Effects of soil warming during spring on photosynthetic recovery in boreal Norway spruce stands

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Abstract

The effect of soil thawing and soil temperature on postwinter recovery of photosynthetic capacity was studied, during late spring and early summer, in Norway spruce stands in northern Sweden. Soil temperature was manipulated by means of buried heating cables. The warming treatment was applied to stands with low (natural) and high (fertilized) availability of nutrients. Soil thawing, expressed as water availability, was followed by means of sapflow in stems, and shoot water potentials. The recovery of photosynthetic capacity was assessed by measuring the rate of light-saturated photosynthesis (A_{max}), and maximum photochemical efficiency of photosystem II in detached shoots, and chlorophyll *a* fluorescence. Accumulation of starch reserves in the needles was followed as an independent indicator of photosynthetic performance *in situ*. Snowmelt and soil thawing occurred more than one month earlier in heated than in unheated plots. This was expressed both as sapflow and as differences in shoot water potential between treatments. During May, the rates of A_{max} were significantly higher on heated than on control plots. The effect of soil warming on A_{max} was, however, not reflected in chlorophyll fluorescence or needle starch content. The time course of the recovery of photosynthetic capacity was mainly controlled by mean air temperature and by the frequency of severe night frosts, and to a lesser extent by earlier soil thawing and higher soil temperatures.

Keywords: boreal, climatic change, fluorescence, *Picea abies*, recovery of photosynthesis, sapflow

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Introduction

Annual carbon gain in conifers growing at high latitudes is largely constrained by low temperatures and frozen soils (see review by Havranek & Tranquillini 1995). Photosynthetic capacity is reduced by the first severe autumn frosts (e.g. Troeng & Linder 1982; Strand 1995), and further reduced by low temperature stress during winter, in combination with photoinhibition during spring (cf. Öquist 1983; Hällgren *et al.* 1991). The combined effect of these stress factors is to reduce the rate of light-saturated photosynthesis (A_{max}) to 10–20% of maximum values found in late summer (Linder & Lohammar 1981; Troeng & Linder 1982). The loss of photosynthetic capacity can be seen not only in A_{max}, but also in terms of chlorophyll fluorescence (e.g. Strand & Lundmark 1987; Lundmark *et al.* 1988a, 1998; Westin *et al.* 1995).

The recovery of photosynthetic capacity in spring and early summer, is strongly temperature-dependent (e.g. Pelkonen & Hari 1980; Linder & Lohammar 1981; Strand & Lundmark 1995), and can be halted, or even set back, by cold days or severe night frosts (Lundmark *et al.* 1988b, 1998). No recovery of photosynthetic capacity was seen in Scots pine, however, before the soil had thawed (Linder & Troeng 1980; Troeng & Linder 1982). This implies that both the timing and the rate of recovery can be subject to large between-year variations (cf. Linder & Flower-Ellis 1992). Once full photosynthetic capacity has been regained, severe summer frost (< -6 °C) can reduce A_{max} by up to 50% (e.g. DeLucia & Smith 1987; Lundmark *et al.* 1988b). Full recovery from such low temperature stress is normally attained within a few days of the frost event (cf. Hällgren *et al.* 1990), which has a minor effect on the annual carbon budget. Recovery in spring and early summer, however, may take up to two months (cf. Linder & Troeng 1980; DeLucia & Smith 1987), and results in a loss of 'potential' photosynthetic production equal

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to 30% of the total annual carbon gain in Scots pine growing in central Sweden (Linder & Lohammar 1981).

The process-based simulation model BIOMASS (McMurtrie *et al.* 1990; McMurtrie & Landsberg 1992), was modified to include the above-mentioned 'boreal' features (cf. Bergh *et al.* 1998a). The modified model was used to simulate annual photosynthetic production (or gross primary production, GPP) for three calendar years, using climatic variables and parameters from boreal Norway spruce stands growing at low and high fertility. The reduction of 'potential' GPP, caused by low-temperature effects, ranged during the three years from 35 to 45%, and was only affected to a small extent by fertility. Variation between years was mainly an effect of differences in spring temperature, which resulted in different rates of repair of the photosynthetic apparatus.

When the carbon balance of boreal forest ecosystems in current or future climates is estimated, it is evident that large errors may be introduced unless the effects of frozen soils and reduced photosynthetic capacity during spring and early summer are considered. Predictions or estimates of the impact of climate change on boreal forests will remain uncertain until results from long-term field studies of carbon gain and losses in boreal ecosystems become available.

