Scots pine responses to elevated temperature and carbon dioxide concentration: growth and wood properties

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Summary Growth and wood properties of 20-year-old Scots pine (Pinus sylvestris L.) trees were studied for 6 years in 16 closed chambers providing a factorial combination of two temperature regimes (ambient and elevated) and two carbon dioxide concentrations ([CO2]) (ambient and twice ambient). The elevation of temperature corresponded to the predicted effect at the site of a doubling in atmospheric [CO2]. Annual height and radial growth and wood properties were analyzed during 1997–2002. Physical wood properties analyzed included early- and latewood widths and their proportions, intra-ring wood densities, early- and latewood density and mean fiber length. Chemical wood properties analyzed included concentrations of acetone-soluble extractives, lignin, cellulose and hemicellulose.

There were no significant treatment effects on height growth during the 6-year study. Elevated [CO2] increased ring width by 66 and 47% at ambient and elevated temperatures, respectively. At ambient [CO2], elevated temperature increased ring width by 19%. Increased ring width in response to elevated [CO2] resulted from increases in both early- and latewood width; however, there was no effect of the treatments on early- and latetwood proportions. Mean wood density, earlywood density and fiber length increased in response to elevated temperature. The chemical composition of wood was affected by elevated [CO2], which reduced the cellulose concentration, and by elevated temperature, which reduced the concentration of acetone-soluble extractives. Thus, over the 6-year period, radial growth was significantly increased by elevated [CO2], and some wood properties were significantly affected by elevated temperature or elevated [CO2], or both, indicating that climate change may affect the material properties of wood.

Keywords: chemical composition of wood, climate change, earlywood, fiber length, height growth, latetwood, radial growth, ring width, wood density.

Introduction

Climate change in northern Europe during the next 100 years is predicted to involve a doubling of atmospheric CO2 concentration ([CO2]), which may increase mean annual temperature by 2–4 °C (IPCC 2001) and winter temperatures by up to 6 °C (Parry 2000). It is also predicted that elevated temperatures will lengthen the growing season (Beuker 1994, Peltola et al. 2002), thereby increasing tree growth. This prediction is supported by observations that fumigation with elevated [CO2] increases radial growth of seedlings of loblolly pine (Pinus taeda L.), longleaf pine (Pinus palustris Mill.), radiata pine (Pinus radiata D. Don) and Scots pine (Pinus sylvestris L.) grown under optimal nutrient conditions (Tinus 1972, Sionit et al. 1985, Surano et al. 1986, Telewski and Strain 1987, Conroy et al. 1990, Prior et al. 1997, Jach and Ceulemans 1999, Telewski et al. 1999, Ceulemans et al. 2002). Elevated [CO2] also enhances height growth in some species, e.g., Scots pine (Jach and Ceulemans 1999) and Norway spruce (Picea abies L. Karst.) (Ske and Nes 1996), but not in Douglas-fir (Pseudotsuga menziesii Mirb. Franco) (Oldeyk et al. 1998, Tingey et al. 2003) or Sitka spruce (Picea sitchensis Bong. Carr.) (Murray et al. 1996). The growth responses of trees to elevated [CO2] or elevated temperature, or both, may be less when trees are grown in competition or at sites with a low nutrient supply, as observed previously in seedlings (Pushnik et al. 1995, Hättenschwiler et al. 1996, Körner 1996, Tissue et al. 1997) and post-juvenile trees (DeLucia et al. 1999, Tognetti et al. 2000, Oren et al. 2001, Peltola et al. 2002, Kilpeläinen et al. 2003).

Independently of any growth response to increases in atmospheric [CO2] and temperature, wood properties such as density, early- and latetwood width and their proportions, fiber length and chemical composition (e.g., acetone-soluble extractives, lignin, cellulose and hemicellulose content) may be affected. So far, the results obtained with seedlings grown in different conditions (pots or containers in chambers or greenhouses, or in the field) have yielded conflicting results both within and between species, as has been shown for loblolly pine (Rogers et al. 1983, Telewski and Strain 1987, Telewski et al. 1999), radiata pine (Donaldson et al. 1987, Conroy et al. 1990), Scots pine (Ceulemans et al. 2002, Kilpeläinen et al. 2003), Norway spruce (Ske and Nes 1996) and Scots pine (Jach and Ceulemans 1999) and Douglas-fir (Oldeyk et al. 1998, Tingey et al. 2003) and Sitka spruce (Murray et al. 1996).
and Norway spruce (Hättenschwiler et al. 1996). The effects of elevated \([\text{CO}_2]\) and temperature on the chemical properties of wood have been less intensively studied, although they are closely related to the physical properties. For example, lignin content is positively related to the proportion of earlywood (Fukazawa and Imagawa 1981), and cellulose and hemicellulose, which are primary constituents of the cell wall, closely parallel changes in wood density (Megraw 1985).

