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Growth of mature boreal Norway spruce was not affected by elevated [CO_2] and/or air temperature unless nutrient availability was improved

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The growth responses of mature Norway spruce (*Picea abies* (L.) Karst.) trees exposed to elevated [CO_2] (C_E; 670–700 ppm) and long-term optimized nutrient availability or elevated air temperature (T_E; +3.9 °C) were studied in situ in northern Sweden in two 3 year field experiments using 12 whole-tree chambers in ca. 40-year-old forest. The first experiment (Exp. I) studied the interactions between C_E and nutrient availability and the second (Exp. II) between C_E and T_E. It should be noted that only air temperature was elevated in Exp. II, while soil temperature was maintained close to ambient. In Exp. I, C_E significantly increased the mean annual height increment, stem volume and biomass increment during the treatment period (25, 28, and 22%, respectively) when nutrients were supplied. There was, however, no significant positive C_E effect found at the low natural nutrient availability. In Exp. II, which was conducted at the natural site fertility, neither C_E nor T_E significantly affected height or stem increment. It is concluded that the low nutrient availability (mainly nitrogen) in the boreal forests is likely to restrict their response to the continuous rise in [CO_2] and/or T_E.

Keywords: boreal forest, global climate change, nitrogen limitation, *Picea abies*.

Introduction

Boreal forests constitute ~30% of the earth's forested area and play a crucial role in the global carbon cycle (e.g., Malhi et al. 1999), and are in many aspects different from other forest biomes. The boreal forests are dominated by coniferous trees growing in cool climates and most of their nitrogen (N) pool is locked up in soil organic matter with low turnover rate. Other forest types typically contain most of their ecosystem N in live biomass (Lukac et al. 2010). In the boreal forest, low nutrient availability (mainly N) has been identified as a key growth-limiting factor (cf. Tamm 1991, Linder 1995, Hyvönen et al. 2007, Lukac et al. 2010).

Atmospheric concentration of CO_2, [CO_2], is predicted to double before 2100, which is likely to lead to an increase in the earth's annual temperature in the range of 2.0–4.5 °C (IPCC 2007). Since CO_2 is the substrate for photosynthesis, the first step in the growth processes of plants, its rise may have a direct effect on forest productivity. Numerous studies have shown that the exposure to elevated [CO_2] almost always leads to an increase in the photosynthetic response (see reviews by Curtis 1996, Saxe et al. 1998, Ainsworth and Long 2005, Hyvönen et al. 2007, Wang et al. 2012). It has, however, also been found that the stimulation of aboveground tree growth in elevated [CO_2] is much more variable than the response of leaf photosynthetic rates (e.g., Koch and Mooney 1996, Curtis and Wang 1998, Nowak et al. 2004, Körner 2006, Hyvönen et al. 2007, Wang et al. 2012). It has therefore been questioned if it is justified to assume a direct relationship between canopy photosynthesis and aboveground growth (cf. Körner 2006, Hyvönen et al. 2007).

While some [CO_2] enrichment studies on field-grown boreal or temperate trees have found significant increases in aboveground growth (e.g., Peltola et al. 2002, Riikonen et al. 2004, Zak et al. 2007), others have not. Notably, a number of CO_2-enrichment studies at sites with low soil fertility have shown no additional aboveground growth or even a slight reduction (Curtis et al. 1994, Kubiske et al. 1998, Oren et al. 2001, Sigurdsson et al. 2001, Pokorný et al. 2010, Norby and Zak 2011). Similar responses have been found when mature trees have been exposed to elevated [CO_2] close to the altitudinal treeline at more southern latitudes (Hättenschwiler and Körner 1998), but the response of different tree species may differ (Dawes et al. 2011). Other studies at sites with low fertility have shown how an initial [CO_2]-induced growth response diminishes in a few years after the start of the exposure, as increased nutrient use caused by enhanced growth lowers the available soil nutrients (Oren et al. 2001, Norby et al. 2010). This has been termed 'progressive nitrogen limitation' (Luo et al. 2004). Some of these studies have included nutrient additions as an experimental factor, which has resulted in a significant increase of the aboveground growth responses to elevated [CO_2] (Hättenschwiler and Körner 1998, Kubiske et al. 1998, Oren et al. 2001, Sigurdsson et al. 2001, Norby et al. 2010). Nutrient inputs do, however, not always enhance the [CO_2]-enrichment effects on aboveground growth. In cold climates such as in the alpine, CO_2 enrichment had no or negative effects on plant growth, irrespective of nutrient inputs (Inauen et al. 2012). When meta-analyses have been used to compare the vast literature on CO_2-exposure experiments at high and low nutrient availability, some have found large effects on aboveground growth (Curtis and Wang 1998, Nowak et al. 2004), but some have not (Ainsworth and Long 2005).

In the boreal region of northern Eurasia, air temperature or temperature sum during the growing season has commonly been identified as the main climatic factor controlling stem diameter or volume growth in Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L. [Karst.]) (e.g., Henttonen 1984, Briffa et al. 1990, Miina 2000, Seo et al. 2008, Lloyd et al. 2011). Changes in ambient temperature may, however, induce a range of responses in trees and in forest ecosystems (Lukac et al. 2010) and strongly interact with other environmental and physiological factors, such as nutrient turnover rate and changed allocation patterns (Morison and Lawlor 1999, Hyvönen et al. 2007, Way and Oren 2010). Many different experimental approaches have been used to evaluate the effects of warming on plant production, including, (i) monitoring of natural variation in temperature and production at single sites, (ii) climate gradient studies, (iii) experimental warming of plants or whole ecosystems and (iv) process-based modelling of plant and ecosystem responses to warming (cf. Rustad 2008). Similar to [CO_2] enrichment, increased ambient temperature can increase photosynthetic rates (e.g., Hall et al. 2013) and plant productivity (Rustad et al. 2001, Saxe et al. 2001, Way and Oren 2010), even if the variability in experimental findings is high (Morison and Lawlor 1999, Bronson et al. 2009). Often, the size of the response has been found to diminish towards lower latitudes or increased mean annual temperatures (Norby and Luo 2004, Way and Oren 2010). Relatively few manipulation studies have focused on changes in biomass growth of field-grown trees in response to elevated temperature in combination with other environmental factors (Lukac et al. 2010). As stated in a recent review on experimental warming on tree growth by Way and Oren (2010), trees from cold environments may show either large positive or negative growth responses to warming depending on other limiting factors, such as water and nutrients.

Nutrient and water optimization experiments have shown that growth and yield of Norway spruce in Sweden is to a large extent limited by both nutrient and water availability in the south, but nutrient availability alone in the north (Linder 1995, Bergh et al. 1999). Bergh et al. (2005) estimated the potential growth for Norway spruce in Sweden and found that in the current climate, potential yield could be increased by 100–300% from south to north, if limitations by water and nutrient availability were eliminated. This potential effect is as large as the range in the observed mean production of Norway spruce across these latitudes (55–68 °N), which highlights the potential importance of interactive effects between nutrients, water and temperature (length of the growing season) in warming experiments.

