Diameter growth of Scots pine (*Pinus sylvestris*) trees grown at elevated temperature and carbon dioxide concentration under boreal conditions

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Received November 20, 2001; accepted February 8, 2002; published online September 2, 2002

Summary  We investigated the impacts of elevated temperature and carbon dioxide concentration ([CO$_2$]) on diameter growth of Scots pine (*Pinus sylvestris* L.), aged about 20 years, grown with a low nitrogen supply in closed chambers at (i) ambient temperature and [CO$_2$] (AT+AC), (ii) ambient temperature and elevated [CO$_2$] (AT+EC), (iii) elevated temperature and ambient [CO$_2$] (ET+AC), and (iv) elevated temperature and [CO$_2$] (ET+EC). Each treatment was replicated four times. Diameter growth was monitored with a band dendrograph at 15-min intervals throughout the growing seasons of 1997, 1998 and 1999.

Over the monitoring period, diameter growth began 2–3 weeks earlier in trees in the ET+EC and ET+AC chambers than in trees in the AT+AC and AT+EC chambers. However, the cessation of growth occurred a week later in trees in the ET+EC, ET+AC and AT+EC chambers compared with the AT+AC chambers. The duration of the growing season was 115 and 108 days in the ET+EC and ET+AC chambers, respectively, and 95 and 84 days in the AT+EC and AT+AC chambers, respectively.

The ET+AC and ET+EC treatments enhanced diameter growth most early in the growing season, whereas in trees in the AT+AC and AT+EC treatments diameter growth rate was greatest in the middle of the growing season. Diameter growth rate leveled off more slowly in trees in the ET+EC and AT+EC treatments than in the other treatments. The growth response to elevated T, elevated [CO$_2$] or both decreased with time and it was less than the maximum observed in other studies for small seedlings and under optimal growth conditions. Nevertheless, cumulative diameter growth for the 3-year period was 67% greater in trees in the ET+EC treatment, and 57 and 26% greater in trees in the AT+EC and ET+AC treatments, respectively, compared with trees in the AT+AC treatment. Over the 3 years, [CO$_2$] had a statistically significant ($P < 0.10$) effect on both absolute and relative diameter growth, but the interaction between [CO$_2$] and temperature was not significant.

Keywords: annual diameter growth, daily diameter growth, factorial design.

Introduction

In northern Europe (above 60° N), tree-ring chronologies of Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) indicate that temperature during the growing season is the main climatic factor affecting diameter growth (Mitcherlich et al. 1966, Jonsson 1969, Henttonen 1984, 1990, Briffa et al. 1988, 1990, Lindholm 1996, Miina 2000). This holds true in both the short and long term; i.e., the initiation, extent and duration of growth over the spring and summer are related to air temperature (Mikola 1950, Mitcherlich et al. 1966, Leikola 1969), with wide year-to-year variability in annual growth reflecting the variation in summer temperatures (Briffa et al. 1988, 1990).

The influence of other environmental factors, such as soil temperature (which is related to air temperature), on diameter growth are less pronounced or nonexistent (Huikari and Paarlari 1967, Leikola 1969). Although a constant supply of water is needed for undisturbed growth (Kramer 1962, Kozlowski 1964), precipitation has little or no effect on radial growth of conifers in northern Europe (Jonsson 1969, Henttonen 1984, 1990, Mielikäinen et al. 1996) because evaporative demand is low relative to precipitation. Only on sandy soils with a low water holding capacity does water supply occasionally affect diameter growth of conifers (Mikola 1950). Tree-ring chronologies have also demonstrated that diameter growth of Scots pine may correlate positively with high winter temperatures (Lindholm 1996). This finding contrasts with the study of Jonsson (1969) showing that diameter growth of Norway spruce is reduced by high temperatures in the previous winter and is enhanced by low temperatures.

