# Effects of elevated carbon dioxide concentration and temperature on needle morphology and shoot growth in Norway spruce

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**HÁSKÓLI ÍSLANDS Raunvísindadeild Líffræðiskor**

Hér með lýsi ég því yfir að ritgerð þessi er samin af mér og að hún hefur hvorki að hluta né í heild verið lögð fram áður til hærri prófgráðu.

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## Abstract (English)

During the past 150 years the amount of $CO_2$ in the atmosphere, [$CO_2$], has increased severely, mostly due to an increase in the burning of fossil fuels and land-use changes. It is predicted that [$CO_2$] will have doubled in the end of this century. Future temperature (T) is also expected to increase due to climate forcing following the increase in [$CO_2$].

In this experiment we studied the effect of elevation of [$CO_2$] and T on needle morphology and shoot growth. It was made by using whole-tree chambers around mature trees. In this research the main goal was to find out what effects elevated [$CO_2$] and T had on specific needle area (SNA), needle density, needle length and width, annual shoot length and shoot needle area at different heights in 40-year-old field-grown Norway spruce trees at the Flakaliden experimental site in northern Sweden. The present study was a part of a larger experiment examining the long-term morphological and physiological responses of the trees.

Elevated T significantly increased SNA ($P<0.04$) and shoot length ($P<0.02$). No significant treatment effects or interactions between [$CO_2$] and T were found for needle area density, needle density, average needle length or width. Most morphological parameters changed significantly with height in the tree.

From the present study it can be concluded that elevated T can possibly increase needle area, through significant changes in annual shoot lengths. Elevated [$CO_2$] is, however, not expected to have a direct effect on needle morphology or needle area of Norway spruce and no interactive changes are expected between elevated [$CO_2$] and T. It is important to note that needle morphology changes more with height in the tree than due to changes in environmental parameters, such as temperature and $CO_2$. When comparing different treatments, care has to be taken that needles from comparable sites within tree canopies are used.

# Ágrip (Abstract in Icelandic)

Titill ritgerðar á íslensku: Áhrif hækkaðs styrks koldíoxíðs og hitastigs á barrnálar rauðgrenis.

Skógar heimsins leika stórt hlutverk í kolefnishringrásinni. Undanfarin 150 ár hefur magn koldíoxíðs aukist verulega í andrúmsloftinu og er það að mestu leiti vegna gjörða mannsins, t.d. vegna aukins bruna á steingerðu kolefni (olíu og kolum) sem orkugjafa auk skógareyðingar í hitabeltinu, en spár gera ráð fyrir að styrkur koldíoxíðs í andrúmslofti muni hafa tvöfaldast í lok þessarar aldar. Við þessa aukningu er einnig gert ráð fyrir hækkuðu hitastigi á jörðinni.

Rannsökuð voru áhrif hækkaðs styrks koldíoxíðs og hitastigs á lögun og vöxt barrnála og sprotavöxt 40 ára gamalla rauðgrenitrjáa (*Picea abies*) sem uxu við náttúrulegar aðstæður í Flakaliden í Norður-Svíþjóð árin 2002-2004. Meðal annars var flatarmál barrnála, lengd, breidd og þéttleika þeirra á árssprotum sem mynduðust meðan á tilrauninni stóð. Einnig var lengd árssprota mæld í mismunandi hæð í trjánum. Þessi rannsókn var hluti af stóru rannsóknarverkefni sem miðaði að því að rannsaka langtímabreytingar á vexti og lífeðlisfræðilegum viðbrögðum trjánna í framtíðar loftslagi. Rannsóknin er frábrugðin flestum eldri rannsóknum á þessu sviði. Þær hafa flestar hafa verið gerðar á rannsóknarstofum við ónáttúruleg skilyrði. Við tilraunina voru byggð loftslagsstýrð gróðurhús (e: whole-tree chambers) utan um hvert tré. Fimm meðhöndlanir voru notaðar með þrem trjám í hverri sem uxu í: a) sama koldíoxíðstyrk og hitastigi sem var í andrúmsloftinu utan gróðurhúsa, b) hækkuðu hitastigi en óbreyttum koldíoxíðstyrk, c) hækkuðum styrk koldíoxíðs en óbreyttu hitastigi, d) hækkuðum styrk koldíoxíðs og hækkuðu hitastigi. e) Einnig voru gerðar sömu mælingar á trjám utan gróðurhúsa.

Helstu niðurstöður voru þær að hitastig jók hlutfall barrflatarmáls og barrvigtar ($P<0,04$; þ.e. barrið varð flatara) og ársvöxt sprota ($P<0.02$).

Engin marktæk meðferðaráhrif eða samspil fundust á aðrar mældar breytur. Lögun barrnála breyttist marktækt með hæð í trénu.

Af þessari rannsókn má álykta að hækkað hitastig getur mögulega gert rauðgreni kleift að mynda þéttari laufkrónur. Þetta gerist vegna þess að hver árssproti lengist og barrnálar verða flatari (hver barrnál hefur meira flatarmál). Hækkaður styrkur koldíoxíðs hefur líklegast ekki áhrif á lögun barrnála eða flatarmál þeirra á rauðgreni.

Það er mikilvægt að gera sér grein fyrir því að lögun barrnála er mjög breytileg eftir staðsetningu þeirra í trénu. Þetta ber að hafa í huga þegar sýnum er safnað til að kanna vöxt barrnála og þegar mismunandi meðferðir eru bornar saman.

# Acknowledgements

I want to thank Bjarni Diðrik for all the help and all the patient towards me and my project.

I want to give special thanks to Ólafur Eggertsson for all the advises and the help with the computer equipment on Mógilsá. I also want to thank Arnór for helping me out with the order analysis and all the other people on Mógilsá for all the nice talks, advises and fun time we had during the time of my analysis.

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## Figures and Tables

# Introduction

## The boreal forests

The boreal forest corresponds with regions of sub-arctic and cold continental climate. The winters are long and severe and summers are short and moderately warm. The range of temperatures between the lows of winter and highs of summer are very wide. Forests cover approximately 33% of the world's land surface and there of boreal forests cover about 11 % of the total world's area (Dixon et al. 1994).

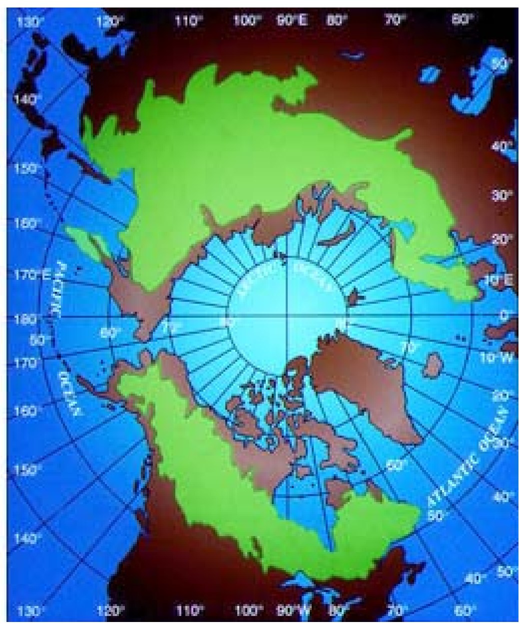



**Figure 1**: the distribution of boreal forest on the northern hemisphere. The green represents the grown area of boreal forests. (Picture taken from Lakehead University (2006))

The boreal forest is south of the Arctic Circle (Figure 1). The northern region accounts for about one third of the planet's total forest area. This area runs through most of Canada, Russia and Scandinavia. The boreal forest has relatively few species but it consists mainly of spruces, firs and pines but also some deciduous trees, mostly along waterways and as a temporary stage after forest fires (Oliver and Larson 1996). The boreal forest corresponds with regions of sub-arctic and cold continental climate with long and severe winters and short summers which can be quite warm.

## Norway spruce

Norway spruce (*Picea abies*) is one of the key species of the boreal forests and is very common in the Nordic countries in Europe. It can grow up to 25 meters in height and can spread up to 12 meters. The crown creates a symmetrical canopy with a regular outline and individuals have more or less identical crown forms. The Norway spruce tolerates most soils and it can tolerate drought very well. (Gilmand and Watson 1993).

## The global carbon cycle

Plants play a big role in the global carbon cycle in and are a major determinant of net primary production (Amthor 1989). The carbon is transferred as $CO_2$ from the atmosphere to the ocean and to the land through photosynthesis of algae and plants, but there it is stored in organic matter before it returns to the atmosphere as $CO_2$ (Grace 2001). The carbon dioxide is also a “greenhouse gas” in the atmosphere. It traps some of the long-wave radiation that would otherwise be lost in space and this causes the warm atmosphere on the Earth. The last 150 years the amount of $CO_2$ in the atmosphere has increased by about 30% (IPCC 2001), mostly due to human activities such as increase in the burning of fossil fuels and land-use changes. Most of the increase in atmospheric [$CO_2$] comes from the use of fossil fuels for energy but about 25% of the increase over the last 150 years came from changes in land use, for example, the clearing of forests and the cultivation of soils for food production. Many people see a potential for reducing the rate at which carbon builds up in the atmosphere by using forests to withdraw carbon from the atmosphere. (Woods Hole Research Centre 2006)

There is a large amount of carbon locked in the boreal forest. When vegetation in the northern hemisphere is in maximum growth phase (during the northern spring and summer) the worldwide levels of carbon dioxide fall and the level of oxygen rises (e.g. Schimel et al. 2001). Coniferous forest cover large land area in the northern hemisphere and therefore play an important role in the global carbon cycle (Schimel el al. 2001). Scientific understanding of the boreal forest's significance in the carbon cycle and its role in control of greenhouse gases and impact on global climate change is incomplete. The present project adds a little information to this, with the focus on how greenhouse gases and climate change affect needle area of Norway spruce, which again is important in how this tree species is going to change its growth and carbon uptake in the future.

Carbon is retained in terrestrial ecosystems in the soil organic matter and in the living biomass. The amount of carbon that is stored in the terrestrial ecosystems at a global level is still quite uncertain but ecosystem models indicate that they will continue to take up some of the carbon dioxide emissions arising from human activities for some decades. After that it is possible that forest ecosystems will become a net source of $CO_2$ (Watson *et al* 2000). There can be several reasons for this. The capacity of ecosystems to sequester carbon may e.g. be limited by nutrients or some biophysical factor (IPCC 2001).

## Climate changes; increasing atmospheric [$CO_2$] and temperature

The carbon dioxide in the atmosphere is increasing each year (Grace 2001). Before the industrial revolution the concentration of $CO_2$ in the atmosphere was ca. 280 µmol/mol (Neftel *et al*. 1985). It has been predicted that in the end of this century, the concentration of carbon dioxide in the atmosphere will rise from about 375 µmol/mol, which it is today (Keeling and Whorf 2005), up to ca. 700 µmol/mol (Grace 2001).

It is also predicted that following this increase in atmospheric carbon dioxide there will be a rise in the global mean temperature. One of the first persons to predict the increase in temperature followed by the elevated carbon dioxide concentration in the atmosphere was the Swedish physicist Svante Arrhenius, late in the $19^{th}$ century. In recent years, global circulation models (GCMs) have been used to predict the change in climate due to increasing greenhouse gas concentrations. Different models predict variable climatic changes during the coming century, but all of them predict warmer global mean temperature (IPCC 2001). In Scandinavia there is one strong GCM modeling group (the Rossby centre) which has made the regional climate model called the Swedish Regional Climate Modelling Programmme (SWECLIM; Christensen et al. 2001). It predicts that in the north Scandinavia (where the present project took place, in Flakaliden in northern Sweden) the temperature increase, in the end of this century, will be ca. +2.8 and +5.6 °C during summer and winter, respectively.

## Effects of elevated [$CO_2$] and temperature on plants

Temperature and $CO_2$ concentration are variables that affect the plant growth, function and development (Jarvis 1998). Much research has been made the last years considering the effects of elevated [$CO_2$] and temperature on plants (see review by Hyvönen et al. 2006). Increasing concentration of $CO_2$ has generally been found to increase the uptake of $CO_2$ (photosynthesis) with a corresponding increase in plant-growth (*e.g*. Poorter 1993, Hyvönen *et al*. 2006). Not all plants react the same way to an increase in the atmospheric $CO_2$ concentration. Hunt *et al*. (1999) showed that 7 out of 27 plant species were unaffected by the concentration whereas others showed a positive response. Another interesting thing is that fast-growing species tend to respond more to elevated [$CO_2$] than slow-growing ones (Poorter et al. 1996).

Most of the older experiments were performed under unrealistic environmental conditions, using glasshouses and pots (Fitter and Hay 2002). Many studies on woody plants have therefore been restricted to seedlings and young (Jarvis 1998). The responses of the seedlings may however differ from those of mature trees (Mousseau and Saugier 1992) and growth in laboratories can differ from growth under the natural circumstances (Drake 1992). That is why it is necessary to investigate these things in the field with mature trees.

Three different techniques have been used to elevate the atmospheric [$CO_2$] out in the field: a) open-top chambers, b) free-air carbon dioxide enrichment, and c) whole tree chambers. The last technique was used in the present experiment. Field experiments with elevated $CO_2$ have also generally resulted in increased growth. In some cases the effects are more in the below-ground biomass than in the above-ground biomass (Norby and Luo 2004). The greater response of root growth is exactly what would be expected from plants growing in water- or nutrient-limited conditions, which are often found in such experiments under natural conditions (Fitter and Hay 2002).

When the literature was searched for relevant information for the present paper, it was apparent that less research has been done on the effect of elevated temperature than on elevated [$CO_2$]. Generally, elevated temperature has been found to increase photosynthesis in northern tree species (Hyvönen *et al*. 2006), but it is not clear how growth will be affected.

Since northern plants are not able to maintain their temperature at a constant optimum temperature, as homeothermic animals can, their metabolism, development and growth are affected by changes in the external temperature. Plants have very complex responses to handle variant temperatures. Increased temperature can have different effects on plant and most often it depends on how tolerant the species is to heat-changes (Fitter and Hay 2002).

When both the [$CO_2$] and temperature increases, how does the tree react? The following hypotheses were made. Could it be that the trees adapt to the changed environment by decreasing the total leaf area so that they can take up the same amount of $CO_2$ from the atmosphere which had higher concentration of carbon dioxide? This could be achieved by growing shorter needles, decreasing the needle area density (NAD) or by decreasing the numbers of the needles per cm of shoot. This could also be achieved by decreasing shoot growth or make fewer buds burst in the spring so that fewer shoots will be made. On the other hand when temperature is increased the cells should become larger and therefore increase needle and shoot growth.

In this research the main goal was to find out what effects elevated carbon dioxide and temperature had on needle morphology, including SNA, needle density and needle length and width in different positions in 40 year old field grown Norway spruce trees.

## Materials and methods

The present study was a small part of a larger experiment that was performed at the Flakaliden experimental research site in northern Sweden (64°07’N, 19°27’E) during the period 2002-2004. In this experiment 40-year old Norway spruce trees were grown in predicted future climate and atmospheric $CO_2$ concentration [$CO_2$] in whole-tree chambers (Figure 2). One PhD thesis has been defended from this experiment (Slaney 2006), which focused on the effect of elevated [$CO_2$] and temperature on phenological development of buds and canopy gas exchange (photosynthesis, respiration and transpiration). The present thesis adds information about needle morphology and shoot growth to those studies.

**Figure 2**: Picture of the whole tree chambers (WTC) used for $CO_2$ and temperature exposure in Flakaliden in Northern Sweden. The chambers

enabled the researchers to control the temperature and the [$CO_2$] inside and therefore find out the effect of these environmental factors (Slaney 2006).

## The study site

The study site, Flakaliden experimental forest, is in northern Sweden, at similar latitude as southern Iceland (64°07'N). It is ca. 100 km from the Baltic sea, at an altitude of 310 m above sea level with minimal slope (<4%) (Slaney 2006). The site consists of a Norway spruce stand which was planted in 1963 with four-year-old seedlings of a local provenance. The stand density is about 2500 trees/ha (Linder 1995).

