

5-2001

## Seasonal Patterns of Photosynthesis in Douglas Fir Seedlings During the Third and Fourth Year of Exposure to Elevated CO<sub>2</sub> and Temperature

James D. Lewis  
*National Research Council*

Melissa S. Lucash  
*Portland State University, lucash@pdx.edu*

David M. Olszyk  
*US Environmental Protection Agency Western Ecology Division*

David T. Tingey  
*US Environmental Protection Agency Western Ecology Division*

**Let us know how access to this document benefits you.**

Follow this and additional works at: [https://pdxscholar.library.pdx.edu/esm\\_fac](https://pdxscholar.library.pdx.edu/esm_fac)

 Part of the [Environmental Monitoring Commons](#), [Other Ecology and Evolutionary Biology Commons](#), [Other Environmental Sciences Commons](#), and the [Plant Biology Commons](#)

---

### Citation Details

Lewis, J. D., Lucash, M., Olszyk, D., & Tingey, D. T. (2001). Seasonal patterns of photosynthesis in Douglas fir seedlings during the third and fourth year of exposure to elevated CO<sub>2</sub> and temperature. *Plant, Cell & Environment*, 24(5), 539-548.

This Article is brought to you for free and open access. It has been accepted for inclusion in Environmental Science and Management Faculty Publications and Presentations by an authorized administrator of PDXScholar. For more information, please contact [pdxscholar@pdx.edu](mailto:pdxscholar@pdx.edu).

# Seasonal patterns of photosynthesis in Douglas fir seedlings during the third and fourth year of exposure to elevated CO<sub>2</sub> and temperature

J. D. LEWIS,<sup>1</sup> M. LUCASH,<sup>2</sup> D. OLSZYK<sup>3</sup> & D. T. TINGEY<sup>3</sup>

<sup>1</sup>National Research Council, <sup>2</sup>Dynamac, Inc. and <sup>3</sup>US Environmental Protection Agency, Western Ecology Division, Corvallis, OR 97333, USA

## ABSTRACT

The interactive effects of elevated atmospheric CO<sub>2</sub> and temperature on seasonal patterns of photosynthesis in Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings were examined. Seedlings were grown in sunlit chambers controlled to track either ambient (~400 p.p.m.) CO<sub>2</sub> or ambient +200 p.p.m. CO<sub>2</sub>, and either ambient temperature or ambient +4 °C. Light-saturated net photosynthetic rates were measured approximately monthly over a 21 month period. Elevated CO<sub>2</sub> increased net photosynthetic rates by an average of 21% across temperature treatments during both the 1996 hydrologic year, the third year of exposure, and the 1997 hydrologic year. Elevated mean annual temperature increased net photosynthetic rates by an average of 33% across CO<sub>2</sub> treatments during both years. Seasonal temperature changes also affected net photosynthetic rates. Across treatments, net photosynthetic rates were highest in the spring and autumn, and lowest in July, August and December–January. Seasonal increases in temperature were not correlated with increases in the relative photosynthetic response to elevated CO<sub>2</sub>. Seasonal shifts in the photosynthetic temperature optimum reduced temperature effects on the relative response to elevated CO<sub>2</sub>. These results suggest that the effects of elevated CO<sub>2</sub> on net photosynthetic rates in Douglas fir are largely independent of temperature.

*Key-words:* *Pseudotsuga menziesii*; acclimation; global climate change; seasonal patterns.

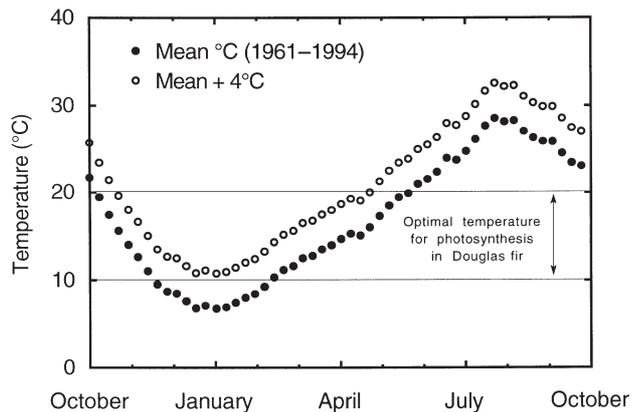
## INTRODUCTION

Increasing carbon uptake by trees in response to increasing atmospheric CO<sub>2</sub> may alter the global carbon cycle by increasing the potential for carbon sequestration in terrestrial ecosystems (Harmon, Ferrell & Franklin 1990; Vitousek 1991). The relative response of carbon uptake to

elevated CO<sub>2</sub> is predicted to vary with temperature as a result of interactive effects on the carboxylation efficiency of ribulose 1·5-bisphosphate carboxylase/oxygenase (Rubisco) (Long 1991). Increasing temperature has been shown to increase the relative photosynthetic response of trees to elevated CO<sub>2</sub> in some studies (Callaway *et al.* 1994; Kellomäki & Wang 1996; Koike *et al.* 1996; Lewis, Tissue & Strain 1996; Tissue, Thomas & Strain 1997; Myers, Thomas & DeLucia 1999), but not in others (Koike *et al.* 1996; Teskey 1997; Wayne, Reekie & Bazzaz 1998). Determining temperature effects on the relative photosynthetic response to elevated CO<sub>2</sub> is critical for predicting climate change effects on carbon uptake in temperate coniferous forests because carbon uptake occurs throughout the year in these forests, and temperatures vary substantially across seasons.

Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) is a dominant tree species in the Pacific Northwest (Franklin & Dyrness 1988; Hermann & Lavender 1990), and half of its annual carbon uptake may occur between October and April (Waring & Franklin 1979; Emmingham 1982). Despite the ecological and economic importance of Douglas fir, few studies have examined temperature effects on Douglas fir responses to elevated CO<sub>2</sub> either experimentally (Olszyk *et al.* 1998a) or through modelling (Franklin *et al.* 1991). Temperature effects may result from seasonal temperature changes and from temperature increases associated with climate change. Mean weekly temperatures in the Pacific Northwest often vary seasonally by 20 °C or more (Franklin & Dyrness 1988; Fig. 1), and low winter temperatures and high summer temperatures suppress photosynthesis in Douglas fir (Brix 1971; Hawkins *et al.* 1995). Mean annual temperatures in this region are predicted to increase by 2–3 °C in coastal areas and 3–4 °C in inland areas by 2080 compared to the 1961–90 means, based on the second Hadley Centre coupled ocean-atmosphere GCM (Johns *et al.* 1997) as provided on the IPCC Data Distribution Centre website (<http://ipcc-ddc.cru.uea.ac.uk>). Increasing temperatures during the winter should reduce temperature limitations on carbon uptake, and increasing temperatures during the summer should exacerbate temperature limitations on carbon uptake.

*Correspondence:* James D. Lewis, The Louis Calder Center and Biological Station, Department of Biological Sciences, Fordham University, 53 Whipoorwill Road, PO Box K, Armonk, NY 10504, USA. Fax: +1 914 273 6346; E-mail: [jdlewis@fordham.edu](mailto:jdlewis@fordham.edu)



**Figure 1.** Weekly mean maximum temperature for the years 1961–94 in Corvallis, Oregon, and weekly mean maximum temperatures after a 4 °C increase in temperature. Horizontal lines at 10 and 20 °C bracket the approximate range of temperatures optimal for photosynthesis in Douglas fir (Helms 1964, 1965; Brix 1967).