Predicted climate change in northern Europe involves a doubling of atmospheric carbon dioxide concentration ([CO$_2$]) and a concurrent increase in mean annual temperature of 2–4 °C (high confidence, IPCC 1996), and up to 6 °C in the winter months, during the next 100 years (Kettunen et al. 1987, Parry 2000). The elevation in temperature is also likely to increase growth by lengthening the growing season, which has been found to correlate positively with total diameter growth in Scots pine under current climatic conditions (Leikola 1969). Elevated atmospheric [CO$_2$] along with enhanced mineralization of nitrogen at higher temperatures may

These inferences are supported by studies demonstrating that diameter growth of seedlings of loblolly pine (Pinus taeda L.), longleaf pine (Pinus palustris Mill.), radiata pine (P. radiata D. Don) and Scots pine, grown without competition and under optimal conditions of nutrient supply, increases in response to increasing atmospheric [CO₂] (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). Increases in diameter growth are particularly striking during the first growing seasons of exposure to elevated [CO₂]. Little or no stimulation of growth in response to elevated [CO₂] has been found, however, when seedlings were grown under near-natural conditions, i.e., in competition with each other and with a limited nutrient supply (Pushnik et al. 1995, Hättenschwiler et al. 1996, Körner 1996, Oren et al. 2001). Olszyk et al. (1998) found no significant effects of elevated [CO₂] and elevated temperature either individually or in combination (factorial design) on the diameter growth of Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) seedlings grown in nitrogen-poor soil with a low soil water content during the summer.

Few studies have focused on changes in diameter growth rate in response to long-term exposure to elevated [CO₂] and temperature alone or in combination on trees past the juvenile stage. In a study of loblolly pines trees (stand age of about 16 years) grown with a low nutrient supply in a free-air CO₂ enrichment experiment (FACE), DeLucia et al. (1999) found a similar increase in diameter growth in response to elevated [CO₂] to that observed in potted loblolly pine seedlings grown with a suboptimal mineral nutrient supply. The response, however, was considerably less than that observed in loblolly pine grown under optimal conditions, and was transient in the absence of nutrient addition (Tissue et al. 1997, Oren et al. 2001). Similarly, decreases over time in growth response to elevated [CO₂] were found by Hättenschwiler et al. (1997) and Tognetti et al. (2000) in studies of stem diameter growth in Mediterranean forest tree species growing close to natural CO₂ springs on soils of low fertility. Thus, extrapolation of findings obtained with young seedlings to mature trees may be misleading, because the morphological, phenological and physiological properties of juvenile trees differ from those of mature trees (Ceulemans and Moussseau 1994). Furthermore, long- and short-term responses may differ, particularly when dynamic changes in nutrient cycles occur as a result of a synergistic effect of [CO₂] and nutrient supply (Oren et al. 2001).

Schweinigruber et al. (1993) postulated that elevated [CO₂] has no effect on trees in the boreal forests of northern Europe. To test this hypothesis, we used a closed [CO₂]- and temperature-controlled chamber system in a boreal forest of Scots pine, aged about 20 years, to investigate the impacts of elevated [CO₂] and temperature alone or in combination on diameter growth (daily and over the growing season) during a 3-year period. Variables examined were: (i) mean absolute and relative growth; (ii) dates and temperature sum for the beginning and cessation of diameter growth; (iii) duration of the growing period; and (iv) differences between treatments in daily and cumulative diameter growth patterns.

Materials and methods

Site and layout

The experiment was performed in a closed [CO₂]- and temperature-controlled chamber system set up in 1996 in a naturally regenerated forest of Scots pine, aged about 20 years and 3 m high, near the Mekrijärvi Research Station (62°47′ N, 30°58′ E, 145 m a.s.l.), of the University of Joensuu, Finland (Kellomäki et al. 2000). The site, which represents the Calluna type in terms of fertility, has a sandy soil and a low supply of nitrogen, and is occupied by a natural Scots pine population of local origin. Climate at the site is characterized by cold winters with a persistent snow cover and a short growing season. Mean annual precipitation (1961–1994) is about 740 mm, of which about 38% is in the form of snow. Mean monthly temperature is –10.4 °C in January and 15.5 °C in July, and an absolute minimum temperature of –40 °C and an absolute maximum temperature of 32 °C were recorded in January and July, respectively. Low evapotranspiration makes the climate more humid in winter than in summer (Wang 1996).