The winters in Flakaliden are similar to Icelandic winters, long and consist of short days (daylight of about 3-5 hours) and cold weather while the summers are rather cool with long days (daylight of about 20-22 hours). The length of the growing season is about 140 days with the mean temperature of 11.6 °C (Bergh *et al.* 1999). Usually the soil freezes in winter and most often does not thaw until May. The mean annual rainfall is about 600 mm with about 1/3 falling as snow which covers the frozen ground from mid-October to early May (Bergh *et al.* 1999). The soil at the site is podzolic, glacial, loamy till with an average depth of about 1.2 m. The mean humus layer depth is about 30-40 mm. (Bergh *et al*. 1999).

The annual mean temperature is about 2.3 °C, which is ca. 2 °C lower than is experienced in southern Iceland (Veðurstofa Íslands 2006). The reason for lower annual temperature in Flakaliden is more continental climate, with much colder winters and slightly warmer summers than those experienced in Iceland. The average temperature in January in Flakaliden is ca. -7.3 °C and in July it is ca. +14.6 °C (Slaney 2006).

The temperature conditions during the study time (2002-2004) had a large variation within and between the years (Figure 3). More information about the climate during the study period can be found in Slaney (2006).

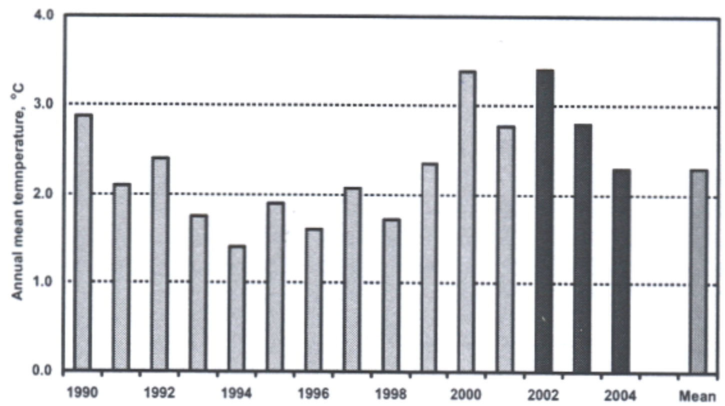



**Figure 3**: Annual mean temperature for each year from 1990 to 2004 and the 15-year mean temperature. Black bars indicate the period in which this experiment was carried out and the stripped bar denotes the 15-year annual mean temperature. (Taken from Slaney 2006)

Flakaliden was chosen in 1986 as a site for a nutrient optimization experiment, which commenced in 1987. For further details about the nutrient treatments and site descriptions see Linder & Flower-Ellis (1992), Linder (1995) and Bergh *et al.* (1999).

## The whole-tree chamber system

During the spring and summer of 2001 twelve whole-tree chambers (WTC) were installed around individual trees. The trees were chosen to represent the average tree size in the non-fertilized control plot in the long term nutrient optimization experiment. Three reference trees were also selected and used as non-chambered control trees. The trees had the average height of 5.6 m in the year 2001 (Slaney 2006).

The chambers were used to examine the long-term morphological and physiological responses of field-grown Norway spruce to ambient (a) and elevated (e) atmospheric carbon dioxide concentration (C) and air temperatures (T). The C and T treatments were randomly assigned to each chamber. In total there were three replicates of the four treatments (CaTa, CaTe, CeTa and CeTe). The [$CO_2$] inside the chambers was maintained at 365 µmol/mol inside the Ca chambers but at 700 µmol/mol inside the Ce chambers. The increase in air temperature inside the Te chambers was altered on a monthly time-step according to estimates made by the Swedish Regional Climate Modelling Programmme, SWECLIM (Christensen *et al.* 2001). They predicted that an [$CO_2$] of 700 µmol/mol will lead to climate forcing in the Flakaliden area of +2.8 and +5.6 °C during summer and winter, respectively (Slaney 2006). Figure 4 shows how monthly temperature elevation was changed throughout the year.

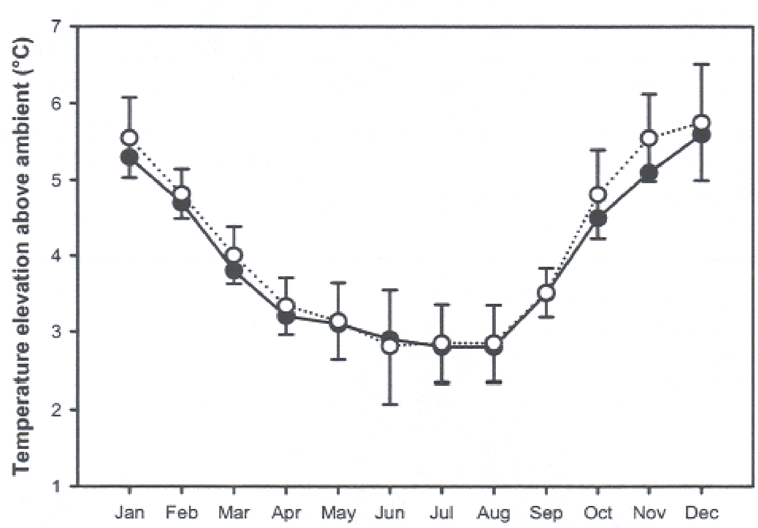



**Figure 4**: The target monthly temperature elevations used at Flakaliden for elevated temperature WTCs. Actual mean monthly temperature elevations for the elevated temperature WTCs (open circles) are shown for the year

2002. Means were calculated by pooling all elevated temperature data for each month. Error bars show ± one standard deviation (n=6) (Taken from Slaney 2006).

## The chambers

The chambers consisted of three main sections; the base (soil compartment), the tree chamber (aboveground compartment) and the cooling unit (Figure 5).

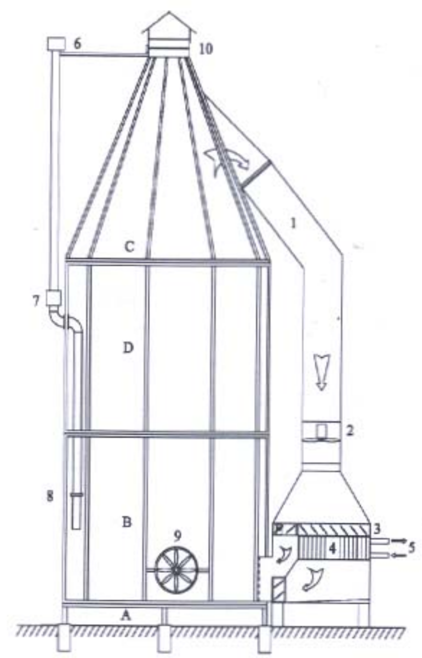



**Figure 5**: A schematic diagram of the whole tree chambers (WTC) used in the long-term manipulation experiments at Flakaliden. The modular chamber design consisted of three main components: the chamber base (soil compartment), the tree chamber (above-ground compartment), and a cooling unit placed directly outside the chamber. The diameter of the WTC was 3.25 m. The chamber base (A) was approximately 0.4 m high. The tree chamber consisted of a bottom (B) and a top (C) section, with a height of 2.5 m and 3.0 m, respectively. Extra sections (D) could be added to the tree chamber to keep up with tree height growth. Some major components of the

system are indicated in the diagram by numbers: (1) pipe (Ø 630 mm) for circulation chamber air through the cooling unit, (2) frequency controlled fan (0-12000 $m^3 h^{-1}$), (3) dampers to regulate the amount of air going through the cooling battery, (4) large surface cooling battery, (5) circulating a glycol/water (30/70) solution maintained at ambient dew point temperature, (6) fresh air inlet, (7) fan for fresh air intake, (8) iris damper for flow control of fresh air intake, (9) safety fan connected to a diesel generator, which starts in case of power failure, and a 12-V controlled safety damper (open-close) working in parallel with a similar damper (10) at the top of the WTC. (taken from Slaney 2006) For further explanations on the chambers and their functioning see Medhurst *et al.* (2006) and Slaney (2006).

The circular frame of the base and the tree chamber was constructed from aluminium. The walls of the base section and tree chamber were sealed with 0.4 mm transparent PVC film. The base section was approximately 0.4 m in height and the lower part of the PVC-film was covered with soil to provide a seal between the base and the ground. The top of the chamber base was sealed with a combination of the PVC-film and transparent Perspex sheets and sealed around the tree stem to prevent air exchange between the soil compartment and the tree chamber. To allow any soil disturbances to subside, the base sections were installed in September 2000, eight months before the tree chambers were installed. Two micro-sprinklers were installed under the chamber floor so that the trees could be irrigated with the same amount of water that was measured by rain gauges outside the chambers. For more information about the chambers see Medhurst *et. al* (2006) and Slaney (2006).

**Table 1**: Whole-tree chamber temperature and $CO_2$ control by temperature and [$CO_2$] treatments. During February the temperature control was deliberately reduced to minimize power consumption over the winter months. Temperatures measured on a 42-min cycle from each WTC were pooled by temperature treatment (n=6). The [$CO_2$] values measured by the central IRGA on a 42-min cycle from each WTC were pooled by [$CO_2$] treatment. Ca is ambient [$CO_2$] and Ce is elevated [$CO_2$], n=6. (Taken from Slaney 2006)

| Treatment | Target elevation | Difference from target | Standard Deviation |
|---|---|---|---|
| **Temperature control** | | | |
| ***14 - 28 February 2002*** | | | |
| Ca | 0 °C | + 0.6 | ± 0.6 |
| Ce | + 4.7 °C | + 4.8 | ± 0.2 |
| ***3 - 17 May 2002*** | | | |
| Ca | 0 °C | 0.0 | ± 0.4 |
| Ce | + 3.1 °C | + 3.1 | ± 0.2 |
| **Carbon dioxide control** | | | |
| ***14 - 28 February 2002*** | | | |
| Ca | 365 µmol/mol | + 20.1 | ± 5.0 |
| Ce | 700 µmol/mol | + 2.4 | ± 3.3 |
| ***3 - 17 May 2002*** | | | |
| Ca | 365 µmol/mol | + 8.9 | ± 14.9 |
| Ce | 700 µmol/mol | - 1.6 | ± 5.8 |

The air in the chamber was drawn over a heat exchanger inside the cooling unit by a powerful fan. The air was then returned from the cooling unit at the base of the tree chamber. Elevated temperature regulation was achieved by a combination of reducing the amount of air passing over the heat exchanger, and the use of two heating elements installed in the circulating air pathway in each chamber. The temperature inside the chambers was measured by a shielded and ventilated thermostat at a height of ca. five meters and the ambient air temperature was also measured with the same technology. The temperature was measured at three minute intervals and the average was logged at 42 minute intervals (Slaney 2006). This whole tree chamber system made the control of temperature during the research easy. The temperature regulation of the chambers with elevated temperature was within ±0.5°C from the target temperature for up to 99% of the time. The good regulation of the temperature inside the chambers can be seen in the small differences in temperature sums between ambient air and inside the Ta chambers (Table 1).

## Harvest measurements of branches

The 15 trees were harvested in September 2004, after three years of C and T treatments. Breast height (BH=1.3 m) and north had been marked on all trees before they were harvested. Each tree was cut at ca. 2 cm with a motor-saw 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 (CD) were recorded. Dead branches below the living crown were cut, counted and weighed for fresh mass (FM). The living crown was divided into five strata of equal depth, with stratum one towards the top (Figure 6)

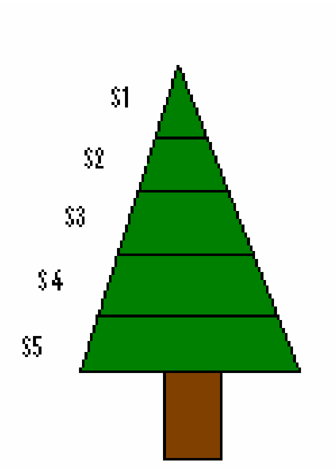



**Figure 6:** The living crown of the tree was divided into 5 strata, starting at the top (S1).

In each stratum, one whorl branch was chosen at random, marked and removed for further analysis. Branch length was recorded and fresh mass (FM) of each branch was measured using EKS PV500 scale (±0.5 g) and the youngest part of the first branch axis, containing ca. 4 age-classes of shoots, was cut and put directly in a freezer at -18 °C. The remaining part of the sample branch was dried at 85 °C for 24 hours before needles and wood was separated. Then both fractions were dried for 24 hours before weighed for dry mass (DM). This yielded the DM:FM quotients for all branches and information about how much of branch DM was in needles and wood. The remaining whorl-, internodal- and dead branches were then removed separately from each stratum, counted and weighed for FM using EKS PV506P scale (±1 g). The stem was then cut into sections and weighed and stem disk were removed for FM:DM determination and for further analysis of wood growth and anatomy.

## Laboratory analyses of sample branches

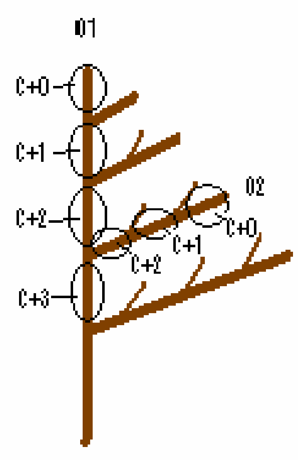



**Figure 7:** Sample branches were divided into current annual, one-, two- and three-year old sections for the fist order axes but from three youngest annual growths were measured for the second order branches.

The stored parts of the 75 sample branches were divided into current annual, one-, two- and three-year old sections (C+0, C+1, C+2 and C+3; annual growth from 2004, 2003, 2002 and 2001) for the fist order axes, but from the second order axis three youngest annual growths were measured (Figure 7).

The length of each annual shoot was measured with digital caliper from bud-scar to bud/bud-scar. A peace of about 20 mm was cut from the middle of each annual shoot and the needles of that part were scanned into a computer which had the program winSEEDLE™ (Version 5.1 A, Regent Instruments inc.,Blain, QC, Canada). The program analyzed the total projected needle area and measured the length and width of each needle. Then the samples were dried at 85 °C for 48 hours. The DM of needles and wood were weighted separately with 0,001 g accuracy.

## Data analysis

Specific needle area was calculated as:

$$SNA = \frac{A}{DM}$$

where A is needle area in $cm^2$ and DM is dry mass of the same needles in g. Needle density was both calculated as number of needles per mm annual shoot and needle area per mm annual shoot. Needle length and width were both studied separately and as a ratio of each other. Finally, total needle area was estimated from the needle mass of the 20 mm long sub-sample, the total shoot length and the measured SNA.

The program SAS 9.1.3 was used for statistical analysis. Two-way ANOVA was used to evaluate chamber effects (difference between outside reference trees and CaTa trees) and if there was any significant difference in needle morphology before the treatments started (C+3 needles compared). Such analyses were also done separately for treatment effects ($CO_2$, T, $CO_2{}^{x}T$) for each age-class, order and stratum. To further study the treatment effects, repeated measures 3-way ANOVA was used, where C+0, C+1 and C+2 needles from the top four strata were analysed simultaneously for the chamber trees.

# Results

## Chamber effects

The term “chamber effect” is used for the difference between the outside reference trees and the CaTa chamber treatment. If the chambers were having unexplained effect on needle anatomy and shoot growth, that would be seen in this difference.

There were only a few examples of significant chamber effects experienced in this study. For example, the only significant difference for SNA between the REF and the CaTa trees was for the oldest shoots (C+3) in the fourth stratum (S4). The shoots from the age-class C+3 were created the year before the chambers were installed, so this apparent difference was not a real chamber effect. The same was true for the needle area density ($cm^2/mm$), besides one age-class in stratum 5 (data not shown). The only measured morphological parameter that showed some indications of significant chamber effects in stratum 2, 3 and 5 was needle width. However, no chamber effects were found for the ratio between width and length of the needles, needle density (#/cm), or total shoot length (data not shown, but for further information see Appendix 2, 3, 4 and 5)

## Initial conditions

By including analysis of the age-class that was created the year before the treatments started (C+3), it was possible to study if the selected trees had in fact been comparable before the experiment started. If any significant treatment effects would be found in measured parameters for C+3 that would indicate that the trees were not comparable. There were no significant differences between C+3 and the other age classes in any of the treatments, except few examples when considering needle length between

CaTa:CeTa and CaTa:CaTe ($CO_2$ and temperature effects). A strong trend was also found for lower needle density for the CeTe treatment compared to others (data not shown, but for further information see Appendix 2).