Effects of elevated temperature on net photosynthetic rates may be moderated by increasing atmospheric CO<sub>2</sub> (Long 1991). Net photosynthetic rates decline rapidly as temperatures increase above the optimal temperature (Larcher 1995; Kozłowski & Pallardy 1996). Elevated CO<sub>2</sub> increases temperature optima for photosynthesis in some C<sub>3</sub> species (Idso & Idso 1994; Eamus, Duff & Berryman 1995). An increase of 200 p.p.m. above current atmospheric CO<sub>2</sub> concentrations may shift temperature optima upward 3–4 °C (Long 1991), paralleling the increase in mean annual temperatures predicted to occur during the next century. By shifting temperature optima upward, elevated CO<sub>2</sub> may ‘acclimate’ photosynthetic processes to future temperature regimes. However, increases in temperature optima may negatively affect net photosynthetic rates when temperatures are suboptimal, as often occurs during the winter months in the Pacific Northwest. Although shifts in temperature optima for photosynthesis alter seasonal patterns of carbon uptake (Berry & Björkman 1980), few studies have examined the effects of elevated CO<sub>2</sub> on seasonal shifts in temperature optima of photosynthesis.

Changes in seasonal patterns of carbon uptake in response to elevated CO<sub>2</sub> and temperature may also reflect changes in phenology (Morison & Lawlor 1999). Although elevated CO<sub>2</sub> does not affect the phenology of Douglas fir seedlings (Olszyk *et al.* 1998a,b), temperature has been widely shown to affect the timing of processes such as bud break, shoot elongation, root elongation, and hardening-off (e.g. Campbell & Sugano 1975; Guak *et al.* 1998; Olszyk *et al.* 1998a,b). These processes may significantly increase carbon utilization (sink activity), changing the relative balance between carbon uptake (source activity) and carbon utilization. Because source–sink balance may regulate photosynthetic response to increasing CO<sub>2</sub> (Arp 1991; Stitt 1991; Thomas & Strain 1991), changes in the seasonal pattern of source–sink balance may alter seasonal patterns

in photosynthetic response to elevated CO<sub>2</sub> (Tissue, Thomas & Strain 1996).

In this study, we examined the effects of seasonal variation in temperature and increased mean annual temperature on the relative photosynthetic response of Douglas fir to elevated CO<sub>2</sub> over a 21-month period, beginning 27 months after treatments were initiated. Specifically, the following questions were addressed: (1) do seasonal changes in temperature affect the relative photosynthetic response to elevated CO<sub>2</sub>? (2) Does increasing the mean annual temperature increase the relative photosynthetic response to elevated CO<sub>2</sub> at a particular measurement period? (3) Does elevated CO<sub>2</sub> increase the temperature optima for photosynthesis?

## MATERIALS AND METHODS

### Growth conditions

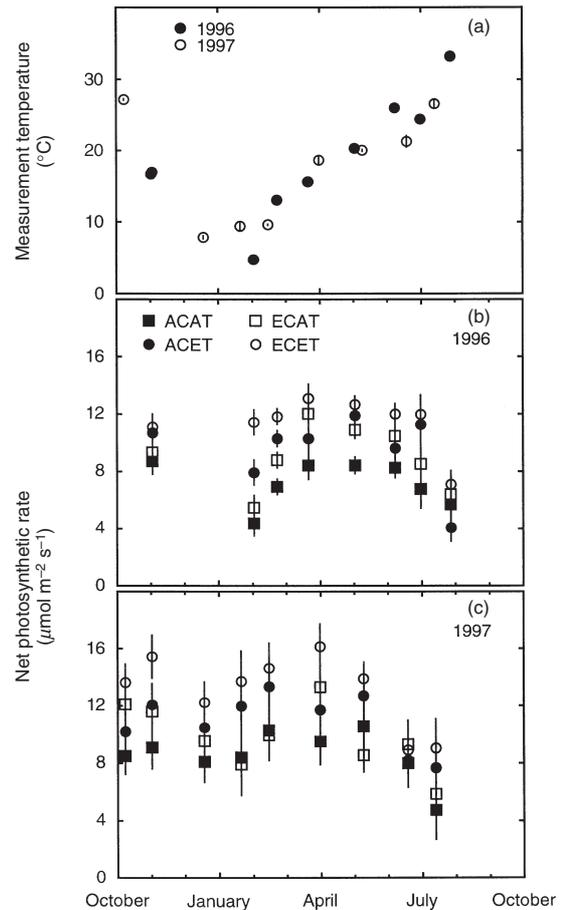
Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) seed lots were collected at five low-elevation seed zones (<500 m) in the Coast Range, Willamette Valley and the west slopes of the Cascade Mountains around Corvallis, Oregon, USA. Seedlings were grown for 1 year in seed beds and 1 year in nursery beds. In June 1993, 14 seedlings were transplanted as bare-root, 2-year-old stock into each 1 m × 2 m surface area chamber at the US Environmental Protection Agency Environmental Research Laboratory in Corvallis, Oregon. Each chamber consisted of a sun-lit upper compartment (1.2–1.5 m high) where air temperature, CO<sub>2</sub> concentration and vapour pressure deficit were monitored and controlled, and a lower soil lysimeter (1.0 m deep) filled with a native coarse-textured sandy loam in which soil parameters such as temperature and soil moisture were monitored (Tingey *et al.* 1996). Initial soil nitrogen concentrations in the A, B and C horizons were 0.12, 0.07 and 0.06%, respectively. Initial phosphorus concentrations in the A, B and C horizons were 7, 3 and 3 p.p.m., respectively. Ambient CO<sub>2</sub> and air temperature were monitored at an adjacent meteorological station, and the chambers were controlled to continuously track either ambient CO<sub>2</sub> or ambient +200 p.p.m. CO<sub>2</sub> and ambient air temperature or ambient +4 °C (Tingey *et al.* 1996). The experimental design was a full factorial with two levels each of CO<sub>2</sub> and temperature resulting in four treatments: ambient CO<sub>2</sub> and ambient temperature (ACAT); ambient CO<sub>2</sub> and elevated temperature (ACET); elevated CO<sub>2</sub> and ambient temperature (ECAT); and elevated CO<sub>2</sub> and elevated temperature (ECET). There were three chambers per treatment combination, and treatments were applied 24 h per day beginning in August 1993 and continuing until the end of the study (July 1997). Mid-day (1000–1400 Pacific standard time) CO<sub>2</sub> concentrations during the growing season in 1996 typically ranged between 360 and 400 p.p.m. in the ambient CO<sub>2</sub> treatment. Seedlings were grown under ambient light, and without supplemental nutrients. Soil moisture content was controlled to reflect seasonal changes in soil moisture typical for the wet winter–dry summer

climate in the Pacific Northwest (Griffiths & Caldwell 1990; Griffiths *et al.* 1991). Weekly water additions to the ambient CO<sub>2</sub>; ambient temperature treatment were calculated on the basis of this pattern of soil moisture content. Water additions to the other treatments were the same as in the ambient CO<sub>2</sub>-ambient temperature treatment. Target dew point depression in the chambers was based on ambient conditions and controlled to have equivalent vapour pressure deficits (VPD) across treatments. Actual chamber conditions during the entire course of the experiment differed slightly from targets: elevated CO<sub>2</sub> averaged 179 p.p.m. above ambient, elevated temperature averaged 3.5 °C above ambient, and the VPD in the elevated temperature treatments averaged 0.10 kPa above the VPD in the ambient temperature treatments.

