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Effects of nutrition and soil warming on stemwood production in a boreal Norway spruce stand

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Abstract

The boreal forest is expected to experience the greatest warming of all forest biomes. The extent of the boreal forest, the large amount of carbon contained in the soil, and the expected climate warming, make the boreal forest a key biome to understand and represent correctly in global carbon models. It has been suggested that an increase in temperature could stimulate the release of CO_2 caused by an increased decomposition rate, more than biomass production, which could convert current carbon sinks into carbon sources. Most boreal forests are currently carbon sinks, but it is unclear for how long in the future the carbon sink capacity of the boreal forest is likely to be maintained. The impact of soil warming on stem volume growth was studied during 6 years, in irrigated (I) and irrigated-fertilized (IL) stands of 40-year-old Norway spruce in Northern Sweden. From May to October heating cables were used to maintain the soil temperature on heated-irrigated plots (Ih and ILh) 5 °C above that on unheated control plots (Ic and ILc). After six seasons' warming, stem volume production ($m^3\,ha^{-1}\,a^{-1}$) was 115% higher on Ih than on unheated (Ic) plots, and on heated and irrigated-fertilized plots (ILh) it was 57% higher than on unheated plots (ILc). The results indicate that in a future warmer climate, an increased availability of nitrogen, combined with a longer growing season, may increase biomass production substantially, on both low- and high-fertility sites. It is, however, too early to decide whether the observed responses are transitory or long lasting. It is therefore crucial to gain a better understanding of the responses of boreal forest ecosystems to climate change, and to provide data to test and validate models used in predicting the impact of climate change.

Keywords: climate change, fertilisation, phenology, *Picea abies*, wood production

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Introduction

Global surface temperature has increased on average by ca. 0.6 °C during the 20th century, most probably because of an increase in the atmospheric concentration of greenhouse gases (GHG) (Houghton *et al*., 2001). Since the concentration of GHG probably will continue to rise, the temperature increase is expected to continue, reaching between 1.4 and 5.8 °C during the 21st century (Houghton *et al*., 2001).

The boreal forest is the second largest terrestrial biome in the world, covering approximately $15.6 \times 10^6\,km^2$ (cf. Gower *et al*., 2001). The soil carbon in this biome is disproportionately larger than that in other forest biomes, because of the deep, often frozen, organic deposits. The boreal forest is expected to experience the greatest warming of all forest biomes, raising concern for the fate of the large quantities of soil carbon (e.g. Wang & Polglase, 1995; Cox *et al.,* 2000; Cramer *et al.,* 2001). The large extent of the boreal forest, the large amount of carbon contained in the soil (Dixon *et al.,* 1994), and the expected climatic warming, make the boreal forest a key biome to be understood and correctly represented in global carbon models.

Growth in a boreal forest is primarily limited by low nutrient availability (Tamm, 1991), but increases in temperature will also increase the rate of nutrient mineralization in the soil (cf. review by Rustad *et al.,* 2001). An increased temperature may, therefore, stimulate biomass production and carbon uptake in the ecosystem. How the nutrient dynamics in the soil is affected is critical for

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improving long-term predictions of the carbon sink strength (Medlyn *et al.*, 2000).

It is suggested that a temperature increase could stimulate respiration of CO_2, caused by increased decomposition rates rather than by net primary production (NPP) (e.g. Cox *et al.*, 2000; Kirschbaum, 2000; Cramer *et al.*, 2001), which could transform the current carbon sink in boreal forests into a carbon source. Most boreal forests are currently carbon sinks (cf. Malhi *et al.*, 1999), but it is unclear for how long the carbon sink capacity of the boreal forest is likely to be maintained. The present small size of the trees, and their low nitrogen content, suggest that the capacity of the system to store carbon will not in itself be limiting, particularly since increases in atmospheric inputs and the rise in temperature may increase the availability of nitrogen.

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

In the present study, a long-term soil-warming experiment in a boreal Norway spruce forest in Northern Sweden was used. Soil warming was accomplished by means of heating cables. This provided a high degree of control over soil temperature, and enabled larger areas to be used, which is an important consideration when working with mature trees. To prevent soil drying, the treated plots were irrigated. Other complementary studies on the effect of soil warming on carbon and nutrient dynamics in a boreal forest have been made in the same experiment (cf. Bergh & Linder, 1999; Majdi, 2001; Strömgren, 2001).