Few studies have examined how increases in temperature and \([\text{CO}_2]\) alone or concurrently affect the radial growth of trees and the physical and chemical properties of the wood. Kilpeläinen et al. (2003) conducted an open-top chamber experiment (1990–1994) and showed that radial growth of 15-year-old Scots pine (\textit{Pinus sylvestris} L.) trees was enhanced by elevated \([\text{CO}_2]\) and elevated temperature over 3 years. Although neither elevated temperature nor elevated \([\text{CO}_2]\) significantly affected ring width or early- and latewood widths or their proportions, elevated \([\text{CO}_2]\) increased latewood and maximum intra-ring density, whereas elevated temperature increased fiber length and lignin concentration and reduced hemicellulose concentration.

We report here on the use of a closed \(\text{CO}_2\) and temperature-controlled chamber system to investigate the impacts of elevations in temperature and \([\text{CO}_2]\) alone or concurrently for the years 1997–2002 on height and radial growth and the physical and chemical properties of wood of 20-year-old Scots pine trees. Treatment effects examined included annual height growth, ring width, early- and latewood widths and their proportions, wood density variables, mean fiber length and the chemical composition of the wood (acetone-soluble extractives, lignin, cellulose and hemicellulose).

**Materials and methods**

**Site and layout**

The experiment was performed in a closed chamber system set up in 1996 in a naturally regenerated forest of Scots pine near the Mekrijärvi Research Station (62°47’N, 30°58’E, 145 m a.s.l.) at the University of Joensuu, Finland (Kellomäki et al. 2000). The site, which corresponds in fertility with the \textit{Calluna} type, has a sandy soil and low nitrogen availability.

The site is characterized by cold winters with persistent snow cover and a short growing season. Mean annual precipitation (1961–1994) is 740 mm, of which about 38% is received as snow. The monthly mean temperature is –10.4 °C in January and 15.5 °C in July, with minimum and maximum temperatures of about –40 and 32 °C recorded in January and July, respectively. Low evapotranspiration makes the climate more humid in winter than in summer (Wang 1996).

The experiment comprised 16 closed chambers, each provided with individual facilities for controlling temperature and \([\text{CO}_2]\). Each chamber consisted of a hexagonal tube with an internal volume of about 19.3 m\(^3\) and a ground area of 5.2 m\(^2\). The four walls facing south and west were made of special heating glass (heating capacity 5640 W for each chamber; Eglas, Alavus, Finland), and the four north- and east-facing walls were made of dual-layer acrylic cell glass (Standard 16 mm BMMA) with three small vents. A computer-controlled heat exchanger linked to a refrigeration unit (CAJ-4511YHR, L’Unité Hermetique, La Verpillière, France) was installed at the top of each chamber.

A fan blower drew unfiltered air into each chamber through a duct about 3.5 m above ground. The airflow rate varied from 0.2 to 0.4 m\(^3\) s\(^{-1}\), depending on the season and weather conditions. Airflow through the duct was determined periodically with a hot wire anemometer and adjusted with a butterfly valve. Air left the chambers through a louvered shutter located about 0.3 m above ground. The computer-controlled heating and cooling system, together with a set of magno-electric valves (controlling the supply of pure CO\(_2\)), automatically adjusted the temperature and \([\text{CO}_2]\) inside the chambers to track ambient conditions, or to achieve a specified elevation in temperature and \([\text{CO}_2]\). The \([\text{CO}_2]\) was elevated continuously (24 h day\(^{-1}\)) throughout the year at a fixed concentration of 700 µmol mol\(^{-1}\) (Figure 1). The warming treatments were designed to correspond to the climatic scenario predicted for the site after a doubling of the atmospheric \([\text{CO}_2]\); i.e., temperature inside the chambers followed the seasonal pattern of outside temperature, with increases depending on the season: 6 °C in winter (December to February), 4 °C in spring and autumn (from March to May and from September to November, respectively) and 2 °C in summer (June to August) (Figure 1).