### Photosynthetic measurements

Net photosynthetic rates were measured using infrared gas analysers built into a leaf cuvette in an open-flow gas exchange system (LI-6400; Li-Cor Inc., Lincoln, NE, USA). All measurements were made on intact fully expanded, unshaded needles from the most recent needle cohort (e.g. measurements made between November 1995 and July 1996 were performed on needles from the 1995 cohort). Needles were arranged in the cuvette such that self-shading was minimized and all needles were parallel to the plane of the leaf chamber. All measurements were made using ambient light. Photosynthetic photon flux densities (PPFD) at the upper leaf surface were typically 1400–2000  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ; no measurements were made below 800  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ . These PPFD are saturating for photosynthesis in Douglas fir needles (Bond *et al.* 1999; Lewis, Olszyk & Tingey 1999; Lewis *et al.* 2000). The airstream entering the cuvette was maintained at the growth CO<sub>2</sub> concentration (either 360 or 560 p.p.m. CO<sub>2</sub>) using a computer-controlled CO<sub>2</sub> mixing system supplied with the LI-6400. Needle, cuvette and air temperatures were measured with thermocouples linked to the LI-6400 computer. Needle temperature was maintained at the desired temperature using a computer-controlled Peltier module mounted on the cuvette. Mean needle temperature at each measurement period in the ambient temperature treatment is shown in Fig. 2. Measurements in the ambient +4 °C treatment were made at temperatures 4 °C higher than the needle temperatures used for the ambient temperature treatment. These temperatures reflect average chamber temperatures between 1000 and 1400 h during a given measurement period. All gas exchange parameters were calculated according to Field, Ball & Berry (1989). Projected surface area of the measured needles was estimated using measurements of needle length and width.

Photosynthetic measurements began 27 months after treatments were initiated, and were measured approximately monthly between November 1995 and July 1997, when the experiment was terminated. Prior to each measurement, needles were equilibrated in the cuvette at



**Figure 2.** Monthly patterns of temperature and net photosynthetic rates for the 1996 and 1997 hydrologic years. Least-square mean ( $\pm$  SE) measurement temperature in the ambient temperature treatment is shown for each measurement period (a). Mean measurement temperatures in the elevated temperature treatment were 4 °C higher than in the ambient temperature treatment. Least-square mean ( $\pm$  SE) net photosynthetic rates are shown separately for 1996 (b) and 1997 (c). Some symbols may not be visible if multiple treatments have similar mean net photosynthetic rates at a particular measurement period. Treatment abbreviations: ACAT, ambient CO<sub>2</sub> and ambient temperature; ACET, ambient CO<sub>2</sub> and elevated temperature; ECAT, elevated CO<sub>2</sub> and ambient temperature; ECET, elevated CO<sub>2</sub> and elevated temperature.  $n = 3$  for all treatments in 1996; in 1997,  $n = 2$  for the ACAT and ECAT treatments,  $n = 3$  for all other treatments.

saturating PPFD, the growth CO<sub>2</sub> concentration, and the measurement temperature. Needles were considered equilibrated if gas exchange parameters were stable for 1 min. Measurements were initiated at approximately 0900 h Pacific standard time, and typically were completed by 1200 h Pacific standard time.

At each measurement period, the relative response of net photosynthetic rates to elevated CO<sub>2</sub> was calculated for each temperature treatment. The relative response was calculated as the ratio of the mean net photosynthetic rate in the elevated CO<sub>2</sub> treatment to the mean net photosynthetic

rate in the ambient CO<sub>2</sub> treatment measured at the growth CO<sub>2</sub>:

$$\text{Relative response} = A_{EC}/A_{AC}, \quad (1)$$

where  $A_{EC}$  is the net photosynthetic rate in the elevated CO<sub>2</sub> treatment and  $A_{AC}$  is the net photosynthetic rate in the ambient CO<sub>2</sub> treatment at the same measurement period. Using this approach, if the relative response = 2 then the net photosynthetic rate in the elevated CO<sub>2</sub> treatment is twice the rate measured in the ambient CO<sub>2</sub> treatment. If the net photosynthetic rate is the same in both CO<sub>2</sub> treatments, the relative response = 1.

The effect of seasonal changes in temperature on net photosynthetic rates in each treatment was examined by comparing the mean net photosynthetic rate versus needle temperature for all measurement periods. An empirically based temperature response curve was calculated for each treatment using the following parabolic model:

$$A = (a \times T^2) + (b \times T) + c, \quad (2)$$

where  $A$  is the net photosynthetic rate and  $T$  is the needle temperature in degrees C. To calculate the temperature optima for the photosynthetic response to seasonal changes in temperature, the equation for each curve was solved for the needle temperature for which the slope was zero.

Seasonal responses (weeks to months) of photosynthesis to temperature reflect acclimation of physiological processes to changing environmental conditions over time, including shifts in the short-term (minutes to hours) temperature optima for photosynthesis (Berry & Björkman 1980). To examine seasonal shifts in short-term temperature optima of photosynthesis, short-term temperature response curves were measured during winter, spring and summer of the 1996 hydrologic year. In February 1996, net photosynthetic rates were measured at five needle temperatures between 12 and 23 °C in all temperature treatments. Similar measurements were made between 17 and 28 °C in May 1996, and between 22 and 35 °C in August 1996. For each curve, leaf temperature was manipulated using the Peltier module mounted on the cuvette. For all measurements at a given measurement period, the water vapour content of the cuvette air was controlled to maintain a constant dew point depression. Prior to each measurement, needles were equilibrated in the cuvette at saturating PPFD, the growth CO<sub>2</sub> concentration, the target water vapour content in the cuvette air, and the measurement temperature. Needles were considered equilibrated if gas exchange parameters were stable for 1 min. Individual measurements typically took 5 min to equilibrate, and temperature response curves generally were completed within 30 min. Measurements were initiated at approximately 0900 h Pacific standard time, and typically were completed by 1200 h Pacific standard time.

### Statistical analyses

Treatment effects on seasonal patterns in photosynthesis were analysed using repeated measures analysis of variance

with growth CO<sub>2</sub> and temperature as the between-subjects factors and measurement period as the within-subjects factor. The effects of short-term temperature changes on net photosynthetic rates were analysed using repeated measures analysis of variance with growth CO<sub>2</sub> and temperature as the between-subjects factors, and needle temperature as the within-subjects factor. Analyses were performed using the multivariate general linear model function (MGLH) in SYSTAT (Systat 1992). In general, photosynthesis was measured on one tree in each chamber per measurement period. Across the study period, individual branches were not repeatedly measured and measurements were made on several trees in each chamber. Because the chamber was the experimental unit, measurements made on multiple trees in a chamber at a given measurement period were combined and the mean value used in the analyses. Data from the 1996 and 1997 hydrologic years were analysed separately. The hydrologic year begins on 1 October in western Oregon, and represents the transition from the dry season to the wet season. One chamber each in the ambient CO<sub>2</sub>: ambient temperature treatment and the elevated CO<sub>2</sub>: ambient temperature treatment were excluded from the 1997 analyses because of extensive insect damage to trees in these chambers.

### RESULTS

The annual patterns in measurement temperatures and net photosynthetic rates during the 1996 and 1997 hydrologic years are shown in Fig. 2. Needle temperatures were lowest in late December and early January, and peaked in late July and early August. Net photosynthetic rates generally were lowest in December–January and July–August, and peaked in March–May and October–November. Elevated CO<sub>2</sub> significantly increased net photosynthetic rates across temperature treatments during both the 1996 (Fig. 2b) and 1997 hydrologic years (Fig. 2c). There was a significant interaction between temperature treatment and measurement period on net photosynthetic rates during the 1996 hydrologic year (Table 1). Elevated temperature increased net photosynthetic rates at all measurement periods except July (Fig. 2b). Throughout the 1997 hydrologic year, elevated temperature increased net photosynthetic rates (Fig. 2c). Although the effects of CO<sub>2</sub> supply and growth temperature on net photosynthetic rates appeared to vary across measurement periods during the 1997 hydrologic year, these interactions were not significant (Table 1).