The purpose of the present study was to determine the effect of soil temperature on the rate of postwinter recovery of photosynthetic capacity in young Norway spruce (*Picea abies* (L.) Karst.) stands in northern Sweden. Soil temperature was experimentally manipulated by means of soil warming, and photosynthetic capacity was assessed in terms of A_{max} and chlorophyll *a* fluorescence. The study was part of a larger project on the ecophysiology of Norway spruce growing in a boreal climate (e.g. Linder & Flower-Ellis 1992; Linder 1995; Stockfors & Linder 1998a,b; Bergh *et al.* 1998a,b).

Materials and methods

Field site

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 (Linder & Flower-Ellis 1992; Linder 1995). The experiment was established in 1986 in a young Norway spruce (*Picea abies* (L.) Karst.) stand, planted in 1963 after clear-felling. The treatments, which began in 1987, included untreated control plots, irrigated plots, and two nutrient optimization treatments. In the present study, only irrigated (I) and irrigated-fertilized (IL) plots were included. For further details regarding treatments, see Linder (1995).

The soil is a thin, podozolic, sandy, glacial till with an average depth of ≈ 120 cm. The humus layer varies in thickness from 2 to 6 cm, with a mean of 4.3 cm. The bulk density of the upper 20 cm of the mineral soil is 1.03 g cm⁻³.

The monthly mean air 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 ≈ 600 mm, and soil moisture is normally not limiting for tree growth (cf. Bergh *et al.* 1998b). The weather at the site was monitored using a standard weather station, and hourly maximum, minimum, and mean temperatures were calculated and stored.

Soil warming

During the early 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 subplots per treatment. Each heated subplot had an unheated control plot. The number of trees per subplot varied between 21 and 28, but the basal area per plot within each treatment was similar. The reason for using treatments including irrigation was to reduce the risk of soil-drying as an effect of soil warming. The (IL) stand was approaching canopy closure, with an estimated crown cover of 80%, while the (I) stand had less than half the crown cover of the (IL) stand.

The performance of the soil-warming system was tested during the autumn of 1994, and the long-term treatment commenced at the beginning of April 1995. The aim of the treatment was to shorten by one month in spring and autumn, respectively, the period during which the soil was frozen. During this period the target was to maintain the soil temperature in heated plots 5 °C above that in control plots (cf. Anonymous 1991).

The design of the soil-warming treatment followed in principle the system described by Peterjohn *et al.* (1993). Six 85 m-long heating cables (DEVI Elektrovärme AB, Vällingby, Sweden) per subplot were buried under the humus layer at a spacing of ≈ 20 cm. When supplied with 230 VAC, the cables had an output of 12.9 W m⁻¹, giving a heating capacity of 65 W m⁻². After slits had been cut with a knife in the moss and humus layer, the cables were placed on the mineral soil, after which the slits were closed. To create a similar disturbance on both heated and unheated plots, slits were cut on the control plots, but cables were not installed.

The control and monitoring of the heating system was carried out by temperature sensors connected to a datalogger (Campbell CR10, Campbell Scientific Inc., Utah, USA). On each plot (heated and control plots), six thermocouples were installed into the first centimetre of the mineral soil. These sensors were monitored each minute, and a mean value was calculated every 10 min.

If the temperature difference between the heated plot and its control was < 4.9 °C, the datalogger activated a relay to supply power to the heating cables, and when the difference was > 5.1 °C, the power was switched off.

Sapflow measurements

Sapflow was monitored in 16 trees, from April to June 1995, by means of a stem tissue heat-balance method (cf. Cermak *et al.* 1973), modified according to Lindroth *et al.* (1995). The principle of this method is that a small portion of the stem surface is supplied with a constant amount of heat and temperature in the conductive xylem is measured by differentially connected thermocouples. One thermocouple is inserted below, and a second sensor within or immediately above the heated area. The monitored stem section is well insulated, to avoid the influence of variations in ambient air temperature. When there is a flow of water in the xylem, the supplied heat will be transported away from the heated section, decreasing the temperature difference between the sensors. This temperature difference can be used to estimate actual sapflow (cf. Lindroth *et al.* 1995).

During the late winter of 1995, a total of 16 sapflow gauges were installed on trees growing on an (I) or an (IL) plot. Of the eight sapflow gauges per treatment, four were installed on trees growing on a heated plot and the other four on trees growing in the unheated control area. The gauges were installed on stem internodes above, but as close as possible to, breast height (130 cm). The diameter of these stem sections ranged between 63 and 85 mm (I) and 73–94 mm (IL).

Each sapflow gauge had a 160 mm long, electric heating element which surrounded and was in close, but light contact with the stem. Two temperature sensors were radially inserted and positioned in the middle of the conductive xylem of the stem, one at the upper edge of the heated area and the other 50 mm below. The temperature sensors were fine wire thermocouples (1.0 mm copper/constantan); temperature was measured continuously and recorded every 10 min by a datalogger (Campbell CR10). The heating element and temperature sensors were insulated with 18 mm thick polyurethane foam wrapped around the stem. The insulation extended 50 mm above and below the position of the temperature sensors, and was covered by highly reflecting foil. To protect the installation from rainwater stemflow, wax was applied to the stem just above the insulation.