![Figure 1. Seasonal patterns of CO\(_2\) concentration ([CO\(_2\)]) and temperature for the years 1997–2002. Treatments: AT+AC = ambient temperature and ambient [CO\(_2\)]; AT+EC = ambient temperature and elevated [CO\(_2\)]; ET+AC = elevated temperature and ambient [CO\(_2\)]; ET+EC = elevated temperature and elevated [CO\(_2\)]; and Cntr = trees outside the closed chambers.](image-url)
A carbon dioxide sensor (GMP111, Vaisala, Helsinki, Finland) located in the middle of the crown of each tree monitored [CO₂]. Relative humidity and temperature within the crown were recorded with a Vaisala RH & T probe (HMP131Y) equipped with a Vaisala Humicap sensor. Global solar radiation (Model SKS1110 silicon pyranometer, Skye Instruments, Llandrindod Wells, U.K.) was measured in the top and middle layers of the crown and volumetric soil water content was measured at depths of 5 and 15 cm with four soil moisture probes (ThetaProbe ML1, Delta-T Devices, Cambridge, U.K.). Measurements were made at 15-s intervals and recorded with a data logger. The chambers were irrigated during the growing season to keep the soil water content close to that of ambient soil, and snow was added during winter to match the snowfall outside. The experimental system has been described in detail by Kellomäki et al. (2000).

In summer 1996, 16 trees of similar age (about 14 years old), diameter (3.8 ± 0.5 cm) and height (3.0 ± 0.3 m) were enclosed in the chambers, and another four trees growing outside the chambers were chosen for comparison (Cntr). To reduce shading of the experimental trees, all trees within 2 m of the chambers were felled 1 year before the experiment. The treatments included four combinations of temperature and [CO₂]: (1) ambient temperature and ambient [CO₂] (AT+AC), (2) ambient temperature and elevated [CO₂] (AT+EC), (3) elevated temperature and elevated [CO₂] (ET+EC), and (4) elevated temperature and ambient [CO₂] (ET+AC). The experiment was closed in the chambers, and another four trees growing outside the chambers were chosen for comparison (Cntr). To reduce shading of the experimental trees, all trees within 2 m of the chambers were felled 1 year before the experiment. The treatments included four combinations of temperature and [CO₂]: (1) ambient temperature and ambient [CO₂] (AT+AC), (2) ambient temperature and elevated [CO₂] (AT+EC), (3) elevated temperature and ambient [CO₂] (ET+AC), and (4) elevated temperature and elevated [CO₂] (ET+EC). The experiment followed a factorial design, with one tree in a chamber as the basic treatment unit, replicated four times. The treatments started on September 1, 1996.

Analyses of wood properties
Sample trees were felled in winter 2003 and their annual height growth determined from the distances between branch whorls. For the analyses of wood properties, small rectangular wood specimens (5 × 5 mm) representing two opposing radii were cut from stem discs taken at about 1.3 m above ground with a twin-bladed circular saw. These specimens, with 12% water content (air dry), were measured in batches with a direct scanning ITRAX X-ray microdensitometer (Cox Analytical Systems, Göteborg, Sweden) with automatic collimator alignment (see Bergsten et al. 2001) at a geometrical resolution of 40 measurements per mm (0.025 × 1 mm). Standard X-ray intensity (30 kV, 35 mA) was used, with an exposure time of 20 ms (see also Kilpeläinen et al. 2003). The ITRAX X-ray images were analyzed with density software (see Bergsten et al. 2001) to determine the characteristics of each ring. The variables analyzed were ring width (mm), early- and latewood widths (mm) and their proportions (%), mean intra-ring wood density (g cm⁻³), minimum and maximum wood densities (g cm⁻³) and early- and latewood densities (g cm⁻³). The mean of the maximum and minimum intra-ring densities was used as the threshold for early- and latewood in each ring; the values above and below this threshold were taken to represent the late- and earlywood, respectively. Each sample originally included about 10 annual rings (juvenile wood), six of which were formed during the treatment period (1997–2002). All the intra-ring variables were measured from the pith toward two opposing radii, averaged for each of these annual rings, and subjected to further analysis.

For fiber length analysis of each annual ring, matchstick-sized wood specimens were chipped away from the same stem disc whors as used for X-ray analysis. These pieces were macerated in a boiling 1:1 (v/v) mixture of acetic acid:hydrogen peroxide and the fiber suspension was fixed on microscope slides. The lengths of 100 undamaged fibers in each growth ring were determined (to the nearest 0.01 mm) with a light microscope connected to an image analysis system (Image Pro Plus 4.0 for Windows, Media Cybernetics, Silver Spring, MD). No distinction was made between early- and latewood fibers.