The relationship between measurement temperature and the relative response of net photosynthetic rates to elevated CO<sub>2</sub> at each measurement period is shown in Fig. 3. The mean relative response was 1.21, and the relative response was >1 (i.e. elevated CO<sub>2</sub> increased net photosynthetic rates) for approximately 90% of the measurement periods. When the correlation between needle temperature and the relative photosynthetic response to elevated CO<sub>2</sub> was analysed separately for each temperature treatment and for each hydrologic year, there were no significant correlations

**Table 1.** Summary of *F*-values and their levels of statistical significance (*P*) from univariate comparisons (repeated measures analysis of variance) on mean light-saturated net photosynthetic rates during the 1996 and 1997 hydrologic years with CO<sub>2</sub> supply and temperature as the between-subjects factors and measurement period as the within-subject factor. Results from multivariate and single degree of freedom polynomial contrasts were similar

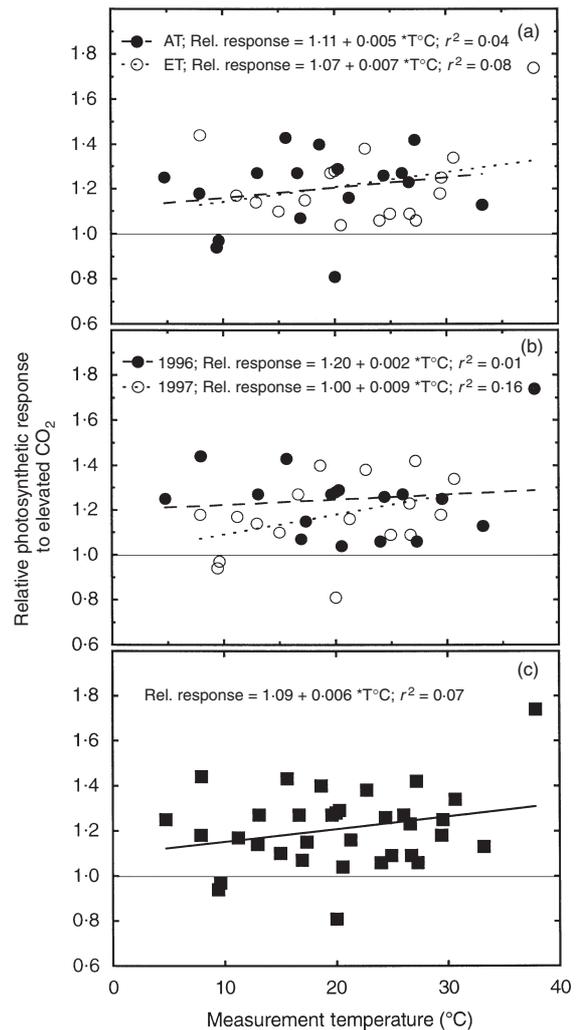
Factor	1996 hydrologic year		1997 hydrologic year	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<b>Between subjects</b>				
CO <sub>2</sub> supply ( <i>C</i> )	14.19	<0.01	5.47	0.06
Temperature ( <i>T</i> )	25.20	<0.01	15.33	<0.01
Temperature × CO <sub>2</sub>	<0.01	0.97	0.42	0.54
<b>Within subjects</b>				
Period ( <i>P<sub>d</sub></i> )	18.62	<0.01	7.13	<0.01
<i>P<sub>d</sub></i> × <i>C</i>	0.94	0.48	1.18	0.34
<i>P<sub>d</sub></i> × <i>T</i>	4.18	<0.01	1.03	0.42
<i>P<sub>d</sub></i> × <i>C</i> × <i>T</i>	0.78	0.61	0.19	0.98

in either temperature treatment ( $P = 0.42, 0.26$  for ambient and elevated temperature, respectively; Fig. 3a) or hydrologic year ( $P = 0.67, 0.10$  for 1996 and 1997, respectively; Fig. 3b). Similarly, when data were grouped across hydrologic years and temperature treatment, there was no significant correlation between needle temperature and the relative photosynthetic response to elevated CO<sub>2</sub> ( $P = 0.14$ ; Fig. 3c).

The effect of seasonal variation in temperature on net photosynthetic rate is shown in Fig. 4. Net photosynthetic rate increased as temperature increased from 5 °C, peaked between 15 and 20 °C, and generally decreased with increasing temperature above 25 °C across treatments. Between 10 and 25 °C net photosynthetic rates were at least 80% of the projected maximum rates (the maximum photosynthetic rate calculated from the model used to fit the temperature-response curve) for a given treatment. Net photosynthetic rates in the elevated temperature treatment generally were higher than in the ambient temperature treatment. In addition to assessing photosynthetic responses to temperature across the study period by combining the entire data set within each treatment, the optimal temperature for photosynthesis was calculated for each chamber in order to examine treatment effects on the temperature optimum. There were no significant effects of CO<sub>2</sub> treatment ( $P = 0.899$ ) or temperature treatment ( $P = 0.663$ ) on the temperature optimum, nor was there a significant interaction between CO<sub>2</sub> treatment and temperature treatment ( $P = 0.291$ ). In the ambient temperature treatment, the mean ( $\pm$  SE) temperature optima were  $18.6 \pm 1.0$  (ambient CO<sub>2</sub> treatment) and  $19.7 \pm 1.3$  (elevated CO<sub>2</sub> treatment). In the elevated temperature treatment, the mean ( $\pm$  SE) temperature optima were  $19.3 \pm 0.7$  (ambient CO<sub>2</sub> treatment) and  $17.9 \pm 1.4$  (elevated CO<sub>2</sub> treatment). These temperature optima vary from the tem-

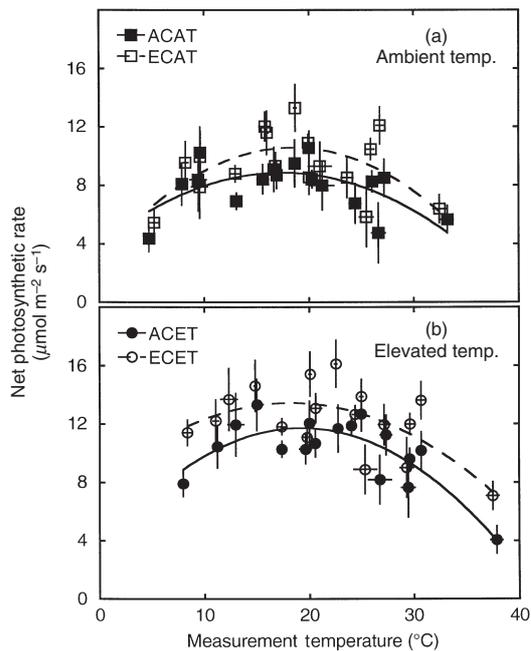
perature optima calculated by combining all three chambers within a treatment because one chamber in each of two treatments was measured for only half of the study period but was given equal weighting in the chamber-based comparison.

In addition to examining the response of net photosynthetic rates to seasonal changes in temperature, we examined the effect of short-term (minutes to hours) changes in temperature on net photosynthetic rates. For a given mea-

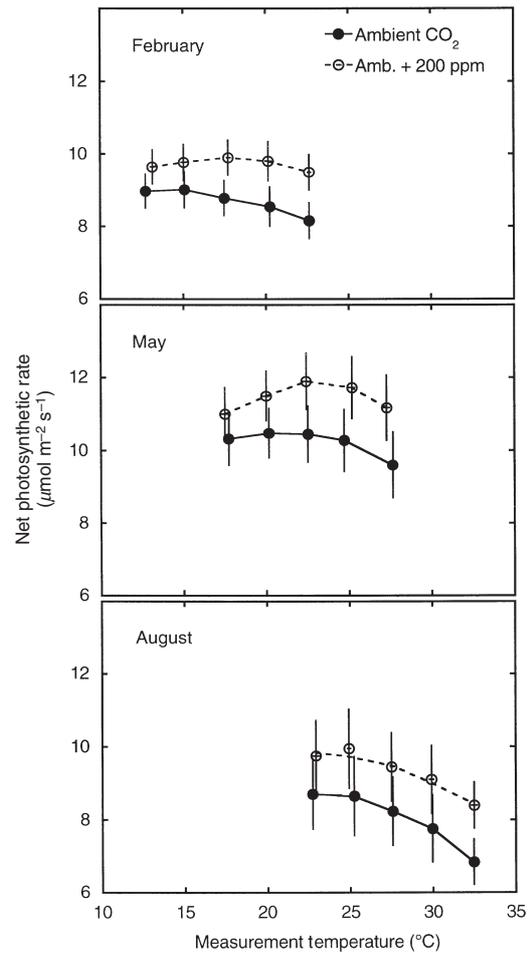


**Figure 3.** Relative response of net photosynthetic rates to elevated CO<sub>2</sub> as affected by measurement temperatures (a), hydrologic year (b), and across measurement temperatures and hydrologic years (c). This relationship was derived by comparing the relative photosynthetic response to elevated CO<sub>2</sub> in each temperature treatment at each measurement period with the mean leaf temperature (approximately ambient air temperature) in each temperature treatment at that measurement period. Regression equations and *r*<sup>2</sup> values for each relationship are shown. The horizontal line at a relative response = 1 indicates the relative response when the net photosynthetic rate was the same in both CO<sub>2</sub> treatments. Each graph shows the same data broken down by the different target factors.