## Treatment effects (elevated $CO_2$ and temperature)

*SNA and needle density*

Figure 8 shows the measured specific needle area (SNA) in first and second order shoots (average for C+0, C+1 and C+2 age-classes). There was a clear trend in the top four strata that elevated $CO_2$ decreased SNA but elevated temperature increased it (Figure 8).

Table 2 shows the statistical analysis for SNA and needle density, when the changes were analysed with repeated measures ANOVA for the top four strata in the tree. The 5$^{th}$ strata was excluded because the branches there were growing in extreme shade, often missing some annual shoots and were generally about to die.

Elevated temperature increased SNA significantly, both when analyzed for C+0, C+1 and C+2 needles on 1$^{st}$ order shoots and 1$^{st}$ and 2$^{nd}$ order shoots together. This effect was, however, not significant when analyzed only for 2$^{nd}$ order shoots (Table 2). The effect of elevated $CO_2$ was not significant and no significant $CO_2$ and temperature interaction was detected (Table 2).

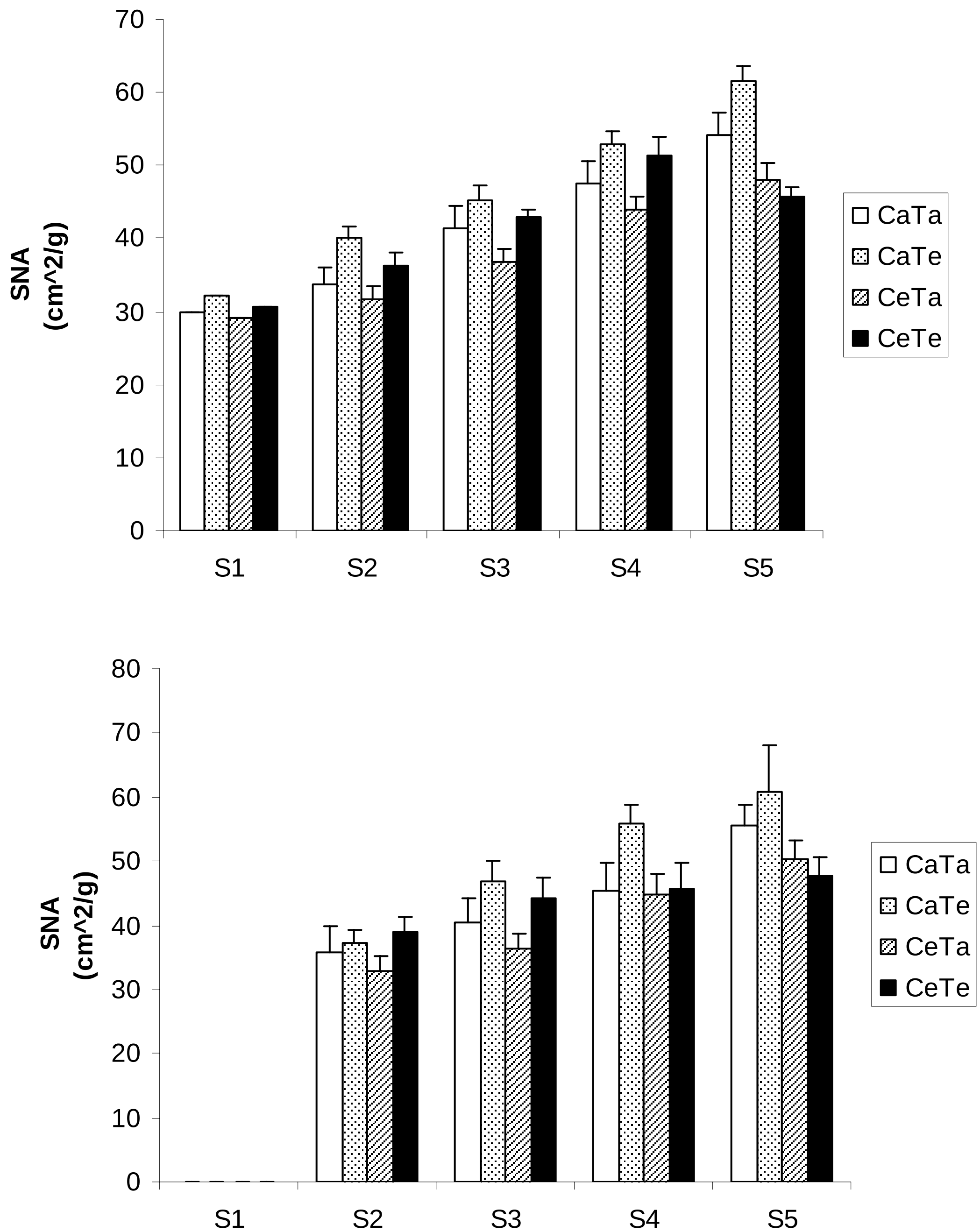


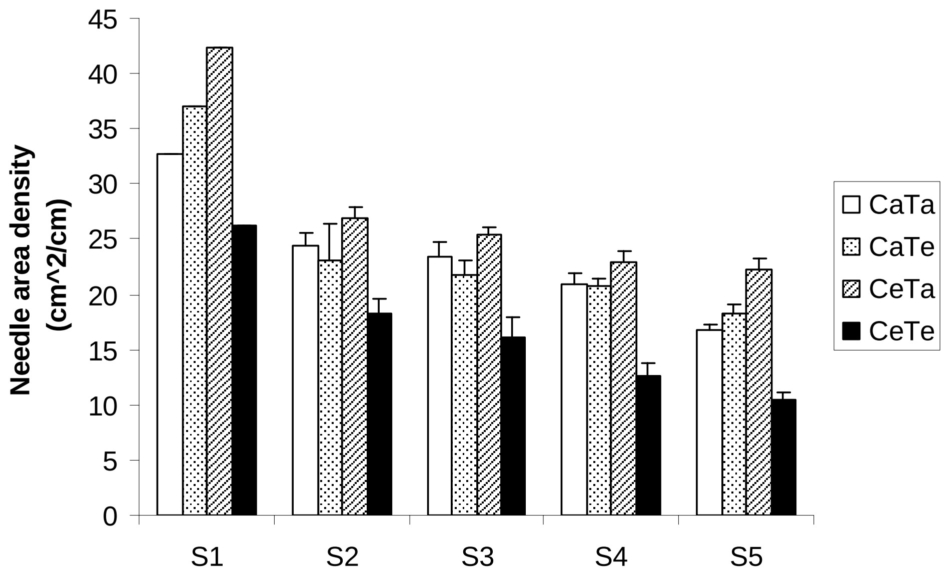

**Figure 8**: Specific needle area for all treatments in each stratum for first order (above) and second order (below) shoots. Standard error is the difference between orders and age classes within stratum.

The SNA was about 40% higher in the lowest strata than in the top strata and the SNA gradually decreased with increasing height in the tree (Figure 8). Most of the observed variability in SNA and needle density was in fact explained by where in the tree the needles were growing (strata in Table 2). The difference in SNA between first and second order shoots was not much (Figure 2).

**Table 2**: P-values from 3-way ANOVA for treatment effects on specific needle area (SNA; $cm^2$ needles/g needles), needle area density ($cm^2$ needles/mm shoot) and needle density (# needles/mm shoots) for Norway spruce growing in elevated temperature (Temp) and atmospheric carbon dioxide concentration ($CO_2$). Also included was the height in the tree (Strata). Analysis was made for $1^{st}$ order shoots (O1), $2^{nd}$ order shoots (O2) and both orders together (O1 + O2).

| Parameters | Temp | CO2 | Strata | TxCxS |
|---|---|---|---|---|
| SNA | | | | |
| O1 | **0.04** | 0.18 | **<0.001** | 0.88 |
| O2 | 0.12 | 0.77 | **<0.001** | 0.61 |
| O1 + O2 | **0.03** | 0.23 | **<0.001** | 0.76 |
| Needle area density | | | | |
| O1 | 0.18 | 0.52 | **<0.001** | 0.14 |
| O2 | 0.12 | 0.58 | **<0.001** | 0.24 |
| O1 + O2 | 0.15 | 0.45 | **<0.001** | 0.12 |
| Needle density | | | | |
| O1 | 0.40 | 0.32 | **<0.001** | 0.36 |
| O2 | 0.49 | 0.57 | 0.59 | 0.64 |
| O1 + O2 | 0.31 | 0.68 | 0.59 | 0.61 |

No significant treatment effects or interactions were found in needle area density or needle density, but both changed significantly with height in the tree (Figure 9 and 10 and Table 2). The apparent low needle area density in the CeTe treatment was also found in the C+3 shoots (data not shown), so this was an artifact caused by some differences in the trees chosen for the experiment. When needle density was calculated as number of needles per mm shoot, this artifact disappeared (Figure 10) and the C+3 shoots were not significantly different between treatments (data not shown).



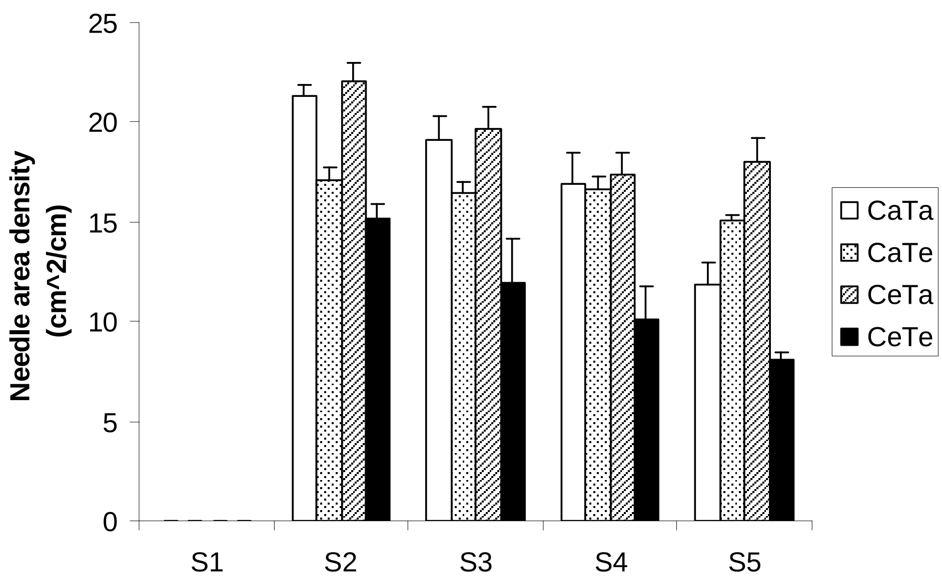




**Figure 9**: Needle area density for all treatments in each stratum for first order (above) and second order (below) shoots. Standard error is the difference between orders and age classes within stratum. Note that the scale on the Y-axis is not the same on both pictures.

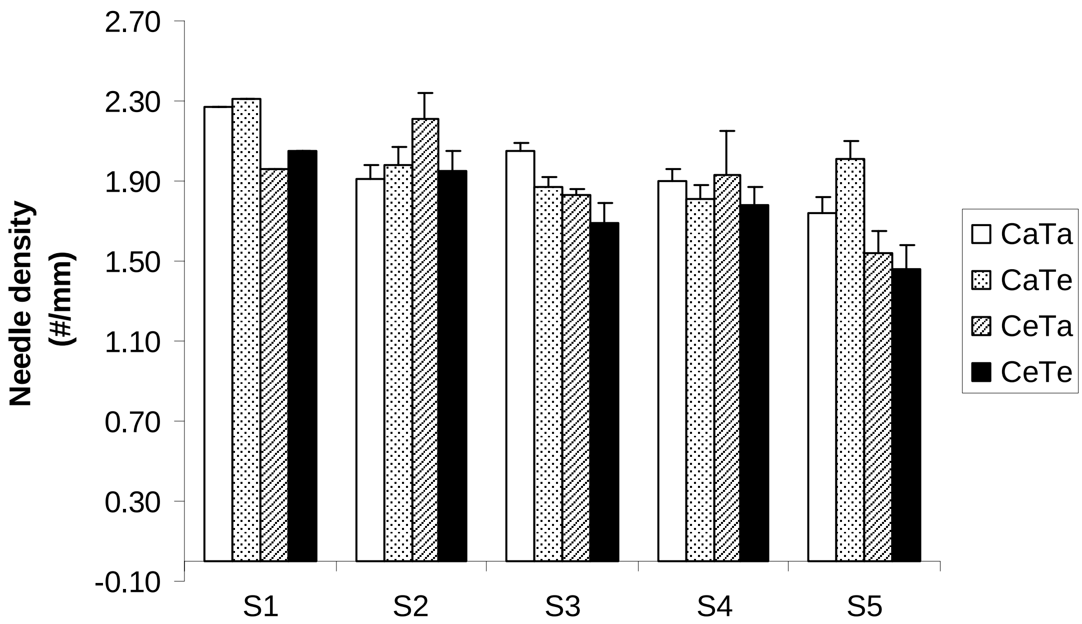



**Figure 10**: Needle density for all treatments in each stratum. Standard error is the difference between orders and age classes within stratum.

*Needle length and width*

The needles in stratum 1 were on average 21% longer than in the other strata lower in the trees (Figure 11). The difference in needle length with height in the tree was highly significant (strata; Table 3). The treatments did not change average needle length significantly nor was there a significant interaction between elevated $CO_2$ and temperature (Table 3). There was, however, a similar trend for shorter needles in the CeTe treatment as was observed for needle density (Figure 10). This was an artifact because of initial differences between trees, as was confirmed by a significant difference for the C+3 needles when compared between treatments (data not shown). This artifact can also been seen in the needle length and width ratio (Figure 13). Hence, the results indicate that elevated temperature and carbon dioxide do not affect needle length in Norway spruce.

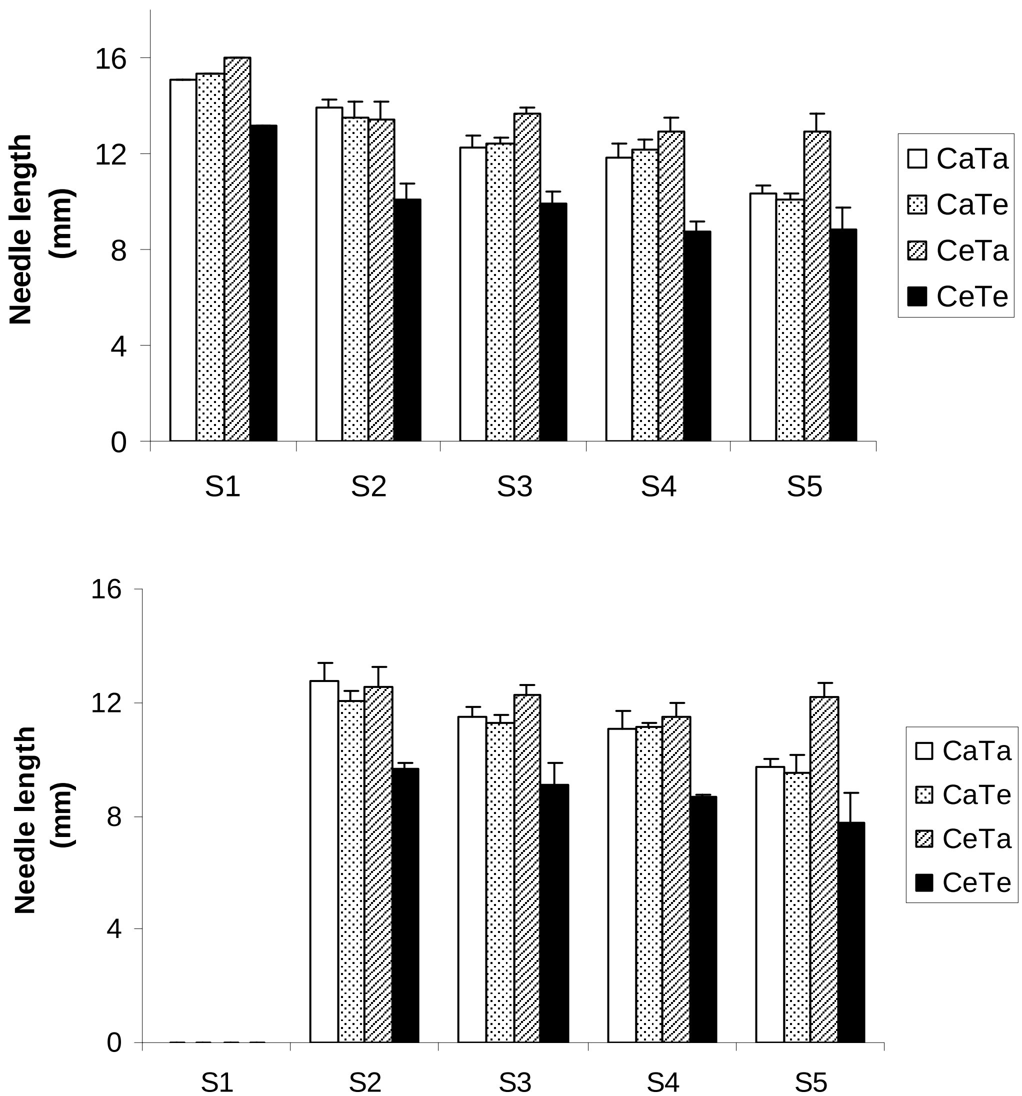



**Figure 11**: Average needle length for all treatments in each stratum. First order shoots (above) and second order shoots (below). Standard error is the difference between orders and age classes within stratum.

