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Physiological adjustment of two full-sib families of ponderosa pine to elevated CO_2

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Summary

Seeds from two full-sib families of ponderosa pine (*Pinus ponderosa*) with known differences in growth rates were germinated and grown in an ambient (350 $\mu l\ l^{-1}$) or elevated (700 $\mu l\ l^{-1}$) CO_2 concentration. Gas exchange at both ambient and elevated CO_2 concentrations was measured 1, 6, 39, and 112 days after the seed coat was shed. Initial stimulation of CO_2 exchange rate (CER) by elevated CO_2 was large (> 100%). On Day 1, CER of seedlings grown in elevated CO_2 and measured at ambient CO_2 was significantly lower than the CER of seedlings grown and measured at ambient CO_2, indicating physiological adjustment of the seedlings exposed to elevated CO_2. Physiological acclimation to elevated CO_2 was complete by Day 39 when there was no significant difference in CER between seedlings grown and measured at ambient CO_2 and seedlings grown and measured at elevated CO_2. After 4 months, the light response of seedlings in the two treatments was determined at both ambient and elevated CO_2. Light compensation point, CER at light saturation, and apparent quantum efficiency of seedlings grown and measured at ambient CO_2 were not significantly different from those of seedlings grown and measured at elevated CO_2. With a short-term increase in CO_2, CER at light saturation (5.16 ± 0.52 versus 3.13 ± 0.30 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$) and apparent quantum efficiency (0.082 ± 0.011 versus 0.045 ± 0.003 $\mu mol\ CO_2\ \mu mol^{-1}$ quanta) were significantly increased. Leaf C/N ratio was significantly increased in the elevated CO_2 treatment. There were few significant differences between families for any response to elevated CO_2. Under the experimental conditions, high growth rate was not correlated with a greater response to elevated CO_2.

Introduction

Predicting carbon and nitrogen relationships at the species level under conditions of elevated CO_2 is the first step in understanding limitations to growth, and potential changes in community structure and ecosystem behavior in response to future increases in atmospheric CO_2 concentrations. Individual species respond differently to elevated atmospheric CO_2 as a result of differences in photosynthetic capacity, phenology, and optimal physical conditions for growth (Strain and Bazzaz 1983, Lemon 1983, Brown 1986). Only one study has investigated intraspecific variability to elevated CO_2 in conifer populations (*Pinus ponderosa*, Sierran and Rocky Mountain varieties, Surano et al. 1986). We have examined whether two full-sib family crosses of *Pinus ponderosa* with known differences in growth rates also exhibit differences in their response to elevated CO_2.

Several mechanisms have been proposed to account for physiological adjustment to elevated atmospheric CO_2. Among these are end-product inhibition or insufficient

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substrate (Sasek et al. 1985, Madsen 1968), reduced nutrient acquisition relative to CO_2-stimulated growth (Herold 1980), and reduced RUBP activity, regeneration, or concentration in elevated CO_2 environments (Wong 1979). Most CO_2-enrichment studies with conifers have been carried out with older seedlings that have relatively high stores of leaf nitrogen and phosphorus, and have had a prolonged period of enhanced carbon assimilation before photosynthetic adjustment occurs. We know of only three studies in which conifer seedlings (*Pinus taeda*) have been grown from seed in ambient or elevated CO_2 for 8 months (Sionit et al. 1985), 12.5 months (Tolley and Strain 1985), or 25 months (Fetcher et al. 1988), but none of these studies focused on physiological adjustment. We have examined the physiological changes that accompany adjustment to elevated CO_2 in ponderosa pine seed germinated and grown in 350 or 700 $\mu l\ l^{-1}$ CO_2 for 4 months.

Methods

Progeny selection

Ponderosa pine seeds of full sibling, controlled crosses were obtained from the USDA, Forest Service, Institute of Forest Genetics (Placerville, CA). Parent trees were from the northern Sierra Nevada Mountains. Family cross (FC) 1 was between Tree 4268 (Lassen National Forest, Hat Creek Road at 1,420 m; average height growth rate of 38.0 cm $year^{-1}$) and Tree 4353 (Shasta Trinity N. F., McCloud Road at 1,260 m; 38.4 cm $year^{-1}$); and FC 2 was between Tree 4579 (57.9 cm $year^{-1}$) and Tree 4361 (47.5 cm $year^{-1}$; both in Shasta Trinity N. F., McCloud Road at 1,613 m).