Small dry wood specimens representing the annual rings for the years 1997–2002 combined were chipped away from the same whors about 1.3 m above ground for analyses of chemical composition. These were further reduced to matchstick-sized pieces and milled to yield samples for analyses of cellulose, hemicellulose, total lignin (Klason lignin and acid-soluble lignin) and acetone-soluble extractives, performed by KCL Services (Oy Keskuslaboratorio-Cent rallaboratorium Ab, Espoo, Finland). Acetone-soluble extractives (% of dry mass, DW) were determined according to SCAN-CM 50 (1994). For this analysis, the milled stem wood (4 g) was extracted with a Soxtec Avanti 2050 automated extraction system (Foss Tecator, Höganäs, Sweden). Total lignin (i.e., Klason plus acid-soluble lignin as a % of DW) was determined from the acetone extractive-free milled wood by the TAPPI Test Method T 222 (TAPPI 2000) as modified by KCL Services. An absorptivity value of 1281 (g cm)⁻¹ at 203 nm was used for soluble lignin, as specified for coniferous species. Because the values for acid-soluble lignin were below the limit of identification (0.1%), the values for Klason lignin were used in the analyses of total lignin. Following acid hydrolysis, carbohydrates (% of DW) in the acetone extractive-free milled wood were analyzed by high performance anion exchange chromatography and pulsed amperometric detection (HPAEC-PAD) according to TAPPI Test Method T 249 (TAPPI 2002), modified by KCL Services. The polysaccharide composition (% of DW) was determined from the acetone extractive-free milled wood by the TAPPI Test Method T 222 (TAPPI 2000) as modified by KCL Services. An absorptivity value of 1281 (g cm)⁻¹ at 203 nm was used for soluble lignin, as specified for coniferous species. Because the values for acid-soluble lignin were below the limit of identification (0.1%), the values for Klason lignin were used in the analyses of total lignin. Following acid hydrolysis, carbohydrates (% of DW) in the acetone extractive-free milled wood were analyzed by high performance anion exchange chromatography and pulsed amperometric detection (HPAEC-PAD) according to TAPPI Test Method T 249 (TAPPI 2002), modified by KCL Services. The polysaccharide composition (% of DW) was calculated according to Janson (1974), with values for the variables as specified for Scots pine.

Statistical analysis
Height and radial growth and the physical properties of wood were tested for effects of [CO₂], temperature and year of tree ring formation and their interactions with a repeated measures analysis of variance (ANOVA) (SPSS for Windows, Version 12.0, SPSS, Chicago, IL). The chemical properties of wood were tested with a two-way ANOVA, because the data for the 6-year treatment period were combined. Studied variables were normalized when needed for the statistical analyses. Differences between treatments were identified at P < 0.05. The only statistically significant interaction was temperature × year of growth for mean wood density, and therefore the main effects of CO₂ and temperature and year of growth are pre-
Results

Height and radial growth

Neither elevated \([\text{CO}_2]\) nor elevated temperature had a statistically significant effect \((P < 0.05)\) on height growth, although total cumulative height growth for the 6-year period was 19, 12 and 9% greater in AT+EC, ET+AC and ET+EC trees, respectively, than in AT+AC trees (Figure 2).

Elevated \([\text{CO}_2]\), but not elevated temperature, increased ring width significantly. The total cumulative ring width for the 6-year period was 66, 19 and 47% greater in AT+EC, ET+AC and ET+EC trees, respectively, than in AT+AC trees (Figure 2). Ring width decreased with time in all treatments.

Earlywood and latewood

The increase in ring width in response to elevated \([\text{CO}_2]\) was the result of significant increases in both early- and latewood width. Earlywood width was 70, 10 and 46% greater in AT+EC, ET+AC and ET+EC trees, respectively, than in AT+AC trees (Table 1). Elevated temperature had no statistically significant effect on earlywood width. Latewood width was 56, 39 and 50% greater in AT+EC, ET+AC and ET+EC trees, respectively, than in AT+AC trees (Table 1). Latewood width increased significantly in response to elevated \([\text{CO}_2]\), whereas elevated temperature had no effect on latewood width.