The present paper presents results from two separate studies on field-grown mature Norway spruce trees using whole-tree chambers (WTCs) with temperature and [CO_2] control. In the first experiment (Exp. I), the effect of site fertility on the response of elevated [CO_2] was studied. In the second experiment (Exp. II), the effects of elevated temperature and [CO_2] were studied separately and in combination at the natural site fertility. Each experiment lasted for 3 years and the treatments were continuous throughout the study periods. Our goal was to test the hypothesis that neither elevated [CO_2] nor elevated aboveground temperature would significantly enhance the growth of mature Norway spruce trees growing in the boreal zone, unless site fertility was improved by fertilization. To avoid the effects of elevated soil temperature on nutrient availability (cf. Strömgren and Linder 2002), only the aboveground part of the trees was warmed.

Material and methods

Twelve WTCs, with temperature and [CO_2] control, were used in two separate experiments with mature Norway spruce (*Picea abies* (L.) Karst.) trees. In the first experiment (Exp. I), the effect of site fertility (nutrient availability) on the response of elevated [CO_2] was studied, and in the second experiment (Exp. II) the

effects of elevated temperature and [CO_2] were studied, at the natural site fertility, separately and in combination.

Site description

The study was conducted in a long-term nutrient optimization experiment at Flakaliden (64°07′N, 19°27′E, 310 m a.s.l.) in northern Sweden. The nutrient optimization experiment was established in 1986 in a Norway spruce stand, planted in 1963 with 4-year-old seedlings of local provenance (Linder 1995, Bergh et al. 1999), after clear-felling and prescribed burning.

Soil at the site is a thin well-developed iron podzolic, sandy, post-glacial till of gneissic origin with a mean depth of ~120 cm, with a 2–6-cm thick humus layer and with soil water content normally not limiting for tree growth (Bergh et al. 1999).

The nutrient treatments, which began in 1987, included untreated control stands, irrigation and two nutrient optimization treatments. The treatments were replicated four times in a randomized block design. Each replicate consisted of 50 × 50 m plots. Only two of the four treatments were used in the present [CO_2]-enrichment study. These treatments were the non-fertilized control (C) and the irrigation combined with liquid fertilization (IL). In the IL treatment, all essential macro- and micronutrients were supplied in irrigation water every second day during the period of active growth (early June–mid-August). The amount of irrigation was set to maintain soil water potential above –100 kPa. In total, the IL treatment had received 900 kg N ha^{-1} and all other nutrients in optimum proportion to N (cf. Linder 1995) when the WCT treatments started. During the WCT treatment period, another 225 kg N ha^{-1} was added. For further details of experimental design of the nutrient treatments, see Linder and Flower-Ellis (1992) and Linder (1995).

Nitrogen deposition in the region averages 3 kg ha^{-1} a^{-1} (cf. SMHI 2009, Karlsson et al. 2011, 2012). The IL treatment has reduced C/N ratios in the organic humus layer from 39 to 32 for the C treatment and increased net mineralization rates from 4 to 18 kg N ha^{-1} a^{-1}, respectively, while nitrification rates are unaffected (from 0.4 to 0.5 kg N ha^{-1} a^{-1}) as well as N leaching (<1 kg N ha^{-1} a^{-1}) (Andersson et al. 2002). Annual fine-root production is lower in the IL treatment than in the C treatment and the turnover rates of fine roots are higher there (Majdi and Öhrvik 2004).

The site belongs to the middle boreal sub-zone (Sjörs 1999). The site has a harsh boreal climate with long cool days in the summer and short cold days in the winter. The mean annual air temperature is 2.4 °C and mean monthly temperature varies from –7.5 °C in February to 14.6 °C in July (mean for 1990–2009). Mean annual rainfall is ~600 mm with approximately one-third falling as snow, which usually covers the frozen ground from mid-October to early May. The length of the growing season (the period with a daily mean air temperature ≥+ 5 °C) averages ~150 days, but with large between-year variations. For detailed information on the climatic conditions for the study period, 1996–2004, see Figure 1 and Table 1.

Chamber design

Briefly, the WTCs consisted of three main sections: the chamber base, containing a sealed soil compartment, the tree chamber (aboveground compartment) and the cooling unit. Additional chamber sections were added when required to accommodate tree height growth during the experiment. Air from the tree chamber was recirculated over a heat exchanger inside the cooling unit by a powerful fan sufficient to maintain turbulent flow around the entire canopy.

Fresh air was continuously added to the WTCs such that the internal chamber volume turned over approximately once per hour. Such slow turnover required that water be condensed by cooling the air in the heat exchanger and CO_2 be added to maintain steady-state conditions within the chamber. An infrared CO_2 gas analyser in each chamber (SBA-1, PP Systems, Hitchin, UK) was used to monitor chamber [CO_2] at 90-s intervals. To maintain the target [CO_2], pure CO_2 was injected into the circulating chamber air through a magnetic valve (Bürket, Germany). The pure CO_2 was supplied from a set of tanks (AGA, Sweden) containing liquefied CO_2. Vapour pressure deficits were maintained within SD = 0.02 of ambient levels.

Two micro-sprinklers were installed under the chamber floor and the trees received irrigation equivalent to precipitation measured with rain gauges outside the WTCs. Trees in the WTCs in the IL-stand were also receiving nutrient solution every second day during the growing season. The equivalent of winter precipitation was applied in the form of irrigation water in early spring.

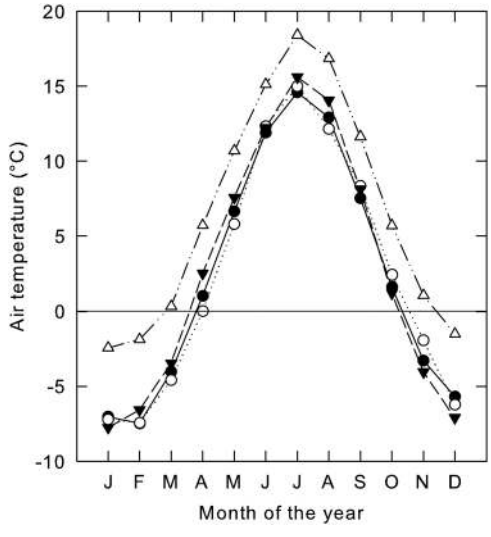

Figure 1. Long-term mean monthly air temperature at Flakaliden (1990–2009; filled circles), during Exp. I (1997–2000; open circles), during Exp. II (2001–04; filled triangles) and in the T_E treatment in Exp. II (open triangles).

Table 1. Some climatic variables for Flakaliden experimental forest in 1996–2004 and the mean values for 20 years (1990–2009). Highest/earliest and lowest/latest values are shown in bold font, indicating how variable individual years can be in the Boreal zone.