Plant culture and growth

Seeds were soaked in aerated, 30% hydrogen peroxide for 6 h at room temperature (Trappe 1961). Seeds (n = 500 for each FC) were then rinsed six times in distilled deionized water, placed on moistened filter paper in petri dishes, and randomly divided between the two growth chambers, set at ambient (350 $\mu l\ l^{-1}$) and elevated (700 $\mu l\ l^{-1}$) CO_2. Seeds and seedlings were switched between chambers every other week to minimize individual chamber effects. Both chambers provided a day/night temperature of 20/16 °C, and a 12-h photoperiod with a photosynthetic photon flux density (PPFD) of 700 $\mu mol\ m^{-2}\ s^{-1}$. After 18 days, 95% of the seeds had germinated and the temperature of both chambers was adjusted to 25/19 °C with all other environmental conditions the same. After 2 months, the photoperiod was extended to 14 h until the end of the experiment.

As each seed produced a radicle, it was planted in a potting tube (4 cm diameter × 25 cm long) filled with a 1/1 mixture of unsterilized organic potting mix (Promix BX) and perlite and covered with a layer of potting mix. Once potted, the seedlings were placed in the growth chambers and fertilized every seventh day with NCSU fertilizer mix (in ppm, N, 106.23; P, 10.41; K, 111.03; Ca, 54.40; Mg, 12.20; Fe, 5.00; S, 13.39; Mn, 0.113; B, 0.24; Zn, 0.013; Cu, 0.005; Co, 0.0003; Mo, 0.05; and Na, 11.04); and watered midweek to reduce build up of minerals. Each seedling was

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labeled with the date when the cotyledon needles expanded sufficiently to discard the seed coat (this date was designated Day 1 of exposure). All physiological measurements were conducted on seedlings with the same emergence date within a sampling period. Cotyledons may have been exposed to the chamber atmosphere for approximately 5–9 days by the time of full emergence from the seed coat. On Day 1, 20 seedlings from each family cross and CO_2 treatment were harvested. Stem diameter to the nearest 0.01 mm and height to the nearest mm were measured. Seedlings were then dried at 65 °C for 24 h and weighed. At the end of the 4-month period of exposure, three seedlings from each family cross and CO_2 treatment were harvested, dried, and weighed.

Carbon dioxide control system and performance

Two chambers were used for the 4-month experiment and a third chamber was available for short-term experimentation. A computer-based control system was designed to measure and control CO_2 concentrations in the three growth chambers. The computer was linked to a data acquisition system (ADC-1, Remote Measurement Systems, Seattle, WA) which monitored PPFD (quantum sensor, Hamamatsu, Bridgewater, NJ), relative humidity (Philips thin film capacitance), and temperature (AD-590 IC) in each chamber every 2 min. The 2-min values were averaged every 30 min and the data were displayed graphically to a monitor and recorded.

Computer-controlled solenoids switched air flow sequentially from chambers to an infrared gas analyzer (due to IRGA failure, either an ADC 225 with zero and span calibration or a Li-Cor LI-6200 with a zero and two-span calibration). Carbon dioxide concentration was determined four times after an equilibration period of 20 s. The IRGA was automatically calibrated every hour; a manual override allowed resetting when necessary. Every 2-min cycle, the CO_2 concentration of each chamber was compared to preset values and the decision to inject CO_2 (compressed gaseous CO_2), scrub CO_2 (air cycled through soda lime columns), or neither (CO_2 concentration $\pm$ 5 $\mu l\ l^{-1}$ around set point) was made based on the rate of CO_2 change from the previous four measurements in that chamber. Manual adjustments in CO_2 scrub (Dwyer rotometers, 0–5 l min^{-1}) and injection flow rates (Dwyer rotometers, 0–50 ml min^{-1}) were made when necessary.