Photosynthesis (A_{max})

The rate of light-saturated photosynthesis (A_{max}) was measured on 11 occasions during the period early April to late June 1995. The measurements were made on detached shoots under controlled conditions. Shoots were sampled, in early morning, from whorl 7 (from the top) of six trees per treatment. The shoots were brought to the laboratory, where the bark was peeled off from the proximal end of the shoot before it was re-cut under water. The detached shoots were supplied with water through a pipette sealed with Parafilm. After the initial preparation, shoots were acclimated for two hours at 10 °C, a photon flux density of 200 µmol m^{-2} s^{-1}, and a relative humidity of more than 60%.

Gas exchange was measured with a portable infrared gas analyser (Li-Cor 6250; Li-Cor Inc., Nebraska, USA) connected to a Perspex cuvette (volume 0.654 L) with a water-cooled top. The gas exchange system was calibrated each day before measurement, using a calibration gas with a known CO_2 concentration.

After acclimation, measurements were made at a temperature of 18 ± 0.5 °C, an ambient CO_2 concentration of 350 ± 5 µmol mol^{-1}, and a photon flux density of *c.* 1400 µmol m^{-2} s^{-1}. The projected needle area of the shoots was measured with a leaf-area meter (Li-Cor 3000, Li-Cor Inc., Nebraska, USA).

Chlorophyll fluorescence

Maximum photochemical efficiency of one-year-old shoots was measured on 23 occasions during the period April to June 1995. On each occasion shoots were sampled from whorl 7 of the trees used for measurement of A_{max}. After one hour of dark acclimation at 0 °C, the shoots were measured at room temperature with a modulation fluorometer (PAM 101 chlorophyll fluorometer, H. Walz, Germany), described by Schreiber *et al.* (1986). The shoots were attached to a strip of transparent tape, then to a bundle of optic fibres (101 F, H. Walz, Germany). A modified Schoot fibre illuminator KL 1500 (FL 103, H. Walz, Germany), with a saturating photon flux density, was used to illuminate shoots. When dark-adapted shoots are illuminated, the fluorescence of photosystem II increases from a minimum (F_0) to a maximum (F_m), then decays to a value close to F_0 (nomenclature according to Schreiber (1983)). The ratio between variable fluorescence ($F_v = F_m - F_0$) and F_m was considered to be an appropriate index of photosystem II activity (cf. Leverenz & Öquist 1987; Lundmark *et al.* 1988a).

Other measurements

Shoots for analysis of starch concentrations in one-year-old (C + 1) needles were sampled on 11 occasions during the spring of 1995. The samples were taken from whorl 7 of six trees per subplot. The shoots were immediately immersed in liquid nitrogen before being stored at – 20 °C until they were further processed and analysed.
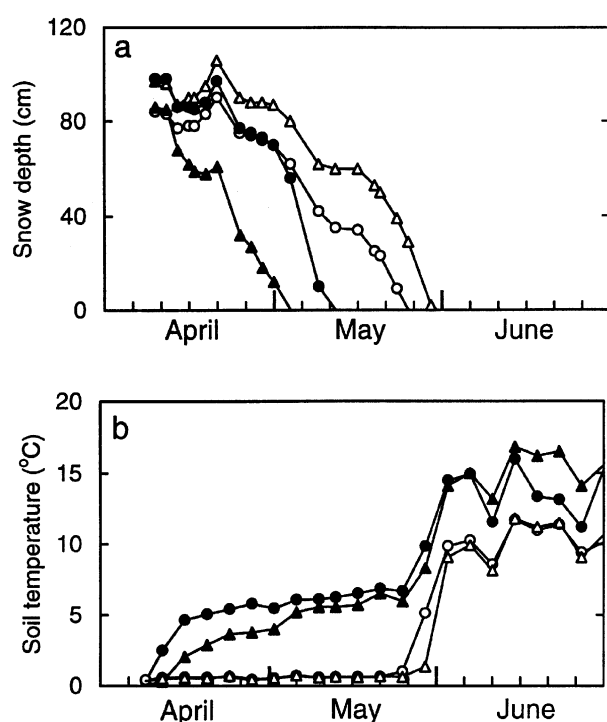
Fig. 1 Snow depth (a) and soil temperature (b) during spring 1995, in heated and unheated plots, respectively. Symbols: Irrigated plots (circles) and irrigated-fertilized plots (triangles). Filled symbols indicate plots with soil warming.