surement period, repeated measures analysis of variance indicated that net photosynthetic rates significantly varied across measurement temperatures ( $P < 0.05$  in all cases). Growth in elevated  $\text{CO}_2$  significantly increased the short-term temperature optima for photosynthesis in February and May ( $P \leq 0.05$  in both cases) but not August ( $P = 0.63$ ). The short-term temperature optima in the ambient  $\text{CO}_2$  treatment were approximately  $13^\circ\text{C}$  in February and approximately  $20^\circ\text{C}$  in May 1996 (Fig. 5); temperature optima in the elevated  $\text{CO}_2$  treatment were approximately  $17^\circ\text{C}$  in February and approximately  $23^\circ\text{C}$  in May. In August 1996, the apparent optimum was approximately  $23^\circ\text{C}$  in the ambient  $\text{CO}_2$  treatment and approximately  $25^\circ\text{C}$  in the elevated  $\text{CO}_2$  treatment. However, because the apparent peak for the ambient  $\text{CO}_2$  treatment occurred at the lowest measurement temperature, the actual temperature optimum may have been lower at this date. The apparent increase in the temperature optimum between February and August was similar to the increase in the weekly mean maximum temperature over this interval (Fig. 1). Temperature treatment did not significantly affect the short-term temperature optima for photosynthesis (data not shown).



**Figure 4.** Relationship between least square mean ( $\pm$  SE) net photosynthetic rates and least square mean ( $\pm$  SE) measurement temperature at each measurement period for trees in the ambient (a) and elevated temperature treatments (b). Within temperature treatments, data are grouped according to  $\text{CO}_2$  treatment. Treatment abbreviations are as in Fig. 2. The equation for each treatment is as follows: ACAT:  $A = -0.016 \times T^2 + 0.572 \times T + 3.89$ ,  $r^2 = 0.40$ ; ACET:  $A = -0.022 \times T^2 + 0.857 \times T + 3.49$ ,  $r^2 = 0.69$ ; ECAT:  $A = -0.022 \times T^2 + 0.823 \times T + 2.97$ ,  $r^2 = 0.36$ ; and ECET:  $A = -0.016 \times T^2 + 0.601 \times T + 7.98$ ,  $r^2 = 0.40$ .  $n = 2-3$  for the ACAT and ECAT treatments,  $n = 3$  for all other treatments.



**Figure 5.** Short-term temperature response curves for photosynthesis measured in February, May and August 1996. Data are summed across temperature treatments.  $n = 4-6$  in February and May,  $n = 2-3$  in August.

## DISCUSSION

Growth in ambient +200 p.p.m.  $\text{CO}_2$  increased net photosynthetic rates of Douglas fir by an average of 21% across the third and fourth years of exposure compared to trees grown in ambient  $\text{CO}_2$ . Over the same time interval, growth in ambient +4  $^\circ\text{C}$  increased net photosynthetic rates an average of 33% in comparison with trees grown in ambient temperature. Although increasing temperature was expected to increase the relative photosynthetic response to elevated  $\text{CO}_2$ , temperature treatment and seasonal changes in temperature did not significantly affect the relative response to elevated  $\text{CO}_2$ . The effects of seasonal changes in temperature on the relative photosynthetic response to elevated  $\text{CO}_2$  have been shown to be limited by photosynthetic acclimation during long-term exposure to elevated  $\text{CO}_2$  (Samuelson & Seiler 1992; Samuelson & Seiler 1994; Curtis *et al.* 1995; Epron, Liozon & Mousseau 1996; Le Thiec & Dixon 1996; Lewis *et al.* 1996). However, because elevated  $\text{CO}_2$  significantly increased net photosynthetic rates across the study period, it is likely that other

factors also mitigated temperature effects on the relative photosynthetic response to elevated CO<sub>2</sub>. The present results suggest that shifts in the short-term temperature optimum for photosynthesis may have reduced the effect of seasonal changes in temperature on the relative response to elevated CO<sub>2</sub>.

Between February and August 1996, the short-term temperature optima for photosynthesis shifted by approximately 10 °C higher in both CO<sub>2</sub> treatments (Fig. 5). As a result of this shift, net photosynthetic rates were generally unaffected by seasonal shifts in temperature between 10 and 25 °C in both CO<sub>2</sub> treatments, and the relative response to elevated CO<sub>2</sub> showed little variation across this temperature range. These results parallel previous studies, which showed that the temperature optimum across seasons for photosynthesis in Douglas fir is approximately 10–20 °C (Helms 1964; Helms 1965; Brix 1967). As ambient temperatures fell within this range for most of the year, seasonal variation in net photosynthetic rates was only observed during early winter and midsummer, and the relative photosynthetic response to elevated CO<sub>2</sub> was generally uniform for most of the year. Broad peaks in the temperature response of photosynthesis across an annual cycle have been observed in several tree species, probably due to seasonal shifts in short-term temperature optima for photosynthesis (Berry & Björkman 1980). Seasonal shifts in short-term temperature optima of as much as 15 °C have been observed in other temperate evergreen (Neilson, Ludlow & Jarvis 1972; Strain, Higginbotham & Mulroy 1976; Drew & Ledig 1981) and deciduous tree species (Aubuchon, Thompson & Hinckley 1978; Dougherty *et al.* 1979). These results suggest that seasonal shifts in short-term temperature optima for photosynthesis may regulate temperature effects on photosynthetic responses to elevated CO<sub>2</sub> in some tree species.

Despite seasonal shifts in the short-term temperature optima for photosynthesis, winter temperatures in this study fell outside the temperature range considered optimal for Douglas fir (Brix 1971; Hawkins *et al.* 1995). As a result, reductions in net photosynthetic rates during the winter in this study probably reflect temperature effects on photosynthesis, particularly in the ambient temperature treatment. In the elevated temperature treatment, reductions in net photosynthetic rates during the winter months were minimized because the 4 °C increase in temperature brought air temperatures closer to the temperature that is optimum for photosynthesis (Fig. 1). During the summer months, measurement temperatures in both temperature treatments exceeded the optimal range for photosynthesis, and may partially account for reductions in net photosynthetic rates. In addition, summer-time carbon uptake may have been suppressed by limited water availability during the warm, dry summers that are characteristic of this region (Waring & Franklin 1979; Emmingham 1982) and that occurred during this study (M. Johnson *et al.* unpublished results).