The total duration of the experiment was 129 days (April 4 to August 11, 1990). Plant and soil respiration at night resulted in elevated nighttime CO_2 concentrations (600–900 $\mu l\ l^{-1}$). At the beginning of each light period, CO_2 set points were reached within 0.25–1.5 h, depending on the CO_2 concentration required and the amount of foliage in the chamber. A similar disturbance in chamber CO_2 concentration occurred when chambers were opened to check for seedling germination, watering, fertilization, switching plants from one chamber to another, or direct experimentation. These perturbations resulted in lack of control 8.4% of the total daylight hours for the 350 $\mu l\ l^{-1}$ chamber and 11.2% for the 700 $\mu l\ l^{-1}$ chamber during the experiment.

Once set points were achieved, the CO_2 concentrations in the ambient and elevated CO_2 chambers were 360 $\pm$ 27 $\mu l\ l^{-1}$ and 698 $\pm$ 24 $\mu l\ l^{-1}$ CO_2 (mean $\pm$ SD), respectively. Irradiance averaged 713 $\pm$ 70 ($\pm$ SD) $\mu mol\ m^{-2}\ s^{-1}$ at canopy height for

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both chambers. Temperature was ± 1.7 °C (SD) for both chambers from the day or night set point. Relative humidity was not controlled, but was 46 ± 12% for the 700 μl l^{-1} chamber and 57 ± 4% for the 350 μl l^{-1} chamber during the light hours and averaged 81 ± 5% for both chambers during the night.

Gas exchange

Gas exchange was measured on the same five plants of each family cross (FC) at their growth CO_2 concentration (350 or 700 μl l^{-1}) on Days 1, 6, 39, and 112 and at the reciprocal CO_2 concentration (700 or 350 μl l^{-1}, respectively) on the subsequent day. The aboveground tissue of the seedling was enclosed in a 0.25-liter cuvette, and gas exchange was determined with a Li-Cor LI-6200 photosynthetic system (Lincoln, NE). Plants were equilibrated in the experimental chamber under saturating light (1600 μmol m^{-2} s^{-1}), a leaf temperature of 25 °C, and the desired CO_2 concentration for 1 h before measurement. All plant containers were watered to saturation 12 h before measurement. Means of each plant were obtained from 2–4 runs (3–4 observations averaged per run). Analyses of variance were applied to the mean photosynthetic value obtained for each plant within a sampling date or under a particular set of conditions.

Carbon dioxide exchange rate (CER) was expressed per needle surface area, which was calculated from the following geometric models of the surfaces. Measures of needle width (W) and length (L) were made non-destructively with a digital micrometer. Cotyledon needles were triangular in cross section, with two wide sides (WS) and one narrow side (NS). Stomata were present on all surfaces of cotyledons and primary needles. The surface area of the cotyledons was calculated as follows: $SA = (2 \times (0.5 \times WS \times L)) + (0.5 \times NS \times L)$, and the surface area of the primary needles was calculated as: $SA = 2 \times (0.5 \times W \times L)$. Primary needles were grouped into several length categories (5–10 mm differences); needles in each length category were counted and multiplied by the average SA of a subsample of 3–5 typical needles in each group.

After gas exchange was measured at full light (1600–1800 μmol m^{-2} s^{-1}; exact measures recorded) on Day 112, gas exchange of three of the five plants in each family at each CO_2 concentration was also measured at 510 μmol m^{-2} s^{-1}, within the range of 100–200 μmol m^{-2} s^{-1} (each irradiance value measured), and in the dark at both the growth and the reciprocal CO_2 concentrations to develop light response curves. A simple leaf model was used to define the relationship: $(CER = P_{max} (1 - e^{-\Phi I/P_{max}})$, where Φ is apparent quantum efficiency and I is PPFD; Thornley 1976). Apparent quantum efficiency and light compensation point were calculated independently for each plant from the initial linear portion of the light response curve as in Ehleringer and Björkman (1977). The following equation was used to test the effects of irradiance, FC, and their interaction: $Y = B_0 + B_1(x_1) + B_2(x_2) + B_3(x_3)$ (Draper and Smith 1981) within a CO_2 treatment, where Y = CER, x_1 = an indicator of FC, x_2 = irradiance (after natural logarithm transformation) and x_3 = light × family = $x_1 \times x_2$.

