. 18). On the ILc and ILh plots, refixation of carbon constituted 5–10% of R_A.

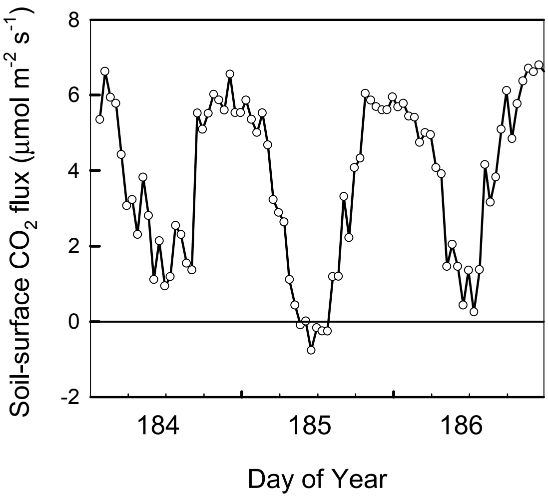


Figure 18. Diurnal variation of soil-surface CO_2 flux for a site with rich ground vegetation on the irrigated-fertilised plot during three days at the end of July 1999. During day 185, there was carbon uptake by the plants for several hours.

Sink or source of carbon?

Aboveground net primary production (ANPP) and net soil-surface CO_2 flux ($F = R - P$) are large components in the C balance of forests (*cf.* Mahli *et al.*, 1999). Therefore, it is crucial to know how this balance will be affected when soil temperature increases.

The first effect of soil warming was an increase in ANPP (Table 4). On the Ic and ILc plots, ANPP increased by 85 and 40%, in comparison with the unheated control plots (Ic & ILc). In 1999, the trees on the Ic and ILc plot had an ANPP of *ca.* 210 and 720 g C m^{-2}, respectively. The estimates of ANPP for Ic, Ih and ILc plots are in the same range, but in the ILh plots higher than has been found in other boreal forests (*cf.* Gower *et al.*, 2001).

Soil warming increased the net soil-surface CO_2 flux (F). In 1999, F was 530 g C m^{-2} on the unheated plots, and the heated plots (Ih & ILh) released 110 and 170 g C m^{-2}, respectively, more than the unheated plots. As was mentioned earlier, the rates of R are within the range reported from other boreal forests. The largest uncertainty relates to P, which would require more detailed study for more accurate estimation. However, even large errors in the estimate of P would **not** change the general conclusions regarding the effect of soil warming in the present study.

In summary, the estimates of ANPP and F in 1999 clearly show that the increase in ANPP is higher than the increase in F on the warmed plots (Table 4). This suggests that increased soil temperatures will increase the carbon sink strength of boreal forest ecosystems.

Table 4. *Aboveground net primary production (ANPP), total soil-surface CO_2 flux (R), photosynthesis of ground vegetation (P) and net soil-surface CO_2 flux (F) for different C fluxes in g C m^{-2} in irrigated (I) and irrigated-fertilised (IL) control (c) and heated (h) in 1999*

Carbon flux (g C m^{-2})	Ic	Ih	ILc	ILh
ANPP	210	390	720	1000
R	650	760	570	740
P	120	120	40	40
F=R−P	530	640	530	700
ANPP−F	−320	−250	190	300

However, ANPP was much lower than *F* on the irrigated plots, showing that carbon allocation to belowground compartments must be included for it to be possible to determine whether an ecosystem is a source or sink for carbon (*cf.* McDowell *et al.*, 2001). The carbon partitioned belowground is used for root production and root respiration, in addition to the growth and respiration of mycorrhizae, and for root exudates which provide carbon for microorganisms in the rhizosphere. Trees growing under poor nutrient conditions usually allocate a higher proportion of total fixed carbon to the roots (*cf.* Linder & Axelsson, 1982; Ericsson, 1995).

Stockfors (1997) estimated that, in 1993, the ratio between carbon allocated to roots and carbon fixed in the aboveground tree biomass at Flakaliden, was 1.4 in the C treatment, but only 0.5 for the IL trees. If this ratio is assumed to have been the same in 1999, carbon allocation to roots would be *ca.* 370 and 340 g C m^{-2} a^{-1} on Ic and ILc plots, respectively. The estimates of the amount of carbon allocated to roots on the Ic and ILc plots are similar to the total belowground carbon allocation estimated by Haynes & Gower (1995), for an unfertilised and fertilised Red pine plantation in northern Wisconsin. Furthermore, an increase in nitrogen availability on the warmed plots may have changed the carbon allocation pattern.