Fig. 2 Daily mean and minimum temperatures at Flakaliden during the period April to June 1995.

(IL) stands. Another effect of the denser canopies on (IL) plots was that snow melt was delayed by one week on the unheated plots, compared to the more open (I) plots (Fig. 1a).

The soil temperature began to increase immediately after soil-warming started, but the target value – a 5 °C difference between heated and unheated plots – was not achieved until the snow cover had disappeared (Fig. 1b). Once the snow was gone, the soil-warming system maintained the temperature difference between heated and unheated plots close to the target value. The reduced difference for the (I) plot in late May, was caused by a power failure.

Sapflow and water potentials

Spring 1995 was cold, and daily mean air temperatures above 0 °C and nights without severe frost did not occur until mid-May (Fig. 2). When weather conditions became milder in early May, with increased air temperatures and water vapour pressure deficits (Fig. 3a), clear diurnal patterns in sapflow were observed (Fig. 3b,c). The effect of soil warming was pronounced, there being an approximately threefold difference between heated and unheated plots in daily peak sapflow values. The daily sapflow during this period, expressed per unit cross-sectional area of xylem and day, was more than twice as large in trees on heated plots as in those on unheated control plots. The differences in sapflow and shoot water potential between trees growing on heated and unheated plots were maintained only until the latter part of May.

The restricted availability of soil water on unheated plots was seen also in the shoot water potentials (Fig. 4a,b). During the first half of May, shoots from trees growing on unheated plots had significantly lower water potentials than those from trees on heated plots. As an effect of the larger canopy, hence of the larger transpiring leaf surface, the difference was most pronounced on (IL) plots (Fig. 4b).

Samples were dried in a ventilated oven (85 °C, 48 h), and pooled within treatments before analysis. Starch and soluble sugars were analysed enzymatically, according to Steen and Larsson (1986), slightly modified (50 mg sample extracted 60 min at 90 °C, Termamyl 300 L). All samples were analysed at the same time and a 'standard' sample of Norway spruce needles, with a known concentration of starch, was included (cf. Linder 1995).

Shoot water potential was measured on five occasions during May. Shoots from whorl 6, from six trees per treatment, were sampled in the early morning ($\approx$ 07.00 hours). To avoid drying of the shoots, they were immediately wrapped in plastic film, moistened with water, and kept in a refrigerator until processed.

Results

Soil warming

When soil warming commenced on 10 April, the snow depth on the studied plots was almost a metre (Fig. 1a). On the heated (IL) plot, the snow disappeared within three weeks, but on the (I) plot it remained for a further week. This difference was caused by heavy snowfall during the latter part of April, when more snow reached the ground in the open (I) stands than in the much denser
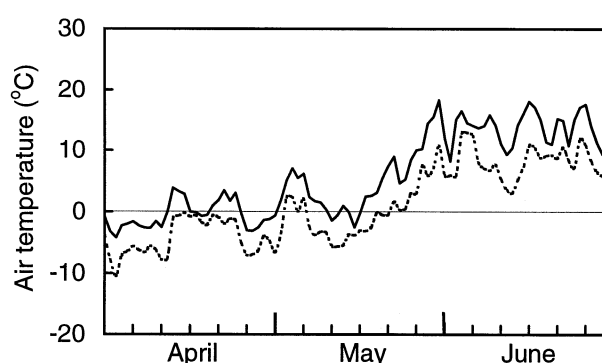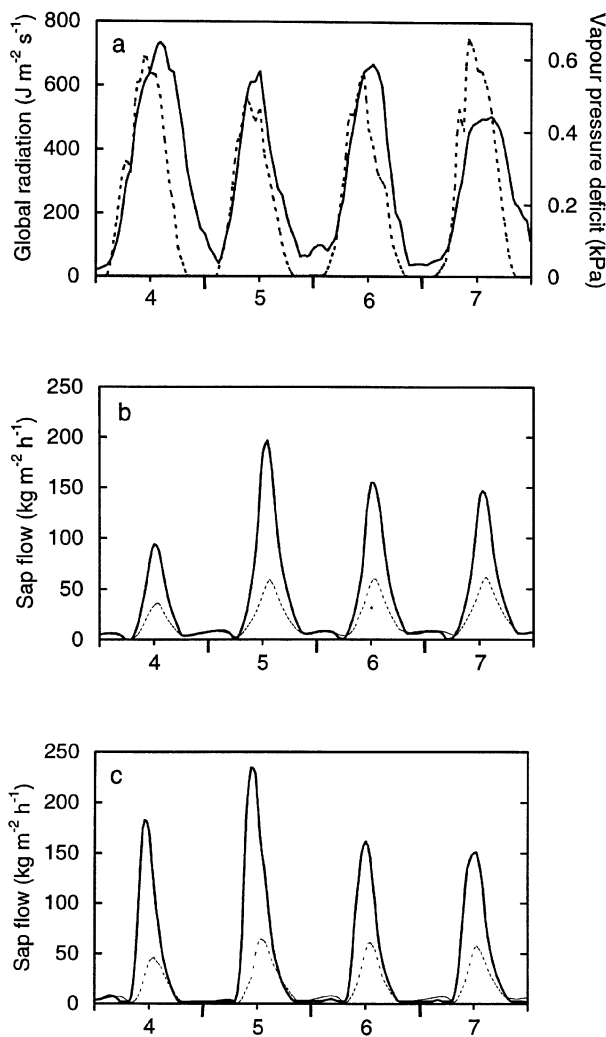
Fig. 3 Diurnal course of (a): total global radiation (broken line) and water vapour pressure deficit (solid line); (b) sapflow in trees growing on irrigated plots without (broken line) or with (solid line) soil warming, and (c) sapflow in trees growing on irrigated-fertilized plots without (broken line) or with (solid line) soil warming, during the period 4–7 May 1995. Presented values for sapflow are hourly means of four trees per treatment and are expressed per unit cross-sectional sapwood area. For further explanations, see text.