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Leaf nitrogen and carbon

Needles were harvested and pooled on the following days after needle expansion: 1 day (20 plants), 5 days (15 plants), 15 days (12 plants), 22 days (10 plants), 39 days (8 plants), and 112 days (3 plants). Total biomass required for tissue nutrient analysis determined the number of plants harvested on a particular sampling date. A one-way ANOVA between plants in the two CO_2 concentrations was conducted within a sampling date. Needle N and C were determined on tissue dried at 65 °C for 24 h and then ground to pass a 40 mesh. Total N and C of needle samples, blanks (2 per 50 samples), replicate subsamples (1 per 6 samples), and a NBS tissue sample (ponderosa pine tissue; 1 per 10 samples) were measured for total N and C with a Carlo-Erba NA1500 Series 2 analyzer. Standard curves were established before and after each run of 35 samples with differing concentrations of atropine. Mean error on true replicates for N and C averaged 0.62%.

Results

Germination and growth responses

Neither the family cross (FC) nor the CO_2 environment had an effect on the rate or total germination of *P. ponderosa* seeds. In both families, foliage biomass on Day 1 was significantly greater in seedlings in the elevated CO_2 treatment (700 μl l^{-1}) than in seedlings in the ambient CO_2 treatment (350 μl l^{-1}), but foliage biomass was not significantly different between families (Figure 1). At the end of the study, foliage biomass was increased by 55% in seedlings in the elevated CO_2 treatment, but there was a significant interaction between FC and CO_2 treatment only for FC 2 (two-way ANOVA, $P = 0.03$). There were no significant differences in stem height or diameter for either FC in either CO_2 treatment ($P > 0.05$).

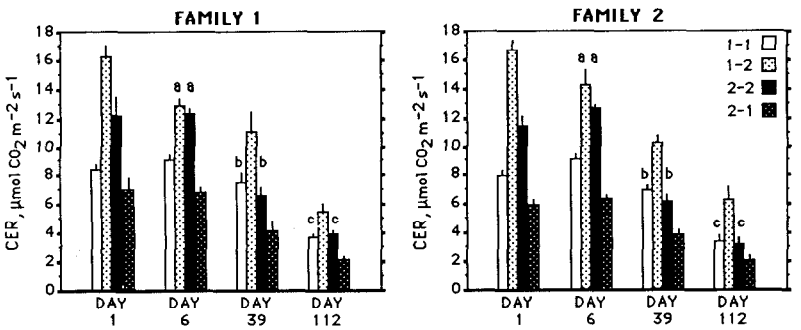

Figure 1. Carbon dioxide exchange rates of seedlings grown in ambient CO_2 and measured at ambient (1-1) or elevated (1-2) CO_2 and of seedlings grown in elevated CO_2 and measured at ambient (2-1) or elevated (2-2) CO_2. The ambient and elevated CO_2 concentrations were 350 and 700 μl l^{-1}, respectively. Bar heights and error lines represent the mean CER ± SE for five plants in each category. Within a sampling date, bars with similar letters are not significantly different at $P = 0.05$.

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Table 1. Summary of growth parameters measured at the end of the exposure period. Values with similar letters within the same row are not significantly different at $P = 0.05$.

Parameter	Family cross 1		Family cross 2	
	350 μl l^{-1} CO_2	700 μl l^{-1} CO_2	350 μl l^{-1} CO_2	700 μl l^{-1} CO_2
Needle dry weight (mg)				
Day 1	19 ± 1a	26 ± 1b	22 ± 1a	26 ± 1b
Day 112	512 ± 43a	490 ± 48a	387 ± 57b	600 ± 51c
Stem height (cm)	14.6 ± 1.4a	11.6 ± 3.8a	20.1 ± 1.9b	15.5 ± 2.5ab
Stem diameter (mm)	2.81 ± 0.20a	2.72 ± 0.25a	2.91 ± 0.17a	2.95 ± 0.11a

Carbon dioxide exchange rate

Short-term stimulation of CER by elevated CO_2 was significant for both FCs (average values for both family crosses were: Day 1, 103 ± 6%; Day 6, 59 ± 9%; Day 39, 47 ± 4%; Day 112, 78 ± 6%, Figure 1), and could be evoked at any time during the experiment. Short-term stimulation was 15 and 12% greater on the first and last sampling days, respectively, for FC 2 than for FC 1, but differences between family responses were not significant ($P > 0.05$).