The effects of seasonal changes in temperature on net photosynthetic rates were expected to be altered

by elevated CO<sub>2</sub> because increasing atmospheric CO<sub>2</sub> is predicted to increase the temperature optimum for photosynthesis by altering the relative balance between photosynthesis and photorespiration (Long 1991). Increasing temperature reduces the CO<sub>2</sub> specificity of Rubisco, increasing the proportion of potential photosynthesis lost to photorespiration (Brooks & Farquhar 1985). In contrast, increasing CO<sub>2</sub> inhibits oxygenase activity (Lorimer 1981), reducing the inhibitory effects of increasing temperature on photosynthesis. Consistent with this prediction, short-term temperature-response curves indicate that elevated CO<sub>2</sub> treatment increased the short-term (minutes to hours) temperature optima for photosynthesis (Fig. 5), as has been observed in other tree species (Idso & Idso 1994; Eamus *et al.* 1995). However, CO<sub>2</sub> treatment did not have a significant effect on the temperature optimum for photosynthesis across seasons. The differential responses of photosynthesis to short-term versus seasonal changes in temperature may reflect the fact that seasonal changes in net photosynthetic rate also occur in response to a variety of abiotic and biotic factors other than temperature. For example, total incident solar radiation (Tolley & Strain 1984a; Lewis *et al.* 1999), nutrient availability (Curtis *et al.* 1995), water availability (Tolley & Strain 1984b; Le Thiec & Dixon 1996), mycorrhizal activity (Lewis & Strain 1996), sink activity (Epron *et al.* 1996; Tissue *et al.* 1997) and leaf age (Aoki & Yabuki 1977; Hickleton & Jolliffe 1980) may influence seasonal patterns in photosynthetic responses to elevated CO<sub>2</sub>. The effects of these and other factors may reduce the direct effects of seasonal changes in temperature on photosynthesis relative to short-term changes in temperature. As a result, although increasing CO<sub>2</sub> may increase the short-term temperature optima for photosynthesis, the overall effect on seasonal responses of photosynthesis to temperature appears to be minimal.

Increased net photosynthetic rates during the third and fourth years of growth in elevated CO<sub>2</sub> are consistent with the photosynthetic response to elevated CO<sub>2</sub> of Douglas fir seedlings during the first year of growth (Hollinger 1987). Additionally, the sustained response of net photosynthetic rates to elevated CO<sub>2</sub> after four years of exposure parallels results from several studies on the effects of long-term (one or more years) exposure of field-grown trees to elevated CO<sub>2</sub> (e.g. Idso, Kimball & Allen 1991; Gunderson, Norby & Wullschleger 1993; Eamus *et al.* 1995; Jones *et al.* 1995; Tissue, Griffin & Ball 1999). The relative increase in net photosynthetic rates due to growth in elevated CO<sub>2</sub> was smaller (21%) than the mean response for tree species (44–66%) reported in recent reviews (Cuelemans & Mousseau 1994; Gunderson & Wullschleger 1994; Curtis 1996; Curtis & Wang 1998; Norby *et al.* 1999). The relatively low photosynthetic response to elevated CO<sub>2</sub> may have resulted from a variety of factors. The reduced response may reflect the relatively low elevated CO<sub>2</sub> treatment in this study (approximately 600 p.p.m.) in comparison with most studies (approximately 700 p.p.m.; Curtis & Wang 1998). However, in a free-air CO<sub>2</sub> enrichment study where the elevated CO<sub>2</sub> treatment was approximately 575 p.p.m.,

long-term exposure to elevated CO<sub>2</sub> increased net photosynthetic rates in *Pinus taeda* by approximately 55% in mid-summer (Ellsworth 1999; Myers *et al.* 1999), and increased net photosynthetic rates of sun leaves by approximately 98% in *Liquidambar styraciflua* (Herrick & Thomas 1999). The relative response observed in this study also reflects 17 measurement periods across 2 years, whereas most studies measure net photosynthetic rates under optimal growth conditions at one or two periods. Additionally, Douglas fir may be relatively unresponsive to elevated CO<sub>2</sub>. Biomass accumulation in Douglas fir is not significantly increased by growth in elevated CO<sub>2</sub> (Hollinger 1987; Mortensen 1994; Gorissen, Kuikman & Van de Beek 1995).

In summary, elevated CO<sub>2</sub> and elevated growth temperature significantly increased net photosynthetic rates during the third and fourth year of exposure. Seasonal changes in temperature did not affect the relative response to elevated CO<sub>2</sub> due to shifts in the short-term temperature optima for photosynthesis. In addition, the relative photosynthetic response to elevated CO<sub>2</sub> in these trees was not affected by temperature treatment, or by light availability (Lewis *et al.* 1999). These results suggest elevated CO<sub>2</sub> may increase carbon accumulation in Douglas fir. However, other studies have shown that long-term exposure to elevated CO<sub>2</sub> does not increase biomass accumulation in Douglas fir. Several factors may limit the biomass response of trees to elevated CO<sub>2</sub> (Norby *et al.* 1999). For example, older needles may be less responsive to elevated CO<sub>2</sub> than the current-year needles measured in this study (Turnbull *et al.* 1998). Reductions in the leaf area ratio (leaf area per unit plant biomass) may also reduce biomass responses to elevated CO<sub>2</sub> (Callaway *et al.* 1994; Lewis & Strain 1996). Similarly, although increasing temperatures associated with climate change may increase net photosynthetic rates and the potential for carbon uptake, increasing temperatures also increase foliar respiration rates in Douglas fir (e.g. Lewis *et al.* 1999), increasing the potential for carbon loss. As a result, increasing CO<sub>2</sub> and increasing temperature associated with climate change are likely to increase needle-level net photosynthetic rates in Douglas fir seedlings, but the effect on biomass accumulation may be smaller than the effect on net photosynthetic rates.

## ACKNOWLEDGMENTS

We thank Joe Greene, Glenn Jarrell, Mark Johnson, Craig McFarlane, Paul Rygielwicz, Ron Waschmann, Jim Weber and Claudia Wise for their technical support in the design and execution of this study. Jacqui Johnson and Dave Myers improved earlier drafts of this manuscript. Seedlings were provided by the Weyerhaeuser Company.

The research described in this article has been funded by the U.S. Environmental Protection Agency. This document has been prepared at the EPA's Western Ecology Division in Corvallis, Oregon, through co-operative agreement CR-824072 with the National Research Council and through

contract 68-C6-0005 with Dynamac, Inc. It has been subject to the agency's peer and administrative review and approved for publication. Mention of trade names or commercial products does not constitute endorsement or recommendation for use.

## REFERENCES

- Aoki M. & Yabuki K. (1977) Studies on the carbon dioxide enrichment of plant growth. VII. Changes in dry matter production and photosynthetic rate of cucumber during carbon dioxide enrichment. *Agricultural Meteorology* **18**, 475–485.
- Arp W.J. (1991) Effects of source-sink relations on photosynthetic acclimation to elevated CO<sub>2</sub>. *Plant, Cell and Environment* **14**, 869–875.
- Aubuchon R.R., Thompson D.R. & Hinckley T.M. (1978) Environmental influences on photosynthesis within the crown of a white oak. *Oecologia* **35**, 295–306.
- Berry J.A. & Björkman O. (1980) Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology* **31**, 491–543.
- Bond B.J., Farnsworth B.T., Coulombe R.A. & Winner W.E. (1999) Foliage physiology and biochemistry in response to light gradients in conifers with varying shade tolerance. *Oecologia* **120**, 183–192.
- Brix H. (1967) An analysis of dry matter production of Douglas fir seedlings in relation to temperature and light intensity. *Canadian Journal of Botany* **45**, 2063–2072.
- Brix H. (1971) Effects of nitrogen fertilization on photosynthesis and respiration in Douglas fir. *Forest Science* **17**, 407–414.
- Brooks A. & Farquhar G.D. (1985) Effect of temperature on the CO<sub>2</sub>/O<sub>2</sub> specificity of ribulose-1, 5-bisphosphate carboxylase/oxygenase and the rate of respiration in the light. *Planta* **165**, 397–406.
- Callaway R.M., DeLucia E.H., Thomas E.M. & Schlesinger W.H. (1994) Compensatory responses of CO<sub>2</sub> exchange and biomass allocation and their effects on the relative growth rate of ponderosa pine in different CO<sub>2</sub> and temperature regimes. *Oecologia* **98**, 159–166.
- Campbell R.K. & Sugano A.I. (1975) Phenology of bud burst in Douglas fir related to provenance, photoperiod, chilling, and flushing temperature. *Botanical Gazette* **136**, 290–298.
- Cuelemans R. & Mousseau M. (1994) Effects of elevated atmospheric CO<sub>2</sub> on woody plants. *New Phytologist* **127**, 425–446.
- Curtis P.S. (1996) A meta-analysis of leaf gas exchange and nitrogen in trees grown under elevated carbon dioxide. *Plant, Cell and Environment* **19**, 127–137.
- Curtis P.S. & Wang X. (1998) A meta-analysis of elevated CO<sub>2</sub> effects on woody plant mass, form, and physiology. *Oecologia* **113**, 299–313.
- Curtis P.S., Vogel C.S., Pregitzer K.S., Zak D.R. & Teeri J.A. (1995) Interacting effects of soil fertility and atmospheric CO<sub>2</sub> on leaf area growth and carbon gain physiology in *Populus × euramericana* (Dode) Guinier. *New Phytologist* **129**, 253–263.
- Dougherty P.M., Teskey R.O., Phelps J.E. & Hinckley T.M. (1979) Net photosynthesis and early growth trends of a dominant white oak (*Quercus alba* L.). *Plant Physiology* **64**, 930–935.
- Drew A.P. & Ledig F.T. (1981) Seasonal patterns of CO<sub>2</sub> exchange in the shoot and root of loblolly pine seedlings. *Botanical Gazette* **142**, 200–205.
- Eamus D., Duff G.A. & Berryman C.A. (1995) Photosynthetic responses to temperature, light flux-density, CO<sub>2</sub> concentration and vapour pressure deficit in *Eucalyptus tetrodonta* grown under CO<sub>2</sub> enrichment. *Environmental Pollution* **90**, 41–49.