The aim of the present study was to investigate the effect of soil warming on growth and phenology of Norway spruce trees, at high and low availability of soil nutrients.

Materials and methods

Site description

The study was performed in a long-term nutrient optimization experiment at Flakaliden (64°07′N; 19°27′E; alt. 310 m a.s.l) in Northern Sweden. The principal aim of the experiment was to demonstrate the potential yield of Norway spruce (*Picea abies* (L.) Karst.), under given climatic conditions and non-limiting soil water, by optimizing the nutritional status of the stands, at the same time as leaching of nutrients to the groundwater was avoided (cf. Linder & Flower-Ellis, 1992; Linder, 1995). The experiment was established in 1986 in a young Norway spruce stand planted in 1963, after prescribed burning and soil scarification, with 4-year-old-seedlings of a local provenance.

The soil is a thin podozolic, sandy, glacial till with an average thickness of ca. 120 cm. The thickness of the humus layer varies between 2 and 6 cm, with a mean thickness of 4.3 cm. The annual mean temperature is 2.3 °C, the monthly mean temperature at the site varies from −8.7 °C in February to 14.4 °C in July, and snow usually covers the frozen ground from mid-October to mid-May Mean annual precipitation is approximately 600 mm, and soil moisture is not normally limiting for tree growth (cf. Bergh *et al.*, 1999). The growing season was assumed to begin on the first day of the period when daily mean air temperature exceeded 5 °C for at least four consecutive days (cf. Odin *et al.*, 1983) and *vice versa* for the end of the growing season.

Nutrient treatments

The treatments, which began in 1987, included untreated control plots, irrigated plots, and two nutrient optimization treatments. Treatments were replicated four times in a randomized block design, and each replicate consisted of 50 × 50 m plots. Each plot contained a net plot (1000 m^2) surrounded by a buffer zone. In the present study, only irrigated (I) and irrigated-fertilized (IL) plots were included. In the IL treatment, all essential macro- and micro-nutrients 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. The reason for using treatments including irrigation was to reduce the risk of drying the soil as an effect of warming. The amount of nutrient elements supplied to the IL plots, before and during (1995–2000) the present study, is given in Table 1.

Soil-warming treatment

During the summer of 1994, a soil-warming treatment was installed in the buffer zone of one irrigated (I) and one irrigated-fertilized (IL) stand, with two 10 × 10 m sub-plots per treatment. Each heated sub-plot (h) had an unheated control plot (c), hereafter referred to as Ic, Ih, ILc, and ILh, respectively. The number of trees per sub-plot varied between 21 and 28, but the basal area per plot was similar within each treatment. All plots were fenced to exclude animals, and boardwalks were installed to prevent trampling of the ground vegetation.

The performance of the soil-warming system was tested during the autumn of 1994, and the long-term treatment commenced in April 1995. The initial aim of the experiment was to study the effect of soil warming on phenology and photosynthetic recovery in spring (Bergh & Linder, 1999), and was later expanded to include carbon and nutrient dynamics (cf. Strömgren, 2001).

The design of the soil-warming treatment followed in principle with the system described by Peterjohn *et al*. (1993). Six, 85-m long, heating cables (DEVI Elektrovärme AB, Vällingby, Sweden) per sub-plot were buried under the humus layer at a spacing of ca. 20 cm. After the moss- and humus-layer was cut through with a knife, the cables were placed on the mineral soil, after which the furrows were closed. The control plots were disturbed in the same way as the warmed plots, but heating cables were not installed. The heating system was controlled and monitored by temperature sensors connected to a data logger (Campbell CR10, Campbell Scientific Inc., Logan, USA). On each plot (heated and control plots), six thermocouples were installed into the first centimetre of the mineral soil. These sensors were monitored and the data stored every 15 min.

Soil warming started in April each year (cf. Table 2), about 5 weeks before the soil thawed in the unheated plots. The soil temperature was increased 1 °C per week, until a 5 °C difference between heated and control plots was reached. In late autumn, when the soil temperature in the control plots approached 0 °C, the soil temperature of the heated plot was decreased by 1 °C per week. If the control plots did not freeze before 1st November, the temperature reduction was still initiated. For further information on the construction and long-term performance of the soil-warming system, see Bergh & Linder (1999) and Strömgren (2001).