The experiment employed 16 closed chambers, each provided with facilities for controlling [CO₂] and temperature. Each chamber consisted of a hexagonal tube with an internal volume of about 19.3 m³ and a ground area of 5.2 m². The four walls facing south and west were made of special heating glass (Standard 16 mm BMMA), with three small vents located in them. A computer-controlled heat exchanger linked to a refrigeration unit (CAJ-4511YHR, L’Unité Hermetique, La Verpilliére, France) was installed at about 0.3 m above ground. The computer-controlled heating and cooling system, together with a set of magneto-electric valves (controlling the supply of pure CO₂), automatically adjusted the temperature and [CO₂] inside the chambers to track ambient conditions, or to achieve a specified elevation in [CO₂] or temperature. The [CO₂] was enriched continuously all day throughout the year and was set at a fixed constant of 700 µmol mol⁻¹. The warming treatments were designed to correspond to the climatic scenario predicted for the site after a doubling of atmospheric [CO₂]; i.e., temperature inside the chambers followed the seasonal pattern of outside temperature (Figure 1), with increases depending on the season: 6 °C in winter (December to February); 4 °C in spring and autumn.
We monitored \([\text{CO}_2]\) with a \(\text{CO}_2\) sensor (GMP111, Vaisala, Helsinki, Finland) located in the middle of the crown of each tree. 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 (Theta-Probe ML1, Delta-T Devices, Cambridge, U.K.). All the sensors were connected to a data logger, enabling measurements to be taken at 15-s intervals. Chambers were irrigated during the growing season to keep soil water content close to that of the ambient soil. During winter, snow was added to the chambers to match snowfall in the surrounding forest. Detailed descriptions of the experimental system have been provided by Kellomäki et al. (2000).

In summer 1996, 16 trees of similar age (about 20 years), diameter \(3.8 \pm 0.5\) cm) and height \(3.0 \pm 0.3\) m were each enclosed in a chamber, and another four trees growing outside the chambers were chosen for comparison (Cntr). To reduce shading of the experimental trees by nearby trees, all trees within 2 m of the chambers were cut down 1 year before the experiment. The treatments comprised four combinations of \([\text{CO}_2]\) and temperature: (i) ambient temperature and \([\text{CO}_2]\) (AT+AC); (ii) ambient temperature and elevated \([\text{CO}_2]\) (AT+EC); (iii) elevated temperature and ambient \([\text{CO}_2]\) (ET+AC); and (iv) elevated temperature and \([\text{CO}_2]\) (ET+EC). The experiment followed a factorial design with one tree in a chamber as the basic treatment unit, replicated four times. The treatment started on September 1, 1996.

**Measurements and analysis of diameter growth**

Daily diameter growth at breast height (1.3 ± 0.14 m above ground) was monitored at 15-min intervals throughout the growing seasons of 1997, 1998 and 1999 by means of a band dendrograph (ELPA 93, University of Oulu, Finland). The dendrograph consists of a stainless steel band and a potentiometer that responds to any displacement. The accuracy of the sensor measurements is 0.5 mm.

To reduce the effect on the results of stem swelling and shrinkage unrelated to growth (see Leikola 1969, Lipas 1978), perimeter measurements made at 15-min intervals were averaged to daily values for further analysis of diameter growth. Some measurements were excluded from analysis because of system malfunction. As a result, only three replicates in each treatment were available for analysis in 1998, with the exception of the AT+EC treatment and the control treatment outside the chambers (Cntr). Similar equipment malfunctions in 1999 affected the ET+AC, ET+EC and AT+EC treatments.

Treatment effects on diameter growth were analyzed for each year and over the entire monitoring period (1997–1999) as follows: (i) mean absolute and relative diameter growth; (ii) dates and temperature sums (degree days, d.d.) for the beginning and cessation of diameter growth; and (iii) the duration (days) of the growing season. The beginning of diameter growth was determined as the beginning of a clear continuous pattern of perimeter growth. Permanent attainment of a given perimeter measurement was regarded as marking the cessation of diameter growth. A threshold value of 5 °C was used for the cumulative temperature sum, based on daily mean temperatures, as used by previous authors (e.g., Cannell et al. 1985, Cannell and Smith 1986, Murray et al. 1989, Kramer 1994). Correspondingly, relative growth rate (%) was determined as the relationship between annual diameter growth (mm) and stem diameter (mm) at the beginning of a growing season.

The data for each year and the entire monitoring period were subjected to two-way analysis of variance performed with the SPSS software package (SPSS, Chicago, IL). Effects were considered significant at \(P < 0.10\). Values of the temperature sum corresponding to 5 and 90% of total growth were used in the statistical analyses (Huikari and Paarlalhti 1967, Leikola 1969).