	Experiment I					Experiment II				20-year mean
	1996	1997[1]	1998	1999	2000[2]	2001	2002	2003	2004[2]	
Annual										
Irradiance (W m^{-2} a^{-1})	3063	**3317**[3]	**2776**[4]	3059	2802	2965	3207	3036	2897	3018
Precipitation (mm a^{-1})	575	549	736	572	**906**[3]	857	**533**[4]	557	634	645
Mean temperature (°C)	**1.6**[4]	2.1	1.7	2.4	**3.4**[3]	2.3	**3.4**[3]	2.8	2.3	2.5
Temperature sum (day degrees ≥5°C)	**839**[d]	1012	849	967	920	1032	**1301**[c]	1016	867	912
Growing season (May–September)										
Irradiance (W m^{-2})	2235	**2454**[3]	**1976**[4]	2330	2074	2177	2448	2248	2092	2226
Precipitation (mm)	271	279	425	**188**[4]	497	**536**[3]	255	337	388	339
Mean temperature (°C)	**10.1**[4]	11.2	10.2	10.9	10.5	11.3	**13.2**[3]	11.2	10.4	10.7
Temperature sum (day degrees ≥5 °C)	**832**[4]	1012	835	959	850	989	**1281**[3]	984	851	912
Start of season (date)	May 20	**May**[4] **30**	April 28	May 17	May 13	May 2	April 21	**April**[3] **18**	April 28	May 2
End of season (date)	Oct 8	Sept **26**	Sept 24	Oct 4	Oct 13	**Oct**[4] **17**	**Sept**[3] **17**	Sept 23	Oct 5	Sept 27
Length of growing season (days)	141	**120**[4]	150	140	153	**168**[3]	150	159	161	148

[1]WTCs installed, but operated at ambient T and [CO_2].
[2]The trees were harvested last week of September 2000 and 2004, respectively.
[3]Highest or earliest values.
[4]Lowest or latest values.

Table 2. Treatment variables in Exp. I and II: nutrient supply (amount added before Exp. I in brackets), treatment variables either as elevated (elev) or ambient (amb), annual mean [CO_2], seasonal means of temperature in air (T_{AIR}) and soil (T_{SOIL}), and vapour pressure deficit (VPD). Variation between chambers and outside reference trees (R) is given as standard deviation. Variation between chambers ($n = 3$) is given as standard deviation. The variables, except for [CO_2], were only measured at one point per plot.

Experiment/ treatments	Treatment variables			[CO_2] Annual mean	Temperature May–Sep		Temperature Oct–Apr		VPD May–Sep	VPD Oct–Apr
	Nutrients[1] (N kg ha^{-1})	CO_2	T	(μmol mol^{-1})	T_{AIR} (°C)	T_{SOIL} (°C)	T_{AIR} (°C)	T_{SOIL} (°C)	(kPa)	(kPa)
Experiment I										
C outside WTCs	0	amb	amb	364 ± 1	10.3	8.6	–3.7	0.0	0.42	0.15
IL outside WTCs	225 (900)	amb	amb	363 ± 0	10.0	8.0	–3.7	–0.2	0.42	0.15
T_AC_A	0	amb	amb	365 ± 2	10.5 ± 0.1	9.5	–2.9 ± 0.3	0.1	0.47 ± 0.02	0.16 ± 0.01
T_AC_A-IL	225 (900)	amb	amb	366 ± 3	10.0 ± 0.3	8.8	–3.3 ± 0.1	0.0	0.40 ± 0.04	0.14 ± 0.01
T_AC_E	0	elev	amb	666 ± 3	10.4 ± 0.1		–3.1 ± 0.2		0.45 ± 0.02	0.15 ± 0.01
T_AC_E-IL	225 (900)	elev	amb	677 ± 3	10.1 ± 0.1		–3.4 ± 0.1		0.41 ± 0.01	0.14 ± 0.01
Experiment II										
Outside WTCs	0	amb	amb	368 ± 1	12.5	10.8	–3.6	0.3	0.59	0.13
T_AC_A	0	amb	amb	374 ± 1	12.6 ± 0.1	10.9 ± 0.8	–2.9 ± 0.2	0.6 ± 0.1	0.61 ± 0.16	0.17 ± 0.02
T_EC_A	0	amb	elev	371 ± 2	15.6 ± 0.0	11.3 ± 0.2	1.4 ± 0.2	1.6 ± 0.4	0.92 ± 0.35	0.34 ± 0.18
T_AC_E	0	elev	amb	697 ± 4	12.6 ± 0.0	10.6 ± 0.3	–2.8 ± 0.2	0.7 ± 0.2	0.62 ± 0.17	0.18 ± 0.01
T_EC_E	0	elev	elev	704 ± 3	15.5 ± 0.0	11.1 ± 0.5	1.4 ± 0.0	1.6 ± 0.1	0.93 ± 0.14	0.35 ± 0.01

[1]Other nutrients in proportion to N (cf. Linder 1995).

Soil temperature and soil volumetric water content were measured with Pt100 thermistors and Theta probes (Thetaprobe ML1, Delta-T Devices Ltd, Cambridge, UK) at 10- and 15-cm depths, respectively, in the mineral soil under the base section of the WTCs and at three nearby positions outside the WTCs. During winter snow cover was simulated by placing insulation material on the floor of the chamber sections.

Further general details on the WTCs and their [CO_2], air temperature and humidity control can be found in Wallin et al. (2001), Medhurst et al. (2006) and Slaney et al. (2007) and specific details regarding Exp. I and Exp. II are given in Table 2.

Air temperature and [CO_2] treatments

Experiment I

In 1996, the 12 WTCs were installed at the site to continuously measure the aboveground gas exchange of individual trees at ambient temperature (T_A) and [CO_2] (C_A) or C_A and elevated [CO_2] (C_E), (cf. Wallin et al. 2001, Medhurst et al. 2006). The

WTCs were installed around individual trees, six in a non-fertilized control stand (C) and six in an irrigated-fertilized (IL) stand.

To compare the variation in gas exchange among the trees, all WTCs were, during the first year (1997), operated at ambient [CO_2]; the elevated [CO_2] treatment commenced in early spring 1998 and continued until last week of September 2000. The temperature in the WTCs continuously tracked the outdoor ambient air temperature, as measured in the stand adjacent to the chambers. The target [CO_2] in the ambient and elevated chambers was 365 and 700 μmol mol^{-1}, respectively. The [CO_2] enrichment was applied to three non-fertilized and three fertilized trees, thus creating a 2×2 factorial experiment. Altogether, four treatments were included in Exp. I (T_AC_A, T_AC_E, T_AC_A-IL, T_AC_E-IL). When the measurements began in 1997 the average height of the chamber trees was 4.3 ± 0.2 m (C) and 7.5 ± 0.4 (IL), respectively. Data on leaf N status of WTC treatment trees can be found in Ceschia (2001).