Fig. 4 Water potential in shoots from whorl 6 (from the top) of Norway spruce growing on irrigated (a) or irrigated-fertilized (b) plots, without (open symbols) and with (filled symbols) soil warming. Vertical bars indicate ± 1 standard deviation, and asterisks denote statistically significant differences (*$P < 0.05$; **$P < 0.01$). $N = 6$. For further explanations, see text.

Recovery of photosynthetic capacity

The rates of light-saturated photosynthesis (A_{max}), measured on detached shoots under controlled conditions in the laboratory, were low during April (Fig. 5a,b). During April there was no significant difference in A_{max} between shoots from heated and those from unheated plots, but throughout May, shoots from heated plots had significantly higher rates. The recovery of photosynthetic capacity, measured as A_{max}, was slow until daily mean temperatures began to increase in mid-May and night f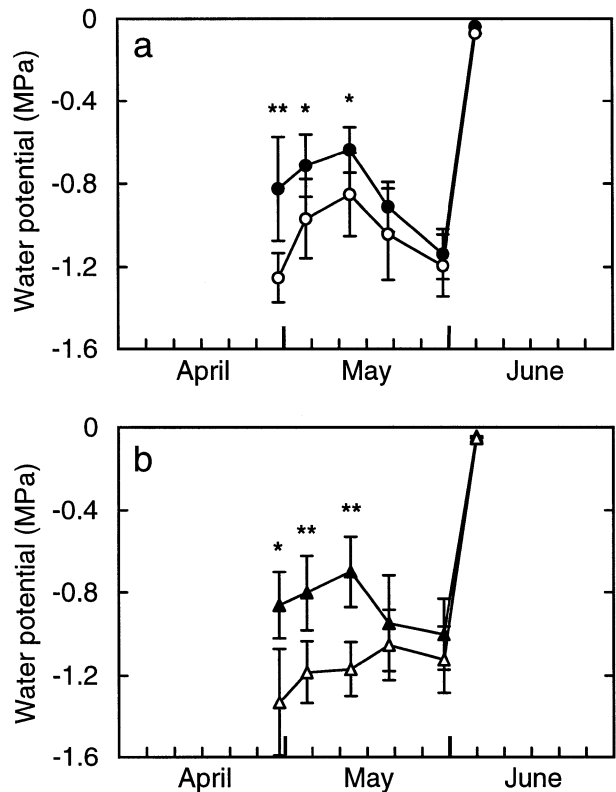rosts were less frequent (cf. Fig. 2). During spells of cold weather or severe night frosts, recovery was even set back, as was seen at the end of April and in mid-May. The rate of recovery was rapid during the second part of May, and by early June, all treatments seemed to have reached 'full' photosynthetic capacity (Fig. 5ab). In absolute terms, the fully recovered rates of A_{max} were 10–15% higher in shoots from (IL) plots than in those from (I) plots.