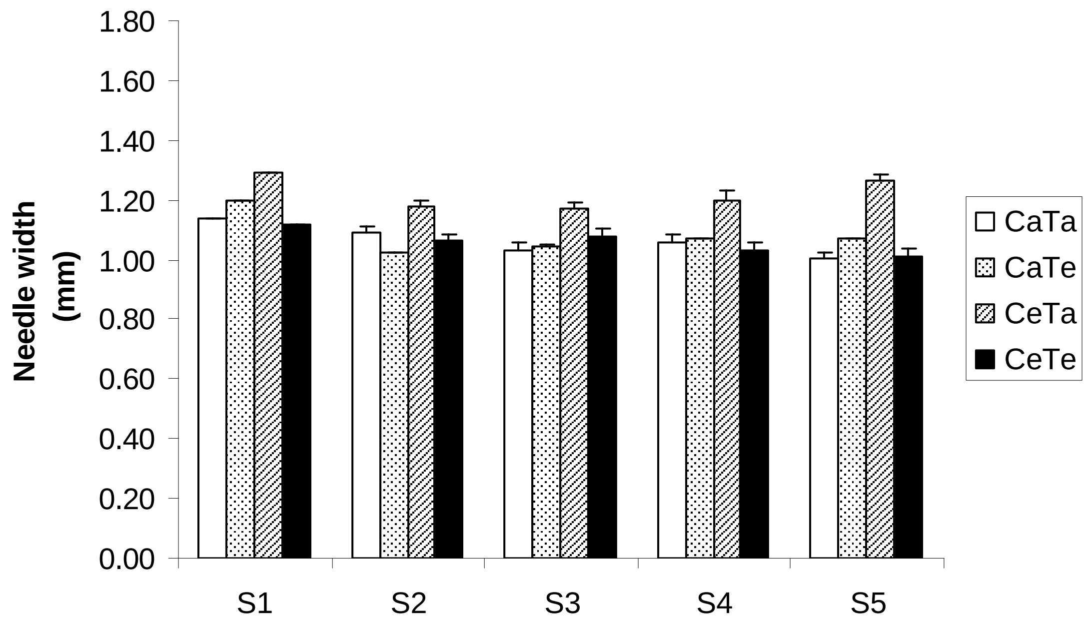



**Figure 12**: Needle width for all treatments in each stratum. Standard error is the difference between orders and age classes within stratum.

**Table 3:** P-values from 3-way ANOVA for treatment effects on needle length (mm), needle width (mm) and needle width and length ratio for Norway spruce growing in elevated temperature (Temp) and atmospheric carbon dioxide concentration ($CO_2$). Also included was the height in the tree (Strata). Analysis was made for 1$^{st}$ order shoots (O1), 2$^{nd}$ order shoots (O2) and both orders together (O1 + O2)

| Parameters | Temp | CO2 | Strata | TxCxS |
|---|---|---|---|---|
| Needle length | | | | |
| O1 | 0.19 | 0.32 | **<0.001** | 0.22 |
| O2 | 0.24 | 0.24 | **<0.001** | 0.52 |
| O1 + O2 | 0.20 | 0.26 | **<0.001** | 0.12 |
| Needle width | | | | |
| O1 | 0.26 | 0.19 | **0.008** | 0.78 |
| O2 | 0.73 | 0.38 | 0.52 | 0.70 |
| O1 + O2 | 0.92 | 0.24 | 0.47 | 0.72 |
| Needle width and length ratio | | | | |
| O1 | 0.32 | 0.10 | **<0.001** | 0.06 |
| O2 | 0.48 | 0.41 | 0.46 | 0.60 |
| O1 + O2 | 0.38 | 0.29 | 0.34 | 0.53 |

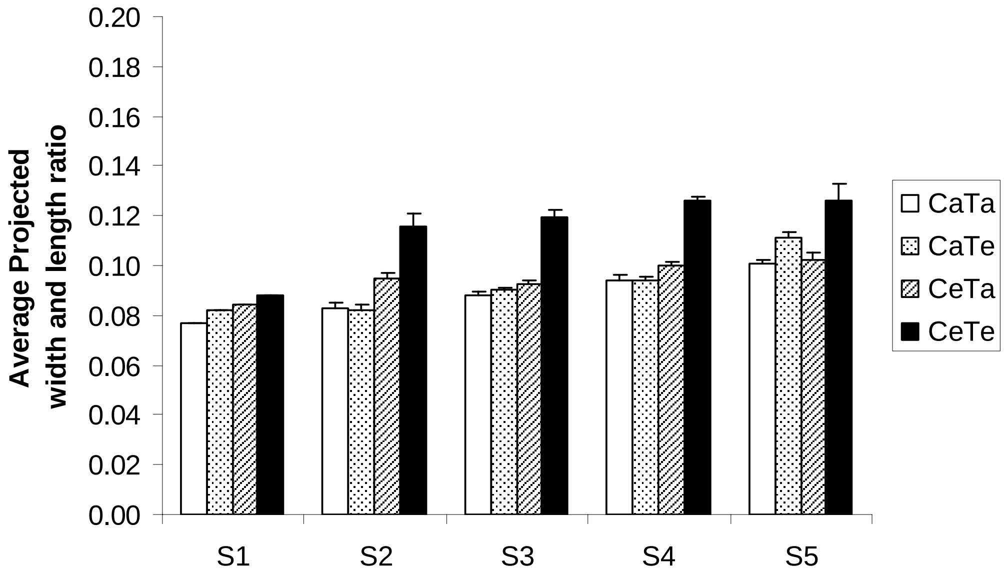



**Figure 13**: The average projected width and length ratio for all treatments in each stratum. Standard error is the difference between orders and age classes within stratum.

There were no significant difference in temperature and carbon dioxide treatments in needle width or the ratio between the width and the length considering the temperature, the carbon dioxide treatment or the combination of the three factors (Figure 12, Figure 13 and Table 3).

*Total shoot length and shoot needle area*

On average for all treatments, the annual shoot length differed from ca. 6 cm in the top stratum to ca. 4 cm in the bottom of the tree crown (Figure 14). The trend that shoot growth increased higher up in the tree was highly significant (Table 4). Temperature elevation also increased shoot growth significantly, both for $1^{st}$ order shoots and $2^{nd}$ order shoots (Table 4). Elevated $CO_2$ did not change shoot growth significantly and there were no clear trends for increased or decreased shoot growth in elevated $CO_2$ (Figure 14 and Table 4). There was no significant interaction between temperature and $CO_2$ for shoot growth (Table 4).

On average, annual shoots had 34% less needle area in the four lower strata than in stratum 1 at the top of the tree (Figure 15), which resulted in highly significant strata effect (Table 4). Total needle area on annual shoots was, however, not significantly affected by temperature or $CO_2$ elevation. It would be expected since both SNA and shoot length were increased in elevated temperature, this would translate into significant effect of elevated temperature on total needle area on annual shoots. However, the variability in shoot length, needle mass and SNA adds up when these parameters were multiplied together to calculate total needle area. When analyzed separately for each age-class, order and stratum, there were some significant temperature effects on total needle area (data not shown, but see Appendix 7 for further information).

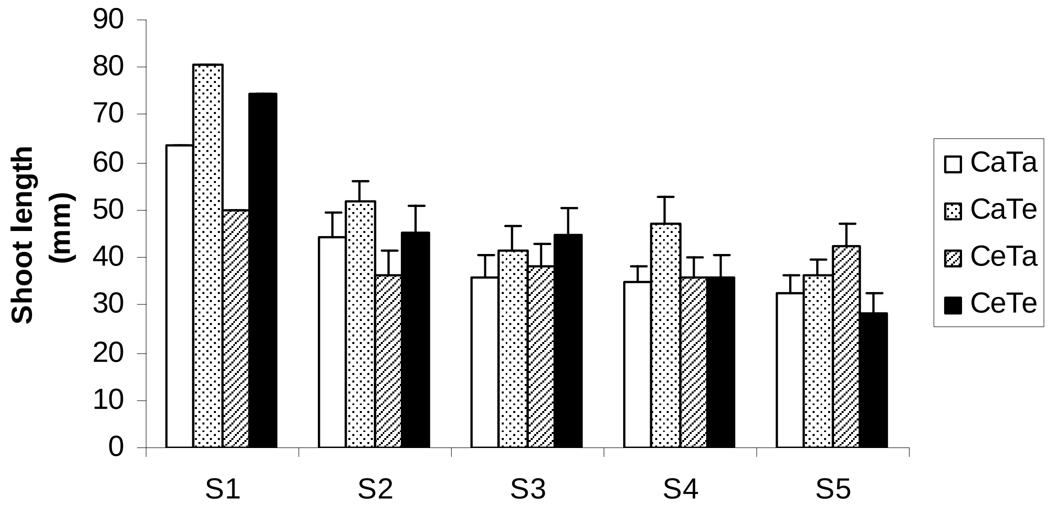



**Figure 14**: Average total shoot length for all treatments in the five strata. Standard error is the difference between orders and age classes within stratum.

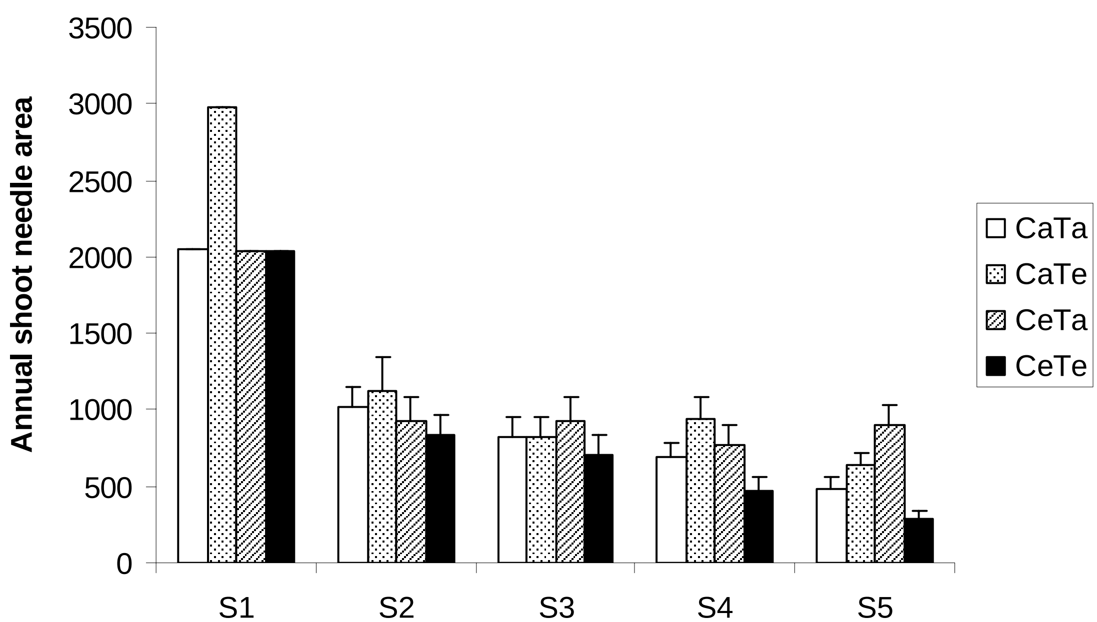



**Figure 15**: Annual shoot needle area for all treatments in each stratum. Standard error is the difference between orders and age classes within stratum.

**Table 4:** P-values from 3-way ANOVA for treatment effects on total shoot length (mm), and total needle area ($mm^2$) for Norway spruce growing in elevated temperature (Temp) and atmospheric carbon dioxide concentration ($CO_2$). Also included was the height in the tree (strata). Analysis was made for 1st order shoots (O1), 2nd order shoots (O2) and both together (O1 + O2).

| Parameters | Temp | CO2 | Strata | TxCxS |
|---|---|---|---|---|
| Total shoot length | | | | |
| O1 | **0.01** | 0.36 | **<0.001** | 0.30 |
| O2 | **<0.001** | 0.32 | 0.14 | 0.68 |
| O1 + O2 | **0.002** | 0.51 | **<0.001** | 0.24 |
| Total needle area | | | | |
| O1 | 0.20 | 0.91 | **<0.001** | 0.66 |
| O2 | 0.37 | 0.35 | **0.001** | 0.28 |
| O1 + O2 | 0.24 | 0.75 | **<0.001** | 0.66 |

## Discussion

It was hypothesized that elevated [$CO_2$] would lead to a decrease in total needle area in the closed canopy of the spruce stand. Because the maximum canopy photosynthesis increased by 35% in elevated [$CO_2$] (Slaney 2006), the trees could allocate some resources to other tissues without decreasing their carbon uptake from what it was before. This could be seen as morphological change in needles created during the experiment, both as a decrease in the needle area density or in the annual shoot growth. All these possible changes were studied in the present project. It was also hypothesized that elevated temperature would increase needle and shoot growth and the interaction between those two environmental factors ($CO_2$ and T) was uncertain. The results were not altogether in agreement with these hypotheses. The total needle area on annual shoots was not significantly affected by temperature or $CO_2$ elevation (Figure 15 and Table 4). Elevated [$CO_2$] was in fact not found to significantly change needle morphology or shoot length (Figures 11, 12, 14 and Tables 3 and 4). Elevated temperature was, however, found to significantly increase both SNA and shoot length (Figures 8 and 14 and Tables 2 and 4), hence partly supporting the hypothesis. Since [$CO_2$] did not significantly change the morphology or growth, no interaction could be found between T and [$CO_2$]. One possible response that also would lead to reduced total needle area is that fewer buds would burst in the spring, resulting in fewer internodal and whorl branches being created. This was not studied in the present project.

*Specific needle area (SNA)*

Specific needle area of needles created during the present experiment increased significantly in elevated temperature (Table 2). Luomala (2005) found significant increase in SNA for Scots pine (*Pinus sylvestris*) seedling needles after exposure to elevated [$CO_2$] and temperature. Zha *et al.* (2001) did a similar study on needle growth on mature Scots pine in Finland. They found that elevated temperature and both elevated [$CO_2$] and temperature increased the SNA by 3-16 % and 1-13% respectively.

There was no significant effect of the elevated [$CO_2$] treatment on SNA, which is in contrast with many other studies of the effects of elevated $CO_2$. Poorter (1993) in this review article said that SNA is frequently reported to decline in elevated $CO_2$ experiments with different herbaceous plant and tree species. Such reductions have even been reported for young Norway spruce saplings and seedlings. Hättenschwiler and Körner (1996) found a significant decrease in SNA  in young Norway spruce saplings after one year exposure to elevated $CO_2$. Zha et. al (2001) also found elevated [$CO_2$] alone reduce the SNA by 2-15% in similar study on mature Scots pine. On the other hand Laitinen *et al* (1998) found out that elevated [$CO_2$] did not affect the SNA of Sots pine significantly, which is the same result as found in the present study on Norway spruce.