Experiment II

In the second experiment, which commenced in mid-August 2001, the effects of elevated temperature (T_E) and [CO_2] (C_E) were studied separately or in combination. WTCs held at ambient temperature (T_A) were continuously tracking the outdoor ambient air temperature as in Exp I. The T_E treatment was designed to simulate the likely air temperature at the site in 2100 as predicted by the Swedish Regional Climate Modelling Programme, SWECLIM (Christensen et al. 2001, Räisänen et al. 2001), using the latitude of Flakaliden and a [CO_2] of 700 μmol mol^{-1}. The temperature elevation target was following the SWECLIM predictions (Figure 1), with a monthly temperature increase above actual T_A ranging between +2.8 °C (July, August) and +5.6 °C (December), resulting in an increase of the mean annual temperature by 3.9 °C, and during the growing season (May–September) by 3.0 °C (Table 1). To simulate these predictions, the temperature target in the T_E treatment was altered on a monthly time step (cf. Medhurst et al. 2006, Slaney et al. 2007).

The targets for [CO_2] were the same as in Exp. I., i.e., 365 and 700 μmol mol^{-1}, for ambient (C_A) and elevated (C_E) WTCs, respectively. Four combinations were studied, T_AC_A, T_EC_A, T_AC_E and T_EC_E, with three replicates of each treatment. The trees were exposed to the treatments throughout the year, from June 2001 to the last week of September 2004.

The air temperature, soil temperature, [CO_2] and vapour pressure deficit inside and outside the WTCs during each of the two experiments are given in Table 2. Data on leaf N status of WTC treatment trees can be found in Hall et al. (2009).

Harvest measurements

At the end of each experimental period, all trees were harvested, using the same sampling protocol. The harvest took place during the last week of September 2000 and 2004, respectively, which was after three complete years of exposure and after the annual growth had terminated.

Breast height (BH, 1.3 m) and northern aspect had been marked on all trees prior to harvest. The stump of each tree was cut 5 cm above the soil surface with a chainsaw and each tree was either lifted out by hand (non-fertilized trees) or by a building crane (IL trees), and laid on trestles with the north side facing upwards. A measurement tape was fitted along the stem and both total height (H) and depth of the living crown was recorded. Dead branches below the living crown were cut, counted and weighed. The living crown was divided into five strata of equal depth, with stratum one located at the top of the crown.

In each stratum, a sample branch was chosen at random and cut. Fresh mass (FM) of each sample branch was measured using a digital scale (±0.5 g), thereafter the branches were stored in a freezer at –18 °C until further processing. The remaining whorl, internodal and dead branches were then removed separately from each stratum, counted and weighed (±1 g).

The location of stem-disks was marked by a waterproof pen: at the base, BH, 40% of height (D40) and on the middle of the annual stem increments of the last 4 years. The length of the last 10 annual height increments was measured on the stem. The stem was then cut with a handsaw into three to four sections, and the FM of each section was determined. Two 5-cm stem disks were cut from each of the seven pre-marked locations, one of which was used for the determination of FM and dry mass (DM). Fresh mass was measured immediately after the disk was cut (±0.01 g). The second disk was used to determine the heartwood diameter (Exp. I only) and for tree-ring analysis. The disks were stored in the freezer at –18 °C until further processing.

Laboratory analyses

Specific needle area (SLA) of different age classes of needles from each sample branch was determined by measuring the projected needle area of ca. 40 needles per age-class and branch with a scanner and the winSEEDLE™ program (Version 5.1 A, Regent Instruments inc., Blain, QC, Canada), and then drying them for 48 h in 80 °C and weighing. All sample branches (Exp. 1 and 2) were also dried at 80 °C in a ventilated oven for 24 h, separated into needles of different age-classes and wood, and then dried for another 24-h period before the DM of each fraction was determined. The whole-tree needle area of each tree was determined by using SLAs, the relative needle age-class distribution on sample branches and their needle mass fraction relative to the total branch mass in each stratum.

Stem disks, for which FM had been recorded, were dried for 72 h at 80 °C, or until they stopped losing weight, whereafter they were weighed for DM. Tree rings and bark fraction were

measured with a LINTAB tree-ring measuring device (Frank Rinn, Heidelberg, Germany) and the software TSAP (version 3.0). Each ring was measured along four lines drawn from the pith (north, east, south, west). The resolution of the tree ring machine was 1/1000 mm. Total carbon concentration of individual tree rings and their mean density were also measured by chemical analysis and X-ray densitometry (cf. Kostiainen et al. 2004, 2009); in Exp. I, the $\delta^{13}C$ of the individual tree rings at BH and needles were also determined (Marshall and Linder, 2013).

Data and statistical analyses

Annual changes in stem volume (V_s) <40% of height of each tree were calculated from the tree ring data by Smalian's formula for the frustum of a paraboloid (Pardé 1980):

$$V_s = L_s \frac{(A_{s1} + A_{s2})}{2} \quad (1)$$

where L_s is the length of the log between two stem disks (base and BH, BH and D40, etc.) and A_{s1} and A_{s2} are the elliptic cross-sectional areas of the two stem disks. Since the trees had reached the D40 height within the past 12 years, L_s was derived from annual height changes after that point. The V_s of the section containing the annual top shoot was calculated as an elliptic cone.

Despite the chamber trees being co-dominant trees, considerable differences in tree size and annual volume increment existed before the exposure periods started. Therefore, before any treatment effects were analysed, the volumes or DM increments were normalized using the average volume or DM increment for the 2 years before the exposure periods started (cf. Asshoff et al. 2006). Another way to compare growth responses of different sized individuals is to calculate their average stem growth efficiency during the exposure period, i.e., average stem growth divided by total needle area, which was also done.

All statistical analyses were performed with SAS 9.2 statistical software. The normality of the data was checked by reviewing normal probability plots and making Shapiro–Wilk tests before comparing any treatment differences. The analysis included repeated measures, with year as a class variable and where the covariance between individuals and treatment was estimated for each year. Treatment differences were compared with two- or three-way analysis of variance (ANOVA), where elevated [CO_2], year of exposure and nutrient treatment (Exp. I) or temperature treatment (Exp. II) were the main factors. When interactions were significant, post-ANOVA Fisher's least significant difference (LSD) tests were used to further investigate the treatment differences.

Results

Basic whole-tree measurements

The long-term nutrient optimization that started in 1987 had produced trees of significantly different stature in Exp. I (Table 3). By year 2000, tree height, DBH, needle, stem,

Table 3. Tree height, diameter at breast height (DBH, on bark), heartwood diameter at breast height (BH), stem, branch (including needles) and total aboveground biomass of Norway spruce trees at the Flakaliden experimental forest in late September 2000 (Experiment I) and 2004 (Experiment II). Values are mean values ± 1 SEM ($n = 3$). Also shown are P values for two-way ANOVA. Significant differences are shown in bold font and nd stands for 'not determined'.