The water potential at 15, 30 and 45 cm depth was measured twice a week by tensiometers at two points per heated plot. These measurements were used to determine irrigation intensity. In addition, soil-water content, at 15 cm depth, was measured continuously by 11 thetaprobes (Delta-T Devices Ltd., Cambridge, England) in Ic and Ih plots, from late summer 1997. To maintain the soil water potential above −100 kPa, the heated plots (Ih and ILh) were given extra irrigation relative to their control plots (Ic and ILc) from July 1997, whenever needed.

Table 1 Amounts of macro- and micro-nutrient elements (kg ha^{-1}) supplied to irrigated-fertilized stands at Flakaliden during the periods 1987–1994 and 1995–2000, respectively. For further details regarding treatments, see Linder (1995)

	N	P	K	Ca	Mg	S	Mn	Fe	Zn	B	Cu
1987–1994	675	115	327	68	58	28	2.6	4.4	0.2	3.5	0.2
1995–2000	450	60	180	0	48	0	1.2	2.2	0.1	0.4	0.1
Total	1125	175	507	68	106	28	3.8	6.6	0.3	3.9	0.3

Table 2 Date of beginning, end, and duration of growing season and period of soil warming, during the years 1995–2000

	Growing season			Soil warming		
Year	Start	End	Duration (days)	Start	End	Duration (days)
1995	May 24	Sep 26	126	Apr 10	Dec 4	238
1996	May 20	Sep 9	113	Apr 15	Nov 4	203
1997	May 6	Oct 3	151	Apr 27	Nov 20	207
1998	Apr 23	Sep 23	154	Apr 6	Nov 30	238
1999	May 17	Oct 4	141	Apr 8	Nov 29	235
2000	May 7	Oct 24	171	Apr 10	Nov 29	233

Additional measurements

Meteorological data from 1995 to 2000 were taken from a standard weather station situated approximately 250 m from the heating experiment, except during periods of sensor or logger failure, when gaps were filled with data from the Svartberget experimental forest, ca. 20 km from Flakaliden. Measurements were taken every minute, and averaged and stored every 10 min by a CR10 logger (Campbell Scientific Inc., Logan, Utah, USA).

Snow depth (four fixed rods per plot) and depth of frozen soil (three fixed sticks per plot) were measured weekly from November 1997. The depth of frozen soil was measured by a frost-depth gauge developed by Gandahl (1957; for an English description, see Rydén & Kostov, 1980), inserted to 50 cm depth.

Soil temperature profiles (0, 2, 5, 10, 20, 50 cm depth of mineral soil) were measured during the first 2 years of soil warming. There were two profiles per heated plot, but none on the control plots (Ic and ILc). Instead, temperature profiles on I and IL plots in the main experiment were used as references.

Growth measurements

Tree height (H) and diameter at breast height (1.3 m; D), were measured annually in autumn after diameter growth ceased. A calliper was used to measure D to 1 mm, using the mean of two measurements at right-angles, and H was measured to 1 dm with a height gauge. For one of the Ic plots, measurements of D were available only from 1997 onwards. For this plot, D was therefore estimated for the years 1994–1996 by a function derived from the trees on the other Ic plot.

$$D_t = k_t D_{97} - m_t \quad (1)$$

where D_t is diameter, cm, for the year in question, k_t and m_t constants, and D_{97} is D measured in 1997. The values of k_t were 0.96, 0.97, and 0.94, and of m_t 0.81, 0.64, and 0.02, for years 1994, 1995 and 1996, respectively ($r^2 = 0.99$ for all years).

Stem volume on bark was estimated by a function, derived by Brandel (1990), for trees exceeding 4.5 cm in D:

$$V = 10^{-0.71101} \cdot D^{2.13529} \cdot (D + 20)^{-0.79437} \cdot H^{3.06616} \cdot (H - 1.3)^{-1.78259} \quad (2)$$

where V is stem volume in dm^3, and D and H are in cm and m, respectively. Since only a minor part of total stem volume on the I and IL treatments (maximum 7.4% and 0.4%, respectively) consisted of trees less then 5 cm in D, the same function was used for all trees. Total stem volume, per unit ground area, was calculated for each plot. Trees less than 1 m from the edges of the plots were 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 normalizing G_t to the volume growth in 1994 (G_{94}), the year before the warming treatment commenced;

$$G_{rel} = 100\left(\frac{G_t}{G_{94}} - 1\right) \quad (3)$$

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.