The CER of plants grown in ambient or elevated CO_2 and measured at the CO_2 concentration in which the plants were grown was compared (Figure 1) to test for physiological adjustment. The CER was significantly different for Days 1 and 6 between plants grown and measured at ambient CO_2 and plants grown and measured at elevated CO_2. On Days 39 and 112, there were no statistical differences between the CERs of plants grown and measured at ambient CO_2 and plants grown and measured at elevated CO_2, indicating full photosynthetic adjustment had occurred in both FCs ($P > 0.05$). Some evidence for physiological adjustment on the first day of cotyledon expansion was provided by the depression (20 ± 5%) of CER, relative to controls, in plants grown in elevated CO_2 and measured at ambient CO_2.

Dark respiration

Although respiration, measured at the end of the study, was greater for plants in the short- and long-term elevated CO_2 environments for both FCs, and FC 1 exhibited greater stimulation of respiration by elevated CO_2 than FC 2, the differences were not significant ($P > 0.05$).

Physiological and phenological changes

The relationships between CER and stomatal conductance (g_s, Figure 2a), CER and internal CO_2 concentration (C_i, Figure 2b), and g_s and C_i (Figure 2c) were plotted for plants grown and measured at ambient and at elevated CO_2 for Days 1, 6, 39, and 112 to show changes due to photosynthetic adjustment and phenology during the 4-month exposure. Stomatal conductance increased from Day 1 through Day 39 and was lower in seedlings in the elevated CO_2 treatment than in seedlings in the ambient CO_2 treatment, indicating greater water use efficiency of seedlings in the elevated

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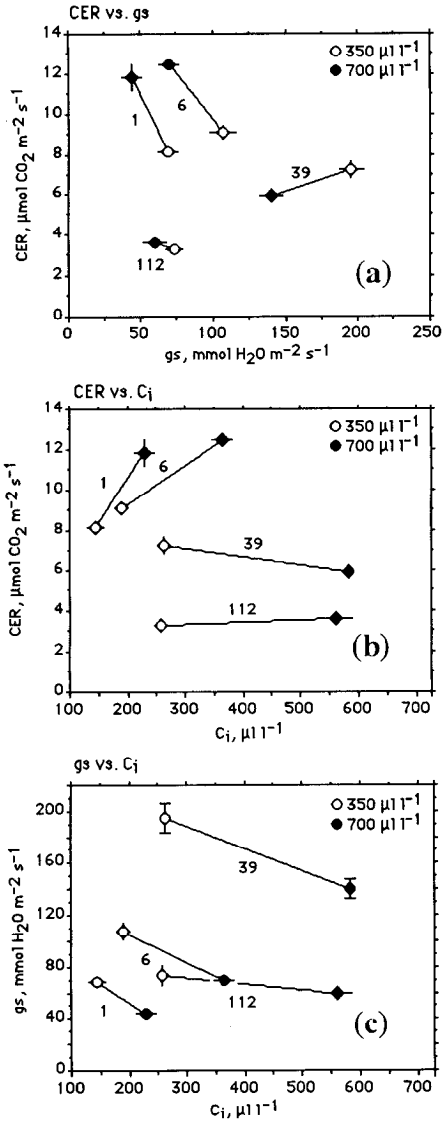

Figure 2. (a) Carbon dioxide exchange rate (CER) versus stomatal conductance (g_s), (b) CER versus internal CO_2 concentration (C_i), and (c) g_s versus C_i for Days 1, 6, 39, and 112 for plants measured grown and measured at ambient CO_2 (○) and plants grown and measured at elevated CO_2 (●). Lines connect the values within each sampling date for clarity and do not imply any response function. The center of each symbol represents the mean value for the two family crosses combined and the error bars denote ± SE.