The proportion of earlywood over the entire treatment period was 7% greater in AT+EC trees than in AT+AC trees, and it was 8 and 3% lower in ET+AC and ET+EC trees, respectively, than in AT+AC trees (Table 1). The proportion of latewood was 15 and 6% greater in ET+AC and ET+EC trees, respectively, compared with AT+AC trees, and it was 14% lower in AT+EC trees than in AT+AC trees (Table 1). Neither elevated \([\text{CO}_2]\) nor elevated temperature had a significant effect on the proportion of either earlywood or latewood.

Fiber length

Over the entire treatment period, fibers were 5 and 6% longer in ET+AC and ET+EC trees, respectively, and 2% shorter in AT+EC trees than in AT+AC trees (Table 1). Fiber length increased significantly in response to elevated temperature, whereas elevated \([\text{CO}_2]\) had no effect on fiber length.

Wood density variables

Mean intra-ring wood density varied between 0.33 and 0.38 g cm\(^{-3}\) (Table 2), increasing by 6% in the ET+AC and ET+EC trees and decreasing by 6% in the AT+EC trees relative to the AT+AC trees. Elevated temperature generally increased mean intra-ring density, but this effect differed over the years (a significant temperature \(\times\) year interaction). Elevated \([\text{CO}_2]\) did not significantly affect mean wood density.

Earlywood density over the entire treatment period was 2 and 6% higher in ET+AC and ET+EC trees, respectively, and 6% lower in AT+EC trees than in AT+AC trees (Table 2). Elevated temperature significantly increased earlywood density; however, the statistical significance of this effect was the result of greater earlywood density in ET+EC trees, where there were only two replicates for the years 2001 and 2002. Elevated \([\text{CO}_2]\) had no significant effect on earlywood density.

Latewood density was 2% higher in ET+AC and ET+EC trees than in AT+AC trees, and it was 1% lower in AT+EC trees than in AT+AC trees (Table 2). There were no significant effects of elevated \([\text{CO}_2]\) and temperature on latewood density.

Minimum density varied from 0.20 to 0.22 g cm\(^{-3}\) over the 6-year treatment period. Maximum density varied within the range 0.67–0.69 g cm\(^{-3}\) (Table 2). Neither elevated \([\text{CO}_2]\) nor elevated temperature had a significant effect on minimum or maximum density.

Chemical composition

Over the treatment period, the concentration of acetone-soluble extractives was 15 and 20% lower in ET+AC and ET+EC trees, respectively, than in AT+AC trees (Table 3). The concentration of acetone-soluble extractives was reduced by elevated temperature, but elevated \([\text{CO}_2]\) had no significant ef-

![Figure 2. Cumulative height and radial growth with standard deviations for the years 1997–2002. Treatments: AT+AC = ambient temperature and ambient carbon dioxide concentration ([CO\(_2\)]; AT+EC = ambient temperature and elevated [CO\(_2\)]; ET+AC = elevated temperature and ambient [CO\(_2\)]; ET+EC = elevated temperature and elevated [CO\(_2\)]; and Cntr = trees outside the closed chambers.](image-url)
Table 1. Early- and latewood widths and proportions and fiber lengths (mean ± standard deviation) over the treatment period (1997–2002) and P values obtained in a repeated measures analysis of variance. Treatments: AT+AC = ambient temperature and ambient carbon dioxide concentration ([CO2]); AT+EC = ambient temperature and elevated [CO2]; ET+AC = elevated temperature and ambient [CO2]; ET+EC = elevated temperature and elevated [CO2]; and Cntr = trees outside the closed chambers.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Ring width (mm)</th>
<th>Proportion earlywood (%)</th>
<th>Fiber length (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Earlywood</td>
<td>Latewood</td>
<td></td>
</tr>
<tr>
<td>AT+AC</td>
<td>1.19 ± 0.05</td>
<td>0.48 ± 0.14</td>
<td>66.05 ± 0.11</td>
</tr>
<tr>
<td>AT+EC</td>
<td>2.03 ± 0.23</td>
<td>0.75 ± 0.27</td>
<td>70.71 ± 0.17</td>
</tr>
<tr>
<td>ET+AC</td>
<td>1.31 ± 0.19</td>
<td>0.67 ± 0.22</td>
<td>60.81 ± 0.21</td>
</tr>
<tr>
<td>ET+EC</td>
<td>1.74 ± 0.06</td>
<td>0.73 ± 0.16</td>
<td>64.16 ± 0.06</td>
</tr>
<tr>
<td>Cntr</td>
<td>1.97 ± 0.15</td>
<td>0.74 ± 0.10</td>
<td>72.60 ± 0.14</td>
</tr>
</tbody>
</table>