The recovery of maximum photochemical efficiency, expressed as the F_v/F_m-ratio (Fig. 6), followed the same general pattern as that seen in A_{max} (Fig. 5). The setback in recovery, seen in A_{max} in late April and mid-May (Fig. 5), was even more pronounced in terms of the F_v/F_m-ratio (Fig. 6). With the exception of one occasion, there was no significant difference in the F_v/F_m-ratio between treatments. There was, however, a tendency during April and May for shoots from trees on the heated (IL) plot to have higher F_v/F_m-values than shoots from the unheated plot (Fig. 6b). Maximum values of A_{max} and the F_v/F_m-ratio were attained in early June, independent of treatment, and were maintained during the remainder of the studied period.
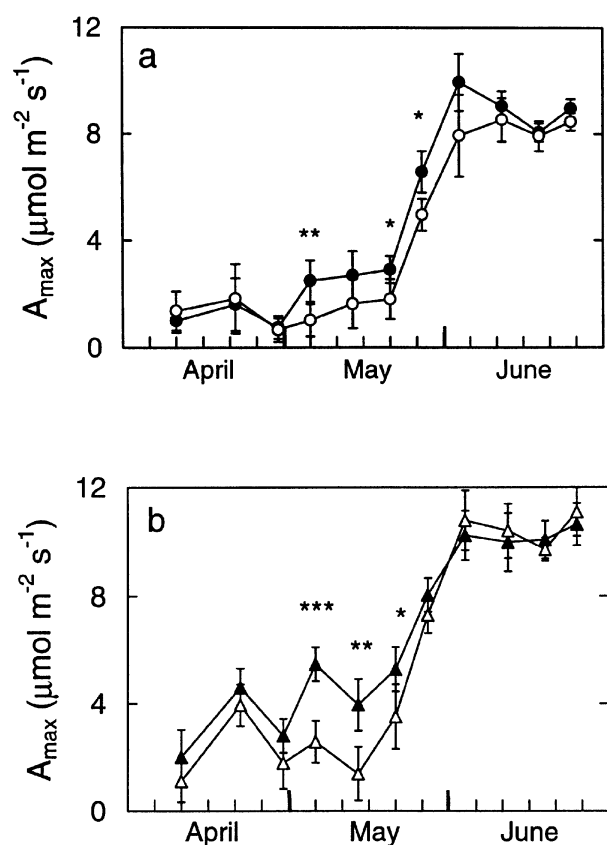
Fig. 5 The rate of light-saturated net photosynthesis (A_{max}) in one-year-old shoots of Norway spruce during spring and early summer. The shoots were taken from whorl 7 (from the top) of trees growing on irrigated (a) or irrigated-fertilized (b) plots, without (open symbols) and with (filled symbols) soil warming. Vertical bars indicate ± 1 standard deviation, and asterisks denote statistically significant differences (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$). $N = 6$. For further explanations, see text.

Fig. 6 Chlorophyll fluorescence (F_v/F_m) in one-year-old shoots of Norway spruce during spring and early summer. The shoots were taken from whorl 7 (from the top) of trees growing on irrigated (a) or irrigated-fertilized (b) plots, without (open symbols) and with (filled symbols) soil warming. On each occasion the standard deviations of the mean were 5% or less. For further explanations, see text.

When A_{max} (Fig. 5) and the F_v/F_m-ratio (Fig. 6) were compared on days when both measurements had been made, strong correlations ($R^2 = 0.88$–0.96) were found between the two methods used to monitor the recovery of photosynthetic capacity (Fig. 7). On irrigated plots (I) there was no difference between trees from heated and unheated plots (Fig. 7a). In trees on heated (IL) plots, however, there was a significantly faster rate (*t*-test, $P < 0.0001$) of recovery of A_{max} in relation to F_v/F_m than for trees from unheated plots (Fig. 7b).

Starch reserves began to accumulate in the needles in mid-April (Fig. 8), and peaked in early June in all treatments. From the latter part of April and throughout May, the starch concentration was higher in needles from (IL) plots, but there was no effect of soil warming. At the peak in June, the needle starch content was ≈ 25% of needle dry mass. The depletion of the starch reserves coincided with budbreak, which occurred around 10 June in all treatments (data not shown).
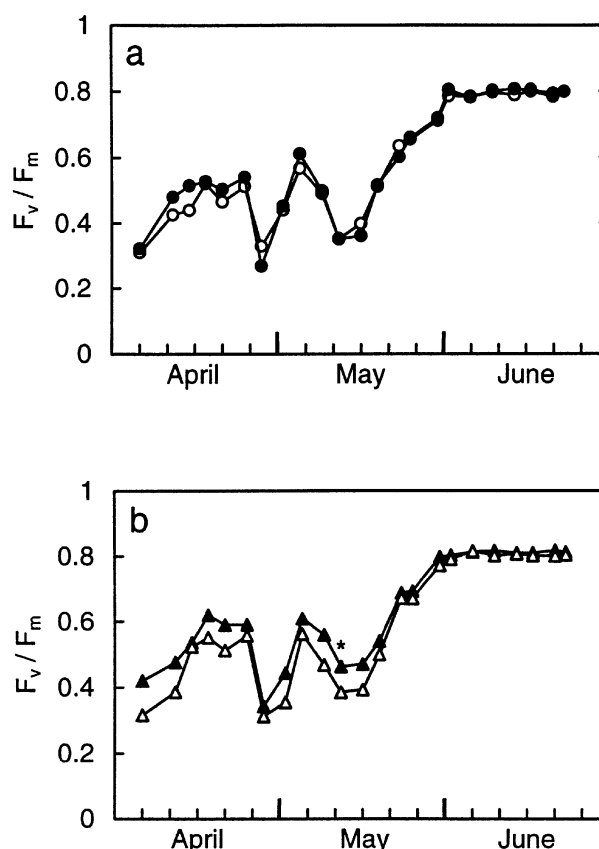
Discussion