Phenology

The date of budburst of apical buds on south-facing branches was monitored during spring 1997–1999 on Ic, Ih, ILc and ILh plots. All trees more than 2 m from the edges of the plots were monitored. In 1997, the buds of the second-order branches (cf. Flower-Ellis, 1996) in whorl 6 were observed and in 1998–1999 the buds of the first-order branches in whorl 3.

The seasonal course of stem diameter increment was measured by using stainless steel band dendrometers, installed at breast height (1.3 m) in April 1997, on all trees with $D > 5$ cm and standing more than 2 m from the edges of the plots. The bark at breast height was smoothed and lichens were brushed off before the bands were installed. The dendrometers were measured manually, to the nearest 0.01 mm, by means of a digital calliper, once a week from April–May to September. To reduce the effects of diurnal variations in diameter, the dendrometers were measured in the same sequence on every occasion, starting at 08:30 h. The dendrometers were loosened in winter. In June 1998, 20 of the manual dendrometers were replaced by automatic band dendrometers (ELPA-93, University of Oulu, Finland). Five automatic dendrometers were installed on one plot of each treatment (Ic, Ih, ILc, ILh). Initially, the dendrometers were read manually, usually twice a week, by means of a multimeter. In July 1998, the automatic dendrometers were connected to a logger (Type Dl2e, Delta-T, Cambridge, UK) and measured hourly. In spring, and in autumn each year after diameter growth had ceased, D was measured in two directions at right-angles on all trees with dendrometer bands.

Statistical analysis

An analysis of variance was carried out to test for treatment effects on growth, using the 'mixed procedure' in SAS statistical software (version 8.01, SAS Institute, Cary, NC). The experiment was considered as a split-plot design, where the fertilization factor (*fert*), i.e. I and IL treatments, was not replicated. The unit of replication for the heating factor (*heat*) was the blocks ($n = 2$). Since the measurements were made on the same plots, they could not be assumed to be independent, and time (T) was used as repeated measure. A complex model was tested as follows:

$$D = \alpha + fert + block(fert) + heat + fert \cdot heat + heat \cdot block(fert) + T + T \cdot fert + T \cdot heat + T \cdot fert \cdot heat + \varepsilon \quad (4)$$

where D is the dependent variable, α is the intercept and ε is an error term T was treated as a variable. Pairwise comparisons of the means for the treatments were used to test significant differences (LSMEANS/pdiff).

Results

During the six years' study, there was a pronounced between-year variation in weather conditions. The beginning of the growing season, defined as the first day of a 4-day-period when daily mean temperature is $> 5\,°C$, varied by 4 weeks, and the end of the growing season varied from 9 September (1996) to 24 October (2000). Mean temperature during the growing season was 11.9 °C and mean precipitation was 304 mm. The growing season in 1997 was unusually warm (15.4 °C), and the precipitation in 1998 and 2000, much higher than normal, 455 and 480 mm, respectively (Table 2). Mean soil temperature during the growing season was 8.7 °C, but was

Table 3 Weather data for Flakaliden during the growing seasons 1995–2000

Year	S_t (MJ m^{-2})	P (mm)	T_{air} (°C)	T_{Soilc} (°C)	T_{Soilh} (°C)	Ψ_c (kPa)	Ψ_h (kPa)
1995	1850	205	11.6	8.5	12.9	−124	−287
1996	1820	209	12.0	7.7	12.4	−88	−278
1997	1810	243	15.4	10.8	15.8	−112	−189
1998	2000	455	10.3	7.9	12.9	−39	−66
1999	2050	234	11.8	8.8	13.8	−95	−128
2000	1860	480	10.3	8.9	13.7	na	na

Abbreviations: Total global radiation (S_t), total precipitation (P), mean air temperature (T_{air}), mean soil temperature on unheated (T_{Soilc}) and heated (T_{Soilh}) plots, and mean minimum water potential measured at 15 cm depth on unheated (Ψ_c) and heated plots (Ψ_h).

as high as 10.8 °C, in 1997. It should, however, be noted that the length of the growing season varied between years (Table 3). The duration of the soil-warming treatment varied less and was in most of the years from early April to the end of November (cf. Table 3).