CO_2 treatment (Figures 2a and 2c). Stomatal conductance declined by Day 112 and was not significantly different ($P > 0.05$) between seedlings in the two treatments. Throughout the experiment, C_i of plants in the elevated CO_2 treatment was significantly greater than that of plants in the ambient CO_2 treatment (Figures 2b and 2c). On Day 1, plants had not adjusted to elevated CO_2 and the ratio of external (C_a) to

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internal CO_2 concentration (C_i) was relatively high (3.11). As plants adjusted to the elevated CO_2 environment, C_a/C_i declined (Day 6, 1.89; Day 39, 1.21; Day 112, 1.25), indicating that the greater water use efficiency observed in the elevated CO_2 treatment declined with time.

Light response

Light response for CER was measured at four irradiances at the end of the exposure period for both FCs. The coefficient for the interaction term (family × irradiance) was not significant ($P > 0.05$), so light responses for both FCs within the same CO_2 concentration were combined. The light compensation point, CER under saturating light, and apparent quantum efficiency were not significantly different between seedlings grown at ambient CO_2 and seedlings grown at elevated CO_2 (Table 2). Short-term exposure of seedlings grown in ambient CO_2 to elevated CO_2 increased the light compensation point ($P = 0.01$), and apparent quantum efficiency ($P = 0.15$). Short-term exposure of seedlings grown in elevated CO_2 to ambient CO_2 depressed the values of the same parameters by a similar amount. It is likely that the light compensation points reported here were high because the seedlings were never exposed to low irradiances in the growth chambers.

Needle nitrogen and C/N

Initial needle N content of both FCs was high until cotyledon needles began to abscise (Days 15–39; Figure 3a). Differences in needle N content were not statistically significant between CO_2 treatments (1.13 versus 0.83% on Day 112, $P > 0.05$; FCs as replicates). The C/N of needle tissue was significantly greater in seedlings grown in elevated CO_2 than in seedlings grown in ambient CO_2 (C/N = 42 versus 55 for elevated CO_2, $P = 0.02$; FCs as replicates). The increase in C/N could be largely accounted for by the reduction in N.

Table 2. Summary of light response parameters for both families combined. The first CO_2 concentration is the concentration during growth and the second CO_2 concentration is the concentration during measurement. Within the same row, values with similar letters are not significantly different at $P = 0.05$.

	Growth CO_2 concentration/measurement CO_2 concentration ($\mu l\ l^{-1}$)			
	350/350	350/700	700/350	700/700
CER at light saturation ($\mu mol\ m^{-2}\ s^{-1}$)	3.13 ± 0.30a	5.16 ± 0.52b	3.51 ± 0.36a	1.95 ± 0.18c
Light compensation point ($\mu mol\ m^{-2}\ s^{-1}$)	109 ± 9a	139 ± 14b	122 ± 15a*[1]	92 ± 13a*
Apparent quantum efficiency	0.045 ± 0.003a	0.082 ± 0.011a	0.052 ± 0.011a*	0.026 ± 0.002a*

[1] Asterisks signify that $P = 0.06$ for that comparison within the row.

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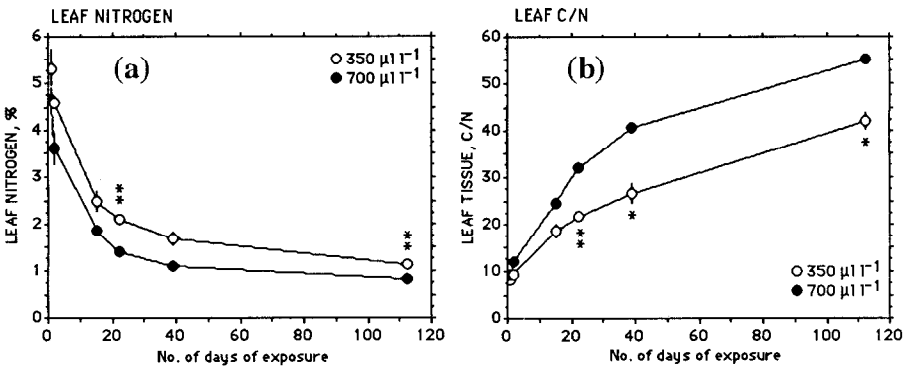

Figure 3. (a) Needle N content (%) and (b) needle C/N during the course of the experiment. The center of each symbol represents the mean value for the two family crosses combined and the error bars denote ± SE. Within a sampling date, significant differences between the two CO_2 treatments are denoted by asterisks, * = $P < 0.05$, and ** = $P < 0.01$.