*Other morphological changes*

In this study the needle length was not significantly affected by the elevated $CO_2$ concentration or the temperature. Luomala (2005) got the same results when studying needle morphology on Scots pine seedlings exposed to elevated $CO_2$ concentration and temperature.

In earlier study at Flakaliden, Stenberg et al. (1999) did not find a significant correlation between openness of the tree crown and length of the needles. In the present study, there seems however to be highly significant relationship between height in the three (openness) and needle length, both on 1$^{st}$ and 2$^{nd}$ order shoots (Table 3; Figure 11).

*Total shoot length and estimated total needle area.*

The present study showed that elevated temperature increased shoot growth significantly, but elevated [$CO_2$] did not change it significantly (Table 4). Hättenschwiler and Kröner (1996) got the same results considering young Norway spruce saplings growing in elevated $CO_2$, where the treatment did not significantly affect the shoot growth.

Slaney (2006), in her Ph.D. thesis from the Flakaliden experiment, found that elevated temperature did not affect the final length of the shoots but affected the time of budburst in the spring. According to her results, the shoots growth started two or three weeks earlier in the treatment with elevated temperature. Slaney (2006) only followed few annual shoots high up in the tree, while in the present study annual shoots were measured at different height in the tree. This can explain why this study showed a significant increase in shoot growth, but Slaney (2006) did not find it. Slaney (2006), however, found that inter-annual variation in shoot growth could be explained by correlation between temperature sum during the active growing season and final shoot length. This finding can also been used to explain more shoot growth in elevated temperature within one growing season, since the temperature sum was higher in the elevated temperature treatment.

Kilpelänien *et al.* (2006) did not find a significant increase in annual shoot length in field-grown Scots pine trees in elevated temperature. However, they only compared the top shoots of the trees.

Total needle area on annual shoots created during the experiment was not significantly affected by temperature or $CO_2$ elevation (Table 4, Figure 15). These results are the opposite to the results of Zha et. al (2001) for Sots pine, where elevated temperature, carbon dioxide and the treatment of both parameters tested together had significant effects on needle area of annual shoots.

*Observed variability with the height in the tree crown*

When the effects of different treatments were studied on different morphological parameters it was obvious that the height in the tree crown (strata) had significant effect. It obviously matters where in the tree the needles grow, and the results obtained from experiment such as the present one are partly dependent on where in the tree the effects are studied. This is important to be aware of when such research is planned.

It is well known that shading has a large impact on both morphology and physiology of leaves and needles (e.g. Larcher 2003). Because of this, foliage is often divided into shade and “sun needles/leaves” in physiological studies. The change in morphology and physiology between “sun” and “shade” types is, however, gradual and in reality it is difficult to only talk about two functional types of foliage. Earlier studies at Flakaliden experimental forest have shown that the morphological parameters change within the tree crown as a function of openness of the crown. (Stenberg et al. 1999). Stenberg et al (1999) found that the SNA of the most shaded needles (lowest in the crown) in the fertilisation treatment had about 2.5 times larger SNA than the most exposed needles at the top of the trees. Canopy openness was found to explain 80% of the variation in the SNA. The present study showed a little less relative change in SNA between the top and the bottom of the tree crown, but the difference can be explained by the fact that the present study took place in the more open non-fertilised control plots.

Steinberg et al (1999) also found out that needle thickness and needle width increased with canopy openness in Norway spruce in Flakaliden, i.e. the

SNA decreased higher up in the tree crown because the needles became more symmetrical in their cross-section.

It is therefore important that people consider where in the tree they are taking samples when comparing variant parameters in the trees. Height and openness of the crown must be considered before sampling.

*Other sources of variation*

The canopy of Norway spruce at Flakaliden consists of ca. 12 age-classes of needles, which are divided between $1^{st}$, $2^{nd}$, $3^{rd}$ and sometimes $4^{th}$ order annual shoots. When the present results on needle morphology on $1^{st}$ and $2^{nd}$ order shoots are compared, it is apparent that there are certain differences between them, even if responses to elevated temperature and [$CO_2$] were similar (Figures 8, 9 and 11 and Tables 2, 3 and 4). This variation should also be kept in mind when sampling of needles is planned. Since $2^{nd}$ order needles make much larger proportion of the total needle area of a spruce tree than $1^{st}$ order needles, studies should rather focus on those.

*Chamber effects*

The whole-tree chamber system (WTC) enabled a very accurate control of temperature and other environmental variables (Slaney 2006). This resulted in almost no significant chamber effects on needle morphology in the present study. In earlier studies with elevated $CO_2$ and WTCs, chamber effects were often apparent on leaf or needle morphology and other growth traits (e.g. Sigurdsson 2001; Sigurdsson et al. 2001; Poorteer 1993). This was presumably because of less strict temperature control, so results from such experiments could have a confounding [$CO_2$] and temperature effects.

Slaney (2006) also found very few examples of significant chamber effects on measured physiological and phonological parameters. This support therefore Slaney's (2006) conclusion that this WTC system had relatively good ability to reproduce natural conditions and provided the conditions for a realistic assessment of tree responses to future climate change.

## Conclusions

From the present study it can be concluded that elevated temperature can possibly have potential to increase needle area, through significant changes in annual shoot lengths. Elevated [$CO_2$] is, however, not expected to have a direct effect on needle morphology or needle area of Norway spruce and no interactive changes are expected between elevated temperature and [$CO_2$].

It is important to note that needle morphology changes more with height in the tree than due to changes in environmental parameters, such as temperature and [$CO_2$]. When comparing different treatments, care has to be taken that needles from comparable sites within tree canopies are used.

The whole-tree chambers themselves had minor effects on needle morphology of the Norway spruce trees (CaTa compared to outside reference trees). This gives confidence in the ability of the system to reproduce the effects of future climate change.

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**Appendix 1:** Average specific needle area (SNA) ± standard error of Norway spruce growing outside chambers (Ref) and in ambient and elevated temperature (Ta, Te) and atmospheric carbon dioxide concentration (Ca, Ce). Also shown P-values from 2-way ANOVA for treatment effects (when ANOVA P<0.05) and interaction. Chamber effects were studied by One-Way ANOVA between Ref and CaTa treatments.

| Strata | Order | Age | REF | CATA | CATE | CETA | CETE | Anova P value | Chmb effect | CO2 effect | Temp effect | CO2xTemp |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 1 | 1 | 32.67 ± 1.3 | 29.99 ± 1.9 | 32.30 ± 2.4 | 29.20 ± 0.8 | 30.75 ± 1.7 | 0.3239 | 0.253 | | | |
| 2 | 1 | 1 | 38.44 ± 3.5 | 37.38 ± 2.5 | 42.74 ± 2.6 | 34.94 ± 2.8 | 39.01 ± 4.3 | 0.5612 | 0.820 | | | |
| 2 | 1 | 2 | 35.74 ± 1.7 | 34.10 ± 1.3 | 41.08 ± 4.2 | 32.31 ± 3.0 | 37.60 ± 2.9 | 0.2908 | 0.688 | | | |
| 2 | 1 | 3 | 31.54 ± 1.3 | 30.07 ± 2.4 | 36.53 ± 4.2 | 28.09 ± 2.1 | 31.87 ± 1.2 | 0.2565 | 0.685 | | | |
| 2 | 1 | 4 | 29.90 ± 2.0 | 27.75 ± 1.4 | 16.75 ± 14.9 | 28.11 ± 1.5 | 28.47 ± 1.9 | 0.4861 | 0.773 | | | |
| 2 | 2 | 1 | 38.66 ± 2.3 | 43.97 ± 5.1 | 41.10 ± 0.5 | 34.67 ± 3.1 | 40.47 ± 2.6 | 0.5542 | 0.354 | | | |
| 2 | 2 | 2 | 38.72 ± 3.4 | 31.85 ± 5.3 | 35.17 ± 13.5 | 35.76 ± 3.3 | 42.16 ± 2.3 | 0.6876 | 0.365 | | | |
| 2 | 2 | 3 | 32.28 ± 2.0 | 31.26 ± 2.7 | 35.41 ± 2.4 | 28.58 ± 2.8 | 34.13 ± 1.9 | 0.4448 | 0.752 | | | |
| 3 | 1 | 1 | 43.28 ± 1.9 | 44.12 ± 1.2 | 46.44 ± 3.9 | 38.57 ± 3.1 | 44.39 ± 3.5 | 0.3850 | 0.831 | | | |
| 3 | 1 | 2 | 42.47 ± 3.4 | 44.72 ± 1.9 | 48.58 ± 2.6 | 39.11 ± 3.2 | 43.53 ± 4.0 | 0.3583 | 0.620 | | | |
| 3 | 1 | 3 | 36.73 ± 2.8 | 35.02 ± 0.9 | 40.57 ± 2.0 | 32.68 ± 1.6 | 41.19 ± 7.6 | 0.4931 | 0.758 | | | |
| 3 | 1 | 4 | 31.95 ± 4.0 | 33.17 ± 4.0 | 32.43 ± 0.2 | 29.34 ± 0.8 | 34.11 ± 4.5 | 0.8325 | 0.779 | | | |
| 3 | 2 | 1 | 43.62 ± 2.7 | 45.26 ± 0.4 | 49.94 ± 2.2 | 39.16 ± 1.4 | 49.20 ± 1.8 | 0.0134 | 0.549 | 0.066 | 0.002 | 0.134 |
| 3 | 2 | 2 | 39.50 ± 3.3 | 43.08 ± 3.3 | 49.99 ± 3.8 | 38.32 ± 0.1 | 45.02 ± 0.8 | 0.1306 | 0.429 | | | |
| 3 | 2 | 3 | 38.56 ± 4.6 | 32.87 ± 1.1 | 40.49 ± 2.0 | 31.82 ± 0.2 | 38.64 ± 2.8 | 0.2388 | 0.214 | | | |
| 4 | 1 | 1 | 50.53 ± 1.4 | 50.15 ± 1.4 | 53.54 ± 2.3 | 45.64 ± 2.6 | 55.49 ± 4.9 | 0.3677 | 0.938 | | | |
| 4 | 1 | 2 | 48.80 ± 3.2 | 50.82 ± 2.8 | 55.94 ± 3.5 | 46.20 ± 2.5 | 52.98 ± 4.6 | 0.3588 | 0.681 | | | |
| 4 | 1 | 3 | 43.29 ± 3.9 | 41.80 ± 1.0 | 48.92 ± 1.0 | 39.90 ± 2.0 | 45.44 ± 1.4 | 0.0999 | 0.633 | | | |
| 4 | 1 | 4 | 38.23 ± 2.3 | 39.52 ± 2.2 | 36.43 ± 1.6 | 33.43 ± 1.6 | 37.65 ± 2.4 | 0.3397 | 0.665 | | | |
| 4 | 2 | 1 | 48.07 ± 3.9 | 53.36 ± 1.4 | 59.90 ± 1.3 | 47.93 ± 1.8 | 38.03 ± 19.2 | 0.0295 | 0.164 | 0.005 | 0.070 | 0.542 |
| 4 | 2 | 2 | 48.77 ± 2.8 | 38.22 ± 16.7 | 57.46 ± 1.9 | 47.90 ± 0.5 | 52.45 ± 2.3 | 0.5252 | 0.355 | | | |
| 4 | 2 | 3 | 88.68 ± 40.9 | 44.70 ± 1.8 | 49.77 ± 1.3 | 38.74 ± 1.5 | 46.46 ± 1.2 | 0.1819 | 0.047 | | | |
| 5 | 1 | 1 | 48.02 ± 4.5 | 57.16 ± 0.3 | 63.75 ± 1.8 | 49.63 ± 7.2 | 45.49 ± 5.5 | 0.2488 | 0.289 | | | |
| 5 | 1 | 2 | 48.20 ± 4.9 | 57.35 ± 5.7 | 64.05 ± 1.2 | 51.77 ± 4.3 | 48.32 ± 6.9 | 0.3192 | 0.283 | | | |
| 5 | 1 | 3 | 43.91 ± 2.5 | 48.13 ± 3.8 | 56.80 ± 0.7 | 43.00 ± 3.8 | 43.12 ± 6.0 | 0.2215 | 0.457 | | | |
| 5 | 1 | 4 | 40.51 ± 1.1 | 45.42 ± 3.0 | 47.04 ± 0.8 | 26.41 ± 11.3 | 35.42 ± 4.8 | 0.2163 | 0.577 | | | |
| 5 | 2 | 1 | 49.79 ± 4.1 | 59.40 ± 6.6 | 51.37 ± 1.5 | 53.21 ± 4.2 | 49.54 ± 5.9 | 0.6444 | 0.208 | | | |
| 5 | 2 | 2 | 48.97 ± 5.1 | 58.22 ± 3.6 | 74.84 ± 10.1 | 53.51 ± 2.3 | 51.81 ± 9.5 | 0.1397 | 0.365 | | | |
| 5 | 2 | 3 | 44.01 ± 2.6 | 49.33 ± 4.1 | 56.53 ± 1.0 | 44.39 ± 2.3 | 41.61 ± 6.3 | 0.1310 | 0.351 | | | |

**Appendix 2**: Average needle area density ± SE of Norway spruce growing outside chambers (Ref) and in ambient and elevated temperature (Ta, Te) and atmospheric carbon dioxide concentration (Ca, Ce). Also shown P-values from 2-way ANOVA for treatment effects (when ANOVA P<0.05) and interaction. Chamber effects were studied by One-Way ANOVA between Ref and CaTa treatments.