A complete carbon balance could not be calculated in the present study, because some C fluxes remain unknown. For instance, there could have been a change in the soil carbon pool, as an effect of the leakage of dissolved organic carbon (DOC) and changed litter accumulation. It is, however, unlikely that leakage of DOC would affect the balance, since the amount of DOC in the soil solution was very small (paper II; *cf.* Currie & Aber, 1996). Finally, the carbon pool in the soil may have changed. Despite the fact that there were no significant differences between ILc and ILh in the total soil carbon pool (data not shown), it is unlikely that changes can be detected over a period of only a few years. The magnitude of the soil carbon pool, and its spatial variation, would require long-term monitoring to establish a change in the soil-carbon stock. Measurement of carbon fluxes can, however, give an indication of the carbon balance of some of the compartments (*e.g.* trees, understorey, roots, soil fauna) which contribute to the total net ecosystem exchange (NEE).

Comparison between soil warming and soil + air warming

The experiment reported here warmed only the soil and not the air, whereas an increase in air temperature will result in a simultaneous increase in soil temperature (*cf.* Gupta *et al.*, 1982). Air temperature directly effects soil temperature, but since soil warms slowly, there is a delay in the response. This result is a hysteresis effect in the relation between air temperature and soil temperature throughout the year (Fig. 19). The insulating effect of snow in winter means that soil temperature is largely unresponsive to changes in air temperature. But after snowmelt in spring, soil temperature begins to rise. As long as the air is warmer than the soil, the soil temperature will increase. After the peak in air temperature in July, air temperature begins to decrease. But soil temperature also decreases more slowly, which results in warmer soil than air in autumn.

In the present study, the unusually warm growing season in 1997, when air temperature was 3 °C higher than the five-year mean, resulted in a 2 °C soil temperature increase. Bonan and Van Cleve (1992) simulated soil temperature at 10 cm depth for different stands, when air temperature was increased by 5 °C. They found that soil temperature increased by 2.6, 3.1 and 4.3 °C for a Black spruce, White spruce and a birch stand, respectively, for the period 20 May–10 September. This implies that the soil temperature increase of 5 °C in the present soil-

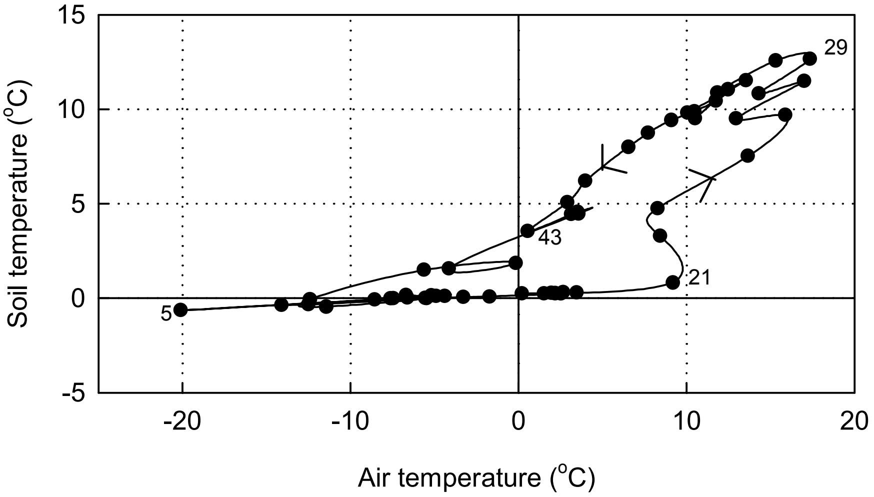


Figure 19. Relationship between air and soil temperature in 1999. Each point corresponds to the mean temperature for one week. The numbers adjacent to a point denote the week number of the year.

warming study would correspond to an increase in air temperature which is probably greater than 5 °C. This is higher than the predictions made by IPCC (Houghton *et al.*, 2001), and the local climate scenarios for the area (SWECLIM, 1998).

Would the effects of soil warming be different if the air had also been warmed? First, an earlier budbreak and onset of diameter growth may be expected, since those processes are controlled by the sum of air temperature (Salisbury & Ross, 1992). This was not observed in the soil-warming study, where budbreak started during the first week of June in all treatments, and after about five days, almost all shoots had flushed. Basal-area growth began at the end of May or beginning of June, and ceased in mid-August in all years. The start and end of basal area growth were not affected by soil warming, but the trees on the IL plots started their growth some days later than the trees on the I plots. Individual trees varied in budbreak and in the start of diameter growth, but this can be explained neither by increased soil temperature, nor by fertilisation.