**Results**

Over the whole monitoring period, diameter growth began first in trees in the ET+EC and ET+AC chambers (on Days 114 and 117 from the beginning of the year, respectively (Fig-
Diameter growth of trees in the AT+EC and AT+AC chambers did not begin until Days 131 and 134, respectively. Elevated T had statistically significant effects on the onset of diameter growth ($P < 0.10$) over the whole monitoring period (and also in each year considered separately), whereas there were no significant effects of elevated [CO$_2$] or a significant CO$_2$ × T interaction on the onset of diameter growth. Correspondingly, the cessation of growth over the whole monitoring period took place about a week earlier in trees in the AT+AC chambers (Day 218) than in the AT+EC (Day 226), ET+AC (Day 225) and ET+EC (Day 229) chambers (Figure 3). Both elevated T and elevated [CO$_2$] separately affected the cessation of growth significantly over the entire monitoring period (but not in the individual years, except in the case of elevated T in 1997). There were no statistically significant CO$_2$ × T interactions on the cessation of diameter growth.

Over the whole monitoring period, the beginning of diameter growth occurred when the temperature sum reached an average of approximately 50 d.d. in the AT+AC treatment and 56 d.d. in the AT+EC treatment, the temperature sum requirement was substantially larger, i.e., 118 and 111 d.d., respectively. The cessation of growth occurred when the temperature sum was about 760 d.d. in the AT+AC chambers, 774 d.d. in the AT+EC chambers, 1197 d.d. in the ET+AC chambers and 1255 d.d. in the ET+EC chambers (Figure 5). Thus, a low temperature sum for the beginning of growth was associated with a low temperature sum at cessation, and vice versa. Elevated T had statistically significant effects on the temperature sum corresponding to both the beginning and for the cessation of diameter growth over the entire monitoring period (and for each year). No significant effects of elevated [CO$_2$] alone or of CO$_2$ × T interactions were found.

For the whole monitoring period, the duration of the growing period was 115 days in the ET+EC treatment, 108 days in the ET+AC treatment, 95 days in the AT+EC treatment and 84 days in the AT+AC treatment (Figure 6). Both elevated T and elevated [CO$_2$] had significant effects on the duration of growth over the entire monitoring period (and for each year, except for the AT+EC treatment in 1998). There were no statistically significant CO$_2$ × T interaction effects on the duration of diameter growth.

The general pattern of daily diameter growth was similar for trees in all treatments, i.e., it gradually increased after an initially low growth rate, reached a maximum and then leveled off. In 1997, however, the relative growth rate of all trees in the AT+AC treatment was unexpectedly low (Figure 7), possibly reflecting the sudden change in growing conditions when the
trees were enclosed in chambers. This chamber effect was presumably obscured by the increases in \([\text{CO}_2]\) and temperature in the other treatments. This assumption is supported by the finding that diameter growth of the trees outside the chambers was greater than that of the trees in the AT+AC chambers. Furthermore, the ET+AC and ET+EC treatments enhanced growth most in the early growing season, whereas the growth pattern of trees in the AT+EC chambers followed that in the AT+AC chambers (with the highest growth rate in the middle of the growing season). However, the growth rate seemed to level off more slowly after the peak in trees in the AT+EC and ET+EC treatments than in trees in the other treatments.

Mean yearly diameter growth, both in absolute and relative terms over the 3-year period, was greater in trees in the ET+EC (5.8 mm, 13.9%) and AT+EC (5.5 mm, 14.3%) treatments than in trees in the ET+AC (4.4 mm, 11.0%) and AT+AC (3.5 mm, 8.9%) treatments (Figures 8 and 9). Thus, relative diameter growth was an average of 3–5 %-units higher in trees in the AT+EC and ET+EC chambers than in trees in the AT+AC and ET+AC chambers. Cumulative diameter growth over the 3 years was 67% higher in trees in the ET+EC treatment (17.5 mm) than in the AT+AC treatment (10.5 mm). By comparison, it was 16.5 mm in the AT+EC treatment (+57%) and 13.2 mm (+26%) in the ET+AC treatment.

Year-to-year variation among treatments was high (Figures 8 and 9).