Treatments	Height (m)	DBH (cm)	BH (cm)	Biomass		
				Stem (kg tree^{-1})	Branch (kg tree^{-1})	Total (kg tree^{-1})
Experiment I						
T_AC_A	6.8 ± 0.5	8.3 ± 0.7	1.0 ± 0.5	7.5 ± 1.8	10.6 ± 3.2	18.1 ± 5.0
T_AC_E	6.3 ± 0.5	8.2 ± 0.2	0.8 ± 0.4	7.0 ± 0.9	10.1 ± 1.5	17.1 ± 2.4
T_AC_E-IL	10.3 ± 0.3	14.7 ± 0.2	1.4 ± 0.5	32.6 ± 8.9	27.2 ± 8.3	59.9 ± 17.1
T_AC_A-IL	10.3 ± 0.7	15.5 ± 1.9	2.4 ± 0.3	27.5 ± 0.3	28.6 ± 2.8	56.1 ± 2.9
Experiment II						
T_AC_A	6.5 ± 0.4	7.7 ± 0.4	nd	7.0 ± 0.9	6.8 ± 0.6	14.3 ± 1.2
T_AC_E	7.1 ± 0.5	8.1 ± 0.8	nd	10.6 ± 3.7	8.7 ± 1.9	20.4 ± 5.9
T_EC_A	7.3 ± 0.4	9.1 ± 2.6	nd	8.3 ± 1.9	6.6 ± 1.6	15.5 ± 3.5
T_EC_E	6.1 ± 0.4	7.4 ± 1.0	nd	6.1 ± 1.0	5.6 ± 1.0	12.1 ± 2.1
Statistical analysis						
Exp. I – ANOVA	**<0.001**	**0.001**	0.12	**0.007**	**0.04**	**0.02**
[CO_2] trees	0.70	0.68	–	0.56	0.93	0.80
Fertilized trees	**<0.001**	**<0.001**	–	**0.001**	**0.006**	**0.002**
[CO_2] × Fertilization	0.61	0.72	–	0.62	0.84	0.88
Exp. II – ANOVA	0.34	0.50	nd	0.48	0.25	0.38
[CO_2] trees	–	–	–	–	–	–
Temperature trees	–	–	–	–	–	–
[CO_2] × Temperature	–	–	–	–	–	–

branch and total aboveground biomass had in the IL treatment, compared with the non-fertilized trees, increased by 57, 83, 286, 314, 170, and 230%, respectively (Table 3). None of the basic whole-tree parameters were, however, significantly altered between C_A and C_E treatments at the end of the 3-year exposure period in Exp. I (Table 3). Similarly, the 3-year exposure to C_E and/or T_E treatments of non-fertilized trees in Exp. II did not significantly affect any of the basic whole-tree parameters compared with the C_A and T_A treatments (Table 3).

Annual height increment

In Exp. I, there was a strong significant interaction between elevated [CO_2] and the nutrient treatment on the height increment (Table 4). This was caused by a 23% increase in mean annual height increment in C_E when nutrients were simultaneously supplied (Figure 2; T_AC_E-IL–T_AC_A-IL, $P < 0.006$, LSD test). However, elevated [CO_2] did not significantly change the mean annual height increment at the natural nutrient availability (T_AC_E–T_AC_A) in either Exp. I (–10%) or Exp. II (–5%; Figure 2; Table 4).

In Exp. II, elevated air temperature did not significantly alter the height increment at the natural nutrient availability (+1 and –6% at T_EC_A and T_EC_E, respectively; Figure 2, Table 4). Mean annual height increment in Exp. II, across all treatments, was 33, 46 and 41 cm in 2002, 2003 and 2004, respectively (data not shown). The smaller height increment in 2002 caused the significant annual variation ($P = 0.03$) seen in Table 4.

Annual stem volume and stem biomass increment in Exp. I

Mean annual stem volume increment in the fertilized T_AC_A-IL treatment was on average 186% higher during 1998 to 2000 than for trees in the non-fertilized control stand (Figure 3a). The fertilization response was highly significant (Table 4). When the mean annual stem growth of the T_AC_A-IL treatment was expressed as biomass (g carbon $tree^{-1}$) (Figure 3b), the relative increase was somewhat smaller, or 148% (Figure 3b), but the fertilization response was still highly significant (Table 4).

Elevated [CO_2] did not significantly change the volume increment across the two nutrient treatments in Exp. I ($P = 0.06$), while the interaction between C_E and fertilization was significant

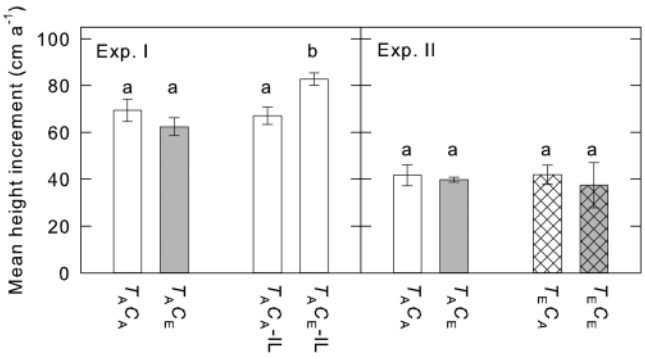

Figure 2. Mean annual height increment of Norway spruce trees grown in WTCs at Flakaliden during 1997–2000 (Exp. I) and 2001–04 (Exp. II), respectively. The treatments were: Exp. I, trees grown for 3 years in ambient or elevated [CO_2] at ambient temperature in non-fertilized (T_AC_A and T_AC_E), and fertilized stands (T_AC_A-IL and T_AC_E-IL), respectively; Exp. II, trees grown for 3 years in a non-fertilized stand at ambient or elevated temperature (T_AC_A and T_EC_E) and ambient or elevated [CO_2], separately or in combination. Lateral bars represent SE ($n = 3$). Different letters show a significant treatment difference ($P < 0.05$) as indicated by post-ANOVA LSD tests. For further statistical analysis of the data, see Table 4.

Table 4. *P* values from two-way and three-way ANOVA for treatment effects on different growth traits of mature Norway spruce trees grown in ambient and elevated [CO_2] at contrasting nutrient availability 1998–2000 (Experiment I), and in ambient or elevated [CO_2] and air temperature, separately or in combination, 2001–04 (Experiment II) at the Flakaliden experimental forest. Significant differences are shown in bold font. Data are shown in Figures 2–4.

ANOVA	Height increment	Volume increment	Biomass increment	Growth efficiency
Experiment I (1998–2000)				
[CO_2]	0.22	0.06	**0.03**	0.83
Fertilization	**0.01**	**<0.001**	**<0.001**	**0.005**
[CO_2] × Fertilization	**0.003**	**0.01**	0.06	0.80
Year	0.07	**<0.001**	**<0.001**	–
[CO_2] × Year	0.57	0.93	0.90	–
Fertilization × Year	0.59	0.06	0.09	–
[CO_2] × Fertilization × Year	0.79	0.73	0.80	–
Experiment II (2002–04)				
[CO_2]	0.40	0.85	0.95	0.61
Temperature	0.78	0.42	0.12	0.52
[CO_2] × Temperature	0.74	0.22	0.10	0.42
Year	**0.03**	**<0.001**	**<0.001**	–
[CO_2] × Year	0.42	0.80	0.79	–
Temperature × Year	0.52	0.38	0.33	–
[CO_2] × Temperature × Year	0.71	0.82	0.80	–