**Table 2**. Intra-ring wood densities (mean ± standard deviation) over the treatment period (1997–2002) with P values obtained in a repeated measure analysis of variance. Treatments: AT+AC = ambient temperature and ambient carbon dioxide concentration ([CO2]); AT+EC = ambient temperature and elevated [CO2]; ET+AC = elevated temperature and ambient [CO2]; ET+EC = elevated temperature and elevated [CO2]; and Cntr = trees outside the closed chambers.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Density (g cm(^{-3}))</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
</tr>
<tr>
<td>AT+AC</td>
<td>0.35 ± 0.06</td>
</tr>
<tr>
<td>AT+EC</td>
<td>0.33 ± 0.04</td>
</tr>
<tr>
<td>ET+AC</td>
<td>0.38 ± 0.03</td>
</tr>
<tr>
<td>ET+EC</td>
<td>0.37 ± 0.06</td>
</tr>
<tr>
<td>Cntr</td>
<td>0.33 ± 0.02</td>
</tr>
</tbody>
</table>

**Discussion and conclusions**

**Height and radial growth**

Height growth of Scots pine trees was not significantly affected by elevated temperature or elevated [CO\(_2\)] (Table 4). The predetermined growth pattern of Scots pine, in which shoot length is determined by the number of primordia formed during the previous year, may limit the height growth response to elevated [CO\(_2\)] because of a low sink capacity (Jach and Ceulemans 1999). In earlier studies, an elevation in [CO\(_2\)] enhanced height growth of seedlings in some species, e.g., Scots pine (Jach and Ceulemans 1999) and Norway spruce (Skre and Nes 1996), but contradictory results also exist (Murray et al. 1996, Olszyk et al. 1998). Oren et al. (2001) found that poor soil fertility was associated with a lack of growth response to elevated [CO\(_2\)]. In our study, however, soil nitrogen content is not a limiting factor for the photosynthetic response to elevated [CO\(_2\)] (Wang and Kellomäki 1997). The effect of elevated temperature on height growth may be associated with earlier onset of the growing season rather than with a longer period of growth (Oleksyn et al. 1998) or a greater amount of growth. In Douglas-fir seedlings, elevated temperature reduced height growth (Olszyk et al. 1998, Tingey et al. 2003). The lack of statistically significant effects in our study may be attributable to the limited number of replicates and the high variation among treatments.
In our study, elevated \([\text{CO}_2]\) had a significant effect on radial growth of Scots pine trees (Table 4), corroborating earlier findings for loblolly pine (Tissue et al. 1997, DeLucia et al. 1999, Telewski et al. 1999) and Scots pine (Ceulemans et al. 2002). Kilpeläinen et al. (2003) reported 25–54% increases in mean radial growth of 15-year-old Scots pines grown in open-top chambers for 3 years at elevated temperature and \([\text{CO}_2]\) alone or concurrently compared with the ambient treatment, whereas we observed increases of 19–66%. In the study by Kilpeläinen et al. (2003), the elevation in \([\text{CO}_2]\) was maintained only during the daytime and between April 15 and September 15, whereas in the present study, elevation in \([\text{CO}_2]\) was maintained day and night throughout the year. There is general agreement that elevated \([\text{CO}_2]\) enhances tree growth by increasing water-use efficiency (Thornley and Cannell 1996, Kellomäki and Wang 1998) and net photosynthesis (e.g., Norby et al. 1999).

### Physical properties of wood

The observed increase in earlywood formation and hence annual ring width in response to elevated \([\text{CO}_2]\) (Table 4) agrees with earlier observations on loblolly pine (Telewski et al. 1999) and Scots pine (Ceulemans et al. 2002). It has been suggested that earlywood formation is regulated by carbohydrate

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**Table 3. Acetone-soluble extractive, lignin, cellulose and hemicellulose concentrations (mean ± standard deviation) over the treatment period (1997–2002) with \(P\) values obtained in a two-way analysis of variance. Treatments: AT+AC = ambient temperature and ambient carbon dioxide concentration ([CO\(_2\)]) ; AT+EC = ambient temperature and elevated [CO\(_2\)]; ET+AC = elevated temperature and ambient [CO\(_2\)]; ET+EC = elevated temperature and elevated [CO\(_2\)]; and Cntr = trees outside the closed chambers.**