Overall, elevated \([\text{CO}_2]\) had statistically significant effects on both absolute and relative diameter growth over the entire monitoring period (and also in each year, except in the case of relative growth in 1998). By comparison, elevated \(T\) had significant effects on total and relative diameter growth only in 1997, although there was no statistically significant \(\text{CO}_2 \times T\) interaction effect on either absolute or relative growth, even in 1997. A significant positive correlation between duration of the growing season and annual diameter growth was found only in the chamberless control treatment (correlation coefficient 0.65). In contrast, the correlation was either poor or negative in the AT+AC (–0.18), AT+EC (–0.24), ET+EC (–0.70) and ET+AC (–0.65) treatments.

**Discussion**

Large year-to-year variation in the onset, cessation, duration and amount of diameter growth, both in absolute and relative terms, occurred within and between treatments, because of the year-to-year variability in temperature (cf. Briffa et al. 1988, 1990, Hättenschwiler et al. 1996). Diameter growth began 2–3 weeks earlier in trees in the ET+AC and ET+EC treat-
ments compared with the other treatments, whereas the cessation of growth took place about a week earlier in trees in the AT+AC and AT+EC treatments than in the other treatments. The duration of the growing period was 115 days in the ET+EC treatment, 108 days in the ET+AC treatment and 95 and 84 days in the AT+EC and AT+AC treatments, respectively. The importance of air temperature and cumulative temperature sum for the onset, cessation and duration of diameter growth has been emphasized in several previous studies (Mikola 1950, Mitcherlich et al. 1966, Leikola 1969). The temperature sum requirement for the beginning of growth was twice as high for trees in the ET+AC and ET+EC treatments than for trees in the AT+EC and AT+AC treatments. This high temperature sum requirement may be associated with the high temperatures that prevailed during the dormant season in the ET+AC and ET+EC chambers compared with the other chamber treatments. For Sitka spruce (Picea sitchensis (Bong.) Carr.), there is evidence that the onset of diameter growth in spring is delayed if temperatures do not fall below a threshold during the dormant season (Cannell et al. 1985, Cannell and Smith 1986). A high temperature sum for the beginning of growth was associated with a high temperature sum for the cessation of growth, and vice versa.

It has been suggested that photoperiod affects the beginning of diameter growth, and even more markedly its cessation (Fraser 1959, Kramer and Kozlowski 1960, Larsson 1964). According to Fraser (1959), the critical photoperiod for diameter growth is 14–15 h. We found that diameter growth ceased at a day length of 15–16 h in trees in all of the treatments except the AT+AC treatment, where the critical day length was nearly 17 h. By comparison, diameter growth started at a day length of 15–16 h in trees in the ET+AC and ET+EC treatments, and at 17 h in the other treatments. We conclude, therefore, that day length did not determine either the beginning or the cessation of diameter growth in our study.

Over the 3-year period, mean yearly diameter growth in both absolute and relative terms was greatest in trees in the ET+EC (5.8 mm, 13.9%) and AT+EC (5.5 mm, 14.3%) chambers and less marked in trees in the ET+AC (4.4 mm, 11.0%) and AT+AC (3.5 mm, 8.9%) chambers. Consequently, mean relative diameter growth rate was 3–5 %–units higher in trees in the AT+EC and ET+EC treatments than in the AT+AC and ET+AC treatments. Correspondingly, cumulative diameter growth over the 3 years was 67% higher in trees in the ET+EC treatment, 57% higher in trees in the ET+AC treatment and 26% higher in trees in the ET+AC treatment than in the AT+AC treatment. The difference between the AT+AC treatment and the other treatments was enhanced by the unexpect-
edly low growth rate of trees in the AT+AC chambers in 1997, which may have been caused by the sudden change in growing conditions when the trees were enclosed in the chambers.

DeLucia et al. (1999) found a 26% increase in basal area growth of loblolly pine trees grown for 2 years in a FACE experiment under conditions of low nutrient supply compared with diameter growth of trees grown under ambient conditions (no response was observed in the first year). A similar response was observed in loblolly pine seedlings grown with suboptimal nutrient supply, but this increase was considerably less than the maximum increase observed for loblolly pine seedlings grown under optimal conditions without nutrient addition (Tissue et al. 1997, Oren et al. 2001). Callaway et al. (1994a, 1994b) also found increased diameter growth in ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) at elevated temperatures compared with ambient temperature, and suggested that transpiration stress at high temperatures increases the demand for sapwood.