| Strata | Order | Age | REF | CATA | CATE | CETA | CETE | Anova P value | Chmb effect | CO2 effect | Temp effect | CO2xTemp |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 1 | 1 | 37.35 ± 1.5 | 32.7 ± 3.5 | 36.99 ± 7.7 | 42.31 ± 5.7 | 26.2 ± 2.3 | 0.614 | 0.541 | | | |
| 2 | 1 | 1 | 25.20 ± 2.3 | 24.0 ± 2.7 | 24.87 ± 4.8 | 24.65 ± 3.6 | 16.6 ± 3.0 | 0.386 | 0.805 | | | |
| 2 | 1 | 2 | 30.70 ± 5.0 | 25.5 ± 3.8 | 30.01 ± 5.4 | 26.40 ± 3.5 | 19.7 ± 2.6 | 0.410 | 0.405 | | | |
| 2 | 1 | 3 | 35.27 ± 4.8 | 26.7 ± 5.4 | 23.02 ± 1.7 | 26.68 ± 0.8 | 21.2 ± 0.9 | 0.102 | 0.103 | | | |
| 2 | 1 | 4 | 23.95 ± 12.9 | 21.7 ± 1.1 | 14.37 ± 13.3 | 29.75 ± 3.6 | 15.9 ± 5.2 | 0.173 | 0.144 | | | |
| 2 | 2 | 1 | 21.22 ± 2.2 | 21.4 ± 2.7 | 18.32 ± 5.4 | 22.91 ± 5.3 | 14.4 ± 3.1 | 0.591 | 0.977 | | | |
| 2 | 2 | 2 | 27.07 ± 1.5 | 22.2 ± 3.4 | 16.49 ± 0.5 | 20.14 ± 4.0 | 16.7 ± 4.6 | 0.260 | 0.333 | | | |
| 2 | 2 | 3 | 24.74 ± 2.5 | 20.3 ± 1.9 | 16.50 ± 1.8 | 23.09 ± 1.6 | 14.3 ± 2.0 | 0.036 | 0.148 | 0.8691 | 0.0188 | 0.2538 |
| 3 | 1 | 1 | 22.86 ± 1.9 | 20.5 ± 4.5 | 20.40 ± 6.6 | 23.47 ± 2.4 | 11.2 ± 4.3 | 0.253 | 0.673 | | | |
| 3 | 1 | 2 | 26.69 ± 1.3 | 25.2 ± 5.3 | 21.34 ± 2.4 | 27.25 ± 4.1 | 16.7 ± 2.3 | 0.230 | 0.765 | | | |
| 3 | 1 | 3 | 27.64 ± 2.8 | 25.9 ± 6.0 | 19.91 ± 4.3 | 25.34 ± 3.6 | 18.4 ± 0.8 | 0.417 | 0.757 | | | |
| 3 | 1 | 4 | 26.22 ± 2.9 | 21.9 ± 2.9 | 25.53 ± 3.4 | 25.24 ± 4.7 | 18.3 ± 0.8 | 0.361 | 0.327 | | | |
| 3 | 2 | 1 | 19.48 ± 1.8 | 17.7 ± 5.0 | 16.26 ± 2.8 | 17.82 ± 1.7 | 7.6 ± 2.6 | 0.115 | 0.690 | | | |
| 3 | 2 | 2 | 20.76 ± 4.5 | 21.5 ± 4.5 | 17.56 ± 0.3 | 21.60 ± 2.9 | 14.0 ± 1.9 | 0.300 | 0.859 | | | |
| 3 | 2 | 3 | 19.27 ± 3.6 | 18.2 ± 4.2 | 15.46 ± 0.5 | 19.65 ± 4.6 | 14.3 ± 1.2 | 0.606 | 0.804 | | | |
| 4 | 1 | 1 | 20.00 ± 3.7 | 17.6 ± 3.7 | 18.80 ± 3.9 | 20.15 ± 1.4 | 10.0 ± 2.9 | 0.150 | 0.567 | | | |
| 4 | 1 | 2 | 25.23 ± 0.7 | 22.0 ± 4.5 | 21.46 ± 5.1 | 24.25 ± 2.6 | 14.0 ± 2.7 | 0.254 | 0.532 | | | |
| 4 | 1 | 3 | 25.23 ± 2.4 | 21.3 ± 4.5 | 20.89 ± 3.0 | 24.53 ± 1.4 | 15.0 ± 2.5 | 0.186 | 0.366 | | | |
| 4 | 1 | 4 | 19.92 ± 1.5 | 22.4 ± 5.7 | 21.67 ± 4.9 | 22.92 ± 1.6 | 11.5 ± 1.7 | 0.218 | 0.630 | | | |
| 4 | 2 | 1 | 14.22 ± 1.6 | 14.0 ± 3.2 | 15.71 ± 3.3 | 15.10 ± 0.8 | 7.0 ± 4.0 | 0.736 | 0.958 | | | |
| 4 | 2 | 2 | 18.21 ± 0.8 | 19.1 ± 3.7 | 17.82 ± 3.5 | 18.98 ± 1.3 | 12.4 ± 2.8 | 0.414 | 0.826 | | | |
| 4 | 2 | 3 | 16.84 ± 2.4 | 17.7 ± 3.4 | 16.41 ± 2.4 | 17.97 ± 0.7 | 11.1 ± 2.9 | 0.446 | 0.817 | | | |
| 5 | 1 | 1 | 22.36 ± 3.1 | 17.9 ± 3.3 | 16.52 ± 2.5 | 21.25 ± 2.7 | 8.5 ± 1.7 | 0.030 | 0.296 | 0.3947 | 0.0168 | 0.0677 |
| 5 | 1 | 2 | 24.51 ± 3.0 | 16.5 ± 2.6 | 19.51 ± 3.9 | 21.96 ± 3.6 | 11.7 ± 3.3 | 0.138 | 0.150 | | | |
| 5 | 1 | 3 | 23.18 ± 1.6 | 17.1 ± 3.4 | 17.36 ± 0.4 | 25.36 ± 2.4 | 11.5 ± 4.9 | 0.068 | 0.196 | | | |
| 5 | 1 | 4 | 16.86 ± 2.4 | 15.4 ± 4.3 | 19.89 ± 5.3 | 20.25 ± 2.1 | 9.9 ± 3.4 | 0.289 | 0.763 | | | |
| 5 | 2 | 1 | 18.39 ± 3.5 | 10.4 ± 2.5 | 14.63 ± 0.8 | 16.39 ± 1.9 | 7.4 ± 0.7 | 0.042 | 0.034 | 0.9492 | 0.1331 | 0.0091 |
| 5 | 2 | 2 | 22.99 ± 2.3 | 14.0 ± 0.9 | 15.10 ± 1.7 | 20.41 ± 2.2 | 8.60 ± 1.3 | 0.001 | 0.005 | 0.9856 | 0.0106 | 0.0039 |
| 5 | 2 | 3 | 17.14 ± 0.4 | 11.2 ± 2.6 | 15.54 ± 0.7 | 17.12 ± 2.0 | 8.33 ± 3.4 | 0.063 | 0.076 | | | |

**Appendix 3**: Average needle density ± SE of Norway spruce growing outside chambers (Ref) and in ambient and elevated temperature (Ta, Te) and atmospheric carbon dioxide concentration (Ca, Ce). Also shown P-values from 2-Way ANOVA for treatment effects (when ANOVA P<0.05) and interaction. Chamber effects were studied by One-Way ANOVA between Ref and CaTa treatments.

| Strata | Order | Age | REF | CATA | CATE | CETA | CETE | Anova P value | Chmb effect | CO2 effect | Temp effect | CO2xT emp |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 1 | 1 | 2.33 ± 0.4 | 2.27 ± 0.2 | 2.31 ± 0.2 | 1.96 ± 0.4 | 2.05 ± 0.1 | 0.837 | 0.883 | | | |
| 2 | 1 | 1 | 2.39 ± 0.3 | 2.14 ± 0.1 | 2.24 ± 0.4 | 2.45 ± 0.3 | 2.58 ± 0.5 | 0.708 | 0.303 | | | |
| 2 | 1 | 2 | 2.06 ± 0.4 | 1.94 ± 0.1 | 2.10 ± 0.2 | 2.42 ± 0.4 | 1.81 ± 0.2 | 0.591 | 0.503 | | | |
| 2 | 1 | 3 | 2.03 ± 0.1 | 1.87 ± 0.3 | 2.09 ± 0.1 | 2.01 ± 0.4 | 1.88 ± 0.0 | 0.685 | 0.313 | | | |
| 2 | 1 | 4 | 1.48 ± 0.7 | 1.66 ± 0.1 | 1.93 ± 0.2 | 1.88 ± 0.1 | 1.80 ± 0.3 | 0.313 | 0.179 | | | |
| 2 | 2 | 1 | 2.08 ± 0.3 | 2.18 ± 0.1 | 2.12 ± 0.5 | 2.70 ± 0.7 | 1.79 ± 0.2 | 0.389 | 0.898 | | | |
| 2 | 2 | 2 | 1.83 ± 0.2 | 1.75 ± 0.0 | 1.61 ± 0.1 | 1.78 ± 0.2 | 1.89 ± 0.1 | 0.179 | 0.094 | | | |
| 2 | 2 | 3 | 1.71 ± 0.1 | 1.83 ± 0.3 | 1.78 ± 0.2 | 2.22 ± 0.4 | 1.87 ± 0.4 | 0.320 | 0.329 | | | |
| 3 | 1 | 1 | 1.82 ± 0.3 | 2.09 ± 0.1 | 1.84 ± 0.3 | 1.82 ± 0.1 | 1.29 ± 0.3 | 0.712 | 0.217 | | | |
| 3 | 1 | 2 | 1.75 ± 0.3 | 2.18 ± 0.1 | 1.84 ± 0.1 | 1.87 ± 0.1 | 1.92 ± 0.2 | 0.789 | 0.377 | | | |
| 3 | 1 | 3 | 1.68 ± 0.2 | 2.01 ± 0.1 | 1.97 ± 0.2 | 1.82 ± 0.2 | 1.78 ± 0.1 | 0.651 | 0.914 | | | |
| 3 | 1 | 4 | 1.67 ± 0.2 | 2.10 ± 0.2 | 2.11 ± 0.2 | 1.84 ± 0.2 | 1.94 ± 0.2 | 0.865 | 0.848 | | | |
| 3 | 2 | 1 | 1.82 ± 0.3 | 2.04 ± 0.1 | 1.92 ± 0.2 | 1.83 ± 0.3 | 1.92 ± 1.0 | 0.229 | 0.121 | | | |
| 3 | 2 | 2 | 1.77 ± 0.3 | 2.07 ± 0.3 | 1.71 ± 0.2 | 1.68 ± 0.1 | 1.51 ± 0.2 | 0.298 | 0.291 | | | |
| 3 | 2 | 3 | 1.43 ± 0.2 | 1.90 ± 0.1 | 1.69 ± 0.0 | 1.97 ± 0.4 | 1.44 ± 0.2 | 0.683 | 0.690 | | | |
| 4 | 1 | 1 | 2.06 ± 0.2 | 2.06 ± 0.2 | 1.75 ± 0.3 | 1.53 ± 0.0 | 1.59 ± 0.5 | 0.359 | 0.947 | | | |
| 4 | 1 | 2 | 1.77 ± 0.2 | 1.93 ± 0.1 | 1.75 ± 0.2 | 1.88 ± 0.2 | 1.74 ± 0.1 | 0.620 | 0.896 | | | |
| 4 | 1 | 3 | 1.64 ± 0.1 | 1.69 ± 0.2 | 1.75 ± 0.1 | 1.58 ± 0.1 | 1.60 ± 0.2 | 0.201 | 0.558 | | | |
| 4 | 1 | 4 | 2.30 ± 0.5 | 2.10 ± 0.1 | 2.22 ± 0.3 | 2.01 ± 0.1 | 1.92 ± 0.2 | 0.344 | 0.458 | | | |
| 4 | 2 | 1 | 1.94 ± 0.2 | 1.88 ± 0.2 | 1.72 ± 0.1 | 3.18 ± 1.6 | 2.14 ± 0.5 | 0.940 | 0.802 | | | |
| 4 | 2 | 2 | 1.77 ± 0.2 | 1.91 ± 0.2 | 1.77 ± 0.2 | 1.72 ± 0.1 | 1.96 ± 0.3 | 0.699 | 0.610 | | | |
| 4 | 2 | 3 | 1.56 ± 0.1 | 1.71 ± 0.1 | 1.75 ± 0.1 | 1.60 ± 0.2 | 1.50 ± 0.0 | 0.738 | 0.336 | | | |
| 5 | 1 | 1 | 1.79 ± 0.1 | 1.99 ± 0.0 | 1.94 ± 0.3 | 1.16 ± 0.3 | 1.45 ± 0.0 | 0.449 | 0.231 | | | |
| 5 | 1 | 2 | 1.77 ± 0.2 | 1.94 ± 0.1 | 2.13 ± 0.2 | 1.54 ± 0.1 | 1.40 ± 0.3 | 0.631 | 0.240 | | | |
| 5 | 1 | 3 | 1.56 ± 0.1 | 1.75 ± 0.2 | 1.78 ± 0.1 | 1.61 ± 0.2 | 1.31 ± 0.6 | 0.609 | 0.211 | | | |
| 5 | 1 | 4 | 1.64 ± 0.2 | 1.79 ± 0.1 | 2.40 ± 0.3 | 2.04 ± 0.4 | 2.01 ± 0.9 | 0.752 | 0.437 | | | |
| 5 | 2 | 1 | 1.66 ± 0.2 | 1.52 ± 0.1 | 2.09 ± 0.0 | 1.51 ± 0.2 | 1.77 ± 0.3 | 0.200 | 0.058 | | | |
| 5 | 2 | 2 | 1.86 ± 0.1 | 1.74 ± 0.2 | 2.04 ± 0.2 | 1.63 ± 0.1 | 1.27 ± 0.3 | 0.461 | 0.409 | | | |
| 5 | 2 | 3 | 1.52 ± 0.1 | 1.45 ± 0.2 | 1.72 ± 0.1 | 1.29 ± 0.2 | 0.98 ± 0.4 | 0.233 | 0.115 | | | |

**Appendix 4**: Average needle length ± SE of Norway spruce growing outside chambers (Ref) and in ambient and elevated temperature (Ta, Te) and atmospheric [$CO_2$] (Ca, Ce). Also P-values from 2-way ANOVA for treatment effects (when ANOVA P<0.05) and interaction. Chamber effects were studied by One-Way ANOVA between Ref and CaTa treatments.

| Strata | Order | Age | REF | CATA | CATE | CETA | CETE | Anova P value | Chmb effect | CO2 effect | Temp effect | CO2xTemp |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 1 | 1 | 14.15 ± 1.2 | 15.05 ± 1.2 | 15.30 ± 1.0 | 16.02 ± 0.9 | 13.13 ± 1.3 | 0.542 | 0.935 | | | |
| 2 | 1 | 1 | 12.68 ± 0.5 | 13.25 ± 0.3 | 13.14 ± 0.5 | 11.59 ± 0.8 | 9.08 ± 1.6 | 0.035 | 0.654 | 0.016 | 0.204 | 0.240 |
| 2 | 1 | 2 | 15.23 ± 0.4 | 14.10 ± 0.6 | 15.31 ± 1.8 | 12.84 ± 1.0 | 11.38 ± 2.1 | 0.281 | 0.572 | | | |
| 2 | 1 | 3 | 15.30 ± 1.0 | 14.72 ± 0.9 | 12.00 ± 0.7 | 15.26 ± 1.2 | 11.11 ± 1.5 | 0.063 | 0.721 | | | |
| 2 | 1 | 4 | 15.49 ± 1.4 | 13.44 ± 1.2 | 13.61 ± 0.5 | 13.86 ± 0.5 | 8.69 ± 2.0 | 0.060 | 0.345 | | | |
| 2 | 2 | 1 | 11.17 ± 0.4 | 11.80 ± 0.6 | 11.60 ± 0.2 | 13.21 ± 1.5 | 9.60 ± 1.1 | 0.180 | 0.597 | | | |
| 2 | 2 | 2 | 14.10 ± 0.7 | 13.95 ± 0.7 | 12.78 ± 1.5 | 11.14 ± 1.8 | 10.06 ± 2.6 | 0.378 | 0.949 | | | |
| 2 | 2 | 3 | 13.59 ± 0.9 | 12.50 ± 1.0 | 11.69 ± 1.0 | 13.27 ± 1.3 | 9.33 ± 1.5 | 0.157 | 0.511 | | | |
| 3 | 1 | 1 | 13.44 ± 1.1 | 11.57 ± 1.8 | 12.48 ± 1.7 | 13.19 ± 0.6 | 8.54 ± 1.9 | 0.187 | 0.379 | | | |
| 3 | 1 | 2 | 14.97 ± 1.6 | 12.18 ± 1.0 | 12.62 ± 1.1 | 14.05 ± 1.5 | 10.37 ± 2.1 | 0.309 | 0.221 | | | |
| 3 | 1 | 3 | 15.88 ± 0.6 | 13.67 ± 1.5 | 11.73 ± 1.6 | 14.16 ± 1.4 | 10.90 ± 0.8 | 0.987 | 0.231 | | | |
| 3 | 1 | 4 | 15.38 ± 0.5 | 11.74 ± 0.5 | 12.92 ± 0.2 | 13.12 ± 0.7 | 9.88 ± 0.9 | 0.025 | 0.290 | 0.236 | 0.150 | 0.009 |
| 3 | 2 | 1 | 12.19 ± 1.0 | 10.75 ± 1.4 | 10.78 ± 1.2 | 12.19 ± 0.8 | 7.73 ± 1.2 | 0.109 | 0.398 | | | |
| 3 | 2 | 2 | 12.79 ± 0.5 | 11.99 ± 0.5 | 11.66 ± 0.6 | 12.91 ± 1.0 | 10.23 ± 1.7 | 0.458 | 0.614 | | | |
| 3 | 2 | 3 | 13.52 ± 0.3 | 11.65 ± 1.5 | 11.37 ± 0.6 | 11.72 ± 1.6 | 9.39 ± 0.9 | 0.197 | 0.284 | | | |
| 4 | 1 | 1 | 11.53 ± 0.9 | 10.31 ± 0.9 | 11.52 ± 0.2 | 12.97 ± 0.5 | 8.45 ± 1.8 | 0.087 | 0.416 | | | |
| 4 | 1 | 2 | 14.72 ± 1.6 | 11.97 ± 1.4 | 12.78 ± 1.3 | 12.72 ± 1.6 | 9.41 ± 2.1 | 0.303 | 0.258 | | | |
| 4 | 1 | 3 | 15.43 ± 1.5 | 13.40 ± 1.2 | 13.08 ± 0.9 | 14.46 ± 1.2 | 9.44 ± 0.8 | 0.038 | 0.244 | 0.253 | 0.035 | 0.056 |
| 4 | 1 | 4 | 10.32 ± 1.1 | 11.60 ± 1.8 | 11.35 ± 1.6 | 11.38 ± 0.3 | 7.59 ± 1.5 | 0.278 | 0.524 | | | |
| 4 | 2 | 1 | 9.61 ± 0.9 | 9.73 ± 1.1 | 10.87 ± 0.4 | 10.64 ± 1.2 | 8.48 ± 2.4 | 0.743 | 0.949 | | | |
| 4 | 2 | 2 | 11.49 ± 0.5 | 11.42 ± 1.5 | 11.30 ± 0.9 | 11.50 ± 0.9 | 8.79 ± 2.0 | 0.523 | 0.970 | | | |
| 4 | 2 | 3 | 11.76 ± 1.5 | 11.97 ± 1.0 | 11.30 ± 0.9 | 12.29 ± 0.9 | 8.67 ± 1.9 | 0.339 | 0.905 | | | |
| 5 | 1 | 1 | 12.98 ± 1.7 | 10.52 ± 0.8 | 9.72 ± 0.6 | 13.10 ± 0.7 | 6.63 ± 0.6 | 0.009 | 0.153 | 0.719 | 0.001 | 0.006 |
| 5 | 1 | 2 | 13.98 ± 1.7 | 9.92 ± 0.2 | 10.43 ± 1.1 | 12.25 ± 1.0 | 8.67 ± 0.3 | 0.050 | 0.039 | 0.733 | 0.046 | 0.041 |
| 5 | 1 | 3 | 14.59 ± 1.6 | 11.22 ± 0.5 | 10.62 ± 0.4 | 15.00 ± 1.1 | 11.14 ± 1.3 | 0.056 | 0.056 | | | |
| 5 | 1 | 4 | 11.14 ± 1.2 | 9.83 ± 1.4 | 9.42 ± 1.3 | 11.36 ± 0.8 | 8.78 ± 1.0 | 0.460 | 0.421 | | | |
| 5 | 2 | 1 | 11.94 ± 1.6 | 9.19 ± 0.9 | 8.73 ± 0.2 | 11.65 ± 0.8 | 6.20 ± 0.2 | 0.010 | 0.066 | 0.728 | 0.002 | 0.008 |
| 5 | 2 | 2 | 12.98 ± 1.1 | 10.14 ± 0.9 | 9.11 ± 0.9 | 11.96 ± 1.1 | 7.48 ± 0.9 | 0.017 | 0.066 | 0.924 | 0.020 | 0.107 |
| 5 | 2 | 3 | 12.18 ± 1.0 | 9.84 ± 0.4 | 10.71 ± 1.0 | 13.07 ± 0.8 | 9.65 ± 1.0 | 0.123 | 0.092 | | | |