The first snow normally fell in October, and maximum snow depth (ca. 1 m), was attained in March. The snow cover persisted to the beginning of May on the heated plots and about 2 weeks longer on the control plots. There were only small differences in snow depth between treatments, but ILh had consistently less snow than the other treatments.

The depth of frozen soil was only a few centimetres on I plots, but 10–20 cm on the IL plots (Table 4). Average soil temperature in the humus layer during winter (i.e. unheated period) was close to 0 °C for all treatments, except during the winter of 1995/96, when both the lowest mean and minimum soil temperatures were recorded. The soil temperature in IL plots was consistently ca. 0.5 °C lower than in I plots. The soil on the heated plots was in general drier than that on control plots during the first years of warming, but supplementary irrigation from 1997 and onwards decreased the difference (Table 3). In April–May, immediately after the soil had thawed and during snowmelt, the soil water content increased rapidly and reached its maximum (Fig. 1).

Soil-warming system

During the growing season, the soil-warming system maintained a temperature difference close to 5 °C between unheated and heated plots (Fig. 1 and Table 2), except during some periods in 1995 and 1996, when

Table 4 The annual mean soil temperature and the mean soil temperature during winter, when the soil-warming system was switched off, and maximum depth of frozen soil on unheated and heated, irrigated and irrigated-fertilized plots, respectively. Minimum temperatures during winter are given in parentheses. Each value is a mean of two plots

		Irrigated		Irrigated-fertilized	
Soil temperature	Year	Unheated	Heated	Unheated	Heated
Annual mean (°C)	1995	3.9	7.4	3.7	7.3
	1996	2.3	4.0	1.7	3.5
	1997	4.5	6.8	4.1	6.3
	1998	4.2	7.3	3.7	6.6
	1999	4.1	7.1	3.6	6.4
	2000	4.9	7.8	4.4	7.1
Winter mean and minimum (°C)	95/96	−1.1 (−3.3)	−1.0 (−3.4)	−2.2 (−5.5)	−2.5 (−7.0)
	96/97	0.9 (0.4)	0.8 (−0.4)	0.4 (−0.2)	0.0 (−1.6)
	97/98	0.5 (−0.2)	0.6 (−0.3)	0.1 (−0.8)	−0.3 (−1.9)
	98/99	0.1 (−1.3)	0.1 (−1.1)	−0.5 (−2.6)	−0.7 (−3.4)
	99/00	0.4 (−0.6)	0.4 (−0.1)	−0.3 (−1.6)	−0.3 (−1.5)
Depth of frozen soil (cm)	97/98	5	7	15	22
	98/99	5	12	22	22
	99/00	6	1	14	12

technical problems occurred. The fall in the temperature difference for a short period in September 1999 (Fig. 1b), was intentional, and was related to a study of soil-surface CO_2 flux (cf. Strömgren, 2001). The temperature difference between plots was more than 5 °C during a few days in spring, when the snow had melted on the heated plots, but the control plots were still covered with snow. This temperature increase was probably due to heating by solar radiation.

Soil warming affected a large part of the soil volume (Fig. 2), and in the first 20 cm of the mineral soil the temperature difference was ca. 5 °C in the middle of the summer. At a soil depth of 50 cm, the warming resulted in a 4 °C difference.

Time of budbreak

In all years, budbreak commenced during the first week of June, and within about 5 days almost all shoots had flushed. There was no difference between different treatments.

Seasonal course in basal area increment

There were no differences in the timing of the beginning, the end, or the peak of basal area growth between the heated and the control plots. The basal area increment began in late May, or at the beginning of June each year, and ceased in mid-August (Fig. 3). The rate of basal area growth peaked in late June, and was always higher on heated (Ih and ILh) plots, than on their unheated control plots (Ic and ILc).

Stem volume growth

Relative volume growth (G_{rel}) varied between years, and the unheated control plots (Ic and ILc) showed similar between-year variation, with the lowest rates at the beginning and end of the study period (Fig. 4).