Discussion

Short-term exposure of *P. ponderosa* seedlings to elevated CO_2 stimulated CER between 50 and 100% (Figure 1), and could be evoked at any time during the 4-month study. A similar stimulation was observed for the same species *in situ* in response to a short-term increase in CO_2 of 150 µl l^{-1} (Green and Wright 1977). In other species of pines exposed for longer periods to elevated CO_2, stimulation of CER was accompanied by increases in stem height and diameter (*P. taeda*, Sionit et al. 1985), and increases in biomass (*P. radiata*, Hollinger 1987, Conroy et al. 1988; *P. echinata*, O'Neill et al 1986; *P. virginiana*, Luxmoore et al. 1986). We observed that needle dry weight was significantly greater in elevated CO_2 only for the faster growing FC 2 at the end of the 4-month exposure (Table 1).

Evidence for photosynthetic adjustment to elevated CO_2 was apparent on Day 1, but full adjustment was not reached until Day 39. *Pinus taeda* germinated and grown at high irradiances (1000 µmol m^{-2} s^{-1}) required 10 weeks of exposure to adjust to elevated CO_2 concentrations, whereas seedlings grown at lower irradiances (250 µmol m^{-2} s^{-1}) adjusted more rapidly to elevated CO_2 (Tolley and Strain 1985). Conifer seedlings grown first in ambient CO_2 and then in elevated CO_2 did not show photosynthetic adjustment within the first season of exposure (Hollinger 1987).

Hollinger (1987) observed a short-term increase in g_s in plants grown in ambient CO_2 and then placed in elevated CO_2, and concluded that the sensitivity of stomata to CO_2 was enhanced in elevated CO_2 concentrations. However, Fetcher et al. (1988) found that, in *P. taeda*, the CO_2 concentration during growth had less effect on g_s than the CO_2 concentration during measurement, because g_s was greater when seedlings grown in either ambient or elevated CO_2 were measured at a CO_2 concentration of 350 µl l^{-1}. In our study, g_s increased from Day 1 through Day 39 and was lower in seedlings grown in elevated CO_2 than in seedlings grown in ambient CO_2, indicating greater water use efficiency of the seedlings grown in elevated CO_2 (Figures 2a

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and 2c). The lack of difference in g_s in the two CO_2 treatments by Day 112 suggests that stomatal sensitivity to elevated CO_2, and elevated CO_2-enhanced water use efficiency, declined near the end of the growing period.

Plants grown at ambient CO_2 and exposed to short-term elevated CO_2 showed a significant increase in CER at high irradiances (Table 2). The light compensation point is expected to decrease because of increasing quantum efficiency at elevated CO_2 concentrations (Ehleringer and Björkman 1977). The increase in light compensation point accompanying exposure to short-term elevated CO_2 concentration may be explained by the increase in dark respiration, although this was not statistically significant (Table 2). Higginbotham et al. (1985) reported that, in *P. contorta*, the light compensation point was similar for different CO_2 concentrations. Apparent quantum efficiency was enhanced by short-term elevated CO_2, and was reversed, as a result of changes in photorespiration, when plants adjusted to elevated CO_2 were placed in ambient CO_2.

In response to elevated CO_2, the needle N content decreased and the C/N of needle tissue increased (Figure 3b). Despite physiological adjustment, plants in the elevated CO_2 treatment continued to sequester C. Shifts in tissue C/N may have significant long-term effects on litter decomposition and ecosystem nutrient cycling (Strain and Bazzaz 1983).

In general, the influence of the CO_2 environment was a much greater factor than the genetic source of the plants. Although the two FCs selected for study had different growth rates, no differences in the magnitude of the response to the elevated CO_2 environment were significant for stem height or diameter, CER, dark respiration, light response, or nutrient relations. Surano et al. (1986) observed that a Sierran population of *P. ponderosa* exhibited greater height increases in response to elevated CO_2 than a population from the Rocky Mountains, possibly because interior populations have greater initial water use efficiency (Monson and Grant 1989). The effect of slow rates of increase in atmospheric CO_2 may not select for more responsive genotypes in the natural population.

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