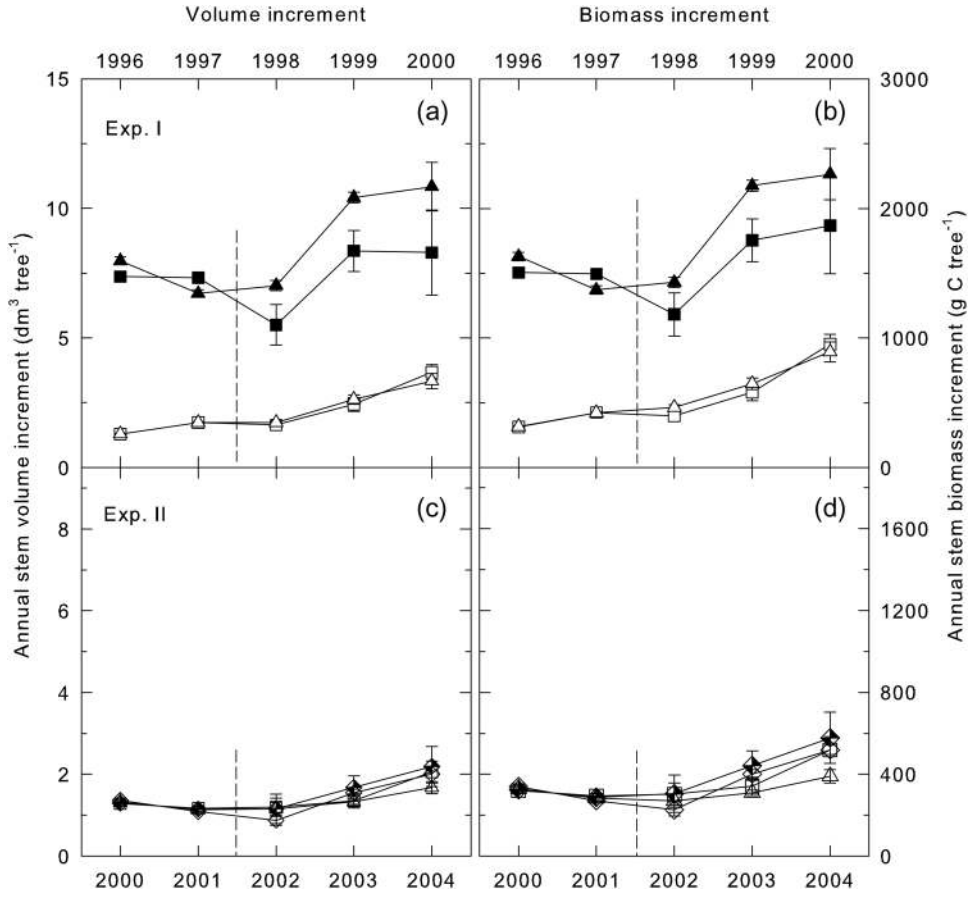

Figure 3. Stem volume increment (a and c) and stem biomass increment (b and d) of Norway spruce trees in WTCs in irrigated-fertilized (filled symbols) or non-fertilized control stands (open or half-filled symbols) in 1996–2000 (Exp. I: a and b) and in 2000–04 (Exp. II: c and d). Squares, triangles, open diamonds and half-filled diamonds indicate trees exposed to ambient air (T_AC_A and T_AC_A-IL), elevated [CO_2] (T_AC_E and T_AC_E-IL), elevated temperature (T_EC_A) or both elevated [CO_2] and temperature (T_EC_E), respectively. Lateral bars represent SE ($n = 3$). Vertical dotted lines indicate when exposure treatments started. For statistical analysis of the data, see Table 4.

($P = 0.01$, Table 4). This was because, similar to height increment, there was a significant +28% C_E-induced increase in average volume increment in T_AC_E-IL across the 3 years ($P < 0.001$, LSD test), while there was no significant response (–1%; $P = 0.98$, LSD test) when the trees were growing in the non-fertilized stand.

When annual stem growth was expressed as biomass instead of volume (Figure 3b), a somewhat different C_E-response appeared. Then, the overall effect of elevated [CO_2] became significant ($P = 0.03$, Table 4), irrespective of nutrient treatment and the interaction with fertilization became insignificant ($P = 0.06$, Table 4). This was because both the average C_E-induced responses were slightly lower in the fertilized trees (+22%, Figure 3b; $P = 0.006$, LSD test) and were marginally higher in the non-fertilized trees, but still not significant (+4% Figure 3b; $P = 0.84$, LSD test). The weak positive C_E-response in the non-fertilized stand was not consistent over the whole period, but disappeared in the last exposure year and became negative (–6%; Figure 3b).

Apart from the exposure treatments, the volume and biomass increment significantly changed during the exposure period (Figure 3a and b; Year effect in Table 4). The average normalized volume and carbon increment across all chamber treatments was 4.0, 6.0, and 6.5 dm^{-3} $tree^{-1}$ a^{-1} and 0.9, 1.3, and 1.5 kg carbon $tree^{-1}$ a^{-1} during 1998, 1999, and 2000, respectively. It was mainly the lower stem volume and biomass increment in 1998 and the high values in 2000 that caused the significant annual variation.

Annual stem volume and stem biomass increment in Exp. II

In Exp. II, which was in a non-fertilized stand only, neither C_E nor T_E significantly changed the average annual increment, irrespective of whether it was expressed as either stem volume or biomass (Figure 3c and d, Table 4). The C_E-induced trends in stem growth in ambient temperature (T_AC_E) were always negative, when expressed as volume (–10%) or carbon (–16%) (Figure 3c and d). Elevated [CO_2] and temperature combined (T_EC_E) showed a trend for more volume or biomass increment (+13 and +15%, respectively; Figure 3c and d). It should also be noted that there were similar annual trends in the C_E responses as was seen in T_AC_E in the non-fertilized stand in

Exp. I, it either became more negative (T_AC_E) or less positive (T_EC_E) during the exposure period (Figure 3c and d). When only air temperature was elevated, there was no additional change in stem growth at ambient temperature (T_EC_A; −4 and −1% for volume and biomass, respectively; Figure 3c and d). The only significant factor affecting stem increment in Exp. II was the year of exposure ($P < 0.001$; Table 4).

Stem growth efficiency

In Exp. I, the trees in the fertilized stand on average produced 29% more stemwood per unit needle area than trees in the non-fertilized stand ($P = 0.005$; Table 4). The C_E treatment did not significantly change stem growth efficiency in non-fertilized or fertilized stands in Exp. I (+4 and 0%, respectively; Figure 4), so the positive C_E-induced growth response in the fertilized trees was accompanied with a corresponding increase in needle area. Similarly, there were no significant treatment differences detected in the stem growth efficiency in the C_E or T_E treatments in Exp. II (Figure 4; Table 4).