In all years, except the first year with heating, G_{rel} was significantly higher on Ih plots compared to Ic plots (Table 5). In the second year, G_{rel} for the Ih plots was 58% higher than the baseline values from 1994, compared to a 17% increase on the control plots. During 1997–1999, G_{rel} was 84–90% on Ih plots, but increased to 115% in year 2000. The ILh plots tended to have a higher stem growth rate compared to ILc plots in all years, except in 1995, the first year of heating (Fig. 4b). The difference was

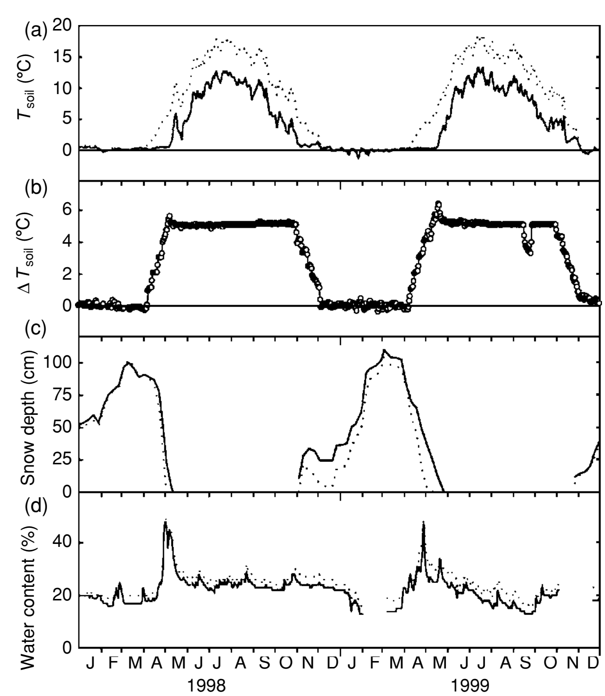

Fig. 1 The variation, during 1998 and 1999, in (a) soil temperature at 1 cm depth in the mineral soil in unheated (solid line) and heated irrigated (dotted line) plots (Ic and Ih), (b) the difference in soil temperature between Ic and Ih, (c) snow depth, and (d) soil water content in per cent of volume, at 15 cm depth.

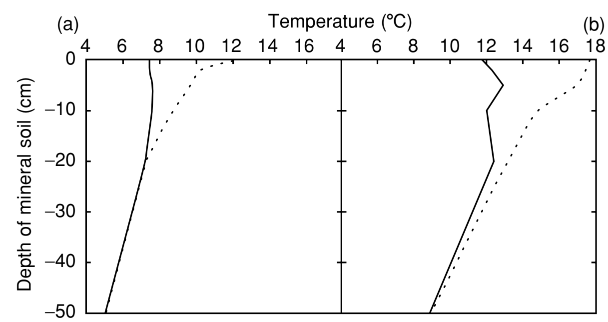

Fig. 2 Soil temperature profiles on an unheated (a), and a heated (b) plot at 03:00 h (solid line) and 15:00 h (dotted line) on a day in mid-July 1997.

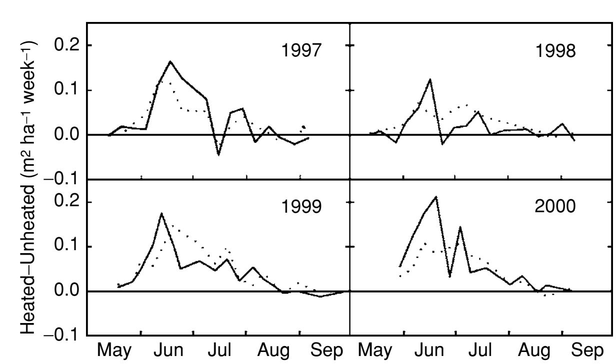

Fig. 3 The difference in weekly basal area increment, between trees on heated and unheated, irrigated (dotted line) and irrigated-fertilized (solid line) plots, during the growing seasons 1997–2000.