- Ellsworth D.S. (1999) CO<sub>2</sub> enrichment in a maturing pine forest: are CO<sub>2</sub> exchange and water status in the canopy affected? *Plant, Cell and Environment* **22**, 461–472.
- Emmingham W.H. (1982) Ecological indexes as a means of evaluating climate, species distribution and primary production. In *Analysis of Coniferous Forest Ecosystems in the Western United States* (ed. R.L. Edmonds), US/IBP Ser. No. 14, pp. 45–67. Dowden, Hutchinson & Ross, Inc., Stroudsburg, PA.
- Epron D., Liozon R. & Mousseau M. (1996) Effects of elevated CO<sub>2</sub> concentration on leaf characteristics and photosynthetic capacity of beech (*Fagus sylvatica*) during the growing season. *Tree Physiology* **16**, 425–432.
- Field C.B., Ball J.T. & Berry J.A. (1989) Photosynthesis: principles and field techniques. In *Plant Physiological Ecology: Field Methods and Instrumentation* (eds R.W. Pearcy, J. Ehleringer, H.A. Mooney & P.W. Rundel), pp. 209–253. Chapman & Hall, New York.
- Franklin J.F. & Dyrness C.T. (1988) *Natural Vegetation of Oregon and Washington*, p. 452. Oregon State University Press, Corvallis, OR.
- Franklin J.F., Swanson F.J., Harmon M.E., *et al.* (1991) Effects of global climatic change on forests in northwestern North America. *Northwest Environmental Journal* **7**, 233–254.
- Gorissen A., Kuikman P.J. & Van de Beek H. (1995) Carbon allocation and water use in juvenile Douglas fir under elevated CO<sub>2</sub>. *New Phytologist* **129**, 275–282.
- Griffiths R.P. & Caldwell B.A. (1990) Douglas fir forest soils colonized by ectomycorrhizal mats. I. Seasonal variation in nitrogen chemistry and nitrogen cycle transformation rates. *Canadian Journal of Forest Research* **20**, 211–218.
- Griffiths R.P., Ingham E.R., Caldwell B.A., Castellano M.A. & Cromack K. Jr (1991) Microbial characteristics of ectomycorrhizal communities in Oregon and California. *Biology and Fertility of Soils* **11**, 196–202.
- Guak S., Olszyk D.M., Fuchigami L.H. & Tingey D.T. (1998) Effects of elevated CO<sub>2</sub> and temperature on cold hardiness and bud burst in Douglas fir (*Pseudotsuga menziesii*). *Tree Physiology* **18**, 671–680.
- Gunderson C.A. & Wullschlegel S.D. (1994) Photosynthetic acclimation in trees to rising atmospheric CO<sub>2</sub>: a broader perspective. *Photosynthesis Research* **39**, 369–388.
- Gunderson C.A., Norby R.J. & Wullschlegel S.D. (1993) Foliar gas exchange responses of two deciduous hardwoods during 3 years of growth in elevated CO<sub>2</sub>: no loss of photosynthetic enrichment. *Plant, Cell and Environment* **16**, 797–807.
- Harmon M.E., Ferrell W.K. & Franklin J.F. (1990) Effects of carbon storage on conversion of old-growth forests to young forests. *Science* **247**, 699–702.
- Hawkins B.J., Davradou M., Pier D. & Shortt R. (1995) Frost hardiness and winter photosynthesis of *Thuja plicata* and *Pseudotsuga menziesii* seedlings grown at three rates of nitrogen and phosphorus supply. *Canadian Journal of Forest Research* **25**, 18–28.
- Helms J.A. (1964) Apparent photosynthesis of Douglas fir in relation to silvicultural treatment. *Forest Science* **10**, 432–442.
- Helms J.A. (1965) Diurnal and seasonal patterns of net assimilation in Douglas fir, *Pseudotsuga menziesii* (Mirb.) Franco, as influenced by environment. *Ecology* **46**, 698–708.
- Hermann R.K. & Lavender D.P. (1990) *Pseudotsuga menziesii* (Mirb.) Franco. In *Silvics of North America, Vol. 1: Conifers* (eds R.M. Burns & B.H. Honkala), pp. 527–540. USDA Forest Service, Washington, DC.
- Herrick J.D. & Thomas R.B. (1999) Effects of CO<sub>2</sub> enrichment on the photosynthetic light response of sun and shade leaves of canopy sweetgum trees (*Liquidambar styraciflua*) in a forest ecosystem. *Tree Physiology* **19**, 779–786.
- Hicklenton P.R. & Jolliffe P.A. (1980) Alterations in the physiology of CO<sub>2</sub> exchange in tomato plants grown in CO<sub>2</sub>-enriched atmospheres. *Canadian Journal of Botany* **58**, 2182–2189.
- Hollinger D.Y. (1987) Gas exchange and dry matter allocation responses to elevation of atmospheric CO<sub>2</sub> concentration in seedlings of three tree species. *Tree Physiology* **3**, 193–202.
- Idso K.E. & Idso S.B. (1994) Plant response to atmospheric CO<sub>2</sub> enrichment in the face of environmental constraints: a review of the past ten years' research. *Agricultural and Forest Meteorology* **69**, 153–203.
- Idso S.B., Kimball B.A. & Allen S.G. (1991) Net photosynthesis of sour orange trees maintained in atmospheres of ambient and elevated CO<sub>2</sub> concentration. *Agricultural and Forest Meteorology* **54**, 95–101.
- Johns T.C., Carnell R.E., Crossley J.F., Gregory J.M., Mitchell J.F.B., Senior C.A., Tett S.F.B. & Wood R.A. (1997) The second Hadley Centre coupled ocean-atmosphere GCM: Model description, spinup and validation. *Climate Dynamics* **13**, 103–134.
- Jones M.B., Brown J.C., Raschi A. & Miglietta R. (1995) The effects on *Arbutus unedo* L. of long-term exposure to elevated CO<sub>2</sub>. *Global Change Biology* **1**, 295–302.
- Kellomäki S. & Wang K.-Y. (1996) Photosynthetic responses to needle water potentials in Scots pine after a four-year exposure to elevated CO<sub>2</sub> and temperature. *Tree Physiology* **16**, 765–772.
- Koike T., Lei T.T., Maximov T.C., Tabuchi R., Takahashi K. & Ivanov B.I. (1996) Comparison of the photosynthetic capacity of Siberian and Japanese birch seedlings grown in elevated CO<sub>2</sub> and temperature. *Tree Physiology* **16**, 381–385.
- Kozlowski T.T. & Pallardy S.G. (1996) *Physiology of Woody Plants*. Academic Press, San Diego, CA.
- Larcher W. (1995) *Physiological Plant Ecology*. Springer-Verlag, Berlin.
- Le Thiec D. & Dixon M. (1996) Acclimation of photosynthesis in Norway spruce and red oak grown in open top chambers and subjected to natural drought and to elevated CO<sub>2</sub>. *Canadian Journal of Forest Research* **26**, 87–94.
- Lewis J.D. & Strain B.R. (1996) The role of mycorrhizas in the response of *Pinus taeda* seedlings to elevated CO<sub>2</sub>. *New Phytologist* **133**, 431–443.
- Lewis J.D., McKane R.B., Tingey D.T. & Beedlow P.A. (2000) Vertical gradients in photosynthetic light response within an old-growth Douglas fir and western hemlock canopy. *Tree Physiology* **20**, 447–456.
- Lewis J.D., Olszyk D. & Tingey D.T. (1999) Effects of elevated atmospheric CO<sub>2</sub> and temperature on seasonal patterns of photosynthetic light response in Douglas fir seedlings. *Tree Physiology* **19**, 243–252.
- Lewis J.D., Tissue D.T. & Strain B.R. (1996) Seasonal response of photosynthesis to elevated CO<sub>2</sub> in loblolly pine (*Pinus taeda* L.) over two growing seasons. *Global Change Biology* **2**, 103–114.
- Long S.P. (1991) Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO<sub>2</sub> concentrations: has its importance been underestimated? *Plant, Cell and Environment* **14**, 729–739.
- Lorimer G.H. (1981) The carboxylation and oxygenation of ribulose 1, 5-bisphosphate: the primary events in photosynthesis and photorespiration. *Annual Review of Plant Physiology* **32**, 349–383.
- Morison J.I.L. & Lawlor D.W. (1999) Interactions between increasing CO<sub>2</sub> concentration and temperature on plant growth. *Plant, Cell and Environment* **22**, 659–682.
- Mortensen L.M. (1994) The influence of carbon dioxide or ozone concentration on growth and assimilate partitioning in seedlings