Discussion

Growth-limiting factors in the Flakaliden experimental forest

Previous studies at Flakaliden have clearly shown that the main limiting factor for tree growth is nitrogen availability and that soil water availability does not limit aboveground growth (Linder 1995, Bergh et al. 1999, 2005). Nitrogen concentration in needles from non-fertilized trees, in both Exp. I and Exp. II, was low and reflected the low fertility of the site (cf. Hall et al. 2009, Uddling and Wallin 2012). Earlier studies at Flakaliden have also indicated that increased aboveground growth in the fertilized treatments has been a combined effect of increased carbon uptake and changed allocation between belowground and aboveground compartments (Stockfors 1997, Bergh et al. 1999, Ivonen et al. 2006). An increased allocation towards stemwood production was also seen as a significantly higher stem growth efficiency of the IL trees in the present study. It is noteworthy that each m^2 of needle area was producing more stemwood on the IL stands, even if the average projected needle area was 52 m^2 $tree^{-1}$, compared with 18 m^2 $tree^{-1}$ in the control stands, with a corresponding increase in self-shading within the canopy.

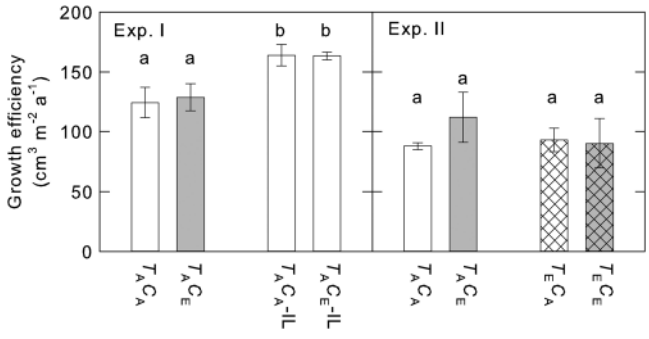

Figure 4. Average stem growth efficiency in Exp. I (left) and Exp. II (right), respectively. Treatments were trees grown for 3 years in (Exp. I) ambient and elevated [CO_2] at ambient temperature in non-fertilized (T_AC_A and T_AC_E) or fertilized stands (T_AC_A-IL and T_AC_E-IL) and (Exp. II) ambient and elevated [CO_2] at ambient or elevated temperature (T_AC_A, T_AC_E, T_EC_A, T_EC_E) in a non-fertilized stand. Different letters above bars indicate significant differences according to Fisher's LSD test. Lateral bars represent SE ($n = 3$). For statistical analysis of the data, see Table 4.

Effects of [CO_2] enrichment on aboveground tree growth

The main finding of the present study is that both height and volume increment of the mature Norway spruce trees was only increased by elevated [CO_2] when nutrient availability was increased by fertilization. A lack of a significant growth response to C_E alone in the trees growing under conditions of low soil N availability was confirmed in the two separate experiments on different individual trees. This supports the hypothesis put forward in the beginning of the experiment and agrees with a number of other whole-tree or ecosystem [CO_2]-enrichment studies on field-grown trees at sites with low soil fertility (e.g., Curtis et al. 1994, Hättenschwiler and Körner 1998, Kubiske et al. 1998, Oren et al. 2001, Sigurdsson et al. 2001, Asshoff et al. 2006, Pokorný et al. 2010). It also agrees with the results in a recent meta-analysis (Dieleman et al. 2010), which found that elevated [CO_2] did not significantly increase aboveground biomass of field-grown trees unless nutrients were added, but resulted instead in a carbon allocation shift towards belowground compartments. Moreover, Dieleman et al. (2010) found that a positive aboveground C_E response was in fact only significant for those manipulation studies where nutrients had been added. These results are, however, in contrast to the findings in a WTC study on 20-year-old field-grown Scots pine on a non-fertile sandy soil in Finland (Peltola et al. 2002, Kilpeläinen et al. 2003), which after 3 years of elevated [CO_2], and/or temperature, found significant increases in cumulative stem diameter growth. A possible explanation to this finding could be that if the soils were disturbed during the WTC installation that could have activated decomposition of organic pools. Even infertile soils can become periodically more fertile if they are disturbed (Archibold et al. 2000).

Effects of [CO_2] enrichment on the ecosystem carbon cycle

There have been several studies at the Flakaliden site, which have looked into treatment effects on shoot and canopy photosynthesis. Wallin et al. (2001) found that the short-term gross primary production (GPP) derived from gas-exchange measurements in T_AC_A-chambers in Exp. I was comparable with GPP derived from eddy covariance measurements from the same area. In an earlier study involving branch-bags, elevated

[CO_2] was found to increase net photosynthesis by 55% (Roberntz and Stockfors 1998). Similarly, Uddling and Wallin (2012) found that in Exp. I and II light-saturated photosynthesis in 1-year-old shoots was increased by 67% by elevated [CO_2] at 20 °C. Hall et al. (2009) reported that the average in situ net photosynthesis measured with automated shoot cuvettes on current-year shoots in each T_AC_E chamber was increased by 34–37% in 2003 and 2004, respectively. Hall et al. (2013) also estimated that in 2003 there was a 50% increase of the annually accumulated photosynthesis in 1-year-old shoots in T_AC_E compared with T_AC_A treatments (Exp. II). Thus, it is clear that [CO_2] enrichment led to an increase in annual canopy photosynthesis in the range of 35–65%. This is a similar response in photosynthesis as found in several other [CO_2]-enrichment studies on field-grown trees (cf. Curtis 1996, Saxe et al. 1998, Ainsworth and Long 2005).

What happened then to the extra assimilated carbon in the non-fertilized control stands, if it was not used for stem growth? There are several avenues along which carbon assimilates can be processed in a tree, and only one among these is the production of aboveground plant biomass. Other possible avenues include: (i) changed metabolism (increased autotrophic respiration), (ii) increased non-woody pools (reproduction, secondary compounds), (iii) increased allocation towards belowground pools (coarse and fine roots, and mycorrhiza) or (iv) increased export processes (volatile compounds or exudation; cf. Körner 2006, Hyvönen et al. 2007).

Some, but not all of these alternatives have been studied at Flakaliden. Roberntz and Stockfors (1998) found an 18% increase in shoot respiration rates in response to elevated [CO_2] in an earlier branch-bag study (avenue i) and Ceschia (2001) reported that in situ maintenance stem respiration increased by a factor of 2.5 in the T_AC_E treatment in Exp. I. He also found that the cost of stemwood construction in elevated [CO_2] was increased by 10% (avenue i). This finding was indirectly supported by the present study, which showed that even if stem volume was not significantly affected by the T_AC_E treatment there was a small, but significant, overall increase in its carbon accumulation (avenue ii). In Exp. II, this small C_E response on carbon accumulation was, however, not significant. This was also reported by Kostiainen et al. (2009), who found no large effects of C_E on wood chemistry or wood density in Exp. II (avenue ii). The C_E treatments did not significantly affect cone production in Exp. I or II (data not shown) (avenue ii).

Fransson et al. (2001) studied the effects of optimized fertilization and elevated [CO_2] on the community structure of ectomycorrhizal fungi in Exp. I. They found significant effects, with the effect of 3 years of C_E being much larger than from 15 years of fertilization (avenue iii). The possibility of an increased belowground allocation, even in the T_AC_E-IL treatment, is further supported by the finding in the present study that stem growth efficiency was not significantly different between T_AC_A-IL and T_AC_E-IL. This seems to indicate that even if the photosynthetic uptake per unit needle area was increased by the T_AC_E-IL treatment, the stem growth was not increased correspondingly, but rather followed the increase in leaf area.