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Acetone-soluble extractives (%)</th>
<th>Lignin (%)</th>
<th>Cellulose (%)</th>
<th>Hemicellulose (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>AT+AC</td>
<td>2.99 ± 0.32</td>
<td>27.75 ± 0.84</td>
<td>41.76 ± 0.94</td>
<td>24.73 ± 0.83</td>
</tr>
<tr>
<td>AT+EC</td>
<td>3.33 ± 0.13</td>
<td>28.58 ± 0.78</td>
<td>40.51 ± 0.69</td>
<td>24.11 ± 0.69</td>
</tr>
<tr>
<td>ET+AC</td>
<td>2.53 ± 0.15</td>
<td>27.55 ± 0.83</td>
<td>42.75 ± 0.16</td>
<td>24.83 ± 1.07</td>
</tr>
<tr>
<td>ET+EC</td>
<td>2.39 ± 0.60</td>
<td>28.50 ± 1.67</td>
<td>41.21 ± 1.27</td>
<td>24.49 ± 1.23</td>
</tr>
<tr>
<td>Cntr</td>
<td>3.31 ± 0.17</td>
<td>27.35 ± 1.06</td>
<td>40.76 ± 1.12</td>
<td>25.48 ± 0.70</td>
</tr>
</tbody>
</table>

**Table 4. Summary of all variables studied. Statistical results from a repeated measures two-way analysis of variance (chemical composition); ns = no effect, + = significant increase \((P < 0.05)\), – = significant decrease \((P < 0.05)\). Interaction terms were not significant for any variable, except a temperature × year interaction for mean wood density (see text) and thus only the main effects of carbon dioxide and temperature are shown. Six-year means are used for the comparison to the AT+AC treatment. Treatments: AT+AC = ambient temperature and ambient carbon dioxide concentration ([CO\(_2\)]) ; AT+EC = ambient temperature and elevated [CO\(_2\)]; ET+AC = elevated temperature and ambient [CO\(_2\)]; and ET+EC = elevated temperature and elevated [CO\(_2\)].**

<table>
<thead>
<tr>
<th>Variable</th>
<th>Effect</th>
<th>Percent change compared with AT+AC treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>[CO(_2)]</td>
<td>Temperature</td>
</tr>
<tr>
<td>Height growth</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Ring width</td>
<td>+</td>
<td>ns</td>
</tr>
<tr>
<td>Earlywood width</td>
<td>+</td>
<td>ns</td>
</tr>
<tr>
<td>Latewood width</td>
<td>+</td>
<td>ns</td>
</tr>
<tr>
<td>Earlywood proportion</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Latewood proportion</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Mean wood density</td>
<td>ns</td>
<td>+</td>
</tr>
<tr>
<td>Earlywood density</td>
<td>ns</td>
<td>+</td>
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reserves stored during the previous growing season, whereas latewood formation is affected by current-year carbon gain (Hättenschwiler et al. 1996). In our study, however, the effects of elevated [CO₂] on both early- and latewood width were already found in the first year of exposure, implying that there were additional reserves readily available to support earlywood formation. An increase in latewood width in response to elevated [CO₂] might result from prolongation of cambial activity (Peltola et al. 2002). Because the transition from earlywood to latewood production occurs after the completion of shoot elongation, more photosynthates will be available for allocation to the stem and to secondary cell wall thickening during latewood development (Antonova and斯塔索夫 1993, Dougherty et al. 1994). Although a positive effect of elevated [CO₂] on latewood width has previously been found in loblolly pine (Telewski et al. 1999), Ceulemans et al. (2002) reported that latewood was unaffected by elevated [CO₂] in Scots pine. Similarly, Kilpeläinen et al. (2003) found no significant effect of either elevated temperature or elevated [CO₂] on early- and latewood widths or their proportions in Scots pine in open-top chambers over 3 years. In our study, the proportion of earlywood or latewood was unaffected by elevated [CO₂], because both early- and latewood widths increased in proportion (Table 4).

Elevated temperature increased mean wood density and earlywood density (Table 4). Generally, an increase in wood density results from a decrease in radial cell diameter or an increase in cell wall thickness, or both. Cell wall thickness depends on the duration of cell wall thickening (Wodzicki 1971, Yasue et al. 2000). Thus, the extension of the growing season (Peltola et al. 2002) may account for the increase in wood density in response to elevated temperature. Alternatively, an increase in earlywood density may be a result of the production of more, but smaller, earlywood cells. Maximum and latewood densities were unaffected by the elevated temperature treatment, although a relationship between maximum wood density or latewood density and summer temperatures has been reported (Briffa et al. 1988, 1990, Da’Arrigo et al. 1992). However, high temperatures have also been found to shorten the duration of cell wall thickening because of increased respiration (Antonova and斯塔索夫 1993), which may explain why maximum wood density and latewood density were unaffected by elevated temperature. Kilpeläinen et al. (2003) found no effect of elevated temperature on wood density parameters in Scots pines grown in open-top chambers for 3 years.