**Appendix 5**: Average needle width ± SE of Norway spruce growing outside chambers (Ref) and in ambient and elevated temperature (Ta, Te) and atmospheric [$CO_2$] (Ca, Ce). Also P-values from 2-way ANOVA for treatment effects (when ANOVA P<0.05) and interaction. Chamber effects were studied by One-Way ANOVA between Ref and CaTa treatments.

| Strata | Order | Age | REF | CATA | CATE | CETA | CETE | Anova P value | Chmb effect | CO2 effect | Temp effect | CO2x Temp |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 1 | 1 | 1.275 ± 0.06 | 1.134 ± 0.08 | 1.200 ± 0.11 | 1.293 ± 0.06 | 1.119 ± 0.03 | 0.634 | 0.362 | | | |
| 2 | 1 | 1 | 1.099 ± 0.01 | 1.006 ± 0.07 | 1.017 ± 0.05 | 1.149 ± 0.05 | 0.989 ± 0.07 | 0.233 | 0.245 | | | |
| 2 | 1 | 2 | 1.227 ± 0.04 | 1.104 ± 0.08 | 1.112 ± 0.03 | 1.182 ± 0.07 | 1.131 ± 0.04 | 0.490 | 0.140 | | | |
| 2 | 1 | 3 | 1.298 ± 0.07 | 1.131 ± 0.05 | 1.095 ± 0.01 | 1.243 ± 0.05 | 1.130 ± 0.03 | 0.043 | 0.026 | 0.883 | 0.016 | 0.546 |
| 2 | 1 | 4 | 1.228 ± 0.09 | 1.173 ± 0.03 | 1.097 ± 0.10 | 1.224 ± 0.06 | 1.097 ± 0.08 | 0.586 | 0.625 | | | |
| 2 | 2 | 1 | 1.124 ± 0.00 | 1.013 ± 0.07 | 0.878 ± 0.03 | 1.143 ± 0.02 | 1.006 ± 0.01 | 0.073 | 0.170 | | | |
| 2 | 2 | 2 | 1.286 ± 0.07 | 1.103 ± 0.11 | 0.992 ± 0.10 | 1.137 ± 0.08 | 1.047 ± 0.10 | 0.298 | 0.174 | | | |
| 2 | 2 | 3 | 1.283 ± 0.08 | 1.087 ± 0.05 | 0.974 ± 0.09 | 1.180 ± 0.06 | 1.052 ± 0.02 | 0.055 | 0.043 | | | |
| 3 | 1 | 1 | 1.159 ± 0.03 | 1.019 ± 0.08 | 1.061 ± 0.11 | 1.169 ± 0.01 | 1.050 ± 0.06 | 0.382 | 0.147 | | | |
| 3 | 1 | 2 | 1.276 ± 0.03 | 1.117 ± 0.12 | 1.128 ± 0.07 | 1.239 ± 0.05 | 1.114 ± 0.03 | 0.325 | 0.122 | | | |
| 3 | 1 | 3 | 1.248 ± 0.04 | 1.073 ± 0.09 | 1.019 ± 0.03 | 1.227 ± 0.03 | 1.159 ± 0.02 | 0.002 | 0.001 | | | |
| 3 | 1 | 4 | 1.229 ± 0.06 | 1.066 ± 0.06 | 1.088 ± 0.06 | 1.140 ± 0.01 | 1.090 ± 0.01 | 0.130 | 0.023 | | | |
| 3 | 2 | 1 | 1.105 ± 0.04 | 0.961 ± 0.10 | 0.984 ± 0.10 | 1.116 ± 0.04 | 0.923 ± 0.06 | 0.280 | 0.188 | | | |
| 3 | 2 | 2 | 1.121 ± 0.08 | 1.027 ± 0.08 | 1.082 ± 0.08 | 1.157 ± 0.03 | 1.083 ± 0.03 | 0.542 | 0.243 | | | |
| 3 | 2 | 3 | 1.184 ± 0.08 | 0.972 ± 0.05 | 0.969 ± 0.10 | 1.168 ± 0.05 | 1.100 ± 0.04 | 0.151 | 0.062 | | | |
| 4 | 1 | 1 | 1.046 ± 0.08 | 1.013 ± 0.08 | 1.116 ± 0.10 | 1.167 ± 0.03 | 0.984 ± 0.07 | 0.376 | 0.744 | | | |
| 4 | 1 | 2 | 1.207 ± 0.03 | 1.137 ± 0.07 | 1.134 ± 0.06 | 1.251 ± 0.03 | 1.100 ± 0.04 | 0.284 | 0.354 | | | |
| 4 | 1 | 3 | 1.220 ± 0.07 | 1.100 ± 0.06 | 1.093 ± 0.08 | 1.341 ± 0.04 | 1.152 ± 0.04 | 0.073 | 0.186 | | | |
| 4 | 1 | 4 | 1.073 ± 0.03 | 1.091 ± 0.08 | 1.049 ± 0.07 | 1.188 ± 0.04 | 0.951 ± 0.07 | 0.201 | 0.844 | | | |
| 4 | 2 | 1 | 0.952 ± 0.07 | 0.941 ± 0.08 | 1.017 ± 0.10 | 1.010 ± 0.05 | 0.925 ± 0.06 | 0.879 | 0.919 | | | |
| 4 | 2 | 2 | 1.106 ± 0.01 | 1.077 ± 0.09 | 1.065 ± 0.06 | 1.187 ± 0.03 | 1.049 ± 0.06 | 0.465 | 0.720 | | | |
| 4 | 2 | 3 | 1.141 ± 0.05 | 1.050 ± 0.06 | 1.018 ± 0.07 | 1.219 ± 0.02 | 1.030 ± 0.05 | 0.117 | 0.297 | | | |
| 5 | 1 | 1 | 1.182 ± 0.04 | 1.040 ± 0.14 | 1.104 ± 0.05 | 1.252 ± 0.04 | 0.945 ± 0.14 | 0.213 | 0.332 | | | |
| 5 | 1 | 2 | 1.228 ± 0.06 | 1.046 ± 0.07 | 1.087 ± 0.01 | 1.332 ± 0.07 | 1.028 ± 0.07 | 0.054 | 0.725 | 0.057 | 0.168 | 0.054 |
| 5 | 1 | 3 | 1.266 ± 0.06 | 1.060 ± 0.05 | 1.143 ± 0.03 | 1.350 ± 0.04 | 1.138 ± 0.05 | 0.010 | 0.011 | 0.008 | 0.174 | 0.012 |
| 5 | 1 | 4 | 1.147 ± 0.06 | 1.025 ± 0.09 | 1.075 ± 0.00 | 1.215 ± 0.02 | 1.059 ± 0.05 | 0.200 | 0.154 | | | |
| 5 | 2 | 1 | 1.161 ± 0.08 | 0.904 ± 0.09 | 1.001 ± 0.10 | 1.158 ± 0.05 | 0.922 ± 0.09 | 0.118 | 0.046 | | | |
| 5 | 2 | 2 | 1.156 ± 0.05 | 1.000 ± 0.07 | 1.014 ± 0.02 | 1.270 ± 0.08 | 0.958 ± 0.09 | 0.037 | 0.123 | 0.156 | 0.061 | 0.044 |
| 5 | 2 | 3 | 1.141 ± 0.01 | 0.946 ± 0.04 | 1.050 ± 0.01 | 1.255 ± 0.05 | 1.021 ± 0.06 | 0.004 | 0.005 | 0.028 | 0.460 | 0.007 |

**Appendix 6**: Average needle width and length ratio ± SE of Norway spruce growing outside chambers (Ref) and in ambient and elevated temperature (Ta, Te) and atmospheric carbon dioxide concentration (Ca, Ce). Also shown P-values from 2-way ANOVA for treatment effects (when ANOVA P<0.05) and interaction. Chamber effects were studied by One-Way ANOVA between Ref and CaTa treatments.

| Strata | Order | Age | REF | CATA | CATE | CETA | CETE | Anova P | Chmb effect | CO2 effect | Temp effect | CO2x Temp |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 1 | 1 | 0.097 ± 0.00 | 0.077 ± 0.00 | 0.082 ± 0.01 | 0.084 ± 0.01 | 0.088 ± 0.01 | 0.294 | 0.297 | | | |
| 2 | 1 | 1 | 0.088 ± 0.00 | 0.076 ± 0.00 | 0.079 ± 0.01 | 0.102 ± 0.00 | 0.116 ± 0.01 | 0.018 | 0.286 | 0.005 | 0.370 | 0.535 |
| 2 | 1 | 2 | 0.083 ± 0.00 | 0.079 ± 0.00 | 0.075 ± 0.01 | 0.094 ± 0.00 | 0.106 ± 0.02 | 0.151 | 0.754 | | | |
| 2 | 1 | 3 | 0.089 ± 0.01 | 0.080 ± 0.00 | 0.095 ± 0.01 | 0.084 ± 0.01 | 0.107 ± 0.02 | 0.380 | 0.522 | | | |
| 2 | 1 | 4 | 0.081 ± 0.00 | 0.091 ± 0.01 | 0.082 ± 0.01 | 0.092 ± 0.01 | 0.142 ± 0.03 | 0.151 | 0.720 | | | |
| 2 | 2 | 1 | 0.102 ± 0.00 | 0.086 ± 0.00 | 0.078 ± 0.00 | 0.089 ± 0.01 | 0.107 ± 0.01 | 0.150 | 0.170 | | | |
| 2 | 2 | 2 | 0.093 ± 0.01 | 0.080 ± 0.01 | 0.081 ± 0.02 | 0.107 ± 0.01 | 0.115 ± 0.02 | 0.364 | 0.517 | | | |
| 2 | 2 | 3 | 0.099 ± 0.01 | 0.090 ± 0.00 | 0.086 ± 0.02 | 0.092 ± 0.01 | 0.120 ± 0.02 | 0.433 | 0.640 | | | |
| 3 | 1 | 1 | 0.088 ± 0.01 | 0.091 ± 0.01 | 0.086 ± 0.01 | 0.090 ± 0.00 | 0.133 ± 0.02 | 0.077 | 0.873 | | | |
| 3 | 1 | 2 | 0.088 ± 0.01 | 0.092 ± 0.00 | 0.091 ± 0.01 | 0.091 ± 0.01 | 0.119 ± 0.03 | 0.526 | 0.835 | | | |
| 3 | 1 | 3 | 0.079 ± 0.00 | 0.080 ± 0.00 | 0.093 ± 0.02 | 0.090 ± 0.01 | 0.109 ± 0.01 | 0.269 | 0.942 | | | |
| 3 | 1 | 4 | 0.081 ± 0.00 | 0.091 ± 0.00 | 0.086 ± 0.01 | 0.089 ± 0.00 | 0.115 ± 0.01 | 0.025 | 0.290 | 0.094 | 0.152 | 0.052 |
| 3 | 2 | 1 | 0.093 ± 0.01 | 0.090 ± 0.00 | 0.092 ± 0.00 | 0.093 ± 0.01 | 0.125 ± 0.02 | 0.148 | 0.841 | | | |
| 3 | 2 | 2 | 0.091 ± 0.01 | 0.086 ± 0.01 | 0.094 ± 0.00 | 0.091 ± 0.00 | 0.112 ± 0.02 | 0.405 | 0.738 | | | |
| 3 | 2 | 3 | 0.089 ± 0.01 | 0.085 ± 0.01 | 0.087 ± 0.01 | 0.103 ± 0.01 | 0.121 ± 0.01 | 0.231 | 0.856 | | | |
| 4 | 1 | 1 | 0.092 ± 0.00 | 0.099 ± 0.00 | 0.098 ± 0.01 | 0.091 ± 0.01 | 0.124 ± 0.02 | 0.186 | 0.635 | | | |
| 4 | 1 | 2 | 0.084 ± 0.01 | 0.098 ± 0.01 | 0.091 ± 0.01 | 0.103 ± 0.01 | 0.128 ± 0.02 | 0.251 | 0.501 | | | |
| 4 | 1 | 3 | 0.081 ± 0.01 | 0.083 ± 0.00 | 0.085 ± 0.01 | 0.095 ± 0.01 | 0.124 ± 0.01 | 0.045 | 0.820 | 0.028 | 0.149 | 0.182 |
| 4 | 1 | 4 | 0.106 ± 0.01 | 0.097 ± 0.01 | 0.099 ± 0.02 | 0.106 ± 0.00 | 0.133 ± 0.02 | 0.407 | 0.640 | | | |
| 4 | 2 | 1 | 0.101 ± 0.01 | 0.099 ± 0.01 | 0.094 ± 0.01 | 0.097 ± 0.01 | 0.121 ± 0.03 | 0.677 | 0.905 | | | |
| 4 | 2 | 2 | 0.097 ± 0.00 | 0.097 ± 0.01 | 0.096 ± 0.01 | 0.105 ± 0.01 | 0.128 ± 0.02 | 0.226 | 0.953 | | | |
| 4 | 2 | 3 | 0.098 ± 0.01 | 0.089 ± 0.00 | 0.092 ± 0.01 | 0.101 ± 0.01 | 0.124 ± 0.02 | 0.331 | 0.571 | | | |
| 5 | 1 | 1 | 0.094 ± 0.01 | 0.100 ± 0.01 | 0.115 ± 0.01 | 0.098 ± 0.01 | 0.142 ± 0.01 | 0.028 | 0.715 | 0.208 | 0.010 | 0.168 |
| 5 | 1 | 2 | 0.091 ± 0.01 | 0.106 ± 0.00 | 0.106 ± 0.01 | 0.110 ± 0.01 | 0.120 ± 0.01 | 0.311 | 0.302 | | | |
| 5 | 1 | 3 | 0.090 ± 0.01 | 0.095 ± 0.00 | 0.109 ± 0.00 | 0.091 ± 0.01 | 0.105 ± 0.01 | 0.450 | 0.664 | | | |
| 5 | 1 | 4 | 0.105 ± 0.01 | 0.107 ± 0.01 | 0.117 ± 0.02 | 0.109 ± 0.01 | 0.125 ± 0.02 | 0.747 | 0.931 | | | |
| 5 | 2 | 1 | 0.100 ± 0.01 | 0.099 ± 0.00 | 0.116 ± 0.01 | 0.101 ± 0.01 | 0.151 ± 0.02 | 0.029 | 0.914 | 0.169 | 0.012 | 0.179 |
| 5 | 2 | 2 | 0.091 ± 0.00 | 0.100 ± 0.01 | 0.115 ± 0.01 | 0.110 ± 0.02 | 0.132 ± 0.02 | 0.298 | 0.662 | | | |
| 5 | 2 | 3 | 0.095 ± 0.01 | 0.097 ± 0.00 | 0.101 ± 0.01 | 0.097 ± 0.01 | 0.108 ± 0.01 | 0.856 | 0.908 | | | |