The experimental manipulation of soil temperature functioned well, soil temperatures increasing almost instantaneously when the power was switched on in early April (Fig. 1). The target value, a temperature difference of 5 °C between unheated and heated plots, was not fully attained until the snow cover had thawed on heated plots. In relation to control plots, the period of unfrozen soil was extended by six weeks in plots with soil warming. It cannot be expected, however, to meet exactly the goal of extending the period with unfrozen soil by one month in spring, because an accurate date of snowmelt for each spring is almost impossible to predict beforehand. The starting date in spring must be based therefore on experience of the 'normal' time for snowmelt instead. This problem does not exist in autumn, when warming can be phased out as soon as the soil in the control plots freezes. Once the snow on the control plots had thawed, there was a rapid increase in soil temperatures, which
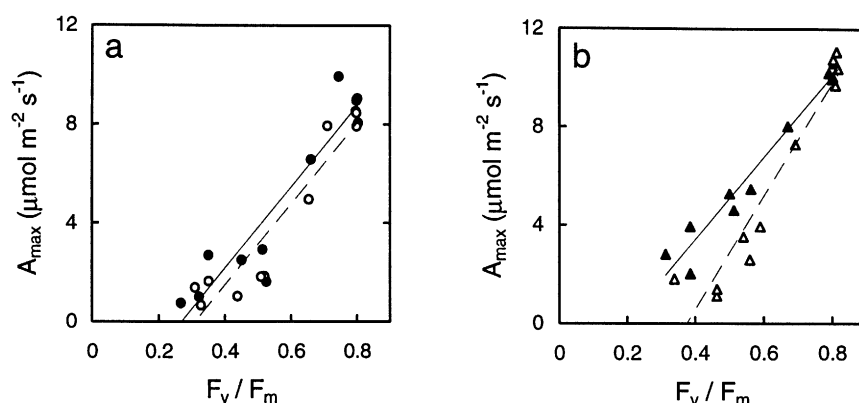
Fig. 7 The relationship between rates of light-saturated photosynthesis (A_{max}) and chlorophyll fluorescence (F_v/F_m) in one-year-old shoots of Norway spruce during late spring and early summer. The shoots were taken from whorl 7 (from the top) of trees growing on irrigated (a) or irrigated-fertilized (b) plots, without (open symbols) and with (filled symbols) soil warming. The linear regression are: Irrigated (I) control plot $y = 16.381x - 5.070$ ($R^2 = 0.896$, $P = 0.001$); heated I-plot $y = 16.455x - 4.429$ ($R^2 = 0.876$, $P = 0.005$); irrigated-fertilized (IL) control plot $y = 23.077x - 8.671$ ($R^2 = 0.916$, $P = 0.0009$), and heated (IL)-plot $y = 16.750x - 3.301$ ($R^2 = 0.963$, $P = 0.0003$).
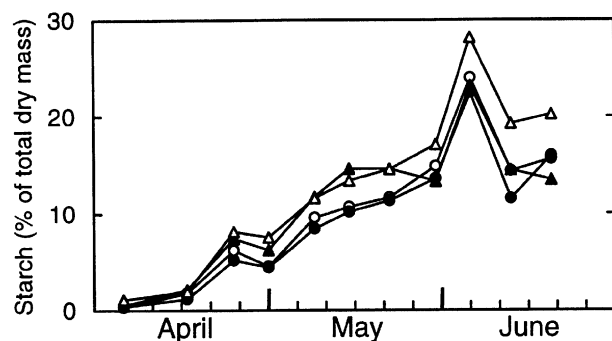

Fig. 8 The concentration of starch (% of dry mass) in one-year-old needles of Norway spruce during spring and early summer. The shoots were taken from whorl 7 (from the top) of trees growing on irrigated (circles) or irrigated-fertilized (triangles) plots, without (open symbols) and with (filled symbols) soil warming. For further details, see text.

agrees with findings by Day *et al.* (1989, 1990) from a study of the performance of Engelmann spruce (*Picea engelmannii*) and lodgepole pine *(Pinus contorta)* during snowmelt in the Rocky Mountains.