- of nine conifers. *Acta Agriculture Scandinavia, Section B: Soil and Plant Science* **44**, 157–163.
- Myers D.A., Thomas R.B. & DeLucia E.H. (1999) Photosynthetic capacity of loblolly pine (*Pinus taeda* L.) trees during the first year of carbon dioxide enrichment in a forest ecosystem. *Plant, Cell and Environment* **22**, 473–481.
- Neilson R.E., Ludlow M.M. & Jarvis P.G. (1972) Photosynthesis in Sitka Spruce [*Picea sitchensis* (Bong.) Carr.]. II. Response to temperature. *Journal of Applied Ecology* **9**, 721–745.
- Norby R.J., Wullschlegel S.D., Gunderson C.A., Johnson D.W. & Ceulemans R. (1999) Tree responses to rising CO<sub>2</sub> in field experiments: implications for the future forest. *Plant, Cell and Environment* **22**, 683–714.
- Olszyk D., Wise C., VanEss E. & Tingey D. (1998a) Elevated temperature but not elevated CO<sub>2</sub> affects long-term patterns of stem diameter and height of Douglas fir seedlings. *Canadian Journal of Forest Research* **28**, 1046–1054.
- Olszyk D., Wise C., VanEss E. & Tingey D. (1998b) Phenology and growth of shoots, needles, and buds of Douglas fir seedlings with elevated CO<sub>2</sub> and (or) temperature. *Canadian Journal of Botany* **76**, 1991–2001.
- Samuelson L.J. & Seiler J.R. (1992) Fraser fir seedling gas exchange and growth in response to elevated CO<sub>2</sub>. *Environmental and Experimental Botany* **32**, 351–356.
- Samuelson L.J. & Seiler J.R. (1994) Red spruce seedling gas exchange in response to elevated CO<sub>2</sub>, water stress, and soil fertility treatments. *Canadian Journal of Forest Research* **24**, 954–959.
- Stitt M. (1991) Rising CO<sub>2</sub> levels and their potential significance for carbon flow in photosynthetic cells. *Plant, Cell and Environment* **16**, 81–86.
- Strain B.R., Higginbotham K.O. & Mulroy J.C. (1976) Temperature preconditioning and photosynthetic capacity of *Pinus taeda* L. *Photosynthetica* **10**, 47–53.
- Systat (1992) *Systat: Statistics. V. 5.2*. Systat Inc., Evanston, IL.
- Teskey R.O. (1997) Combined effects of elevated CO<sub>2</sub> and air temperature on carbon assimilation of *Pinus taeda* trees. *Plant, Cell and Environment* **20**, 373–380.
- Thomas R.B. & Strain B.R. (1991) Root restriction as a factor in photosynthetic acclimation of cotton seedlings grown in elevated CO<sub>2</sub>. *Plant Physiology* **96**, 627–634.
- Tingey D.T., McVeety B., Waschmann R., Johnson M., Phillips D., Rygiel P.T. & Oslzyk D. (1996) A versatile sun-lit controlled-environment facility for studying plant and soil processes. *Journal of Environmental Quality* **25**, 614–625.
- Tissue D.T., Griffin K.L. & Ball J.T. (1999) Photosynthetic adjustment in field-grown ponderosa pine trees after six years of exposure to elevated CO<sub>2</sub>. *Tree Physiology* **19**, 221–228.
- Tissue D.T., Thomas R.B. & Strain B.R. (1996) Growth and photosynthesis of loblolly pine (*Pinus taeda*) after exposure to elevated CO<sub>2</sub> for 19 months in the field. *Tree Physiology* **16**, 49–59.
- Tissue D.T., Thomas R.B. & Strain B.R. (1997) Atmospheric CO<sub>2</sub> enrichment increases growth and photosynthesis of *Pinus taeda*: a 4 year experiment in the field. *Plant, Cell and Environment* **20**, 1123–1134.
- Tolley L.C. & Strain B.R. (1984a) Effects of CO<sub>2</sub> enrichment on growth of *Liquidamber styraciflua* and *Pinus taeda* seedlings grown under different irradiance levels. *Canadian Journal of Forest Research* **14**, 343–350.
- Tolley L.C. & Strain B.R. (1984b) Effects of CO<sub>2</sub> enrichment and water stress on growth of *Liquidamber styraciflua* and *Pinus taeda* seedlings grown under different irradiance levels. *Canadian Journal of Botany* **62**, 2135–2139.
- Turnbull M.H., Tissue D.T., Griffin K.L., Rogers G.N.D. & Whitehead D. (1998) Photosynthetic acclimation to long-term exposure to elevated CO<sub>2</sub> concentration in *Pinus radiata* D. Don is related to age of needles. *Plant, Cell and Environment* **21**, 1019–1028.
- Vitousek P.M. (1991) Can planted forests counteract increasing atmospheric carbon dioxide? *Journal of Environmental Quality* **20**, 348–354.
- Waring R.H. & Franklin J.F. (1979) Evergreen coniferous forest of the Pacific Northwest. *Science* **204**, 1380–1386.
- Wayne P.M., Reekie E.G. & Bazzaz F.A. (1998) Elevated CO<sub>2</sub> ameliorates birch response to high temperature and frost stress: implications for modeling climate-induced geographic range shifts. *Oecologia* **114**, 335–342.

Received 9 September 2000; received in revised form 24 January 2001; accepted for publication 24 January 2001