**Appendix 7**: Average total needle area ± SE of Norway spruce growing outside chambers (Ref) and in ambient and elevated temperature (Ta, Te) and atmospheric carbon dioxide concentration (Ca, Ce). Also shown P-values from 2-way ANOVA for treatment effects (when ANOVA P<0.05) and interaction. Chamber effects were studied by One-Way ANOVA between Ref and CaTa treatments.

| Strata | Order | Age | REF | CATA | CATE | CETA | CETE | Anova P value | Chmb effect | CO2 effect | Temp effect | CO2x Temp |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 1 | 1 | 1731.05 ± 315.4 | 2045.13 ± 690.3 | 2980.91 ± 624.9 | 2035.40 ± 103.4 | 2035.61 ± 684.7 | 0.675 | 0.906 | | | |
| 2 | 1 | 1 | 830.15 ± 78.4 | 831.82 ± 156.8 | 1286.95 ± 477.0 | 532.17 ± 171.9 | 663.14 ± 296.6 | 0.416 | 0.997 | | | |
| 2 | 1 | 2 | 1692.54 ± 329.6 | 1399.99 ± 209.4 | 2347.19 ± 694.3 | 1421.16 ± 264.8 | 1371.50 ± 331.4 | 0.432 | 0.619 | | | |
| 2 | 1 | 3 | 1536.06 ± 253.7 | 1419.91 ± 259.7 | 1099.72 ± 297.8 | 1105.94 ± 302.3 | 1128.02 ± 144.2 | 0.650 | 0.757 | | | |
| 2 | 1 | 4 | 1087.51 ± 600.1 | 1230.50 ± 117.0 | 709.35 ± 640.2 | 1374.15 ± 74.6 | 902.06 ± 419.7 | 0.457 | 0.444 | | | |
| 2 | 2 | 1 | 368.55 ± 62.0 | 488.27 ± 132.3 | 836.00 ± 473.2 | 327.11 ± 117.5 | 354.68 ± 113.4 | 0.532 | 0.696 | | | |
| 2 | 2 | 2 | 842.26 ± 11.8 | 1001.88 ± 271.0 | 858.96 ± 147.3 | 820.07 ± 248.5 | 826.07 ± 307.8 | 0.977 | 0.635 | | | |
| 2 | 2 | 3 | 673.54 ± 78.6 | 794.08 ± 31.4 | 728.83 ± 209.5 | 922.77 ± 15.7 | 584.67 ± 191.2 | 0.502 | 0.501 | | | |
| 3 | 1 | 1 | 698.51 ± 80.0 | 527.77 ± 244.6 | 636.81 ± 257.2 | 694.36 ± 132.2 | 463.70 ± 254.3 | 0.882 | 0.552 | | | |
| 3 | 1 | 2 | 1262.04 ± 105.7 | 1234.13 ± 322.7 | 1250.26 ± 136.8 | 1603.28 ± 352.3 | 1084.23 ± 342.3 | 0.746 | 0.944 | | | |
| 3 | 1 | 3 | 1384.52 ± 119.9 | 1154.74 ± 277.1 | 984.04 ± 182.2 | 1243.06 ± 295.2 | 1063.55 ± 194.2 | 0.744 | 0.484 | | | |
| 3 | 1 | 4 | 1148.98 ± 141.1 | 1029.85 ± 141.1 | 1182.27 ± 45.8 | 1105.48 ± 314.9 | 906.03 ± 181.6 | 0.809 | 0.642 | | | |
| 3 | 2 | 1 | 474.41 ± 84.5 | 357.49 ± 163.9 | 273.81 ± 74.6 | 331.89 ± 38.0 | 105.11 ± 30.8 | 0.145 | 0.388 | | | |
| 3 | 2 | 2 | 723.11 ± 192.0 | 796.63 ± 192.0 | 789.05 ± 97.8 | 851.68 ± 177.7 | 693.33 ± 117.0 | 0.958 | 0.754 | | | |
| 3 | 2 | 3 | 766.09 ± 216.9 | 653.76 ± 195.7 | 642.12 ± 11.8 | 675.50 ± 321.2 | 642.46 ± 155.6 | 0.990 | 0.717 | | | |
| 4 | 1 | 1 | 477.40 ± 165.5 | 501.05 ± 165.5 | 1006.23 ± 293.5 | 586.74 ± 73.0 | 347.69 ± 215.9 | 0.205 | 0.931 | | | |
| 4 | 1 | 2 | 1162.10 ± 68.9 | 641.11 ± 232.8 | 1631.97 ± 580.8 | 1225.72 ± 105.1 | 818.88 ± 348.6 | 0.303 | 0.284 | | | |
| 4 | 1 | 3 | 1119.66 ± 129.4 | 978.61 ± 250.3 | 967.16 ± 120.4 | 1155.25 ± 120.9 | 647.95 ± 154.2 | 0.270 | 0.553 | | | |
| 4 | 1 | 4 | 639.68 ± 94.9 | 1004.21 ± 356.7 | 855.68 ± 235.2 | 895.29 ± 127.7 | 410.69 ± 170.8 | 0.377 | 0.264 | | | |
| 4 | 2 | 1 | 216.17 ± 58.7 | 308.00 ± 110.6 | 506.17 ± 179.8 | 260.38 ± 84.1 | 203.93 ± 145.2 | 0.532 | 0.604 | | | |
| 4 | 2 | 2 | 580.87 ± 62.0 | 784.19 ± 187.3 | 1038.42 ± 324.8 | 672.05 ± 151.1 | 620.70 ± 251.8 | 0.590 | 0.518 | | | |
| 4 | 2 | 3 | 409.41 ± 23.7 | 603.41 ± 158.8 | 556.80 ± 81.6 | 575.29 ± 40.9 | 236.80 ± 67.4 | 0.184 | 0.228 | | | |
| 5 | 1 | 1 | 945.07 ± 315.5 | 609.12 ± 53.3 | 520.92 ± 297.4 | 790.82 ± 171.1 | 215.60 ± 95.2 | 0.220 | 0.331 | | | |
| 5 | 1 | 2 | 1435.72 ± 330.5 | 796.22 ± 48.7 | 1054.15 ± 398.9 | 1369.00 ± 354.6 | 606.18 ± 245.6 | 0.317 | 0.208 | | | |
| 5 | 1 | 3 | 1026.24 ± 167.8 | 548.63 ± 122.4 | 582.99 ± 69.5 | 1271.53 ± 267.4 | 288.49 ± 115.4 | 0.009 | 0.055 | 0.015 | 0.128 | 0.015 |
| 5 | 1 | 4 | 599.46 ± 98.8 | 491.48 ± 166.9 | 670.15 ± 308.6 | 640.11 ± 60.7 | 217.18 ± 69.3 | 0.204 | 0.576 | | | |
| 5 | 2 | 1 | 556.34 ± 238.3 | 180.26 ± 59.6 | 442.70 ± 65.0 | 449.74 ± 66.9 | 111.96 ± 30.3 | 0.127 | 0.058 | | | |
| 5 | 2 | 2 | 923.95 ± 111.8 | 491.99 ± 46.5 | 632.89 ± 147.0 | 1096.40 ± 211.8 | 338.37 ± 92.7 | 0.014 | 0.046 | 0.297 | 0.057 | 0.012 |
| 5 | 2 | 3 | 538.85 ± 41.5 | 292.43 ± 69.7 | 581.59 ± 143.0 | 659.73 ± 139.4 | 206.71 ± 79.8 | 0.042 | 0.097 | 0.695 | 0.692 | 0.012 |

**Appendix 8**: Average total shoot length ± SE of Norway spruce growing outside chambers (Ref) and in ambient and elevated temperature (Ta, Te) and atmospheric carbon dioxide concentration (Ca, Ce). Also shown P-values from 2-way ANOVA for treatment effects (when ANOVA P<0.05) and interaction. Chamber effects were studied by One-Way ANOVA between Ref and CaTa treatments.

| Strata | Order | Age | REF | CATA | CATE | CETA | CETE | Anova P value | Chmb effect | CO2 effect | Temp effect | CO2x Temp |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 1 | 1 | 46.14 ± 7.9 | 63.44 ± 20.2 | 80.70 ± 8.0 | 49.96 ± 7.1 | 74.38 ± 20.3 | 0.602 | 0.6113 | | | |
| 2 | 1 | 1 | 33.31 ± 3.9 | 34.63 ± 4.5 | 47.98 ± 12.4 | 20.79 ± 4.8 | 35.59 ± 12.1 | 0.3329 | 0.9147 | | | |
| 2 | 1 | 2 | 54.48 ± 2.6 | 57.96 ± 12.2 | 74.53 ± 10.4 | 53.15 ± 2.7 | 68.23 ± 8.1 | 0.3417 | 0.7712 | | | |
| 2 | 1 | 3 | 43.67 ± 4.4 | 53.63 ± 2.6 | 47.41 ± 10.9 | 40.81 ± 10.4 | 52.83 ± 4.7 | 0.6903 | 0.3645 | | | |
| 2 | 1 | 4 | 48.83 ± 4.0 | 57.47 ± 7.9 | 55.99 ± 7.2 | 46.97 ± 3.4 | 52.26 ± 13.8 | 0.8381 | 0.3744 | | | |
| 2 | 2 | 1 | 17.25 ± 1.1 | 22.09 ± 3.8 | 41.63 ± 13.5 | 13.84 ± 1.9 | 24.13 ± 2.6 | 0.1144 | 0.5719 | | | |
| 2 | 2 | 2 | 31.28 ± 1.5 | 44.93 ± 8.4 | 52.38 ± 10.4 | 38.70 ± 6.5 | 45.74 ± 8.3 | 0.4045 | 0.2014 | | | |
| 2 | 2 | 3 | 27.17 ± 1.0 | 39.88 ± 3.8 | 43.32 ± 8.0 | 40.12 ± 2.1 | 39.08 ± 7.6 | 0.2958 | 0.1041 | | | |
| 3 | 1 | 1 | 30.38 ± 1.2 | 22.68 ± 7.2 | 32.06 ± 14.1 | 29.39 ± 3.7 | 36.68 ± 6.8 | 0.7215 | 0.4550 | | | |
| 3 | 1 | 2 | 47.22 ± 2.6 | 47.91 ± 2.7 | 58.77 ± 3.7 | 57.63 ± 4.0 | 61.58 ± 12.5 | 0.4103 | 0.9396 | | | |
| 3 | 1 | 3 | 50.27 ± 1.4 | 44.28 ± 3.2 | 49.99 ± 2.2 | 47.89 ± 4.6 | 57.20 ± 8.6 | 0.4538 | 0.3912 | | | |
| 3 | 1 | 4 | 44.03 ± 3.1 | 47.16 ± 3.1 | 47.49 ± 4.5 | 42.13 ± 4.6 | 48.84 ± 8.6 | 0.8737 | 0.6722 | | | |
| 3 | 2 | 1 | 23.97 ± 2.6 | 18.28 ± 3.4 | 16.74 ± 4.3 | 18.62 ± 1.1 | 15.80 ± 3.0 | 0.4199 | 0.2185 | | | |
| 3 | 2 | 2 | 33.62 ± 1.6 | 36.46 ± 1.6 | 44.77 ± 4.7 | 38.69 ± 3.2 | 49.56 ± 3.6 | 0.0877 | 0.6164 | | | |
| 3 | 2 | 3 | 39.02 ± 4.0 | 35.41 ± 2.7 | 41.55 ± 0.7 | 32.32 ± 8.7 | 43.80 ± 8.0 | 0.7355 | 0.7275 | | | |
| 4 | 1 | 1 | 23.50 ± 4.7 | 27.37 ± 4.7 | 51.97 ± 6.3 | 29.69 ± 5.0 | 29.84 ± 10.8 | 0.0771 | 0.6850 | | | |
| 4 | 1 | 2 | 46.00 ± 1.9 | 35.05 ± 14.9 | 72.30 ± 7.9 | 51.04 ± 3.9 | 53.67 ± 12.2 | 0.1643 | 0.4344 | | | |
| 4 | 1 | 3 | 44.44 ± 3.8 | 44.97 ± 2.5 | 46.52 ± 0.9 | 47.66 ± 6.8 | 43.75 ± 10.9 | 0.2011 | 0.5578 | | | |
| 4 | 1 | 4 | 31.90 ± 3.0 | 42.41 ± 9.0 | 39.07 ± 4.3 | 38.90 ± 3.9 | 33.42 ± 9.1 | 0.9902 | 0.9523 | | | |
| 4 | 2 | 1 | 14.62 ± 2.6 | 20.73 ± 2.7 | 30.30 ± 4.8 | 17.01 ± 5.4 | 22.98 ± 6.0 | 0.1729 | 0.3587 | | | |
| 4 | 2 | 2 | 31.93 ± 3.3 | 40.45 ± 1.7 | 55.96 ± 6.2 | 35.11 ± 7.2 | 46.75 ± 8.4 | 0.0970 | 0.3318 | | | |
| 4 | 2 | 3 | 25.03 ± 5.0 | 33.13 ± 2.6 | 33.96 ± 1.3 | 32.28 ± 3.5 | 21.23 ± 0.6 | 0.0684 | 0.0954 | | | |
| 5 | 1 | 1 | 40.37 ± 7.8 | 34.64 ± 3.4 | 29.51 ± 13.6 | 36.24 ± 4.0 | 22.36 ± 8.1 | 0.5075 | 0.6294 | | | |
| 5 | 1 | 2 | 57.24 ± 6.2 | 50.01 ± 10.9 | 52.03 ± 10.0 | 60.38 ± 6.1 | 45.70 ± 10.8 | 0.7376 | 0.5886 | | | |
| 5 | 1 | 3 | 43.82 ± 4.4 | 32.82 ± 7.0 | 33.51 ± 3.3 | 49.40 ± 5.9 | 27.20 ± 4.3 | 0.0689 | 0.1557 | | | |
| 5 | 1 | 4 | 35.45 ± 2.8 | 30.36 ± 5.6 | 31.83 ± 7.0 | 32.36 ± 5.0 | 22.89 ± 1.4 | 0.3825 | 0.4241 | | | |
| 5 | 2 | 1 | 27.83 ± 6.5 | 16.62 ± 1.5 | 30.11 ± 2.8 | 27.24 ± 1.0 | 15.73 ± 5.2 | 0.1147 | 0.0845 | | | |
| 5 | 2 | 2 | 40.12 ± 2.0 | 35.94 ± 5.9 | 41.18 ± 7.7 | 52.79 ± 4.3 | 39.24 ± 8.5 | 0.4153 | 0.6421 | | | |
| 5 | 2 | 3 | 31.57 ± 3.1 | 26.67 ± 5.7 | 36.82 ± 7.5 | 38.11 ± 3.8 | 25.40 ± 0.9 | 0.3473 | 0.4884 | | | |