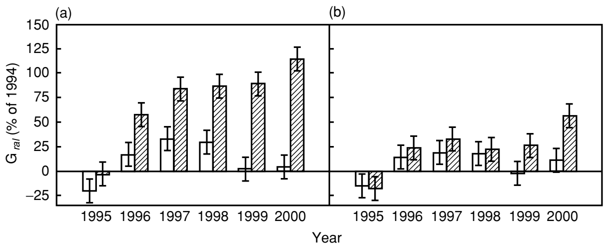

Fig. 4 The relative annual volume growth (G_{rel}), in relation to the growth in the year before the soil-warming treatment began (1994), on irrigated (a) and irrigated-fertilized (b) plots. Unheated plots (open bars) and heated plots (hatched bars). Vertical error bars indicate ± 1 standard error.

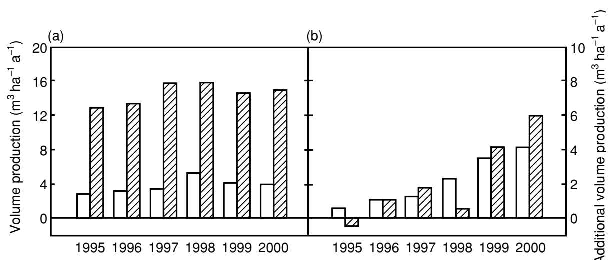

Fig. 5 (a) The annual volume growth, 1995–2000, on irrigated (open bars) and irrigated-fertilized (hatched bars) plots ($n = 4$) within the nutrient optimization experiment at Flakaliden, and (b) the additional volume growth obtained each year on irrigated (Ih) and irrigated-fertilized (ILh) plots ($n = 2$), as an effect of soil warming.

Table 5 Statistical difference in relative volume growth (G_{rel}), relative growth of basal area (B_{rel}) and relative height growth (H_{rel}), between heated and unheated plots on irrigated (Ih–Ic) and irrigated-fertilized (Ilh–ILc) treatments

	Ih-Ic			Ilh-ILc		
Year	G_{rel}	B_{rel}	H_{rel}	G_{rel}	B_{rel}	H_{rel}
1995	ns	ns	ns	ns	ns	ns
1996	*	**	ns	ns	ns	ns
1997	**	**	ns	ns	ns	ns
1998	**	*	***	ns	ns	ns
1999	***	***	**	ns	ns	ns
2000	***	***	***	*	**	ns

$P > 0.05$ denotes not significant (ns); * $P < 0.05$; ** $P < 0.01$; and *** $P < 0.001$.

significant only in 2000 (Table 5). Relative growth in basal area (B_{rel}) showed a similar trend as G_{rel}, while relative height growth (H_{rel}) differed significantly only during the last 3 years on Ih plots compared to Ic plots (Table 5).

There was a three-fold difference in absolute volume growth between unheated I and IL plots, with a small decrease in volume production, in both treatments, during the last 2 years (Fig. 5a). The additional volume production obtained as an effect of soil warming was similar in absolute terms in Ih and ILh, and increased steadily during the period of study (Fig. 5b).

Discussion

Weather conditions at the beginning of winter are important for the development of frozen soil. An early, thick snow cover on top of unfrozen soil may prevent soil freezing (Odin, 1992). When the snow has reached a certain depth, its effect on soil temperature is very small, but it acts as an efficient insulation. Since the IL plots had a dense canopy compared to the I plots, the snow depth at the beginning of winter was lower on IL plots than on I plots, which could have caused the lower temperature and the increased depth of frozen soil (Table 4). Odin (1992) found that in 6 years out of 10, there was hard-frozen soil to a maximum depth of at least 10 cm in an old spruce forest 20 km from Flakaliden.

A large proportion of the soil profile was affected by soil warming and in the middle of the season, the temperature difference was 4 °C at a depth of 50 cm in the mineral soil (Fig. 2). Most fine roots in the stand are found in the uppermost 20 cm of the mineral soil (Majdi, 2001), which means that most of the roots should be affected by the warming treatment.

The growth of basal area and volume in the different treatments, exhibited pronounced between-year variations (Figs 3–5), but cannot directly be related to the variations in weather conditions (cf. Tables 2–4). Growth is, however, not only affected by weather conditions in the current season, but also by weather conditions in the previous year (e.g. Peterson & Peterson, 1994; Mäkinen *et al.*, 2001). The poor growth in 1995 could have been an effect of root damage when the heating cables were installed, but 1995 was also a year with an extremly high cone production. Cones may be a strong sink for both carbon and nutrients, which results in decreased diameter growth (cf. Eis *et al.*, 1965; Koppel *et al.*, 1987). The observed reduction in volume growth in 1999 and 2000 is probably the effect of a severe infection of the fungus *Chrysomyxa ledi*, which resulted in considerable needle loss. In addition, heavy snowfalls during the winter of 1998/99 caused shoot and stem breakages, which also affected the amount of stemwood production in the following years.