We observed no significant effects of elevated [CO₂] on wood density parameters, in agreement with most earlier studies on the effects of elevated [CO₂] on mean wood density (e.g., Rogers et al. 1983, Telewski and Strain 1987, Telewski et al. 1999, Ceulemans et al. 2002), although there were changes in ring width (Table 4). In contrast, Hättenschwiler et al. (1996) reported significant increases in the wood density of Norway spruce seedlings in elevated [CO₂] relative to the ambient treatment even though ring width growth was not stimulated. Similarly, an increase in wood density was found in radiata pine seedlings, even though there were no differences in the proportions of early- and latewood (Conroy et al. 1990).

In contrast to our results, Kilpeläinen et al. (2003) reported that elevated [CO₂] increased latewood density and maximum intra-ring density.

Fiber length increased significantly in response to elevated temperature (Table 4), even though an increase in growth rate generally indicates a decrease in fiber length in conifers (Zobel and van Buijtenen 1989, Dutilleul et al. 1998). Kilpeläinen et al. (2003) also found an increase in fiber length in Scots pines grown at elevated temperature in open-top chambers. The production of longer fibers in response to elevated temperature may be the result of an increase in latewood with longer fibers (Goggans 1962). Richardson (1964) reported that high temperatures increased fiber length in Sitka spruce (Picea sitchensis (Bong.) Carr.). We found no effect of elevated [CO₂] on fiber length, which is in agreement with the results for radiata pine seedlings (Donaldson et al. 1987, Conroy et al. 1990) and Scots pine trees (Kilpeläinen et al. 2003).

Chemical composition of wood

The concentration of acetone-soluble extractives decreased over the 6-year treatment period in response to elevated temperature (Table 4), which may have been associated with increased maintenance respiration at high temperatures (Zha et al. 2001). Although an increase in growth and vigor should lead to an increase in extractive content (Kramer and Kozlowski 1979), elevated [CO₂] had no effect on the concentration of acetone-soluble extractives.

No significant effect of elevated [CO₂] on lignin concentration was observed, even though earlywood formation, which has a higher lignin content than latewood (Fukazawa and Imagawa 1981), increased in response to elevated [CO₂] (Table 4). Earlier studies also showed that lignin concentrations in the wood of Norway spruce (Hättenschwiler et al. 1996), longleaf pine (Entry et al. 1998) and radiata pine (Atwell et al. 2003) are unaffected by elevated [CO₂]. Elevated temperature had no significant effect on lignin concentration, despite the lengthened growing season due to the elevated temperature treatment (Peltola et al. 2002). Gindl et al. (2000) found that earlier termination of the growing season for Norway spruce resulted in lower lignin content of the last forming latewood cells. In contrast to our study, Kilpeläinen et al. (2003) found an increase in lignin concentration in the wood of Scots pine in response to elevated temperature in open-top chambers. The reason we failed to find such an effect may be associated with the high cellulose concentration observed in ET+AC trees (Table 4). The decrease in cellulose concentration in response to elevated [CO₂] may be related to the wider earlywood bands, with narrower cell walls, which reduce the concentration of cellulose. In contrast to our study, elevated [CO₂] had no effect on the cellulose concentrations in stem wood of longleaf pine (Entry et al. 1998).

In conclusion, we examined the effects of a continuous (24 h day⁻¹) year-round elevation in [CO₂] and temperature on height and radial growth and wood properties of juvenile Scots pine trees. Over the 6-year study, radial growth of trees was significantly increased by elevated [CO₂], and some physical and chemical wood properties were affected significantly by
elevated temperature or elevated [CO\textsubscript{2}], or both (e.g., mean wood density, earlywood density, early- and latewood width, fiber length, acetone-soluble extractives, cellulose concentration). An increase in ring width in response to elevated [CO\textsubscript{2}] indicates enhanced wood production. An increase in mean wood density and fiber length in response to elevated temperature would affect the material properties of the wood. Extrapolation of these findings to mature trees should be made with care, because the wood properties of juvenile Scots pine trees differ from those of mature trees. Our study highlights the need for additional studies on wood properties, because even small changes in the material properties of wood may be important economically.

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