While snow still covered the ground on control plots, and their soil temperature remained close to 0 °C (Fig. 1), sapflow was strongly reduced as compared to trees on heated plots (Fig. 3), resulting in lower shoot water potentials on unheated than on heated plots (Fig. 4). The differences in rate of sapflow and water potential disappeared as soon as the snow had thawed and soil temperatures had increased. Similar results were reported by Day *et al.* (1990) from a short-term experiment in which soil temperature was manipulated during the period of snowmelt. In the present study, it was not possible to decide whether the differences observed in sapflow were the effect of soil temperature, water availab-

ility or both. It should be noted that, in the present study, sapflow measurements were not used to quantify sapflow, but as an indirect measure of water availability during the period of snowmelt and soil thaw. The sapflow gauges were installed in internodes close to breast height (130 cm), which means that a small proportion of the transpiring foliage was below the point at which sapflow was monitored (cf. Flower-Ellis 1996).

Most studies on the effects of soil temperature on water relations, gas exchange or both, in conifers have been made on potted seedlings, which have varied in terms of pretreatment and degree of hardening (cf. Day *et al.* 1990, 1991 and references therein). In consequence, the threshold at which soil temperature has been reported to have a pronounced effect on gas exchange varies by more than 10 °C. Results concerning gas exchange from long-term field manipulations of soil temperature are lacking, but in a short-term field experiment, DeLucia and Smith (1987) found a significant correlation between soil temperature and photosynthesis in Engelmann spruce (*P. engelmannii*).

The course of postwinter recovery of light-saturated photosynthesis (A_{max}) and chlorophyll *a* fluorescence (F_v/F_m) during April and May (Figs 5, 6), confirms earlier reports on the effect of air temperature, and severe night frosts (< -6 °C), on the rate of recovery in Norway spruce (Lundmark *et al.* 1988a, 1998; Hällgren *et al.* 1990; Strand & Lundmark 1995). The time course of A_{max} (Fig. 5) and chlorophyll fluorescence (Fig. 6) closely followed the trend in daily mean and minimum temperatures (Fig. 2), with recovery during mild days and reduced values after cold spells. The strong correlation between A_{max} and F_v/F_m (Fig. 7), and the lack of a significant soil warming effect on the rate of recovery during April, indicates that the observed recovery in

A_{max} was controlled by air temperature, rather than by soil temperature or the availability of soil water. The significant differences in A_{max}, between heated and unheated plots, were observed during the period in May when major differences in the rate of sapflow occurred (Fig. 3), as well as significant differences in shoot water potentials (Fig. 4). These observations indicate that water availability, or soil temperature, may have some effect on the rate of recovery. The major part of the recovery, however, occurred during the second half of May, when air temperatures rose and night temperatures stayed above freezing, which is in agreement with other studies on the recovery of photosynthetic capacity in Norway spruce (Lundmark *et al.* 1988a, 1998; Strand & Lundmark 1995).

The time course of starch accumulation (Fig. 8) followed the general pattern normally seen in needles of Scots pine (Ericsson 1978) and Norway spruce (Flower-Ellis 1993; Linder 1995) growing at high latitudes. The effect of soil warming on A_{max} during May (Fig. 5), was not reflected in the needle starch content (Fig. 8). The reason for the lack of agreement between A_{max} and needle accumulation of starch reserves may be that carbohydrates are accumulated rather as the result of photosynthetic performance, than of photosynthetic capacity. In the present study, all gas-exchange measurements were made on detached shoots, supplied with water and acclimated to room temperature, which implies that the results cannot be regarded as reflecting the performance of shoots in the field.

Soil warming had no effect on the timing of budbreak. An absence of effects of soil warming on the phenology of conifers has previously been reported by Van Cleve *et al.* (1990) and Lükewille & Wright (1997). No effects of soil cooling on the phenology of Norway spruce and Scots pine were found during a three-year field experiment in Finnish Lapland (Huikari & Paarlahti 1967).

In the limited number of long-term soil warming experiments in forest ecosystems, the major effects, during the initial stage, have been increased soil emissions of CO_2, increased uptake of methane (Peterjohn *et al.* 1993, 1994), and increased decomposition of the forest floor, resulting in increased amounts of extractable nitrogen and phosphorus (Van Cleve *et al.* 1990), and increased concentrations of nitrate and ammonium in runoff (Lükewille & Wright 1997). It is still unclear whether some of these effects may be transient, which emphasizes the need for long-term soil warming experiments. Such experiments are especially important at high latitudes, where the structure, function, and biogeochemistry of forest ecosystems may change drastically in response to climatic warming (cf. Melillo *et al.* 1990; Bonan 1993; Kirschbaum & Fischlin 1996).

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