The annual stemwood production relative to annual production in 1994 (G_{rel}) was significantly higher on Ih plots compared to Ic plots in all years after the first year with warming (Fig. 3a). In all years, except the first year of warming, ILh tended to have a higher stemwood growth compared to ILc (Fig. 4b), but the difference was significant only in 2000. Since there were only two replicates in every treatment, a heating effect on IL might have been obscured by the variation within the ILh and ILc plots. Relative growth in basal area (B_{rel}) showed a similar trend as G_{rel}, but height growth (H_{rel}) had no clear trend. The height increments were, however, affected by snow damage, especially on IL plots with high leaf-area indices.

The lack of a significant heating effect on G_{rel} in the first year of warming, may be explained by the predetermined growth pattern of Norway spruce, and by the fact that, during the first year, increased nutrient availability will not be seen in terms of increased growth in temperate and boreal conifers (cf. Linder & Rook, 1984). The increase in stemwood production on the Ih plot was higher than the 33% increase found after 2 years of warming (8–10 °C) in a black spruce stand in boreal Canada (Van Cleve *et al.*, 1990; Bonan, 1993) or in model estimates of effects of a temperature increase of 5 °C on production in a stand of black spruce (Bonan & Van Cleve, 1992).

An increase in growth may be explained by two main factors: (i) increased soil temperature, giving an earlier thaw of the frozen soil and a prolonged period for the uptake of water, nutrients, and photosynthesis (cf. DeLucia, 1986; DeLucia & Smith, 1987; Bergh *et al.*, 1998; Wan *et al.*, 1999); and (ii) an increased availability of soil nutrients, as an effect of increased mineralization (cf. Van Cleve *et al.*, 1990; Chapin III *et al.*, 1995; Lükewill & Wright, 1997; Rustad & Fernandez, 1998; Rustad *et al.*, 2000).

Direct effects of increased air temperature on plant growth may be smaller than often is expected, because of thermal acclimation (Mooney *et al.*, 1999; Kirschbaum, 2000). Indirect effects of warming on changes in species composition, litter quality and nutrient availability, may however, cause changes in the carbon balance of forest ecosystems, large enough to provide significant feedbacks to global warming.

Assuming that the IL treatment was not limited by nutrient availability (Linder, 1995; Bergh *et al.*, 1999), then the increased growth on ILh plots (20–60%) would be the effect of an earlier soil thaw and a longer season, and the large increase in the Ih plots (115%), a combined effect of a longer season and increased N mineralization. However, when the additional growth obtained in Ih and ILh plots was compared, the absolute increase in volume production was similar (Fig. 5). This indicates that even the ILh plots had benefitted from increased nutrient mineralization. This was supported by the fact that, when the accumulated N uptake, during the 6 years of warming, was estimated, the increased N uptake was similar on Ih and ILh plots (Strömgren 2001).

At this stage we cannot determine whether the increased growth and N uptake on the ILh plots was the effect of increased nutrient demand, as a consequence of a longer growing season, or whether the nutrient supply on the IL treatment (cf. Linder, 1995; Bergh *et al.*, 1999) was sub-optimal.

When the increased carbon uptake, as an effect of soil warming, is compared with soil-surface CO_2 fluxes measured in the same experiment (Strömgren, 2001), there is no indication that this boreal site is becoming a C source instead of a sink. In fact, the response to 6 years of soil warming was that the C sink strength had increased as an effect of the treatment.

The results indicate that in a future warmer climate, an increased availability of nitrogen, combined with a longer growing season, may increase biomass production in boreal forests substantially, on both low- and high-fertility sites. It is, however, too early to determine whether the observed responses are transitory or long-lasting. It is therefore crucial to gain a better understanding of the responses of boreal forest ecosystems to climate change, and new, long-term manipulation experiments should be established to provide more data to test and validate models used in predicting the impact of climate change on forest ecosystems (cf. Rustad *et al.*, 2001).

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