Several atmospheric CO₂ enrichment experiments have shown much greater increases in diameter growth of small seedlings of loblolly pine, longleaf pine, radiata pine and Scots pine than we observed, especially during the first year of exposure (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). For example, Telewski et al. (1999) found a 93% increase in ring width of loblolly pine in the first year of exposure to elevated [CO₂] and a 15–37% increase in the following 2 years. We note that these findings were obtained from experiments with young seedlings grown without competition and with an optimal nutrient supply, whereas we used mature trees grown with a low nitrogen supply. By comparison, no stimulation of growth has been found in response to elevated [CO₂] when seedlings were grown under near-natural conditions with a low nutrient supply (Pushnik et al. 1995, Hättenschwiler et al. 1996, Körner 1996).

The ET+AC and ET+EC treatments enhanced diameter growth most early in the growing season, whereas the highest diameter growth rates were observed in the middle of the growing season in trees in the AT+EC and AT+AC treatments. On the other hand, growth rate leveled off at a lower value in the AT+EC and ET+EC treatments than in the other treatments. In the control treatment, there was a positive correlation between duration of the growing season and annual diameter growth, as found by Leikola (1969) for Scots pines grown under current climatic conditions, but this correlation was not significant for the other treatments. Gregg et al. (1988)
also found that diameter growth of loblolly pine was positively related to mean daily temperature in early summer, but negatively related to it in late summer, reflecting the influence of high-temperature stress on growth. This may partly explain our findings of a poor correlation between duration of the growing season and total diameter growth of trees in the ET+AC treatment. On the other hand, Zha et al. (2001), who made measurements at our site, found that the rate of maintenance respiration in needles was enhanced in the ET+AC and ET+EC treatments compared with that in the AT+EC or AT+AC treatments. Also, the increase in maintenance respiration rate in needles in the ET+AC treatment was greater than that in the ET+EC treatment. The maintenance respiration rate of needles in the AT+EC treatment seemed to be enhanced early in the growing season but reduced later in the growing season (Zha et al. 2001).

Our finding that diameter growth was enhanced toward the end of the growing season in trees in the AT+EC treatment, compared with the ET+AC treatment, may also be attributable to decreased stomatal conductance and reduced transpiration in elevated [CO₂] (cf. Ceulemans and Mousseau 1994, Kellomäki and Wang 1998). Increased water-use efficiency in response to elevated [CO₂] may compensate for any decrease in availability of water (Telewski and Strain 1986, Guehl et al. 1992, Tschaplinski et al. 1993, Tissue et al. 1997, Kellomäki and Wang 1998, Mäkipää et al. 1999), thereby reducing the water stress that trees may otherwise experience in response to elevated temperature (Thorley and Cannell 1996). However, the soil water data indicate that water availability had no direct effect on diameter growth in any treatment (Kellomäki and Wang 1998, Kellomäki et al. 2000).

In conclusion, trees growing in a forest for decades may show a different response to climate change than young seedlings in the juvenile phase. The response of forest trees may also differ from that of more mature trees grown in chambers, because trees in chambers are protected from wind-induced stem movement, which enhances diameter growth (Telewski 1990). We found that the trees grown outside the chambers had greater diameter growth than trees grown in the AT+AC chambers (see Figure 8), even though the air temperature was always lower outside the chambers than inside. We conclude that it is difficult to generalize findings obtained in experiments with trees in the juvenile phase to mature trees or to trees grown under different environmental conditions.

**Acknowledgments**

This work was funded through the Finnish Center of Excellence Programme (2000–2005), under the Center of Excellence for Forest Ecology and Management (Project No. 64308), co-ordinated by Prof. Seppo Kellomäki, University of Joensuu, Faculty of Forestry. Support provided by the Academy of Finland, the National Technology Agency (Tekes) and the University of Joensuu is acknowledged. Alpo Hassinen and Matti Lemettinen, at the Mekrijärvi Research Station, University of Joensuu, are thanked for technical assistance. We thank Tomi Löfman, Ismo Rouvinen and Sanna Leinonen for helping with data processing and Malcolm Hicks for revising the English of the manuscript.

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**TREE PHYSIOLOGY VOLUME 22, 2002**