Comstedt et al. (2006) measured forest-floor CO_2 efflux and its $\delta^{13}C$ signature in Exp. II. They found on average 48 and 62% increase in forest-floor CO_2 efflux in 2002 and 2003, respectively, as a response to elevated [CO_2]. The data on $\delta^{13}C$ indicated that this increase in CO_2 efflux was from increased root/rhizosphere respiration of recently fixed carbon (avenues iii and iv). Similarly, the finding in the present study that C_E significantly decreased foliar [N] (cf. Hall et al. 2009, Uddling and Wallin 2012) may be an indication of changed source/sink ratio, which could cause an increased belowground allocation (avenues iii and iv).

Based on the above-mentioned studies, an increased belowground allocation of carbon seems to be the most plausible explanation for the lack of a significant increase in aboveground growth, when the trees were growing under the low natural N availability in Exp. I and II. It is, however, not clear what was the main use of the extra carbohydrates: root production and/or mycorrhizal symbiosis (avenue iii) or root exudation (avenue iv)? Increased aboveground respiration (avenue i) and wood chemistry (avenue ii) can only explain a small part of the observed response.

Effects of elevated air temperature on aboveground tree growth

There was no significant T_E effect on aboveground stem volume or biomass increment of trees growing at the natural and low N availability in Exp. II, where soil temperature was kept close to ambient. When soil temperature in a long-term soil-warming experiment at Flakaliden was elevated by 5 °C at 10-cm depth throughout the growing seasons for 6 years, the cumulative stem volume production on non-fertilized plots was increased by >60% (Strömgren and Linder 2002), which was interpreted as an effect of increased nitrogen mineralization.

The correlation between air temperature and wood production commonly found at a regional scale or in long-term tree ring analyses at higher latitudes (Henttonen 1984, Miina 2000, Seo et al. 2008) may therefore be more complex than previously considered. The present study seems to indicate that the relationship between aboveground growth and air temperature at the Flakaliden site is controlled by soil processes and site fertility rather than through a direct effect of canopy photosynthesis on cell production and/or expansion (cf. Bergh et al. 1999, Jarvis and Linder 2000).

Elevated air temperature in Exp. II was found to lengthen the active growing season by ca. 2 weeks by an earlier bud burst (Slaney et al. 2007), which was also found by Bronson et al. (2009) in a warming experiment in young black spruce (*Picea*

mariana (Mill.)) in Canada. Elevated temperature also resulted in an earlier photosynthetic development in current-year shoots (Hall et al. 2009) and faster photosynthetic spring recovery in 1-year-old shoots Wallin et al. 2013). When compared at a constant foliar N, the annual photosynthesis was increased by 44% in $T_E C_A$ compared with $T_E C_A$, to a large extent depending on a longer season (Hall et al. 2013).

Most temperature manipulation studies have warmed both the air and the soil (cf. Saxe et al. 2001, Way and Oren 2010). While that may give a sound prediction of what will be the net effect of a future climate change, it may hide some important causal relationships on how temperature changes affect the growth and physiological processes of boreal trees. In the present study, the direct positive effect of higher air temperature on shoot phenology, gas exchange and shoot growth did not translate into increased stem growth. This agrees with earlier reports that elevated [CO_2] did not increase stem growth when not accompanied with increased N availability (Curtis et al. 1994, Oren et al. 2001, Sigurdsson et al. 2001, Pokorný et al. 2010). Hence, effects of change in temperature on forest productivity in the boreal zone should rather be modelled through its effects on the soil-N cycle and the interaction between changed N availability and growth, rather than only through its direct effect on gas exchange and/or phenology.

It was noteworthy that stem growth efficiency in Exp. II was marginally (20–27%) higher in C_E at ambient temperature than in any other treatments. Since the absolute amount of annual stemwood increment was, however, lowest in this treatment in 2004, this indicated a trend for relatively less canopy area per unit stemwood production in $C_E T_A$, a phenomenon also found in $C_E T_A$ in the study of Sigurdsson et al. (2001) in nutrient-limited conditions. This trend was, however, not statistically significant. In large, expensive and technically demanding manipulation experiments, as the present studies, sample size is necessarily small. This means low statistical power to detect differences, which is an inherent problem of all such manipulation studies. Therefore, some notice should also be paid to strong (insignificant) trends when results are evaluated, without drawing too radical conclusions from such trends, of course. A recent global meta-analysis on the effect of T_E and C_E on plant growth (Wang et al. 2012) concluded that it was important to further improve our mechanistic understanding of how plants respond to the interactive effect of elevated [CO_2] and other abiotic factors, particularly temperature, N deposition and altered patterns of precipitation, all of which are expected to change in the future.

Will the responses change with time?

A central problem for most manipulation experiments of long-lived organisms, such as forest trees, is that the environmental conditions are normally only altered for few years. Some exposure studies have shown that an initial positive response of stem growth to elevated [CO_2] decreased later because N availability did not increase proportionally (cf. Hyvönen et al. 2007, Norby et al. 2010). The present study supports these findings, where an initial positive trend in the C_E response became negative after 3 years of exposure (Exp. I) or became more negative with time in non-fertilized trees (Exp. II; Figure 3) when the trees became more N-limited.

The key question for the long-term effects of elevated [CO_2] at the Flakaliden site is whether increased belowground carbon allocation in elevated [CO_2] could lead to increased N availability with time. Availability may potentially increase through increased fine root exploration (Iversen 2010, Iversen et al. 2011), increased root exudation and stimulated microbial and fungal activity (Drake et al. 2011, Phillips et al. 2012). This was, however, not seen in the present study during the 3-year exposure periods. In the long-term Duke Forest FACE experiment, however, a stimulation of microbial activity had after 12 years resulted in an increased rate of N uptake (cf. Drake et al. 2011), but this positive effect on N cycling was not seen after the first 5 years of CO_2 fumigation (Finzi and Schlesinger 2003).

Conclusions

The general assumption in most process-based simulation models of forest growth is that increased canopy photosynthesis, as stimulated by elevated [CO_2] and/or temperature, will inevitably result in increased tree growth and forest productivity (Landsberg 2003). This is also true for some of the coupled climate-carbon-cycle models used in the IPCC's fourth assessment report (IPCC 2007). The findings of the present study do not support such a modelling approach for the nutrient-poor boreal forests. Rather, it seems that soil nutrient availability will determine if the enhanced photosynthesis will result in increased aboveground growth or not. The present study, together with the results from other manipulation experiments at Flakaliden (fertilization, irrigation, soil warming), convincingly show that the effect of air temperature on tree growth is not through aboveground processes, but rather through an indirect effect on soil temperature that is likely to increase nutrient availability.

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Change - Manipulation Experiments in Terrestrial Ecosystems) and the Nordic research networks: Nordic Centre of Advanced Research on Environmental Services (CAR-ES) and Forest Soil Carbon-sink Nordic Network (FSC-Sink).

Conflict of interest

None declared.

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