If the air were warmed, it could also be assumed that the recovery of photosynthesis from winter damage would occur even faster, since it is dependent on air temperature (*e.g.* Lundmark *et al.*, 1988). This would further enhance photosynthesis, hence biomass production during spring.

The soil-warming experiment could not take into account effects on respiration and photosynthesis caused by elevated air temperature. If respiration increases more than photosynthesis, biomass production will decrease. However, as mentioned earlier, a model simulation with a 4 °C increase in air temperature increased NPP (the difference between gross photosynthetic productivity and respiration) by 18% at Flakaliden (Bergh, 1997). That simulation included the effect of faster recovery of winter damage, and increased respiration caused by increased air temperature. However, it did not take into account an increased nutrient mineralisation rate, caused by increased soil temperature, nor an acclimatisation of respiration to warmer temperature (*cf.* Gifford, 1994; Kirschbaum, 2000a; Oechel *et al.*, 2000;). Therefore, it is likely that NPP will be even higher in a warmer climate.

The results from the soil-warming experiment would be valid for the soil compartment, but since it is possible that NPP may be different, there may be secondary effects in the soil.

Are the soil-warming results valid for a general climate-change scenario?

An increase in soil temperature by 5 °C is probably higher than would be expected if the predictions of air-temperature increase made by IPCC (Houghton *et al.*, 2001) or SWECLIM (1998) are correct. If so, the increase in soil-surface CO_2 flux will be smaller than our predictions. But since the difference between the heated and unheated plots in soil-surface CO_2 flux during summer was already small, the treatment effects were mainly caused by an earlier thaw and delayed freezing of the soil. Therefore, it is expected that the main findings of the present experiment will still be valid for the IPCC and SWECLIM predictions.

The observed increase in nitrogen uptake on the warmed plots will probably be lower under the IPCC and SWECLIM predictions, since nutrient mineralisation is dependent on temperature. This will result in a smaller increase of biomass production than in our estimates. However, it is still likely that biomass production will increase more than the soil-surface CO_2 flux for boreal Norway spruce forests, *i.e.* the carbon sink will be stronger.

Conclusions

Soil warming increased stemwood production. The increase in growth between warmed and control plots was largest at the beginning of the season. Increased mineralisation had a stronger effect on growth than the direct effect of warming or the indirect effect of a prolonged growing season.

There are several indications that soil warming has increased nitrogen mineralisation, such as the increases in stemwood production, total N uptake by trees and ^{15}N content in the needles.

Soil warming increased N uptake by trees, but this was reflected only by an increase in N content in the needles during the first year of warming. During the subsequent years, the increased N availability was used to increase biomass production rather than to increase N concentration (growth dilution).

Soil warming increased soil-surface CO_2 by 10–30%, instead of the expected 50–80% if there had been no acclimation. This emphasises (*i*) that the positive feedback from soil, due to a climate change, may be overestimated (*cf.* Kirschbaum, 1995; Wang & Polglase, 1995; Cox *et al.*, 2000; Lenton, 2000), and (*ii*) that the relationship between soil-surface CO_2 flux and temperature should not be used outside the temperature range or location for which they were derived (*cf.* Lloyd & Taylor, 1994).

For periods during the day, the C uptake of the field- and bottom-layer vegetation can be greater than the release from the soil. This should be accounted for when carbon budgets for ecosystems are estimated. For locations with dense ground vegetation in the present study, photosynthesis by ground vegetation refixed 20% of total annual soil-surface CO_2 flux (*cf.* Goulden & Crill, 1997).

Soil warming increased carbon uptake by trees (ANPP) more than carbon losses by soil-surface CO_2 flux. This shows that a warmer climate may strengthen the carbon sink, rather than converting boreal forests into sources.

However, there are still many questions left to study and to answer. Why is the increase of the soil-surface CO_2 flux so small? What are the physiological adaptations? To answer this, study of the different processes involved in the soil-surface CO_2 flux is required. In particular effects of soil warming on root growth and turnover, on acclimation of autotrophic and heterotrophic respiration, and on carbon allocation to the roots must be studied and quantified. But there is also a need to develop better measurement techniques for these processes. Another question to be answered is whether these results concerning growth and soil-surface dynamics are valid in the long term (decades/centuries), or whether they are transitory. There is a need for long-term field studies on the effects of elevated air and soil temperature in forest ecosystems.

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